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Sonia Gasmi

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THÈSE PRÉSENTÉE

POUR OBTENIR LE GRADE DE

DOCTEUR DE

L'UNIVERSITÉ DE BORDEAUX

ÉCOLE DOCTORALE

Sciences et environnement

SPÉCIALITÉ
Biogéochimie et écosystèmes

Sonia GASMI

Écologie trophique et reproduction d'une population sauvage d'huître creuse *Crassostrea gigas* dans un écosystème macrotidal, peu profond : cas du Bassin d'Arcachon

Sous la direction de : Gwenaël Abril
(Co-directeurs : Valérie David et Philippe Soudant)

Soutenue le 22 juin 2017

Membres du jury :

M. de Montaudouin, Xavier	Université de Bordeaux, UMR EPOC	Président
M. Parrish, Christopher	Memorial University of Newfoundland	rapporteur
M. Lefebvre, Sébastien	Université de Lille 1, UMR LOG	rapporteur
M. Olivier, Frédéric	Muséum National d'Histoire Naturelle, UMR BOREA	examinateur
Mme. Maurer, Danièle	IFREMER	invité

Titre: Écologie trophique et reproduction d'une population sauvage d'huître creuse *Crassostrea gigas* dans un écosystème macrotidal, peu profond : cas du Bassin d'Arcachon.

Résumé :

Le fonctionnement écologique des écosystèmes côtiers est soumis à l'action synergique des changements climatiques et des pressions anthropiques. Au sein du Bassin d'Arcachon, l'huître *Crassostrea gigas*, montre depuis quelques années une modification du cycle reproductif (*i.e.* faible formation des gamètes, retard de ponte), qui semble lié aux modifications globales des conditions thermiques et trophiques du milieu. L'objectif de ce travail consiste à réaliser un état des lieux de la variabilité spatio-temporelle de l'état reproductif des huîtres dans le Bassin d'Arcachon, en lien avec l'origine, la quantité et la qualité de la ressource trophique. Les résultats obtenus ont permis de révéler d'importants gradients spatiaux de variabilité du développement gonadique et du signal trophique chez *C. gigas*, entre les parties internes sous influences des rivières (sud-est et nord-est), et la partie externe sous influences océaniques. Deux facteurs clés se sont révélés en partie explicatifs de cette variabilité, le temps d'immersion et le temps de renouvellement océanique. Un comparatif de la gamétogenèse et du pool nutritif entre les parties sud-est et nord-est du bassin a permis de démontrer une variabilité temporelle de la composition phytoplanctonique associée à une variabilité des apports en acides gras essentiels à la formation et la maturité des gamètes. La dynamique de la mise en réserves ainsi que le déclenchement des pontes chez *C. gigas* se sont révélés synchrones à la variabilité saisonnière de la quantité et la qualité du pool nutritif. Ces résultats représentent une première étape vers le développement d'un modèle prédictif des besoins énergétiques de l'espèce sous l'effet des changements globaux des conditions environnementales.

Mots clés : reproduction, hydrodynamisme, variabilité spatio-temporelle, pool nutritif, phytoplancton, isotopes stables, acides gras

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Title: Trophic ecology and reproduction in the wild population of the Pacific oyster *Crassostrea gigas* from a shallow macrotidal ecosystem: case of Arcachon Bay.

Abstract :

The ecological functioning of coastal ecosystems is subjected to the synergistic action of climate change and anthropogenic pressures. In Arcachon Bay, the reproductive cycle of the oyster *Crassostrea gigas* has changed in recent years (*e.g.* weak gametogenesis, spawning delay). This pattern seems to be associated with global changes in thermal and trophic conditions. The aim of this work was to characterize the spatio-temporal variability in the reproductive investment of oysters in Arcachon Bay. This variability has been investigated in relation to the origin, quantity and quality of the trophic resources. The results revealed important spatial gradients of variability in gonadal development and trophic signal in *C. gigas*, between inner parts of the bay influenced by river inputs (south-east and north-east) and the external part of the bay, which is influenced by oceanic inputs. Two hydrodynamic factors explained most of the observed variability: immersion time and oceanic water renewal. A comparison of *C. gigas* gametogenesis and the nutritional value of available food sources between the south-eastern and north-eastern parts of the bay revealed temporal variability in the composition of phytoplankton. This variability was associated with variability in the amounts of essential fatty acids, necessary for gametogenesis. Changes in energy reserves and gamete release cycle were synchronized with the seasonal nutrient variability. These results constitute a first approach in the development of a model predicting the evolution of the energetic needs of *C. gigas* under the global change in environmental conditions.

Keywords : reproduction, hydrodynamics, spatio-temporal variability, nutrition, phytoplankton, stables isotopes, fatty acids

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Unité de recherche

[EPOC, 5805, Station Marine d'Arcachon, 2 Rue du Professeur Jolyet, 33120 ARCACHON]

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Principales abréviations

Abréviation	Définition
BMA	Benthic Microalgae
Dfw	Dry flesh weight
FAs	Fatty Acids
I_L	Immersion Level
Is_V	Intra-station Variation
LoFt	Local oceanic Flushing time
LS_{CI}	Lawrence & Scott Condition Index
NL	Neutral Lipids
PL	Polar Lipids
PUFA	Polyinsaturated Fatty Acids
SPOM	Suspended Particulate Organic Matter
TAG	Triacylglycerol

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Contexte général et objectifs de l'étude

Les écosystèmes côtiers peu profonds font partie des **écosystèmes les plus productifs** au monde (Agardy et al. 2005). Ils sont caractérisés par un fonctionnement hydrodynamique complexe, modulé par une action simultanée des apports **d'eaux océaniques et continentales** (Zimmerman 1976). Ce fonctionnement induit dans ces milieux une forte variabilité spatio-temporelle des conditions environnementales. Toutefois, ceci n'empêche pas le développement d'une forte production primaire, bénéficiant des nutriments entraînés dans le système par les eaux douces et marines (Cloern et al. 2014 ; Watanabe & Kuwae 2015). La richesse biologique qui les caractérise leur offre une attractivité particulière pour le développement d'activités industrielles et récréatives. Ainsi, de par leur proximité, ces environnements offrent plusieurs **services écosystémiques** directs (*e.g.* aquaculture, tourisme) et indirects (*e.g.* recyclage des nutriments, régulation du climat). Cependant, ces écosystèmes évoluent sensiblement sous l'effet des **changements globaux** qui affectent leurs capacités biologiques et les services qui en découlent (Kirby et al. 2009). L'action synergique des changements climatiques et des pressions anthropiques (*e.g.* surexploitation, pollution) est difficilement dissociable (Goberville et al. 2010 ; Goberville et al. 2011). Toutefois, les répercussions se manifestent de plus en plus et les effets sont considérables : dégradation de la qualité de l'eau, perturbation des cycles biogéochimiques, pertes d'habitats etc. (Brook et al. 2008 ; Ver et al. 1999). La mise en place d'approches spécifiques à court et moyen termes est devenue cruciale afin de comprendre les mécanismes qui modulent ces changements et de **prédire leur évolution**. Ceci permettrait d'assurer une **meilleure gestion** des zones côtières, dans le but de préserver leur capacité de résilience et les services écosystémiques qu'elles fournissent (Hosack et al. 2009).

Parmi les services écosystémiques exploités dans les zones côtières françaises, la **conchyliculture**, et principalement l'élevage de **l'huître creuse *Crassostrea gigas***, fait partie de l'une des principales activités humaines de production de nourriture. Cette production ostréicole, estimée en moyenne à 130 000 tonnes par an, a été en 2013 la première source de revenus aquacole en France, devançant la pêche thonière (389 millions d'euros ; FranceAgriMer 2016). Elle est assurée grâce à la maîtrise, depuis près de 160 ans, de l'activité de **captage de naissains** (ou recrutement larvaire : collecte de larves d'huîtres issues des populations cultivée et sauvage, par fixation sur substrat dur dans le milieu naturel).

Cependant, la production ostréicole française se trouve dépendante de cet approvisionnement, qui est fortement modulé par des processus biologiques. Ces processus régis par les conditions environnementales du système ostréicole (*i.e.* qualité des eaux, pressions climatiques, pathogènes), peuvent constituer un facteur limitant pour le **volume de production** en fin du cycle d'élevage. Cette limite s'est révélée au niveau de différentes **crises** traversées par la filière française depuis le début du 20ème siècle (Mortensen et al. 2006 ; Murray & Peeler 2005). En 2008, la production de l'huître connait l'une des crises les plus sévères depuis 40 ans en France, caractérisée par une **mortalité massive des naissains** destinées à l'élevage, *i.e.* entre 60 et 90 % de pertes pour tous les sites d'élevages (Cochennec-Laureau et al. 2011). Ces pertes ont largement entravé la production des années 2009 et 2010.

Cette dernière crise, touchant l'ensemble des bassins conchylicoles français, souligne l'importance de **l'approvisionnement initial en naissains**, dont la principale source reste le captage naturel (seulement 30% des naissains sont produits en écloserie). Dans ce contexte, de par sa capacité historique à produire du naissain, le Bassin d'Arcachon occupe une place centrale. En effet, les conditions clémentes et le savoir-faire technique local et patrimoniale ont fait du bassin un centre spécialisé dans l'activité de captage. La production arcachonnaise fournit 60 à 70% des 4 milliards et demi de juvéniles d'huître nécessaires à l'ensemble de la production annuelle française (Comité Régional Conchyliculture Arcachon Aquitaine), et représente la **première nurserie d'huîtres en France et en Europe**. Cette production de naissain est fortement dépendante de l'environnement. Des études précédentes ont en effet montré que les fluctuations de température avaient un rôle certain sur le captage et l'activité des entreprises ostréicoles arcachonnaise selon leur spécificité : *i.e.* vente d'huîtres, vente de naissain (Irichabeau 2011). Toutefois, de fortes fluctuations interannuelles de captage ont été observées dans le Bassin d'Arcachon depuis 1995 : déficits prononcés avec moins de 100 naissains par tuile (1998, 2002, 2005 et 2007, 2009 à 2011 ; Pouvreau 2016) *versus* des années pléthoriques comme en 2003, 2006 et 2008 sans que la température ne joue un rôle direct sur cette production (David et al. Soumise). Ces fluctuations ne sont pas sans conséquence sur **l'économie** française, et en particulier l'économie arcachonnaise, plaçant l'huître au centre de ses activités industrielles et touristiques.

L'origine de ces fluctuations fait office de **plusieurs hypothèses** à de changements à **court et long termes**, influençant la vie et le recrutement larvaire, mais aussi la variabilité de la

reproduction de l'huître, elle-même fortement dépendante de la **qualité trophique** du milieu qui prévalent pendant la période de **constitution des gamètes** chez les adultes. Ces deux phases du cycle biologique de l'huître ont aussi montré une évolution récente dans le bassin d'Arcachon. Des études soulignent, une **diminution** du nombre de **larves** au premier stade de vie (particulièrement dans la **zone est** du bassin), et donc une **baisse de la fécondité et/ou de la survie larvaire**, associée à un **recul de la date de ponte** principale depuis 1995 (Maurer et al. 2016 ; David et al. Soumise).

Trois pistes de recherche ont été investiguées pour approcher ces évolutions du statut reproductif et des fluctuations de l'activité de captage dans le bassin d'Arcachon, en adressant des questions spécifiques :

1. **Hypothèse « Modifications locales des populations » :** Les huîtres arcachonnaises présentent elles des problèmes spécifiques (dégénérescence génétique) ? la nature et l'emplacement de ces différents stocks (huîtres triploïdes, diploïdes cultivées ou sauvages) peuvent-il être à l'origine des problèmes de captage ?
2. **Hypothèse « Pollution anthropique » :** les concentrations de contaminants dans le bassin d'Arcachon sont-elles en mesure d'induire une perturbation de la gamétogenèse (déficit de maturation, retard de ponte) ou de la survie larvaire ?
3. **Hypothèse climatique :** Le changement climatique influencerait-il les communautés de proies des huîtres au point de causer des anomalies de captage ?

Ces hypothèses sont étudiées dans le cadre de travaux collaboratifs impliquant différents organismes : l'université de Bordeaux (UMR EPOC[1]), l'Ifremer[2], le CRCCA[3], le SIBA[4], la DDTM [5] Gironde, et l'Agence des Aires Marine Protégées. La participation de l'UMR EPOC dans ces travaux de recherche pour tenter d'expliquer le schéma émergeant de l'activité de captage, s'articulent autour de trois axes pilotés dans le cadre de 3 **projets** : (1) le projet **OSQUAR 2** financé par la Région Aquitaine et le SIBA qui a posé le cadre général des études et qui s'est attelé plus spécifiquement à l'impact des contaminants sur la qualité de l'eau, (2) le projet

[1] Environnements et Paléoenvironnements Océaniques et Continentaux (Unité Mixte de Recherche, CNRS, Université de Bordeaux, 5805)
[2] Institut Français de Recherche pour l'Exploitation de la mer
[3] Comité Régional Conchylicole Arcachon Aquitaine
[4] Syndicat Intercommunal du Bassin d'Arcachon
[5] Direction Départementale des Territoire et de la Mer

FéLiBA financé par différents organismes (*i.e.* SIBA, Région Aquitaine, Ministère de l'Ecologie, du Développement Durable et de l'Energie, Fond Européen pour la Pêche, Agence Nationale de la Recherche) qui s'est focalisé essentiellement sur l'hypothèse « Modifications locales des populations », (1) le projet **CLEEO** financé par le Labex COTE qui se propose d'étudier la relation entre captage et facteurs climatiques pour expliquer les difficultés de la filière ostréicole arcachonnaise, notamment en comprenant le rôle de la qualité de la nourriture dans la gamétogenèse. C'est dans ce dernier cadre que ma thèse s'insère.

Les résultats des projets FéliBA et OSQUAR 2 ont permis de limiter l'impact des hypothèses 1 et 2 sur les anomalies de captage bien qu'elles agissent probablement en synergie avec la dernière hypothèse. En effet, les huîtres arcachonnaises ne semblent pas atteintes d'une dégénérescence génétique particulière. Par ailleurs, au vue des bons résultats du captage de l'année 2013, la forte compétition entre les stocks de filtreurs n'est plus plausible, il est peu probable que les densités aient été modifiées considérablement depuis les dernières années de très faible captage (2009 à 2010). La diminution des stocks d'huîtres cultivées dans les zones internes du bassin ne semble pas non plus avoir un impact considérable sur le nombre de larves. Leur remplacement par de vastes surfaces d'huîtres sauvages semble pouvoir largement compenser leur moindre fécondité par rapport à celle des huîtres cultivées. En ce qui concerne les contaminants, des expérimentations en laboratoire ont démontré l'impact que peuvent avoir certaines concentrations réalistes de composés chimiques (*i.e.* cuivre, métolachlore) dans le Bassin d'Arcachon, sur le développement et la survie larvaire (Gamain 2016). Toutefois, malgré les concentrations élevées en HAP (Hydrocarbures Aromatiques Polycycliques) et modérées en cuivre mesurées dans les tissus des huîtres sauvages dans le Bassin d'Arcachon, les seuils atteints ne semblent pas pouvoir expliquer la baisse de fécondité et le retard des pontes (Bernard et al. 2014). Par opposition, les premiers résultats du projet CLEEO montrent que, sur le long-terme, le changement climatique a profondément modifié les communautés phytoplanctoniques du bassin d'Arcachon au profit a priori d'espèces à faibles qualité nutritive (David et al. Soumise).

Cette étude se propose donc de participer à l'avancement de la réflexion autour de la reproduction de l'huître creuse dans le bassin d'Arcachon. Elle fait **partie intégrante du projet CLEEO**, mais a aussi contribué dans la réalisation de l'un des objectifs du projet FéLiBA. L'**objectif principal** est de dresser un schéma actuel de la reproduction de l'huître creuse dans le Bassin

d'Arcachon en relation avec la qualité trophique du milieu. Plus précisément, il s'agira d'une part de travailler à l'échelle de l'écosystème pour dresser un état des lieux spatial de l'état reproductif et du régime alimentaire de l'huître en période de gamétogenèse. D'autre part, de travailler à l'échelle locale pour suivre la dynamique temporelle de la gamétogenèse, en caractérisant le pool nutritif et sa mobilisation dans le processus reproductif. Ces deux parties constituant cette étude ont été approchées en lien avec le fonctionnement hydrodynamique du Bassin d'Arcachon, modulé dans les zones externes principalement par les eaux océaniques et dans les zones internes par les eaux océaniques et continentales. Les outils mis en place pour répondre à ces problématiques font l'originalité de cette étude qui se caractérise principalement par une haute résolution spatiale et temporelle, ainsi qu'une utilisation d'une multitude d'approches analytiques complémentaires pour l'étude de l'hydrodynamisme (*i.e.* modèle hydrodynamique), de la qualité trophique du milieu (*i.e.* diversité et composition du seston, acides gras essentiels), du régime alimentaire (*i.e.* isotopes, acides gras), et du statut reproductif de l'huître creuse (*i.e.* indice de condition, lipides, histologie). Le choix d'étudier les populations sauvages a émergé de la prise de conscience de leur importance écologique et leur rôle central dans l'activité du captage dans le Bassin d'Arcachon.

Organisation du manuscrit

L'organisation de ce manuscrit suit le plan suivant : un **contexte bibliographique** composé de trois parties, une **première partie** décrivant le fonctionnement hydrodynamique et trophique des écosystèmes côtiers peu profonds, une **deuxième partie**, décrivant l'écologie et la biologie de l'huître creuse, et son développement au sein du Bassin d'Arcachon, et une **troisième partie** détaillant les approches méthodologiques utilisées pour répondre aux objectifs de ce travail. Les résultats de cette étude sont présentés sous la forme de 3 articles constituant chacun un chapitre. A l'échelle de l'écosystème, un **premier chapitre** exposant les patrons spatiaux des indices de condition de l'huître sauvage en relation avec les processus hydrodynamiques (Gasmi et al. 2017) et un **deuxième chapitre** exposant les patrons spatiaux des régimes alimentaires en lien avec les origines de la matière organique et inorganique. Un **troisième chapitre** sera dédié au suivi, sur deux stations influencées différemment par les influences continentales, de la dynamique temporelle de la gamétogenèse en lien avec la variabilité saisonnière des conditions trophiques. En fin, une **discussion générale** et des **perspectives** seront présentées à la fin de ce manuscrit.

Introduction générale

Partie I

Fonctionnement hydrodynamique et trophique des écosystèmes peu profonds

1. Généralité sur les écosystèmes côtiers

L'étude du fonctionnement écologique d'un écosystème côtier commence par la compréhension de son fonctionnement hydrodynamique, premier responsable de la structuration de ses processus physico-chimiques et biologiques (Monsen et al. 2002 ; Zimmerman 1976 ; Cloern 1996). En effet, le mouvement et la dynamique des masses d'eau conditionnent le transport et la dilution des différents éléments essentiels du système (*i.e.* plancton, matière en suspension, nutriments, etc.), influençant ainsi les flux d'énergie et de matière disponible pour les organismes benthiques. L'étude de ces processus reste complexe dans les écosystèmes côtiers peu profonds, caractérisés par des gradients bathymétriques marqués et la présence de larges zones intertidales (Plus et al. 2009), où se mélangent les eaux marines poussées par les courants tidaux et les eaux douces des fleuves (Rynne et al. 2016). Ces milieux constituent des zones importantes d'un point de vue biogéochimique, où une forte production primaire bénéficie d'un important apport de nutriments et de carbone en provenance des écosystèmes adjacents (Cloern et al. 2014). Toutefois, les influences, océaniques (*i.e.* les marées), atmosphériques (*i.e.* les vents), et continentales (*i.e.* précipitations et affluentes des rivières), engendrent dans ces milieux une grande dynamique spatio-temporelle du fonctionnement hydrologique et trophique de la colonne d'eau (Grangeré et al. 2012 ; Cloern 1996). Ces échelles de variabilité conditionnent la distribution, la croissance et l'état physiologique des organismes benthiques (Wildish & Kristmanson 1997).

1.1 Courants tidaux

Les faibles profondeurs et les courant tidaux jouent un rôle fondamental dans la modulation des processus hydrodynamiques et des flux de matière au sein des écosystèmes côtiers peu profonds. Les faibles profondeurs permettent à la couche de mélange de s'étendre de la surface jusqu'au fond, ce qui permet un enrichissement de la colonne d'eau par la remise en suspension de la matière sédimentée (*i.e.* détritus) et la remise à disposition des sels nutritifs (Saint-Béat et al. 2014). Cette matière devient alors disponible pour les communautés planctoniques et est rapidement utilisée dans l'activité photosynthétique (Mann & Lazier 2006). En association avec d'autres facteurs physiques (*i.e.* vents, vagues, morphologie du fond, advection), les courants tidaux sont les premiers générateurs de cette connexion benthos-pélagos, contrôlant ainsi la transformation de la matière, le recyclage des nutriments et la dynamique sédimentaire (Ubertini et al. 2012). De plus, l'induction de turbulences par l'énergie tidale limite les phénomènes de stratification, qui peuvent constituer un facteur limitant pour la production primaire (Mann & Lazier 2006). Les courants tidaux agissent aussi dans le transport de particules phytoplanctoniques d'origine marine, renforçant ainsi le potentiel trophique des écosystèmes côtiers. Ce déplacement peut même permettre l'initiation des efflorescences phytoplactoniques locales (Glé et al. 2007 ; Trigueros & Orive 2000). Ce fonctionnement hydrodynamique fait des bassins tidaux des pièges à matière organique en suspension et de nutriments dissous qui sont produits de sa minéralisation (Zimmerman 1976).

1.2 Apports fluviaux

Conjointement au contrôle de l'hydrodynamisme et des flux de matière par les courants tidaux dans les écosystèmes côtiers peu profonds, les apports fluviaux jouent un rôle important dans la dynamique biogéochimique du système (Canton et al. 2012). En fonction des caractéristiques du bassin versant (*i.e.* taux d'occupation par les activités agricoles et industrielles, activité biologique en amont des eaux douces, nature du sédiment), les eaux douces apportent un enrichissement nutritif, soutenant la production primaire côtière (Glé et al. 2008). En opposition avec les vents et les courants tidaux générateurs de phénomènes de turbulence, les eaux douces tendent à provoquer un phénomène de stratification de la colonne d'eau. Etant plus légères que les eaux salées, elles peuvent en restant en surface, empêcher le processus de mélange tidal (Mann & Lazier 2006). Cette stratification est l'un des facteurs clé dans

l'apparition d'efflorescences phytoplanctoniques (Cloern 1996). Elle peut apparaître périodiquement dans les systèmes côtiers bien mélangés (*i.e.* macrotidaux), sous l'influence d'épisodes climatiques ou hydrologiques exceptionnelles (Mann & Lazier 2006). Toutefois, cette stratification est dépendante des quantités d'eaux douces affluentes. En période de forts débits fluviaux, l'hydrodynamisme peut provoquer l'expulsion de communauté phytoplanctonique estuarienne et empêcher l'apparition de blooms (Rendell et al. 1997) . La complexité et l'opposition spatiale des processus hydrodynamiques continentaux et océaniques dans les écosystèmes côtiers peu profonds, induit, sous l'influence d'autres facteurs physiques (*i.e.* vents, bathymétrie), une mise en place de larges gradients horizontaux conditionnant la distribution de la salinité, de la chaleur, des nutriments et de plusieurs autres facteurs (Mann & Lazier 2006).

1.3 Interaction courants-herbiers : modification de l'hydrodynamisme

Les herbiers de phanérogames marines connaissent depuis quelques décennies un déclin mondial considérable. De par leur rôle clé dans le fonctionnement écologique des écosystèmes côtiers, ils font l'objet aujourd'hui de nombreux réseaux de surveillance à long terme afin de permettre leur restauration et assurer leur durabilité (*i.e.* Short et al. 2014 ; van Katwijk et al. 2016). L'un des rôles clés attribués aux phanérogames marines est leur influence sur le fonctionnement hydrodynamique. En effet, leur densité et leurs larges étendues génèrent une modification des caractéristiques des courants. Leur interaction avec l'hydrodynamisme à l'interface eau-sédiment, induit localement une réduction significative des vitesses des courants et une altération des processus de turbulence (Fonseca et al. 1982 ; Gacia et al. 1999). Des expériences sur l'espèce *Zostera marina* montrent sa capacité à atténuer entre 50 et 90% de la vitesse des flux à l'intérieur de l'herbier (Gambi et al. 1990). Cette interaction entre courant et herbier entraîne une dynamique sédimentaire (dépôt ou érosion) importante au sein de la zone végétalisée, mais aussi les milieux environnants (Madsen et al. 2001). Les espèces qui forment des herbiers sont donc considérées comme des espèces ingénieures, capable de former une barrière physique et de modifier la circulation des eaux. Les herbiers participent donc à la variabilité spatiale des conditions hydrologiques au sein de l'écosystème. A cette variabilité spatiale, s'ajoute une variabilité temporelle liée à l'état biologique de l'herbier (croissance, dégénérescence). Ce fonctionnement module la dynamique des flux de

nutriments, car les herbiers agissent comme des réservoirs en stockant de larges quantités de carbone et d'azote organique et inorganique (Fourqurean et al. 2012).

2. L'hydrodynamisme dans le Bassin d'Arcachon

Localisé au sud du Golfe de Gascogne, le Bassin d'Arcachon (44°40'N, 1°10'O) résulte d'une longue évolution d'un système primitivement estuarien modulé par la principale rivière actuelle, l'Eyre (Labrid 1969). Sa forme triangulaire caractéristique décrite pour la première fois par Waleursee en 1928, a été provoquée par l'allongement vers le sud du cordon littoral du Cap-Ferret (Bouchet 1968). L'hydrodynamisme dans le bassin d'Arcachon est influencé en premier lieu par les courants tidaux et en second lieu par les vents (Salles et al. 2015). Le cycle tidal est semi-diurne et les amplitudes de marée varient entre 0,8 et 4,5 m, pour un échange d'eaux avec l'océan de 384.10^6 m^3 et 264.10^6 m^3, pour mortes et vives eaux, respectivement (Cayocca 2001). Les courants tidaux s'introduisent dans la baie au travers de ses deux passes (nord et sud ; Figure 1), ils progressent uniformément (et refluent au jusant) en respectant l'embranchement complexe des chenaux principaux. Ce fonctionnement hydrodynamique en « piston » est semblable à celui observé dans les milieux estuariens (Plus et al. 2009). La circulation des courants à l'intérieur de la baie permet son découpage en deux zones : une zone interne où l'on trouve de faibles courants et flux résiduels, et une zone externe qui s'étend de l'entrée du bassin jusqu'à l'amont des chenaux du Cap-Ferret et du Teychan (Figure 1), où l'on trouve de forts courants avec des flux résiduels en direction de l'océan (Plus et al. 2009).

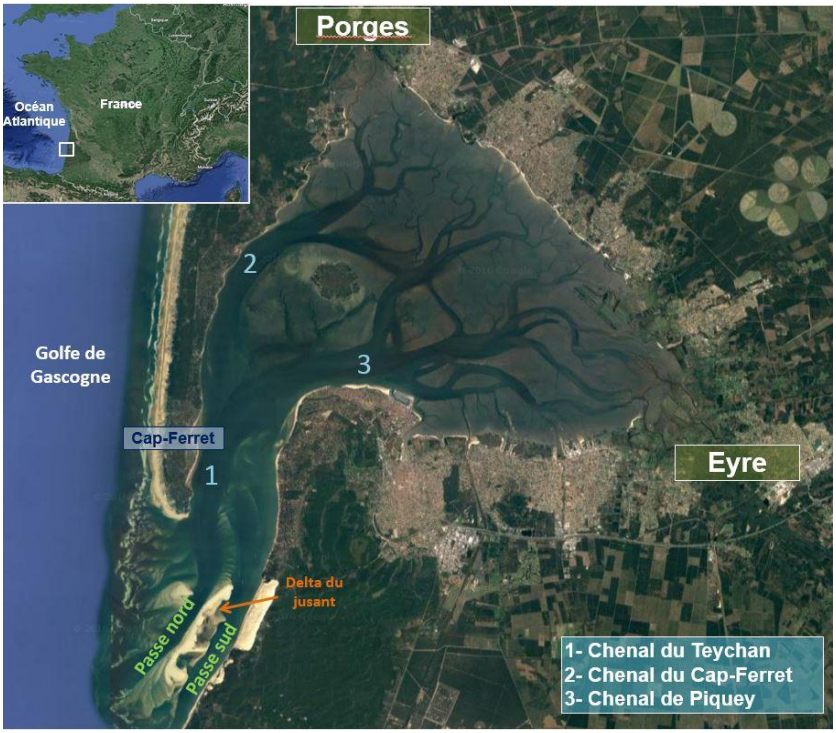

Figure 1 : Carte du Bassin d'Arcachon représentant les principales composantes hydrodynamiques et géomorphologiques.

2.1 Courants tidaux

Le taux de renouvellement océanique moyen, est de 13,3 et 19,5 jours sous l'effet des vents nord et ouest, respectivement, avec un meilleur renouvellement de la zone externe de la baie (Plus et al. 2009). Bien que dominants, les courants tidaux n'assurent pas un bon renouvellement des eaux, l'eau se retirant avec la marée basse pénétrante dans le bassin à la prochaine marée haute. Les courants tidaux jouent tout de même un rôle important dans la dynamique des communautés phytoplanctoniques au sein du Bassin d'Arcachon. Par le biais d'une surveillance à haute fréquence, Glé et al. (2007) décrivent pour la première fois la récurrence annuelle de l'introduction d'un inoculum phytoplanctonique hivernal (fin février) en provenance du Golfe de Gascogne, initiant la période de productivité dans le système. Les auteurs soulignent la variabilité spatiale de cette efflorescence qui trouve des conditions favorables et se développent principalement dans les zones externes avant d'atteindre les zones internes (Figure 2). Cette influence océanique est aussi soulignée par Auby & Maurer (2004) pour la période estivale. Les auteurs décrivent la communauté phytoplanctonique du bassin d'Arcachon comme étant ***«typique d'une eau marine côtière»***, avec une dominance de picoprocaryotes (*Synechococcus*) d'origine océanique, l'existence d'une importante communauté de picoeucaryotes (Partensky et al. 1996), et la présence d'une communauté

nanoplanctonique abondante et diversifié (Auby et al. 2000). Ces communautés phytoplanctoniques montrent aussi un pattern spatial lié à ces influences océaniques. Les eaux de l'entrée du bassin se caractérisent par les *Synechococcus*, qui pénètrent largement en saison estivale, tandis que les grandes cellules eucaryotes sont plus typiques des masses d'eaux internes (Auby & Maurer 2004).

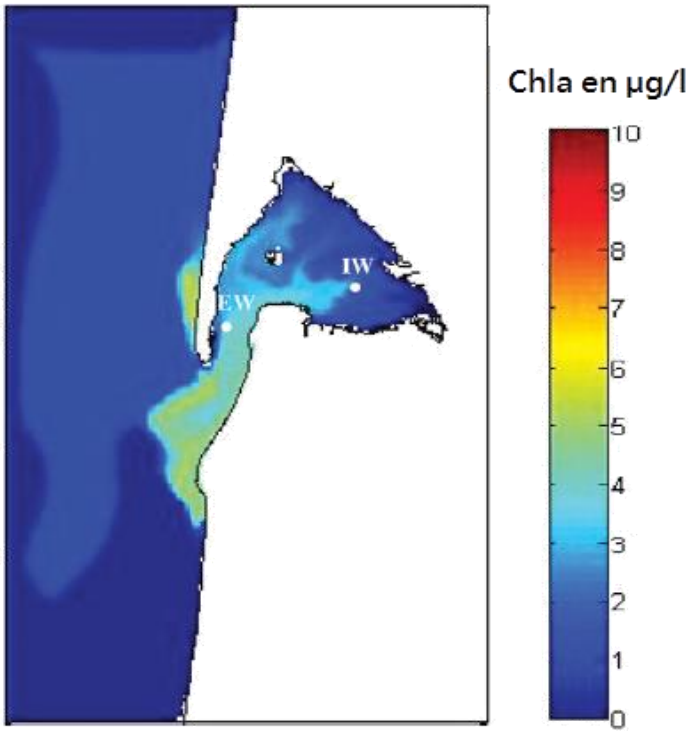

Figure 2 : Modélisation (MARS2D) de la pénétration et de la dispersion des cellules phytoplanctoniques entre février et mars 2003 dans les eaux externes (EW) et les eaux internes (IW). Figure extraite de Glé et al. (2007).

2.2 Apports fluviaux

Un bassin versant de 4 136 km² draine dans le bassin d'Arcachon une quantité d'eau douce annuelle d'environ 1,25 milliard de m^3, dont 83% arrivent dans le système par écoulement superficiel, 11% par l'apport directe des précipitations et 6% par un écoulement des nappes phréatiques. Sur les façades «sud» et «est», 19 rivières correspondant à une surface de bassin versant de 3000 km² sont responsables des apports en eaux douces. Ces apports sont supplémentés par les lacs et les canaux au nord et au sud du bassin (1136 km²). Les sources des flux continentaux sont multiples, toutefois deux principales rivières assurent la majorité des apports annuels d'eaux douces dans le bassin, 70% de L'Eyre et 24% du Porges (Plus et al. 2009 ; Figure 1). Les débits mensuels moyens varient pour l'Eyre entre 8,4 et 38,6 $m^3 s^{-1}$ et entre 1,8

et 12,9 m^3 s^{-1} pour le Porges (Plus et al. 2009). Le Bassin d'Arcachon est classé parmi les écosystèmes bien mélangés par les courants tidaux. La couche de mélange correspond à toute la hauteur de la colonne d'eau, les phénomènes de stratification qui peuvent être générés par les rivières ne sont donc pas notables (Glé et al. 2007). Les fleuves jouent un rôle important dans le fonctionnement écologique du bassin d'Arcachon. Ils constituent le source majeure d'apports en nutriments (*i.e.* azote et silicium) (Castel et al. 1996 ; Rimmelin et al. 1998 ; De Wit et al. 2005). Ces apports expliquent la majeure partie de la variabilité saisonnière, spatiale et interannuelle de la production primaire phytoplanctonique dans le Bassin d'Arcachon (Glé et al. 2008).

2.3 Interaction courants-herbiers

Le Bassin d'Arcachon abrite dans ses vastes zones intertidales le plus large herbier de *Zostera noltei* en Europe (Auby & Labourg 1996). Cette espèce cohabite avec l'espèce *Zostera marina* qui colonise les bords des chenaux en zone subtidale. Ces deux espèces ont subi entre 1988 et 2008 un sévère déclin, estimé à 33% pour *Z. marina* et 74% pour *Z. noltei* (Figure 3 ; Plus et al. 2010). Ce déclin serait responsable d'une diminution de la capacité de séquestration du carbone qui passerait de 24 846 ± 6030 tonnes C/an en 1989 à 16 564 ± 4020 tonnes C/an en 2007 à l'échelle du bassin d'Arcachon (Ribaudo et al. 2016). En plus de son impact sur la biogéochimie, ce déclin jouerait sans doute un rôle dans la modification de l'hydrodynamisme au sein du système. De ce fait, plusieurs études se mettent en place pour comprendre les variabilités saisonnières et spatiales de l'interaction courant-herbier-sédiment (Kombiadou et al. 2014 ; Mutterlein et al. 2016 ; Ganthy et al. 2013). Ces variabilités sont induites principalement par l'espèce *Z. notlei*, qui montre de forts changements saisonniers en terme de densités, avec une période de croissance se situant entre février et septembre, et une période de dégénérescence le reste de l'année (Auby & Labourg 1996). Cette variabilité saisonnière, en plus du déclin des herbiers à *Z. noltei*, engendre des changements significatifs dans la propagation de l'onde tidale, influençant le niveau des eaux et l'asymétrie des courants, particulièrement dans la partie interne du bassin (Mutterlein et al. 2016).

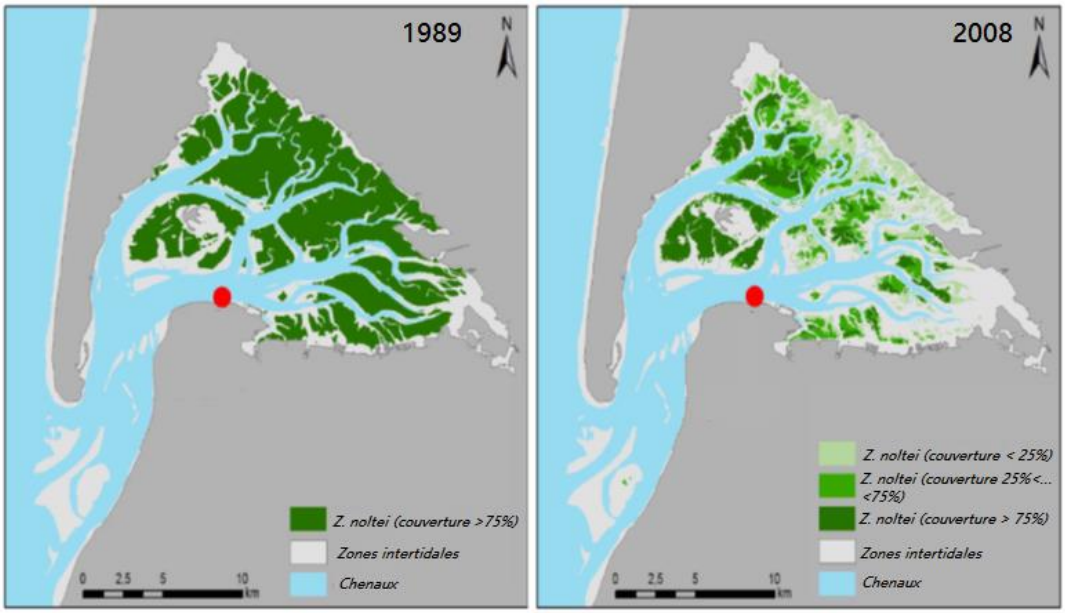

Figure 3 :Cartographie des changements de biomasse de *Z. noltei* entre 1989 et 2008 dans le bassin d'Arcachon d'après Plus et al. (2010).

Partie II

Écologie et biologie de l'huître creuse *Crassostrea gigas*

1. Répartition géographique et biomasses de *C. gigas* sur les côtes françaises

1.1 Exploitation ostréicole

L'huître creuse du Pacifique *Crassostrea gigas* (Thunberg 1793), est une espèce native des côtes japonaises. Pour des besoins de production aquacole, elle a été introduite avec succès par l'homme dans différents écosystèmes des deux hémisphères : *i.e*. une quinzaine de pays au cours du 20ème siècle tels que, le Canada vers 1912, l'Australie et la Tasmanie vers 1950, la Nouvelle-Zélande et la France vers 1970 (Grizel 1996). L'espèce est connue pour sa grande capacité d'adaptation à une large gamme de conditions environnementales et une résistance aux pathogènes. Ces introductions répondaient principalement à deux problématiques, les maladies et la surexploitation qui touchaient les espèces indigènes (Grizel 1996). En France, *C. gigas* a permis de maintenir la filière ostréicole, en montrant une grande capacité de résistance aux différentes maladies affectant à l'époque l'huître portugaise *Crassostrea angulata* (Viroses) et l'huître plate *Ostrea Odulis* (*Marteilia refringens* et *Bonamia ostreae*) (Grizel 1983 ; Grizel & Heral 1991). La disparition de *C. angulata* (1971-1973) des côtes françaises avait infligé des pertes considérables au secteur ostréicole, *C. gigas* constituait donc une alternative permettant de sauvegarder les emplois et la production (Grizel & Heral 1991). De ce fait, de grandes quantités de géniteurs et de juvéniles d'huîtres (naissain) importés respectivement du Canada et du Japon, ont été implantées dans différents bassins français (*i.e*. Baie de Bourgneuf, Pertuis Charentais, Bassin d'Arcachon). Aujourd'hui, l'activité conchylicole française repose en majeure partie sur le recrutement naturel de naissain (captage) provenant principalement de deux centres naisseurs historiques, le Bassin d'Arcachon et les Pertuis Charentais, mais aussi de façon de plus en plus significative de bassins situés plus au nord, la Baie de Bourgneuf et la Rade de Brest (Pouvreau et al. 2016).

L'huître creuse *C. gigas* reste toutefois l'espèce de mollusque bivalve la plus produite mondialement, avec un tonnage global estimé à 625 925 tonnes (FAO, 2014). La France occupe la première place européenne et la 4ème place après la Chine, le Japon et la Corée. Environ

110 000 tonnes sont produites chaque année, dont 47 000 tonnes provenant du plus grand bassin conchylicole français de Poitou-Charentes (5100 ha, IFREMER).

Mis à part quelques années de faibles recrutements (1972, 1981, 1986) associées à des anormalités de températures, *C. gigas* trouve des conditions favorables pour son développement en France (Grizel & Heral 1991). Toutefois, depuis 2008, des mortalités massives chez les juvéniles de *C. gigas* sont observées dans tous les écosystèmes français (Pernet et al. 2012 ; Petton et al. 2013), mais aussi en Irlande (Lynch et al. 2012) et dans les îles Anglo-Normandes (Martenot et al. 2011). Ces mortalités qui peuvent toucher jusqu'à 90% de la production (Martenot et al. 2011) ont été reliées à l'infection par l'herpès virus OsHV-1, fortement virulent sous l'effet des température élevées en période estivale (Segarra et al. 2010). Cette crise écologique est la plus marquante dans l'histoire de l'industrie française de l'huître creuse depuis son introduction dans les années 1970 (Pernet et al. 2012). En parallèle de cette crise de mortalité, touchant principalement les huîtres ayant moins d'un an, des fluctuations de recrutement larvaire sont observés dans les différents centres naisseurs français (Pouvreau et al. 2016).

1.2 Développement des gisements naturels

Dans la plupart des régions côtières où elle a été introduite, *C. gigas* ne s'est pas limitée aux zones de culture, mais s'est dispersée en colonisant de nouveaux environnements (Ayres 1991 ; Cardoso et al. 2007 ; Dinamani 1991). En Europe, elle est devenue une espèce établie, d'importance écologique et est arrivée à s'installer du sud de la Norvège jusqu'au sud du Portugal (Cardoso et al. 2007 ; Cognie et al. 2006 ; Wehrmann et al. 2000). Étant naturellement présente dans les eaux chaudes (Drinkwaard 1999), *C. gigas* montre un recrutement variable selon les étés (Borgne et al. 1973). Les faibles températures et les conditions climatiques estivales maussades ne permettent pas le déclenchement des pontes et la survie larvaire. L'élévation des températures ces dernières décennies, ainsi que l'augmentation des biomasses phytoplanctoniques semblent avoir favorisé ces processus biologiques, permettant la survie et la dispersion des larves et donnant lieu à un meilleur recrutement naturel (Cognie et al. 2006 ; Diederich et al. 2005 ; Thomas et al. 2015). Par exemple, des croissances spectaculaires des gisements naturels sont rapportées au Pays-Bas : l'espèce totalement absente en 1976 dans la partie orientale de l'estuaire de l'Escaut, occupe entre 15 et 35 ha en 1980 et atteint 640 ha en

2002 (Kater & Baars 2003 dans Diederich et al. 2005). En France, les estimations des gisements naturels sont rares, une étude réalisée au niveau de 21 secteurs en Poitou-Charentes rapportent une biomasse totale de 35 000 tonnes (Soletchnik et al. 2012), mais le même phénomène d'invasion est aussi documentée notamment en Bretagne (Le Berre et al. 2009). Dans le Bassin d'Arcachon, les quantités sont passées de 38 000 tonnes en 2004 à 65000 tonnes en 2011 (Blanchet 2004 ; Soletchnik et al. 2012). *C. gigas* semble trouver, sous l'effet des changements climatiques, un meilleur optimum thermique pour sa gamétogenèse, sa ponte et sa survie larvaire en direction des pôles (Thomas et al. 2015).

2. Biologie de l'huître

Les huîtres font partie de l'embranchement des mollusques, de la classe des bivalves, de l'ordre des ostréidés. Ce sont des animaux sédentaires, fixés sur des substrats durs. Ils peuplent les zones marines (intertidales et infralittorales) et estuariennes. Les huîtres ont une grande capacité de tolérance à un large panel de conditions environnementales, ce sont des organismes eurythermes et euryhalins (Delaporte 2005).

2.1 Anatomie

Chez les huîtres, une coquille calcaire, constituée de deux valves asymétriques, renferme une masse viscérale maintenue par un muscle adducteur (Figure 4). Cette masse viscérale est enveloppée dans un manteau, qui joue un rôle fondamental dans la formation de la coquille et dans l'accumulation des réserves pour la reproduction. Au printemps et à partir de ces réserves, la gonade se développe progressivement sous le manteau et autour de la glande digestive, jusqu'à occuper plus de 50% de la masse viscérale. Le manteau abrite aussi les branchies, qui assurent une double fonction, la respiration et la nutrition. Ces dernières sont tapissées de filaments ciliés qui permettent une circulation de l'eau à l'intérieur de la cavité palléale, et donc une oxygénation et un apport de particules sestoniques. Ces particules sont dirigées vers les palpes labiaux, puis transférées vers la bouche avant d'être ingérées. L'appareil circulatoire chez l'huître est constitué d'un cœur, d'artères et de veines. Le système nerveux est peu développé, il est réduit à deux ganglions, un premier près de la bouche et un deuxième sous le muscle adducteur.

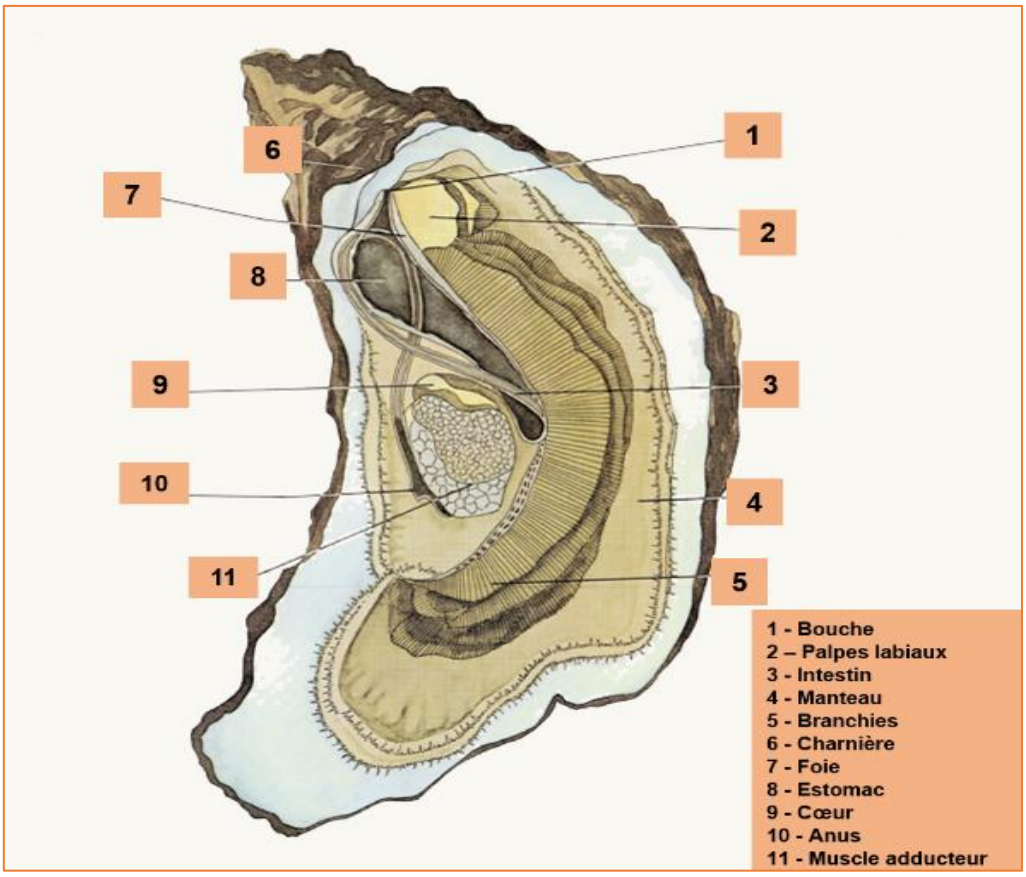

Figure 4 : Schéma représentant les principaux organes chez l'huître creuse *Crassostrea gigas*.

2.2 Reproduction et développement

Différentiation sexuelle

L'huître creuse *Crassostrea gigas* est hermaphrodite avec une sexualité alternative irrégulière. Les individus matures sont ainsi soit mâles soit femelles, les cas simultanés sont rares. Les pourcentages de mâles sont généralement élevés chez les individus d'un an et peuvent représenter 70% de la population. L'équilibre mâles/femelles est mieux observé au cours de la deuxième année, puis s'installe chez les huîtres âgées une tendance à la domination des femelles (Auby & Maurer 2004). La différenciation sexuelle s'effectue à l'automne, avant le début de la saison de reproduction (Galtsoff 1964 ; Lubet 1980 ; Auby & Maurer 2004 ; Fabioux 2004). Des facteurs externes (*i.e.* température, nourriture, polluants) peuvent avoir une forte influence sur ces différentiations et conditionner donc les sex-ratios dans la population (Gerard et al. 1995 ; Lango-Reynoso et al. 1999).

Gamétogenèse et ponte

L'activité gamétogénétique chez l'huître est saisonnière, elle induit différentes variations physiologiques et biochimiques. L'initiation de la constitution des cellules sexuelles est observée en hiver (Fabioux 2004) puis la gamétogénèse s'accélère en corrélation avec l'augmentation de la nourriture et de la température. Selon les conditions climatiques et environnementales du milieu, la maturité sexuelle est atteinte en début de période estivale. En fin de cycle de gamétogenèse, la gonade se trouve très développée et les huîtres deviennent très sensibles aux stimuli extérieurs (*i.e.* température, efflorescence phytoplanctonique, conditions météorologiques, cycle des marées, Bernard et al. 2016). La fécondation étant externe, ces stimuli permettent le déclenchement de la ponte et l'émission des gamètes. En fonction de la localisation géographique, la ponte peut avoir lieu une ou plusieurs fois par an (Goulletquer 1995 ; Chavez-Villalba et al. 2000, Bernard et al. 2016). L'huître possède aussi la capacité de reconstruire rapidement ses cellules sexuelles après une ponte. Dans une même saison de reproduction, certains individus pourraient pondre plusieurs fois (His 1991 ; Auby & Maurer 2004). Les pontes peuvent être synchrones ou asynchrones entre les individus dans un même milieu. Elles peuvent être aussi totales ou partielles pour un même individu et sont suivies par une phase automnale de résorption gonadique, permettant la restructuration des tissus reproductifs et l'élimination des cellules sexuelles restantes par cytolyse et phagocytose (Lubet 1991). Le cycle se termine par une période de repos sexuel de la fin de l'automne à l'hiver, durant laquelle l'activité gonadique est très réduite avant l'initiation de la prochaine saison de reproduction. Durant cette période, les huîtres construisent leurs réserves énergétiques sous forme de glycogène stocké principalement dans le manteau (Berthelin et al. 2000a). Ces réserves servent, en plus de l'apport nutritif printanier, de support énergétique majeur de la gamétogenèse (Deslous-Paoli & Héral 1988 ; Berthelin et al. 2000a). Cet apport est en particulier essentiel pour les femelles qui fournissent de grandes quantités lipidiques aux ovocytes. Ces contributions seront utilisées pendant l'embryogenèse et les premiers jours de la vie larvaire (His & Maurer 1988)

Fécondation et vie larvaire

L'émission des gamètes mâles et femelles directement dans le milieu permet une fécondation externe. Une larve pélagique se forme au bout de 24h (pour une température entre 22 et 24°C),

en passant du stade trochophore au stade véligère (ou larve D). La larve à ce stade possède les principaux organes (*i.e.* coquille, couronne ciliée, appareil digestif), ce qui lui permet de nager et de s'alimenter. Elle évolue progressivement et développe son organe de fixation, le « pied», pour atteindre le dernier stade de la vie pélagique et former une larve pédivéligère (Figure 5). La durée totale du cycle pélagique est variable (2 à 3 semaines), elle est conditionnée par la température et la quantité de nourriture disponible. La vie benthique débute dès lors que la larve trouve un support adéquat. La métamorphose continue après la fixation, le développement complet pour atteindre la forme adulte se fait en 6 mois.

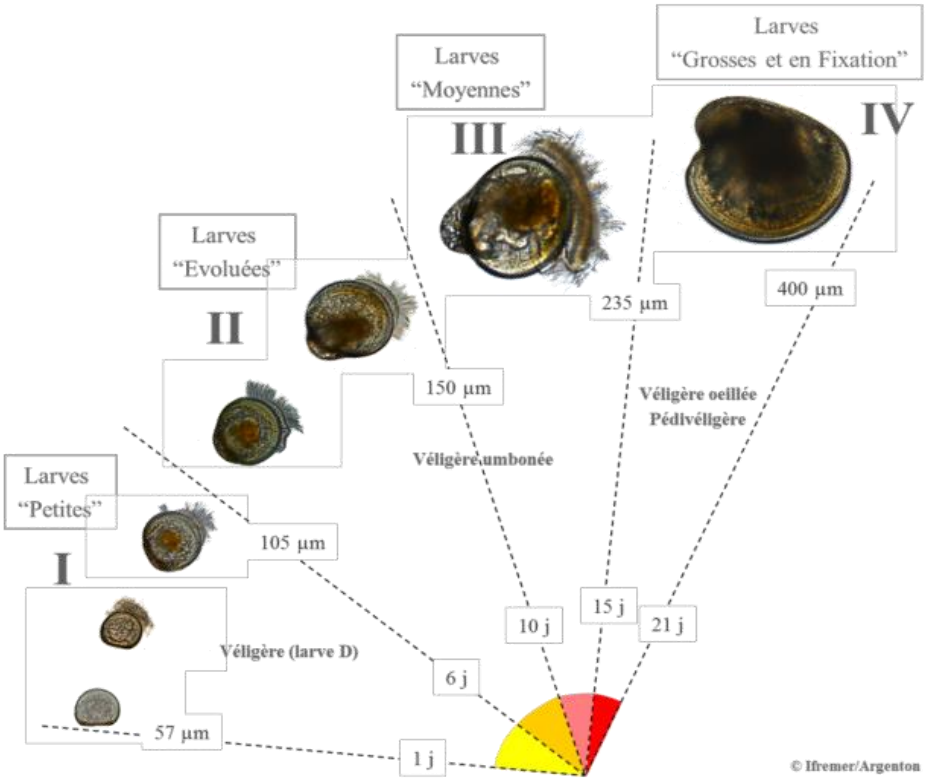

Figure 5 : Représentation des différents stades larvaires chez l'huître creuse, *Crassostrea gigas*, d'après (Le Pennec 1978 ; His 1991), tiré de (Pouvreau et al. 2016).

2.3 Régime alimentaire

L'huître adulte, au stade benthique, fait partie des bivalves filtreurs qui se nourrissent de matériel particulaire en suspension dans la colonne d'eau (seston). Son régime alimentaire est

connu pour être principalement constitué de phytoplancton et de microphytobenthos (Marchais et al. 2013 ; P Riera & Richard 1996 ; Leal et al. 2008). Une fois les particules sestoniques collectés au niveau des branchies, *C. gigas* est capable de les trier avant leur ingestion, moins de 10% des particules de taille de 1µm et 50 % des particules de tailles supérieures à 3 µm sont retenues (Heral 1985). La taille optimale d'ingestion se situe pour *C. gigas* entre 7 et 20 µm mais ceci dépend de la charge sestonique présente dans le milieu (L Barillé et al. 1993). Chez *Crassostrea virginica*, l'efficacité diminue lorsque la charge sestonique est très forte (Haven & Morales-Alamo 1970). Comme les branchies, les palpes labiaux participent aussi au processus de tri pré-ingestif. La sélection s'effectue non seulement en fonction de la taille des particules mais encore de leurs propriétés biochimiques (Ward et al. 1997 ; Espinosa et al. 2007). Ces rejets pré-ingestifs démontrent la sensibilité de *C. gigas* à la qualité trophique du milieu, ils présentent une importance considérable dans le bilan énergétique de l'espèce (Raillard et al. 1993). Pendant la phase planctonique, les larves de *C. gigas* se nourrissent dès le stade véligère en captant les particules sestoniques (taille de 1 à 20µm) grâce à leur couronne cilié (Auby & Maurer 2004). La capacité de tri et de sélection a été observée aussi chez les larves (Baldwin 1991).

3. Historique de reproduction de l'huître creuse dans le Bassin d'Arcachon

3.1 La forme cultivée

Depuis les années 1970, le Bassin d'Arcachon fait partie des plus grands centres naisseurs de l'huître creuse en France. Les conditions climatiques clémentes de la région ont fait de cet écosystème un centre spécialisé dans le captage naturel (rétention sur collecteur) de larves d'huître. Le Bassin d'Arcachon fournit 60 à 70% des 4 milliards et demi de juvéniles d'huître nécessaires à l'ensemble de la production annuelle française (Comité Régional Conchyliculture Arcachon Aquitaine). De plus, le bassin assure un approvisionnent international, en alimentant en naissains plusieurs bassins ostréicoles européens.

Cette activité fortement dépendante de la qualité de l'environnement a connu toutefois des périodes de crises entravant la capacité de production du bassin d'Arcachon. La crise la plus marquée dans l'histoire de la production Arcachonnaise a été la succession d'années sans captages, de 1977 à 1981. Les recherches effectuées pour comprendre ce phénomène à cette époque avaient mis en évidence le rôle du TBT (Tributyl Etain, composant des peintures

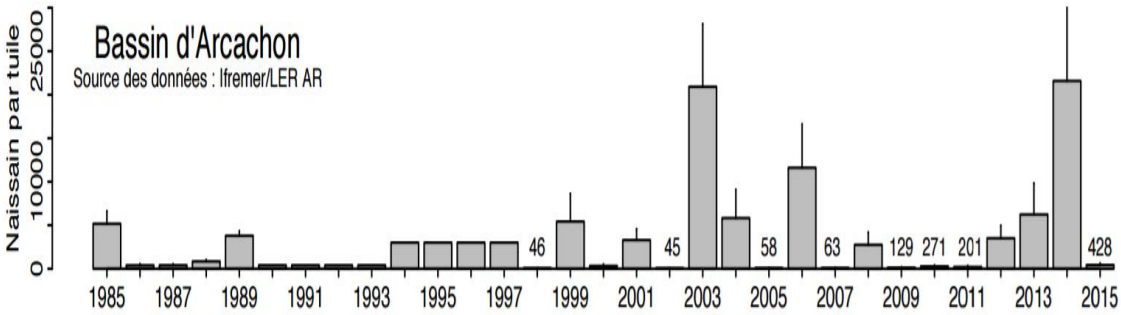

Figure 6 : Série temporelle de l'évolution du recrutement larvaire pour l'activité ostréicole dans le bassin d'Arcachon, tiré de (Pouvreau et al. 2016).

antisalissure) dans la perturbation du potentiel trophique du bassin, affectant potentiellement la nutrition et la croissance larvaire (His et al. 1984 ; His & Robert 1983). Mais plus récemment, depuis 1998, de fortes fluctuations du captage sont aussi observées. Des années à très faible captage (*i.e.* 2009, 2010, 2011) alternent avec des années à captage exceptionnel (*i.e.* 2003, 2006, 2008, 2014, 2015 ; Figure 6).

Ces fluctuations du captage ont fait l'objet d'une première étude intégrée de l'état reproductif de l'huître creuse dans le bassin d'Arcachon, cette dernière a permis d'identifier les facteurs déterminant du succès du captage. Deux phases clés et très sensibles aux conditions environnementales sont soulignées : 1- la survie larvaire, mise en relation avec la température de l'eau au moment du développement des larves, 2- la quantité initiale de larves émises par les géniteurs adultes, mise en relation avec la biomasse phytoplanctonique entre la fin de la période hivernale et printanière (Auby & Maurer 2004). Le captage a été ensuite suivi chaque année dans le bassin d'Arcachon, jusqu'à la mise en place en 2008 du réseau Velyger de l'Ifremer pour « Observer, Analyser, et Gérer la variabilité de la reproduction et du recrutement de l'huître creuse en France». Dans cinq bassins ostréicoles français, Velyger assure un suivi de trois descripteurs de la reproduction de *C. gigas* : (1) suivi annuel de la croissance et de la maturation d'un lot d'huîtres sentinelles, (2) suivi estival de l'abondance et du développement larvaire, (3) estimation automnale du captage sur collecteur professionnel. En parallèle de ces descripteurs de l'état de condition de *C. gigas*, il assure un suivi annuel de la température, du phytoplancton et de la salinité (Pouvreau et al. 2016). Le réseau Velyger a permis de rendre compte de l'émergence plus marquée des phénomènes de fluctuations du captage dans le Bassin d'Arcachon par rapport aux autres systèmes ostréicoles français pour la période récente.

Ces phénomènes y existent mais s'avèrent être beaucoup moins marqués (*i.e.* Pertuis Charentais ; Pouvreau et al. 2016).

En comparaison avec d'autres écosystèmes français, l'effort de reproduction et la maturation de *C. gigas* sont décrites comme faibles dans le bassin d'Arcachon (Bernard et al. 2014). Ceci est attribuable à la capacité trophique du milieu, naturellement plus faible que dans les autres systèmes (*i.e.* système mésotrophe à faible production primaire, Glé et al. 2008). Toutefois, ces deux processus subissent aussi localement des changements considérables depuis quelques années, faisant émerger un nouveau schéma reproductif au sein du bassin. Ces changements sont reflétés par un faible investissement dans la formation des gamètes, associé à un recul de la date de ponte (Auby et al. 2012 ; Bernard et al. 2014). Depuis 1995, mis à part quelques années exceptionnelles (*i.e.* 1994, 2003, 2006), une tendance à la baisse du nombre moyen de larves au stade «Petites», et donc l'intensité des pontes principales et secondaires, est révélée dans le bassin d'Arcachon (Figure 7 ; Maurer et al. 2016). Un constat qui s'associe au mauvais captage des années 2009 à 2011 (Maurer et al. 2011), et qui se poursuit en 2012, 2014 et 2015 (Maurer et al. 2016). Dans le même temps, un recul de la date d'émission des gamètes dans le milieu est constaté entre 1987 (début juillet) et 2015 (fin juillet) ; (Figure 8 ; Maurer et al. 2016). Ces retards sont associés dans les zones les plus internes du bassin d'Arcachon à des pontes partielles, les huîtres n'émettant pas la totalité des gamètes produites (Bernard et al. 2014).

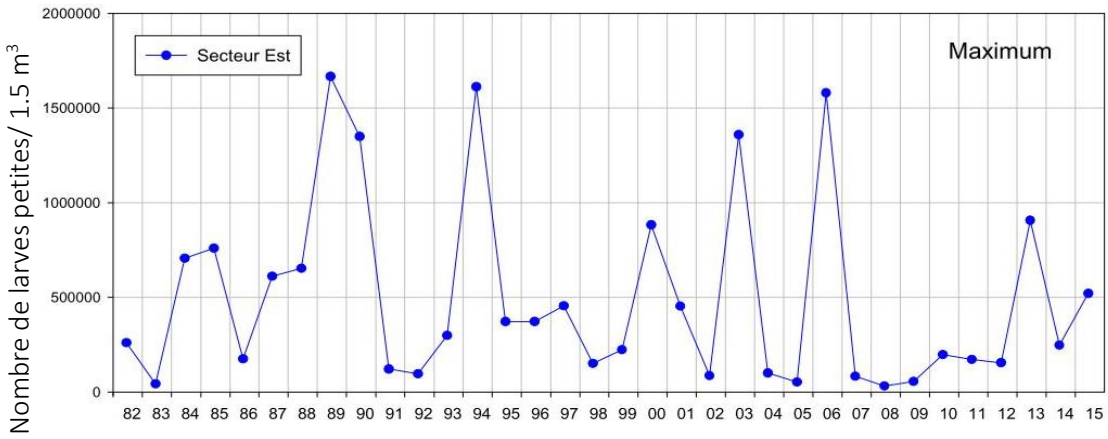

Figure 7 : Evolution des abondances maximales de larves «Petites» en période ponte principale «juillet-aout» de 1982 à 2015 dans le secteur «est» du Bassin d'Arcachon, tiré de Maurer et al. (2016).

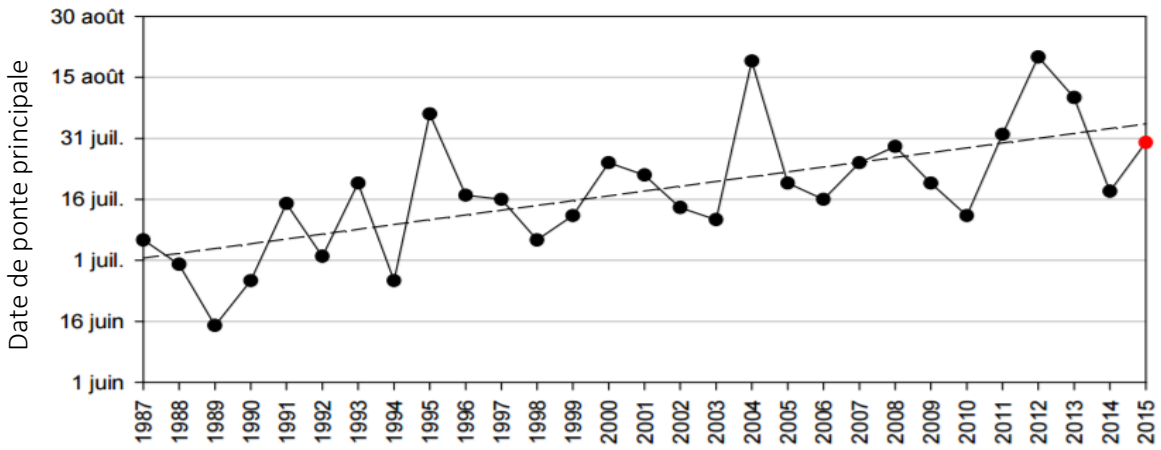

Figure 8 : Évolution de date la ponte principale des huîtres localisées dans la zone est du Bassin d'Arcachon entre 1987 et 2015, tiré de Maurer et al. (2016).

3.2 La forme sauvage

Les huîtres creuses sauvages ont été très peu étudiées dans le bassin d'Arcachon. Toutefois, la diminution des parcs à huîtres cultivées depuis les années 70s et leur déplacement vers les zones externes du bassin (Maurer. D, *com. pers*), a redéfinie l'importance de ces gisements naturels. De plus, représentant 79% de la biomasse (**sauvage** : 65 000 tonnes, **cultivée** : 16 600 tonnes ; Scourzic et al. 2012), ils occupent un emplacement écologique important et constituent la première source productrice de larves du Bassin d'Arcachon. Cette importance a été soulignée dans le cadre du projet FéLiBA, et elle provient de leur localisation dans les zones internes du bassin, propices à la rétention des larves. Les huîtres sauvages semblent contribuer majoritairement au captage puisque la zone interne contribue à 46% des larves qui restent dans le bassin, alors que les larves produites sur les zones externes se dispersent vers l'extérieur sous l'effet de l'hydrodynamisme (Figure 9 ; Bernard et al. 2014).

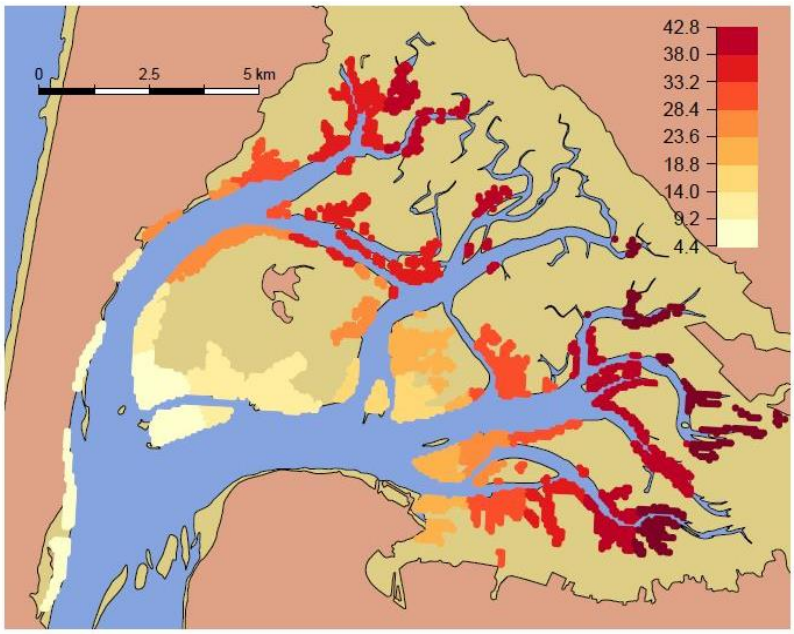

Figure 9 : Pourcentage de rétention moyen des larves dans le bassin d'Arcachon d'après un modèle hydrodynamique selon la répartition de 35 gisements naturels d'huîtres creuses. Extraite de (Bernard et al. 2014).

Partie III

Approches méthodologiques

1. Hydrodynamisme : bathymétrie et temps de renouvellement des masses d'eaux

1.1 Mesures bathymétriques LIDAR

Comprendre le fonctionnement hydrodynamique des écosystèmes côtiers peu profonds débute impérativement par la caractérisation de leur bathymétrie, premier facteur influençant la circulation des courants, ainsi que les processus d'émersion et d'immersion des zones intertidales. Plusieurs outils permettent de réaliser des cartographies bathymétriques en zones côtières (*i.e.* sondeur hydrographique, GPS différentiel) et le couplage de ces méthodes et parfois nécessaire pour améliorer l'exactitude des mesures (Hein et al. 2002). Depuis quelques décennies, la technologie LIDAR (Light Detection And Ranging) connaît un essor considérable dans les études consacrées à la morphologie et l'évolution des zones côtières (Brock & Purkis 2009). Cette technique de télédétection par laser est utilisée en zones côtières pour différents types d'études comme la caractérisation d'habitats d'espèces (Sellars & Jolls 2007) ou la cartographie des herbiers (Ishiguro et al. 2016). Elle permet de réaliser des mesures bathymétriques à large échelle acquise grâce à un double système d'émission/réception de lumière. Le temps écoulé entre l'émission et la réception du signal permet de calculer la distance franchie. Les mesures bathymétriques en zones côtières sont acquises grâce à un télémètre laser aéroporté (Guenther 2007).

1.2 Modèle hydrodynamique MARS

Plusieurs outils et concepts se sont développés en modélisation pour permettre de comprendre le fonctionnement hydrodynamique complexe des systèmes côtiers (Zimmerman 1976 ; Brooks et al. 1999 ; Monsen et al. 2002 ; Pascalis et al. 2016). Ces modèles permettent de *«simuler la dispersion de substances solubles avec des emprises et des résolutions spatiales variables»* (Ouahsine 2014). Les modèles hydrodynamiques, basée sur les équations mathématiques de la mécanique des fluides (Navier-Stokes), permettent de simuler finement les hauteurs d'eau et vitesses de courant résultant de la propagation de la marée, des apports d'eaux continentales par les rivières, et du vent. La prise en compte de l'advection et de la diffusion de traceurs (e.g.

substances dissoutes ou particulaires, sédiments, etc) permet entre autre de calculer différentes grandeurs telles que : flux résiduels, temps de renouvellement, suivi de dispersion larvaire etc. Reposant sur ces principes, le modèle MARS (Lazure & Dumas 2008) développé par IFREMER a été appliqué pour la première fois dans le bassin d'Arcachon dans sa version 2D par Plus et al. (2009). Ce travail a permis de caractériser le fonctionnement hydrodynamique du système sous l'influence de 3 grands forçages physiques (marées, vents et rivières). Il en résulte une caractérisation saisonnière à l'échelle de la baie des processus de mélange et de transport des masses d'eaux (*i.e.* temps de renouvellement des eaux marines et des eaux douces, vitesse des courants, prisme tidal etc.). Le modèle mit en place par Plus et al. (2009) a par la suite été amélioré afin de prendre en compte l'effet des herbiers à zostères sur l'hydrodynamique (Kombiadou et al. 2014) puis appliqué au bassin d'Arcachon dans sa version 3D.

La modélisation des temps de renouvellement, proxy de l'hydrodynamisme local, réalisé à l'échelle du bassin d'Arcachon reflète comme décrit par Plus et al. (2009) *«le temps nécessaire pour un remplacement significatif d'une portion d'eau avec une autre arrivant des systèmes adjacents, i.e. océan ou rivières».*

2. Conditions trophiques du milieu

La compréhension du fonctionnement hydrodynamique d'un écosystème apporte des informations précieuses sur la dynamique des conditions environnementales locales et le transport de matière dans un milieu. Toutefois, des analyses *in situ* permettent de les caractériser et d'estimer le potentiel trophique du milieu, à travers la détermination de la nature de la matière organique en suspension et les forçages environnementaux qui la régissent. La caractérisation de la qualité hydrologique repose sur le suivi de ses composantes physico-chimiques (*i.e.* température, salinité, oxygène) et surtout biologiques (*i.e.* bactéries, phytoplancton). Ceci permet de caractériser la nature de la matière organique en suspension et les forçages environnementaux qui les régissent. Si les mesures physico-chimiques font appel généralement à un appareillage classique, les mesures biologiques exigent des moyens humains et techniques plus sophistiqués. L'analyse du phytoplancton peut être réalisée par le biais de différentes méthodes qui peuvent donner des informations quantitatives et/ou qualitatives. L'indicateur le plus couramment utilisé pour déterminer la biomasse phytoplanctonique, est la **chlorophylle *a*** (Chla). Elle est généralement mesurée par des

méthodes d'excitation lumineuse et mesure de la fluorescence (*i.e.* fluorimétrie, **spectrofluorimétrie** ; Yentsch & Menzel 1963 ; Holm-Hansen et al. 1965). Cette approche opérationnelle fournit une information exclusivement quantitative et doit s'accompagner d'une approche en **microscopie optique**, en vue d'une identification des espèces phytoplanctoniques. Cette dernière méthode permet l'identification de cellules de différentes tailles, le microplancton (10-20µm), quelques ordres du nanoplancton (<20µm) et quelques classes de l'ultraplancton (<10µm). Les plus petites cellules nanoplanctoniques et les cellules picoplanctoniques (<2-3µm) ne peuvent pas être abordées par cette technique. Il peut toutefois être mesuré par **cytométrie en flux**, une méthode récente qui permet de dénombrer les plus petites formes présentes dans le milieu qu'elles soient hétérotrophes (bactéries), autotrophes procaryotes (cyanobactéries) ou eucaryotes (pico-ultra et nanoplancton). Comme la fluorimétrie, cette technique repose sur l'excitation lumineuse des pigments naturels des cellules (phytoplancton) ou leur marquage (bactérie) (Marie et al. 1997 ; Olson et al. 1988). La caractérisation de la matière organique et de son potentiel trophique pourrait aussi être abordée par des approches chimiques et biochimiques en analysant les **isotopes stables du carbone et de l'azote**, ainsi que les **acides gras biomarqueurs** qui peuvent caractériser différents niveaux taxonomiques (*i.e.* diatomées, bactéries, dinoflagellés, plantes terrestres, etc. ; Dalsgaard et al., 2003). Le couplage de toutes ces méthodes apporte des informations quantitatives et qualitatives complémentaires sur le potentiel trophique de la colonne d'eau.

3. Régime alimentaire de l'huître

3.1 Isotopes stables

Initialement utilisés par les géochimistes et les paléo-océanographes pour des études fondamentales sur les cycles de la matière ou encore les conditions climatiques anciennes, les isotopes stables ont par la suite suscité l'intérêt dans la communauté des écologistes et des biologistes, qui les ont adapté aux travaux sur les transferts de matière au sein des écosystèmes (Michener & Lajtha 2007). L'abondance naturelle de ces marqueurs permet d'étudier à l'échelle des populations les relations trophiques entre un consommateur et ses sources potentielles de nourriture (Marchais et al. 2013 ; Nerot et al. 2012), et à l'échelle de l'écosystème le fonctionnement des réseaux trophiques (Grall et al. 2006 ; Schaal et al. 2008 ; Davenport & Bax 2002). Les isotopes stables permettent aussi de décrire les patrons de variabilité spatiaux et

temporels des flux de matière et les échanges entre systèmes adjacents (Raymond & Bauer 2001 ; Mortillaro et al. 2014). Mesuré dans les tissus d'organismes sédentaires comme les bivalves ou les algues, les isotopes stables peuvent également renseigner sur l'apport exogène de substances chimiques, introduites dans les écosystèmes côtiers par voie anthropique (Costanzo et al. 1997 ; Riera et al. 2000 ; Piola et al. 2006 ; Fertig et al. 2009).

Chimie des isotopes stables

Les isotopes stables sont des formes d'un même élément chimique (*i.e.* C, N, O, H) qui diffèrent par le nombre de neutrons qu'abrite leur noyau. Ils se retrouvent dans l'environnement avec des proportions différentes, principalement sous leur forme légère (^{12}C, ^{14}N), les isotopes lourds étant trouvés à l'état de traces (^{13}C, ^{15}N). En écologie, les teneurs en isotopes stables sont exprimées sous la forme d'un rapport entre isotopes lourds et légers, δ, exprimé en ‰. Composants structuraux principaux du vivant, le carbone (^{13}C) et l'azote (^{15}N) sont les éléments les plus utilisés en écologie trophique.

Le rapport entre isotopes stables est calculé conventionnellement comme suit :

$$\boldsymbol{\delta^{13}C_{\text{échantillon}}} \textbf{ ou } \boldsymbol{\delta^{15}N_{\text{échantillon}}} = \left(\frac{\mathbf{R_{\text{échantillon}}}}{\mathbf{R_{\text{standard}}}} - \mathbf{1}\right) \mathbf{x\ 1000}$$

Avec R= $^{13}C/^{12}C$ ou $^{15}N/^{14}N$ de l'échantillon ou du standard. Pour le carbone ($\delta^{13}C$), la composition isotopique du standard correspond à celle de la Pee Dee Belemnite (roche fossile) et pour l'azote ($\delta^{15}N$) le standard correspond à celle de l'azote atmosphérique.

Les isotopes comme marqueurs trophiques

Les isotopes stables sont considérés comme des outils robustes pour la compréhension des transferts entre les compartiments benthiques et pélagiques. En milieu côtier peu profond (où les échanges à l'interface eau-sédiment sont prononcés), ils se sont révélés être performants pour étudier la composition et l'origine de la matière organique en suspension ingérées par les organismes benthiques (Dubois et al. 2014 ; Le Loc'h et al. 2008). Le traçage isotopique de l'alimentation est rendu possible grâce à la composition isotopique spécifique de chaque producteur primaire. Cette composition est caractérisée par les sources de nutriments

inorganiques utilisées et par les mécanismes métaboliques impliqués dans leur utilisation par l'organisme (Raven et al. 2002).

La stabilité de la composition isotopique de la source après les processus de digestion et de transfert dans les tissus du consommateur est l'un des principes de base sur lequel s'appuie l'utilisation des isotopes stables en écologie trophique. Toutefois, un léger enrichissement en isotopes lourds est observé chez le consommateur, du fait de l'élimination rapide des isotopes légers par respiration ou excrétion. Le passage d'un niveau trophique à un autre se traduit donc par un enrichissement en isotopes lourds, qui est appelé fractionnement trophique (Fry & Sherr 1989 ; Fry 2007). La caractérisation du fractionnement est cependant compliquée par sa variation en fonction de plusieurs facteurs (groupes taxinomiques, nature des sources de nourriture, physiologie du consommateur ; Emmery 2012). Les fractionnements utilisés en écologie trophique des bivalves filtreurs proviennent le plus souvent d'expériences en milieu contrôlé sur des espèces ciblées, et leurs niveaux d'incertitudes est encore débattus (Paulet et al. 2006 ; Dubois et al. 2007 ; Deudero et al. 2009).

Les isotopes stables comme traceurs de l'origine de la matière

En plus de l'identification des relations trophiques entre un consommateur et ses sources potentielles de nourriture, les isotopes stables permettent de tracer l'origine marine ou terrestre de la matière. Le carbone inorganique dissous (CID) qui arrive dans le système par la voie océanique et qui est utilisé par les producteurs primaires se trouve enrichi en ^{13}C, à l'opposé du CID des rivières qui est appauvri en ^{13}C, de la même façon qu'en milieu limnique (Faganeli et al. 1995). Par conséquent, le $\delta^{13}C$ se trouve plus au moins enrichi chez les consommateurs primaires, selon l'origine et la composition de la matière organique particulaire ingérée. Le $\delta^{13}C$ de la MOP drainée par les rivières est estimé entre -29,2 et -27,4‰ (P Riera & Richard 1996), tandis que le $\delta^{13}C$ de la MOP marine se situe entre -21,7‰ et -19,6‰ (Riera 2007). Comme pour le carbone, le marquage isotopique de l'azote inorganique dissous (AID) peut aussi être informatif des influences continentales sur le pool de matière organique en milieu côtier. Ces influences sont principalement liées à l'introduction dans les rivières de l'azote dérivant des activités humaines (*e.i.* agriculture, élevage, urbanisation, etc.). En pénétrant dans les zones côtières, ces apports induisent un enrichissement en ^{15}N (Voss et al. 2011).

Dynamique et métabolisation des isotopes stables dans les tissus de C. gigas

L'intégration des isotopes stables du carbone et de l'azote dans les tissus animaux est soumise aux variations saisonnières et spatiales de l'environnement trophique, mais aussi aux variations des activités métaboliques (*i.e.* croissance, reproduction) qui modulent le temps de renouvellement des tissus. Chez *C. gigas,* la croissance interviendrait à 74% dans le renouvellement du carbone et à 35% dans le renouvellement de l'azote (Malet 2005). Ce renouvellement s'effectue de façon hétérogène entre les différents organes (*i.e.* glande digestive, manteau, branchies), selon la physiologie de l'organisme et leur composition biochimique. Pour son faible taux de renouvellement tissulaire, le muscle de l'huître est connu pour être l'organe le plus intégrateur de la signature isotopique nutritionnelle (Paulet et al. 2006). Le renouvellement de la composition isotopique dans le muscle de *C. gigas* s'effectue entre 60 et 92 jours (Malet 2005), ce qui fait du muscle un organe informateur à long terme.

3.2 Acides gras

Nomenclature et biosynthèse des acides gras

Les acides gras se distinguent par la longueur de leur chaîne carbonée et par le nombre et la position des doubles liaisons. La chaîne peut être linéaire ou ramifiée et comprendre entre 4 et 40 atomes de carbone. Les acides gras sont notés sous la forme C:Xn-Y, où C est le nombre de carbones, X est le nombre de doubles liaisons et Y est la position de la première double liaison comptée à partir du groupe méthyl terminal. Les acides gras saturés ne présentent aucune double liaison, contrairement aux acides gras monoinsaturés ou polyinsaturés qui présentent une ou plusieurs doubles liaisons, respectivement.

Les organismes vivants ont majoritairement la capacité de synthétiser des acides gras saturés avec 16 (acide palmitique) et 18 carbones (acide stéarique), à partir desquels une diversité d'acides gras polyinsaturés peut être obtenue par des processus enzymatiques d'élongation et de désaturation à partir de précurseurs métaboliques (bioconversion). Les différences de composition d'acides gras entre les groupes taxonomiques résultent des capacités différentes à réaliser ces processus. A la base de la chaîne alimentaire, les producteurs primaires sont dotés des enzymes nécessaires (Δ15-désaturase et Δ12-désaturase) pour la bioconversion du 18:1n-9 (acides oléique) en 18:2n-6 (acide linoléique) et 18:3n-3 (acide linoléique). Ces deux acides

gras sont biosynthétisés en milieu marin par les microalgues, ainsi que l'ensemble des acides gras à longues chaînes des séries n-6 et n-3 (Figure 10). La plupart des espèces animales ne sont pas capables de synthétiser *de novo* le 18:2n-6 et le 18:3n-3 et l'acquièrent donc par voie nutritionnelle. Les vertébrés terrestres peuvent ensuite les utiliser comme précurseurs pour la synthèse des acides gras polyinsaturés à longues chaînes (AGPI) tandis que les organismes marins sont peu ou pas capables de le faire. Ces derniers étant indispensables aux activités métaboliques, les organismes marins doivent les extraire des leurs sources de nourriture. Les AGPI identifiés comme essentiels pour la survie, la croissance et la reproduction des organismes marins sont : le 20:4n-6 (acide arachidonique, ARA), le 20:5n-3 (acide eicosapentaénoïque, EPA) et le 22:6n-3 (acide docosahexaenoïque, DHA) (Kelly & Scheibling 2012).

Les acides gras sont rarement trouvés libres, étant en général liés à d'autres molécules (*i.e.* alcools, glycérol, composés azotés). Ils forment deux grandes classes en fonction de leur polarité, la classe des lipides neutres (*i.e.* triglycérides, esters de stérols, glycérides éther) et la classe des lipides polaires (*i.e.* glycolipides, lipoprotéines, phospholipides, sphingolipides). Les acides gras associés aux lipides neutres servent de réserves énergétiques, alors que les acides gras des lipides polaires ont un rôle structurel et contribuent à la constitution des membranes

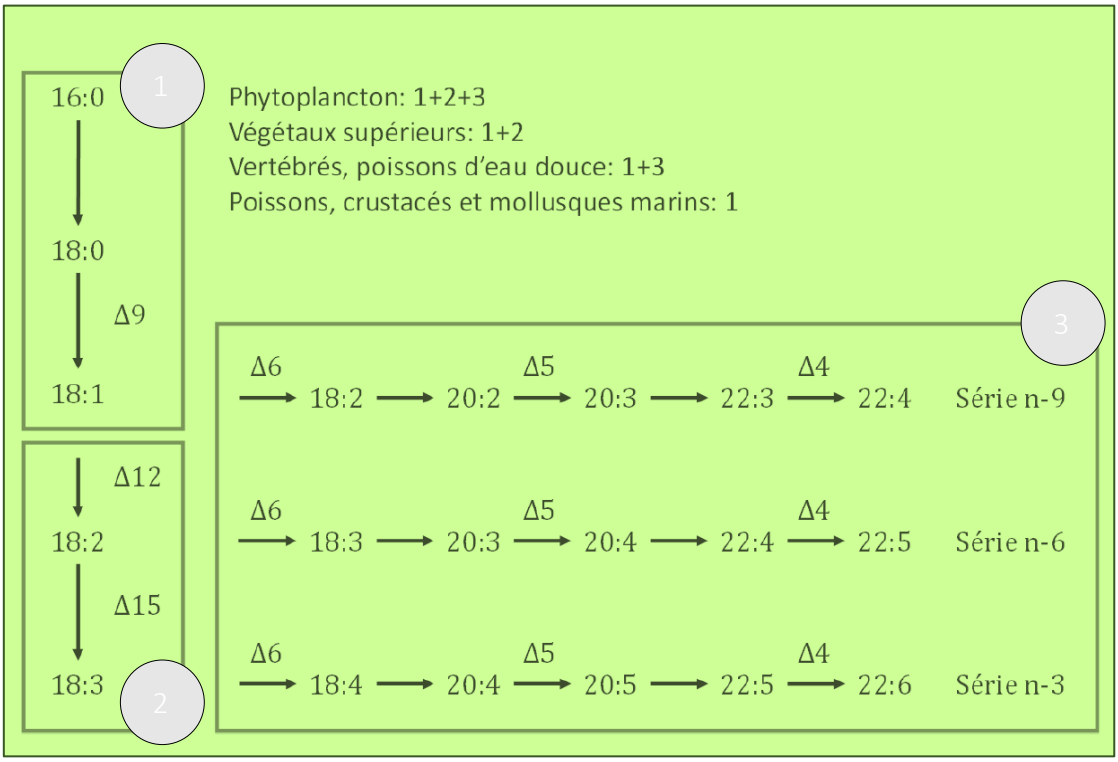

Figure 10 : Les voies de synthèse des principaux acides gras pour le phytoplancton, les végétaux supérieurs, les vertébrés et les poissons d'eau douce, et les organismes marins tiré de (Delaunay 1992).

cellulaires. Les lipides structuraux des membranes (phospholipides) des organismes marins sont généralement enrichis en acides gras à longues chaînes polyinsaturés de type n-3 et sont impliqués dans diverses activités membranaires (Pernet 2016). La composition des acides gras dans les lipides polaires est donc très régulée pour assurer un fonctionnement optimal de ces activités. Les acides gras dans les lipides neutres sont moins soumis à régulation métabolique et donc reflètent plus directement les apports trophiques. Par conséquent, leur analyse est plus adaptée à l'étude des relations trophiques (Dalsgaard et al. 2003 ; Ackman 1983).

Dynamique et métabolisation des acides gras dans les tissus de C. gigas

Les acides gras sont des composants structuraux de la vie biologique, dont la composition dépend des besoins métaboliques et énergétiques des organismes. Cette modulation s'effectue en fonction de facteurs endogènes (*i.e.* physiologie, reproduction) et de facteurs exogènes (*i.e.* température, nourriture). Chez *C. gigas*, la modulation des classes de lipides et de leur composition en acides gras est principalement liée à la reproduction et aux efflorescences phytoplanctoniques (Berthelin et al. 2000 ; Dridi et al. 2007 ; Pazos et al. 1996). La gonade enveloppée par le manteau est l'organe le plus concerné par cette dynamique biochimique, suivi par la glande digestive et de façon très limitée par le muscle (Soudant et al. 1999). En période de mise en réserve, l'accumulation énergétique s'effectue essentiellement sous forme de glycogène (Berthelin et al., 2000). Ce dernier est converti en lipides au démarrage de la croissance gonadique et sert de précurseur pour la construction des gamètes. Pendant la gamétogenèse, *C. gigas* bénéficie des efflorescences phytoplanctoniques printanières. Une accumulation des lipides neutres (réserves), essentiellement composés de triglycérides, est alors observée dans les ovocytes. Les triglycérides servent de réservoirs d'acides gras polyinsaturés (AGPI), qui peuvent être transférés vers les lipides polaires (structure) ou être investis directement dans les voies métaboliques (Ackman 1983 ; Pazos et al. 1996). Avec la libération des gamètes, les taux de triglycérides se réduisent drastiquement, faisant chuter la contenance en lipides neutres. Les lipides polaires montrent chez *C. gigas* une stabilité et des variations saisonnières beaucoup moins notables que les lipides neutres. Dans les deux classes de lipides, les acides gras essentiels (DHA, EPA, ARA) à la reproduction subissent aussi ces variations saisonnières, mais ils se trouvent incorporés principalement dans les lipides polaires (Dagorn et al. 2016 ; Soudant et al. 1999). Le 22:6n-3 (DHA) est le plus corrélé à la croissance gonadique, il joue chez les bivalves un rôle structurel et fonctionnel dans les

membranes des cellules impliquées dans les processus d'ovogenèse (Soudant et al. 1996). Le 20:5n-3 (EPA) est impliqué chez les bivalves dans des processus énergétiques. Delaporte et al. (2003) ont également démontré son rôle dans les fonctions immunitaires chez *C. gigas*. Le 20:4n-6 (ARA) est essentiel pour la synthèse d'eicosanoïdes, comme la prostaglandine, connue pour être impliquée dans les processus reproductifs chez les huîtres (Hurtado et al. 2009). Pour la survie, la croissance et la reproduction l'équilibre biochimique réside dans le maintien d'un ratio AGPI (n-3)/(n-6) élevé (Thompson et al. 1996). Ceci serait le reflet d'un environnement trophique de bonne qualité nutritionnelle.

Les acides gras comme marqueurs/indicateurs trophiques

En écologie trophique, relier un consommateur à ses sources potentielles de nourriture est basé sur l'identification chez le premier d'acides gras spécifiques aux groupes d'espèces ingérées (*i.e.* diatomées, bactéries, dinoflagellés, macroalgues), sans qu'ils soient modifiés lors des processus de digestion et de métabolisation (Kelly & Scheibling 2012). La limite à l'utilisation des acides gras réside dans la rareté de ces marqueurs (réellement spécifique à une source). Certains acides gras sont majoritairement ubiquistes et ne peuvent être utilisés dans ce cas que comme indicateurs trophiques. Leur interprétation doit prendre en considération les caractéristiques écologiques de l'écosystème étudié, et en particulier la disponibilité des différentes sources trophiques pour le consommateur d'intérêt.

Retracer qualitativement le régime alimentaire des bivalves filtreurs réside dans la caractérisation des acides gras contenus dans la matière organique particulaire (MOP). La MOP est principalement constituée de cellules phytoplanctoniques et la variabilité de sa composition biochimique est liée à la dynamique de deux groupes principaux : les diatomées et les dinoflagellés (Budge et al. 2001). Les diatomées sont caractérisées par différentes marqueurs, le 16:1n-7 (Dijkman & Kromkamp, 2006), le 16:2n-4 et le 16:4n-1 (Viso & Marty 1993) et le 20:5n-3 (Volkman et al. 1989). Les dinoflagellés sont caractérisés par le 18:4n-3 (Volkman et al. 1989), le 18:5n-3 (Dijkman & Kromkamp, 2006) et le 22:6n-3 (Volkman et al. 1989). D'autres compartiments biologiques peuvent être identifiés dans la MOP grâce aux acides gras : les bactéries (acides gras saturés ramifiés, *iso/anteiso* 15:0 et 17:0, et non ramifiées 15:0 et 17:0, Dalsgaard et al. 2003), les algues vertes (*i.e.* chlorophycées, 18:3n-3, Dijkman et Kromkamp, 2006). Il est toutefois important de noter que des groupes taxonomiques différents peuvent

montrer des acides gras communs. Par exemple, le 20:5n-3 et le 18:3n-3, pourraient être présent de façon abondante chez certains flagellés (*i.e.* Prasinophycées, Prymnésiophycées ; Reitan et al. 1994 ; Robert et al. 2004).

Dans la littérature certains rapports d'acides gras peuvent également être utilisés comme indicateurs trophiques, ces rapports sont listés dans la Table 1.

Table 1 : Liste des ratios d'acides gras utilisés comme indicateurs trophiques.

Indicateurs	Sources	Références
16:1n-7/16:0	Diatomées ; bactéries	Viso & Marty 1993 ; Budge et al. 2001
20:5n-3/22:6n-3	<1 dinoflagellés >1 diatomées	Dalsgaard et al. 2003 ; Kelly and Scheibling 2012
18:5n-3/18:3n-3	dinoflagellés	Viso & Marty 1993
18:2n-6+18:3n-3	Matériel terrestre	Budge & Parrish 1998 ; Budge et al. 2001 ; Kelly & Scheibling 2012
∑ AG ramifiés (iso/anteiso 15:0 et 17:0) et non ramifiés (15:0 et 17:0)	Bactéries	Budge & Parrish 1998, Budge et al. 2001
18:1n-9/18:1n-7	Bactéries	Volkman et al. 1980

4. Suivi quantitatif et qualitatif du statut reproductif de l'huître

4.1 Indice de condition gonado-somatique

L'étude du cycle biologique d'une espèce animale permet d'identifier des périodes clés telles que la croissance ou la reproduction. Ces périodes se traduisent par des modifications de la quantité de tissus somatiques produite, ce qui définit la «condition» de l'individu. Plusieurs indicateurs ont été développés pour estimer cette condition, surtout chez l'huître. Ces indicateurs appelés communément «indices de condition» reposent tous sur des mesures biométriques (*i.e.* poids total, poids sec, longueur, largeur). Selon le choix des mesures à utiliser dans le calcul de l'indice, différents niveaux de sensibilité y sont attribués. Dans une étude comparative de Bodoy et al. (1986) sur 21 indices de condition mesurés chez *C. gigas,* l'indice de Lawrence et Scott (1982) montre la meilleure sensibilité. Cet indice est un ratio entre la quantité de chair contenue dans l'huître et un estimateur du volume intervalvaire. Il traduit ainsi le degré de remplissage des huîtres. C'est l'indice le plus couramment utilisé pour l'huître creuse et ce calcul selon la formule suivante :

$$\mathrm{LS_{IC}} = \frac{\text{Poids sec (g)}}{\text{Poids total} - \text{Poids de coquille (g)}} \times 100$$

Cet indice correspond à toute la masse gonado-somatique, toutefois, en période de reproduction les tissus gonadiques représentent plus de 65% de la masse totale chez l'huître (Cigarria 1999 ; Pouvreau et al. 2006a ; Ren et al. 2003). Cet indice présente aussi l'avantage d'être indépendant de la taille de l'individu, il est donc un bon proxy du volume gonadique.

4.2 Histologie

Chez les bivalves, la gonade subie au cours d'un cycle de reproduction des changements quantitatifs mais aussi qualitatifs. Les cellules sexuelles mâles et femelles se différencient progressivement jusqu'à atteindre la maturation et soient libérées. La structure anatomique de la gonade et la détermination des différents stades de maturité sont généralement réalisées par l'analyse d'une section histologique d'environ 4 à 5 µm (*i.e.* Chávez-Villalba et al. 2002).

Après des colorations spécifiques (Figure 11), ces sections sont analysées qualitativement et quantitativement par la visualisation d'images réalisées par microscopie (Fabioux 2004).

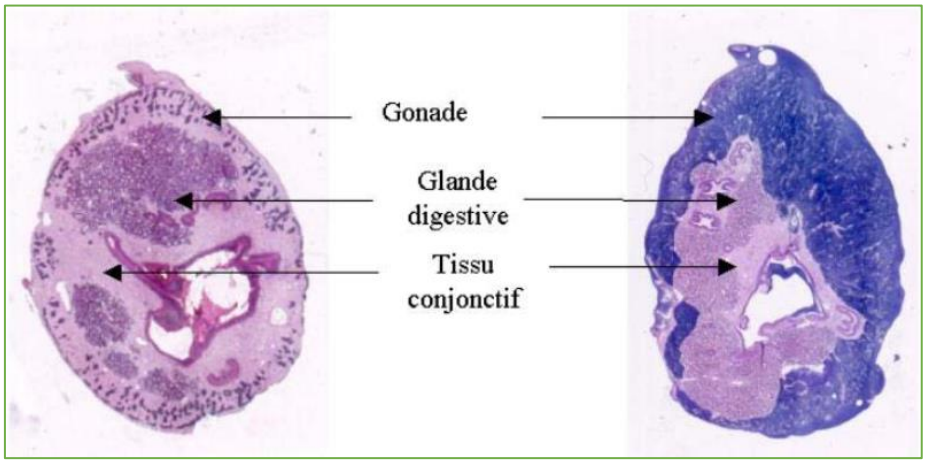

Figure 11 : Coupes histologiques de masse viscérale d'une huître creuse adulte, les différents tissus sont différenciés par leur coloration, tiré de (Fabioux et al. 2005).

Chapitre I :

Variabilité spatiale de l'effort reproductif chez l'huître creuse *Crassostrea gigas*:

Influence des processus tidaux

Résumé

Dans les écosystèmes côtiers macrotidaux, l'hétérogénéité spatiale des propriétés physico-chimiques et biologiques de la colonne d'eau est induite à la fois par des influences océaniques et continentales. Les processus hydrodynamiques génèrent un gradient de variabilité océan-continent des conditions environnementales, affectant les performances biologiques des organismes sédentaires. L'objectif de cette première étude est d'établir une évaluation spatiale exhaustive de l'investissement reproductif de l'huître sauvage *Crassostrea gigas* dans le Bassin d'Arcachon. Ceci en lien avec les processus hydrodynamiques qui conditionnent l'accès des bivalves filtreurs à la nourriture.

Pour ce faire, nous avons cherché des relations entre l'indice Lawrence et Scott (LS_{CI}) et deux processus tidaux : le niveau d'immersion (I_L) et le temps de renouvellement des eaux (LoFt). Le niveau d'immersion comme proxy de la durée maximale disponible pour la filtration, et le temps de renouvellement comme proxy de la probabilité pour une huître de filtrer une eau renouvelée. Le LS_{CI} de *C. gigas* a été mesuré, juste avant la période de libération des gamètes, au niveau de 68 stations d'échantillonnage dans le Bassin d'Arcachon. A cette période, la gonade représente plus de 50% de la masse somatique de *C. gigas*. Le LS_{CI} est donc considéré comme un proxy de l'investissement reproductif.

Globalement, les résultats démontrent une faible condition de *C. gigas* et une variabilité spatiale importante. Une différence significative est notée pour le LS_{CI} entre les parties internes et externes de la baie. Les bancs d'huîtres localisés à l'entrée du bassin montre un LS_{CI} élevé (entre 9 et 11), alors que les bancs localisés à l'intérieur du bassin, en particulier dans la partie Sud-Est à l'embouchure du fleuve de l'Eyre, montrent des valeurs de LS_{CI} plus faibles (inférieures à 6). Des régressions linéaires ont permis de mettre en évidence des effets significatifs des deux processus tidaux, I_L et LoFt, sur le gradient obtenu pour LS_{CI}. Les deux processus expliquent 33% de la variabilité spatiale observée pour LS_{CI} (I_L= 3% ; LoFt=17% ; LoFt + I_L: 13%), 6% ont été attribué à la variabilité intra-station (ISv). Ainsi, un temps d'immersion long et un renouvellement rapide des eaux permettent un meilleur développement gonadique, grâce à un temps d'accès à la nourriture prolongé et un niveau d'apports élevé de matière d'origine océanique par les flux tidaux. La détermination des effets de I_L et du LoFt sur le LS_{CI} a

permis de décrire une partie du schéma spatial révélé pour LS_{CI}, 61% de la variabilité reste non expliquée par les deux processus hydrodynamiques étudiés.

Dans le but d'etablir une comparaison spatiale uniquement de l'environnement nutritif, indépendamment des facteurs physiques d'accès à la nourriture. Les indices LS_{CI} ont été corrigés des effets de I_L et LoFt. Un gradient résiduel dirigé du Sud-Est vers le Nord-Ouest souligne la présence d'autres facteurs, pouvant avoir impact négatif sur la performance reproductive de *C. gigas* dans la partie interne de la baie.

Les patrons spatiaux révélés dans le cadre de cette étude mettent en évidence la variabilité et la complexité du fonctionnement des écosystèmes côtiers peu profonds. La faible condition de *C. gigas* dans la partie Sud-Est de la baie nécessite des études plus intégrées et plus approfondies, permettant de regarder l'effet d'autres facteurs pouvant perturber la gamétogenèse de l'huître (*i.e.* salinité, qualité de l'environnement trophique, contaminants).

Spatial patterns in the condition index of the wild Pacific oyster *Crassostrea gigas* in a macrotidal coastal ecosystem: influence of tidal processes and beyond

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Abstract

In macrotidal coastal ecosystems, spatial heterogeneity of the water column properties is induced by both oceanic and continental influences. Hydrodynamic processes generate a land-sea gradient of environmental conditions, affecting the biological performances of sedentary organisms. The aim of the present study is to establish an extensive spatial assessment in the reproductive investment of the wild Pacific oyster *Crassostrea gigas* in Arcachon Bay. This is done by looking for a relationship between the Lawrence and Scott condition index (LS_{CI}) and two tidal processes: the immersion level (I_L) and the local oceanic flushing time (LoFt). The LS_{CI} of *C. gigas* was assessed, just before gamete release, at 68 sampling stations in Arcachon Bay. Oyster performance was overall low and spatially variable. Significant differences in the LS_{CI} were detected between the outer and inner bay. Oyster reefs located toward the mouth of the bay exhibited high LS_{CI} (between 9 and 11), while oyster reefs located in inner bay, especially in south-eastern part around the Eyre River, had low LS_{CI} (below 6). Linear modelling allowed to highlight significant effects of both tidal processes I_L and LoFt on the obtained LS_{CI} gradient. I_L, LoFt explained 33% of the spatial variability observed on LS_{CI} (I_L= 3%; LoFt=17%; LoFt + I_L: 13%), 6% were attributed to the intra-station variation (ISv). Thus, high I_L and rapid LoFt favor a better development of somatic-gonadal volume, probably because of longer feeding time and higher supply of food from the ocean by tide flows. Disentangling the effects of I_L and LoFt on LS_{CI} allowed to describe the spatial pattern in 61% of variability not explained by both tidal factors. A residual gradient directed southeast-northwest highlighted that others factors, independent from I_L and LoFt seem to hamper inner bay oyster reproductive performance. Consequently, investigating the ecological functioning (Eyre influences), trophic potential and anthropogenic pressures of this zone seem crucial in the understanding of *C. gigas* reproductive pattern in Arcachon Bay.

Keywords: reproductive investment, *Crassostrea gigas*, macrotidal lagoon, immersion level, oceanic flushing, environmental variability

Abbreviations:

LS_{CI}: Lawrence and Scott condition index

I_L: Immersion Level

LoFt: Local oceanic Flushing time

ISv: Intra-station variation

1. Introduction

In marine aquaculture areas, natural spat collection of the Pacific oyster *Crassostrea gigas* depends on the reproductive output of both farmed and wild stocks. However, although natural beds can significantly contribute to the overall gamete release, few studies have assessed their reproductive capacities (Lango-Reynoso et al. 1999; Cardoso et al. 2007a; Dutertre et al. 2010). Monitoring of natural populations has mostly been limited to the evaluation of livestock biomass and distribution (Martin et al. 2005; Cognie et al. 2006; Scourzic et al. 2012; Soletchnik et al. 2012). In contrast, more research on oyster reproductive effort has focused on farmed stocks (Berthelin et al. 2000b; Lango-Reynoso et al. 2000; Dutertre et al. 2009; Enríquez-Díaz et al. 2009). Recently in Arcachon Bay, the high inter-annual fluctuations in spat collection raised some question on the reproductive output of wild oyster beds (Bernard 2011). It seems that, in addition to the monitoring of farmed stock, it is crucial to focus on the reproductive output of wild populations. This is of special importance for the assessment of aquaculture health and in the development of spat production predictive models, particularly for coastal ecosystems where spat collection constitutes an important economic activity, such as Arcachon Bay.

Reproductive performance of *C. gigas* is primarily conditioned by local environment (Bourlès et al. 2009; Alunno-Bruscia et al. 2011a). Both temperature and food supply constitute the main drivers of *C. gigas* gametogenetic cycles (Kang et al. 2000; Chávez-Villalba et al. 2002a ; Chávez-Villalba et al. 2002b ; Fabioux et al. 2005 ; Dridi et al. 2007b ; Enríquez-Díaz et al. 2009 ; Dutertre et al. 2010). Temperature triggers gametogenesis, gonadal development dynamics and egg maturation, while food quantity and composition enhance fertility and gametes quality (Fabioux et al. 2005; Enríquez-Díaz et al. 2009). In response to local and regional differences in these main factors, *C. gigas* reproductive output exhibits significant geographical and spatial variability (Bernard et al. 2011a ; Cardoso et al. 2007a ; Royer et al. 2007 ; Pouvreau et al. 2016).

In macrotidal coastal ecosystems, tides and freshwater inflow from adjacent rivers are responsible for most of food supply variability (Cloern et al. 1989 ; Powell et al. 1989 ; Monbet 1992a ; Trigueros & Orive 2000). Consequently, the biological condition and feeding of *C. gigas* is known to be spatially variable within their ecosystem habitat (Riera & Richard 1996; Royer et al. 2007 ; Leal et al. 2008 ; Marchais et al. 2013). Differences can arise between suspension-

feeders living at different tidal levels on the shore: the time of aerial exposure increases with elevation, reduces feeding time and increases the intensity of abiotic factor effects for high-shore communities (Gillmor 1982a ; Goulletquer et al. 1987). On the other hand, tidal forcing (*i.e.* current velocity, tide amplitude, flushing time) induces large variability of the quantity and quality of food available to suspension-feeders (Newell 2004 ; Prins et al. 1997). Food supply is ensured by water renewal, material resuspension, and allochthonous organic matter inputs from the nearshore zone (Grant 1996 ; Roegner 1998 ; Roegner & Shanks 2001), in addition to local primary production, which can be enhanced by nutrient inputs from the drainage basin and adjacent rivers (Mallin et al. 1993).

This study was carried out in Arcachon Bay, a semi-enclosed bay of French Atlantic coast (southwest of France), characterized by a macrotidal regime. The bay is marked by strong spatial and temporal heterogeneity of the water column (Glé et al. 2008 ; Plus et al. 2009). The water renewal is mostly ensured by oceanic flushing from the Bay of Biscay and, to a lesser extent, by freshwater inflows from adjacent rivers (Castel et al. 1996 ; Plus et al. 2009) (see material and methods ; **Figure 12**). Arcachon Bay is not affected by eutrophication events since nutrient inputs are moderate and tidal water exchange with the ocean sufficient (De Wit et al. 2001 ; Plus et al. 2009). Depending on the seasonal balance between tidal flushing and freshwater inflows, temporal and spatial hydrobiological changes in the land-sea gradient can occur, affecting the dynamics of the autotrophic compartment (Glé et al. 2008) and potentially the availability of trophic resources for *C. gigas* (Grangeré et al. 2012).

Arcachon Bay historically provides an important amount of spat for oyster farming in France. High annual fluctuation in spat production of *C. gigas* in Arcachon Bay has been reported since 1998 (Auby et al. 2014). These variations occur in parallel with two trends in Arcachon Bay: (i) decreasing abundance of the first larval stage of *C. gigas*, and (ii) delay spawning period (see for instance Pouvreau et al. 2016). Since reproductive effort seems to be involved in this variability of spat collection, the main objective of this study is to describe the spatial pattern in the condition index of wild *C. gigas* stock at the bay scale, in relation with the tidal processes. Firstly, through an extensive spatial assessment of *C. gigas* somatic-gonadal index just before spawning, and secondly by the investigation of the role of immersion level (I_L) and the local oceanic flushing time (LoFt), that may control the reproductive pattern in Arcachon Bay.

2. Material and Methods

2.1. Study site

Arcachon Bay (44°40′ N, 1°10′ W) is located at the southeast of the Bay of Biscay, on the Atlantic coast (**Figure 12**). This semi-enclosed lagoon covers a water surface of about 174 km² at high tide and is characterized by a semi-diurnal mesotidal regime. The tidal amplitude ranges between 0.8 and 4.6 m for neap and spring tides, respectively. The bay communicates with the Atlantic Ocean through two narrow channels separated by the Arguin sand-bank. Freshwater inputs originate from two main rivers, the Eyre and the Porges Canal, which contribute to more than 95% of total annual freshwater inflows (Plus et al. 2009), and by several small streams (at the north-eastern and southern parts of the bay). A strong heterogeneity of flushing time occurs inside the bay, causing

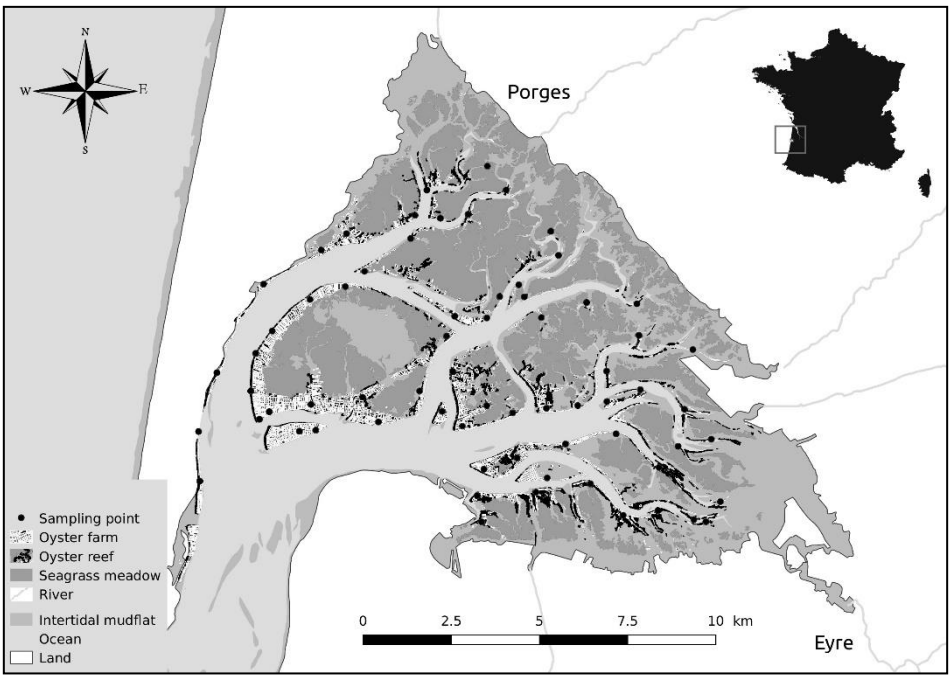

Figure 12: Map of Arcachon Bay with its principal ecological components: Eyre and Porges rivers; seagrasses beds (*Zostera noltei*), oyster reefs (Lafond, 2012) and oyster farms.

different confinement levels. Areas close to the ocean are flushed much faster than north-eastern and southern zones (Plus et al. 2009). Indeed, the water located near the lagoon inlets and the river mouths is rapidly renewed (below 1 day), while in others parts of the lagoon, it takes between 12.4 and 17.4 days (Plus et al. 2009). On the basis of the land-sea salinity gradient, three distinct water masses were clearly identified in the bay by Bouchet (1968): (i) external neritic waters, (ii) median neritic waters, (iii) inner neritic waters, shaped

proportionally to the distance from the ocean by marine and freshwater inputs. Median waters appear hydrologically closer to external than internal waters, which seem hydrologically isolated (Guillocheau 1988).

The main ecological habitats characterizing the Arcachon Bay ecosystem are seagrass meadows and *Crassostrea gigas* reefs. In the inner part of the lagoon (156 km²), the *Zostera noltei* bed covers an intertidal surface of 70 km² (**Figure 12**). Seagrasses cohabitate with wild oyster reefs whose mean density is estimated at 1000 oysters per m² (Scourzic et al., 2012; **Figure 12**). Primary production is ensured by different contributors: autochthonous macroproducers (mainly *Zostera noltei*), microphytobenthos on intertidal mudflats and phytoplankton (Dubois et al. 2014). The bay is characterized by low to moderate phytoplankton primary production estimated at 103 g $C.m^{-2}$ $year^{-1}$ (Glé et al. 2008).

2.2. Sampling strategy

Sampling was carried out on 68 stations of wild oyster reefs in Arcachon Bay according to a stratified random sampling strategy, in June 2013 (**Figure 12**). This period was at the end of the seasonal gametogenic cycle and before the release of eggs by oyster genitors in Arcachon Bay (Pouvreau et al. 2016). For each station, 30 adult wild oysters were collected. A minimum whole weight of 18 g was fixed to prevent juvenile individuals being considered.

2.3. The somatic-gonadal index

Biometric analyses were made prior to the calculation of the Lawrence and Scott condition index (LS_{CI}). Although this index is a proxy of the somatic-gonadal volume, the LS_{CI} was used here as a proxy of gonadal development, as *C. gigas* gonadal tissues can account for up to 65% of the total soft body weight in gametogenesis period (Cigarria 1999; Ren et al. 2003; Pouvreau et al. 2006b). LS_{CI} is size-independent and thus a good indicator of gonadal volume, independently of oyster age.

The whole weight (Ww) of each oyster was measured after cleaning the shell from epibionts and other debris. Oysters were then opened to separate the flesh from the shell. Soft tissues were drained on absorbent paper and wet weighed before being freeze-dried for 48 h for dry flesh weight (Dfw) measurements. Shells were weighed (Shw) after being wiped and air dried.

The LS_{CI} was calculated for each individual oyster according to the weighing method described by (Lawrence & Scott 1982) and calculated as follows:

$$LS_{CI} = \frac{\text{Dfw (g)}}{\text{Ww} - \text{Shw (g)}} \times 100$$

As demonstrated in Lawrence and Scott (1982), the weight of cavity contents (Ww-Shw) is highly correlated to the cavity volume, thus LS_{CI} represents the oyster somatic-gonadal volume.

Among the 2040 sampled oysters, 45 oysters showing a biased LS_{CI} were excluded from the analysis.

2.4. Tidal processes indices

2.4.1. Immersion level (IL)

Sampling site elevation was used as a proxy of immersion level (I_L) and considered as an index of the maximal duration available for oyster feeding. Substrate elevation was extracted for each sampling point from the Lidar bathymetric survey realized by the SIBA (Syndicat Intercommunal du Bassin d'Arcachon) in 2011.

2.4.2. Local oceanic Flushing time (LoFt)

The local oceanic flushing time LoFt was used as the time required for a replacement of a significant and localized water fraction by another one coming from the ocean or nearest rivers (Zimmerman 1976). The LoFt were calculated for the whole bay using the MARS3D numerical model (Lazure & Dumas 2008) and then extracted for each station. The latest version of the model improved by Kombiadou et al. (2014) from Plus et al. (2009) was used to re-assess the flushing times over the bay. This 3-dimensional version allowed to take into account the hydrodynamic modifications induced by *Z. noltei* beds.

As our study aimed to examine the relationship between oceanic waters impact on the bay and oyster reproductive performance, the numerical simulation was run without taking into account river discharges in order to remove influences of freshwater inputs in LoFt computation. Because oyster sampling was performed in June 2013, the model was run over the period May-June 2013, using realistic seagrass characteristics (in terms of spatial cover and development stage) in order to obtain the most representative LoFt.

2.5. Data analysis

2.5.1. Spatial mapping

Maps were used in this work to represent spatial patterns of oysters somatic-gonadal index LS_{CI}. Linear regressions between LS_{CI} and geographic coordinates (longitude and latitude) allowed to explore the spatial structure of the data. When significant, the spatial gradient was represented by a continuous arrow.

2.5.2. Statistical modeling

Linear models

A first approach was undertaken on the mean oysters somatic-gonadal index LS_{CI} values to explore independently the relationships with both proxies of tidal processes (I_L and LoFt). Two linear models were applied according to the following equations:

$$\text{Linear model } (\mathrm{LM}_1) = \mathrm{LS}_{\mathrm{CI}} \sim \mathrm{I}_{\mathrm{L}} + \varepsilon$$

$$\text{Linear model } (\mathrm{LM}_2) = \mathrm{LS}_{\mathrm{CI}} \sim \mathrm{LoFt} + \varepsilon$$

where I_L and LoFt represented the fixed effects and ε was the "error term" to represent the deviations from the models predictions due to all the random factors that affect LS_{CI}, independently from I_L and LoFt.

Mixed models and variance partitioning

A second approach was undertaken in order to study the LS_{CI} response to multiple factors effects. In this part, the total set of LS_{CI} data was used to integrate the intra-station variation (IS_v) into the analysis.

A mixed model incorporating both fixed effect of tidal processes I_L and LoFt, in addition to a random effect of IS_v was constructed as follows:

$$\text{Linear mixed model } (\mathrm{LMM}_1) = \mathrm{LS}_{\mathrm{CI}} \sim \mathrm{I}_{\mathrm{L}} + \mathrm{LoFt} + (1|\mathrm{IS}_{\mathrm{v}}) + \varepsilon$$

$(1|IS_v)$ was applied to precise in the model the use of different random intercepts for each station.

I_L and LoFt data were centred and reduced prior to the model application in order to compare their effects on LS_{CI}.

The statistical significance of the linear mixed model was verified using the Likelihood Ratio Test. The method was based on the comparison of the full linear mixed model (LMM_1) against a reduced model incorporating only one fixed effect I_L or LoFt (X, LMM_2). When ANOVA tests revealed a difference between the likelihood of these two models, we concluded on the significance of the tested fixed effect (X).

$$\text{Linear mixed model } (\mathrm{LMM_2}) = \mathrm{LS_{CI}} \sim \mathrm{X} + (1|\mathrm{IS_V}) + \varepsilon$$

Finally, a variance partitioning based on multiple linear regression was applied in order to partition the LS_{CI} variation into components accounted for the three explanatory variables (I_L, LoFt, IS_v) and their combined effects.

The tendencies resulted from the linear and linear mixed models were removed to obtain a LS_{CI} corrected for fixed I_L, LoFt effects and IS_v random effect.

All maps and the statistical modeling were elaborated using the R Software (R Development Core Team 2013) and several associated packages (sp, maptools, rgdal, geosphere, SDMTools, Hmisc and RColorBrewer, vegan, lme4). The homoscedasticity and normality of the models residuals were previously verified by examining plots of residuals distribution against fitted values.

3. Results

3.1. Spatial gradient in the somatic-gonadal index of Lawrence and Scott (LS_{CI})

A significant gradient oriented toward the west-south-west was found in the somatic-gonadal index LS_{CI} (Fisher test, p-value < 0.001). The lowest condition indices of *Crassostrea gigas* were found in the inner part of the bay, while oysters with highest condition indices were found at the vicinity of the mouth of the bay (**Figure 13**). At the scale of the whole bay, the average LS_{CI}

ranged between 4.1 and 11. All southeastern oyster reefs showed weak condition indices (39 sites; LS_{CI} below 6), at the opposite of all southwestern reefs where oysters exhibited the highest condition indices (10 sites; LS_{CI} between 9 and 11).

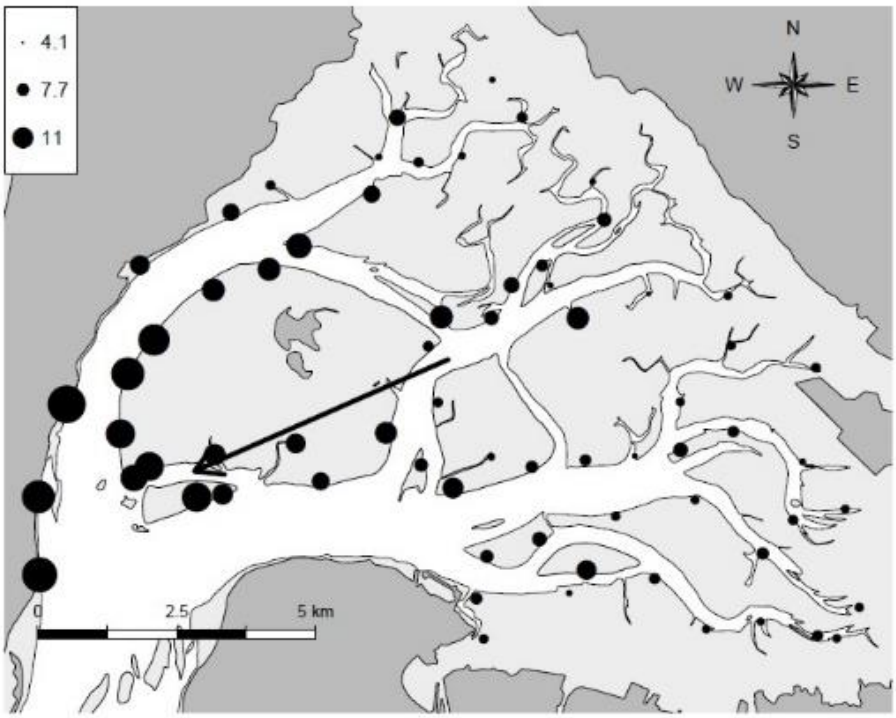

Figure 13: Spatial pattern of the Lawrence and Scott condition index LS_{CI} of the wild Pacific oyster *Crassostrea gigas* in Arcachon bay. Black arrow indicates a significant gradient at 1% level (p=8.16 e^{-17}; n=68).

3.2. Spatial variability on tidal processes I_L and LoFt

Both immersion level (I_L) and local oceanic flushing time (LoFt) exhibited a spatial heterogeneity. On the 68 stations, highest shore oysters were located at 2.19 m and lowest shore-level oysters at 0.52 m. For LoFt, the hydrodynamic model revealed high water renewal (low LoFt, below 15 days) near the mouth of the bay and low water renewal (high LoFt, up to 22 days) in the inner parts of the bay (Figure 14).

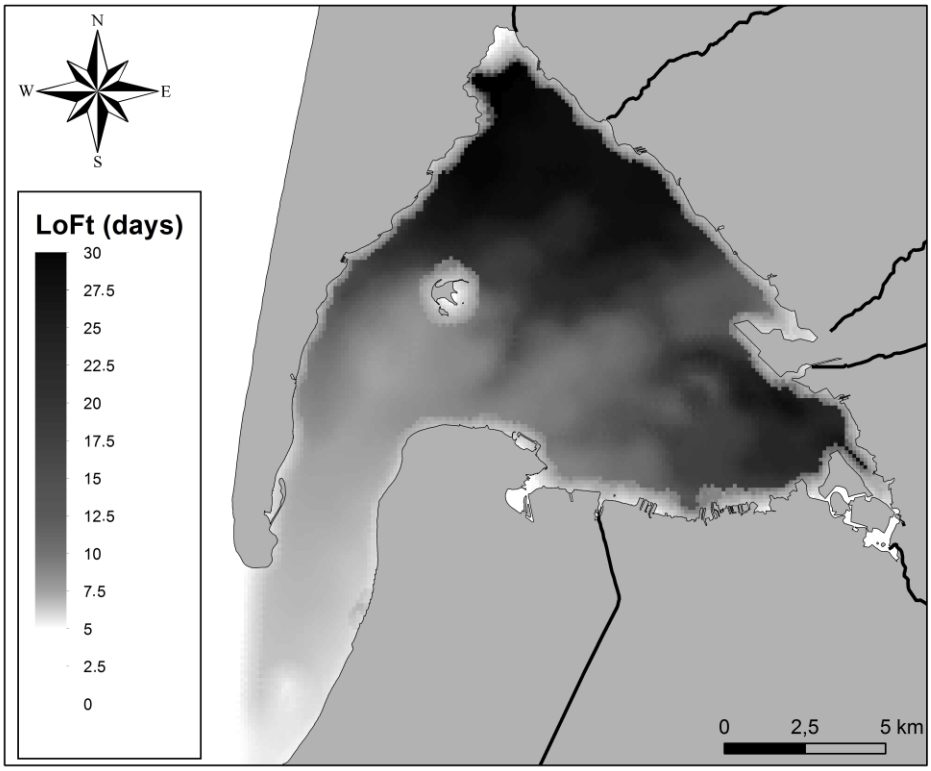

Figure 14: Local oceanic flushing time (LoFt) calculated over the whole Arcachon Bay using MARS3D numerical model.

3.3. Tidal processes control on oysters LS_{CI}

3.3.1. Linear models

The two linear models applied on the mean somatic-gonadal index LS_{CI} as a function of both immersion time I_L and local oceanic flushing time LoFt were significant (p-value < 0.001; Adjusted R-squared= 0.33 and 0.5, respectively; **Figure 15**).

3.3.2. Linear mixed models

The full linear mixed model (LMM_1) highlighted weak variability for the random effect of the intra-station variation IS_v (std. dev=1.097). For the fixed effects, the Likehood Ratio Test reported the significance of both I_L and LoFt explanatory variables. I_L affected LS_{CI} ($\chi^2(1)=14.52$, p=0.000138), lowering it by 0.60 ± 0.15 (standard error), while LoFt affected LS_{CI} ($\chi^2(1)=34.82$, $p=3.61e^{-09}$), lowering it by 1 ± 0.15 (standard error).

The partitioning of the LS_{CI} variability on both tidal processes I_L and Loft, in addition to the site effect IS_v allowed to explain 39% of the global variance, pure effects: I_L=3%; LS_{CI}=17% and IS_v=

4% and combined effects: I_L+Loft= 13% and I_L+IS_v=2%. Thus, I_L and LoFt explained 33% of LS_{CI} variability.

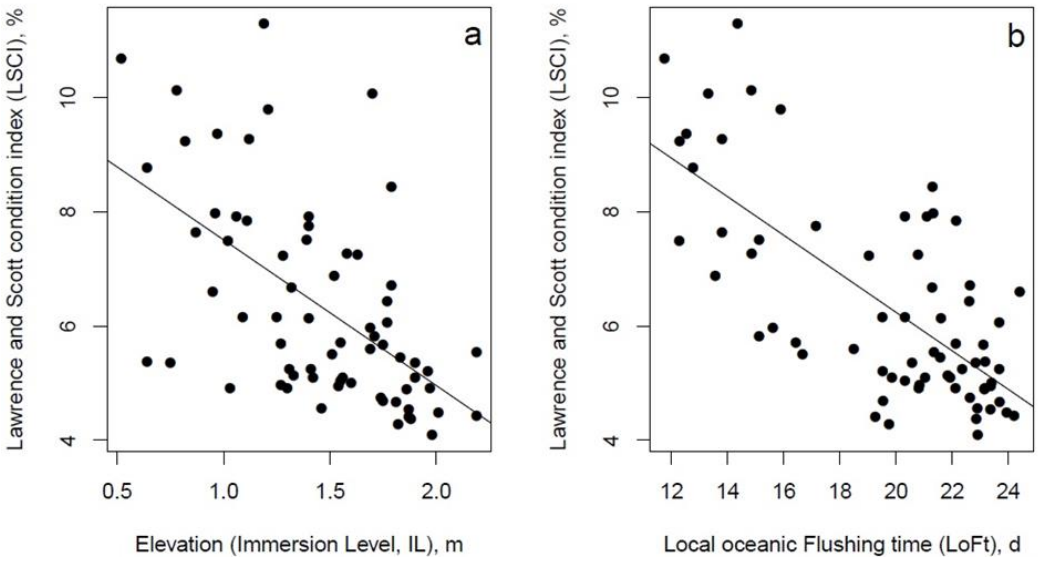

Figure 15: Linear regressions between Lawrence and Scott condition index (LS_{CI}) of *Crassostrea gigas* and both tidal process: (a) LS_{CI} *vs* Immersion Level in metres (I_L), and (b) LS_{CI} *vs* Local oceanic Flushing time in days (LoFt). The adjusted R^2 values were 0.33 and 0.5 respectively ($p < 0.001$).

3.4. Oysters LS_{CI} without I_L and LoFt effects

The relationships described above between the somatic-gonadal index LS_{CI} and tidal processes parameters were statistically removed in order to obtain the spatial distribution of LS_{CI} corrected for I_L, LoFt and I_L+LoFt+IS_V effects. This analysis resulted in a marked change on the direction of LS_{CI} residual gradient, revealing a significant gradient of increasing LS_{CI} scores from south-east to the north-west (p-value < 0.001, Figure 16).

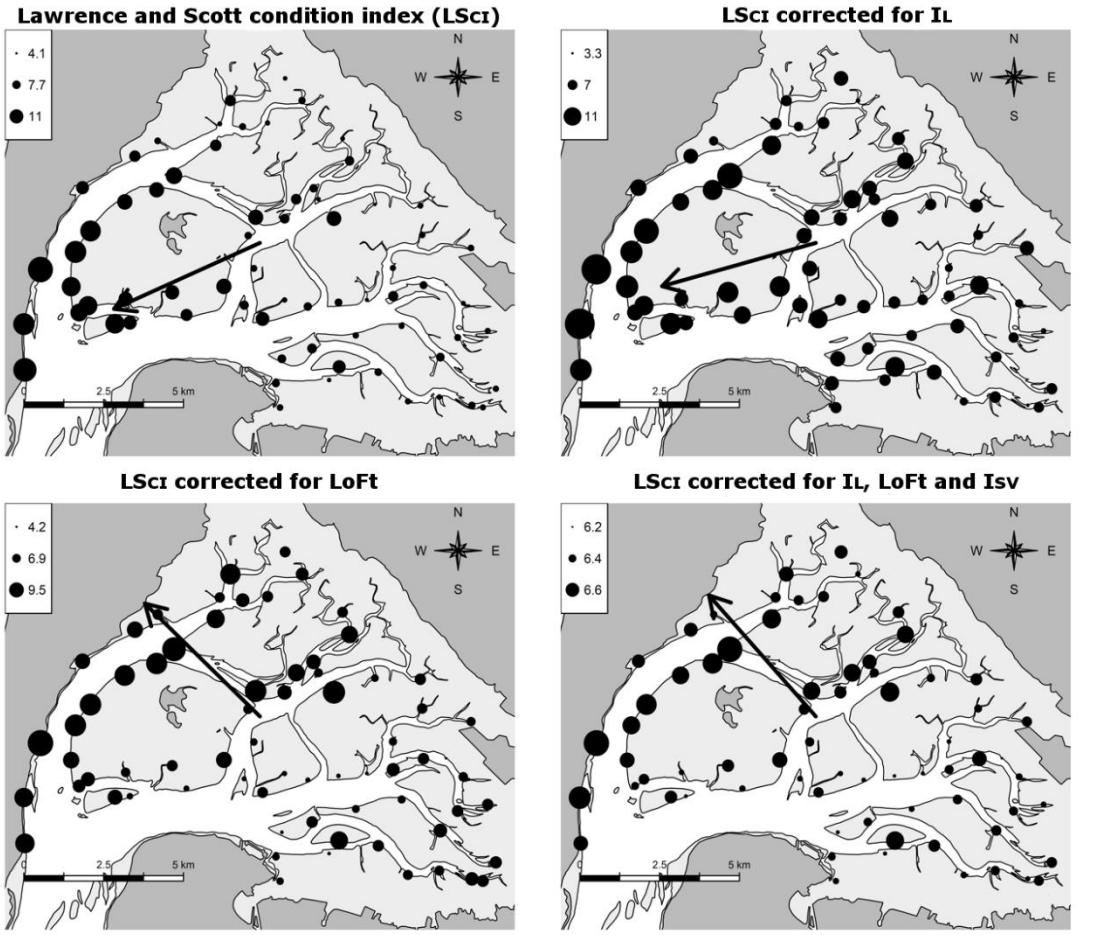

Figure 16: Spatial pattern of the Lawrence and Scott condition index (LS_{CI}) of the wild Pacific oyster *Crassostrea gigas* in Arcachon Bay before (a) and after the removing of the Immersion level (I_L, b), the Local oceanic Flushing time (LoFt, c) effects and multiple effects of I_L, LoFt and the intra-station variation I_{SV} (d). Black arrows indicate a significant residual gradient at 1% level (b: p= 1.6 e^{-10}; c: p= 0.0001; d: p= 9 e^{-10}; n=68).

4. Discussion

4.1. Spatial variability of oyster condition index at regional and local scale

This work confirmed variability in the condition index of the Pacific oyster *Crassostrea gigas* along the European Atlantic coast. In comparison with other French oyster culturing sites, such as Brest and Marennes-Oléron Bays, where, in 2013, the Lawrence and Scott condition index LS_{CI} reached 14.4 and 12.3 respectively, low oyster condition indices were observed in Arcachon Bay (Bourlès et al. 2009 ; Bernard et al. 2011a ; Pouvreau et al. 2016). Indeed, out of the 68 sampled sites, all south-eastern sites showed condition indices below 6. In general, LS_{CI} values above 8 are indicative of oysters in good physiological state (Barillé et al. 2000). In Arcachon bay, this threshold was reached only in south-western sites with a maximum value of 11. This

result is in accordance with the south-north gradient of growth and reproductive output drawn for *C. gigas* along the west European coast. Wild oyster populations show an increase in gonadal-mass from France to The Netherlands (Cardoso et al. 2007a ; Enríquez-Díaz et al. 2009). Besides differences in temperature, the most likely explanation of this biological condition of oysters in Arcachon Bay is the low phytoplankton primary productivity (103 g C m^{-2} y^{-1}; Glé et al., 2008). Indeed, *C. gigas* is known to produce a higher amount of gametes in eutrophic than oligotrophic conditions (Kang et al. 2000).

At the bay scale, higher condition index in ocean-influenced areas was revealed in contrast with inner-bay areas. The LS_{CI} showed a significant gradient in the west-south-west direction. As it has been shown in both Brest Bay and Veys Bay, marine-influenced environment seems to provide better trophic conditions, enhancing *C. gigas* physiological condition (Costil et al. 2005; Royer et al. 2007). Indeed, lower reproductive performance was observed in inner areas, especially around the Eyre River outlet. These findings confirmed the potentially food-depleted conditions of bivalves in south-eastern part of the bay suggested by earlier studies (Dang et al. 2010 ; Caill-Milly et al. 2012 ; Robert et al. 1993). Other bivalves such as the Manila clam *Ruditapes philippinarum* were also revealed to be in poor condition in this area (Dang et al. 2010 ; Caill-Milly et al. 2012). As oceanic water inputs are apparently beneficial to the development of bivalves (Bacher & Goulletquer 1989 ; Robert et al. 1993), relationships between tidal processes and *C. gigas* reproductive investment might explain the spatial pattern revealed in Arcachon Bay.

4.2. LS_{CI} *vs* tidal processes

The significant relationships revealed between *C. gigas* LS_{CI} and both proxies of tidal influence did corroborate the positive effect of oceanic influence on the functioning of invertebrate populations in coastal bay. In fact, 33% of the spatial variability observed on *C. gigas* LS_{CI} was explained by pure and combined effects of the immersion level and the local oceanic flushing time (I_L= 3%; LoFt: 17%; LoFt + I_L: 13%).

Since I_L referred to the bathymetric elevation of the sampled site, it did not exhibit any spatial gradient. Indeed, longer immersion time enhanced the LS_{CI} for *C. gigas* because of longer feeding time and lower exposure to biotic interactions and variation in environmental conditions during emersion. Such positive correlation between the quantity of gametes

released and the immersion time was previously observed in bivalves (Gillmor 1982a ; Goulletquer et al. 1987). A significant increase of oyster somatic-gonadal index when immersed for longer periods was also reported (Goulletquer et al. 1987 ; Walles et al. 2016). The common mussel *Mytilus edulis* produces larger eggs when immersion time is longer (Honkoop & van der Meer 1998).

The positive correlation between LS_{CI} and LoFt in the western part may reveal a better feeding environment in the outer part of the bay, potentially due to the rapid and repeated introduction by tide flows of phytoplankton from the Bay of Biscay, where the primary production ranges between 145 and 170 g $C.m^{-2}$ $year^{-1}$ (Laborde et al. 1999 ; Glé et al. 2007). Indeed, tidal flushing is one of the main bottom-up factors controlling phytoplankton dynamic and biomass in high-shore ecosystems (Monbet 1992a ; Trigueros & Orive 2000 ; Glé et al. 2007). In the inner part of the bay, longer LoFt limits replenishment of water with oceanic-originating phytoplankton. Oceanic waters reaching the inner part of the bay have already been filtered by outer bay communities, possibly reducing its content in nutritive particles (Herman et al. 1999). In addition, tidal flushing allows organic material resuspension such as microphytobenthos, which has been shown to contribute significantly to *C. gigas* diet in macrotidal estuaries (Ubertini et al. 2012 ; Marchais et al. 2013). The contrasted reproductive response of *C. gigas* between the outer and the inner bay highlights the ecological isolation of inner water masses. In this area, the trophic potential is mainly controlled by autochthonous primary production and influenced by the seasonal changes of the Eyre River inflows (Guillocheau 1988 ; Castel et al. 1996 ; Desclaux et al. 2004 ; Glé et al. 2008).

The feeding environment in the river-influenced part of the bay may also have been hampered by a higher competition for food within wild oyster stock. Indeed, for at least a decade, oyster farming areas in the inner bay have been progressively abandoned, which resulted in the development of wild oyster reefs. In 2011, total amount of oyster stock was estimated in Arcachon Bay to be 82500 t, with only 16600 t of farmed oysters, localized mostly in the outer part of the bay (Fig. 1, Scourzic et al. 2012). In addition, an interspecific competition may take place in the inner part of the bay, where the biomass of clams, represented mainly by *Venerupis philippinarum,* was estimated in 2014 at 7138 t (Sanchez et al. 2014). This clam biomass represents a competition for food and may exacerbate the observed gradient in oyster LS_{CI} between the outer and the inner part of the bay.

Besides the variability of the trophic environment, several physico-chemical land-sea gradients are enhanced by LoFt or simply correlated with it (*i.e*. temperature, salinity, turbidity). Their interactions and role on the spatial pattern of food availability and oysters feeding activity must be taken into account in the understanding of the observed pattern of *C. gigas* condition index. South-eastern areas exhibited higher amplitude in temperature, salinity and higher turbidities. Reduced salinity has been observed to negatively affect *C. gigas* growth (Brown & Hartwick 1988). Moreover, salinity below 30 is known to delay *C. gigas* gonad development (Muranaka & Lannan 1984). Even though temperature increases strongly enhance bivalves gamete maturation (Fabioux et al 2005 ; Enríquez-Díaz et al. 2009), temperature at 25°C decreases oysters filtration rate while oxygen consumption increases, affecting feeding activity and energy allocation (Bougrier et al. 1995).

4.3. Beyond I_L and LoFt effects: the residual spatial gradient of LS_{CI}

The reproductive pattern of *C. gigas* is a response to complex interactions and variations in several environmental parameters, mostly modulated in macrotidal ecosystems by tidal processes. It is therefore difficult to disentangle the effects of each factor on oyster reproductive performance. In this study, a rapid and useful approach had been undertaken to discriminate tidal effects from other independent factors. The effect of both I_L and LoFt on LS_{CI} has been statistically removed and a new spatial pattern was drawn with LS_{CI} residual values. Regardless of the elevation level and the distance from ocean, the residual pattern revealed a significant gradient of LS_{CI} directed to the north-west. The 61 % of variability in the LS_{CI} condition index of *C. gigas* not explained by either of the tidal processes seem linked to others factors, independent from I_L and LoFt. Surprisingly, this residual pattern did not oppose inner waters to ocean-influenced waters and takes place in the median bay (Bouchet 1968). This new gradient suggests that other biological processes or anthropogenic impacts may affect oyster condition. Higher contamination level of PAHs (polycyclic aromatic hydrocarbons) and Copper in *C. gigas* from the south-eastern bay have been already recorded (Bijoux 2014; Bernard, unpublished data), especially in the vicinity of the city of Arcachon. The many harbors and human uses, in addition to freshwater inputs from the Eyre River, could represent a source of various pollutants for bivalves. Understanding this residual gradient, and especially the effects of various pollutants on the reproductive ecology of oysters in this area, would be useful for a thorough understanding of Arcachon bay ecological functioning.

5. Conclusion

The reproductive performance of wild Pacific oyster *Crassostrea gigas* was shown to be poor and spatially variable in Arcachon Bay. Important differences in the Lawrence and Scott somatic-gonadal index (LS_{CI}) were recorded between outer and inner bay. The LS_{CI} increased significantly along the land-sea gradient and was related to tidal processes. Both immersion level (I_L) and oceanic local flushing time (LoFt) explained 33% from the spatial variability of LS_{CI}. Oysters benefitting from high I_L and rapid and repeated LoFt showed the best biological condition. In the south-eastern areas, oysters appeared affected by the low LoFt and the influence of the Eyre River inputs, reflecting the presence of two hydrographical regions with different characteristics and ecological functioning (Marcovecchio et al. 2006). Around the entrance of the bay by the ocean, a better trophic environment seems to enhance oyster condition.

This work also allowed to reveal the presence of a second north-west oriented gradient on oysters reproductive performance. Independently from tidal processes, other factors seem to explain the remaining forty-two percent of the LS_{CI} variability. The residual gradient once again indicated the low biological state of *C. gigas* in south-eastern part of the bay.

This study suggests that oyster production in the bay could benefit from being displaced to the entrance of the bay, where better growth conditions prevail. In contrast, because larval dispersal to the sea is higher in these areas, spat collection should be performed in the inner bay, where the highest retention rates have been observed (Bernard et al. 2014). Indeed, although inner bay oysters had lower physiological condition, they are the main contributors to spat collection in Arcachon Bay. Thus, finding a compromise between good fecundity and low larval dispersion must be considered in the farming practices. The next step to undertake in order to understand the reproductive performance of *C. gigas* in Arcachon Bay would cover the temporal changes in the environmental conditions during the gametogenetic cycle of *C. gigas*, specifically using more specific tools to quantify the trophic potential of the water column in parallel to the physiological response of *C. gigas*.

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Chapitre II

Effet de l'hydrodynamisme local sur la variabilité du régime alimentaire : approche par les isotopes stables ($\delta^{13}C$ et $\delta^{15}N$)

Résumé

La relation mise en évidence entre l'indice de condition et les conditions d'accessibilité à la nourriture dans le Chapitre I suggérent une différence de régime alimentaire de l'huître entre les parties internes et externes de la baie. Pour vérifier cette hypothèse, un schéma spatial des signatures isotopiques du carbone et de l'azote ($\delta^{13}C$ et $\delta^{15}N$) dans le muscle de *C. gigas* a été réalisé à l'échelle de l'écosystème. Les résultats montrent un régime alimentaire assez homogène et composé principalement de microalgues benthiques et pélagiques. Toutefois, bien que de faibles différences de ratios isotopiques aient été observées entre les 68 stations échantillonnées (2‰), des patrons spatiaux significatifs apparaissent entre les zones sous influences océaniques vs. continentales. Les valeurs enrichies en ^{13}C dans les zones à fort renouvellement océanique (LoFt) démontrent une consommation plus importante de phytoplancton d'origine marine. Cette variabilité spatiale du $\delta^{13}C$ est expliquée à 29% par LoFt. Une fois cet effet corrigé mathématiquement, un gradient de variabilité se dessine entre le sud-est et le nord-ouest de la baie. Ce nouveau gradient suggère une différence de la contribution des microalgues benthiques vs. pélagiques dans le régime alimentaire de C. gigas. Contrairement au $\delta^{13}C$ et indépendamment de l'effet de LoFt, le $\delta^{15}N$ dans le muscle de C. gigas montre un gradient nord-sud, un enrichissement est observé de l'embouchure du fleuve de l'Eyre vers la sortie de la baie. Les apports continentaux via les eaux douces étant faibles dans le Bassin d'Arcachon, ce schéma pourrait être attribué à une contribution plus forte de protistes hétérotrophes dans la partie sud-est, même si cette contribution semble légère. La relation trouvée entre le $\delta^{13}C$ et le poids sec révèle une influence de la physiologie sur la composition isotopique de *C. gigas*, une étude supplémentaire est donc nécessaire pour dissocier le rôle de la nourriture et de la physiologie dans les schémas spatiaux observés dans le Bassin d'Arcachon.

Effect of local hydrodynamic variability on the $\delta^{13}C$ and $\delta^{15}N$ ratios in the wild Pacific oyster *Crassostrea gigas* in Arcachon Bay, France

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1. Introduction

The Japanese native oyster, *Crassostrea gigas* is the most farmed mollusk bivalve in the world with a global harvest reaching 4 million tonnes (FAO, 2014). This species has been introduced for farming in several countries (*e.g.* Canada, Australia, New Zealand, and France ; Grizel 1996) due to drastic decreases in indigenous oyster stocks. Although natural oyster reefs are of significant ecological value, providing valuable ecosystem services including enhancement of water quality, shoreline stabilization and support to aquaculture through the furniture of juvenile or spat (Grabowski et al. 2012), *C. gigas* is clearly recognized as an invasive species which strongly modify the ecological and economical integrity of ecosystems (Bishop et al. 2010). Owing to its high adaptive capacity, *C. gigas* has dispersed beyond farmed systems, creating extensive wild reefs. Along the European coasts, *C. gigas* is now well-established from Norway to Portugal (Cardoso et al. 2007a ; Cognie et al. 2006 ; Wehrmann et al. 2000). However, differences in physiology and reproductive investment have been observed in a variety of local and regional environmental conditions for the species (Bernard et al. 2011b ; Royer et al. 2007 ; Cardoso et al. 2007a). Food supply and temperature are the main drivers of these differences (Chávez-Villalba et al. 2002b ; Dridi et al. 2007b ; Kang et al. 2000). In Arcachon Bay, large scale spatial variability in the oyster condition index has been previously evidenced, highlighting a significant gradient of *C. gigas* condition index in relation to oceanic influence within the bay (Gasmi et al. 2017). Thirty-three percent of condition index variability is related to two tidal processes, immersion level and local oceanic flushing time. Both parameters are known to control filter-feeders feeding period (Gillmor 1982b ; Goulletquer et al. 1987 ; Walles et al. 2016) , as well as phytoplankton dynamics and transport (Monbet 1992b ; Trigueros & Orive 2000).

Crassostrea gigas feeds by filtering suspended particulate organic matter (SPOM), derived in coastal waters from a complex mixture of endogenous and exogenous sources (Duce & Duursma 1977 ; Faganeli et al. 1995 ; Hopkinson et al. 1998). SPOM supply to the water column is provided by diverse primary producers inhabiting coastal environments (*i.e.* benthic and planktonic microalgae, seagrass, macroalgae; Watanabe & Kuwae 2015). In addition, allochtonous inputs driven by active oceanic tidal flushing, riverine-terrestrial runoff, and atmospheric loadings contribute to these pools (Raymond & Bauer 2001 ; Voss et al. 2011). *Crassostrea gigas* adapts its feeding behavior according to variations in the water column

trophic conditions (Decottignies et al. 2007). Although phytoplankton (seston/pelagic microalgae) seems to be the dominant contributor to *C. gigas* diet, other SPOM components such as benthic microalgae (BMA), flagellates, ciliates and debris of macroalgae or seagrass beds have been reported as important nutritive sources which may provide different palatabilities and/or nutritive qualities for oysters (Delaporte et al. 2006 ; Dupuy et al. 1999 ; Marchais et al. 2013 ; Xu & Yang 2007). SPOM availability and composition are thus major factors that determines habitat suitability for *C. gigas* physiology and reproductive success (Chávez-Villalba et al. 2002a ; Enríquez-Díaz et al. 2009).

Natural stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are well-established tools for assessing the origin of SPOM coastal waters and subsequently in animal tissues (Fry 2007 ; Michener & Lajtha 2007). These tracers are commonly used to understand bentho-pelagic coupling and trophic ecology in coastal organisms (Hobson et al. 1995 ; Grall et al. 2006 ; Davenport & Bax 2002). Primary producers contributing to SPOM exhibit distinct stable isotope ratios, as a consequence of nutrient sources and diverse physiological processes (Raven et al. 2002). Dissolved inorganic carbon (DIC) pools are ^{13}C-depleted in freshwater environments due to the low $\delta^{13}C$ of C3 plants in European catchments (Coleman & Fry 1991). On the other hand, marine environments are characterized by ^{13}C enriched DIC pools, resulting in high $\delta^{13}C$ in most marine primary producers (Faganeli et al. 1995). In contrast, $\delta^{15}N$ is routingly used as a proxy for organism trophic level (Post 2002), and anthropogenic inputs influences on SPOM (Fertig et al. 2009 ; Ning et al. 2013).

Arcachon Bay is a shallow, semi-enclosed lagoon subject to dynamic oceanic water exchange with the Atlantic Ocean and freshwater inputs, mainly from the Eyre and Porges rivers (Castel et al. 1996 ; Plus et al. 2009). The input of SPOM into the system is ensured by the abundant diversity of primary producers (Dubois et al. 2012). In particular, the largest European seagrass, *Zostera noltei*, plays a crucial role in the nutrient cycle at this location (Ribaudo et al. 2016). In the bay, *C. gigas* is abundant as both farmed and wild stocks, with 16,600 and 65,000 tons, respectively (Scourzic et al. 2012). For these reasons, Arcachon bay is a suitable area to study oyster diet variability. In this work we use stable isotope ($\delta^{13}C$, $\delta^{15}N$) in *C. gigas* muscle to infer spatio-temporal variability in origin and composition of SPOM consumed by *C. gigas* across Arcachon Bay. Because stable isotopes are time-integrated markers of trophic subsidies to oysters, they provide unique insights into the main patterns that characterize the trophic

ecology of oysters at the Bay scale. Based on previous results showing a strong link between connectivity to the open ocean and oysters conditions indices, we investigate the trophic side of this relationship, through 1) an extensive spatial sampling of *C. gigas* and 2) a seasonal survey for 2 stations localized in outer and in inner bay in Arcachon Bay, in various areas differentially connected to the open ocean.

2. Material and methods

2.1. Study site

Arcachon Bay (44°40′ N, 1°10′ W) is located at the southeast of the Bay of Biscay, on the Atlantic coast **Figure 17**. This semi-enclosed lagoon covers a surface of about 174 km² at high tide and is characterized by a semi-diurnal macrotidal regime. The tidal amplitude ranges between 0.8 and 4.6 m for neap and spring tides, respectively. The bay communicates with the Atlantic Ocean through two narrow channels separated by the Arguin sand-bank. The catchment's surface is about 3000 km² and drains the Eyre River and 15 smaller streams that flow directly into the inner part of the lagoon (Canton et al. 2012). The Eyre and the Porges rivers contribute to more than 95% of total annual freshwater inflows (Plus et al. 2009 ; Canton et al. 2012). A strong heterogeneity of flushing time occurs inside the bay, causing different confinement levels: areas close to the ocean are flushed much faster than north-eastern and southern zones (Plus et al. 2009).

The main ecological habitats characterizing the Arcachon Bay ecosystem are bare mudflats, seagrass meadows and *C. gigas* reefs. In the inner part of the lagoon (156 km²), *Zostera noltei* beds cover an intertidal surface of 70 km². Seagrasses cohabitate with wild oyster reefs whose mean density is estimated at 1000 oysters per m² (Scourzic et al. 2012 ; **Figure 17**). The bay is characterized by a large diversity of autochthonous primary producers: *Z. noltei, Z. marina, Spartina* spp. and other salt marsh plants, macroalgae, benthic microalgae and phytoplankton (Dubois et al. 2012). Continental inputs are mainly composed of soil and litter of terrestrial C3-plants (Polsenaere et al. 2012). The bay is characterized by low to moderate phytoplankton primary production estimated at 103 g $C.m^{-2}$ $year^{-1}$ (Glé et al. 2008).

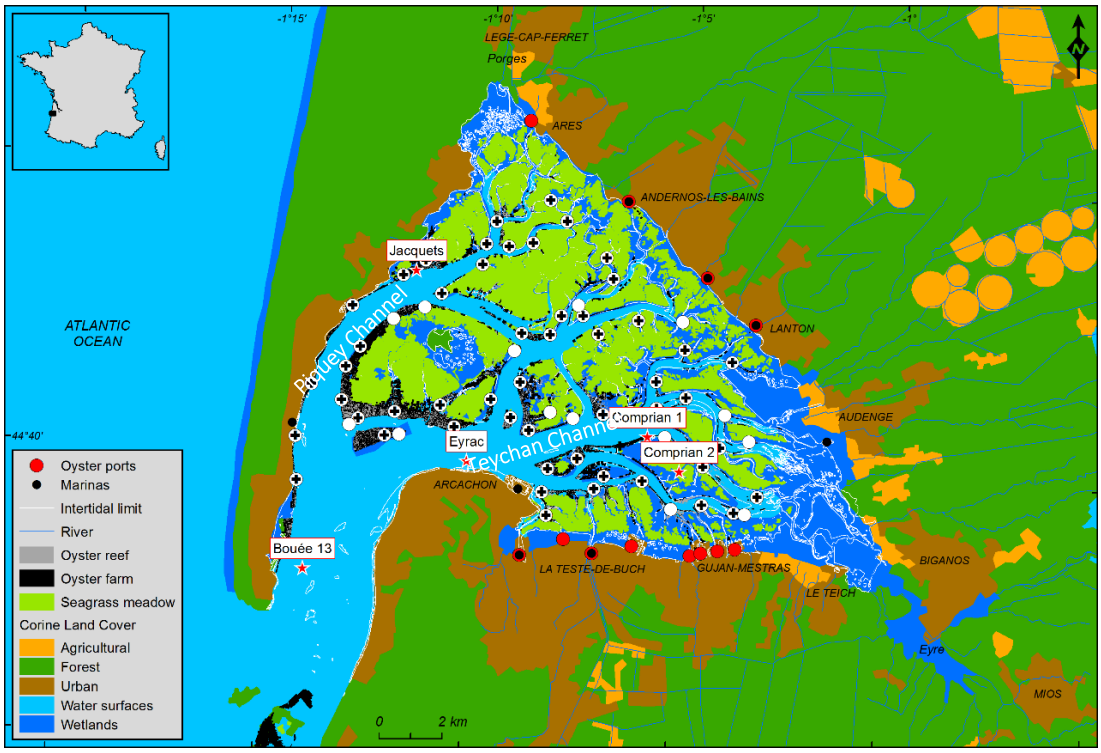

Figure 17: Map of Arcachon Bay with its main ecological components and nearshore land uses and activities. Sampled stations are identified as follows: red stars for water, white circles for microphytobenthos and white/black circles for oyster.

2.2. Sampling strategy and sample processing

2.2.1. *Crassostrea gigas*

Sampling for the spatial variability of *C. gigas* stable isotope composition was carried out in June 2013 at 67 stations on wild oyster reefs in Arcachon bay, according to a stratified random strategy. Sampling for the temporal study of *C. gigas* isotopic signatures was performed monthly from March to September 2014 at Comprian (south-east) and Jacquets (north-west ; **Figure 17**) stations. For each station, 3 adult wild oysters (whole weight > 18 g) were randomly sampled and transported to the laboratory. Adductor muscles were then dissected and rinsed with distilled water. Samples were then stored into HCl-cleaned, precombusted glass vials and stored at -80°C. Before stable isotope analyses, muscles were freeze-dried and ground into a homogeneous powder using a ball mill. For N isotopic analysis, ca. 0.4 mg of powder was placed in a tin cup without further processing. For C isotopic analysis, C analysis, *ca* 0.6 mg of powder was placed in a silver cup, was in-cup decarbonated using 50 µl of 1.2 N HCl, and then dried (Kennedy et al. 2005).

2.2.2. SPOM and phytoplankton

Seawater was sampled at four sites (Comprian 2, Eyrac, Jacquets, Bouée 13, **Figure 17**). It was sampled bimonthly at high tide from March to June 2013 and from December 2013 to September 2014 within the framework of the French Coastal Monitoring Network SOMLIT (http://somlit.epoc.u-bordeaux1.fr/fr/). It was additionally sampled weekly, alternatively at high and low tide, at Comprian, Jacquets, Eyrac and Bouée 13 from March to June 2013 from ARCHYD survey (Ifremer). Water samples were filtered through GF/F filters (∅ 47 mm) for chlorophyll a (Chl*a*) and through pre-combusted (4 h, 450°C) GF/F filters (∅ 47 mm) for particulate organic carbon (POC) and for C and N isotopic ratios. Chl*a* filters were stored frozen at -80°C. Filters for other parameters were dried overnight at 50°C and then stored in a dark desiccator.

Chlorophyll *a* was extracted using 90% acetone and analyzed by fluorescence (Turner Design 10 AU Fluorometer) following Yentsch and Menzel (1963).

Prior to analysis, filters for elemental and isotopic analyses were decarbonated by contact with HCl vapour (4h; Lorrain et al. 2003). One piece of each filter was punched (∅ 11 mm) and analyzed for POC. The rest of the filter was used for the analysis of the isotopic ratios.

Isotopic data associated with POC:Chl*a* ratio lower than 200 were considered as phytoplankton-dominated (Savoye et al. 2003 and references therein) and were used for the determination of the phytoplankton isotopic signature (Savoye et al. Soumise).

2.2.3. Benthic sources (BMA and macrophytes)

The top 0.5 centimeters of sediment were collected from 49 stations. 400 cm^2 of mixed benthic microalgae and sediment were scraped and placed in aluminium containers. Samples were stored at -20°C until the microalgae-sediment separation. Benthic microalgae (BMA) was extracted from the sediment following a modified method of Bolch (1997) based on density gradient using pre filtered (0.2 µm) seawater (density of *ca* 1) and a solution of sodium polytungstate (density of 2) separated by centrifugation. At the end of the process microalgae in pre-filtered seawater was recovered and filtrated through pre combusted (4h-450°C) GF/F filters (∅ 25 mm). The filters were dried overnight at 50°C and then stored in a dark desiccator. The filters were then processed and analyzed as described above.

Macroalgae and phanerogam isotopic signatures for the system are from Dubois et al. (2014).

2.3. Isotopes analyses

N and C compositions were measured using an elemental analyser (EA; NC2500, CarloErba ®) coupled to an isotope ratio mass spectrometer (IRMS; Isoprime, GV Instruments ®). The IRMS was daily calibrated by home-made standards and reference material (IAEA-N2), its drifts were corrected using home-made (casein, glycine) or commercial (acetanilide) standards with known isotopic and elemental signatures. Analytical uncertainties for $\delta^{13}C$ and $\delta^{15}N$ were assessed through repeated measurements of in-house standards and were less than 0.2‰. Inter-individual variability (median of the standard deviations of the 67 triplicates) was 0.3‰ in both $\delta^{13}C$ and $\delta^{15}N$.

Isotopic ratios were expressed in the conventional delta notation:

$$\boldsymbol{\delta^{13}C_{sample}\ or\ \delta^{15}N_{sample} = \left(\frac{R_{sample}}{R_{reference}} - 1\right) x\ 1000}$$

with $R={}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ and the reference is vPDB for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

The trophic enrichment used to explore the trophic link between *C. gigas* and its potential food sources was 1.7‰ for $\delta^{13}C$ and 3‰ for $\delta^{15}N$ as described in Malet (2005).

2.4. Oysters dry weight

Biometrics analyses were measured for 30 individuals per station as detailed in Gasmi et al. (2017). Briefly, the whole weight (Ww) of each oyster was measured after cleaning the shell from epibionts and other debris. Oysters were then opened to separate the flesh from the shell. Soft tissues were drained on absorbent paper and wet weighted before being freeze-dried during 48 h for dry flesh weight (Dfw) measurements.

2.5. Local oceanic flushing time

Local oceanic flushing time (LoFt) was calculated for the whole bay using the MARS3D numerical model (Lazure & Dumas 2008) as detailed in Gasmi et al. (2017). LoFt was used as the time required for local water masses renewal.

2.6. Statistical analyses and spatial mapping

Linear regressions between $\delta^{13}C/\delta^{15}N$ and geographic coordinates were applied to explore the spatial structure of oyster and BMA isotopic signatures. Significant gradients were tested using Fisher tests. Temporal dynamics of oyster $\delta^{13}C$ and $\delta^{15}N$ were tested using Friedman (non-parametric approach) tests to take into account for temporal pairing between stations Comprian and Jacquets.

In order to obtain bay scale distribution maps for $\delta^{13}C$ and $\delta^{15}N$ of *C. gigas* and BMA, the Inverse Distance Weighted (IDW) interpolation method was used. Interpolations were calculated as the difference between each sampled data and its associated interpolation cell, and summarized in Table 2.

Hydrodynamic processes control on *C. gigas* $\delta^{13}C$ and $\delta^{15}N$ spatial variation were examined using simple linear regressions between LoFt and both isotope ratios. When significant, the resulting trends were statistically removed to obtain isotopic ratios corrected for LoFt effects.

Statistical analyses were realized using the R software (R Development Core Team, 2013) and several associated packages (sp, maptools, rgdal, geosphere, SDMTools, Hmisc and RColorBrewer, vegan, lme4). IDW interpolation method was processed with ArcGIS for Desktop 10.3 software (Esri 2014).

Table 2: Summary of Inverse Distance Weighted interpolation errors

	Points	Max error	Mean error (ME)	Standard deviation (SD)	Points [ME ± SD]
$\delta^{13}C$ *C. gigas*	67	0.171	0.006	0.054	50
$\delta^{15}N$ *C. gigas*	67	0.285	0.004	0.079	55

3. Results

3.1. Stable isotope ratios of *Crassostrea gigas* and its potential food sources

Overall, the stable isotope composition of *C. gigas* in Arcachon Bay ranged spatially between -20.6‰ and -18.1‰ for $\delta^{13}C$, and from 7.2‰ to 9.23‰ for $\delta^{15}N$. A significant west-east gradient for $\delta^{13}C$ and a significant north-south gradient was observed for $\delta^{15}N$ (Fisher tests, p-values <

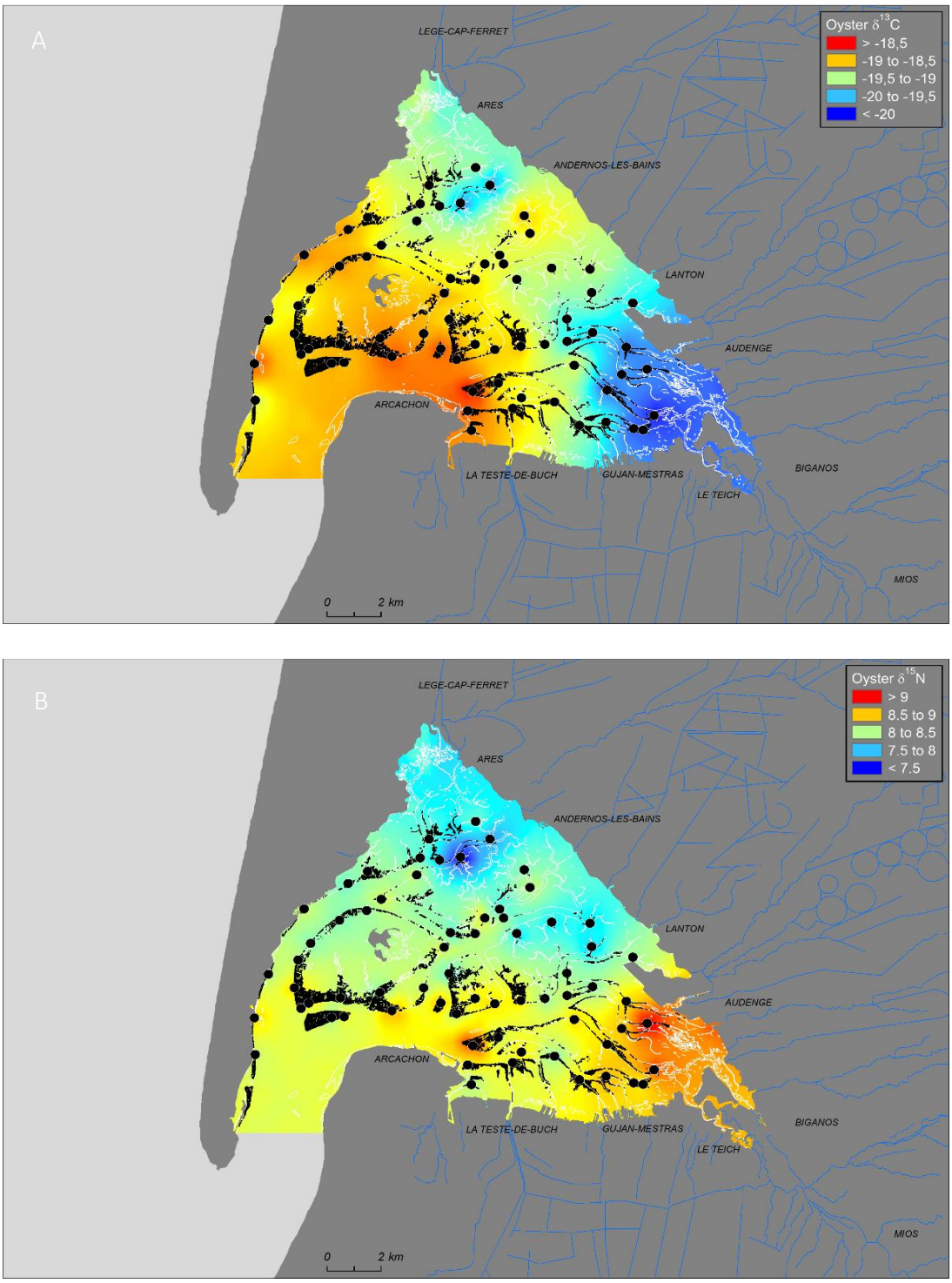

Figure 18: Spatial patterns of $\delta^{13}C$ (A) and δ15N (B) in *C. gigas* muscles using IDW interpolation method. Oyster reefs are delimited in black and black dots represents the 67 sampled stations.

0.001). Low $\delta^{13}C$ (<-20‰) were observed in inner areas, especially near the Eyre River mouth and, to a lesser extent, around the Porges river mouth. At the opposite, high $\delta^{13}C$ (>-19‰) were recorded in marine-influenced areas (**Figure 18A**). Low $\delta^{15}N$ (<8‰) were recorded in the north

of the bay and high $\delta^{15}N$ (>8.5‰) in the south of the bay with a maximum of 9.2‰ near the Eyre River mouth (**Figure 18B**).

The temporal monitoring of *C. gigas* stable isotope ratios only did not reveal any significant variations of both $\delta^{13}C$ and $\delta^{15}N$ (typically lower than 1‰; Friedman tests, $p>0.05$). However, a slight $\delta^{13}C$ increase from ca. -18.7‰ to ca. -18.0‰ was observed at both stations between March and September. No significant differences were detected between the two stations for both parameters (Friedman tests, $p>0.05$), although a slight ^{15}N enrichment was recorded at Comprian compared to Jacquets from July to September (0.3‰ enriched on average).

The spatio-temporal monitoring of SPOM isotopic composition revealed mean $\delta^{13}C$ values of -22.9 ± 1.6‰ and -21.4 ± 1.2‰, between March and June 2013 and March and September 2014 respectively and mean $\delta^{15}N$ values of 4.6 ± 1‰ and 5.4 ± 1.2‰, for the same periods in 2013 and 2014 respectively (**Figure 19**). In 2013, lowest and highest isotopes ratios were recorded in March, they ranged from -26.9‰ to -20.1‰ for $\delta^{13}C$ and from 2.7 to 7.3‰ for $\delta^{15}N$. In 2014, $\delta^{13}C$ values ranged from -23.6‰ to -19.2‰ in March and June, respectively. For $\delta^{15}N$, values ranged from 3.6 ‰ to 7.4‰ in February and June, respectively.

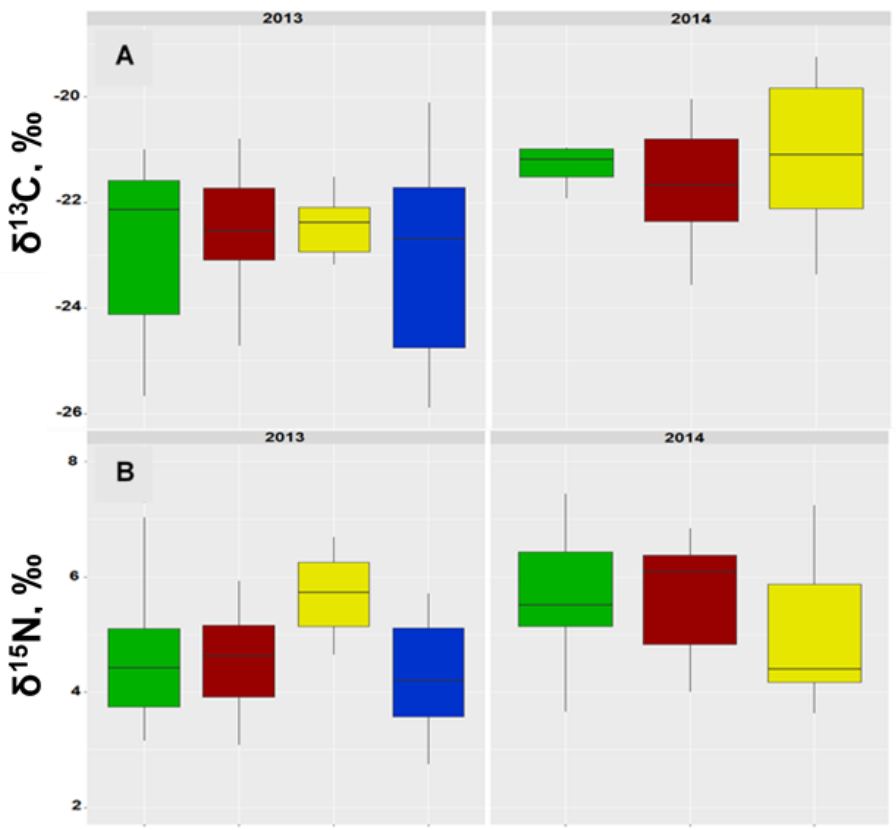

Figure 19: Spatial variability of SPOM isotopic composition in 2013 and 2014 at Bouée 13 (green), Comprian (red), Eyrac (yellow) and Jacquets (blue). Boxplots show median, interquartile ranges (boxes), and ranges (vertical lines).

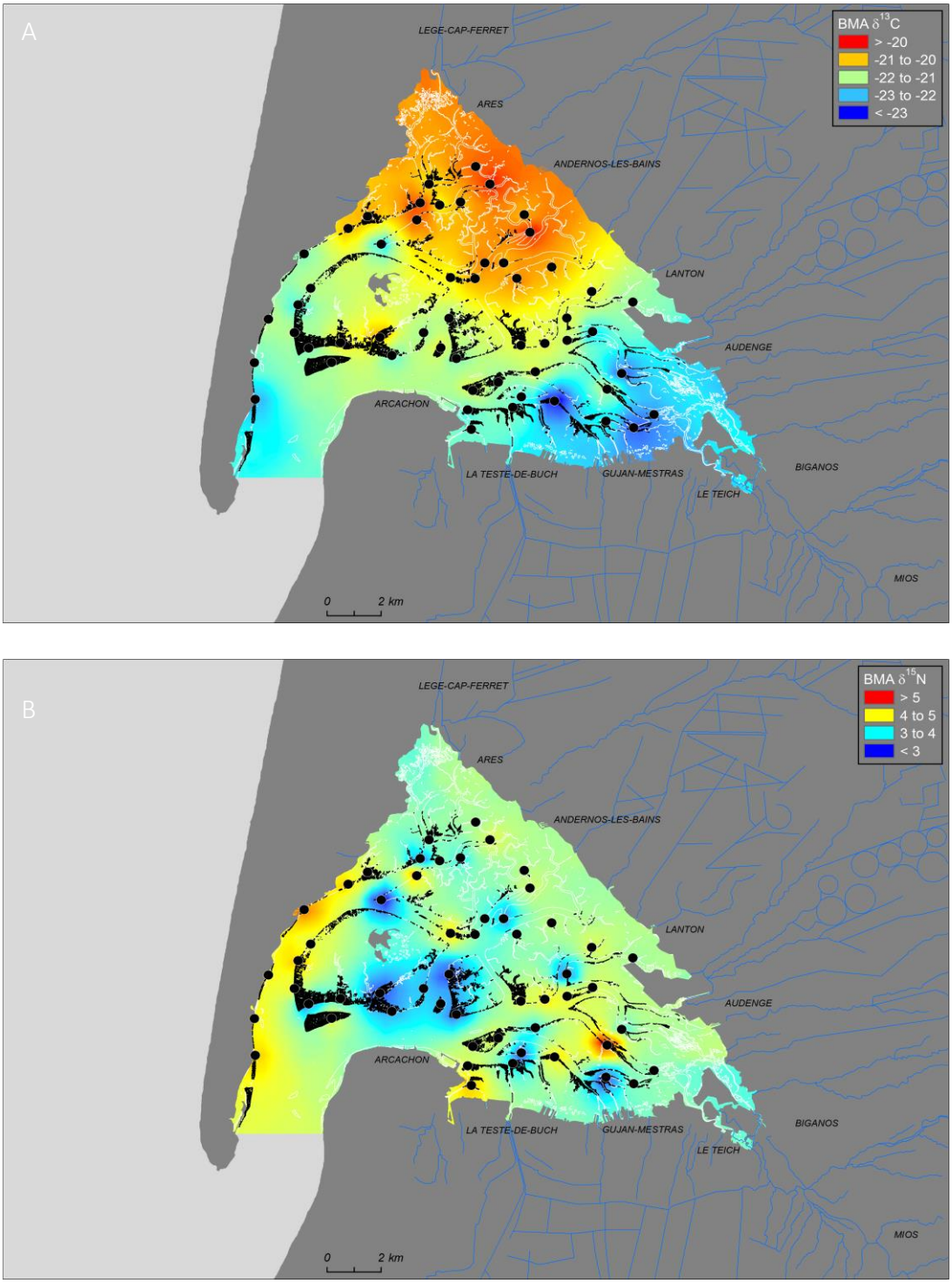

Figure 20: Spatial patterns of $\delta^{13}C$ (A) and δ15N (B) in BMA using IDW interpolation method. Oyster reefs are delimited in black and black dots represents the 67 sampled stations.

The spatial mapping of benthic microalgae (BMA) revealed mean values of -21.1 ± 1.1‰ for $\delta^{13}C$ and of 4.0 ± 0.9‰ for $\delta^{15}N$. A significant south-north gradient was observed for $\delta^{13}C$ (Fisher tests, p-values < 0.001; **Figure 20A**). Low $\delta^{13}C$ (<-20‰) were observed in south areas, while high $\delta^{13}C$ (>-19‰) were observed in north area near the Porges River. No significant spatial pattern was observed for $\delta^{15}N$ (**Figure 20B**). Low values (<3‰) were observed locally and in particular in front of the Eyrac station. High values (>4‰) were observed along the Piquey channel (**Figure 17**).

3.2. Relationship between *C. gigas* dry flesh weight and isotopic ratios

Oysters $\delta^{13}C$ showed a significant and linear positive relationship with Dfw (**Figure 21A**; Fisher test, p-value < 0.01; Adjusted R-squared=0.23). Oysters $\delta^{15}N$ was not correlated to Dfw (Fisher test, p-value=0.9; Adjusted R-squared=$1.6e^{-05}$).

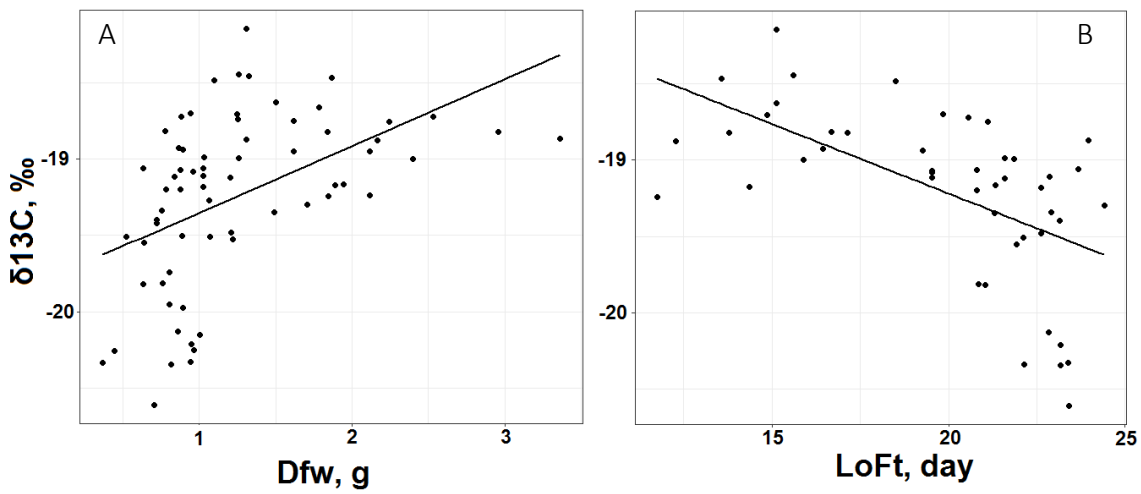

Figure 21: Linear regressions between $\delta^{13}C$ and both Dfw (A) and LoFt (B). The adjusted R^2 values were 0.23 and 0.29, respectively.

3.3. LoFt effects on *C. gigas* isotopic ratios

Oysters $\delta^{13}C$ showed a significant and linear negative relationship with local oceanic flushing time (LoFt) (**Figure 21B**; Fisher test, p-value < 0.01; Adjusted R-squared= 0.29). Oysters $\delta^{15}N$ was significantly but weakly linearly correlated to LoFt (Fisher test, p-value <0.05; Adjusted R-squared = 0.04).

3.4. Variance partitioning of Dfw and LoFt effects on *C. gigas* $\delta^{13}C$

The partitioning of the $\delta^{13}C$ variability on both Dfw and LoFt allowed to explain 32% of the global variance, pure effects: LoFt= 16% and combined effects= 16%.

3.4. *C. gigas* $\delta^{13}C$ and $\delta^{15}N$ corrected from LoFt effect

After statistical correction by LoFt-related spatial gradients, a marked change in the direction of the residual $\delta^{13}C$ gradient was observed, revealing a significant $\delta^{13}C$ enrichment from south-east to the north-west (p-value<0.001, **Figure 22**). Only slight changes in the direction of the $\delta^{15}N$ gradient towards the south-east were observed after correction (p-value<0.001).

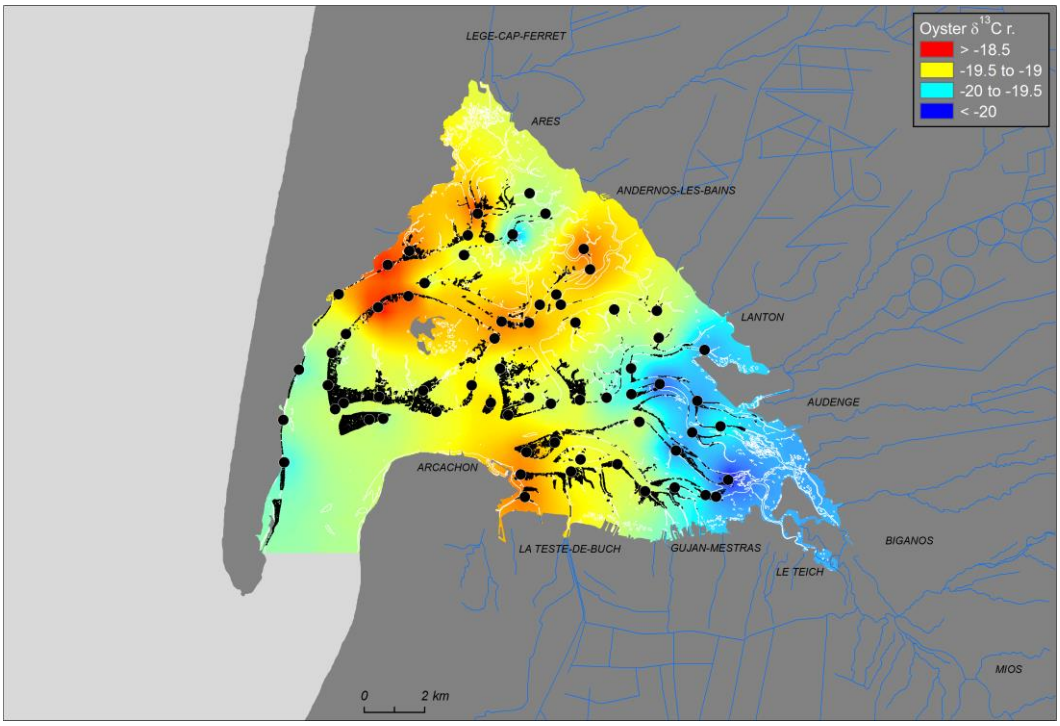

Figure 22: Spatial patterns of $\delta^{13}C$ in *C. gigas* muscle corrected from LoFt effect using IDW interpolation method. Oyster reefs are delimited in black and black dots represents the 67 sampled stations.

4. Discussion

4.1. *Crassostrea gigas* food sources

Several food sources have been reported in the literature to enter the diet of *C. gigas*: phytoplankton, benthic microalgae, decayed macroalgae and seagrass, and microzooplankton (Riera & Richard 1996 ; Decottignies et al. 2007 ; Marchais et al. 2013 ; Dupuy et al. 1999). The

composition of SPOM is known to vary seasonally depending on temperature, nutrient supply and hydrodynamic processes. It is thus necessary to consider the diversity of factors potentially affecting the dynamics of SPOM composition to fully understand the trophic ecology of oystersThe isotopic composition of oysters was very close to microalgae (phytoplankton and microphytobenthos; **Figure 23**) suggesting that these sources represent the large majority of oysters diet, as already observed for many other enclosed coastal systems (*e.g.* Kang et al. 2003). Although reported in previous studies (*e.g.* Dupuy et al. 1999), the consumption of zooplankton seems to be negligible in the bay in term of ingested carbon and thus assimilated material (Salvo, personal communication). Furthermore, our results clearly indicate that detrital matter derived from seagrass beds and macroalgae does not contribute to oysters diet, which is confirmed by fatty acids analysis conducted on the same temporal survey (unpublished data). Although oysters are generalist consumers that filter a mixture of organic matter

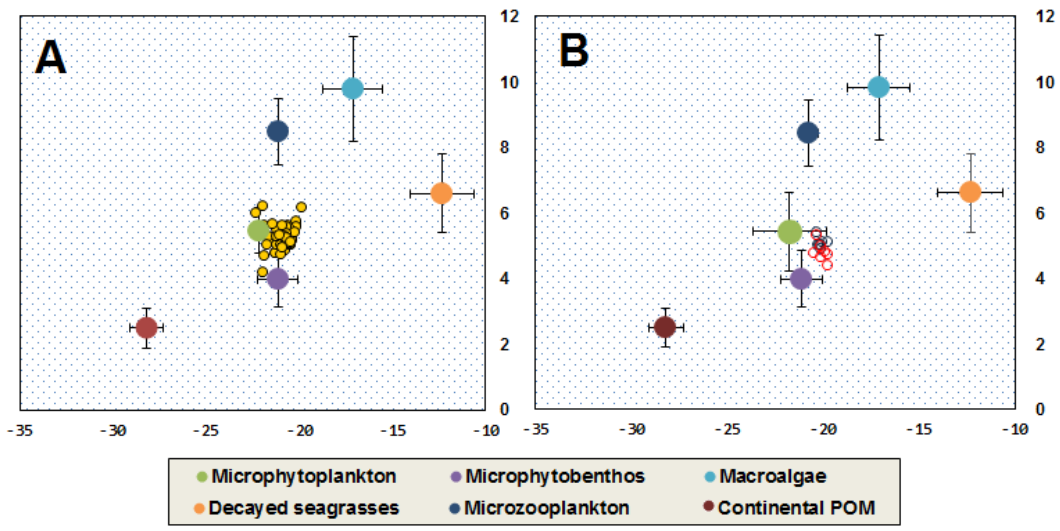

Figure 23: Stable isotope biplots of nitrogen and carbon in *C. gigas* muscle after subtraction of trophic isotope enrichment. (A) Yellow dots represents oysters isotopic ratios from the 67 sites sampled in June 2013. (B) Blue and red circles represents oysters isotopic ratios from respectively Comprian and Jacquets, monthly sampled from March to September 2014. BMA isotopic ratios (green dots) originated from the 49 sites sampled in June 2013. Macroalgae, decayed seagrasses and Continental POM are Dubois et al. (2014). Microzoplankton isotopic ratios were estimated from phytoplankton assuming a trophic enrichment of 3 ± 1 for $\delta^{15}N$ and 1 ± 0.5 for $\delta^{13}C$.

suspended in the water column, they have been proven to exhibit high pre- or post-ingestion selectivity toward the most nutritive components of SPOM (Dame 1996; Tamburri & Zimmer-Faust 1996).

In shallow coastal environments, tidal flushing and river runoff are the main bottom-up factors controlling phytoplankton dynamics and BMA resuspension (Glé et al. 2007 ; Monbet 1992 ; Trigueros & Orive 2000). Phytoplankton is generally to be a dominant component of *C. gigas* diet, while BMA contribution is more controversial. Some authors defend the focus on phytoplankton since its seasonal dynamics fits perfectly with *C. gigas* growth cycle (Alunno-Bruscia et al. 2011b), while other authors argue for a significant contribution of BMA, in particular based on stable isotope results (Marchais et al. 2013 ; Pascal Riera & Richard 1997). Comparing the trophic functioning of two coastal ecosystems of the Cotentin Peninsula (France), Gaudron et al. (2016) showed that *C. gigas* exposed to marine influences on the west coast relied mainly on pelagic SPOM, while on the east coast benthic food sources appeared to be a major contributor. The authors attributed this difference to the nature of the sediment, which controls BMA erodibility and therefore availability via tidal hydrodynamic processes (Gaudron et al. 2016). Under the right conditions (*i.e.* sand-mud equilibrium, biofilm stability, high hydrodynamism; Ubertini et al. 2015), benthic resuspension constitutes an important source of chlorophyll a and several benthic micro-organisms such as microphytobenthos cells input into the water column (Guarini et al. 1998 ; Ubertini et al. 2012; David et al. 2016 ; Saint-Béat et al. 2014) , which supports the idea of its contribution to filter-feeders' diets.

Considering the overall similarity between oysters and microalgae stable isotope compositions (**Figure 23**), continental inputs do not represent a large fraction of *C. gigas* diet. SPOM inputs from the Eyre river are indeed known to be highly ^{13}C-depleted (Dang et al. 2009), and any important contribution would have resulted in lower $\delta^{13}C$ than those observed here. The low contribution of continental material to oysters diet confirms the outcomes of previous studies (e.g. Kang et al. 2003), where the lower nutritive value of continental material had been suggested to explain its absence of assimilation by coastal bivalves (Deegan & Garritt 1997 ; Page 1997). A slight ^{13}C-depletion was however observed in oysters at the immediate vicinity of the Eyre river mouth, suggesting that continental inputs (detritus of freshwater phytoplankton) could locally represent a minor part of *C. gigas* diet. These inputs are quickly diluted and do not seem to enter the diet of *C. gigas* in the outer part of the bay.

4.2. Spatio-temporal variability of oyster diets

In a previous paper, we found that the spatial variability of condition index (Laurence and Scott condition index, LS_{CI}) was mainly explained by local oceanic flushing time and immersion level (Gasmi et al. 2017). We hypothesized that longer feeding time and higher phytoplankton supply from the open ocean by tide flow did result in better oysters' physiological condition (Gasmi et al. 2017). The main objective here was thus to analyze how stable isotopes can bring other information about these assumptions and how they can be used here as significant tools to assess oyster feeding spatial and temporal variability. Here, we found that the spatial variability of *C. gigas* stable isotope composition was quite similar to previous studies carried out in coastal enclosed systems (*e.g.* Fertig et al. 2009; Marchais et al. 2013). Although the range of variation was typically below 2‰ at the bay scale for both $\delta^{13}C$ and $\delta^{15}N$, it still allowed detecting statistically significant patterns, revealing small scale variability in sources supporting *C. gigas* growth or in local physiological aspects. In contrast we found no temporal variability in the stable isotope composition of oysters. This absence of temporal variability has to be related to the analysis of muscle tissues, which are known to integrate trophic signals over longer periods than other tissues (Tieszen et al. 1983).

The present study revealed a statistically significant relationship between dry weight and oyster $\delta^{13}C$. Furthermore, *C. gigas* $\delta^{13}C$ showed a significant relationship with local oceanic flushing time (LoFt), which explained 29% of the total $\delta^{13}C$ variability. This was to be expected since oysters condition indices have been reported to be correlated to oceanic flushing time in the bay by Gasmi et al. (2017). Rapid and repeated entrance of tide flow in the outer bay (LoFt: 15 days ± 2.24) contributes to oyster ^{13}C enrichment. In contrast, longer LoFt and higher freshwater inputs from the Eyre (LoFt: 20.5 ± 2.3) and the Porges rivers (LoFt: 23 days ± 1) in the inner bay result in oyster ^{13}C depletion.

This correlation is probably partly explained by a higher reliance towards oceanic phytoplankton near the entrance of the bay. However, the correlation observed between oysters $\delta^{13}C$ and their dry flesh weight (R^2=0.23) suggests that physiological aspects might contribute to the observed pattern. Higher growth rate have indeed been reported for oysters near the entrance, while those from the inner bay were characterized by lower growth and condition index (Gasmi et al. 2017). Physiological aspects are under recognized factors affecting

trophic fractionation, but can heavily affect consumer stable isotope composition. For instance, Pecquerie et al. (2010) inferred from a modelling approach that individuals fed different levels and displaying contrasted growth rates would significantly differ in the stable isotope fractionation. This alternative explanation thus cannot be ignored, and further investigation is required to determine the relative parts of diet *vs* physiology in the observed stable isotope patterns.

As BMA is typically 13C enriched compared to phytoplankton (France 1995), it could be hypothesized that oysters in the oceanic part of the bay rely more on BMA, while those in the inner part of the bay rely on phytoplankton, therefore creating the observed east-west gradient of oyster $\delta^{13}C$. However, sediment from the outer bay is mostly sandy, diatoms are epipsammic and not easily detachable from sand, which limits their availability for *C. gigas* (Gaudron et al. 2016 ; Marín Leal et al. 2008). In contrast, sediments from the inner bay are mostly muddy, where migrating diatoms are known to be subject to resuspension by tide flow (Ubertini et al. 2015). The hypothesis of significant BMA contribution at the vicinity of the bay entrance is also not supported by stable isotope data in local SPOM (Liénart et al. Soumise). The observed east-west gradient of oyster $\delta^{13}C$ may alternatively reflect a $\delta^{13}C$ gradient in phytoplankton bloom dynamic in the Bay. Marine SPOM inputs from the adjacent waters of the Bay of Biscay are recurrent, and set the period of phytoplankton productivity inside the bay (Glé et al., 2007). Phytoplankton blooms start in the outer bay and reaches the inner bay in 7 days, where microalgae benefit from nutrient inputs from rivers (Glé et al. 2007). However, although monitoring of Jacquets and Comprian revealed phytoplankton $\delta^{13}C$ values ranging from -20.8 to -24.7‰, there was no obvious spatial phytoplankton isotope pattern supporting the above hypothesis. For instance, in March and April, phytoplankton showed two ^{13}C depletion events (< -23‰), in the inner and outer bay simultaneously. In a parallel study, the monitoring from March to June 2013 of the three stations localized along the east-west axis of the bay did not evidence a $\delta^{13}C$ gradient in the phytoplankton/SPOM whatever the sampling months (N. Savoye, pers. comm.). It is in agreement with previous studies stating that the well-mixed regime maintained by tidal inflows ensure spatially homogenous isotope composition of phytoplankton (Dang et al. 2009).

Contrary to $\delta^{13}C$, *C. gigas,* $\delta^{15}N$ was only slightly correlated to the LoFt gradient (4% of $\delta^{15}N$ variability explained by LoFt). A marked north-south gradient was observed, the highest values

being observed in the south-east of the bay, and the highest in the northern bay. Although continental inputs from the Eyre river could contribute to the observed enrichment in the southern part of the bay, the catchment is mostly rural, and lacks significant urban zones. Furthermore, no ^{15}N enrichment was observed in BMA for this area, supporting the lack of anthropogenic inputs from the Eyre river. An alternative explanation involves a higher contribution of heterotrophic protists to the diet of oysters in this freshwater-influenced area, as already suggested in an estuarine environment by Riera (1998) even if this contribution seems limited. Nutrients and DOM inputs from the Eyre might stimulate the microbial food web in the south-east bay, while oysters in the northern bay, where continental inputs are lower, mostly rely on autotrophic phytoplankton. This hypothesis is supported by in situ observation from REPHY survey (Ifremer) that shows for the same period a higher contribution of heterotrophic protists in the southern part of the bay (Maurer, pers. comm.)

BMA $\delta^{13}C$ spatial variability exhibited a south-north gradient that do not appear to contribute to the east-west gradient of oyster $\delta^{13}C$, suggesting at least a partial trophic decoupling between BMA and oysters. BMA isotope signatures recorded spatially (-23.8‰ to -19.1‰ and 2.3 to 6.0‰, for $\delta^{13}C$ and $\delta^{15}N$, respectively) are similar to signatures recorded for other coastal systems (Dubois et al. 2007 ; Jaschinski et al. 2008), but are ^{13}C-depleted compared to values recorded in Aiguillon and Marennes-Oléron Bays (France ; Riera & Richard 1996, 1997) and South Korean coastal bays (Kang et al. 2003). This may be linked to the differences in temperature and/or species that dominate the BMA community (Oakes et al. 2005) but no data are available about local BMA species composition to confirm this assumption. No temporal variability in BMA stable isotopes was reported in Arcachon Bay (Dubois et al. 2012). The ^{13}C-depletion observed in the northern bay could reveal a contribution of *Zostera spp*. originating nutrients. Eelgrasses are abundant in this area of the bay (Ganthy et al. 2013) and are known to display extremely ^{13}C depleted stable isotope compositions, and release dissolved organic matter (DOM), especially when undergoing desiccation during emersion (Wetzel & Penhale 1979). This DOM can then be remineralized in the sediments, hence contributing to the productivity of BMA.

4.2.1 Oyster isotopic variability in the inner parts of Arcachon bay

After correcting oysters' $\delta^{13}C$ by the LoFt-related spatial gradient, a south-east-north west gradient was revealed explaining the remaining 71% of residual $\delta^{13}C$ variability. This new gradient was similar to the one displayed by BMA, ^{13}C-enriched in the northern part of the Bay. This suggests that BMA, although being a secondary source compared to phytoplankton, significantly contribute to the diet of *C. gigas* in Arcachon Bay. However, the contribution of BMA to oysters diet seems to be highly variable at the bay scale.

The north-west region of the Bay is characterized by a higher percentage of silt and clay in the sediments (Binias et al. 2014), which favors resuspension processes (Ubertini et al. 2015). This is in agreement with the diversified diet described for *Ruditapes philippinarum* along the northern Piquey channel, where BMA appeared as the major component of clam diet (Dang et al. 2009). These authors also observed that *R. philippinarum* did not seem to use BMA in the south-east part of the bay but rather fed more heavily on phytoplankton. They attributed this finding to a reliance on outer bay phytoplankton transported by tidal flushing within the bay. Indeed, 60 % of tidal inputs follow the southern Teychan channel compared to just 15% for Piquey channel (**Figure 17** ; Plus et al. 2006). Furthermore, in our study, BMA $\delta^{15}N$ was too low at the Eyre mouth to support the hypothesis of a significant BMA consumption by oysters.

4.3. Conclusion

The extensive characterization of stable isotopes in both BMA and oysters in Arcachon Bay allowed disentangling different spatial patterns, which have been linked to differential phytoplankton *vs* BMA contribution to the diet of oysters. In our study, the weak discrimination between phytoplankton and BMA stable isotope composition did not allow to use mixing models to infer the respective contributions of these two sources. In spite of the weak spatial variability of *C. gigas* isotopic ratios in Arcachon Bay, this study allowed to detect significant spatial patterns. We inferred that the main spatial gradient, highly correlated to the local connectivity to the open ocean, was likely indicative of marine phytoplankton contribution. After mathematically correcting stable isotope compositions from this major trend, a secondary gradient emerged, and revealed the importance of BMA to the diet of oysters. We suggest that in case stable isotopes do not allow discriminating among different food sources, such

extensive spatial sampling, although time and coast consuming, might represent a promising alternative (Leclerc et al. 2013 ; Marchais et al. 2013).

Chapitre III

Variabilité des acides gras essentiels et de la composition phytoplanctonique pendant un cycle reproductif de l'huître creuse *Crassostrea gigas* dans le Bassin d'Arcachon

Variability in essential fatty acids and phytoplankton composition over a gametogenesis cycle of the Pacific oyster *Crassostrea gigas* in Arcachon bay (France)

1. Introduction

Assessing the carrying capacity of coastal ecosystems is crucial to avoid system collapse and ensure their sustainable exploitation (Filgueira et al. 2014 ; Kluger et al. 2016). Few studies have investigated the capacity of a system characterized by bivalve farming to answer species requirements in terms of lipid compounds and more especially essential fatty acids (EFAs) (Budge et al. 2001). EFAs are as described in Dunstan et al. (1992) as: "fatty acids which cannot be synthesized in sufficient quantities by animals to maintain good growth and survival". For fishes and mollusks, these active biological molecules are implicated in vital physiological functions such as reproduction and immune response (Hurtado et al. 2009 ; Parrish 2009). Many studies have focused on bivalve EFA requirements in the last decades while less is known about how cultivated and exploited bivalves acquire them from their environment (Parrish 2009). More research is needed in this field to correctly assess and model the trophic state of aquaculture ecosystems (*i.e.* EFA origins, availability, and fate). This is particularly important in the current context of climate change, which is predicted to affect both phytoplankton fatty acid composition (Hixson & Arts 2016) and shellfish production (Guyondet et al. 2015).

During the gametogenesis cycle, energetic reserves invested by mollusks in oocyte building processes are in the form of lipids derived mainly from food. These storage lipids (or neutral lipids) are transferred from storage organs (*i.e.* digestive gland, mantle) to the gonad (Berthelin et al. 2000). Fatty acid composition of dietary lipids is therefore an important driver of oogenesis processes and success. In many hatchery-reared species (*e.g. Pecten maximus)*, dietary fatty acids have been revealed as determinant factors for the quality of the gametes and the reproductive output (Soudant et al. 1996). Among EFAs, the long-chain polyunsaturated FAs (LC-PUFAs): 20:5n-3 (acids eicosapentaenoic, EPA), 22:6n-3 (docosahexaenoic acid, DHA) and 20:4n-6 (arachidonic acid, ARA) are the most important and have different nutritional interests for bivalve growth and reproduction (Hendriks et al. 2003). However, bivalves have very limited or no ability at all to synthesize these EFAs and require them from their environment for their own metabolism (Knauer & Southgate, 1997). Nevertheless, bivalves are able to *de novo* synthesise some peculiar fatty acids (FAs) called non-methylene interrupted fatty acid (NMIs) (Monroig et al. 2013) which are thought to have

functional and structural roles in membranes (Kraffe et al. 2004). They may also substitute for EFAs (Klingensmith 1982) but their proportions depend on the dietary supply of their precursors, *i.e.* 16:1n-7 and 18:1n-9. EFAs and their precursors originate in suspension-feeding bivalves from suspended particulate organic matter (SPOM) (Monroig et al. 2013)

Thus, the nutritive value of POM for bivalves will depend, at least partially, upon the presence of essential polyunsaturated fatty acids (PUFAs) especially arachidonic acid (AA, 20:4n-6), eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) as well as the presence of NMI precursors. Also, it is generally accepted that an optimal POM quality for marine animals is characterized by high n-3/n-6 fatty acid ratios (Sargent et al. 1995). SPOM is composed of several sources including phytoplankton, bacteria, zooplankton, macrophytes and terrestrial detritus (Lowe et al. 2014). In marine environments, EPA, DHA and ARA concentrations in SPOM are driven by three major functional group of phytoplankton, diatoms, dinoflagellates and prymnesiophyceae (Bergé & Barnathan 2005 ; Dalsgaard et al. 2003). Heterotrophic protists and autotrophic bacteria also synthesize EFAs (Dalsgaard et al. 2003 ; Monroig et al. 2013). EPA and DHA are the major synthesized phytoplankton-derived EFAs, as well as ARA to a lesser extent (Boelen et al. 2013).

Each phytoplankton group contributes differently to the composition of FA available in the SPOM bulk (Volkman et al. 1998). Due to their specific fatty acids biosynthesis pathways, diatoms are characterized by high production of C16 and C20 fatty acids, such as 16:1n-7 (Dijkman and Kromkamp, 2006), 16:2n-4 and 16:4n-1 (Viso & Marty 1993), and 20:5n-3 (Volkman et al. 1989). In contrast, dinoflagellates are rich in C18 and C22 polyunsaturated fatty acids (PUFA), such as 18:4n-3 (Volkman et al. 1989), 18:5n-3 (Dijkman & Kromkamp 2006) and 22:6n-3 (Volkman et al. 1989). The dominance of diatoms relative to dinoflagellates can thus be assessed by a ratio 20:5n-3/22:6n-3>1 (Dalsgaard et al. 2003). Prymnesiophyceae exhibits FA profile relatively similar to dinoflagellates. Pepin et al. (2011) have proposed the sum of 18:1n-9 and 18:4n-3 as a biomarker of their contribution to the composition of POM. For other taxonomic groups, the green algae and vascular plants contribution is mainly in the form of 18:2n-6 and 18:3n-3 (Kelly & Scheibling, 2012) while bacteria biomarkers are straight and branched odd numbered 15:0 and 17:0 saturated fatty acids (Volkman et al. 1989).

EFA concentrations in SPOM are strongly dependent on seasonal changes in hydrodynamics and environmental conditions (*e.g.* temperature, light, nutrients) which are the main drivers of phytoplankton growth and species composition (Dalsgaard et al. 2003). In a study conducted by Galloway and Winder (2015) which compared fatty acids composition of six major taxonomic groups cultured in a wide range of environmental conditions, changes in taxonomic group induced 3-4 times more variation in phytoplankton fatty acids composition than most important environmental conditions. Across the Beaufort Sea shelf, seasonal shift in SPOM fatty acids correspond to shift in the ratio of abundance between diatoms *vs.* dinophyceae, prymnesiophyceae and/or prasinophyceae (Connelly et al. 2016). These groups are present in the water column at different sizes, microplankton (20-200µm), nanoplankton (2-20µm) and picoplankton (0.2 - 2µm). Nano- and picoplankton significantly contribute to primary production and carbon biomass because of their highest metabolic and growth rates (Marañón 2015 ; Moynihan et al. 2016).

Arcachon Bay is a shallow coastal lagoon which supports great biological production of the oyster *Crassostrea gigas*. Historically, the bay provides an important amount of spat for oyster farming in France. The reproductive effort of *C. gigas* appeared highly variable at both local and regional scales (Bernard et al. 2014 ; Gasmi et al. 2017). This variability was related to differences in the trophic environment. The bay is characterized by low to moderate phytoplankton and high local gradients of variability in nutrients and primary production (Glé et al. 2008). For these reasons, Arcachon Bay appeared as a great area to study the trends of variability in fatty acids composition of SPOM and their role in the gametogenesis process of *C. gigas*.

The primary goal was to assess the nutritional value of the fatty acids pools in SPOM, able to answer *C. gigas* gametogenesis requirements. Fatty acids profiles were analyzed together with the composition and biomass of phytoplankton communities in order to identify the main groups contributing to POM fatty acids. The spatial and temporal variability of EFAs and their precursors in POM were investigated over a reproductive cycle of *C. gigas* in Arcachon Bay, from March to September 2014. Nano- and pico-sized POM biomass were monitored as well to investigate its contribution to fatty acid pools. To assess the quality of the trophic environment, proportions of the different functional groups of saturated and unsaturated fatty acids, EFAs and n-3/n-6 ratios were compared. Dietary fatty acids and their involvement in *C.*

gigas gametogenesis processes were studied by the determination of fatty acids composition of neutral and polar lipids in oysters' digestive gland and gonad plus mantle tissue.

2. Material and methods

2.1. Study area

Arcachon Bay (44°40′ N, 1°10′ W, **Figure 24**) is a semi-enclosed lagoon of 174 km², located at the southeast of the Bay of Biscay (France). It opens into the Atlantic Ocean through tow narrow channels. During each tidal cycle, approximately two third of the lagoon total volume is flushed in and out (Plus et al. 2009). The average tidal amplitude ranges from 0.8 to 4.6 m (mesotidal regime) at neap and spring tide, respectively. Mean oceanic flushing time range between 13.3 and 19.5 days under north and west winds, respectively; highest water renewal occurs in the outer bay (Plus et al. 2009). Tidal currents and wind are the main drivers of tidal mixing in the bay (Salles et al. 2015). In addition to marine influences, Arcachon Bay is submitted to freshwaters inflows from several streams and rivers. Eyre (southeast) and Porges (north) rivers are the main sources of annual freshwater inputs into the system, with 70% and 24%, respectively (Plus et al. 2009). The presence of this two major freshwater sources creates, towards the ocean, two gradients of hydrobiological parameters, east-west and north-south (Binias et al. 2014), and affect suspension-feeders trophic environment (Dang et al. 2009 ; Dubois et al. 2014).

2.2. Sampling strategy

Focusing on the north-south gradient of variability in oyster reproductive condition (Gasmi et al. 2017), hydrobiological features were monitored in two sites: Comprian (44° 40' N, 1° 05' W) in the southern part at the vicinity of the Eyre river mouth, and Jacquets (44°43' N, 1°11' W) in the north-western part (**Figure 24**).

Sampling was performed at these two stations from February 24th to September 23th 2014, a period including oyster gametogenesis, gamete releases and larval development (Auby et al. 2014).

Water sampling was carried out weekly at ebb tide, when oysters were found to have the maximum opening rate amplitude, suggesting highest feeding activity (Tran et al. 2011). Seawater was sampled for the analysis of the suspended matter, organic nitrogen and carbon,

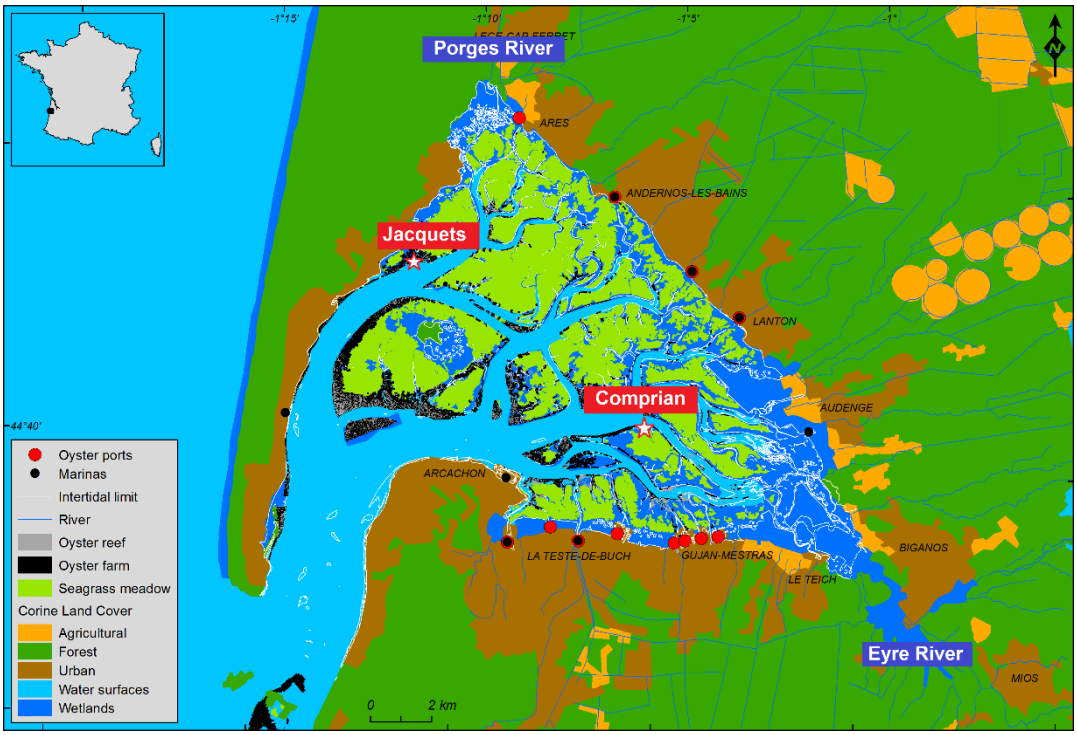

Figure 24: Map of Arcachon Bay with its main ecological components and nearshore land uses and activities. Red stars represents sampled stations.

chlorophyll *a* and phaeopigment concentrations, seston diversity and abundances, lipid classes and fatty acids in particulate organic matter. The water was sampled 1m above the bottom using a 30L Niskin bottle.

Forty individuals of adult wild *C. gigas* (whole weight > 18g) were collected at Comprian and Jacquets every two weeks at low tide by hand and transported to the laboratory. Biometrics and condition index measurements were carried on 30 individuals, while 10 individuals were examined for lipid classes/fatty acids contents and histology.

2.3 Water column samples processing

2.3.1. SM, POC and PON

Between 1 and 2 liters of seawater were directly filtered for suspended matter (SM) and particulate organic carbon and nitrogen measurements (POC and PON) on pre-weighed and pre-combusted (4 h at 450°C) fiberglass filters (Whatman GF/F, Ø 47 mm). After filtration, filters were dried overnight at 50°C and then placed in a dark desiccator. Dry filters were then weighed and suspended matter weight was determined by subtracting the filter weight.

Measurements of POC and PON elemental compositions were measured on the same filter using a Flash Elemental Analyser Series 1112 (ThermoFinnigan®). Previously, to the analysis, filters were decarbonated with HCl vapors (4 h; Lorrain et al. 2003). One piece of each filter was punched (Ø 11 mm) and used to determine POC and PON concentrations according to the procedure adopted in the framework of the French Coastal Monitoring Network SOMLIT (http://somlit.epoc.u-bordeaux1.fr/fr/).

2.3.2. Chlorophyll a and phaeopigments

For chlorophyll *a* and phaeopigment measurements, 300 ml of seawater were directly filtered on fiberglass filters (Whatman GF/F, Ø 47 mm). Filters were stored at -80°C until the analysis. Pigment extraction was performed protected from heat and light. Filters were placed in glass tubes with 90% acetone (final concentration), hand-crushed using a glass stick and kept overnight in the dark at 4°C. Chlorophyll *a* and phaeopigment concentrations were then measured using a spectrofluorimeter according to the method described in Aminot et al. (2004). Wavelength excitation and emission peaks of pigments were calibrated with a standard solution (Sigma-Aldrich: Anacystis nidulans, C-6144) at 428 and 670 nm respectively.

2.3.3. Prokaryotes, picoeukaryotes and nanoeukaryotes

Seawater sampling for the analysis of pico-and nano-eukaryote communities was realized without turbulence and immediately fixed with 25% glutaraldehyde. 1.5 mL of seawater was aliquoted in cryotubes containing 60 µl of glutaraldehyde for a final concentration of 1%. Samples were stored on board in liquid nitrogen and then at -80°C until flow cytometry analysis.

Flow cytometric analyses were performed at the Platform (Core facility) of Cytometry and Imagery of the University of La Rochelle, using a FACS Canto II cytometer according to (Troussellier et al. 1993).

2.3.4. Phytoplankton determination and biomass

Samples for the identification of phytoplankton species composition were fixed on board with a Lugol acid solution and protected from heat and light. In the laboratory, phytoplankton cells were identified at the lowest possible taxonomic level and counted using an inverted microscope (Zeiss) (magnification of ×200) after a 24h sedimentation using Utermöhl settling chambers (Utermöhl 1958).

2.3.5. Fatty acids in particulate organic matter

Particulate organic matter was sampled by filtration of seawater on pre-combusted (450°C, 4h) fiberglass filters (Whatman GF/F, Ø 150 mm). Seawater samples were previously sieved using a 200 µm mesh size to eliminate coarse particles and zooplankton. On board, filters were stored in pre-combusted aluminum foil in liquid nitrogen and then at -80°C.

For fatty acids analysis, each filter was placed in a glass tube with 6 mL of chloroform/methanol (2/1; v/v), sonicated and centrifuged (453 x g, 5 min, 4°C). The supernatant (6 mL) was transferred in a new glass tube. To optimize the extraction, the operation was repeated 2 more times for a final extraction volume of 18 mL. The final tube was centrifuged (453 x g, 5min, 4°C) and stored at least 24h for the extraction of fatty acids. As some filters still contained some water after filtration, two layers were formed, separating the methanol+water (approximatively 2 mL) from the chloroform containing the lipid extract (approximatively 16 mL). The first layer was eliminated and 3 mL was sampled from the second layer, evaporated then to dryness under nitrogen flux. Lipid extract was then re-suspended in 1 mL of chloroform/methanol (2/1; v/v) and conserved at -20°C.

Fatty acids in total extracted lipids were analyzed as fatty acid methyl esters (FAME) after transesterification using sulfuric acid in methanol (3.4%; v/v). 1 ml of the extraction solution was evaporated to dryness and re-suspended in 800µl of $H2SO_4$-MeOH and heated at 100°C for 10 min. To recover FAME, 800 µL of hexane and 1.5 mL of distilled water saturated with hexane were added. Tubes were mixed and centrifuged (1000 rpm, 1 min, 20°C) and the

aqueous phase was eliminated. This washing operation was repeated twice, the last added aqueous phase was conserved and frozen by placing the vials at -20°C for 4h. FAME were recovered from the organic liquid phase.

Fatty acid analyses were performed using a gas chromatograph (VARIAN CP 3800) equipped with a flame ionization detector and a splitless injector and using hydrogen as carrier gas. Two columns operated in parallel allowed fatty acids separations on a polar one (ZBWAX 30 m x 0.25 mm ID; 0.25 µm film thickness) and a non-polar one (ZB5HT 30 m x 0.25 mm ID; 0.2 µm film thickness). The identification of fatty acids was accomplished by comparing their retention times with those of commercial standards or with lab made standards of marine phytoplankton and bivalves (Soudant et al. 1995). Fatty acid peak integration and identification was performed using Galaxy software (version 1.9.3.2) for chromatograms analysis. Fatty acids quantities were calculated proportionally to the internal standard (C23:0), and were expressed as percentage of the total amount of fatty acids.

2.4. Oysters processing

2.4.1. Oysters biometry and condition index

Biometric analyses and condition indices calculations were carried out as detailed in Gasmi et al. (2017).

2.4.2. Oysters lipid-class contents in digestive gland and gonad+mantle

Digestive gland and gonad+mantle from 5 oysters were dissected and stored in pre-combusted glass vials at -80°C until the analysis. Both organs were then freeze-crushed in liquid nitrogen into a fine and homogeneous powder using a ball mill. Lipid extraction on about 200 mg of fresh tissue was processed in 6 mL of a chloroform:methanol solution (2:1; v:v). Samples were sonicated for 10 minutes and stored at least during 24h for lipid extraction. Then, 1 mL and 3 mL from each sample was transferred into separate glass vials for lipid class and fatty acid analyses, respectively. Samples were stored at -20°C until the analysis.

Lipid classes were separated and quantified using a high performance, thin-layer chromatography (HPTLC) on HPTLC glass plates (1010 mm) pre-coated with silica gel 60 from Merck (Darmstadt, Germany).

For neutral lipids (NL), classes were analysed as described by Haberkorn et al. (2010). A preliminary run was conducted to remove possible impurities using hexane:diethyl ether (97:3;v:v), and the plate was activated for 30 min at 120°C. Samples (5 and 20µl) were then spotted on the plates by the CAMAG automatic sampler (CAMAG, Switzerland). A double development with two distinct solvent systems allowed the separation of triglycerides from other NL classes. The first solvent system contained hexane:diethyl ether:acetic acid (20:5:0.5,v:v:v), whereas the second was composed of hexane:diethyl ether (97:3,v:v).

For polar lipids (PL), a preliminary run was conducted to remove possible impurities using methyl-acetate:iso-propanol:chloroform:methanol:KCl 0.25% (10:10:10:4:3.6; v:v:v:v:v), and the plate was activated for 30 min at 120°C. Samples (5 and 20µl) were then spotted on the plates by the CAMAG automatic sampler (CAMAG, Switzerland). PLs were separated using the above solvent system.

Neutral and polar lipids classes were revealed as black spots on the HPTLC plates after dipping in a cupric-sulfate, phosphoric-acid solution and heating for 20 min at 160°C. The plates were then read by scanning at 370 nm, and quantified using Wincats software (CAMAG, Switzerland). Six neutral lipid classes (free fatty acids, steryl esters, glyceryl ethers, triacylglycerols, fatty alcohols, and free sterols) and six polar lipid classes (phosphatidylinositol, phosphatidylserine, phosphatidylcholine, phosphatidylethanolamine and cardiolipid that migrate together) were identified based on Sigma-Aldrich standards (Sigma–Aldrich, France) and colouring techniques. Results were calculated as mg of each identified lipid class per g of analysed tissue wet weight, and then expressed as percentage of total NL or PL lipids.

2.4.3. Oyster fatty acids in digestive gland and gonad+mantle

Fatty acid analyses on oyster tissues were performed as described above for particulate organic matter. However, fatty acids in neutral (NL) and polar lipids (PL) were treated separately. NL and PL were separated on a silica gel micro-column according to Marty et al. (1992). The 3 mL sample with total lipid extract (conserved after oyster organ freeze-crushing and extraction, section 2.9) was evaporated to dryness under liquid nitrogen flux and resuspended in 500 µl of chloroform/methanol (98/2; v/v). The aliquot was placed on the top of 4cm silica micro-column (Silica 60A 63-200 µm (70-230 mesh)). The operation was repeated 3 times, a total volume of 1.5 mL was injected in the column. NL were eluted with 10 mL of chloroform/methanol (98/2;

v/v), and PL with 20 mL of methanol. As internal standard, an amount of 2.3µg of C23:0 was added in both NL and PL extracts.

Fatty acids in NL and PL were trans-esterified and analyzed using gas chromatography (VARIAN CP 3800) as described for particulate organic matter analyses (section 2.7).

2.4.4. Oysters histology

Oysters for histological monitoring of reproductive state and spawning were directly dissected, the adductor muscle and the gills were separated from the visceral mass (the gonad and the digestive gland). Histological examination was carried on 3-mm cross section from the visceral mass sampled at the anterior of the pericardial region as described in (Pouvreau et al. 2016). Sections were directly fixed in Bouin's solution and kept at 4°C for at least 48h (Howard & Smith 1983), then dehydrated in ascending ethanol solution and embedded in paraffin. Five micrometer sections were cut, mounted on glass slide, stained with Harris' hematoxylin–eosin Y (Martoja & Martoja-Pierson 1967) and coverslipped. Histological slides were examined under a LEICA DMIRB inverted microscope (Leica Microsystems) to examine gametogenetic stage according to Steele & Mulcahy (1999) classification. Six stages of gonad maturity were determined: 0 (undifferentiated), 1 (early development), 2 (late development), 3 (ripe), IV (partially spent), 4 (total spent) and 5 (post-spawning). Pictures of each stage were taken using a Retigua 2000R color camera and ImageJPro software.

2.5. Statistical analysis

To assess differences according to date and stations for environmental parameters and oyster condition index (suspendend matter, PON, POC, Chla and pheopigments) the parametric one-way ANOVA followed by Tukey’s HSD tests was used and if the condition of normality and homogeneity were not respected the non-parametric Kruskal-Wallis testing of variance was applied.

Similarity of percentages analysis (SIMPER) was used to identify the fatty acids that were the most discriminant between dates and stations.

Permutational Multivariate Analysis of Variance (PERMANOVA) were used to compare fatty acids compositions of oysters according to stations, date, organ and fraction.

Principal components analysis (PCA) was performed to investigate the variation in fatty acids profiles composition between dates and stations for neutral and polar lipids in both oyster digestive gland and gonad+mantle. Correlations between fatty acids were discussed only for for high loading (> 0.7). One way- ANOVA followed by Tukey's HSD tests of Kruskal-Wallis were performed on PCA scores of the proportional fatty acid profiles to determine spatial and temporal variability.

Spearman correlations were used to test relationships among phytoplankton groups or fatty acids.

Analyses were performed using R studio software (Version 1.0.136).

3. Results

3.1. Spatio-temporal variability in the water column trophic conditions

3.1.1. Suspended matter, PON and POC

Suspended matter (SM) was generally below 10 mg L^{-1}, although a slight increase was observed in March for both Comprian and Jacquets stations (19.65±1.2 mg L^{-1}; **Figure 25a**). Two other noticeable peaks were observed on April 28th and June 2nd. These increases were significantly different between stations, and higher at Comprian (one-way ANOVA, $p<0.05$) (59.7±4.9 mg L^{-1} and 37.5±10.7 mg L^{-1} for April and June, respectively) than at Jacquets (19.9±2.4 mg L^{-1} and 24.6±0.2 mg L^{-1} for April and June, respectively).

Particulate organic carbon and nitrogen (PON and POC) showed the same temporal patterns (**Figure 25 b & c**). In March, POC reached a mean value of 818±27.7 µg L^{-1} and PON reached a mean value of 100.4± 3.1 µg L^{-1}. As observed for SM, noticeable peaks were observed on April 28th, higher at Comprian (POC: 2072.6±158.9 µg L^{-1}, PON: 231.9±18.7 µg L^{-1} for PON) than at Jacquets (POC: 935.2±59.6, PON: 113.8±10.2; one-way ANOVA, $p<0.05$).

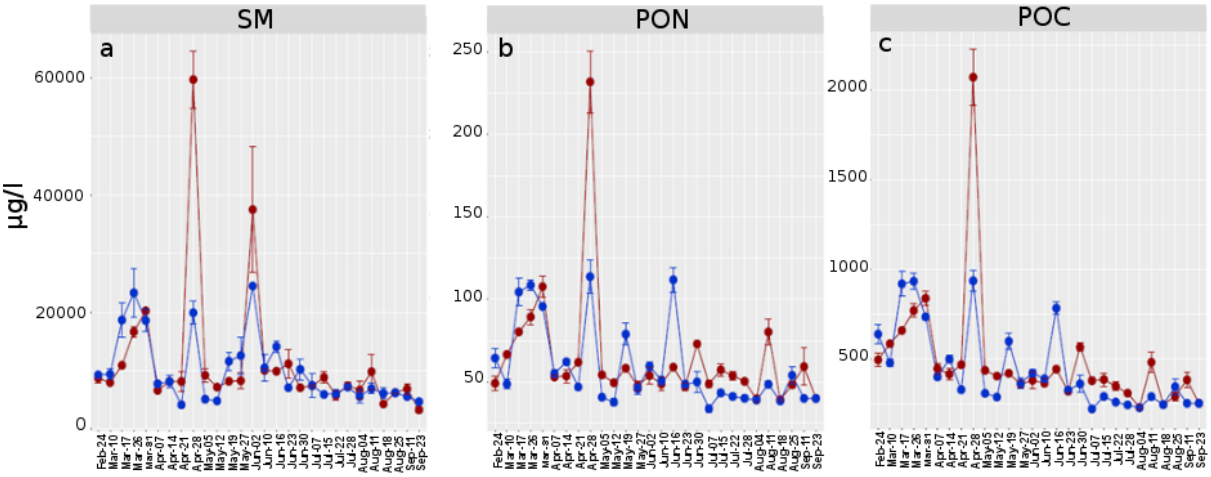

Figure 25: Seasonal variability (February 24th - September 23rd) of suspended matter (a), particulate organic nitrogen (b), and particulate organic carbon (c) for Comprian (red) and Jacquets (blue) stations. (means±SD).

3.1.2. Chl*a* and pheopigments

The main Chl*a* peak occurred at the end of March (7.8±1.3 µg L^{-1}), and was followed by four peaks, which were synchronized at both stations, on April 28th, May 19th, June 10th and July 22nd (**Figure 26 a**). Their concentrations ranged between 3.0±0.6 µg L^{-1} and 5.4±1.8 µg L^{-1}. Overall, no significant spatial differences were observed between stations (log-transformed ANOVA, p-value > 0.05). Phaeopigment (Phe*a*) concentrations were generally low (>2.5 µg L^{-1}), and showed two small peaks in March and April, concomitantly with the first two Chl*a* peaks (**Figure 26 b**).

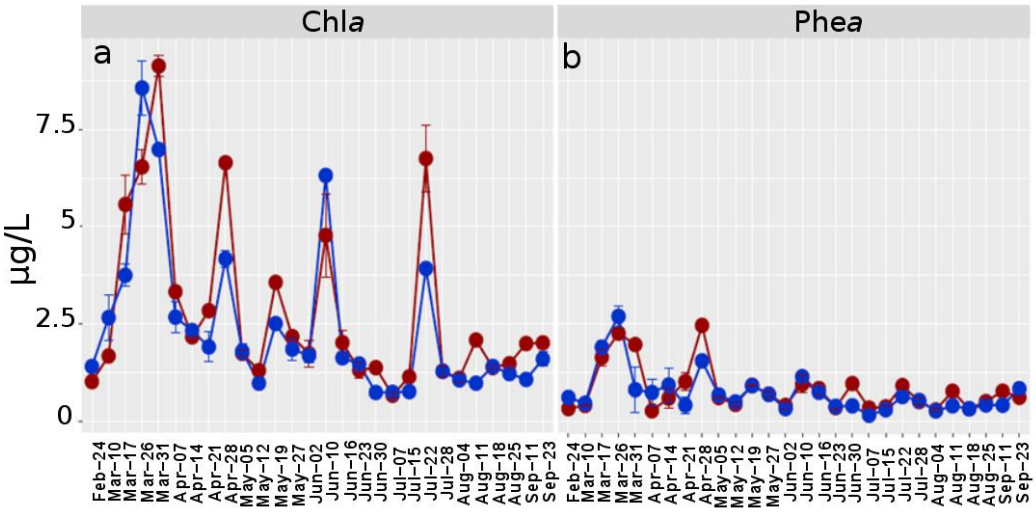

Figure 26: Seasonal variability (February 24th – September 23rd) of Chl*a* (a) and Pheopigment (ba) for Comprian (red) and Jacquets (blue) stations. (means±SD).

3.1.3. POC/Chla ratio

In general, the POC/Chl*a* ratio was below 300 at both sampling stations (**Figure 27**). The lowest values (≤ 100) were observed during the productive period in March and on May 19th, June 10th and July 22nd. The highest values (> 300) were reached between June 23rd and July 7th. Significant differences were observed between Comprian and Jacquets on June 16th and July 7th (one-way ANOVA, $p < 0.05$).

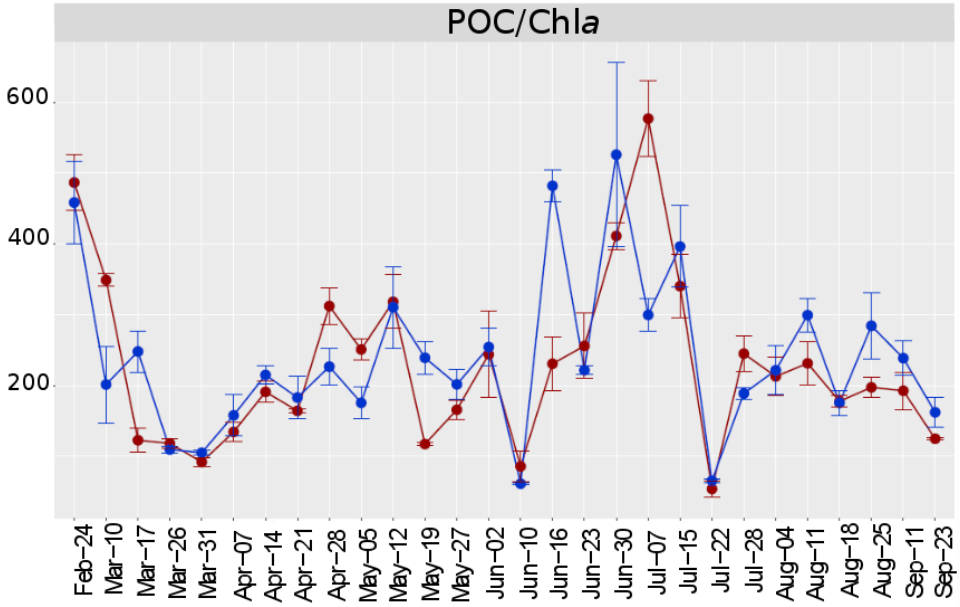

Figure 27: Seasonal variability (February 24th – September 23rd) of POC/Chla ratio for Comprian (red) and Jacquets (blue) stations. (means±SD).

3.1.4. Microphytoplankton

Over the monitoring period, the highest diatom concentrations were recorded in March with values reaching 2.6 x 10^6 and 1.5 x 10^6 cell L^{-1} for Comprian and Jacquets, respectively. Increase in dinoflagellates biomass was observed between late April and early June (**Figure 28a**). Noticeable differences of their contribution to microphytolankton biomass between stations were observed on April 28th (5 and 36% at Comprian and Jacquets, respectively). Dinfolagellates concentration reached 2.5 x 10^4 cell L^{-1} at Jacquets, while it reached 3 x 10^5 cell L^{-1} at Comprian (**Figure 28b**). The highest concentrations were recorded on May 19th (3.9 x 10^4 and 4 x 10^6 for Comprian and Jacquets, respectively). A noticeable decrease in dinfolagellates was observed at the end of May. In contrast, diatoms showed slight increases in June, July and September at both Comprian and Jacquets stations.

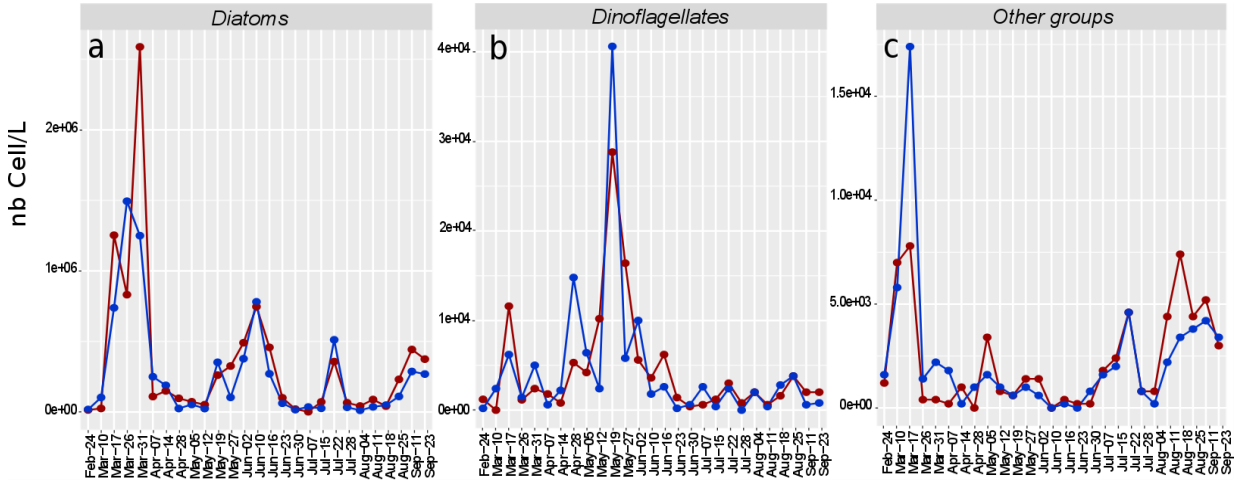

Figure 28 Seasonal variability (February 24th – September 23rd) of diatoms (a), dinoflagelates (b) and other groups of phytoplankton concentrations for Comprian (red) and Jacquets (blue) stations. (means±SD).

During the spring bloom, the dominant diatom populations were mostly composed of the species *Asterionellopsis glacialis*, which reached its maximum concentration on March 31st (2.4 x 10^6 cells L^{-1} and 1.26 x 10^6 cells L^{-1} at Comprian and Jacquets, respectively). This period was also characterized by the main presence of *Nitzschia longissima* and *Pseudonitzschia* spp. On April, diatoms concentrations decreased, only a small bloom was observed for the species *Rhizosolenia imbricata* (~ 7000 cells L^{-1}) at both stations. On June 10th, diatom concentrations increased mainly becauce of both *Chaetoceros spp.* (~ 5 x 10^5 cells L^{-1}) and *Leptocylindrus spp.* (~ 1.7 10^5 cells L^{-1}). On July 22nd, *Leptocylindrus spp.* showed a second increase associated to a great increase of the diatom *Lithodesmium undulatum* (2 x 10^5 and 3 x 10^5 cells L^{-1} at Comprian and Jacquets, respectively) (**Figure 29**).

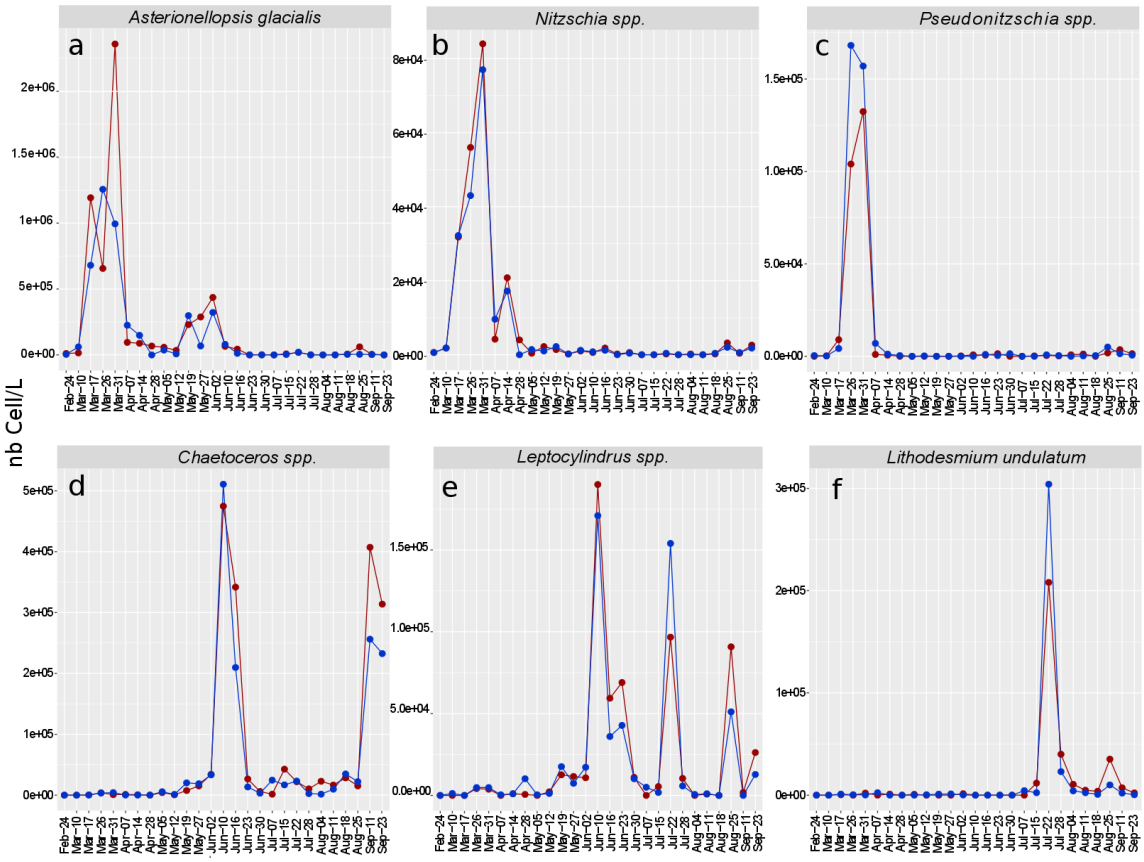

Figure 29 Seasonal variability (February 24th – September 23rd) of the principal diatoms species for Comprian (red) and Jacquets (Blue) stations. (means±SD).

The increase of dinoflagellates biomass between late April and early June was mainly linked to *Neocentrum spp.* (> 9 x 10^3 cells L^{-1}) and *Prorocentrum spp.* (8.2 x 10^3 and 1.4 x 10^4 cells L^{-1} at Comprian and Jacquets, respectively) **Figure 30**).

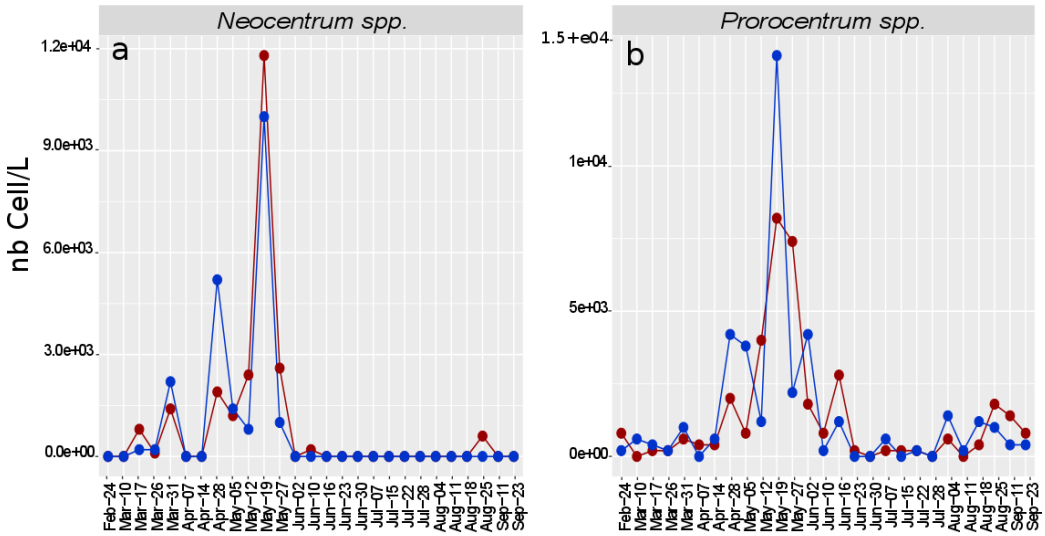

Figure 30 Seasonal variability (February 24th – September 23rd) of the principal dinoflagellates species for Comprian (red) and Jacquets (Blue) stations. (means±SD).

3.1.4. Prokaryotes and pico-nanoeukaryotes

Flow cytometry results showed the dominance of picoeukaryotes, their concentrations ranged between 5.9 x 10^6 and 5.5 x 10^7 cells L^{-1} at Comprian and between 6.6 x 10^6 and 7.7 x 10^7 cells L^{-1} at Jacquets (**Figure 31a**). Lowest concentrations were recorded in March and on April 28th at both stations. Highest concentrations were observed at Jacquets on April 7th, May 5th, May 12th and July 22nd. Nanoeukaryotes concentrations ranged between 8.3 x 10^5 and 4.9 x 10^6 at Comprian and between 6.2 x 10^5 and 4.72 x 10^6 at Jacquets (**Figure 31b**). Highest concentrations were reached between March 26th and 31st, on April 28th and on June 10th at both stations. Nanoeukaryotes and picoeukaryotes showed different temporal patterns. Both groups were negatively correlated (Spearman correlation, r= -0.5, p-value<0.001). Similarly to the spatial pattern observed for picoeukaryotes, highest concentrations of Cryptophceae were observed at Jacquets during the spring and early summer periods. Values ranged between 0 and 2.4 x 10^5 cells L^{-1} (**Figure 31c**).

Total bacteria showed high temporal variability without clear patterns at both Comprian and Jacquets stations. Several successive peaks were observed over the sampled period. Concentrations ranged between 6.7 x 10^2 cells L^{-1} and 2.44x 10^3 cells L^{-1} (**Figure 31d**).

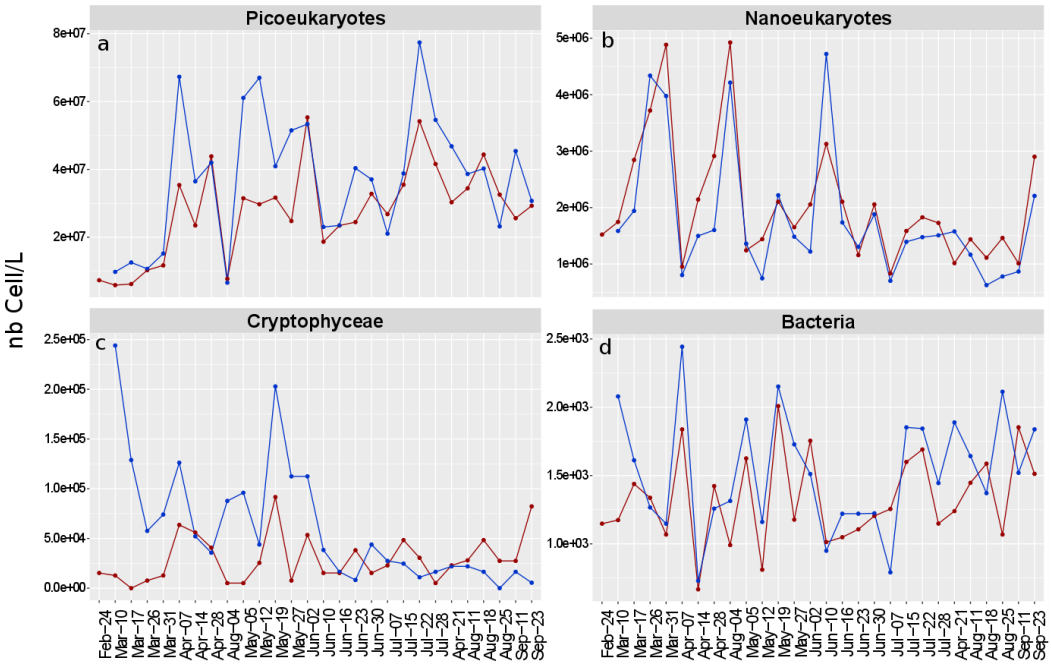

Figure 31 Seasonal varibility in cytometric groups: (a) Picoeukaryotes, (b) nanoeukaryotes, (c) Cryptophycea, (d) Bacteria for Comprian (red) and Jacquets (blue). (means±SD).

3.1.5. Fatty acids

Saturated fatty acids (SFAs) were the dominant functional group over the sampled period, they accounted for more than 30 % of total fatty acids in both Comprian and Jacquets. Lowest percentages (30-41%) were observed between February and May except in May 5th were SFA reached 68% at Jacquets. Highest SFA percentages (>50%) were recorded in summer and particulary at Comprian (>65%) **(Figure 32a)**. In contrast, highest percentages of monounsaturated fatty acids (MUFA) (23-25%) were observed during spring and lowest values (14-19%) in early summer **(Figure 32b)**. Polyunsaturated fatty acids (PUFAs) proportions ranged between 11% and 27% **(Figure 32c)**. Noticeable differences between stations were observed in May (20.5±4.3% and 13.6±5.1% at Comprian and Jacquets, respectively) and August (19.5±6.1% and 12.3±3.6% at Comprian and Jacquets, respectively). Branched fatty acids (BFA) group showed the weakest proportions with values ranging between 2 and 3 % **(Figure 32d).**

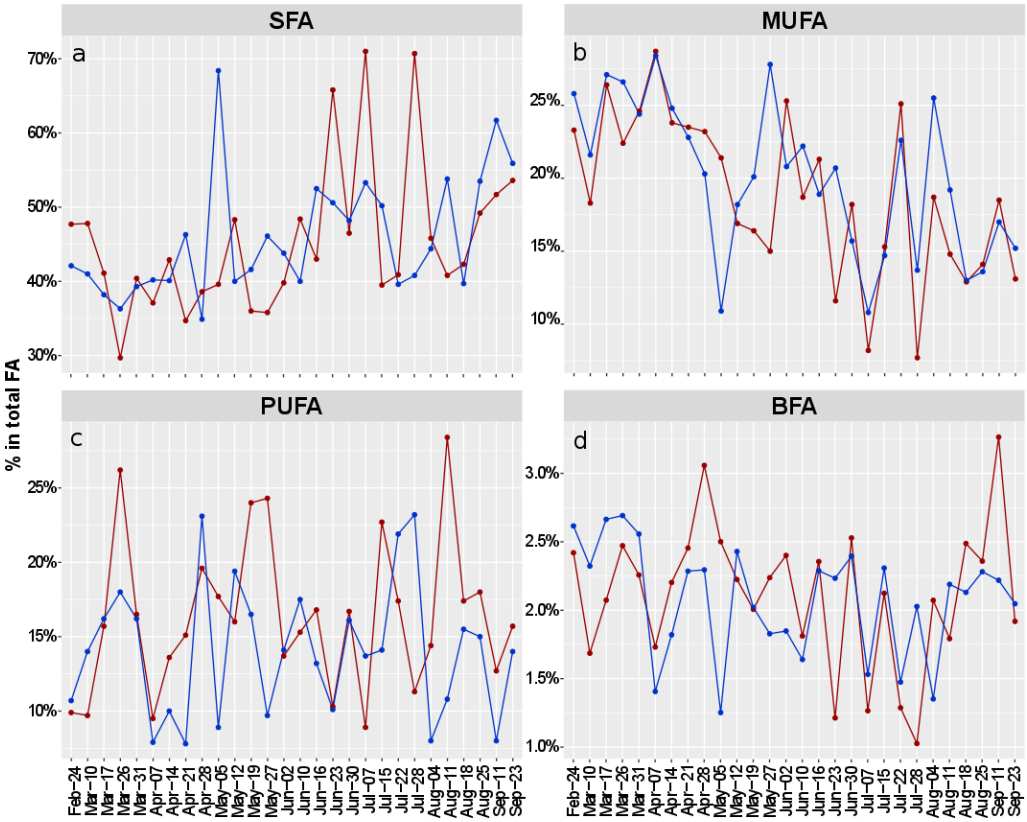

Figure 32 Seasonal variability in fatty acids groups of suspended particulate matter: (a) saturated, (b) monounsaturated (c) polyunsaturated, and (d) branched fatty acids for Comprian (red) and Jacquets (blue) stations. (means±SD).

Most influential fatty acids which generated significant monthly dissimilarity in SPOM composition were identified by One-way SIMPER analysis **(Erreur ! Source du renvoi introuvable.)**. High contribution to the dissimilarity was attributed to the 18:0 FA. The MUFAs 16:1n-7, 18:1n-9 and the PUFA 20:5n-3 contributed each between 10 and 12% of the dissimilarity between March and April. Between April and June, C18 FAs (18:0 and 18:1n-9) and the PUFA 22:6n-3 were the most influential FAs, explaining 35% of the dissimilarity. In summer, 16:0, 16:1n-7 and 20:5n-3 were the most influential FAs. Dissimilarities between Comprian and Jacquets were attributed mainly to 18:0, 16:1n-7, 20:5n-3, 18:1n-9 and 16:0.

Seasonal variation of most influential FAs is shown in **Figure 33**.

Table 3 Cumulative contribution of most influential fatty acids in suspended particulate matter (One-way SIMPER Analysis)

Cumulative contribution of most influential fatty acids in POM (One-Way SIMPER Analysis)										
Temporal dissimilarities										
March - April	16:1n-7	18:1n-9	20:5n-3	18:0	16:0	14:0	18:2n-6	22:6n-3	18:4n-3	16:4n-1
	12%	22%	32%	40%	47%	54%	61%	65%	68%	71%
April - May	18:0	18:1n-9	22:6n-3	16:1n-7	20:5n-3	18:2n-6	16:0	14:0	18:5n-3	
	13%	24%	35%	43%	51%	57%	63%	68%	73%	
May - June	18:0	22:6n-3	18:1n-9	16:0	14:0	20:5n-3	18:5n-3	14:0	16:1n-9	18:1n-7
	18%	28%	37%	43%	49%	55%	60%	65%	70%	73%
June - July	18:0	16:1n-7	20:5n-3	16:0	14:0	18:1n-9	16:1n-9	22:6n-3	18:2n-6	18:4n-3
	20%	31%	40%	47%	54%	59%	64%	67%	70%	72%
July - Aug	18:0	20:5n-3	16:1n-7	18:1n-9	16:0	14:0	22:6n-3	18:4n-3	18:5n-3	
	20%	29%	37%	45%	53%	59%	64%	68%	72%	
Aug - Sept	18:0	20:5n-3	16:0	18:1n-9	22:6n-3	18:4n-3	18:3n-3	18:5n-3	16:1n-7	18:2n-6
	20%	28%	36%	44%	51%	57%	61%	67%	69%	73%
Spatial dissimilarity										
Comprian - Jacquets	18:0	16:1n-7	20:5n-3	18:1n-9	16:0	22:6n-3	14:0	18:2n-6	18:5n-3	18:4n-3
	16%	26%	34%	42%	50%	56%	62%	66%	69%	72%

The highest proportions of EFAs in SPOM were recorded for 20:5n-3 and 22:6n-3 which reached values around 15% of the total fatty acids. In general, highest values for both fatty acids were recorded monthly at Comprian. The 20:4n-6 values ranged between 0.3 and 1%.

Proportions of total n-3 PUFAs ranged between 13 and 41% while n-6 PUFAs proportions ranged between 3 and 15%. Noticeable spatial difference was observed in May between 34±6.9% and 22.7±8.2% at Comprian and Jacquets, respectively) and July (22.3±9.2 and 29.5±4.3%, at Comprian and Jacquets, respectively). The ratio of n-3/n-6 reached its highest value of 8±2.3% at Jacquets in May, when Comprian exhibited very low value of 3.9±1%. The highest value of 7.48±1.5% was recorded at Comprian in August.

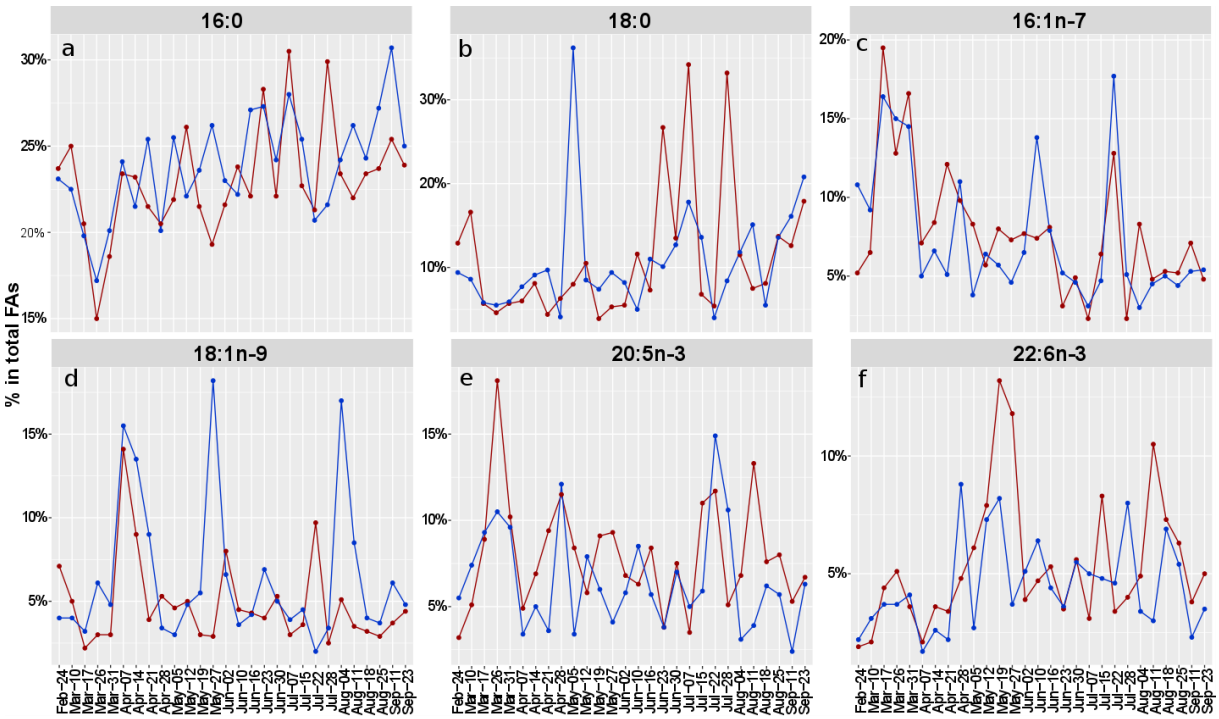

Figure 33 Seasonal variability of most influential fatty acids as revealed by one-way SIMPER analysis for Comprian (red) and Jacquets (blue) stations (means±SD).

Suspended matter fatty acids seasonal variability is detailed in **Table** .

3.2. Spatio-temporal variability in oyster condition and reproductive behavior

3.2.1. Lawrence and Scott condition index LS_{CI}

During the survey, LS_{CI} mean values ranged between 2.95±0.2 and 7.33±0.6 (**Figure 34**). The two sites displayed the same general trend for this index, progressively increasing until April-May, before a marked decrease in July, followed by a relative temporal stability. The highest mean values (>6) were recorded on April 28th and on July 07that Jacquets and on June 10th at Comprian. At each date, no significant spatial differences were observed between sites (Kruskal-wallis, $p < 0.05$).

Table 4 Fatty acids profiles (mean % of total fatty acids ± standard deviation) of suspended particulate matter collected from two stations between February and September; (n) denotes number of date sampled per month.

Month	**February**		**March**		**April**		**May**		**June**		**July**		**August**		**September**	
Site (n)	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**
	n = 1	*n = 1*	*n = 4*	*n=4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 4*	*n = 2*	*n = 2*
Fatty acids (%)																
iso 15:0	1.0 -	1.0 -	0.7 ± 0.2	0.9 ± 0.1	0.9 ± 0.2	0.7 ± 0.2	0.9 ± 0.0	0.7 ± 0.3	0.8 ± 0.2	0.7 ± 0.2	0.4 ± 0.1	0.7 ±0.2	0.8 ± 0.2	0.7 ± 0.2	1.0 ± 0.3	0.9 ± 0.0
*ai*15:0	0.7 -	0.8 -	0.4 ± 0.1	0.6 ± 0.1	0.7 ± 0.2	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.1	0.3 ± 0.1	0.4 ±0.2	0.5 ± 0.1	0.4 ± 0.2	0.6 ± 0.2	0.6 ± 0.1
iso 17:0	0.8 -	0.8 -	1.0 ± 0.2	1.0 ± 0.2	0.8 ± 0.2	0.6 ± 0.2	0.8 ± 0.2	0.6 ± 0.1	0.8 ± 0.2	0.7 ± 0.1	0.6 ± 0.3	0.7 ±0.1	0.9 ± 0.2	0.8 ± 0.3	0.9 ± 0.5	0.6 ± 0.1
∑ mean BFA	**2.4 -**	**2.6**	**2.1 ± 0.3**	**2.6 ± 0.2**	**2.4 ± 0.3**	**1.9 ± 0.4**	**2.2 ± 0.3**	**1.9 ± 0.5**	**2.1 ± 0.3**	**2.1 ± 0.3**	**1.4 ± 0.3**	**1.8 ±0.4**	**2.2 ± 0.3**	**2.0 ± 0.4**	**2.6 ± 0.3**	**2.1 ± 0.1**
14:0	4.4 -	4.3 -	8.6 ± 4.6	8.3 ± 2.2	5.4 ± 1.2	5.4 ± 1.3	6.3 ± 1.1	5.5 ± 1.8	6.0 ± 1.6	7.4 ± 1.8	6.2 ± 3.9	7.3 ±3.4	6.9 ± 0.2	6.5 ± 0.8	8.0 ± 1.4	6.6 ± 1.5
15:0	1.8 -	1.4 -	0.9 ± 0.2	1.1 ± 0.2	1.2 ± 0.2	1.3 ± 0.5	1.1 ± 0.4	1.1 ± 0.1	1.5 ± 0.3	1.7 ± 0.5	0.9 ± 0.2	1.1 ±0.3	1.2 ± 0.2	1.2 ± 0.5	1.3 ± 0.1	1.6 ± 0.6
16:0	23.7 -	23.1 -	19.8 ± 4.2	19.9 ± 2.2	22.1 ± 1.4	22.8 ± 2.4	22.2 ± 2.8	24.3 ± 1.9	23.6 ± 2.8	24.8 ± 2.3	26.1 ± 4.8	23.9 ±3.4	23.1 ± 0.8	25.5 ± 1.5	24.6 ± 1.1	27.8 ± 4.0
17:0	0.8 -	0.6 -	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.2	0.6 ± 0.1	0.8 ± 0.1	0.8 ± 0.3	0.7 ± 0.3	0.7 ±0.3	0.9 ± 0.1	0.7 ± 0.4	0.8 ± 0.0	1.0 ± 0.4
18:0	12.9 -	9.4 -	8.1 ± 5.7	6.4 ± 1.4	6.2 ± 1.5	7.6 ± 2.5	6.9 ± 2.9	15.4 ± 13.9	12.9 ± 8.3	9.4 ± 2.9	19.9 ± 16.0	10.9 ±6.0	10.2 ± 2.9	11.5 ± 4.2	15.2 ± 3.7	18.4 ± 3.3
20:0	1.0 -	0.8 -	0.6 ± 0.1	0.7 ± 0.2	1.0 ± 0.3	0.9 ± 0.3	1.0 ± 0.4	0.8 ± 0.2	1.1 ± 0.2	0.9 ± 0.2	0.7 ± 0.1	0.7 ±0.2	0.7 ± 0.1	0.7 ± 0.3	0.9 ± 0.1	1.1 ± 0.3
22:0	1.3 -	1.0 -	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.2	0.5 ± 0.3	0.9 ± 0.2	0.8 ± 0.3	0.3 ± 0.1	0.5 ±0.2	0.6 ± 0.1	0.7 ± 0.5	0.6 ± 0.1	0.8 ± 0.2
24:0	1.8 -	1.5 -	0.8 ± 0.1	1.0 ± 0.1	1.2 ± 0.4	1.0 ± 0.2	1.1 ± 0.4	0.8 ± 0.3	1.9 ± 0.5	1.4 ± 0.6	0.6 ± 0.1	0.8 ±0.3	0.8 ± 0.1	0.9 ± 0.4	1.0 ± 0.0	1.2 ± 0.4
∑ mean SFA	**47.7 -**	**42.1 -**	**39.7 ± 7.5**	**38.7 ± 2.0**	**38.3 ± 3.4**	**40.4 ± 4.7**	**39.9 ± 5.9**	**49.0 ± 13.2**	**48.7 ± 10.1**	**47.0 ± 5.1**	**55.5 ± 17.7**	**46.0 ±6.8**	**44.5 ± 3.8**	**47.8 ± 7.0**	**52.6 ± 1.3**	**58.8 ± 4.1**
16:1n-9	3.8 -	2.1 -	0.7 ± 0.2	1.0 ± 0.5	2.1 ± 0.5	2.3 ± 1.4	1.4 ± 0.6	1.1 ± 0.4	3.1 ± 1.4	2.3 ± 1.7	0.8 ± 0.1	1.0 ±0.3	1.5 ± 0.7	1.6 ± 1.0	1.5 ± 0.6	1.8 ± 1.0
16:1n-7	5.2 -	10.8 -	13.8 ± 5.6	13.8 ± 3.2	9.3 ± 2.1	6.9 ± 2.8	7.3 ± 1.2	5.1 ± 1.2	6.2 ± 2.2	7.6 ± 3.7	5.9 ± 5.0	7.6 ±6.8	5.9 ± 1.6	4.2 ± 0.9	5.9 ± 1.6	5.3 ± 0.1
18:1n-9	7.1 -	4.0 -	3.3 ± 1.2	4.5 ± 1.2	8.1 ± 4.6	10.3 ± 5.4	3.9 ± 1.1	7.9 ± 7.0	5.2 ± 1.6	5.2 ± 1.5	4.7 ± 3.4	3.4 ±1.1	3.7 ± 1.0	8.3 ± 6.2	4.0 ± 0.5	5.4 ± 0.9
18:1n-7	2.7 -	4.7 -	2.7 ± 1.0	3.6 ± 1.1	3.5 ± 0.7	3.1 ± 0.5	3.5 ± 0.9	3.3 ± 0.9	2.5 ± 1.0	2.7 ± 0.5	2.0 ± 1.1	2.3 ±0.6	2.9 ± 1.0	3.0 ± 0.9	3.3 ± 1.8	2.7 ± 0.5
20:1n-9	2.2 -	1.2 -	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.5 ± 0.2	0.4 ± 0.2	0.7 ± 1.0	1.3 ± 0.9	1.1 ± 0.6	0.2 ± 0.1	0.3 ±0.1	0.4 ± 0.3	0.2 ± 0.1	0.3 ± 0.0	0.3 ± 0.1
22:1n-9	2.3 -	3.0 -	2.0 ± 0.9	1.7 ± 0.5	1.3 ± 0.4	1.0 ± 0.8	0.8 ± 0.5	1.0 ± 0.6	0.6 ± 0.2	0.7 ± 0.3	0.3 ± 0.1	0.7 ±0.4	0.8 ± 0.5	0.5 ± 0.2	0.8 ± 0.2	0.4 ± 0.1
∑ mean MUFA	**23.3 -**	**25.8 -**	**22.9 ± 3.5**	**24.9 ± 2.5**	**24.8 ± 2.6**	**24.08 ± 3.4**	**17.4 ± 2.8**	**19.2 ± 6.9**	**19.0 ± 5.0**	**19.7 ± 2.5**	**14.1 ± 8.1**	**15.4 ±5.0**	**15.1 ± 2.5**	**17.8 ± 5.8**	**15.8 ± 3.8**	**16.1 ± 1.3**
16:2n-4	0.4 -	0.9 -	2.2 ± 1.3	2.0 ± 0.9	1.1 ± 0.5	0.7 ± 0.5	0.9 ± 0.2	0.5 ± 0.2	1.0 ± 0.5	1.0 ± 0.5	0.9 ± 1.0	1.0 ±0.7	0.8 ± 0.2	0.5 ± 0.2	1.0 ± 0.1	0.5 ± 0.0
16:3n-3	0.5 -	0.6 -	0.9 ± 0.2	0.9 ± 0.2	0.6 ± 0.2	0.5 ± 0.2	0.7 ± 0.2	0.4 ± 0.2	0.8 ± 0.4	0.6 ± 0.2	0.5 ± 0.3	0.6 ±0.1	0.6 ± 0.2	0.5 ± 0.2	0.5 ± 0.0	0.3 ± 0.2
16:4n-3	2.8 -	1.5 -	1.0 ± 0.5	1.0 ± 0.4	1.9 ± 1.0	2.0 ± 1.2	2.1 ± 0.3	2.0 ± 0.7	2.1 ± 0.9	1.9 ± 0.6	1.2 ± 0.6	1.8 ±0.7	2.1 ± 0.7	2.5 ± 0.9	1.6 ± 0.1	2.0 ± 0.6
16:4n-1	0.5 -	1.0 -	2.8 ± 1.7	2.5 ± 0.6	1.5 ± 0.8	1.2 ± 1.0	1.2 ± 0.3	0.7 ± 0.2	1.1 ± 0.6	1.0 ± 0.5	1.1 ± 0.8	0.8 ±0.7	0.8 ± 0.2	0.5 ± 0.2	0.7 ± 0.1	0.4 ± 0.2
18:2n-6	2.4 -	1.9 -	2.1 ± 1.1	2.0 ± 0.4	4.4 ± 3.0	6.5 ± 4.7	2.1 ± 0.4	2.8 ± 1.4	1.9 ± 0.4	2.6 ± 1.0	2.4 ± 1.5	2.7 ±0.9	1.7 ± 0.3	3.3 ± 1.9	2.4 ± 1.3	2.6 ± 0.8
18:3n-6	0.2 -	0.1 -	0.2 ± 0.1	0.4 ± 0.2	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.4	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ±0.1	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
18:3n-3	2.4 -	3.5 -	1.8 ± 1.7	1.7 ± 1.2	2.3 ± 1.2	2.3 ± 1.0	2.0 ± 0.3	1.6 ± 0.4	1.9 ± 0.3	2.2 ± 0.5	2.0 ± 1.1	2.8 ±1.4	2.8 ± 1.0	3.5 ± 2.3	1.8 ± 0.1	1.2 ± 0.4
18:4n-6	1.2 -	1.0 -	0.8 ± 0.5	0.8 ± 0.5	1.2 ± 0.3	1.1 ± 0.9	0.7 ± 0.4	1.0 ± 0.6	1.3 ± 0.7	1.1 ± 0.4	0.8 ± 0.3	1.0 ±0.6	0.9 ± 0.2	0.9 ± 0.1	1.4 ± 0.2	1.7 ± 1.3
18:4n-3	3.8 -	5.8 -	4.2 ± 1.4	4.4 ± 1.4	3.9 ± 1.5	3.5 ± 0.3	4.4 ± 0.9	3.4 ± 1.3	3.3 ± 0.8	3.7 ± 0.7	3.2 ± 1.4	4.7 ±0.9	5.4 ± 1.2	4.9 ± 2.1	3.1 ± 0.1	1.9 ± 1.1
18:5n-3	2.6 -	2.5 -	2.0 ± 0.7	2.0 ± 0.6	2.8 ± 0.9	3.1 ± 1.6	5.6 ± 1.7	3.4 ± 1.3	2.1 ± 0.6	2.6 ± 0.7	1.6 ± 0.9	2.6 ±1.0	3.3 ± 1.5	3.2 ± 1.6	1.9 ± 0.2	1.0 ± 0.5
20:2n-6	0.6 -	0.1 -	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.4	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ±0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
20:3n-6	0.2 -	0.0 -	0.0 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.0 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.1	0.2 ±0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
20:3n-3	1.4 -	0.6 -	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.7 ± 0.2	0.6 ± 0.3	0.4 ± 0.2	1.2 ±0.8	0.7 ± 0.3	07 ± 0.5	1.0 ± 0.6	1.4 ± 0.4
20:4n-6	0.1 -	0.3 -	0.4 ± 0.1	0.5 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	0.5 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.2	0.6 ±0.2	0.8 ± 0.4	0.5 ± 0.2	0.5 ± 0.1	0.4 ± 0.2
20:4n-3	0.7 -	0.5 -	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.7 ± 0.2	0.6 ± 0.2	0.4 ± 0.1	0.5 ±0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.6 ± 0.4
20:5n-3	3.2 -	5.5 -	10.6 ± 5.5	9.2 ± 1.3	8.2 ± 2.9	6.0 ± 4.1	8.1 ± 1.6	5.3 ± 2.0	6.6 ± 1.7	6.2 ± 1.7	7.8 ± 4.1	9.1 ±4.6	8.9 ± 3.0	4.7 ± 1.5	6.0 ± 1.0	4.3 ± 2.8
22:2n-6	1.2 -	0.9 -	0.6 ± 0.1	1.0 ± 0.4	0.5 ± 0.2	0.4 ± 0.2	0.5 ± 0.3	0.5 ± 0.3	0.6 ± 0.2	0.5 ± 0.3	0.3 ± 0.1	0.4 ±0.3	0.3 ± 0.2	0.3 ± 0.4	1.0 ± 0.8	0.3 ± 0.8
22:2n-5	0.4 -	0.3 -	0.3 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.4 ± 0.3	0.5 ± 0.2	0.4 ± 0.1	0.1 ± 0.1	0.2 ±0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.0	0.3 ± 0.8
22:5n-3	0.2 -	0.2 -	0.2 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.4 ± 0.2	0.4 ±0.1	0.6 ± 0.3	0.7 ± 0.5	0.4 ± 0.0	0.4 ± 0.8
22:6n-3	1.9 -	2.2 -	3.8 ± 1.3	3.6 ± 0.4	3.5 ± 1.1	3.8 ± 3.3	9.7 ± 3.3	5.5 ± 2.7	4.6 ± 0.9	5.0 ± 1.1	4.7 ± 2.4	5.6 ±1.6	7.2 ± 2.4	4.7 ± 1.8	4.4 ± 0.8	2.9 ± 0.8
∑ mean PUFA	**9.9 -**	**10.7 -**	**17.0 ± 6.8**	**16.1 ± 1.6**	**14.4 ± 4.2**	**12.2 ± 7.3**	**20.5 ± 4.3**	**13.6 ± 5.1**	**14.6 ± 2.7**	**14.2 ± 2.8**	**15.1 ± 6.2**	**18.2 ±5.0**	**19.5 ± 6.1**	**12.3 ± 3.6**	**14.2 ± 2.1**	**11.0 ± 4.2**
Trophic indices																
∑ n-3	19.3 -	22.9 -	25.3 ± 5.6	24.1 ± 1.6	24.3 ± 5.3	22.4 ± 8.2	34.0 ± 6.9	22.7 ± 8.2	23.1 ± 3.5	23.9 ± 3.7	22.3 ± 9.2	29.5 ±4.3	32.2 ± 5.3	25.9 ± 9.2	21.3 ± 1.3	16.2 ± 5.3
∑ n-6	6.3 -	4.7 -	4.9 ± 1.3	5.1 ± 0.7	7.5 ± 2.7	9.2 ± 4.7	4.3 ± 0.4	5.8 ± 1.4	5.0 ± 1.1	5.3 ± 1.3	4.5 ± 1.6	5.3 ±1.7	4.35 ± 0.3	5.4 ± 1.3	5.9 ± 2.3	5.8 ± 0.0
n-3/n-6	3.1 -	4.9 -	5.4 ± 1.5	4.8 ± 0.6	3.7 ± 1.9	3.6 ± 3.6	8.0 ± 2.3	3.9 ± 1.0	4.7 ± 0.7	4.6 ± 1.1	5.0 ± 1.3	6.0 ±2.1	7.48 ± 1.5	5.1 ± 2.3	3.8 ± 1.3	2.9 ± 0.9
18:1n-9/18:1n-7	2.6 -	0.9 -	1.3 ± 0.4	1.4 ± 0.7	2.4 ± 1.4	3.5 ± 2.1	1.1 ± 0.4	2.3 ± 1.8	2.2 ± 0.6	2.0 ± 0.5	2.8 ± 2.5	1.5 ±0.3	1.49 ± 0.9	3.3 ± 3.4	1.5 ± 1.0	2.1 ± 0.7
20:5n-3/22:6n-3	1.8 -	0.9 -	2.7 ± 0.7	1.4 ± 0.2	2.4 ± 0.3	3.5 ± 0.3	0.9 ± 0.3	2.3 ± 0.2	1.4 ± 0.3	2.0 ± 0.1	1.8 ± 1.1	1.5 ±1.0	1.24 ± 0.1	3.3 ± 0.2	1.4 ± 0.0	2.1 ± 0.5
16:4n-3+18:3n-3/∑ n-3	0.3 -	0.2 -	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.2 ±0.1	0.15 ±0.0	0.2 ±0.1	0.2 ±0.0	0.2 ±0.1

BFA – Branched fatty acids, SFA – saturated fatty acids, MUFA – monounsaturated fatty acids, PUFA – polyunsaturated fatty acids. The prefix *ai* denotes branched fatty acids from the anteiso series

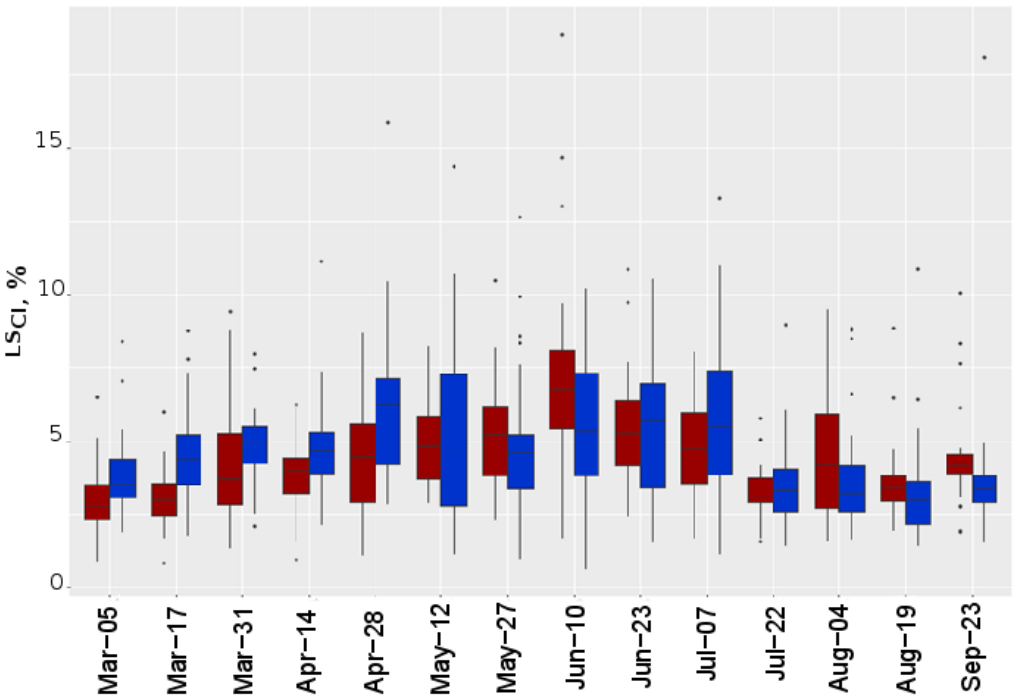

Figure 34 Seasonal variability of *C. gigas* condition index LS_{CI} for Comprian (red) and Jaquets (blue) stations. Boxplots show median, interquartile ranges (boxes), and ranges (vertical lines). Black dots represent the outliers data.

3.2.2. Gonadal development and spawning

Histological monitoring of *C. gigas* gonad germ cell from March to August allowed the identification of 6 stages of development. Overall, individuals from Comprian and Jacquets were at each date at the same gametogenic stage. Early gonad development (stage 1) was observed from March 17th to 31st. Late gonad development (stage 2) was observed from April 14th to 28th. At this period, some individuals contained ripe gametes (stage 3). Partial spawning phase (stage 4) started on early May. However, from May 28th until July 07th most of individuals were at stage 3. On July 22nd and August 4th total spawning (stage 5) was observed at Jacquets for all individuals while some individuals had spawned partially at Comprian. At both station, post-spawning (stage 6) was observed on the 19th August.

3.2.3. Neutral and polar lipids classes in digestive gland and gonad+mantle

Neutral and polar lipid classes showed significant differences as function of sampling date, stations and organ (PERMANOVA, $p < 0.05$). The NL proportion in *C. gigas* digestive glands ranged between 17±9% and 47±0.5% **(Figure 35a)**. From March to early June, NL proportions increased at Comprian from 20±3% to 37±4%. They were higher at Jacquets as compared to

Comprian from March 05th to May 12th (39±6% and 45±4%, respectively). On May 27th, NL values decreased noticeably at Jacquets reaching 17±9%. On July 22nd, after gametes release, oysters at Jacquets exhibited high NL proportion (40±3%), while oysters at Comprian exhibited low NL proportion (19±1%). This pattern was contrasted in August and September, were highest NL class proportions were observed in Comprian than Jacquets.

The NL class proportions in *C. gigas* gonad+mantle were assessed only in female *C. gigas,* since very low NL proportions were measured in males. NL values ranged between 17±2% and 57±2% **(Figure 35b)**. They increased at Comprian from 19±1% to 51±4% between March 5th and May 12th, while meantime NL proportions were higher at Jacquets than Comprian from March 5th till April 28th (between 29±5% and 57±10%). A first decrease was observed at Comprian between June 10th and 23rd (27±7%). After gametes release, on July 22nd, NL mean values decreased at both stations, with NL mean percentages falling to 24±3% and 34±2% at Comprian and Jacquets, respectively. From August to September, NL proportions were high at Comprian (29±7% to 44±4%), while at Jacquets NL values showed stable proportions (±30%) as compared to Comprian.

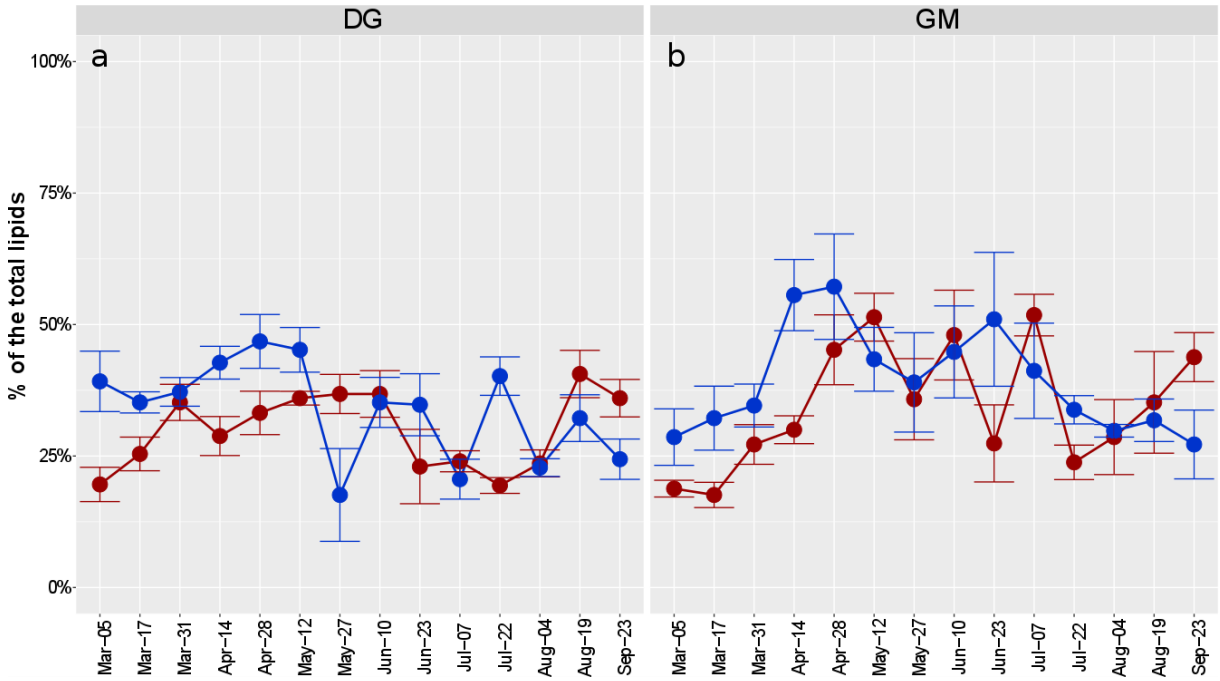

Figure 35 Seasonal variability of neutral lipids in *C. gigas* digestive gland (a), and gonad+mantle (b) for Comprian (red) and (Jacquets). (means±SE).

Neutral lipids class composition

Neutral lipid class composition showed significant differences as function of sampling date, station and organ (PERMANOVA, $p < 0.05$). In *C. gigas* digestive gland, triacylglycerol (TAG) constituted the major component over the sampling period **(Figure 36A)**. The proportion of TAG increased at Comprian from 17±7% to 56±2% between March 05th and April 28th. During the same period, TAG values were more stable at Jacquets, they ranged from 57±9% to 65±2%. The first decrease was observed on May 27th, down to 21±5% at Comprian and to 28±4% at Jacquets. On July 22nd, after gametes release, the proportion of TAG was higher at Jacquets as compared to Comprian (52±2% and 26±5%, respectively). In contrast, on September 23rd, oysters at Comprian exhibited higher TAG values (46±2% and 25±8% for Comprian and Jacquets, respectively). The sterol ester (SE) and the glyceryl ether (GE) proportions were in general lower than 10%. The highest proportions of SE were recorded in March 17th at Jacquets and July 7th at Comprian (16±2% and 19±7%, respectively). The highest proportions of GE were recorded on July 22nd at Jacquets and August 19th at Comprian (15±3% and 18±6%, respectively). The proportion of free fatty acids (FFA) was highly variable and ranged from 0.3±0.2% to 47±9%. Noticeable increases were observed in May and June at both Comprian and Jacquets stations. The proportion of free sterols (FS) ranged from 13±2% to 51±8%. Highest values were recorded at Comprian as compared to Jacquets particulary in March 05th and August 04th.

In female *C. gigas* gonad+mantle, TAG was also the major NL class over the sampled period. The proportion of TAG ranged from 9±1% to 65±4% at Comprian and from 30±12% to 69±4 at Jacquets between March 05th and April 14th **(Figure 36B)**. Several decreases and increases were observed in TAG proportions at both stations between April and June. After gametes release, TAG proportions dropped to 29±4% at Comprian and to 34±5% at Jacquets. Higher TAG proportion was recorded in September 23rd at Comprian (54±4%) as compared to Jacquets (19±8%). SE and GE did not display a clear temporal patterns, their proportions ranged between 4% and 23%. FFA showed low and steady proportions (<6%), the highest value (10±6%) was recorded at Comprian in March 5th. FS proportion was high in March and during the summer at both stations. FS value decreased from 64±8% to 6±1 at Comprian and from 36±8% to 8±4% at Jacquets between March 5th and July 7th. An increase was observed in summer with values

reaching more than 40%. Jacquets showed noticeable highest FS proportion as compared to Comprian in Sept 23th (64±13% and 20±5%, respectively).

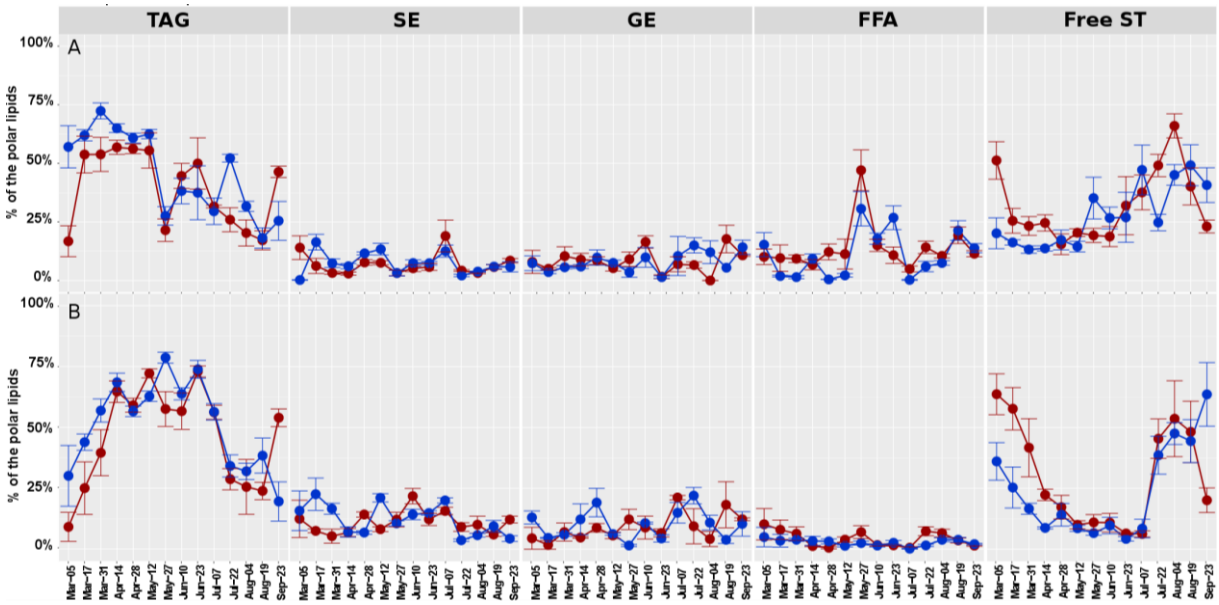

Figure 36 Sesonal variability of neutral lipid classes in *C. gigas* DG (A) and gonad+Mantle (B) for Comprian (red) and Jacquets (blue) stations. (means±SE).

Polar lipids class composition

Polar lipid class composition showed significant differences as function of sampling date, station and organ (PERMANOVA, $p< 0.05$). In *C. gigas* digestive gland, phosphatidylcholine (PC) and phosphatidylethanolamine+cardiolipid (PE+CL) were the major PL classes over the sampling period **(Figure 37A)**. PC proportions were in general around 40% at both stations, a noticeable fall to 15±0.4 was observed at Jacquets on May 12th. For PE+CL, the proportions were constant around 30%. PE+CL percentages increased at Jacquets on May 12th reaching 45±0.3%. The phosphatidylserine (PS) class showed stable proportions (<11%) at both stations. The phosphatidylinositol (PI) showed proportions around between 20% and 30%. At both Comprian and Jacquets PI proportions slightly increased in late summer.

In female *C. gigas* gonad+mantle, PC and PE+CL were also the major components of polar lipids throughout the sampling period (**Figure 37B**). The proportion of PC ranged from 22±6% to 52±2%. The highest values (>40%) were recorded at both Comprian and Jacquets stations on July 7th. The proportion of PE+CL ranged between 25±1% and 42±3%. The highest (>40%) and

the lowest values (<30%) were recorded at both Comprian and Jacquets stations on June 10th and July 7th, respectively. The proportion of PS was in general below 11%, a noticeable increase from ~5% to ~13% was observed between July 7th and June 22nd (after gametes release) at both stations. The proportion of PI was in general stable between 20 and 30%. An increase was observed on August 18th at both stations.

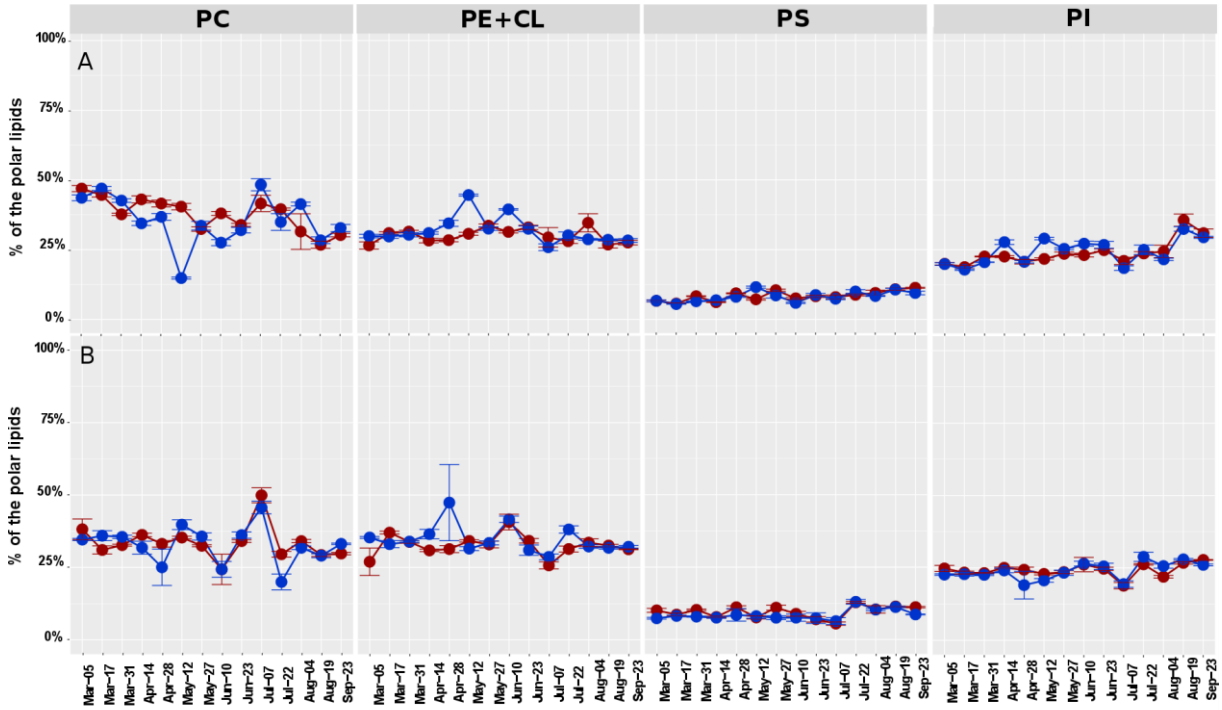

Figure 37 Sesonal variability in polar lipid classes of *C. gigas* digestive gland (A) and gonad+mantle (B) for Comprian (red) and Jacquets stations. (means±SE).

3.2.4. Fatty acid composition of neutral and polar lipids classes in DG and GM

For all sampling dates and organs, the FAs composition of both NL and PL fractions differed significantly (Two-way PERMANOVA, $p<0.001$), with no significant effect of station. In DG and GM, two-way PERMANOVA revealed significant differences according to date and lipid fractions with interaction between both factors ($p<0.001$).

Spatio-temporal variability of FAs composition in DG NL and PL fractions

Principal component analysis (PCA) performed separately in DG NL and PL FAs composition showed a clear spatio-temporal variability driven on the first component (PC1) (29.7% and 28.4% for NL and PL, respectively;**Figure 38 a** & **c**).

In **DG NL** fraction, positive correlations with PC1 were found for iso 17:0, 17:0, 18:0, 18:5n-3, 20:1n-9 and both NMI FAs 22:2i and 22:2j while negative correlations were found for 16:1n-7, 16:2n-4 and 20:5n-3. The 16:0 FA showed positive correlation with PC2. C18 FAs 18:1n-9 and 18:2n-6 showed positive correlations with PC3, which accounted for 11% of the total variability. Significant differences were recorded between Comprian and Jacquets for FAs associated to PC1 on July 22nd (Kruskal-Wallis; $p<0.05$). Significant temporal variability was recorded for FAs associated with PC1 and PC3 (Kruskal-Wallis; $p<0.05$).

In **DG PL** fraction, positive correlations of FAs with PC1 were found for ant17:0, 17:0, 18:5n-3, 20:4n-6, 16:1n-7DMA while negative correlations were found for 14:0, 16:1n-7, 18:1n-7, 20:5n-3, 21:5n-3. No spatial variability were recorded for FAs associated with PC1, while significant temporal variability was observed at both stations (ANOVA; $p<0.05$).

Spatio-temporal variability of FAs composition in GM NL and PL fractions

Principal component analysis (PCA) performed separately in GM NL and PL FAs compositions showed spatio-temporal variability driven on the first component (PC1) (26.8% and 30.8%, respectively; **Figure 38 b** & **d**).

In **GM NL** fraction, positive correlations with PC1 were found for 18:0, 20:1n-9, 20:1n-7, 20:4n-6, 22:2i and 22:2j while negative correlations were found for 16:1n-7, 18:2n-6, 18:3n-3, 18:4n-3 and 18:5n-3. Strong positive correlation with PC2 was found for 20:5n-3 (loading=0.9). No spatial variability was recorded between stations for FAs associated with PC1 and PC2. Significant temporal variability was recorded for FAs associated with PC1 between early spring (March 31st) and early summer (June 23rd and July 22nd) (Kruskal-Wallis; $p<0.05$). For FAs associated to PC2, significant temporal variability was observed between early spring (March 31st-April 14th) and all other sampled dates (ANOVA; $p<0.05$).

In **GM PL** fraction, positive correlation with PC1 were found for ant15:0, 14:0, 16:1n-7, 20:1n-9, 16:4n-1, 18:3n-4, 20:4n-6, 22:3nmi, 22:4n-6, 16:0 DMA and 17:0 DMA while negative

correlations were found for 18:5n-3 and 16:1n-7DMA. On PC2, positive correlations were found for 18:3n-6, 18:4n-3, 21:5n-3 while negative correlations were found for 18:5n-3 and 16:1n-7DMA. Positive correlations were found for saturated FAs 15:0 and 17:0, 16:4n-3 and negative correlations for 20:5n-3 with PC3 (accounted for 11% of the total variability). Significant temporal variability was observed for FAs associated to all axis at both stations.

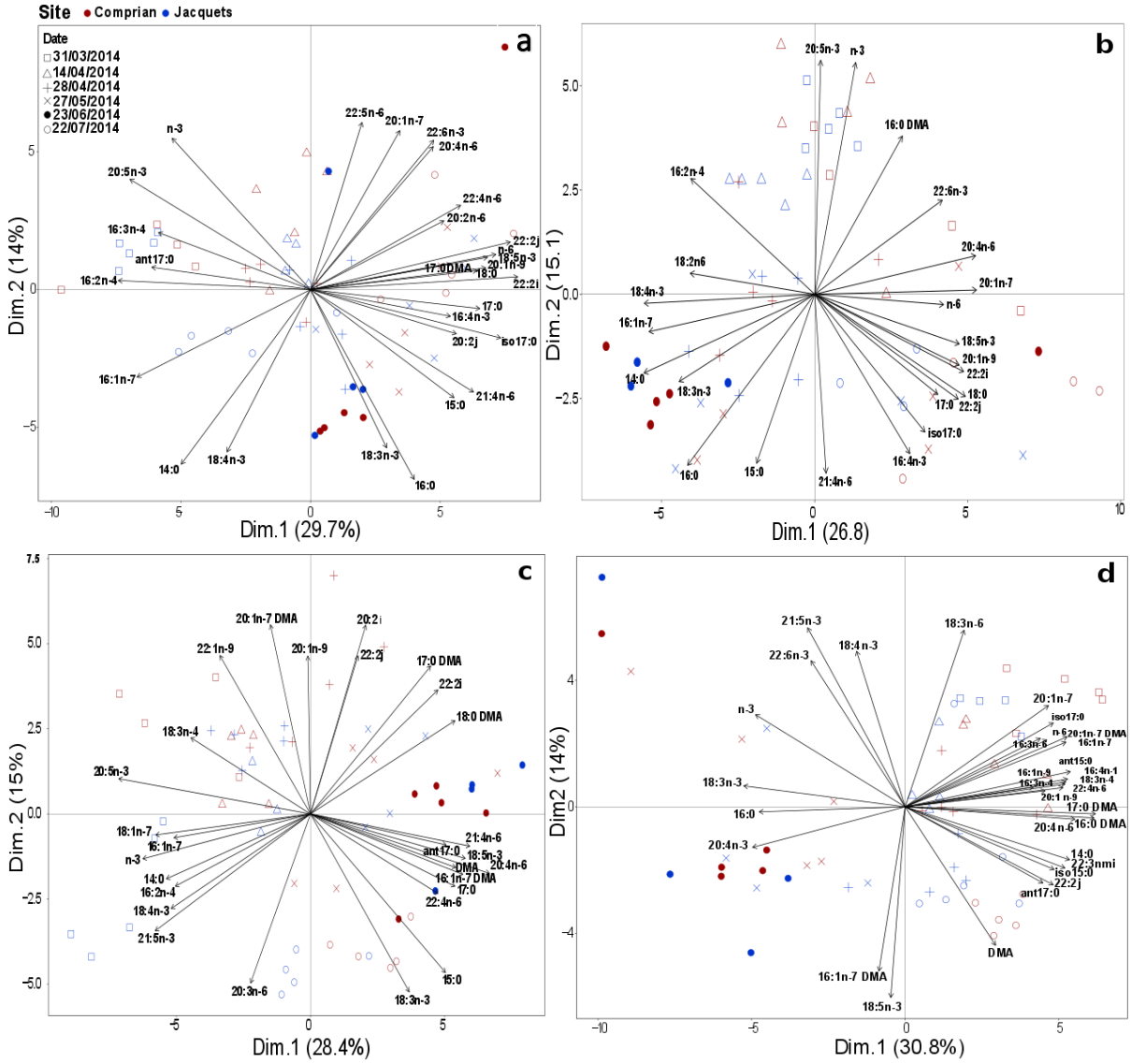

Figure 38 PCA analysis on neutral and polar lipids of *C. gigas* digestive gland and gonad+mantle. (a) DG NL, (b) GM NL, (C) DG PL, (d) GM PL. Only fatty acids with cos2 > 0.35 were represented to improve the reading.

3.2.5. A focus on EFAs and n-3/n-6 ratios

In DG NL, EPA proprotions showed a clear decrease between March 31st May 27th at Comprian and Jacquets. EPA values decreased from about 29% to 17% at both stations. Significant

difference was observed on July 22nd, higher values were recoreded at Jacquets as compared to Comprian (Kruskal-wallis; p>0.05). DHA proportions were more stable with values ranging from 8% to 11%. A slight increases were observed on April 14th. ARA showed stable and low proportions (1% - 2%) at both stations. Ratio of n-3/n-6 in DG NL ranged from 6±0.7% to 11±1% at Comprian and from 7±0.3 to 12±0.3% at Jacquets. Highest values were recorded in March 31st. Significant difference between Comprian and Jacquets was observed July 22nd (Kruskal-wallis; p>0.05).

In DG PL, EPA proportions decreased between spring and summer from about 21% to 14% at Comprian and Jacquets stations. A slight increases were observed on July 22nd. DHA proportions were more stable with values ranging from 12% to 15%. Highest values were recorded on May 27th at both stations. ARA showed also stable propotions (~3%). Ratio of n-3/n-6 in DG PL ranged from 6±0.3% to 7±0.5% at Comprian and from 5±0.2% and 8±0.2% at Jacquets. Highest values were recorded on March 31st.

In GM NL, EPA proportions showed a continual decrease between spring and summer from about 22% to 15%. Highest values were recorded on March 31st and April 14th at Jacquets and Comprian, respectively. DHA proportions ranged from about 7% to 11% at both stations. Highest values were recorded on March 31st and July 22nd. DHA values were significantly higher at Comprian on April 14th (Kruskal-Wallis, p<0.05). The lowest values were observed on April 28th at both stations. ARA proportions ranged from 1 to 3%, highest values were recorded on March 31st and July 22nd. Significant difference between Comprian and Jacquets was observed on March 31st (Kruskal-Wallis, p<0.05). The ratio of n-3/n-6 in GM NL ranged from 6±1 to 8±0.7 at Comprian and from 6±1 to 9±1 0.8 at Jacquets. Highest values were recorded on March 31st and April 14th at Jacquets and Comprian, respectively.

In GM PL, EPA proportions ranged from about 12% to 19% with a noticeable increase between April 28th and June 23rd. The lowest values were recorded on July 22nd. DHA proportions ranged from 14% to 16%. Significant difference was observed between Comprian and Jacquets on March 31st (Kruskal-Wallis, p<0.05). DHA values increased between April 28th and June 23rd. ARA proportions were stable and ranged from 3% to 4%. The highest values were recorded on March 31st and July 22nd. The ratio of n-3/n-6 in GM PL ranged from 4±0.2 to 7±0.5 at Comprian

and from 5±0.5 to 7±0.4 at Jacquets. Highest values were recorded on May 27th and June 23rd at both stations.

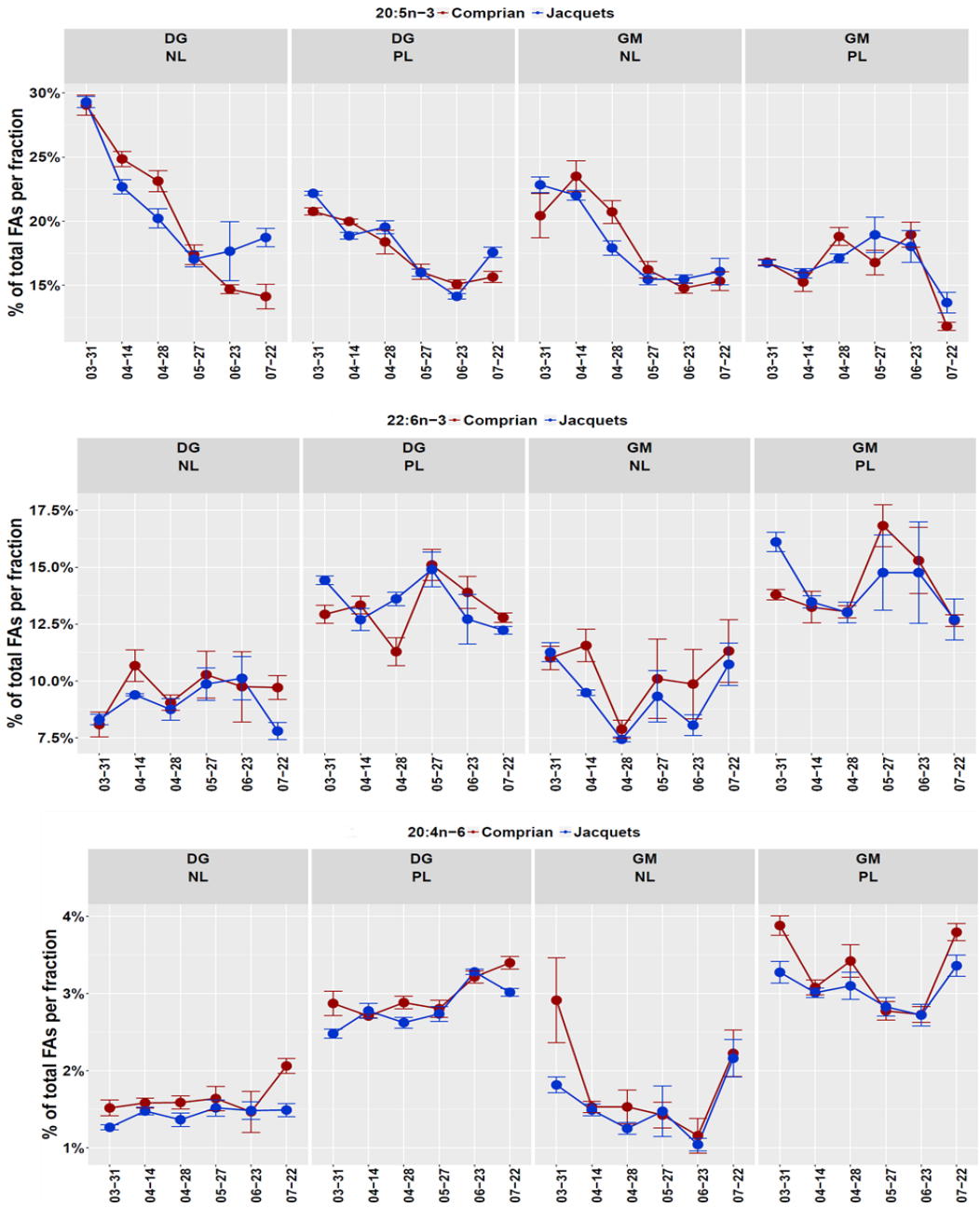

Figure 39 Seasonal variability of essential fatty acids for oyster neutral and polar lipids in digestive gland and gonad+mantle (DG NL, DG PL, MG NL, MG PL) for Comprian (red) and Jacquets (blue) stations. (means±SE).

4. Discussion

4.1. Spatio-temporal variability in oyster trophic environment

In shallow coastal environments, phytoplankton blooms can be episodic, seasonally recurrent or rare events associated to specific climatic or hydrological conditions (Cloern 1996). This variability plays a prominent role in the biological functioning of the ecosystem. Primary producers are the major sources of marine lipids and particularly essential fatty acids (EFAs) for higher trophic levels (Dalsgaard et al. 2003). EFAs are crucial for marine organisms that cannot sufficiently synthetized them (Monroig et al. 2013). Spatio-temporal variability of EFAs is therefore associated to that of phytoplankton communities. In Arcachon Bay, nutrients inputs mostly from the Eyre River (south-eastern part) and with lesser extent from the Porges River (northeastern part) modulate phytoplankton communities (Glé et al. 2008, 2007). In accordance to this pattern, the variability in the nutritional value of *C. gigas* trophic resources, including essential fatty acids, were monitored at two sites, Comprian and Jacquets, localized in southern and northeastern areas, respectively. Relationships between the contribution of functional groups (*e.g.* diatoms, dinoflagellates), the size-class structure of phytoplankton (microphytoplankton, nano- and pico-eukaryotes) and fatty acids pools available in the POM were explored at both spatial and seasonal scales.

On the onset of the spring productive period (March), the increase of Chl*a* concentrations (> 7.5 µg L^{-1}) was associated to large colonies of the diatom *Asterionellopsis glacialis* (>10^6 Cell L^{-1}). This species is typical of spring phytoplankton communities and grows under nutrients-rich conditions (López 1958). The species *A. glacialis* dominated microphytoplankton in association with other diatoms such as *Thalassiosira* spp*., Pseudonitzschia* spp. *and Nitzschia longissima.* As reported in the bay by Glé et al. (2008), microscopic species identification revealed a 99% dominance of diatoms in March. In the same study, the authors showed that *A. glacialis* spring blooming provides the highest primary production rate in the bay (496.6 mg C m^{-3} d^{-1}). This is in agreement with previous studies of the continental shelf of the Bay of Biscay (Gohin et al. 2003 ; Herbland et al. 1998). In March, nanoeukaryotes biomass showed similar tendency with microphytoplankton (~4 x 10^6 cell L^{-1}). In contrast, picoeukaryotes exhibited noticeably low biomass when compared to the rest of the monitored period (~6 x 10^6 cell L^{-1}). This antagonistic dynamics between micro- and nanophytoplankton *vs.* picophytoplankton have been previously

described in Arcachon Bay by Auby and Maurer (2004). High freshwater inflows from the Eyre River in late winter (January-February) support large-size phytoplankton development (Glé et al., 2008). A POC/Chl*a* ratio lower than 100 also indicates fresh particulate organic matter composed of living phytoplankton during this period (Savoye et al., 2003). This high primary production allowed an increase in the amount of PUFA (>15%), in particular the EFA 20:5n-3 that is associated to diatoms (Volkman et al. 1989).The ratios of n-3/n-6 were higher than 5 and in the range of optimal dietary ratios reported for marine fishes (Sargent et al. 1995).

Immediately after the early spring bloom, a noticeable decrease occurred on microphytoplankton and nanoeukaryotes biomasses. This pattern was reported linked to nutrients depletion because of the massive and fast development of *A. glacialis* (Glé et al. 2008). In contrast, picoeukaryotes increased greatly, showing highest biomass at Jacquets station (7 x 10^7 cell L^{-1}). This shift between larger nano- and microplankton and tiny picoplankton is in agreement with the increasing importance of picophytoplankton in nutrient-poor waters reported by Agawin et al. (2000). Nutrient limitation (*i.e.* nitrogen, phosphorus) is actually the dominant factor controlling phytoplankton cell size (Peter and Sommer, 2015). Over the monitored period, the highest picoeukaryotes biomasses were recorded at the northern station Jacquets. This result is in agreement with previous study that compared this station with other localities in the Bay (Auby & Maurer 2004). Lower nutrient inputs from the Porges River seem to provide better environment for small-size plankton development in northern bay.

Since diatoms and dinoflagellates are major components of nano- and microplankton, their decrease in early April generated a decrease in PUFA (<15%) and in particular the EFA 20:5n-3. In contrast, an increase was observed for C18 FAs 18:1n-9 (~15%) and 18:2n-6 (~10%), which were highly correlated along the monitored period (r=0.7). The FA 18:1n-9 has been attributed to picoeukaryotes such as *Prymnesiophyceae* (Boelen et al. 2013 ; Dalsgaard et al. 2003 ; Volkman et al. 1989). This group has been reported as important pico-sized representatives across all major ocean basins worldwide (Kirkham et al. 2013). In a study on the diet of copepods, Escribano and Pérez (2010) reported higher 18:1n-9 proportions in copepods fed on pico- and nanoplankton than those fed on microplankton. Their highest proportions in POM at the northern station reinforce the hypothesis of picoeukaryotes contribution to the POM. The literature attributed 18:2n-6 predominantly to vascular plants, in association with 18:3n-3

(Kelly & Scheibling 2012). However, a low correlation (r= 0.23) was observed between both FAs, suggesting different origins. This result highlights the weak contribution of the large seagrass *Zostera noltei* beds to the pool of organic matter in Arcachon Bay. High 18:2n-6 were also found in *Cryptophycea* (*e.g. Rhodomonas salina*) and *Chlorophycea* (Dunstan et al. 2005, 1992). Low n-3/n-6 ratios (lower than 2.5) were recorded after the early spring blooming at both stations, revealing poorer nutritional environment for marine organisms according to Sargent et al. (2015).

On the 28th, at the end of April, dinoflagellates contribution to microphytoplankton was higher at Jacquets (36%), than at Comprian (5%). Dinoflagellates cell number increased mainly due to the presence of the species *Prorocentrum micans*, *Neocentrum fusus* and *Scrippsiella spp*.The significant increase in POC concentrations on April 28th supports the importance of dinoflagellates as a carbon resource within the bay, as observed in the Mediterranean Thau lagoon (Dupuy et al. 2000). However, POC concentrations recorded at Comprian (2000 µg L^{-1}) were higher than concentrations recorded at Jacquets (1000 µg L^{-1}) and chl*a* concentrations showed similar pattern (6.6 µg L^{-1} at Comprian and 4.2 µg L^{-1} at Jacquets), suggesting that the importance of dinoflagellates is not homogeneous at the bay scale. Moreover, the POC/Chla ratio higher than 300 at Comprian indicated a larger contribution of non-photosynthetic organisms (mixotrophs and/or heterotrophs) and/or non-living material. Increase in the dinoflagellates biomarkers 18:5n-3 (Dijkman & Kromkamp 2006) and 22:6n-3 (Volkman et al. 1989) suggest that dinoflagellates may significantly contribute to the pool of mixotrophs and heterotrophs and to the increase of n-3/n-6 ratios (4.5 for Comprian and 8 for Jacquets). These results highlight the important contribution to oyster food of dinoflagellates with various nutritional modes in shallow coastal waters.

Late spring (May-June) microphytoplankton communities were characterized by the presence of the same diatom species, *A. glacialis,* as well as *Chaetoceros spp.* and *Leptocylindrus danicus.* Both species are the main summer diatoms in Arcachon Bay (Auby et al. 2000), and reached their maximum biomass on June 10th. Chl*a* concentrations were higher than 5 µg L^{-1} at both Comprian and Jacquets. *Chaetoceros spp. and Leptocylindrus spp.* blooms appeared in parallel to the increase of nanoeukaryote biomass. In May, PUFAs were high (~20%) mainly due to the increase in 18:5n-3 and 22:6n-3. Higher proportions of dinoflagellate biomarkers were observed at Comprian, while higher large-size dinoflagellate abundance was recorded at

Jacquets. which could be attributed to the contribution of small-size dinoflagellates, not detected in the micro-plankton (Moynihan et al. 2016). However, picoeukaryotes exhibited the highest concentrations at Jacquets, with high levels of 18:1n-9 in particular on May 27th (3% at Comprian *vs.* 17.5% at Jacquets). Thus, pico-sized phytoplankton composition appeared different between both stations. More studies are needed to identify their contribution to the n-3 PUFAs and the 18:1n-9. Similar spatial pattern was observed for the EFA 20:5n-3 (~8%). Moreover, the n-3/n-6 ratios reached 10 at Comprian and were around 5 at Jacquets.

During summer, phytoplankton development in Arcachon Bay is limited by nutrient inputs (Glé et al., 2008), the primary production decreased as compared to spring. Low primary production was sustained by the diatoms *Chaetoceros spp.*, *Leptocylindrus danicus, Ceratoneis closterium.* Moreover, poor-nutrient conditions enhance picoeukaryotes development. In July, POC/Chl*a* ratios higher than 500 revealed noticeable decrease of the autotrophs biomass at the expense of mixotrophs/heterotrophs or non-living particles. Besides, at the end of July, Chl*a* concentrations were below 2.5 µg L^{-1}, Chl*a* concentrations reached 6.7 µg L^{-1} at Comprian and 3.9 µg L^{-1} at Jacquets after the bloom of the species *Lithodesmium undulatum*. Highest n-3/n-6 ratios at Jacquets (8.4 *vs.* 3.4 at Comprian) indicated higher non-autotrophic enrichment at this station, potentially from heterotrophic compartment especially to the gonad. Heterotrophic protists are actually able to biosynthesize n-3 PUFAs when fed on microalgae lacking 20:5n-3 and 22:6n-3 (Veloza et al. 2006).

4.2. Oyster diet and energy reserves building

In accordance with the higher quality trophic status of the water column in March, *C. gigas* showed an increase in reserve lipids (or neutral lipids NL) in the digestive gland. This increase was observed at Comprian during March (from 20% to 37%). At the northern station, stable NL contents (from 40% to 45 %) were observed at this period. NL fraction in *C. gigas* DG was composed mainly of triglycerides (TAG), which reached on March 31st at about 70% of the total NL. Similarly to the dynamic of FAs in SPOM, high levels of 16:1n-7, 16:2n-4, and 20:5n-3 were recorded in TAGs. In mollusks, fatty acid composition of NL reflects their diet (Soudant et al., 1996). Thus, high contribution of diatoms (*A. glacialis*) to *C. gigas* diet occurred in early spring. In marine organisms, TAGs dominates NL and constitutes an energetic reserve of FAs destined to provide energy (ATP) or to be incorporated in structural lipids (polar lipids PL) (Bergé and

Barnathan, 2005). Digestive gland plays a transitory role for TAGs storage as this organ is implicated in the transfer of assimilated food to other compartments especially to the gonads (Berthelin et al., 2000). Before early March, *C. gigas* at Jacquets benefited potentially from better trophic environment, allowing building larger TAGs reserves. Since SPOM nutritional value showed similar trends at Comprian and Jacquets in March, differences cannot be attributed to spatial differences in the nutritional environment at this period. Future monitoring on *C. gigas* diet at Arcachon Bay should include late winter trophic conditions. At the end of March, n-3/n-6 ratios in DG NL showed the highest values over the monitored period. (11.0±0.6 and 12.0±0.1 at Comprian and Jacquets, respectively). These ratios were greater than ratios recorded in natural and artificial *C. gigas* cultivated stocks from Marennes-Oléron Bay (Soudant et al. 1999).

In early April, *C. gigas* TAGs percentages in DG were stable and similar to those recorded in late March. However, following the pattern observed for FAs in SPOM, diatoms biomarkers dropped in contrast with 22:6n-3 and C18 FAs (18:1n-9, 18:2n-6). Dinoflagellates and picoeukaryotes (*e.g. Prymnesiophyceae*) appeared as prominent sources of dietary fatty acids for *C. gigas*. In the lagoon of Thau, Dupuy et al. (2000) argued that picoeukaryotes do not significantly contribute to *C. gigas* diet because of its low retention capacity of small-size cells (<5µm). The authors suggested that picoplanktonic production was transferred to oyster via their assimilation of hetero-/mixotrophic protists (Dupuy et al. 1999). However, *Crassostrea virginica* showed experimentally to have significant ability to ingest picoplankton-sized embedded within aggregates (Kach & Ward 2008). Seychelles et al. (2009) demonstrated that some picoeukaryotes species are of high biochemical value and provide essential fatty acids such as 20:5n-3. Similar result was found for the 18:1n-9 in marine fish diet, the authors attributed this pattern to small-size plankton (Le Croizier et al. 2016). Thus, although microphytoplankton is assumed to be the main food sources of *C. gigas* in Arcachon Bay (Salvo 2010), feeding directly or indirectly on pico-size POM production may contribute to oyster diet in period of low microphytoplankton primary production, with potentially a higher contribution in northern part.

Between late April and early June, dinoflagellates constitute an important food source for *C. gigas.* Bivalves can ingest dinoflagelates selectively among other food sources (Shumway et al. 1985). Dinoflagellates biomarkers in *C. gigas* DG NL showed different patterns. The 18:5n-3

increased gradually at both stations, reaching its maxima on the 27th May. However, the 22:6n-3 decreased on late April. This is could be related to a mobilisation process for reproductive issues, since 22:6n-3 decreased concomitantly in gonad+mantle NL fraction. The steady decrease of 20:5n-3, even with the bloom of diatoms *Leptocylindrus danicus* and *Chaetoceros spp.*, generates a decrease in n-3/n-6 ratios at both stations (to around 8). Energy demand seems high to allow reserves building in gametes at this period of the end of gametogenesis process.

On July 22nd, noticeable difference in the FA composition of *C. gigas* DG NL revealed different trophic environments between Comprian and Jacquets. At Comprian, an increase of the diatom biomarkers 16:4n-1 and 16:2n-4 (Viso & Marty 1993), bacteria biomarkers iso17:0, 15:0 and 17:0 (Volkman et al. 1989) and of both dinoflagellate biomarkers 18:5n-3 and 22:6n-3 was observed, while at Jacquets, FAs increase was observed for the diatom biomarkers 20:5n-3, 16:1n-7 and bacteria biomarker ant17:0 increased (Volkman et al. 1989). This differences in FA composition appeard related to the patterns observed in SPOM on July 7th. Indeed, higher abundance of diatoms was found in total microphytoplancton abundance at Jacquets (90% *vs.* 40% for Comprian). These different trophic environements may explain the pattern of full spawning observed at Jacquets in contrast with Comprian where partial release of gametes occurred.

4.3. Energy reserves and essential fatty acids investment in gametogenesis process

The reproductive cycle of *C. gigas* was monitored from March (early stage of gametes development) to late July (after spawning). A constant increase in the somatic-gonadal index LS_{CI} was observed from March to mid-April. LS_{CI} recorded at Jacquets (4.5±0.2) were higher than those recorded at Comprian (3.5±0.3). Similarly, TAG in neutral lipids of gonad plus mantle tissue increased at both stations (about 75%), with slightly higher energy reserves observed at Jacquets in early March. In addition to digestive gland, gonad and surrounding mantle represent an important storage tissue supporting *C. gigas* reproductive effort (Berthelin et al. 2000). Thus, oyster at Jacquets started their gametogenesis cycle with better energy reserves condition. On late March, at early stage of gametes maturation, high n-3 PUFAs levels were observed in NL, n-3/n-6 ratios were around 7 and 9 at Comprian and Jacquets, respectively. Both EFAs 20:5n-3 and 22:6n-3 in NL showed similar spatial patterns between stations, around

22% and 11%, respectively. Difference between stations was observed for the 20:4n-6, which showed higher proportions in gonad+mantle NL and PL fractions at Comprian.

From late April to late June, gamete maturation reached ripeness stage and several episodes of partial spawning were observed at both Comprian and Jacquets stations. A first slight decrease in TAGs was observed on late April, in accordance with the beginning of partial gametes release as revealed by the histological monitoring. Several increases and decreases events of TAG levels followed these partial spawning dynamic. Mean temperature between mid-April and mi-May was around 15.6 ±1°C (Surval Ifremer network), which is too low for *C. gigas* spawning in Arcachon Bay (Maurer et al. 2016). High amount of n-3 PUFAs and in particular the EFA 22:6n-3 from dinoflagellates bloom seems to drive this pattern. The drop of LS_{CI} (~3.5) and TAGs (less than 50%) that occurred between the 7th and the 22nd July was concomitant with the beginning of total spawning period. TAGs in gonad+mantle is stored mainly in the female gametes to serve as energy source for larval development (Gallager & Mann 1986). After the spawning, TAG contents were maintained at Jacquets (about 25%), while it decreased at Comprian (~12%). These results confirmed the better energy reserves building in northern bay.

In contrast to what is usually noticed for *C. gigas* in other ecosystems (*e.g.* Marennes-Oléron Bay ; Soudant et al. 1999), the amounts of 20:5n-3 decreased constantly in gonad + mantle NL between March and late May. In mollusks, this essential fatty acids is mobilized for energy purposes (Delaunay 1992). Its high proportion in *C. gigas* tissue NL fraction confirms this role. The constant decrease confirms the elevated energy demand by oyster in Arcachon Bay suggesting a moderate trophic “quality” compared with other bays (Bernard et al. 2014). Energy building is allowed only at the onset of the productive period when feeding on large amounts of *A. glacialis*. However, this species is recognized for its low nutritional value (David et al. Soumise). Both EFAs 22:6n-3 and 20:4n-6 showed higher proportions in PL fraction in accordance with their biological role. The 22:6n-3 have been reported to be implicated in structural and functional lipids of cell membranes and involved in oogenesis and embryogenesis processes in the female of the scallop *Pecten maximus* (Soudant et al. 1996). The 20:4n-6 is a major precursor of reproductive hormone (prostaglandin) (Hurtado et al. 2009). Their presence in *C. gigas* PL confirms their physiological needs. Similar proportions of 22:6n-3 in PL were

found for *C. gigas* in Marennes-Oléron Bay, while 20:4n-6 was highest at Arachon Bay (Soudant et al. 1999).

Similarities in the increase of 18:1n-9 in the digestive gland and gonad+mantle in April revealed a potential role of this FA in oyster reproductive process. The 18:1n-9 is precursor of NMI PUFAs in bivalves. NMIs in oysters are influenced by dietary supply (Delaporte et al 2005), they are thought to have functional and structural roles in bivalve membranes (Kraffe et al. 2004; Zhukova 1991). The high correlation found between 18:1n-9 and C20 NMI: 20:2i (r=0.66) and 20:2j (r=0.83) in *C. gigas* tissue total lipids support this hypothesis.

4.4. Conclusion

The spatio-temporal monitoring of *C. gigas* gametogenesis in 2014 confirmed the south-est north-west gradient of variability in the reproductive effort observed in 2013 by Gasmi et al. (2017). Oyster in south-eastern areas exhibited lower energy reserves as revealed by the lower amounts of neutral lipids in digestive glands and gonad+mantle tissues. Changes in the water column trophic condition was more pronounced at the temporal scale than the spatial scale and related to changes in planktonic communities. Microphytoplanktonic and naneukaryote biomass appeared similar at both Comprian and Jacquets stations, while picoeukaryotes showed in general higher biomass at Jacquets. Dissimilarities in the SPOM fatty acids composition between station were attributed essentially to diatom biomarkers (20:5n-3 and 16:1n-7) and C18 FAs (18:0 and 18:1n-9), suggesting spatial differences in the contribution of autotrophic groups and/or heterotrophs to SPOM fatty acids composition between north-west and south-east areas. Increases in diatom biomarkers were observed in relation to increases in micro and nano-eukaryotes communities, while 18:1n-9 were observed in relation to increase in picoeukaryotes ones. Increases of 18:1n-9 in *C. gigas* digestive gland reserves in low primary production periods suggests a trophic transfer from picoeukaryotes communities. Since their contribution to oyster diet is still debated because their tiny size seems to not allow their retention by oyster gill, feeding on protists may explain this pattern (Dupuy et al. 2000, 1999). Although microphytoplankton is assumed to be the major food source in Arcachon Bay, in period of low primary production, this input of 18:1n-9 (directly from picoeukaryotes or indirectly through protists) could be precious since this fatty acid is a precursor of NMIs fatty acids, as demonstrated by the correlation found with 20:2i and 22:2j. Their higher contribution

to fatty acids pools at Jacquets in April and May may contribute to explain the better physiological state. Indeed, dietary EFAs in both the digestive gland and gonad+mantle appeared to differ between stations only on July 22nd. More studies are needed to investigate the origin of 18:1n-9 FA and variability in heterotrophic contribution to *C. gigas* diet in Arcachon Bay.

Overall, Arcachon Bay revealed the low trophic potential of the system to answer *C. gigas* reproductive requirements. Although diatoms appeared as the dominant group in microphytolankton communities, the EFA 20:5n-3 dropped in both *C. gigas* digestive gland and gonad+mantle over gametogenesis period. This result is contrasted with the physiological state of oyster in other aquaculture ecosystems (*e.g.* Marennes-Oléron Bay), where 20:5n-3 increases along with the gonad growing gametes (Soudant et al. 1999). Since 20:5n-3 is involved in providing energy reserves for reproductive process, this result gives new insights into the differences in gonadal development observed between different ecosystems (Bernard et al. 2014). At the onset of the productive period, the massive development of *A. glacialis* did not result in an increase of the n-3/n-6 ratio, which confirms the low nutritional value of the species as reported in others studies (David et al. submitted). The highest n-3/n-6 ratios in SPOM were recorded during dinoflagellate blooms, highlighting their important contribution to food quality improvement in the bay.

Discussion générale et perspectives

Discussion générale, synthèse et perspectives

Le paysage ostréicole français connait depuis quelques années une évolution importante de ses pratiques. La mécanisation des cabanes ostréicoles (*e.g.* chaîne de triage, calibreuses automatiques), le plein essor de la production du naissain dans les écloseries, ainsi que le développement de la culture des huîtres triploïdes contribue à l'évolution de la filière. Toutefois, de nouvelles crises rappelant des crises anciennes (*e.g.* éradication de l'huître portugaise) font régner un climat d'inquiétude sur son devenir. Les phénomènes de mortalité à raisons épidémiologiques observés depuis 2007 dans tous les bassins ostréicoles français soulignent la fragilité de la filière face à sa dépendance aux conditions environnementales (Bernard 2011). A ces problématiques épidémiologiques se rajoutent des problématiques biologiques et écologiques. Depuis une vingtaine d'année, une diminution de l'effort reproductif associé à un retard de ponte est observée dans plusieurs bassins. Un ostréiculteur de Marennes-Oléron affirmait : *"Avant [...], j'ai vu naviguer au cœur du Bassin dans du lait ! Les huîtres perdaient toutes leur lait en même temps : vous étiez dans un bain de lait ! C'est fou ! On ne voit plus ça"* (Toulhoat 2008). Le Bassin d'Arcachon est l'un des bassin les plus touché par ces phénomènes (Pouvreau et al. 2016). L'effort reproductif chez l'huître est dépendant de deux facteurs principaux : la température et la nourriture (Enríquez-Díaz et al., 2009). Ces facteurs évoluent sous l'effet des changements globaux, qui sont en train de faire émerger chez l'huître des nouveaux optimums écologiques (Thomas et al. 2015). Dans un bassin mésotrophe comme le Bassin d'Arcachon, caractérisé par une production primaire faible à modéré (Glé et al. 2008), il est donc primordial de dessiner un schéma actuel de la reproduction de l'huître et de son environnement nutritif naturel, afin d'appréhender au mieux leurs variations futures.

Dans ce contexte, ce travail consiste à dresser un état des lieux spatio-temporel du régime alimentaire et de l'effort reproductif des bancs sauvages d'huître creuse *Crassostrea gigas* dans le Bassin d'Arcachon, en étudiant la disponibilité de la ressource trophique et la variabilité de sa valeur nutritive durant la période de gamétogenèse. L'approche adoptée est présentée selon deux angles: **(Chapitre I & II)** l'étude des variations spatiales de l'effort reproductif et du régime alimentaire étudiée en relation avec des facteurs hydrodynamique à l'échelle de l'écosystème, et **(Chapitre III)** l'étude spatio-temporelle des variations du pool nutritif (*e.g.* composition, quantité et qualité) afin de caractériser la réponse du milieu aux besoins énergétiques de

l'espèce en période de gamétogenèse. Les méthodes utilisées dans ces études et les résultats mis en évidence seront discutés conjointement.

Gradients de variabilité de l'effort reproductif de l'huître creuse dans le Bassin d'Arcachon

Les résultats de cette étude mettent en évidence des gradients de variabilité spatiale claires de l'effort reproductif de l'huître creuse *Crassostrea gigas* dans le Bassin d'Arcachon. Cet effort de reproduction, approché à large échelle spatiale par les indices de condition gonado-somatique de Lawrence & Scott (1982), se révèle contrasté entre les parties internes et les parties externes de la baie. Une meilleure fécondité est observée chez les huîtres localisées dans les régions océaniques. Ce gradient spatial s'avère en partie en relation avec les conditions d'accès à la nourriture: principalement le temps de renouvellement océanique ("LoFt") et en moindre mesure le niveau d'immersion ("I_L"). Comme précédemment observé chez plusieurs espèces de bivalves, un renouvellement rapide et fréquent par des eaux marines adjacentes et un temps d'alimentation plus long favorise la croissance somatique (Wildish 1991). La relation trouvée en entre "LoFt" et le ratio isotopique du $\delta^{13}C$ mesuré à l'échelle de la baie dans le muscle de *C. gigas* suggère une consommation plus élevée de matière organique d'origine marine dans la partie externe. Ceci se révèle par l'enrichissement du muscle ^{13}C dans les parties plus renouvelées et son appauvrissement au niveau des principaux points d'apports des eaux douces (*e.g*. fleuve de l'Eyre et du Porges). L'entrée dans la baie de phytoplancton marin en provenance du Golf de Gascogne (Glé et al. 2007) semble donc créer un environnement trophique plus favorable dans les parties externes. Toutefois, le lien trouvé entre le $\delta^{13}C$ et le poids sec des huîtres suggère une influence de la physiologie sur la composition isotopique de l'huître (Pecquerie et al. 2010). D'autres études sont donc nécessaires pour dissocier le rôle de la nourriture et de l'état physiologique dans l'explication des patterns observés pour *C. gigas* entre les parties interne et externes de la baie.

Un nouveau gradient de l'effort reproductif chez *C. gigas* apparaît après correction de l'indice de condition des effets d'accessibilité à la nourriture. Pour un même temps de renouvellement et un niveau d'immersion similaire, les huîtres du sud-est du bassin présentent des indices de condition plus faibles que les huîtres du nord-ouest. Cet état reproductif observé dans le sud-est pour l'huître se rapproche du bilan de croissance dressé pour la palourde japonaise *Ruditapes philippinarum* (Caill-Milly et al., 2012; Dang et al., 2009). Les conditions

environnementales locales dans la partie sud-est s'avèrent donc moins propices pour répondre aux besoins énergétiques de ces deux espèces. En période de reproduction, la gamétogenèse chez *C. gigas* est soutenue par une mise en réserve biochimique importante (Berthelin et al. 2000). Cette mise en réserve qui se fait sous forme de lipides, stockés dans des organes cibles (*e.g.* glande digestive, manteau) est l'un des moteurs clés du succès reproductif de l'espèce (Soudant et al. 1999). Le suivi temporel des réserves biochimiques en période de gamétogenèse est en accord avec les résultats obtenus par l'indice de condition, une meilleure mise en réserves lipidiques (lipides neutres) est observée en début de période de gamétogenèse dans la partie nord-ouest du bassin. Chez les organismes marins, ces lipides de réserves qui se font principalement sous forme de triglycérides constituent une source d'acides gras polyinsaturés (*i.e.* 20:5n-3, 22:6n-3, 20:4n-6) indispensables à la survie et la reproduction (Delaporte et al. 2003; Hurtado et al. 2009). Ces acides gras acquis majoritairement via la nourriture (*i.e.* phytoplancton) sont transférés de la glande digestive vers la gonade afin d'assurer la formation et la maturation des gamètes (Berthelin et al. 2000). Les proportions plus élevées de lipides neutres mesurées dans la glande digestive et la gonade des huîtres au nord-ouest suggèrent que dans la partie sud-est les huîtres sont soumises soit à un environnement trophique de qualité nutritive moins propice, et/ou une dépense énergétique plus importante en lien avec une réponse à des stress potentiellement généré par des apports continentaux du fleuve principal de l'Eyre dans cette partie de la baie.

Variabilité spatio-temporelle des conditions trophiques du milieu et du régime alimentaire de *C. gigas*

Le suivi de la dynamique des biomasses phytoplanctoniques réalisé en période de gamétogenèse révèle une variabilité temporelle marquée mais une faible variabilité spatiale entre les parties nord et sud du bassin. Ce résultat est en accord avec l'homogénéité de la distribution de la matière organique décrite par Dubois (2012) dans les parties internes, ainsi que la faible variabilité spatiale des ratios isotopiques $\delta^{13}C$ et $\delta^{15}N$ observée dans cette étude. Toutefois, tout au long du suivi des abondances plus élevées des biomasses des communautés picoeucaryotes sont observées dans la partie nord-ouest. Ces patrons de distribution ont déjà été décrits dans d'autres études dans le Bassin d'Arcachon (Auby and Maurer 2004). L'apport de nutriments l'Eyre semble favoriser le développement de communautés phytoplanctoniques de grandes tailles, les cellules planctoniques de de petites tailles se développant mieux dans

des milieux pauvres en nutriments (Agawin et al. 2000). Le développement antagoniste observé entre le micro et nano-plancton vs. le pico-plancton révèle une dynamique alternée qui semble intiment liée aux concentrations en éléments nutritifs dans le bassin (Peter and Sommer, 2015). L'apport moins important d'eaux douces par le Porges dans la partie nord (24% vs. 70% pour l'Eyre ; Plus et al., 2009) semblent créer des conditions nutritives différentes de celles observées dans la partie sud. Ces conditions peuvent fortement influencer la structure et la composition des communautés phytoplanctoniques, et donc la valeur nutritive du pool nutritif (Galloway and Winder, 2015). Ces résultats montrent que bien qu'un fort hydrodynamisme permette la dilution des apports des fleuves dans les écosystèmes côtiers bien mélangés, des variations locales du fonctionnement écologique peuvent s'y dessiner. Ce constat est appuyé par les ratios isotopiques de $\delta^{13}C$ et de $\delta^{15}N$ contrasté dans le microphytobenthos entre les parties nord-ouest et sud-est du bassin.

La spatialisation des signatures isotopiques $\delta^{13}C$ et $\delta^{15}N$ dans le muscle de *C. gigas* a permis de détecter des patterns de variabilité entre la partie sud-est et la partie nord-ouest pouvant être en lien avec des différences dans la composition du pool nutritif. Toutefois, la contribution des différentes sources trophiques assimilées à ces patrons de distribution est apparue difficile à aborder. La comparaison des signatures de *C. gigas* avec les signatures des sources potentielles de nourriture révèle une dominance du phytoplancton et du microphytobenthos à l'échelle de la baie comme cela est observé dans d'autres écosystèmes côtiers (*e.g.* Kang et al. 2003). La similarité de la composition isotopique des deux sources n'a pas permis d'estimer leur contribution relative au régime alimentaire de *C. gigas.* Toutefois, la comparaison des gradients spatiaux après correction de l'effet du renouvellement océanique (donc de la contribution du phytoplancton d'origine marine) suggère une utilisation plus importante de microphytobenthos dans la partie nord-ouest de la baie. Cette hypothèse peut être soutenue par la nature plus fine du sédiment favorisant la remise en suspension (Ubertini et al. 2015). Le $\delta^{15}N$ dans le muscle de *C. gigas* apparait variable entre la partie nord et la partie sud. Cette variabilité ne semble pas liée aux apports de matière organique continentale apportée par le fleuve de l'Eyre. Ces derniers sont décrits comme faibles et ne contribuent pas significativement au régime alimentaire des bivalves filtreurs dans le Bassin d'Arcachon (Dubois 2012). En plus, le $\delta^{13}C$ dans le muscle de *C. gigas* est apparue très enrichi en ^{13}C par rapport à la MOP continental. Une hypothèse d'une contribution plus forte de sources trophiques

hétérotrophes dans la partie sud et de sources trophiques autotrophes dans la partie nord est suggérée. En effet, l'enrichissement en ^{15}N dépend du régime alimentaire du consommateur et de la qualité de sa nourriture (Adams & Sterner 2000, McCutchan et al. 2003, Vanderklift & Ponsard 2003, Robbins et al. 2005). En effet, *C. gigas* est connue pour sa capacité à osciller entre plusieurs modes alimentaire : la phytophagie, la détritivorie et l'omnivorie comme décrit par Riera (1998). La diversité des facteurs affectant la composition isotopique d'un consommateur souligne ainsi la nécessité d'employer des approches multi-outils pour s'affranchir de ces biais potentiels.

Capacité du Bassin d'Arcachon à répondre aux besoins énergétiques de *C. gigas* pendant la gamétogenèse

Les résultats obtenus soulignent la variabilité des capacités trophiques des bassins ostréicoles à répondre aux besoins énergétiques des espèces cultivées. Les travaux menés dans le cadre de cette étude montrent une faible capacité trophique du Bassin d'Arcachon en termes de qualité et de quantité du pool nutritif à soutenir un fort effort reproductif de l'huître creuse *Crassostrea gigas*. Ces résultats sont conformes aux précédents travaux décrivant une faible croissance gonadique dans le Bassin d'Arcachon en comparaison avec d'autres écosystèmes conchylicoles français (*i.e.* Bassin de Marennes-Oléron; Bernard et al. 2014). Le suivi spatio-temporel de la qualité biochimique de la matière organique en suspension révèle un faible potentiel du pool nutritif dans la baie. Il est généralement considéré dans la littérature qu'une qualité optimale de la ressource trophique implique un ratio d'acides gras polyinsaturés n-3/n-6 entre 5 et 15 pour assurer les demandes énergétiques des adultes et des larves de bivalves (Napolitano et al. 1992;Thompson et al. 1993; Pazos et al. 1997). Les ratios n-3/n-6 autour de 5 observés même en période de forte production primaire soulignent les limitations auxquelles sont soumises les huîtres en termes d'acides gras essentiels dans le Bassin d'Arcachon. Ces limitations trophiques sont également illustrées par la chute de la teneur en 20:5n-3 durant la gamétogénèse dans le Bassin d'Arcachon, ce qui contraste avec les résultats observés dans le bassin voisin de Marennes-Oléron, où sa teneur augmente ou cours de la production des gamètes (Soudant et al. 1999). Enfin, il apparaît que la composition de la SPOM au moment critique du début de la période productive est très largement dominée par un espèce, *Asterionellopsis glacialis*, conue dans la littérature pour n'offrir qu'une qualité trophique limitée (David et al., soumis). Cette efflorescence ne se traduit en effet que par une faible modification

des rapports n-3/n-6 chez les huîtres, illustrant l'apport limité de cette efflorescence phytoplanctonique printanière sur les capacités de gamétogénèse des huîtres.

Conclusion

Cette étude souligne la complexité des processus écologiques intervenant dans les écosystèmes côtiers soumis aux influences océaniques et continentales. Appréhender à la fois la variabilité spatiale et temporelle peut se confronter aux limites des techniques utilisées. L'approche mutli-outils combinée à un échantillonnage à fines échelles spatiales et temporelles a permis de mettre en évidence différents patrons de variabilité dans la condition des huîtres et la qualité nutritive de son environnement trophique. Si les différents mécanismes identifiés dans le cadre de cette thèse concourent à décrire le bassin d'Arcachon comme apportant une capacité trophique limitée pour le développement et la gamétogénèse de *Crassostrea gigas*, il convient toutefois de garder à l'esprit que ces mécanismes peuvent être soumis à une forte variabilité inter-annuelle, illustrée par l'importante variabilité des rendements de captage dans le système (voir introduction). La reproduction de ce type d'étude dans le temps permettra d'apprécier de rôle des mécanismes écologiques mis en évidence dans les tendances à long terme de rendements ostréicoles dans le Bassin d'Arcachon. Par ailleurs, si ces résultats semblent illustrer le rôle fondamental des aspects trophiques dans le maintien des stocks d'huîtres sauvages, leurs effets sur la phase larvaire, potentiellement bien plus sensible et susceptible d'être affectée par les phénomènes ponctuels, restent à établir. Enfin, les principales limites à la croissance et la gamétogénèse des huîtres dans le Bassin d'Arcachon semblent liées au caractère mésotrophe du milieu. La comparaison avec d'autres systèmes ostréicoles contrastés pourrait permettre d'élargir les conclusions de ce travail à plus grande échelle, et contribuer à mieux comprendre les phénomènes affectant ces socio-écosystèmes.

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Annexes

Annexe 1: Means ± SE of neutral and polar lipid classes in *C. gigas* digestive gland for Comprian and Jacquets stations. The results are expressed as percentages of total neutral and polar lipids.

		Neutral lipids (%)										Polar lipids (%)							
Date	**Site *(n)***	**SE**		**GE**		**TAG**		**FFA**		**FS**		**PI**		**PS**		**PC**		**PE+CL**	
March 5th	Comprian *(5)*	14.0	± 5.0	7.9	± 4.9	16.7	± 6.6	10.1	± 3.3	51.2	± 8.0	20.0	± 0.4	6.6	± 0.3	46.9	± 1.1	26.5	± 1.3
	Jacquets *(5)*	0.2	± 0.1	7.3	± 3.2	57.0	± 9.0	15.3	± 5.1	20.1	± 6.6	19.9	± 0.5	6.7	± 0.3	43.6	± 1.0	29.9	± 0.6
March 17th	Comprian *(5)*	6.2	± 3.2	5.0	± 0.5	53.8	± 7.9	9.6	± 5.6	25.5	± 5.3	18.8	± 0.6	5.7	± 0.1	44.6	± 0.8	30.9	± 0.5
	Jacquets (4)	16.4	± 3.3	3.6	± 0.6	61.9	± 2.4	1.9	± 0.4	16.2	± 1.1	17.9	± 0.3	5.5	± 0.1	46.9	± 0.7	29.7	± 0.6
March 31st	Comprian *(5)*	3.2	± 0.6	10.4	± 4.0	53.8	± 7.3	9.3	± 1.6	23.3	± 4.0	22.6	± 0.2	8.3	± 0.1	37.7	± 0.4	31.5	± 0.5
	Jacquets *(5)*	7.4	± 1.9	5.6	± 0.7	72.4	± 3.4	1.4	± 0.7	13.2	± 1.6	20.6	± 0.1	6.5	± 0.1	42.6	± 0.6	30.3	± 0.8
April 14th	Comprian *(5)*	2.9	± 0.6	8.9	± 2.7	56.8	± 3.0	6.8	± 2.2	24.6	± 3.5	22.6	± 0.4	6.2	± 0.2	43.0	± 1.3	28.3	± 0.8
	Jacquets *(4)*	6.1	± 1.1	5.9	± 0.8	65.0	± 1.9	9.3	± 2.0	13.7	± 1.1	27.8	± 0.8	6.9	± 0.2	34.4	± 0.8	31.0	± 0.4
April 28th	Comprian *(5)*	7.7	± 1.2	8.5	± 1.6	56.2	± 2.1	12.2	± 3.4	15.5	± 4.4	20.7	± 0.8	9.3	± 0.2	41.5	± 1.2	28.4	± 0.6
	Jacquets *(5)*	11.6	± 0.6	9.8	± 3.3	60.8	± 2.1	0.5	± 0.1	17.3	± 4.2	20.7	± 0.4	8.1	± 0.2	36.8	± 1.2	34.4	± 1.1
May 12th	Comprian *(5)*	7.6	± 0.9	5.3	± 1.2	55.5	± 7.5	11.3	± 6.4	20.4	± 1.7	21.7	± 0.4	7.2	± 0.3	40.4	± 1.2	30.7	± 0.5
	Jacquets *(5)*	13.3	± 2.5	7.5	± 1.2	62.5	± 2.0	2.2	± 0.8	14.5	± 2.3	29.0	± 0.4	11.6	± 0.4	14.8	± 0.4	44.6	± 0.3
May 27th	Comprian *(5)*	3.2	± 1.1	9.1	± 3.1	21.5	± 4.8	47.0	± 8.7	19.2	± 3.0	23.6	± 0.6	10.5	± 0.4	32.4	± 0.8	33.6	± 0.6
	Jacquets *(5)*	3.2	± 1.3	3.5	± 2.1	27.6	± 3.9	30.6	± 7.3	35.2	± 8.9	25.4	± 0.4	8.6	± 1.0	33.6	± 1.6	32.5	± 0.6
June 10th	Comprian *(5)*	5.2	± 1.4	16.4	± 2.6	44.6	± 5.3	15.0	± 2.6	18.8	± 4.3	23.1	± 0.7	7.5	± 0.3	38.0	± 0.7	31.4	± 0.4
	Jacquets *(5)*	7.4	± 1.4	9.9	± 4.2	38.2	± 5.4	17.8	± 2.4	26.7	± 4.6	27.2	± 0.9	5.9	± 0.2	27.5	± 1.1	39.4	± 0.3
June 23rd	Comprian *(5)*	5.7	± 1.5	1.6	± 0.8	49.9	± 11.0	10.8	± 3.5	32.0	± 12.4	24.9	± 0.5	8.3	± 0.4	33.9	± 0.5	33.0	± 0.8
	Jacquets *(5)*	7.4	± 0.8	1.4	±0.5	37.5	± 11.5	26.8	± 5.0	27.0	± 10.7	26.8	± 1.2	8.7	± 0.6	32.0	± 1.0	32.5	± 1.0
July 7th	Comprian *(5)*	19.0	± 6.8	6.9	± 3.2	31.6	± 0.6	4.9	± 1.3	37.6	± 7.4	21.0	± 1.3	8.0	± 0.8	41.6	± 2.9	29.4	± 3.5
	Jacquets *(5)*	12.5	± 2.6	10.4	± 8.3	29.5	± 5.6	0.3	± 0.2	47.2	± 10.6	18.4	± 0.8	7.4	± 0.3	48.3	± 2.2	25.9	± 1.2
July 22nd	Comprian *(5)*	4.2	± 0.4	6.6	± 1.3	25.9	± 5.1	14.2	± 2.6	49.1	± 4.7	23.7	± 0.7	8.8	± 0.4	39.5	± 0.4	28.0	± 0.8
	Jacquets *(5)*	2.1	± 0.5	15.0	± 3.2	52.2	± 1.6	6.0	± 2.2	24.8	± 3.5	25.0	± 1.7	10.0	± 0.6	34.9	± 3.0	30.1	± 1.2
Aug 4th	Comprian *(5)*	3.2	± 0.3	0.0	± 0.0	20.3	± 5.6	10.5	± 0.9	66.0	± 5.1	24.4	± 2.2	9.5	± 1.0	31.5	± 6.4	34.6	± 3.3
	Jacquets *(5)*	3.8	± 0.2	12.1	± 4.9	31.6	± 2.2	7.5	± 1.0	45.0	± 4.4	21.6	± 0.4	8.4	± 0.1	41.3	± 0.7	28.7	± 0.3
Aug 19th	Comprian *(5)*	5.7	± 1.0	17.7	± 5.9	17.2	± 4.1	19.3	± 3.5	40.1	± 7.9	35.6	± 2.2	10.8	± 0.4	26.7	± 1.3	26.8	± 1.3
	Jacquets *(5)*	5.9	± 1.0	5.5	± 5.5	18.1	± 4.3	21.3	± 4.2	49.2	± 8.7	32.5	± 0.8	10.7	± 0.5	28.4	± 1.2	28.5	± 0.3
Sept 23rd	Comprian *(5)*	8.5	± 0.9	10.7	± 0.4	46.4	± 2.4	11.4	± 1.3	23.0	± 2.8	31.0	± 1.5	11.3	± 0.2	30.2	± 0.6	27.5	± 0.8
	Jacquets *(5)*	5.8	± 2.2	14.2	± 3.0	25.5	± 8.3	13.8	± 1.9	40.7	± 7.4	29.5	± 0.4	9.5	± 0.6	32.8	± 1.3	28.3	± 0.6

Annexe 2: Means ± SE of neutral and polar lipid classes in *C. gigas* gonad+manle for Comprian and Jacquets stations. The results are expressed as percentages of total neutral and polar lipids.

		Neutral lipids (%)										Polar lipids (%)							
Month	**Site (n)**	**SE**		**GE**		**TAG**		**FFA**		**FS**		**PI**		**PS**		**PC**		**PE+CL**	
March 5th	Comprian *(5)*	12.5	± 7.7	4.5	± 4.5	9.1	± 5.9	10.3	± 6.4	63.7	± 8.4	24.8	± 1.1	10.1	± 0.7	38.2	± 3.5	27.0	± 4.8
	Jacquets *(5)*	15.8	± 8.1	13.1	± 2.7	30.1	± 12.5	5.0	± 4.0	36.1	± 7.7	22.7	± 0.3	7.4	± 0.3	34.6	± 0.4	35.3	± 0.3
March 17th	Comprian *(3)*	7.5	± 0.8	1.8	± 1.8	25.0	± 10.8	8.0	± 4.0	57.7	± 8.7	22.8	± 0.5	7.9	± 0.2	32.9	± 1.0	36.5	± 0.6
	Jacquets *(4)*	22.6	± 6.6	4.7	± 0.2	43.9	± 3.3	3.5	± 2.6	25.4	± 8.4	22.6	± 0.8	8.1	± 0.3	37.2	± 1.6	32.1	± 1.0
March 31st	Comprian *(3)*	5.4	± 2.9	7.0	± 3.7	39.5	± 9.5	6.4	± 2.9	41.7	± 12.0	23.0	± 0.0	10.6	± 0.1	32.5	± 0.4	33.8	± 0.4
	Jacquets *(3)*	16.6	± 2.2	6.0	± 0.7	56.9	± 4.8	3.9	± 0.7	16.6	± 2.2	22.9	± 0.2	7.8	± 0.2	35.2	± 0.5	34.0	± 0.3
April 14th	Comprian *(3)*	6.9	± 1.7	4.8	± 0.3	64.7	± 4.4	1.3	± 0.2	22.3	± 2.3	24.7	± 0.2	7.5	± 0.3	36.4	± 0.3	31.3	± 0.1
	Jacquets *(3)*	7.1	± 2.1	12.3	± 6.4	68.5	± 3.7	3.4	± 1.9	8.8	± 0.4	24.9	± 0.4	7.6	± 0.3	29.7	± 2.0	37.8	± 2.2
April 28th	Comprian *(3)*	14.3	± 1.0	8.8	± 1.8	59.1	± 2.9	0.6	± 0.5	17.3	±4.9	25.4	± 0.6	10.5	± 0.2	34.0	± 0.8	30.1	± 1.1
	Jacquets *(4)*	6.9	± 0.7	19.2	± 5.8	56.6	± 2.2	3.2	± 1.0	14.2	± 4.7	23.8	± 0.4	10.6	± 0.1	31.3	± 0.3	34.2	± 0.5
May 12th	Comprian *(4)*	8.2	± 1.0	5.7	± 1.3	72.2	± 1.8	3.9	± 1.1	10.0	±1.7	23.1	± 0.4	7.9	± 0.6	35.0	± 0.3	34.1	± 0.5
	Jacquets *(4)*	21.1	± 1.7	6.2	± 0.5	62.8	± 2.2	1.4	± 0.4	8.6	±1.3	21.1	± 0.6	8.1	± 1.0	38.7	± 1.7	32.1	± 0.4
May 27th	Comprian *(3)*	12.2	± 3.0	12.3	± 4.2	57.5	± 7.2	7.0	± 2.6	11.0	± 3.2	22.8	± 0.4	9.7	± 0.6	32.6	± 0.6	34.8	± 0.2
	Jacquets *(3)*	10.6	± 1.1	1.5	± 0.4	78.6	± 2.3	2.5	± 0.8	6.6	± 0.9	24.2	± 1.3	6.5	± 0.4	35.5	± 1.9	33.8	± 1.0
June 10th	Comprian *(4)*	21.8	± 3.2	8.9	± 4.7	56.7	± 7.5	1.7	± 0.5	10.9	± 3.8	27.1	± 3.0	8.8	± 1.1	21.9	± 6.0	42.2	± 2.8
	Jacquets *(3)*	14.3	± 2.2	10.7	± 0.4	63.8	± 2.5	1.5	± 0.6	9.7	± 3.4	26.5	± 1.1	6.2	± 0.8	26.3	± 1.4	41.1	± 0.6
June 23th	Comprian *(4)*	12.3	± 2.5	6.7	± 1.6	73.0	± 2.3	1.6	± 0.3	6.5	± 0.5	24.8	± 0.7	6.1	± 0.2	34.4	± 0.4	34.7	± 0.8
	Jacquets *(3)*	14.9	± 0.9	4.4	± 1.5	73.8	± 3.7	2.6	± 0.9	4.2	± 0.9	26.1	± 1.3	5.6	± 0.3	35.8	± 1.4	32.6	± 0.9
July 7th	Comprian *(4)*	15.7	± 1.5	21.2	± 0.9	56.2	± 2.9	0.6	± 0.4	6.3	± 1.3	17.9	± 0.7	5.0	± 0.2	52.0	± 2.0	25.2	± 1.4
	Jacquets *(4)*	20.0	± 1.1	15.0	± 4.3	56.4	± 3.4	0.2	± 0.2	8.5	± 3.8	20.0	± 1.3	5.4	± 0.8	45.5	± 2.8	29.2	± 1.0
July 22nd	Comprian *(4)*	9.1	± 1.8	9.4	± 7.2	28.7	± 4.4	7.4	± 1.9	45.4	± 8.1	26.3	± 0.1	13.3	± 0.2	28.7	± 1.3	31.7	± 1.1
	Jacquets *(3)*	3.7	± 0.5	22.0	± 3.4	34.1	± 4.6	1.6	± 0.4	38.6	± 7.8	26.3	± 0.1	12.5	± 0.9	22.5	± 1.7	38.6	± 0.8
Aug 4th	Comprian *(3)*	10.1	± 3.5	4.2	± 3.1	25.5	± 11.3	6.6	± 1.6	53.6	± 15.6	21.9	± 0.5	10.4	± 1.3	34.1	± 0.6	33.6	± 1.3
	Jacquets *(5)*	5.8	± 0.8	10.9	± 3.0	31.9	± 3.3	3.9	± 0.8	47.6	± 4.5	25.6	± 0.7	10.3	± 0.4	31.8	± 0.6	32.2	± 0.6
Aug 19th	Comprian *(5)*	6.0	± 0.7	18.3	± 9.5	23.9	± 3.6	3.6	± 1.0	48.2	± 12.6	26.7	± 0.4	11.4	± 0.1	29.3	± 0.5	32.6	± 0.4
	Jacquets *(5)*	9.4	± 2.4	3.9	± 1.5	38.4	± 7.2	3.9	± 1.0	44.4	± 8.8	27.9	± 0.3	11.2	± 0.2	29.1	± 0.7	31.8	± 0.5
Sept 23rd	Comprian *(5)*	12.2	± 1.4	12.3	± 0.6	53.9	± 3.6	1.5	± 0.3	20.1	± 5.1	27.7	± 0.1	11.2	± 0.2	29.8	± 0.4	31.3	± 0.1
	Jacquets *(5)*	4.4	± 1.2	10.4	± 5.0	19.5	± 8.1	2.1	± 0.3	63.6	± 13.1	26.0	± 0.3	8.7	± 0.1	33.1	± 0.3	32.1	± 0.4

Annexe 3: Fatty acids composition of the neutral lipids in *C. gigas* digestive gland at both Comprian and Jacquets stations from March 31st to July 22nd. The results are expressed as percentage of total fatty acids (means ± SD).

Sampled date	**March 31st**		**April 14th**		**April 28th**		**May 27th**		**June 23rd**		**July 22nd**	
Site (n)%	**Comprian** *n = 4*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n = 5*
Fatty acids (%)												
iso 15:0	0.3 ± 0.2	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
*ai*15:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
iso 17:0	0.5 ± 0.1	0.4 ± 0.0	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.8 ± 0.1	0.7 ± 0.0	0.8 ± 0.0	0.7 ± 0.0	0.7 ± 0.0	0.9 ± 0.1	0.6 ± 0.1
*ai*17:0	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.4 ± 0.1
∑ BFA	1.1 ± 0.2	0.9 ± 0.0	1.0 ± 0.2	1.1 ± 0.1	1.0 ± 0.0	1.2 ± 0.1	1.2 ± 0.1	1.2 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.5 ± 0.1	1.3 ± 0.1
14:0	5.1 ± 0.5	5.0 ± 0.2	3.2 ± 0.3	3.8 ± 0.1	4.9 ± 0.6	4.5 ± 1.3	3.7 ± 1.3	3.5 ± 1.0	5.4 ± 2.5	4.2 ± 1.0	3.1 ± 0.8	6.0 ± 1.0
15:0	0.4 ± 0.0	0.4 ± 0.0	0.5 ± 0.1	0.6 ± 0.0	0.5 ± 0.0	0.6 ± 0.0	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.9 ± 0.3	0.6 ± 0.1
16:0	13.2 ± 0.7	14.6 ± 0.7	16.1 ± 0.8	17.4 ± 0.8	18.3 ± 1.9	19.7 ± 1.4	19.5 ± 3.0	19.7 ± 1.6	23.2 ± 5.5	21.9 ± 3.9	20.5 ± 2.7	20.1 ± 0.7
17:0	1.2 ± 0.2	0.9 ± 0.0	1.2 ± 0.1	1.2 ± 0.1	1.1 ± 0.2	1.5 ± 0.1	1.5 ± 0.3	1.6 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	2.2 ± 0.4	1.3 ± 0.1
18:0	2.9 ± 0.5	3.2 ± 0.8	4.1 ± 0.3	3.4 ± 0.2	4.0 ± 0.4	4.2 ± 0.3	4.7 ± 0.7	5.3 ± 0.9	4.6 ± 0.9	4.1 ± 0.1	8.2 ± 1.3	4.8 ± 0.6
22:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.3	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
∑ SFA	23.0 ± 0.5	24.1 ± 1.5	25.1 ± 1.0	26.4 ± 1.0	28.8 ± 2.3	30.6 ± 2.4	30.1 ± 4.2	30.9 ± 1.6	35.3 ± 7.3	32.2 ± 5.2	34.9 ± 4.6	32.9 ± 0.9
16:1n-9	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
16:1n-7	6.0 ± 0.9	5.7 ± 0.3	3.4 ± 0.3	3.9 ± 0.1	4.5 ± 0.6	4.1 ± 0.7	3.3 ± 0.8	3.2 ± 1.0	3.6 ± 1.3	3.9 ± 0.7	3.4 ± 0.7	7.5 ± 1.3
16:1n-5	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1
18:1n-9	2.9 ± 0.2	3.4 ± 1.4	4.2 ± 0.3	4.8 ± 0.3	3.0 ± 0.6	4.3 ± 0.2	3.9 ± 0.6	4.2 ± 0.3	3.7 ± 0.3	3.8 ± 0.2	3.1 ± 0.2	2.8 ± 0.3
18:1n-7	6.4 ± 0.5	5.6 ± 1.7	6.3 ± 0.7	6.2 ± 0.4	6.2 ± 0.5	6.3 ± 0.7	6.5 ± 0.9	6.4 ± 0.5	5.1 ± 0.7	5.3 ± 0.3	5.1 ± 1.1	5.9 ± 0.4
18:1n-5	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0
20:1n-9	0.4 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.4 ± 0.2	0.4 ± 0.0	0.5 ± 0.1	0.3 ± 0.0
20:1n-7	3.6 ± 0.2	3.1 ± 0.3	3.6 ± 0.7	2.7 ± 0.4	3.3 ± 0.4	2.9 ± 0.4	4.0 ± 0.6	3.6 ± 0.7	3.1 ± 1.5	3.0 ± 0.8	4.0 ± 0.4	3.1 ± 0.3
22:1n-9	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.2	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.0	0.1 ± 0.0
∑ MUFA	20.2 ± 0.8	18.7 ± 0.7	18.7 ± 0.6	18.9 ± 0.3	18.3 ± 0.7	19.1 ± 1.1	19.5 ± 1.1	19.0 ± 0.6	17.0 ± 1.2	17.3 ± 0.8	16.9 ± 1.2	20.4 ± 0.9
16:2n-4	1.1 ± 0.2	1.1 ± 0.3	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.9 ± 0.2
16:3n-4	1.0 ± 0.2	0.7 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.0	0.2 ± 0.1	0.4 ± 0.2
16:3n-6	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.0
16:4n-3	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.2 ± 0.0	0.1 ± 0.0
16:4n-1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.4 ± 0.1	0.2 ± 0.0
18:2n-6	1.5 ± 0.1	1.4 ± 0.1	2.2 ± 0.2	2.4 ± 0.1	1.8 ± 0.3	2.1 ± 0.2	1.8 ± 0.1	1.9 ± 0.3	1.7 ± 0.3	2.0 ± 0.1	1.3 ± 0.1	1.4 ± 0.2
18:2n-4	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.2	0.4 ± 0.1	0.4 ± 0.0
18:3n-6	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0
18:3n-4	0.4 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0
18:3n-3	1.1 ± 0.1	1.3 ± 0.2	1.2 ± 0.1	1.5 ± 0.1	1.2 ± 0.2	1.4 ± 0.4	1.5 ± 0.2	1.5 ± 0.4	2.1 ± 0.4	2.2 ± 0.7	1.7 ± 0.3	1.8 ± 0.3
18:4n-3	3.9 ± 0.2	4.2 ± 0.3	3.5 ± 0.5	3.9 ± 0.2	3.4 ± 0.3	3.8 ± 0.5	3.7 ± 0.6	3.6 ± 0.6	4.2 ± 1.0	4.6 ± 0.8	3.2 ± 0.5	3.6 ± 0.2
18:5n-3	0.7 ± 0.2	0.9 ± 0.2	1.0 ± 0.1	1.2 ± 0.1	1.1 ± 0.4	1.4 ± 0.3	1.5 ± 0.3	1.6 ± 0.3	1.3 ± 0.5	1.1 ± 0.1	2.3 ± 0.5	1.3 ± 0.2
20:2i	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.1 ± 0.0
20:2j	0.5 ± 0.1	0.6 ± 0.1	0.9 ± 0.2	1.0 ± 0.2	1.1 ± 0.2	1.1 ± 0.2	1.0 ± 0.2	0.9 ± 0.1	0.9 ± 0.0	0.9 ± 0.1	0.8 ± 0.2	0.7 ± 0.1
20:2n-6	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.2	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0
20:3n-6	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:4n-6	1.5 ± 0.2	1.3 ± 0.1	1.6 ± 0.1	1.5 ± 0.1	1.6 ± 0.2	1.4 ± 0.2	1.6 ± 0.4	1.5 ± 0.2	1.5 ± 0.6	1.5 ± 0.2	2.1 ± 0.2	1.5 ± 0.2
20:4n-3	0.5 ± 0.0	0.6 ± 0.0	0.5 ± 0.0	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.6 ± 0.0	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1
20:5n-3	29.1 ± 1.6	29.3 ± 1.0	24.9 ± 1.3	22.7 ± 1.1	23.1 ± 1.8	20.2 ± 1.7	17.4 ± 1.7	17.0 ± 1.4	14.7 ± 0.8	17.7 ± 4.6	14.1 ± 2.2	18.7 ± 1.6
21:4n-6	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.2	0.6 ± 0.1	0.7 ± 0.3	0.3 ± 0.2	0.2 ± 0.1	0.4 ± 0.1	0.2 ± 0.0
21:5n-3	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.3	1.3 ± 0.7	0.8 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.8 ± 0.0	0.8 ± 0.2	0.8 ± 0.1	0.7 ± 0.1	0.7 ± 0.1
22:2i	0.1 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.2	0.4 ± 0.0	0.5 ± 0.1	0.2 ± 0.0
22:2j	1.2 ± 0.2	1.1 ± 0.1	2.0 ± 0.4	1.6 ± 0.3	2.2 ± 0.2	1.8 ± 0.2	2.5 ± 0.5	2.6 ± 0.8	2.6 ± 1.3	2.2 ± 0.0	3.4 ± 0.5	1.6 ± 0.3
22:3nmi	0.1 ± 0.0	0.2 ± 0.1	0.3 ± 0.2	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.7 ± 1.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0
22:4n-6	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0
22:5n-6	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0
22:5n-3	1.2 ± 1.0	0.7 ± 0.1	0.9 ± 0.2	0.7 ± 0.0	0.8 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.2	0.8 ± 0.1	0.9 ± 0.1	0.7 ± 0.1
22:6n-3	8.1 ± 1.1	8.3 ± 0.5	10.7 ± 1.5	9.4 ± 0.1	9.0 ± 0.7	8.7 ± 1.1	10.3 ± 2.3	9.9 ± 1.6	9.7 ± 3.5	10.1 ± 1.9	9.7 ± 1.2	7.8 ± 0.8
∑ PUFA	54.8 ± 0.9	54.8 ± 1.4	54.0 ± 1.5	51.4 ± 1.4	50.5 ± 1.5	47.9 ± 2.5	48.1 ± 4.2	47.4 ± 2.1	45.7 ± 6.5	48.5 ± 4.8	45.3 ± 3.3	44.6 ± 1.2
16:0 DMA	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
16:1n-7 DMA	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.6 ± 0.2	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.0
17:0 DMA	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0
18:0 DMA	0.3 ± 0.1	0.7 ± 0.2	0.6 ± 0.2	1.0 ± 0.1	0.6 ± 0.4	0.5 ± 0.2	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.2	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
20:1n-7 DMA	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.0
∑ DMA	0.8 ± 0.1	1.4 ± 0.3	1.2 ± 0.3	2.2 ± 0.4	1.3 ± 0.7	1.3 ± 0.3	1.1 ± 0.3	1.4 ± 0.4	0.9 ± 0.2	0.8 ± 0.2	1.3 ± 0.4	0.9 ± 0.1
Trophic indices												
∑ n-3 (%)	45.4 ± 1.2	46.0 ± 1.2	43.6 ± 1.5	41.4 ± 1.4	40.2 ± 1.5	37.8 ± 3.1	36.9 ± 3.5	36.0 ± 1.4	34.4 ± 3.5	38.0 ± 4.9	33.4 ± 3.5	35.4 ± 1.2
∑ n-6 (%)	4.2 ± 0.4	3.8 ± 0.1	5.1 ± 0.2	5.3 ± 0.2	4.7 ± 0.1	4.9 ± 0.4	5.4 ± 0.5	5.4 ± 0.3	4.8 ± 0.6	5.0 ± 0.3	5.2 ± 0.3	4.2 ± 0.4
n-3/n-6	11.0 ± 1.1	12.2 ± 0.3	8.5 ± 0.6	7.8 ± 0.3	8.6 ± 0.4	7.8 ± 1.1	6.8 ± 0.3	6.6 ± 0.3	7.1 ± 0.5	7.6 ± 1.0	6.5 ± 0.7	8.5 ± 0.7
18:1n-9/18:1n-7	0.5 ± 0.1	0.8 ± 0.8	0.7 ± 0.1	0.8 ± 0.1	0.5 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.5 ± 0.1
20:5n-3/22:6n-3	3.7 ± 0.8	3.5 ± 0.3	2.4 ± 0.4	2.4 ± 0.1	2.6 ± 0.4	2.3 ± 0.2	1.7 ± 0.3	1.8 ± 0.4	1.6 ± 0.4	1.7 ± 0.1	1.5 ± 0.1	2.4 ± 0.4

BFA – Branched fatty acids, SFA – saturated fatty acids, MUFA – monounsaturated fatty acids, PUFA – polyunsaturated fatty acids. The prefix ai denotes branched fatty acids from the anteiso series

Annexe 4: Fatty acids composition of the polar lipids in *C. gigas* digestive gland at both Comprian and Jacquets stations from March 31st to July 22nd. The results are expressed as percentage of total fatty acids (means ± SD).

Sampled date	**March 31st**		**April 14th**		**April 28th**		**May 27th**		**June 23rd**		**July 22nd**	
	Comprian	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**	**Comprian**	**Jacquets**
Site (n)	*n = 4*	*n = 5*	*n = 5*	*n = 4*	*n = 5*	*n = 5*	*n = 5*	*n = 5*	*n = 5*	*n = 4*	*n = 5*	*n = 5*
Fatty acids (%)												
iso 15:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
*ai*15:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
iso 17:0	0.7 ± 0.1	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.0	0.6 ± 0.7
*ai*17:0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.1	0.3 ± 0.0
∑ BFA	1.1 ± 0.2	1.0 ± 0.1	1.0 ± 0.0	1.1 ± 0.0	1.1 ± 0.1	1.0 ± 0.1	1.2 ± 0.1	1.1 ± 0.0	1.2 ± 0.1	1.3 ± 0.2	1.3 ± 0.1	1.1 ± 0.1
14:0	1.8 ± 0.1	1.8 ± 0.1	1.3 ± 0.1	1.3 ± 0.0	1.2 ± 0.1	1.6 ± 0.2	1.1 ± 0.2	1.0 ± 0.0	0.9 ± 0.1	0.9 ± 0.2	1.5 ± 0.1	1.8 ± 0.0
15:0	0.4 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.7 ± 0.1
16:0	12.9 ± 0.6	13.1 ± 0.3	13.2 ± 0.6	13.4 ± 1.0	13.4 ± 0.7	13.0 ± 0.3	14.4 ± 1.8	15.3 ± 2.2	13.8 ± 1.7	14.9 ± 1.4	15.0 ± 1.5	15.4 ± 0.6
17:0	1.2 ± 0.1	1.2 ± 0.0	1.3 ± 0.0	1.3 ± 0.0	1.3 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.4 ± 0.0
18:0	4.7 ± 0.3	5.2 ± 0.3	6.0 ± 0.3	5.8 ± 0.4	6.3 ± 0.5	5.1 ± 0.5	5.2 ± 0.5	5.6 ± 0.6	4.8 ± 0.5	5.3 ± 0.8	5.7 ± 0.5	5.3 ± 0.2
22:0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0
∑ SFA	21.3 ± 0.6	21.8 ± 0.5	22.3 ± 0.4	22.4 ± 1.1	22.8 ± 1.1	21.3 ± 0.7	22.7 ± 1.3	23.8 ± 1.9	21.7 ± 1.6	23.4 ± 1.6	24.5 ± 1.2	24.7 ± 0.5
16:1n-9	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
16:1n-7	1.5 ± 0.2	1.3 ± 0.1	1.1 ± 0.1	1.0 ± 0.2	1.0 ± 0.1	1.2 ± 0.2	0.7 ± 0.1	0.7 ± 0.0	0.9 ± 0.1	0.8 ± 0.1	1.1 ± 0.1	1.3 ± 0.2
16:1n-5	0.2 ± 0.2	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.9	0.3 ± 0.0	0.4 ± 0.1	0.5 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.1
18:1n-9	1.8 ± 0.1	1.8 ± 0.1	2.1 ± 0.2	2.5 ± 0.1	1.9 ± 0.2	2.0 ± 0.2	1.9 ± 0.1	1.9 ± 0.1	2.5 ± 0.1	2.4 ± 0.3	1.7 ± 0.1	1.7 ± 0.1
18:1n-7	4.6 ± 0.2	4.8 ± 0.9	4.0 ± 0.5	4.4 ± 0.2	4.2 ± 0.2	4.3 ± 0.4	3.2 ± 0.3	3.1 ± 0.2	3.4 ± 0.3	3.2 ± 0.4	3.6 ± 0.3	4.3 ± 0.2
18:1n-5	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
20:1n-9	0.7 ± 0.1	0.6 ± 0.2	0.7 ± 0.0	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.0	0.4 ± 0.0
20:1n-7	5.0 ± 0.3	5.2 ± 0.3	5.1 ± 0.3	4.9 ± 0.3	5.5 ± 0.6	4.5 ± 0.2	4.6 ± 0.3	4.4 ± 0.2	4.1 ± 0.1	4.1 ± 0.1	3.9 ± 0.1	3.9 ± 0.2
22:1n-9	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
∑ MUFA	14.3 ± 0.5	14.3 ± 0.8	13.4 ± 0.6	14.0 ± 0.6	13.8 ± 0.9	13.4 ± 0.5	11.9 ± 0.6	11.4 ± 0.2	12.2 ± 0.4	11.7 ± 0.6	11.5 ± 0.4	12.2 ± 0.7
16:2n-4	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
16:3n-4	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.4 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
16:3n-6	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
16:4n-3	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
16:4n-1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
18:2n-6	1.0 ± 0.1	1.1 ± 0.1	1.4 ± 0.1	1.8 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.1 ± 0.1	1.2 ± 0.1	1.2 ± 0.1	1.0 ± 0.0	1.0 ± 0.1
18:2n-4	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
18:3n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0
18:3n-4	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
18:3n-3	0.5 ± 0.0	0.7 ± 0.0	0.7 ± 0.1	0.9 ± 0.0	0.5 ± 0.1	0.7 ± 0.0	0.8 ± 0.1	0.9 ± 0.1	1.1 ± 0.1	1.0 ± 0.1	1.1 ± 0.0	1.0 ± 0.1
18:4n-3	1.8 ± 0.2	1.9 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.0 ± 0.2	1.6 ± 0.2	1.5 ± 0.4	1.3 ± 0.2	1.3 ± 0.1	1.1 ± 0.1	1.5 ± 0.1	1.5 ± 0.1
18:5n-3	1.2 ± 0.1	0.9 ± 0.2	1.6 ± 0.3	2.0 ± 0.0	1.9 ± 0.2	1.7 ± 0.1	1.8 ± 0.3	1.8 ± 0.2	2.1 ± 0.3	2.3 ± 0.4	2.7 ± 0.2	2.2 ± 0.2
20:2i	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
20:2j	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
20:2n-6	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:3n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:4n-6	2.9 ± 0.3	2.5 ± 0.1	2.7 ± 0.0	2.8 ± 0.2	2.9 ± 0.2	2.6 ± 0.2	2.8 ± 0.2	2.7 ± 0.2	3.2 ± 0.2	3.3 ± 0.1	3.4 ± 0.2	3.0 ± 0.1
20:4n-3	0.5 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.0	0.5 ± 0.0	0.5 ± 0.0
20:5n-3	20.8 ± 0.6	22.2 ± 0.4	20.0 ± 0.4	18.9 ± 0.4	18.4 ± 2.1	19.5 ± 1.1	16.0 ± 1.3	16.0 ± 0.5	15.1 ± 0.8	14.1 ± 0.4	15.7 ± 1.0	17.6 ± 0.9
21:4n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
21:5n-3	0.7 ± 0.1	0.9 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.5 ± 0.1	0.6 ± 0.0	0.6 ± 0.1	0.5 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.0	0.7 ± 0.0
22:2i	0.8 ± 0.1	0.6 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.0	0.9 ± 0.2	0.8 ± 0.1	0.9 ± 0.1	0.9 ± 0.2	0.8 ± 0.0	0.7 ± 0.8
22:2j	4.4 ± 0.4	4.6 ± 0.3	5.1 ± 0.4	5.0 ± 0.4	6.2 ± 0.7	4.9 ± 0.4	5.1 ± 0.8	4.8 ± 0.7	5.0 ± 0.6	4.9 ± 0.7	4.6 ± 0.2	4.1 ± 0.2
22:3nmi	0.3 ± 0.2	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
22:4n-6	0.4 ± 0.1	0.3 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0
22:5n-6	0.5 ± 0.0	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.4 ± 0.0
22:5n-3	1.3 ± 0.1	1.4 ± 0.1	1.4 ± 0.2	1.2 ± 0.0	1.2 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.3 ± 0.1
22:6n-3	12.9 ± 0.8	14.4 ± 0.4	13.3 ± 0.9	12.7 ± 0.9	11.3 ± 1.4	13.6 ± 0.7	15.1 ± 1.5	14.9 ± 1.5	13.9 ± 1.6	12.7 ± 2.2	12.8 ± 0.5	12.2 ± 0.4
∑ PUFA	52.2 ± 0.6	54.6 ± 0.5	52.8 ± 1.0	51.8 ± 0.7	49.3 ± 2.6	52.0 ± 1.3	50.6 ± 2.4	49.8 ± 1.0	49.3 ± 1.3	47.0 ± 1.5	49.5 ± 1.1	48.9 ± 0.4
16:0 DMA	0.8 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.4 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.0	0.4 ± 0.1
16:1n-7 DMA	0.9 ± 0.5	1.7 ± 0.2	1.8 ± 0.3	1.7 ± 0.7	2.5 ± 0.6	2.3 ± 0.6	3.1 ± 0.5	3.1 ± 0.2	3.2 ± 0.6	3.1 ± 0.4	3.2 ± 0.4	2.8 ± 0.2
17:0 DMA	0.8 ± 0.1	0.5 ± 0.0	0.6 ± 0.0	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.6 ± 0.0	0.6 ± 0.1
18:0 DMA	5.1 ± 0.7	2.9 ± 0.7	4.4 ± 0.3	4.6 ± 0.2	5.1 ± 1.0	5.0 ± 0.6	5.2 ± 0.8	5.8 ± 0.6	6.4 ± 1.0	6.9 ± 1.2	4.7 ± 0.4	5.1 ± 0.4
20:1n-7 DMA	0.9 ± 0.3	0.3 ± 0.2	0.6 ± 0.1	0.3 ± 0.0	0.7 ± 0.2	0.7 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.6 ± 0.2	0.2 ± 0.0	0.3 ± 0.1
∑ DMA	8.5 ± 0.5	5.8 ± 0.9	7.8 ± 0.5	7.6 ± 0.9	9.4 ± 1.2	9.2 ± 0.5	9.9 ± 1.5	10.6 ± 1.0	11.3 ± 1.6	12.1 ± 1.9	9.4 ± 0.7	9.2 ± 0.5
Trophic indices												
∑ n-3	39.8 ± 0.8	43.0 ± 0.4	39.7 ± 1.0	38.4 ± 0.9	35.2 ± 3.4	39.4 ± 1.9	37.8 ± 3.1	37.3 ± 1.5	36.0 ± 1.7	33.6 ± 2.0	36.3 ± 1.1	37.1 ± 0.6
∑ n-6	5.5 ± 0.4	5.1 ± 0.2	5.7 ± 0.1	6.1 ± 0.2	5.5 ± 0.1	5.4 ± 0.3	5.5 ± 0.2	5.2 ± 0.1	6.0 ± 0.17	6.1 ± 0.3	6.2 ± 0.2	5.6 ± 0.2
n-3/n-6	7.3 ± 0.5	8.4 ± 0.2	7.0 ± 0.3	6.3 ± 0.0	6.4 ± 0.7	7.3 ± 0.7	6.8 ± 0.7	7.1 ± 0.3	6.0 ± 0.3	5.5 ± 0.2	5.9 ± 0.3	6.6 ± 0.3
18:1n-9/18:1n-7	0.4 ± 0.0	0.4 ± 0.1	0.5 ± 0.0	0.6 ± 0.0	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.8 ± 0.05	0.8 ± 0.1	0.5 ± 0.0	0.4 ± 0.0
20:5n-3/22:6n-3	1.6 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.5 ± 0.1	1.6 ± 0.2	1.4 ± 0.0	1.1 ± 0.1	1.1 ± 0.1	1.1 ± 0.13	1.1 ± 0.2	1.2 ± 0.1	1.4 ± 0.1

BFA – Branched fatty acids, SFA – saturated fatty acids, MUFA – monounsaturated fatty acids, PUFA – polyunsaturated fatty acids. The prefix ai denotes branched fatty acids from the anteiso series

Annexe 5: Fatty acids composition of the neutral lipids in *C. gigas* gonad+mantle at both Comprian and Jacquets stations from March 31st to July 22nd. The results are expressed as percentage of total fatty acids (means ± SD).

Sampled date	**March 31st**		**April 14th**		**April 28th**		**May 27th**		**June 23rd**		**July 22nd**	
Site (n)	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 3*	**Comprian** *n = 4*	**Jacquets** *n = 4*
Fatty acids (%)												
iso 15:0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.0	0.2 ± 0.1	0.3 ± 0.1
*ai*15:0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
iso 17:0	0.8 ± 0.2	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.0	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.1
*ai*17:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.2
∑ BFA	1.1 ± 0.1	1.1 ± 0.1	1 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.2 ± 0.1	1.1 ± 0.2	1.2 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.2 ± 0.1	1.3
14:0	2.4 ± 1.2	3.3 ± 0.2	3.2 ± 0.2	4.0 ± 0.2	5.3 ± 1.3	5.5 ± 1.4	4.5 ± 2.4	5.0 ± 2.1	6.3 ± 2.9	5.9 ± 0.9	2.2 ± 1.0	3.2 ± 0.9
15:0	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.7 ± 0.2	0.7 ± 0.2
16:0	16 ± 1.6	17.7 ± 0.6	16.9 ± 1.6	18.3 ± 0.9	20.2 ± 3.1	22.3 ± 1.8	21.8 ± 4.0	23.0 ± 4.4	24.9 ± 4.2	25.2 ± 2.1	19.0 ± 3.4	18.5 ± 3.9
17:0	1.3 ± 0.3	1.3 ± 0.1	1.2 ± 0.2	1.3 ± 0.1	1.2 ± 0.1	1.4 ± 0.2	1.6 ± 0.4	1.4 ± 0.4	1.3 ± 0.2	1.3 ± 0.1	1.9 ± 0.2	1.7 ± 0.3
18:0	5.4 ± 2.4	3.9 ± 0.2	4.0 ± 0.8	3.5 ± 0.4	4.1 ± 0.4	4.1 ± 0.5	4.7 ± 1.0	4.4 ± 0.9	4.1 ± 1.0	3.7 ± 0.6	7.1 ± 0.9	5.8 ± 0.4
22:0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.2	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
∑ SFA	25.9 ± 1.2	26.9 ± 0.8	26 ± 2.8	27.8 ± 1	31.5 ± 3.9	34.1 ± 2.5	33.3 ± 5.3	34.6 ± 5.5	37.3 ± 5.8	36.9 ± 2.5	30.9 ± 4.3	30
16:1n-9	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.4 ± 0.3
16:1n-7	3 ± 1.0	3.4 ± 0.3	3.1 ± 0.4	3.9 ± 0.2	4.5 ± 0.8	4.7 ± 0.5	3.5 ± 1.4	4.2 ± 1.6	4.0 ± 1.4	4.9 ± 0.8	2.2 ± 0.6	3.3 ± 0.9
16:1n-5	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.4 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.2 ± 0.2	0.4 ± 0.2	0.2 ± 0.1	0.3 ± 0.0	0.2 ± 0.1	0.7 ± 0.9
18:1n-9	4 ± 1.3	3.4 ± 0.4	4.4 ± 0.1	4.6 ± 0.4	3.4 ± 0.5	4.5 ± 0.3	4.0 ± 0.8	4.7 ± 1.8	3.3 ± 0.3	3.7 ± 0.2	3.8 ± 0.8	3.3 ± 0.9
18:1n-7	6.2 ± 1.0	6.1 ± 0.6	6.3 ± 0.8	6.4 ± 0.7	6.4 ± 0.7	6.0 ± 0.7	6.1 ± 1.2	4.8 ± 0.9	4.8 ± 0.9	5.0 ± 0.3	5.7 ± 1.7	5.0 ± 1.4
18:1n-5	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.2
20:1n-9	0.8 ± 0.5	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	0.2 ± 0.0	0.4 ± 0.1	0.5 ± 0.1
20:1n-7	5.9 ± 2.5	3.0 ± 0.6	2.9 ± 0.3	2.3 ± 0.3	3.0 ± 0.6	2.6 ± 0.4	3.3 ± 0.9	2.9 ± 1.2	2.6 ± 1.7	1.8 ± 0.3	4.0 ± 0.9	3.8 ± 0.6
22:1n-9	0.3 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.2	0.1 ± 0.0	0.4 ± 0.2	0.2 ± 0.0
∑ MUFA	20.9 ± 2.6	17.1 ± 1.1	17.8 ± 0.4	18.5 ± 0.7	18.9 ± 0.8	19.1 ± 0.8	18.5 ± 2	18.2 ± 1.8	15.8 ± 1.9	16.5 ± 1.1	17.3 ± 2.2	17.3
16:2n-4	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	0.3 ± 0.1
16:3n-4	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.1
16:3n-6	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1
16:4n-3	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
16:4n-1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
18:2n-6	1.2 ± 0.3	1.4 ± 0.1	2.2 ± 0.3	2.3 ± 0.1	2.0 ± 0.4	2.2 ± 0.2	1.8 ± 0.1	1.9 ± 0.2	1.8 ± 0.2	2.2 ± 0.1	1.4 ± 0.4	1.4 ± 0.2
18:2n-4	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.6 ± 0.2	0.4 ± 0.0	0.4 ± 0.1	0.3 ± 0.1
18:3n-6	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
18:3n-4	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.1
18:3n-3	0.8 ± 0.3	1.5 ± 0.4	1.1 ± 0.1	1.6 ± 0.3	1.3 ± 0.2	1.6 ± 0.3	1.4 ± 0.4	1.6 ± 0.5	2.4 ± 0.7	2.7 ± 0.1	1.3 ± 0.5	1.2 ± 0.3
18:4n-3	2.8 ± 0.9	3.7 ± 0.5	3.5 ± 0.3	4.1 ± 0.4	3.6 ± 0.4	4.0 ± 0.4	3.7 ± 1.4	3.9 ± 1.2	5.1 ± 1.5	5.8 ± 0.4	2.4 ± 0.5	2.3 ± 0.7
18:5n-3	1.2 ± 0.3	1.4 ± 0.5	1.0 ± 0.1	1.2 ± 0.1	1.1 ± 0.3	1.2 ± 0.2	1.7 ± 0.7	1.3 ± 0.6	1.0 ± 0.6	0.9 ± 0.1	2.7 ± 0.8	2.4 ± 0.3
20:2i	0.2 ± 0.0	0.1 ± 0.0	0.6 ± 1.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:2j	1.1 ± 0.2	0.8 ± 0.0	0.9 ± 0.3	1.1 ± 0.2	1.2 ± 0.2	1.1 ± 0.2	1.1 ± 0.2	1.0 ± 0.1	0.8 ± 0.0	0.9 ± 0.1	1.1 ± 0.1	1.0 ± 0.2
20:2n-6	0.3 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.4	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0
20:3n-6	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:4n-6	2.9 ± 1.2	1.8 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	1.5 ± 0.5	1.3 ± 0.2	1.4 ± 0.4	1.5 ± 0.7	1.2 ± 0.5	1.0 ± 0.1	2.2 ± 0.6	2.2 ± 0.5
20:4n-3	0.5 ± 0.1	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.4 ± 0.1	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.1
20:5n-3	20.4 ± 3.9	22.8 ± 1.4	23.5 ± 2.7	22.0 ± 0.9	20.7 ± 2.0	17.9 ± 1.2	16.2 ± 1.4	15.5 ± 0.9	14.8 ± 0.9	15.5 ± 0.6	15.3 ± 1.5	16.1 ± 2.0
21:4n-6	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.5 ± 0.3	0.6 ± 0.3	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.0
21:5n-3	0.9 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	1.0 ± 0.0	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.6	0.7 ± 0.2
22:2i	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.3	0.3 ± 0.0	0.5 ± 0.2	0.6 ± 0.4
22:2j	2.6 ± 1.0	1.6 ± 0.2	1.5 ± 0.3	1.4 ± 0.1	1.8 ± 0.3	1.6 ± 0.3	2.3 ± 0.5	2.1 ± 0.5	2.1 ± 1.3	1.7 ± 0.3	3.8 ± 1.0	3.5 ± 1.4
22:3nmi	0.1 ± 0.1	0.5 ± 0.3	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.4 ± 0.1
22:4n-6	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	1.3 ± 2.2	0.3 ± 0.1
22:5n-6	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.4 ± 0.1	0.4 ± 0.1
22:5n-3	1.2 ± 0.8	0.9 ± 0.1	0.9 ± 0.1	0.7 ± 0.0	0.6 ± 0.1	0.6 ± 0.0	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	1.0 ± 0.2	0.9 ± 0.3
22:6n-3	11 ± 1.2	11.3 ± 0.9	11.6 ± 1.6	9.5 ± 0.3	7.9 ± 0.9	7.4 ± 0.2	10.1 ± 3.9	9.3 ± 2.5	9.9 ± 3.4	8.1 ± 0.8	11.3 ± 2.8	10.7 ± 1.9
∑ PUFA	50.9 ± 3.1	52.7 ± 1.2	53.4 ± 2.5	50.3 ± 0.6	46.7 ± 2.9	44.4 ± 1.8	45.9 ± 4.1	44.3 ± 4.1	44.9 ± 4	44.6 ± 1.5	49.1 ± 5	47.2
16:0 DMA	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.3
16:1n-7 DMA	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.6 ± 0.9	0.9 ± 1.0	0.3 ± 0.1	0.3 ± 0.2	0.5 ± 0.4	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.2	1.0 ± 1.2
17:0 DMA	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.4 ± 0.3
18:0 DMA	0.5 ± 0.3	1.1 ± 0.3	0.8 ± 0.3	1.0 ± 0.2	0.5 ± 0.2	0.6 ± 0.2	0.5 ± 0.3	0.8 ± 0.6	0.4 ± 0.1	0.5 ± 0.0	0.6 ± 0.3	2.1 ± 2.8
20:1n-7 DMA	0.2 ± 0.1	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.2	0.3 ± 0.3
∑ DMA	1.3 ± 0.4	2.3 ± 0.5	1.6 ± 0.6	2.3 ± 1.1	1.8 ± 1.1	1.4 ± 0.4	1.2 ± 0.6	1.8 ± 1.2	0.9 ± 0.1	0.9 ± 0.1	1.5 ± 0.5	4.1
Trophic indices												
∑ n-3 (%)	39.1 ± 5	43.1 ± 1.4	43.0 ± 3.6	40.7 ± 0.8	36.7 ± 2.8	34.2 ± 1.5	35.4 ± 4.3	33.7 ± 3.3	35.3 ± 1.5	35.1 ± 1.2	35.7 ± 2.5	35 ± 0.8
∑ n-6 (%)	5.8 ± 1.4	4.7 ± 0.3	5.2 ± 0.2	5.2 ± 0.2	4.8 ± 0.4	5.2 ± 0.3	4.9 ± 0.4	5.3 ± 1.0	4.4 ± 0.8	4.6 ± 0.2	6.4 ± 2.3	5.2 ± 0.7
n-3/n-6	7.2 ± 2.3	9.2 ± 0.8	8.2 ± 0.7	7.8 ± 0.4	7.7 ± 0.5	6.6 ± 0.3	7.3 ± 1.1	6.5 ± 1.3	8.2 ± 1	7.6 ± 0.3	6 ± 1.3	6.8 ± 1
18:1n-9/18:1n-7	0.7 ± 0.3	0.6 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.5 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	1 ± 0.5	0.7 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.7 ± 0.1
20:5n-3/22:6n-3	1.9 ± 0.5	2 ± 0.3	2 ± 0.3	2.3 ± 0.1	2.6 ± 0.2	2.4 ± 0.1	1.7 ± 0.4	1.7 ± 0.4	1.6 ± 0.5	1.9 ± 0.1	1.4 ± 0.4	1.6 ± 0.4

BFA – Branched fatty acids, SFA – saturated fatty acids, MUFA – monounsaturated fatty acids, PUFA – polyunsaturated fatty acids. The prefix ai denotes branched fatty acids from the anteiso series

Annexe 6: Fatty acids composition of the polar lipids in *C. gigas* gonad+mantle at both Comprian and Jacquets stations from March 31st to July 22nd. The results are expressed as percentage of total fatty acids (means ± SD).

ampled date	**March 31st**		**April 14th**		**April 28th**		**May 27th**		**June 23rd**		**July 22nd**	
Site (n)	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n = 5*	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n = 4*	**Comprian** *n = 5*	**Jacquets** *n =5*
Fatty acids (%)												
iso 15:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
*ai*15:0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
iso 17:0	1.0 ± 0.1	0.9 ± 0.1	1.0 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.2	1.0 ± 0.0	0.9 ± 0.1
*ai*17:0	0.6 ± 0.1	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.4 ± 0.1
∑ BFA	1.8 ± 0.2	1.5 ± 0.2	1.6 ± 0.1	1.5 ± 0.1	1.4 ± 0.2	1.5 ± 0.1	1.2 ± 0.1	1.2 ± 0.2	1.1 ± 0.1	1.2 ± 0.2	1.8 ± 0.1	1.5 ± 0.1
14:0	1.5 ± 0.1	1.4 ± 0.1	1.4 ± 0.2	1.3 ± 0.1	1.3 ± 0.1	1.4 ± 0.1	1.0 ± 0.1	1.1 ± 0.1	1.0 ± 0.2	0.9 ± 0.2	1.3 ± 0.1	1.7 ± 0.3
15:0	0.6 ± 0.3	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.2	0.7 ± 0.1	0.7 ± 0.2	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.2	1.1 ± 0.1	1.0 ± 0.3
16:0	11.2 ± 0.9	11.3 ± 1.0	13.3 ± 1.5	12.2 ± 0.8	11.6 ± 0.6	12.4 ± 1.3	16.3 ± 0.6	16.1 ± 1.3	15.0 ± 2.7	16.8 ± 3.8	14.2 ± 1.0	14.3 ± 3.4
17:0	1.4 ± 0.1	1.4 ± 0.2	1.7 ± 0.2	1.4 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	1.3 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	1.4 ± 0.2	1.6 ± 0.1	1.6 ± 0.2
18:0	4.1 ± 0.4	5.1 ± 0.5	6.8 ± 0.9	5.8 ± 0.1	4.7 ± 0.1	4.9 ± 0.3	3.7 ± 0.1	4.2 ± 0.3	4.1 ± 0.6	4.3 ± 0.9	5.7 ± 0.3	5.5 ± 0.8
22:0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
∑ SFA	18.7 ± 0.6	19.9 ± 1.8	23.8 ± 2.7	21.4 ± 0.9	19.6 ± 0.7	20.7 ± 1.5	23.0 ± 3.3	23.3 ± 1.9	22.0 ± 2.2	24.1 ± 3.7	24.0 ± 1.1	24.1 ± 4.8
16:1n-9	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0
16:1n-7	1.3 ± 0.2	1.1 ± 0.1	1.0 ± 0.1	0.9 ± 0.2	1.0 ± 0.1	0.9 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.7 ± 0.1	1.1 ± 0.2
16:1n-5	0.4 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	0.4 ± 0.0	0.4 ± 0.1	0.6 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	0.5 ± 0.1
18:1n-9	2.1 ± 0.2	1.8 ± 0.2	2.0 ± 0.2	2.3 ± 0.3	1.8 ± 0.1	2.1 ± 0.1	1.8 ± 0.1	1.8 ± 0.1	1.8 ± 0.2	1.8 ± 0.2	2.0 ± 0.1	1.8 ± 0.1
18:1n-7	4.1 ± 0.2	3.6 ± 0.8	3.4 ± 0.4	3.9 ± 0.3	3.6 ± 0.2	3.4 ± 0.4	3.1 ± 0.2	2.4 ± 0.4	2.4 ± 0.5	2.6 ± 0.8	3.0 ± 0.4	3.8 ± 0.8
18:1n-5	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1
20:1n-9	1.0 ± 0.1	0.9 ± 0.2	0.9 ± 0.1	0.9 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.2	0.7 ± 0.1	0.7 ± 0.0
20:1n-7	4.9 ± 0.4	4.9 ± 0.2	5.2 ± 0.6	4.5 ± 0.3	4.7 ± 0.2	4.4 ± 0.2	4.0 ± 0.2	3.8 ± 0.2	3.8 ± 0.4	3.5 ± 0.4	4.2 ± 0.2	4.2 ± 0.5
22:1n-9	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
	14.2 ± 0.8	12.9 ± 0.8	13.2 ± 1.1	13.2 ± 0.5	12.5 ± 0.2	12.6 ± 0.3	10.8 ± 0.5	9.9 ± 1	9.8 ± 0.9	9.7 ± 1.0	11.3 ± 0.3	12.5 ± 1.2
16:2n-4	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.2	0.3 ± 0.1	0.1 ± 0.2	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0
16:3n-4	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
16:3n-6	0.7 ± 0.2	0.3 ± 0.1	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.1	0.3 ± 0.1
16:4n-3	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
16:4n-1	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
18:2n-6	1.1 ± 0.2	1.0 ± 0.1	1.2 ± 0.2	1.6 ± 0.2	1.0 ± 0.3	1.4 ± 0.1	1.3 ± 0.3	1.2 ± 0.1	1.2 ± 0.3	1.2 ± 0.2	1.0 ± 0.0	1.0 ± 0.1
18:2n-4	0.3 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.0
18:3n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
18:3n-4	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.2 ± 0.1
18:3n-3	0.5 ± 0.0	0.4 ± 0.0	0.5 ± 0.1	0.6 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.9 ± 0.2	0.8 ± 0.2	0.6 ± 0.1	0.6 ± 0.1
18:4n-3	1.3 ± 0.1	1.1 ± 0.1	1.0 ± 0.1	1.1 ± 0.2	0.8 ± 0.1	0.9 ± 0.1	1.0 ± 0.1	1.0 ± 0.1	1.2 ± 0.1	1.0 ± 0.2	0.7 ± 0.0	0.8 ± 0.1
18:5n-3	1.3 ± 0.3	1.2 ± 0.1	1.5 ± 0.2	2.0 ± 0.1	1.8 ± 0.2	1.9 ± 0.3	1.8 ± 0.2	2.0 ± 0.3	2.1 ± 0.5	2.4 ± 0.9	3.3 ± 0.4	2.6 ± 0.5
20:2i	0.1 ± 0.0	0.1 ± 0.0	0.3 ± 0.2	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1
20:2j	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.2	0.4 ± 0.0	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.0	0.3 ± 0.1
20:2n-6	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.0
20:3n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
20:4n-6	3.9 ± 0.3	3.3 ± 0.3	3.1 ± 0.2	3.0 ± 0.1	3.4 ± 0.5	3.1 ± 0.4	2.8 ± 0.5	2.8 ± 0.4	2.7 ± 0.2	2.7 ± 0.3	3.8 ± 0.2	3.4 ± 0.3
20:4n-3	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.3 ± 0.0
20:5n-3	16.8 ± 0.5	16.7 ± 0.5	15.3 ± 1.6	15.9 ± 0.7	18.8 ± 1.5	17.1 ± 0.8	16.8 ± 1.5	18.9 ± 0.8	19.0 ± 2.2	18.0 ± 2.5	11.8 ± 0.7	13.7 ± 1.9
21:4n-6	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.0	0.2 ± 0.1
21:5n-3	0.5 ± 0.1	0.5 ± 0.0	0.4 ± 0.0	0.5 ± 0.0	0.4 ± 0.0	0.4 ± 0.0	0.6 ± 0.0	0.4 ± 0.0	0.5 ± 0.2	0.5 ± 0.2	0.3 ± 0.0	0.4 ± 0.1
22:2i	1.1 ± 0.1	0.9 ± 0.1	1.1 ± 0.2	1.0 ± 0.1	1.0 ± 0.1	1.1 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.8 ± 0.2	2.0 ± 2.5	1.1 ± 0.1	1.1 ± 0.1
22:2j	4.5 ± 0.7	4.2 ± 0.4	4.7 ± 0.6	4.5 ± 0.3	5.2 ± 0.4	4.8 ± 0.2	3.8 ± 0.4	4.0 ± 0.2	3.7 ± 0.9	2.9 ± 1.5	5.1 ± 0.2	4.7 ± 0.4
22:3nmi	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.4 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.4 ± 0.0	0.4 ± 0.1
22:4n-6	0.6 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.4 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.0	0.4 ± 0.1	0.6 ± 0.1	0.5 ± 0.1
22:5n-6	0.7 ± 0.0	0.9 ± 0.1	0.9 ± 0.1	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.6 ± 0.1
22:5n-3	1.3 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.2 ± 0.1	1.3 ± 0.0	1.3 ± 0.0	1.4 ± 0.0	1.4 ± 0.0	1.6 ± 0.1	1.6 ± 0.1	1.3 ± 0.1	1.3 ± 0.2
22:6n-3	13.8 ± 0.5	16.1 ± 0.8	13.2 ± 1.5	13.5 ± 0.5	13.0 ± 0.6	13.0 ± 1.0	16.8 ± 0.6	14.8 ± 1.0	15.3 ± 3.3	14.8 ± 4.5	12.7 ± 0.6	12.7 ± 2.2
∑ PUFA	50.7 ± 0.8	51.1 ± 2.0	48 ± 2.4	49.0 ± 0.8	51.2 ± 1.9	49.4 ± 0.6	51.2 ± 1.2	51.3 ± 0.3	52.5 ± 0.6	51.4 ± 2.3	45.8 ± 1	46.2 ± 4.4
16:0 DMA	1.1 ± 0.2	0.9 ± 0.1	0.7 ± 0.2	0.8 ± 0.1	0.9 ± 0.2	0.7 ± 0.1	0.5 ± 0.2	0.5 ± 0.1	0.5 ± 0.2	0.3 ± 0.2	1.0 ± 0.1	0.7 ± 0.2
16:1n-7 DMA	2.3 ± 0.5	1.9 ± 0.3	1.7 ± 0.6	2.3 ± 0.3	2.1 ± 0.6	3.6 ± 0.3	3.0 ± 0.6	3.0 ± 0.3	3.3 ± 0.9	3.0 ± 1.2	3.4 ± 0.4	3.0 ± 1.0
17:0 DMA	1.0 ± 0.1	1.1 ± 0.1	0.9 ± 0.2	1.0 ± 0.1	1.0 ± 0.1	0.9 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.6 ± 0.1	0.5 ± 0.2	0.9 ± 0.1	0.9 ± 0.1
18:0 DMA	5.0 ± 1.0	5.8 ± 1.0	5.2 ± 1.2	5.7 ± 0.4	6.2 ± 1.3	5.6 ± 0.5	5.1 ± 1.3	5.7 ± 0.5	5.8 ± 1.7	5.3 ± 2.4	6.0 ± 0.2	5.7 ± 1.2
20:1n-7 DMA	0.8 ± 0.1	1.0 ± 0.2	0.7 ± 0.2	0.7 ± 0.1	0.9 ± 0.3	0.3 ± 0.0	0.3 ± 0.3	0.4 ± 0.0	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.6 ± 0.2
∑ DMA	10.3 ± 1.4	10.7 ± 1.1	9.2 ± 1.9	10.5 ± 0.5	11.1 ± 2.2	11.1 ± 0.9	9.6 ± 2.2	10.3 ± 1.4	10.4 ± 2.9	9.6 ± 4.1	11.7 ± 0.2	11.0 ± 2.2
Trophic indices												
∑ n-3 (%)	35.8 ± 0.8	37.9 ± 1.4	33.7 ± 3.2	35.3 ± 0.5	36.9 ± 1.7	35.5 ± 0.7	39.5 ± 1.7	39.5 ± 0.7	41.1 ± 1.2	39.6 ± 4.2	31.0 ± 1.0	32.4 ± 3.7
∑ n-6 (%)	7.4 ± 0.4	6.4 ± 0.4	6.5 ± 0.3	6.5 ± 0.3	6.2 ± 0.4	6.1 ± 0.4	5.8 ± 0.4	5.5 ± 0.4	5.6 ± 0.4	5.6 ± 0.5	6.9 ± 0.2	6.3 ± 0.6
n-3/n-6	4.9 ± 0.3	5.9 ± 0.4	5.2 ± 0.3	5.4 ± 0.2	6 ± 0.5	5.8 ± 0.4	6.8 ± 0.5	7.2 ± 0.4	7.4 ± 0.4	7.0 ± 0.9	4.5 ± 0.2	5.2 ± 0.5
18:1n-9/18:1n-7	0.51 ± 0.0	0.5 ± 0.1	0.6 ± 0.0	0.6 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.6 ± 0.0	0.8 ± 0.1	0.7 ± 0.1	1.3 ± 0.2	0.9 ± 0.1	0.5 ± 0.1
20:5n-3/22:6n-3	1.22 ± 0.0	1 ± 0	1.1 ± 0.1	1.2 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	1.02 ± 0.1	1.4 ± 0.2	1.3 ± 0.3	0.7 ± 0.4	0.7 ± 0.0	1.1 ± 0.2

BFA – Branched fatty acids, SFA – saturated fatty acids, MUFA – monounsaturated fatty acids, PUFA – polyunsaturated fatty acids. The prefix ai denotes branched fatty acids from the anteiso series.