



Ifremer

## THÈSE

Présentée à l'Université de Pau et des Pays de l'Adour

École Doctorale Sciences Exactes et leurs Applications – ED 211

**Par Mme Nathalie Caill-Milly**

Pour obtenir le grade de docteur

Spécialité : Physiologie et biologie des organismes-populations-interactions

**Relations entre l'état d'une ressource et son exploitation via la compréhension et la formalisation des interactions de socio-écosystèmes.**

**Application à la palourde japonaise (*Venerupis philippinarum*) du bassin d'Arcachon.**

Soutenue le 11 décembre 2012

Devant le jury constitué de :

<b>M. Philippe GAUDIN</b> , Directeur de Recherche, INRA - Saint-Pée-sur-Nivelle	Président
<b>M. Angel BORJA</b> , Directeur de Recherche, AZTI - TECNALIA - San Sebastian, Espagne	Rapporteur
<b>M. Olivier LE PAPE</b> , Professeur des Universités, AGROCAMPUS OUEST - Rennes	Rapporteur
<b>M. Benoit SAUTOUR</b> , Professeur des Universités, Université de Bordeaux 1 - Arcachon	Examineur
<b>M. Frank D'AMICO</b> , Maître de Conférences, HDR, Université de Pau et des Pays de l'Adour - Anglet	Directeur de thèse
<b>M. Olivier GUYADER</b> , Chargé de Recherche, HDR, IFREMER - Brest	Co-directeur de thèse









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## Résumé

Composante importante de l'écosystème marin benthique, les bivalves exploités sont surtout situés dans la zone littorale dont les caractéristiques spatiales et temporelles engendrent des fluctuations populationnelles naturelles et contribuent à de fortes variations de biomasse et de structure démographique s'ajoutant aux effets d'activités anthropiques. La compréhension des interactions entre l'espèce, son environnement et son exploitation est cruciale. Leur formalisation, y compris pour la gestion, passe par le développement de modèles mathématiques qui visent à décrire le fonctionnement du système, expliquer des phénomènes observés en termes de cause à effet ou prédire l'effets de nouvelles causes. Espèce introduite en France dans les années 1980, la palourde japonaise (*Venerupis philippinarum*) constitue une ressource économique importante pour des zones littorales. Pour le bassin d'Arcachon, les pêcheurs à pied professionnels capturent quelques 600 tonnes par an. Outre la réglementation européenne qui fixe une taille minimale de capture, des mesures de gestion complémentaires sont établies par les structures professionnelles locales de la pêche dans un cadre de cogestion impliquant ces structures, scientifiques et administration.

Ce travail de thèse s'inscrit dans ce contexte en intégrant les traits d'histoire de vie de la population dans le modèle de simulation utilisé à des fins de gestion. A l'échelle locale, l'analyse de forme conventionnelle basée sur des mesures métriques et pondérales établit des relations d'allométrie entre des paires de descripteurs avec un changement significatif de morphologie à partir d'une longueur de 16-20 mm. La variabilité phénotypique intra-site s'articule en trois patrons morphologiques. Dans le bassin d'Arcachon, le caractère globuleux, décrit pour la première fois ici, est associé à de faibles densités et à de fortes proportions d'individus affectés par la maladie du muscle marron, maladie émergente sur le bassin. A l'échelle de la façade atlantique française, trois ratios morphométriques (indices d'élongation, de densité de la valve et de poids de la valve sur sa longueur) discriminent les populations des sites nord (Banc du Guer, golfe du Morbihan) de celles des sites sud (Bellevue, bassin d'Arcachon). Une corrélation significative entre ces ratios et les conditions trophiques approchées par la concentration en chlorophylle a ainsi qu'un lien entre l'indice de densité de la valve et le pourcentage de températures comprises entre 12 et 20°C sont démontrés. La complexité des facteurs intervenant sur la morphologie intra et inter-sites laisse supposer l'intervention d'autres facteurs comme la nature du substrat, ce qui est conforté par des premières analyses de contours. Les travaux ont confirmé l'importance de la température sur les variables d'état du stock notamment lors de la période de reproduction. Pour ces mêmes variables, un rôle majeur des ressources trophiques a aussi été démontré avec des réponses différant selon les stades. Une partie de ces résultats a contribué à des modifications dans le modèle de simulation. Elles ont surtout concerné l'intégration de l'effet des ressources trophiques sur le recrutement, la révision de la production de juvéniles et des taux de croissance par classe de taille, la précision de données de captures et l'ajout d'un effet prix sur les stratégies de pêche. En parallèle à la validation du modèle, l'analyse de sensibilité a mis en évidence la sensibilité du modèle aux paramètres environnementaux et aux variables relatives aux stades les plus jeunes. Dans un contexte de cogestion, l'outil a été utilisé pour réaliser des projections sur le devenir de la population selon différents scénarios de gestion. Les différences de tendances d'évolution de la biomasse en réponse à ces dispositifs d'action ont servi aux gestionnaires pour la définition des mesures de gestion actuellement en vigueur. Au final, le modèle renforce la démarche participative engagée.

**Mots-clés** : bivalve, morphométrie, allométrie, dynamique des populations, système dynamique, gestion, palourde japonaise, *Venerupis philippinarum*

## Abstract

Significant component of the marine benthic ecosystem, exploited bivalves are mainly located inside the coastal area, which temporal and spatial features generate natural population fluctuations and contribute to considerable biomass and demographic structure changes added to anthropogenic activities' effects (fishing, pollution,...). Understanding of the relationships between the species, its environment and its exploitation is crucial and their formalization, including for management purposes, requires development of mathematical models that aim at describing the functioning of the system, to explain the observed phenomenon in terms of cause and effect or predict effects of new causes. Originating from venerid culture trials carried out in France in the 80s, Manila clam (*Venerupis philippinarum*) is an important economic resource for coastal areas. Inside the Arcachon Bay, professional fishermen catch about 600 tonnes annually. Whereas the minimum legal harvest size is set by European legislation, complementary management measures are established by regional and departmental professional organizations in the framework of a co-management approach involving professional, scientists and administration.

This doctoral thesis is part of this objective of co-management by integrating life history traits of the population in a simulation model used for management purposes. At local scale, conventional shape analysis methods using metric weights and measures establish allometric relationships between pairs of descriptors with a significant morphological change detected from a length of ca. 16-20 mm. Intra-site phenotypic variability is structured in three morphological patterns. Occurrence of globular character inside the Arcachon Bay, described here for the first time, is associated to low densities and to high proportions of individuals affected by brown muscle disease, an emerging disease in the Bay. At the scale of the French Atlantic coast, three morphological ratios (elongation, valve density and weight related to length indices) discriminate populations from northern (Banc du Guer and Morbihan Gulf) and southern sites (Bellevue and Arcachon Bay). Significant relationships between those ratios and trophic conditions expressed by chlorophyll a concentrations, as well as a link between weight surface ratios and percentage of seawater temperature ranging from 12 to 20°C are demonstrated. Complexity of factors involved in intrasite and intersite morphology suggests intervention of other factors such as sediment characteristics, which is supported by a first outlines analysis. This work confirmed the importance of seawater temperature on stock state variables particularly during the reproduction period. For those same variables, a major role of trophic conditions has also been demonstrated with answers depending on development stages. Part of this result contributed to modifications within the simulation model dedicated to this population. The modifications mainly concerned integration of trophic resources effect on recruitment level, juveniles' production and growth rates per length class revision, accuracy of catches by professional fishermen and addition of a price effect on the fishing strategies. In conjunction with the model validation, the sensitivity analysis undertaken highlighted the sensitivity of the model to environmental parameters and to variables related to the younger stages. In a co-management context, this tool was used to perform projections on the future of the population according to various management scenarios. The differences in the patterns of biomass evolution in response to those action schemes were used by the stakeholders to identify management measures currently in force. In the end the model reinforces the engaged participatory process.

**Keywords** : bivalve, morphometry, allometry, population dynamics, dynamic system, management, Manila clam, *Venerupis philippinarum*





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## **Introduction générale et objectifs**



## Introduction générale et objectifs

Présents sous toutes les latitudes à l'échelle du globe et à toutes les profondeurs des océans, les bivalves constituent une composante importante de l'écosystème marin benthique (Berke et al., 2012). Les bivalves exploités, regroupant essentiellement les moules, les huîtres, les pétoncles et les clams, sont surtout localisés dans les zones intertidales et subtidales ; certains peuvent malgré tout atteindre des profondeurs de l'ordre de 200 m (Gosling, 2003). La plupart des milieux de vie occupés par ces bivalves exploités sont par conséquent situés à l'interface de la mer et du continent. Ils sont caractérisés par des perturbations fréquentes, variées et spatialement hétérogènes par rapport aux systèmes marins hauturiers. Elles engendrent pour les populations des fluctuations naturelles au sein des différents stades du cycle biologique et contribuent à des variations importantes de biomasse et de structure démographique auxquelles s'intéresse la dynamique des populations (Daget & Le Guen, 1975). Cette sensibilité aux variations des conditions environnementales se traduit spatialement, elle peut même s'exprimer à l'échelle de quelques mètres (Caddy & Defeo, 2003), mais aussi temporellement par des niveaux de recrutement extrêmement variables d'une année à une autre (Miyawaki & Sekiguchi, 1999 ; Munroe & McKinley, 2007).

La gestion durable de ces espèces, à des fins de conservation et/ou d'exploitation par l'homme, suppose par conséquent la connaissance de l'effet de l'environnement sur la dynamique de ces populations. Cela s'applique en particulier sur les espèces peu mobiles ou sédentaires qui peuvent de plus présenter des mécanismes densité-dépendants à différentes phases de leur cycle biologique (Caddy & Defeo, 2003). Dans le cas des espèces exploitées, l'interaction des effets naturels et anthropiques complexifie la compréhension des phénomènes observés. Les effets anthropiques sont eux même souvent difficiles à appréhender dans la mesure où ils supposent des données fiables dans le temps en particulier pour l'ensemble des activités de prélèvement, à savoir la pêche professionnelle et la pêche de loisir. Ils peuvent de plus ne pas se limiter à la pêche (effet de la pollution par exemple).

Ainsi, alors que l'estimation des abondances de la plupart des espèces exploitées dans ces écosystèmes littoraux est facilitée par leur faible mobilité et leur localisation proche, Defeo (2011) relève que les pêcheries dépendant de ces ressources comptent parmi les systèmes les moins bien appréhendés pour ce qui est de leur structure et de la dynamique des stocks<sup>1</sup>.

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<sup>1</sup> Le stock étant défini comme l'ensemble des animaux exploitables (Laurec & Le Guen, 1981).

## Introduction générale et objectifs

La compréhension des interactions entre l'espèce, son environnement et son exploitation est un gage à l'appréhension du fonctionnement de la dynamique de la population et de ses facteurs de contrôle. Leur formalisation passe par le développement de modèles mathématiques dont la finalité est la description du fonctionnement du système, l'explication des phénomènes observés en termes de cause à effet ou la réalisation des prédictions d'effets de nouvelles causes. Ce dernier point est un besoin récurrent en matière d'aide à la gestion des ressources exploitées. Ces considérations revêtent toute leur importance lorsque l'on considère que les bivalves sont destinés à l'alimentation humaine<sup>2</sup>, qu'ils génèrent des revenus directs importants pour les communautés de pêcheurs (Defeo, 2011) alors que les écosystèmes qu'ils occupent sont identifiés comme particulièrement vulnérables au changement climatique (Paskoff, 2001).

### *Production mondiale de bivalves*

La production mondiale de bivalves est estimée à 14,6 millions de tonnes en 2010. La pêche fournit 12 % de ces apports, le reste provient de l'aquaculture (source : <http://www.fao.org/fishery/statistics/fr>). En termes de groupes d'espèces, ces productions sont dominées par les clams/coques/arches et les huîtres avec respectivement 38 et 31 % des apports globaux. En fonction des groupes d'espèces, les contributions de la pêche et de l'aquaculture diffèrent fortement. Entre 2001 et 2010, la pêche représente moins de 5 % des apports d'huîtres et participe à quelques 38 % des apports de coquille Saint Jacques. Le groupe des clams/coques/arches se place dans une situation intermédiaire avec une contribution comprise entre 12 et 23 % sur la période considérée (Figure 1). Pour ce dernier, alors que la production globale enregistre une augmentation de 53 % entre 2001 et 2010, la part des apports issus de la pêche a diminué de près de 47 % au profit de l'aquaculture notamment en provenance de Chine.

Parmi ce groupe des clams/coques/arches, la palourde japonaise occupe une place importante avec deux tiers des apports (pêche et aquaculture confondues). En Europe, les pays contribuant habituellement aux captures par la pêche sont la France, l'Irlande et le Portugal. Concernant l'aquaculture, les principaux pays européens producteurs sont l'Italie, l'Espagne, la France et l'Irlande. Les productions européennes fournies par la FAO semblent cependant sous-estimées pour certains pays (cas par exemple de la France et de l'Italie).

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<sup>2</sup> La catégorie « Mollusques et autres » contribue pour 13 % de l'alimentation humaine en « Produits de la mer » (source : <http://www.fao.org/fishery/statistics/global-consumption/fr>).

## Introduction générale et objectifs

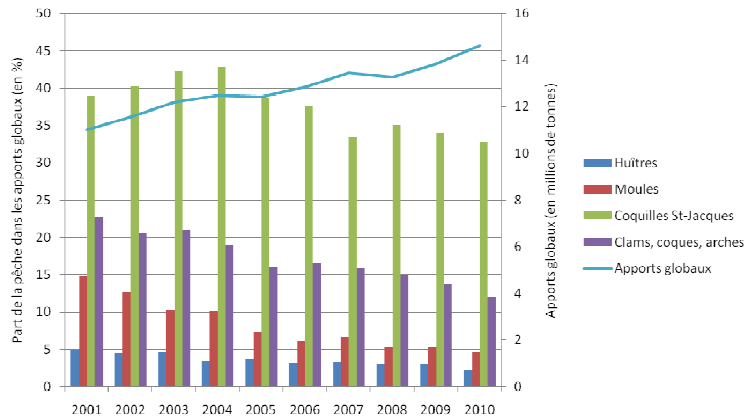


Figure 1. : Évolution de la contribution de la pêche dans les apports globaux (pêche et aquaculture) par groupe d'espèces de bivalves (source : <http://www.fao.org/fishery/statistics/fr>).

### *Production de palourde japonaise (*Venerupis philippinarum*) en France*

En France, la pêche professionnelle de la palourde japonaise est pratiquée sur différents sites depuis la Basse-Normandie jusqu'à l'Aquitaine. Les deux principaux lieux de production sont le bassin d'Arcachon et le golfe du Morbihan avec respectivement 614 t en 2011 [source : Base Pêche Aquitaine (BPA)/Comité Régional des Pêches Maritimes et des Élevages Marins (CRPMEM) Aquitaine] et 578 t en 2010 [source : Comité Local des Pêches Maritimes et des Élevages Marins (CLPMEM) Auray/Vannes]. Les autres gisements exploités sont essentiellement localisés du nord au sud : sur la côte ouest du Cotentin (ex : Grand Vey, Brévands) ; dans les Côtes d'Armor (ex : Banc du Guer) ; dans le Morbihan (ex : en Baie de Vilaine) ; en Charente Maritime (ex : Bonne Anse, Bellevue). En fonction des zones, les captures sont réalisées à la main (avec ou sans râteau ou griffe), à la drague ou en apnée. Les apports sont opérés par trois types d'exploitants professionnels :

- des marins pêcheurs (inscrits maritimes travaillant depuis un navire) ;
- des conchyliculteurs dont le navire est armé en conchyliculture petite pêche mixte. Au côté de leur activité principale de conchyliculture, ils sont autorisés à utiliser leur embarcation pour mettre en œuvre des engins de pêche professionnels ;
- des pêcheurs à pied professionnels qui doivent posséder un permis de pêche à pied délivré par les Affaires Maritimes.

Ces différents statuts combinés à la refonte fin 2008 du système français en charge de la production de statistiques de captures opérées par les pêcheurs professionnels (le Système d'Informations Pêche et Aquaculture de la Direction des Pêches Maritimes et de



## Introduction générale et objectifs

l'Aquaculture - DPMA), font qu'il est actuellement délicat d'avancer un chiffre de production globale pour les côtes françaises. Avec ces réserves, la production globale déclarée s'élève à 1 200 tonnes en 2008 (source DPMA – flux déclaratif). La palourde japonaise constitue une source de revenus importante pour les zones littorales accueillant les principaux gisements.

Des captures sont également opérées par la pêche de loisir. Il n'y a cependant aucune statistique permettant à l'heure actuelle de jauger l'importance de ces prélèvements par rapport à la pêche professionnelle. Le niveau d'exploitation par la pêche de loisir est probablement différent d'un gisement à un autre.

### *Réglementation en vigueur*

La pêche de la palourde japonaise est encadrée par un règlement européen fixant une taille minimale de capture qui correspond à la longueur antéropostérieure de la coquille. Pour les zones 1 à 5 excepté Skagerrak/Kattergat (cf. Figure 2) qui comprennent les eaux de l'Atlantique Nord, de la Manche et de la mer du Nord, la taille est établie à 35 mm depuis 2008 (Règlement CE n°40/2008) hormis dans le cas de la Basse-Normandie pour laquelle la taille minimale de capture est 40 mm (Arrêté du 15/07/2010 - JORF n°0171) essentiellement pour des raisons de marché. Le règlement CE 40/2008 n'encadre cependant qu'un régime dérogatoire du règlement CE n°850/1998, ce dernier devant être revu d'ici fin 2012. Une nouvelle proposition du règlement est en cours d'élaboration actuellement, la taille minimale serait confirmée à 35 mm.

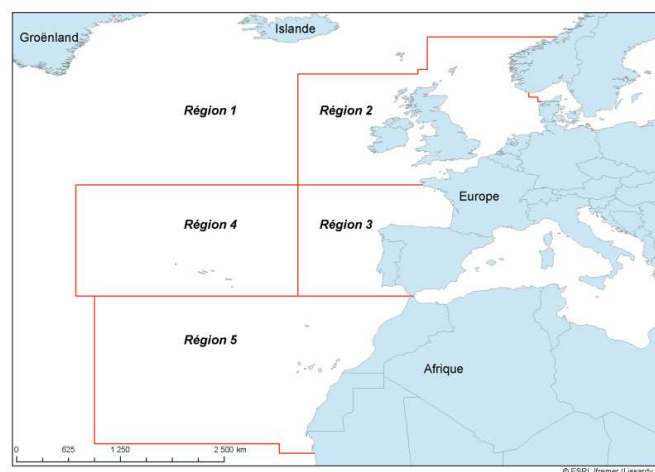


Figure 2. : Localisation des zones concernées par la taille minimale de capture pour la palourde japonaise – zones 1 à 5 excepté Skagerrak/Kattergat.

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Au niveau national, l'exercice de la pêche à pied professionnelle est depuis 2010 soumis à la détention d'un permis de pêche national (Décret du 28/12/2010 n° 2010-1653). Il est délivré pour une durée de douze mois par le préfet du département dans lequel le demandeur envisage de pratiquer principalement son activité ou, le cas échéant, par l'autorité compétente définie par le décret n°90-95 du 25 janvier 1990.

À ces réglementations européenne et nationale s'ajoute une réglementation spécifique pour chaque gisement. Elle est du ressort des Comités Départementaux et Régionaux des Pêches Maritimes et des Élevages Marins<sup>3</sup> (CDPMEM et CRPMEM) dont les statuts prévoient qu'ils participent à l'organisation de la gestion responsable de ressources halieutiques. Ces mesures complémentaires peuvent concerner le contingent de licences, des périodes de fermeture de la pêche, des zones de réserve de pêche, des quotas, la définition d'une taille minimale supérieure... Elles sont décidées en Conseils et mises en application de manière indépendante par les différents comités des pêches.

### *Relations structures professionnelles/scientifiques/administration*

En fonction des gisements, les décisions prises par les structures professionnelles reposent ou non sur un avis scientifique. Ils s'appuient alors soit sur des résultats de visites de gisement (cas des petits gisements) ou sur des campagnes d'évaluation de stock (cas des deux principaux gisements). Dans les deux cas, une collaboration étroite existe entre les structures professionnelles et scientifiques pour la réalisation de ces campagnes régulières (depuis 12 ans pour le bassin d'Arcachon et 16 ans pour le golfe du Morbihan).

Certaines mesures telles que la mise en place de zones de réserve de pêche, une taille minimale de capture supérieure à la législation européenne, nécessitent la promulgation d'arrêtés préfectoraux. L'administration, représentée par les services de l'État en région, contribue par conséquent également au processus de gestion de ces ressources.

La gouvernance appliquée à la palourde japonaise correspond dans ces conditions aux critères de cogestion définis par Gutiérrez et al. (2011) et Uchida & Wilen (2004). En référence à la classification proposée par Nielsen & Vedsmand (1999), cette cogestion est de type coopératif ou délégué en fonction des zones (Tableau 1).

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<sup>3</sup> Organismes interprofessionnels paritaires regroupant tous les professionnels se livrant aux activités de production, de premier achat et de transformation des produits des pêches maritimes et des élevages marins.

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Type	Descriptif
Consultatif	La cogestion se traduit par une consultation à un niveau central. Une large gamme d'usagers est représentée. Ils peuvent formuler aux pouvoirs publics des avis sur les mesures de régulation et sur la délégation de mesures de gestion.
Coopératif	La cogestion se traduit par un processus coopératif entre les pouvoirs publics et les usagers impliquant des groupes de travail.
Délégué	La cogestion se traduit par une délégation de gestion aux groupes d'usagers à un niveau régional. Les pouvoirs publics restent uniquement informés des décisions prises.

Tableau 1. : Classification de la cogestion en trois types d'organisation proposée par Nielsen & Vedsmand (1999).

### *Cas spécifique du bassin d'Arcachon*

Pour le bassin d'Arcachon, les comités des pêches intervenant sont le Comité Départemental des Pêches Maritimes et des Élevages Marins de Gironde<sup>4</sup> (CDPMEM) et le Comité Régional des Pêches Maritimes et des Élevages Marins d'Aquitaine (CRPMEM). Observant une diminution des rendements et étant confrontés à des difficultés de valorisation à la fin des années quatre-vingt dix, ces structures ont sollicité les scientifiques pour la réalisation d'une étude sur le gisement. La première étude porte sur une partie du gisement et a été réalisée en 2000 (Bertignac et al., 2001). Depuis, des campagnes régulières (d'abord conduites tous les trois ans puis tous les deux ans à partir de 2006) couvrant l'ensemble de la zone exploitée sont menées (Caill-Milly et al., 2003, 2006, 2008 ; Sanchez et al., 2010). L'organisation, la réalisation et le traitement des données sont partagés depuis 2006 entre les structures professionnelles et scientifiques.

Un groupe de travail palourde (également appelé comité de pilotage) associant des scientifiques, des professionnels ainsi que leurs représentants, des acheteurs et l'administration est instauré depuis 2003. Outre la définition des zones à prospecter, les résultats des campagnes y sont présentés et les retombées en matière de gestion discutées. Les propositions sont ensuite formulées par écrit par l'Ifremer et les décisions incombent aux structures professionnelles en lien avec l'administration. Les mesures de gestion adoptées au fur et à mesure de ces campagnes sont synthétisées dans la Figure 3.

<sup>4</sup> Appelé Comité Local des Pêches Maritimes et des Élevages Marins jusqu'en 2012.

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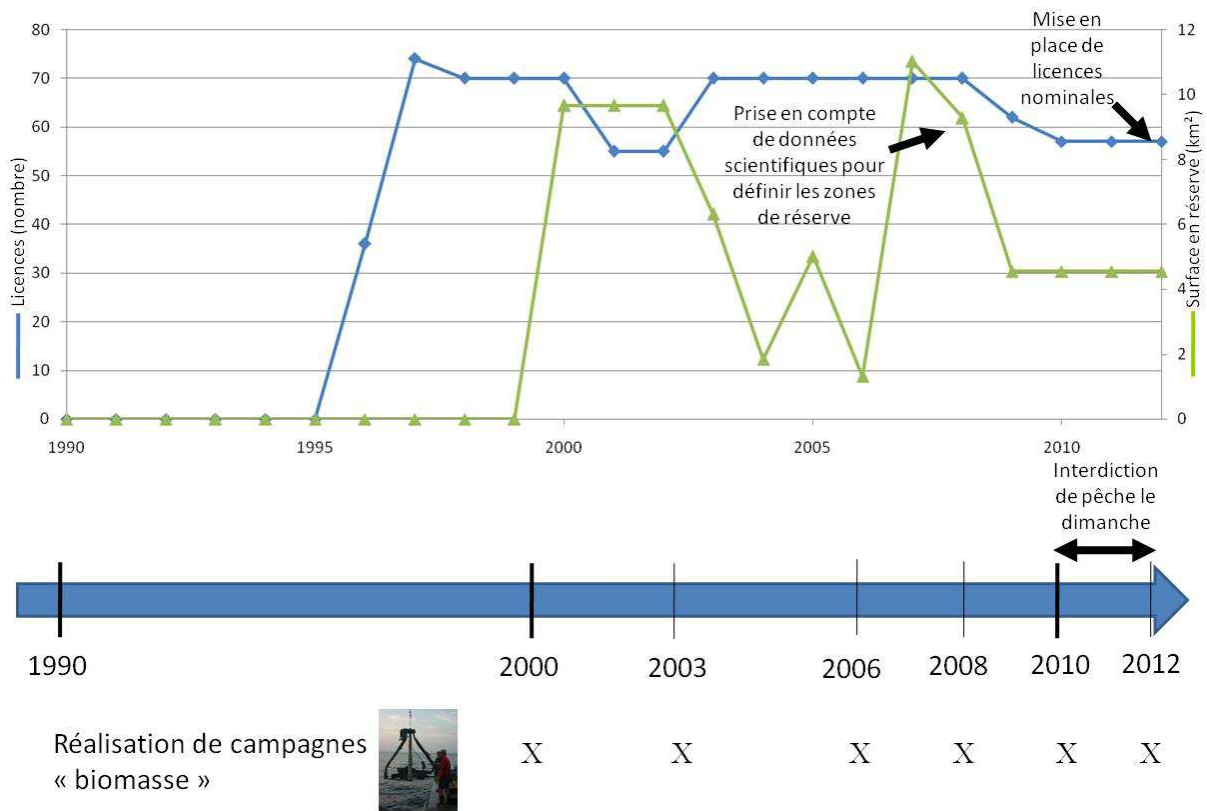


Figure 3. : Synthèse des mesures de gestion appliquées au stock de palourde japonaise du bassin d'Arcachon.

Au côté de cette activité d'expertise, des travaux de recherche ont été développés à partir de 2006 pour répondre à des questions spécifiques du comité de pilotage. Le point commun de ces travaux est qu'ils ont pour objectif de mieux comprendre la dynamique de la population intra-bassin et ainsi de renforcer les connaissances mobilisées pour formuler les recommandations aux gestionnaires (continuum « observation-expertise-recherche » synthétisé à la Figure 4).

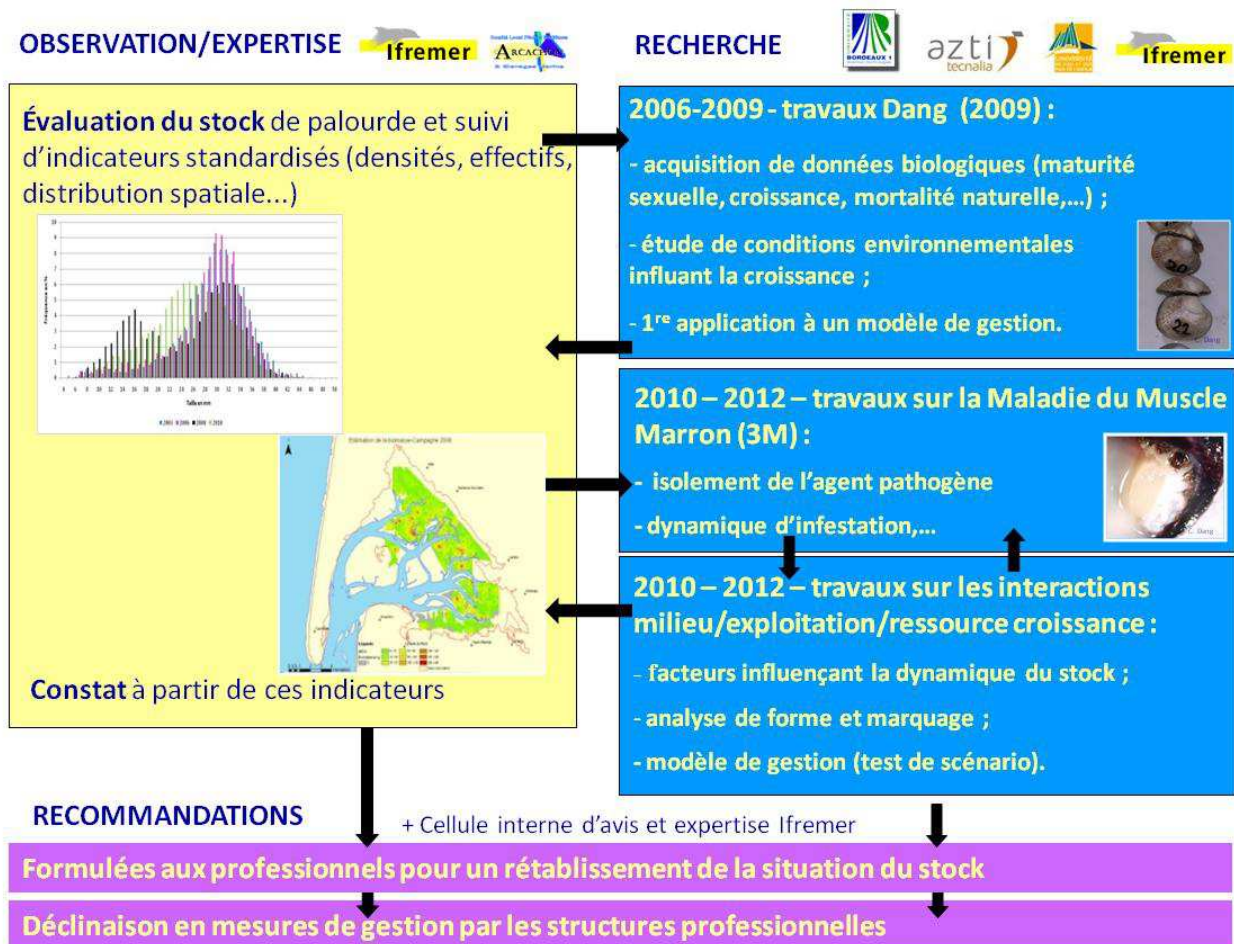


Figure 4. : Synthèse de la démarche engagée.

Au côté de l'acquisition des données biologiques valables pour le bassin sur la maturité sexuelle, la croissance, la mortalité naturelle, ces travaux ont permis de définir les paramètres de croissance de la population locale, de mettre en évidence l'émergence d'une nouvelle pathologie (la Maladie du Muscle Marron) et d'adapter un modèle de simulation spécifique à cette population (Bald et al., 2009 ; Dang, 2009 ; Dang et al., 2008 et 2010).

En comparaison avec d'autres sites, une croissance ralentie à partir de 32 mm a été démontrée pour le bassin. La coquille des bivalves présente des modifications allométriques non seulement définies génétiquement mais également phénotypiques (Ohba, 1959 ; Seed, 1968 ; Eagar et al., 1984 ; Costa et al., 2008). La question qui se pose est donc de savoir si cette mesure linéaire de la croissance masque des différences morphométriques de coquille pouvant avoir des incidences pour la gestion ?

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La présente thèse a été mise en place pour considérer cette question et, plus globalement, pour poursuivre la compréhension des traits d'histoire de vie écologique de la population et intégrer ces connaissances dans le modèle de simulation utilisé à des fins de gestion.

Elle s'articule en quatre chapitres :

- Chapitre 1 – Présentation de l'espèce, du site d'étude ainsi que de l'activité de pêche ;
- Chapitre 2 – Étude des caractéristiques morphométriques de la population intra-bassin ;
- Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population. Cela porte d'une part sur l'identification de patterns morphométriques de populations de palourdes et leur lien avec les conditions environnementales. D'autre part, les relations entre les facteurs environnementaux et des descripteurs du stock sont considérées ;
- Chapitre 4 - Évolutions apportées au modèle, simulations de scénarios de gestion et utilisation pour la gestion.

Une conclusion générale synthétise les principaux résultats de ce travail de recherche et ouvre sur les perspectives de recherche.

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# **Chapitre 1 – Présentation de l'espèce étudiée, du site d'étude et de l'activité de pêche**





## 1. Généralités sur l'espèce

### 1.1. Position systématique et description de l'espèce

La position systématique de la palourde japonaise est détaillée dans le Tableau 1.1<sup>5</sup>.

Tableau 1.1. Position systématique de la palourde japonaise (source : World Register of Marine Species, <http://www.marinespecies.org>).

Phylum ou Embranchement :	Mollusca
Classe	Bivalvia (Linné, 1758)
Sous-classe	Heterodonta (Neumayr, 1884)
Infra-classe	Euheterodonta
Ordre	Veneroidea (Adams et Adams, 1956)
Super-famille	Veneroidea (Rafinesque, 1815)
Famille	Veneridae (Rafinesque, 1815)
Genre	<i>Venerupis</i> (Chiamenti, 1900)
Espèce	<i>Venerupis philippinarum</i> (A. Adams et Reeve, 1850)

La palourde japonaise possède une coquille composée de deux valves également développées et de forme plus ou moins ovoïde (Figure 1.1.). L'extérieur de la coquille présente de nombreuses stries concentriques et des stries rayonnantes quelque peu espacées et s'entrecroisant. L'ornementation est par ailleurs souvent asymétrique. À l'intérieur de la coquille, le sinus palléal est régulièrement arrondi et développé sans atteindre la ligne médiane des valves. Les siphons inhalant et exhalant sont soudés aux deux tiers (Le Treut, 1986 ; Quéro & Vayne, 1998).

<sup>5</sup>Des changements sont intervenus pendant ce travail de thèse sur les noms scientifiques acceptés pour cette espèce. *Ruditapes philippinarum* était accepté, il ne l'est plus (source : World Register of Marine Species). En fonction de la date de soumission des articles, ce nom a pu être utilisé (articles 1 et 3).

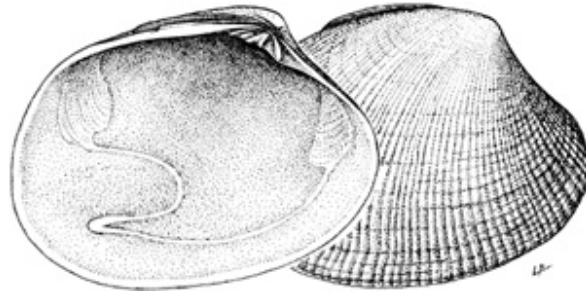


Figure 1.1. : Représentation schématique des valves de la palourde japonaise

(source : [http://www.fao.org/fishery/culturedspecies/Ruditapes\\_philippinarum/fr](http://www.fao.org/fishery/culturedspecies/Ruditapes_philippinarum/fr)).

L'espèce peut être confondue avec la palourde européenne *Venerupis decussata* (Linnaeus, 1758) mais cette dernière présente une coquille de forme plus rectangulaire, des stries concentriques et rayonnantes fines et serrées, une ornementation symétrique, un sinus palléal anguleux dorsalement et des siphons libres et plus longs. Quéro & Vayne (1998) mentionnent également une confusion possible avec la palourde bleue *Venerupis corrugata* (Gmelin, 1791), cette dernière présentant malgré tout un sinus palléal atteignant ou dépassant la ligne médiane de la valve.

## 1.2. Aire de répartition

La palourde japonaise est originaire de la région Indo-Pacifique et a vu sa distribution spatiale s'étendre au début du 20<sup>ème</sup> siècle suite à son importation accidentelle avec du naissain d'huître japonaise *Crassostrea gigas* (Thunberg, 1793) ou volontaire à des fins d'aquaculture (Le Treut, 1986). Elle est désormais présente le long de la côte pacifique américaine, des côtes atlantiques européennes, de l'Adriatique et de la mer Egée (Kim, 1995 ; Goulletquer, 1997 ; Jensen et al., 2004, 2005). À l'échelle du globe, elle est distribuée entre les latitudes 25°N et 45°N (Dang, 2009) ; Gérard (1978) reporte par ailleurs que l'espèce est connue à Java (10°S) et autour des Iles Kouriles méridionales (50°N). Les populations néonaturelles d'Europe sont observées depuis les côtes britanniques et norvégiennes jusqu'aux lagunes du Portugal pour les côtes atlantiques mais également en Méditerranée et en Adriatique. La Figure 1.2. reprend l'aire de répartition de l'espèce proposée par Paul-Pont (2010) ; elle distingue l'aire originale des zones où des populations se sont développées suite à leur introduction.

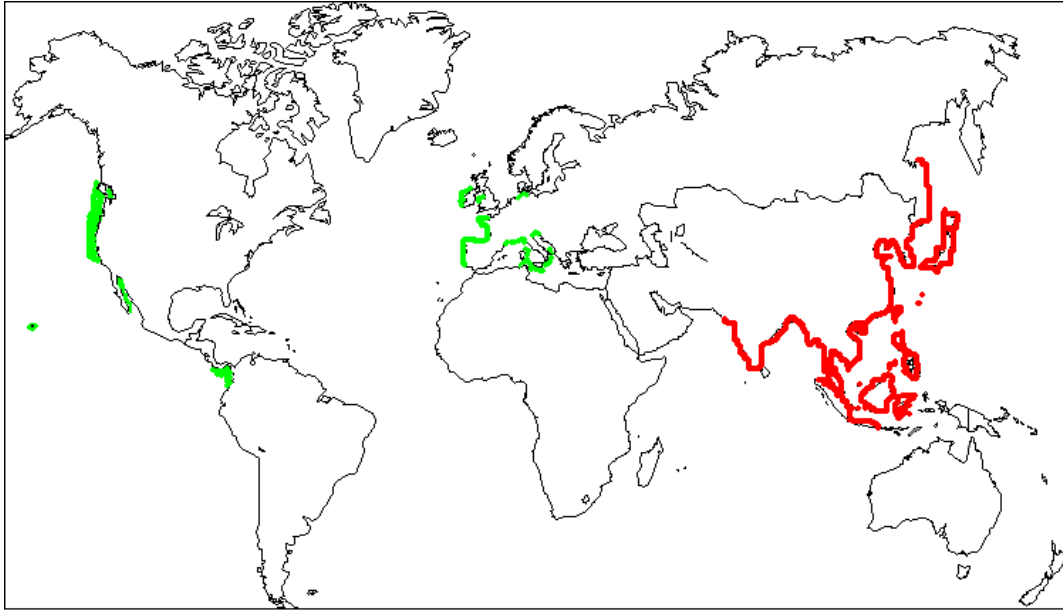


Figure 1.2. : Aire de répartition de la palourde japonaise *Venerupis philippinarum* proposée par Paul-Pont (2010) d'après Flye-Sainte-Marie (2007). En rouge, l'aire originale de répartition. En vert, les zones où des populations introduites se sont développées.

Dans le bassin d'Arcachon, l'introduction de la palourde japonaise date des années 1980 et provient d'essais de vénériculture (Robert & Deltreil, 1990). Localement cette activité d'élevage a rapidement été abandonnée en raison de difficultés économiques (prix au kilogramme divisé par deux en une dizaine d'années et mortalités élevées notamment sous l'action de prédateurs). Les individus introduits et laissés sur place ont cependant trouvé dans le bassin des conditions favorables au développement d'une population néonaturelle (Auby, 1993).

### 1.3. Habitats et déplacements

La palourde japonaise est une espèce fouisseuse (en position de vie verticale), de l'étage médiolittoral (Le Treut, 1986). Elle est présente dans des sédiments variés (vaseux, sablo-vaseux, sableux). Elle est également observée dans des zones associant des cailloutis et de la vase (Gérard Véron, comm. pers.), des débris coquillers d'huîtres.

La distribution spatiale des adultes est de type agrégatif (Kalyagina, 1994). L'espèce est sédentaire, cependant des déplacements latéraux limités d'individus atteignant six mètres par mois ont été reportés (Tamura, 1970).

Sa distribution verticale dans le sédiment est variable en fonction des périodes de l'année et de l'âge des individus. Les juvéniles se répartissent plus en surface alors que les adultes vivent généralement à une profondeur comprise entre 7 et 12 cm. La profondeur maximale d'enfouissement connue est 12 cm (Le Treut, 1986).

En position de vie (hors déplacements), les siphons de la palourde affleurent la surface du sédiment (Figure 1.3.).

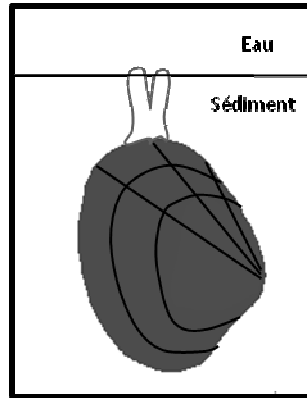


Figure 1.3. : Représentation de la position de vie (hors déplacement) de la palourde dans le sédiment.

#### 1.4. Alimentation

La palourde est dépositivore ; elle aspire la matière organique déposée à l'interface eau-sédiment. De ce fait, son régime alimentaire est complexe (Flye-Sainte-Marie, 2008). Il est majoritairement composé de phytoplancton, (Kasai et al., 2004 ; Kanaya et al., 2005 ; Yokoyama et al., 2005 ; Spillman et al., 2008) mais aussi de bactéries (Kharlamenko et al., 2001), de diatomées, de matières organiques particulières (dont celles d'origine détritique provenant de feuilles de *Zostera noltii* ; Dang, 2009), de petits rotifères (Sorokin and Giovanardi, 1995), de dinoflagellés (Li et al., 2001), de microphytobenthos (Kang et al., 2007). La diversification des sources trophiques serait fonction de l'âge ; les stades larvaires consommant des diatomées et des dinoflagellés (Loosanof et al., 1963 ; Le Treut, 1986).

#### 1.5. Croissance

En tant que mollusque bivalve, la palourde présente un corps mou se développant au sein d'une coquille calcique. La coquille assure les fonctions de squelette externe permettant la fixation des muscles et de protection à la fois contre les prédateurs et en protégeant la cavité

branchiale du sédiment (Gosling, 2003). Alors que la croissance de la masse viscérale de l'animal est assurée par l'apport de matière organique, la coquille grandit par incréments sous l'effet conjoint de l'accumulation de matières organique et minérale (Le Treut, 1986).

La coquille est élaborée par le manteau et est organisée en trois couches : le *péριοstracum*, l'*ostracum* et l'*hypostracum*. La composante organique est limitée au *péριοstracum* ; la composante minérale constitue les deux autres couches et est essentiellement formée de carbonate de calcium cristallisé sous des formes variées (Timmermans, 1969 ; Wilbur & Saleuddin, 1983 ; Wheeler, 1992 ; Mc Connaughey & Gillikin, 2008).

La croissance de la coquille en circonférence s'effectue par l'accumulation de matière depuis le bord du manteau alors que sa croissance en épaisseur des valves est la conséquence de dépôts issus de l'activité de l'ensemble de la surface du manteau (Gosling, 2003). Ces éléments sont synthétisés dans la Figure 1.4.

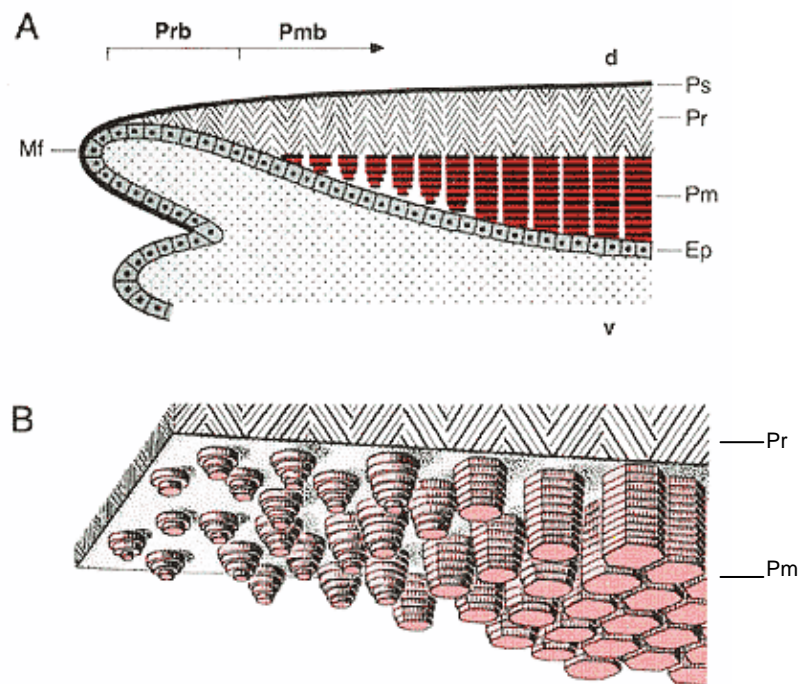


Figure 1.4. : Représentation schématique [(A) en coupe longitudinale (B) en trois dimensions] des zones de croissance d'un bivalve (source : Wehner & Gehring, 1995).

Ps : péριοstracum ; Pr : ostracum ; Pm : hypostracum ; Ep : épithélium palléal ; Mf : manteau ; d : dos ; v : ventre ; Prb : croissance de l'ostracum ; Pmb : croissance de l'hypostracum

Des opérations de marquage de la coquille au strontium et à la calcéine (Poulain et al., 2011 ; Fujikura et al., 2003 ; Caill-Milly et al., 2011) ont mis en évidence le rythme tidal de la formation des micro-incréments en bordure de valve (Figure 1.5.). Des ralentissements de croissance se produisent l'hiver mais également au moment de la reproduction ou lors de conditions environnementales défavorables chez les palourdes européennes et japonaises (Garcia, 1993 ; Kanazawa & Sato, 2008). Ces éléments font que le nombre des stries externes visibles à l'œil nu sur la coquille ne peut être utilisé pour estimer l'âge des individus.

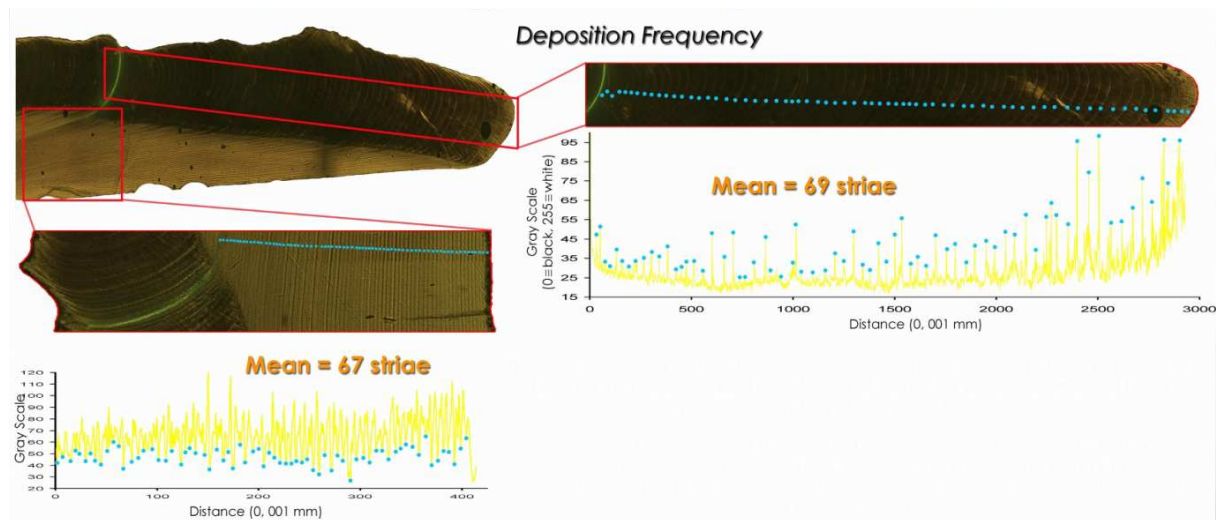


Figure 1.5. : Visualisation de la périodicité tidale de formation des micro-incréments en bordure de valve pour la palourde japonaise à partir d'opération de marquage à la calcéine (source : Caill-Milly et al., 2011).

La longueur antéro-postérieure de la coquille est la dimension usuelle utilisée pour décrire la croissance chez cette espèce. Sa croissance est influencée par la température de l'eau de mer (Toba, 1987 in Nakamura et al., 2002 ; Fan et al., 2007), mais également par les ressources trophiques (Yamamoto et al., 1956 ; Maître-Allain, 1982) et la durée d'immersion (Gouletquer et al., 1987).

La durée de vie maximum de la palourde est inconnue (Dee Boersma et al., 2006). Gillespie et al. (1999) indique qu'elle excède rarement 10 ans dans le cas de populations exploitées.

La longueur maximale des valves est estimée dans la bibliographie à 7,5 cm environ (Gosling, 2003). Un individu mesurant 9 cm a été pêché dans le golfe du Morbihan en 2011<sup>6</sup>. De fortes différences de longueur maximale sont observées en fonction des zones (Obha, 1959 ; Nosho & Chew, 1972).

### *1.6. Reproduction, phase larvaire et recrutement*

Espèce gonochorique, la palourde japonaise est considérée comme sexuellement mature à partir d'une vingtaine de millimètres (Holland & Chew, 1974). Une augmentation de la production des gonades avec l'âge (exprimée en kj/an) est observée chez une espèce proche, la palourde européenne (Urrutia et al., 1999), tout comme chez de nombreux bivalves. Quatre principaux facteurs environnementaux sont décrits dans la littérature pour leurs effets sur la gamétogénèse et la ponte : la température, la photopériode, la disponibilité en ressources trophiques et la salinité (Delgado & Pérez Camacho, 2007 ; Devauchelle, 1990 ; Le Pennec & Benninger, 2000 ; Park & Choi, 2004 ; Toba & Miyama, 1995).

Le déroulement du cycle reproducteur est marqué par d'importantes variations, non seulement d'un site géographique à un autre, mais également à l'échelle interannuelle (Miyawaki & Sekiguchi, 1999 ; Dang, 2009). Plusieurs pontes peuvent être effectuées au cours d'une même année (généralement une à deux pontes). La métamorphose et le recrutement des jeunes individus se produisent après une période larvaire pélagique de 2 à 3 semaines (Le Treut, 1986). L'éclosion des œufs requiert des conditions spécifiques de température (Emmett et al., 1991), de même la survie larvaire est influencée par ce paramètre (Robinson & Breese, 1984). D'autres facteurs sont cependant décrits pour affecter le niveau de recrutement comme par exemple la prédation et les pathogènes (Williams, 1980 ; Ishii et al., 2001).

Des travaux récents (Hurtado et al., 2011) en génétique et en cytologie ont mis en évidence l'hybridation entre la palourde japonaise et la palourde européenne dans le nord-ouest de l'Espagne.

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<sup>6</sup> Article de presse consultable sur : <http://www.letelegramme.com/local/morbihan/vannes-auray/cantonvannes/sene/sene-56-une-palourde-geante-decouverte-dans-le-golfe-du-morbihan-08-06-2011-1329628.php>



*1.7. Mortalité naturelle*

Outre la sénescence, les facteurs contribuant à la mortalité naturelle sont :

- la prédation par des crustacés (*Carcinus maenas*,...), par des mollusques gastéropodes (*Ocenebra erinacea*, *Natica spp.*,...), par des astéridés (*Asteria forbesi desus*,...), par des poissons des familles des pleuronectidés et des sparidés, par des oiseaux (*Haematopus ostralegus* pour les jeunes individus,...). En fonction des espèces, la prédation peut intervenir soit lorsque la palourde est enfouie dans le sédiment ou lorsqu'elle est en mouvement vertical dans le sédiment (Le Treut, 1986) ;
- les pathologies (Maladie de l'Anneau Brun, Perkinsose, ...). Localement, elles peuvent occasionner des mortalités massives pour l'espèce (Dang, 2009).

## **Connaissances spécifiques relatives à la population de palourdes du bassin d'Arcachon**

### ***Croissance***

Les paramètres de croissance de l'équation de Von Bertalanffy ont été établis par Dang et al. (2010) à partir d'expérimentations en cages réparties sur cinq stations (quatre intra-bassin et une océanique). Ils reflètent une croissance ralentie à partir de 32 mm par comparaison avec d'autres sites (français et étrangers) (Dang, 2009).

### ***Reproduction***

Deux pontes sont habituellement observées (avril à juin et août à octobre). Elles se produisent lorsque la température de l'eau de mer est comprise entre 15°C et 22°C (Dang et al., 2010). Le niveau de recrutement pour l'année n, appréhendé par l'effectif des individus de longueur inférieure à 17 mm l'année n+1, présente des variations allant du simple au triple d'une observation à une autre (Sanchez et al., 2010).

### ***Pathologie***

Une pathologie émergente, la Maladie du Muscle Marron, a été récemment mise en évidence sur Arcachon par Dang et al. (2008). Elle n'a jusqu'à présent jamais été décrite ailleurs.

### ***Descripteurs du stock***

Les descripteurs du stock sont estimés à partir des campagnes scientifiques standardisées. Leurs évolutions relatives sont considérées pour appréhender l'état de la population dans le bassin (Tableau 1.2.).

	<b>2003</b>	<b>2006</b>	<b>2008</b>	<b>2010</b>
Biomasse totale (tonnes)	7 992	7 307	4 457	5 773
Abondance totale (millions d'individus)	1 101	1 091	828	1 194
Biomasse moyenne (g/m <sup>2</sup> )	172	152,4	95,2	123
Abondance moyenne (nombre d'individus/m <sup>2</sup> )	23,6	22,8	17,6	25,6
Abondance individus de longueur supérieure à 35 mm (millions d'individus)	193	134	90	71
Biomasse individus de longueur supérieure à 35 mm (tonnes)	2 730	1 710	1 159	916
Abondance individus de longueur inférieure à 17 mm (millions d'individus)	51	69	180	129

Tableau 1.2. : Évolution des principaux descripteurs du stock de palourde japonaise intra-bassin (sources : Caill-Milly et al., 2003, 2006, 2008 ; Sanchez et al., 2010).

## 2. Site d'étude

Situé sur le littoral sud-ouest de la France, le bassin d'Arcachon (44°40'N, 1°10'W) est une lagune semi-fermée insérée dans la plaine côtière de Gascogne (Figure 1.6.). Il pénètre à 20 km à l'intérieur des terres. Sa superficie est de 180 km<sup>2</sup> y compris avec les passes. Ces dernières sont au nombre de deux (3 km de large, 20 km de long) et connectent le bassin à l'océan Atlantique. La côte noroît désigne le secteur allant du Lège au Cap Ferret ; la côte est désigne le secteur allant d'Arès à Audenge (Manaud, 1997). Les chenaux principaux ont une profondeur maximale de 20 m ; ils sont prolongés par un réseau secondaire peu profond, les « esteys » (Dang, 2009).

La surface de zone intertidale est estimée à 110 km<sup>2</sup> intra-bassin. La nature du sédiment de ces zones exondables est essentiellement constituée de « slikkes » sablo-vaseuses et de sables terrigènes envasés (Bouchet, 1994). De vastes herbiers à zostère (*Zostera noltii*) colonisent l'estran.

Le bassin est à la fois influencé par les eaux néritiques externes et par les apports continentaux. Le rythme est de type macro-tidal semi-diurne. Le volume d'eau oscillant à chaque marée est compris entre 130 et 200.10<sup>6</sup> m<sup>3</sup> en période de mortes eaux ; il est compris entre 370 et 400.10<sup>6</sup> m<sup>3</sup> en période de vives eaux. Les courants de marée s'élèvent à 1,75 m/s au niveau des passes et dans la partie médiane du bassin. Ils sont inférieurs à 1 m/s dans le fond du bassin (Dang, 2009).

Le bassin versant du bassin d'Arcachon comprend deux systèmes hydrographiques :

- le système des cours d'eau qui débouche directement dans le bassin. Le principal cours d'eau est l'Eyre situé au sud-est ;
- le système des étangs qui se déversent dans le bassin par des canaux. Les principaux tributaires sont le Canal des Étangs au nord et le Canal des Landes au sud.

Les apports d'eau douce sont estimés à 1,25 milliards m<sup>3</sup> par an. Près de 80 % proviennent des cours d'eau, environ 12 % des précipitations directes dans le bassin et le reste du ruissellement de la nappe phréatique (Manaud, 1997).

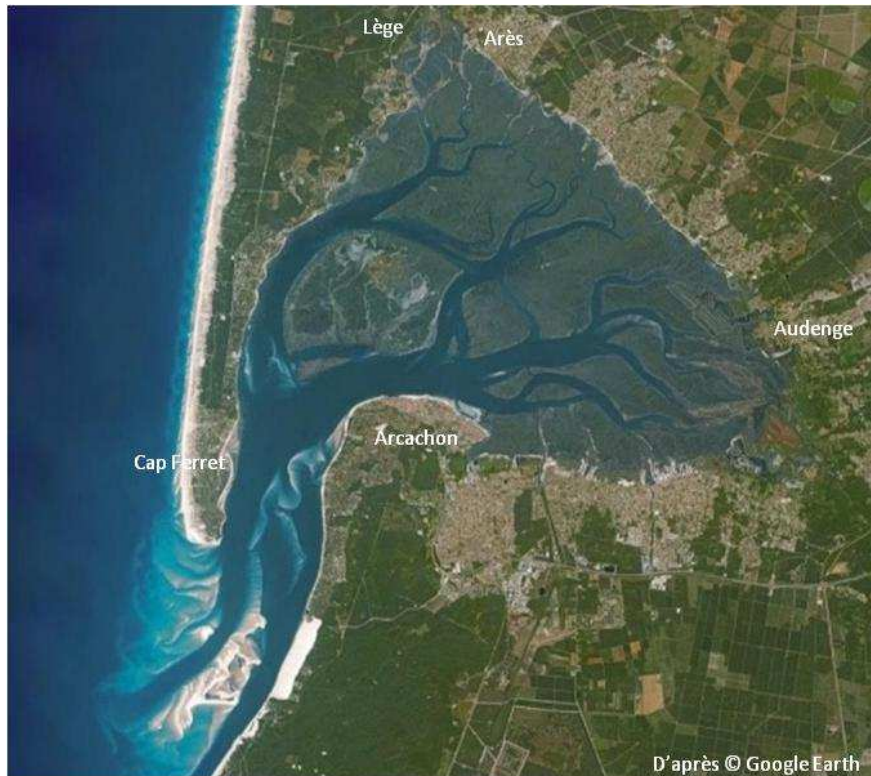


Figure 1.6. : Vue du bassin d'Arcachon.

### **3. Exploitation de la palourde japonaise sur le bassin d'Arcachon**

#### *3.1. Technique de pêche*

Intra-bassin, la pêche est réalisée à la main et à marée basse dans la zone intertidale. Les pêcheurs se rendent sur les zones de pêche en bateau, puis se déplacent sur l'estran à pied munis de patins (Photo 1.1.). Une à deux marées est réalisée par jour. La pêche n'est généralement pas pratiquée lors des coefficients de marée inférieurs à 50.

Bien qu'autorisée, la pêche en bordure de chenaux depuis un bateau et à l'aide d'un râteau d'une largeur maximum de 50 cm fixé sur une perche n'est plus exercée. Cette pratique concernait un nombre très limité de pêcheurs professionnels (Photos 1.2. et 1.3.).



Photo 1.1 : Pêche à la main en zone intertidale.

Photos 1.2 et 1.3. : Pêche au râteau en bordure de chenaux.

### 3.2. Productions déclarées

Les premières déclarations de captures ont été enregistrées en 1992 avec 1,3 t (source CRTS). Rapidement, l'activité s'est développée pour atteindre 1 028 t en 2007 et se stabiliser actuellement vers 500-600 tonnes annuelles (Fig. 1.7.).

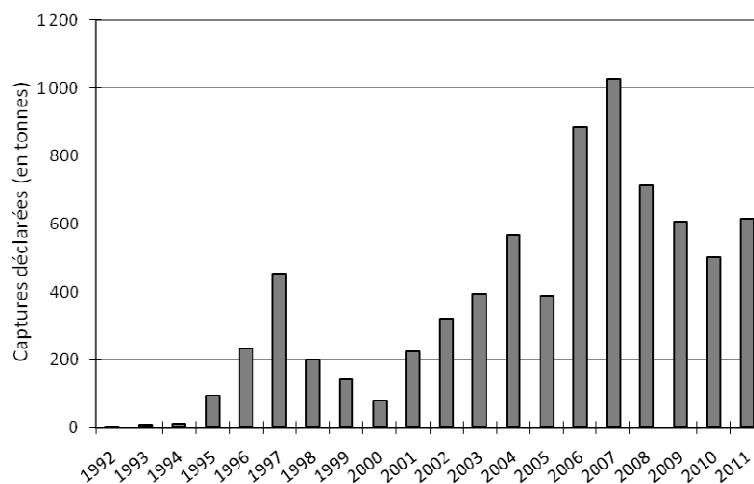


Figure 1.7. : Évolution des captures de palourdes japonaises déclarées par les pêcheurs professionnels pour le bassin d'Arcachon [sources : CRTS, Ifremer, BPA (CRPMEM Aquitaine), valeur estimée pour 1999].

### 3.3. Saisonnalité des apports

Les apports déclarés les plus importants sont réalisés entre mars et septembre. Une baisse des captures est observée entre novembre et janvier (Figure 1.8.).

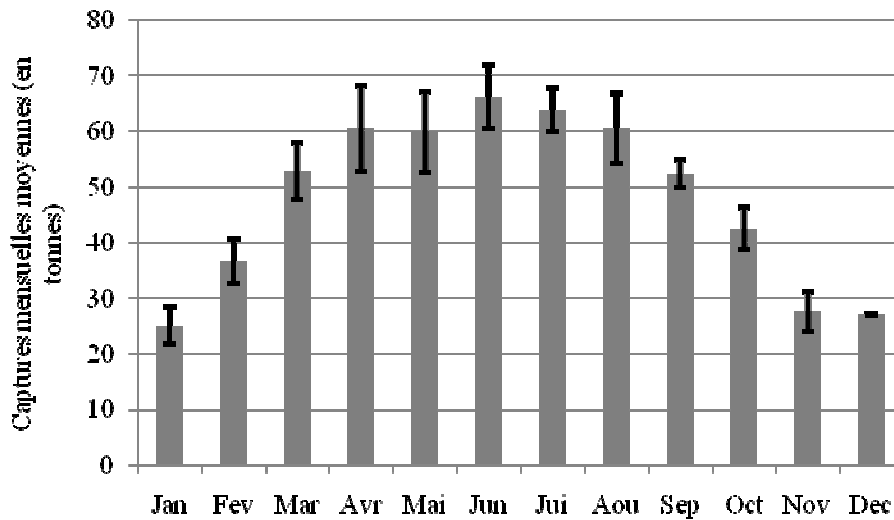


Figure 1.8. : Saisonnalité des apports de palourdes japonaises déclarées par les pêcheurs professionnels pour le bassin d'Arcachon – moyenne et erreur-type calculée sur 2009-2011 [source : BPA (CRPMEM Aquitaine)].

### 3.4. Captures par unité d'effort

Avant 2006, les informations issues des déclarations de captures sont disponibles à l'échelle de la journée pour moins de la moitié des navires pratiquant la pêche de la palourde ; elles ne sont pas considérées comme représentatives. A partir de 2006, les déclarations journalières sont renseignées pour pratiquement tous les navires. Elles permettent d'estimer les Captures journalières moyennes Par Unité d'Effort (CPUE), exprimées en kg/h. Les rendements horaires moyens sont caractérisés par d'importantes variations d'une année à l'autre (Tableau 1.2.).

Cette mesure de l'effort ne peut être utilisée pour considérer l'évolution de l'abondance du stock. En effet, l'attribution d'une licence autorise un ou deux pêcheurs à travailler en même temps mais les déclarations de captures journalières étaient regroupées jusqu'en 2011. La prise par unité d'effort ainsi calculée dépend donc non seulement de l'abondance de palourde mais également de la stratégie de chaque entreprise qui peut moduler le nombre de personnes opérant les captures au cours de l'année. Depuis 2012, le CRPMEM d'Aquitaine a mis en place des déclarations nominatives.

## Chapitre 1 – Présentation de l'espèce étudiée, du site d'étude et de l'activité de pêche

<b>Année</b>	<b>CPUE moyenne (kg/h) et erreur type entre parenthèse</b>
2006	20,7 (0,2)
2007	24,0 (0,2)
2008	18,7 (0,1)
2009	17,9 (0,2)
2010	15,8 (0,2)
2011	17,9 (0,1)

Tableau 1.3. : Captures Par Unité d'Effort (CPUE) moyennes et erreur type entre 2006 et 2011 [sources : Caill-Milly et al., 2008, BPA (CRPMEM Aquitaine)].

## **Chapitre 2 – Caractéristiques morphométriques de la population intra-bassin**





L'étude de la dynamique d'une population repose sur la connaissance des paramètres de base que sont la croissance, la mortalité et la reproduction. Chez les mollusques, la croissance est classiquement appréhendée par un suivi des dimensions de la coquille (Seed, 1980). Chez les bivalves, le critère le plus fréquemment utilisé est la plus grande longueur correspondant à la mesure antéropostérieure des valves (Gosling, 2003). Cette mesure peut néanmoins s'avérer insuffisante car elle ne renseigne que sur un axe de croissance alors que cette dernière peut se réaliser selon plusieurs dimensions et que la plupart des bivalves présentent des modifications de formes au cours de leur développement (Fan et al., 2007). Ces changements allométriques progressifs sont clairement contrôlés par le génotype des individus et se déroulent pendant l'ontogénie (Gosling, 2003 ; Hoffman, 1978). Pour de nombreuses espèces, l'influence des conditions environnementales a également été démontrée (Ohba, 1959 ; Seed, 1968 ; Rosenberg, 1972 ; Brown et al., 1976 ; Gérard, 1978 ; Lucas, 1981 ; Eagar et al., 1984 ; Stirling & Okumus, 1994 ; Kwon et al., 1999 ; Costa et al., 2008). Elle conduit à l'expression de phénotypes variés. L'identification de ces groupes d'individus aux échelles inter et intra-sites constitue dans ces conditions une connaissance complémentaire utile pour la compréhension de la dynamique du stock. Cette connaissance a potentiellement des répercussions dans le choix des mesures de gestion adaptées à la population étudiée. Elle vient étayer les modalités de gestion spatialisées qui s'avèrent particulièrement adaptées pour les espèces peu mobiles ou sédentaires et à fortes dispersions (Caddy & Defeo, 2003).

Dans le cas de la population de palourde japonaise (*Venerupis philippinarum*) du bassin d'Arcachon, les travaux de Dang (2009) ont permis de proposer une modélisation de la croissance en longueur selon la méthode de Von Bertalanffy. Par rapport aux données disponibles dans la littérature, ils indiquent que les performances de croissance sont relativement faibles à l'intérieur de la lagune. La taille asymptotique maximale estimée à partir d'expérimentations de marquage/recapture présente une variabilité importante intra-bassin et s'élève en moyenne à 43,9 mm. Le paramètre représentatif du taux de croissance, K, présente des valeurs élevées qui sont homogènes à l'échelle du bassin. Ces travaux mettent également en exergue un ralentissement de la croissance à partir de 32 mm. La taille minimale réglementaire de capture repose uniquement sur la longueur et est fixée pour l'ensemble des eaux de l'Atlantique Nord, de la Manche et de la mer du Nord à 35 mm (cf. Chapitre 1). Dans le cas où le ralentissement de croissance observé sur la longueur était compensé par une croissance plus élevée dans d'autres dimensions aboutissant au final à une morphométrie

## Chapitre 2 - Caractéristiques morphométriques de la population intra-bassin

particulière chez les individus adultes, l'adéquation de la taille minimale en vigueur pour l'ensemble des gisements exploités sur les côtes atlantiques pourrait-elle être discutée ?

Afin d'apporter des éléments de réponse, cette thèse débute par la présentation d'une analyse de forme des palourdes japonaises du bassin d'Arcachon, objet d'un premier article (**Article 1**). Cette étude morphométrique fait appel à des descripteurs traditionnels morphologiques basés sur des paramètres métriques et pondéraux. Elle permet de considérer non seulement la variabilité intra-site à l'échelle du bassin d'Arcachon mais également la variabilité inter-site au regard de la littérature disponible. Elle définit les relations allométriques pour la population du bassin d'Arcachon et renseigne ainsi sur la croissance relative des critères retenus. La variabilité spatiale des patrons de formes est discutée en fin d'**Article 1** au regard des facteurs densité et pathologie.

**Article 1**

Titre : Shell Shape Analysis and Spatial Allometry Patterns of Manila Clam (*Ruditapes philippinarum*) in a Mesotidal Coastal Lagoon

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## Chapitre 2 - Caractéristiques morphométriques de la population intra-bassin

## Research Article

# Shell Shape Analysis and Spatial Allometry Patterns of Manila Clam (*Ruditapes philippinarum*) in a Mesotidal Coastal Lagoon

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While gradual allometric changes of shells are intrinsically driven by genotype, morphometrical shifts can also be modulated by local environmental conditions. Consequently the common use of a unique dimension (usually length) to assess bivalves' growth may mask phenotypic differences in valve shape among populations. A morphometric exhaustive study was conducted on Manila clam, *Ruditapes philippinarum*, by acquiring data in the French Arcachon Bay (intrasite phenotypic variability) and by comparing with other sites in the literature (intersite phenotypic variability). 2070 shells were subsampled, weighted, and automatically measured using TNPC software. Some ratios' values indicate a relatively round and globular shape shell in comparison with other sites confirming poor conditions for some individuals. Among adult clams, three main morphological groups were identified and discussed according to spatial considerations. Allometric relations for pairs of shell descriptors were determined by testing classical linear and piecewise regression models on log-transformed relation of Huxley. A significant shape change correlated to size was observed; it corresponds to the second year of life of the clam. Relationships between density, disease, and shell shape are demonstrated and discussed related to other potential factors affecting shell shape. Finally, consequences on population regulation are addressed.

## 1. Introduction

Growth of individuals is commonly assessed by correlating the evolution of the largest dimension of the individuals along time. For bivalves, this dimension can be the valve's length as for cockle, clam, mussel, razor shell, the valve's height as for oyster, scallop [1]. The shape changes of the shell are induced by the differential growth vectors operating at distinct locations around the mantle edge [2], organ that plays a key role in the shell secretion. This highlights the need of taking into account several allometric ratios.

Those gradual allometric changes are clearly driven by genotype and occur during ontogeny; they are usually associated with the conservation concept of physiological favorable surface area to volume ratios [1]. At the same time, those morphometrical shifts can also be modulated by local environmental conditions [3–12].

So, the convenient approach which consists in considering growth through a unique dimension can mask phenotypic plasticity responses in valve shape. While bivalves allocate a significant portion of their total energy budget to shell growth [13], apparent disparities concerning length could occur among individuals even if they dedicate the same amount of energy to shell growth. Shell increments could indeed shift to other dimensions such as height, width, and thickness of the valve. This concern is important because it gives new arguments to suggest that deficient growth in length is not always due to problems of energy input deficit (e.g., phytoplankton) but could also be related to intrinsic considerations leading to specific morphological patterns.

In order to investigate the question of growth in the fullest possible way for ecological and commercial purposes, an exhaustive morphometric study is proposed by acquiring data in Arcachon Bay (intrasite phenotypic variability) and

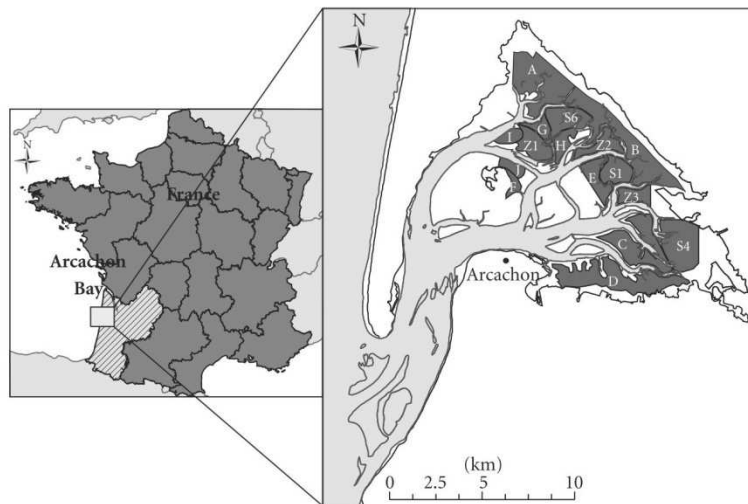


FIGURE 1: Maps showing the studied site Arcachon Bay (France) and localization of the sampled strata (Sources: ESRI, BD Carthage, Ifremer—M. Lissardy).

by comparing with other sites in the literature (intersite phenotypic variability). The chosen biological model is Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) which supports an important commercial fishing activity with around 550 to 1.000 tons per year for the Arcachon Bay located in the southwest coast of France, hoisting it at the first rank of French production sites.

Various ecological factors are identified for their effect on bivalve shell shape: wave impact, trophic conditions, water depth, density... [2, 14]. In this study, we decided to focus on two factors integrating a populational dimension and be susceptible to influence the growth and the shell shape: density and brown muscle disease—emerging pathology. Several studies have already been conducted on density dependence of the Manila clam's shell shape but without consensus [15–18]. One of the supposed effects is that the dorso-ventral shell axis (height) should be the most affected by space competition since buried clams present their anteroposterior axis (length) almost perpendicular to the substrat [18]. Concerning pathology, we considered it challenging to study relationships between the prevalence of BMD affection which is known for having negative impact on the functioning of the adductor muscles involved in the shell's closure [19] and shell shape. Those features were preferred to other potential factors such as perkinsosis or brown ring disease since their low impacts on the Arcachon Bay population were demonstrated [20]. For other environmental modulators, (such as type of sediment, shore level, etc) data at sufficient fine scale are not currently defined.

## 2. Materials and Methods

**2.1. Study Site.** Arcachon Bay is a 156 km<sup>2</sup> semi sheltered lagoon in the southwest coast of France (Figure 1). Mostly composed of tidal flats (110 km<sup>2</sup> within the inner lagoon);

this mesotidal system is characterized by a sediment composition ranging from mud to muddy sands and colonized by vast *Zostera noltii* seagrass meadows. Both influenced by external neritic waters and by continental inputs [20], this bay presents a semidiurnal macrotidal rhythm. Temperature and salinity gradients within the bay are controlled by the characteristics of these water masses as well as the slow renewal of water by tides [21]. With an average salinity of 30 (source Archyd network) which is higher than freshwater salinity and lower than seawater one's, the investigated area is considered as brackish water [22].

**2.2. Origin of the Data.** *R. philippinarum* shells were collected in Arcachon Bay during the last biomass survey in 2010. Henceforth biennial, this field survey is carried out with a standardised protocol (stratified random sampling) with 14 strata located at intertidal level (excluding channels) investigated for a total of 490 sampling stations. Sediments, core of 0.25 m<sup>2</sup> (0.5 m × 0.5 m) on a 0.2 m depth, were sampled with a Hamon grab at the high tide and filtered onboard with running water over a set of three sieves with 2, 1, and 0.5 cm mesh sizes. On the whole collected shells, 2070 shells were randomly subsampled.

**2.3. Shells Preparation and Morphology Descriptors of Individuals.** In laboratory, all the shells were first cleaned and dried at 38°C for 48 h. Then, the valves were separated and analyses on two high-resolution pictures (lateral and ventral views) were performed with the TNPC software (Digital Processing for Calcified Structures, <http://www.TNPC.fr>) on left valve. To describe the morphology of the individuals, seven classical parameters were retained:

- (i) length ( $L$ ), defined as the longest distance from front edge to back edge (mm). It is the reference length obtained from lateral view;



TABLE 1: Morphometric variables for arcachon bay.

Descriptor	Formulae	Minimum	Maximum	Mean	Ecart-type
Elongation index	$= H/L$	0.66	0.86	0.75	0.02
Compacity index	$= W/L$	0.19	0.38	0.28	0.02
Convexity index	$= W/H$	0.35	0.51	0.37	0.03
Circle index lateral view	$= AL/0.25 \times L^2 \times \pi$	0.65	0.85	0.73	0.02
Circle index ventral view	$= 2 \times AV/0.25 \times LVent^2 \times \pi$	0.36	0.70	0.48	0.04
Reference Ellipse index lateral view	$= AL/0.25 \times L^2 \times \pi$	2.63	3.43	2.94	0.10
Reference Ellipse index ventral view	$= 2 \times AV/0.25 \times LVent^2 \times \pi$	0.73	1.40	0.95	0.08
Weight ratio 1	$= SM/L$	0.06	1.76	0.57	0.27
Weight ratio 2	$= SM/H$	0.08	2.17	0.76	0.35
Weight ratio 3	$= SM/W$	0.23	5.80	2.02	0.88

- (ii) ventral length ( $LVent$ ), as the longest distance from front edge to back edge (mm). It is the reference length obtained from ventral view;
- (iii) height ( $H$ ), as distance from the umbo to edge (mm). It is obtained from lateral view;
- (iv) width ( $W$ ), as the longest distance of the valve in a lateral plane across the valve (mm). It is obtained from ventral view;
- (v) weight or shell mass ( $SM$ ), as dry mass of the left valve (mg);
- (vi) area lateral ( $AL$ ), as area of the left valve projection ( $mm^2$ ) from lateral view;
- (vii) area ventral ( $AV$ ), as area of the left valve projection ( $mm^2$ ) from ventral view.

These seven parameters consist in linear or surface measures directly obtained from the shape analysis (lateral or ventral views) and weight measure of each left valve. Respective accuracies of almost  $1.10^{-3}$  millimeter and 0.1 mg are associated to linear and weight measures. Taken separately, those parameters do not allow describing the shell morphology because of a size effect. So not only to characterize the general morphology tendencies at the bay and at the strata scales, but also to examine allometric patterns for this population, 10 shape descriptors were defined from these parameters (Table 1). Such indices are supposed to give synthetic information on growth [23].

- (i) Elongation index, Compactness index, and Convexity index to consider the coupled ratios between the 3 dimensions of the valve: a compact and convex bivalve has its width greater than 50% of its height which means a Convexity index greater than 0.5 [24];
- (ii) Circle index lateral view (CIL) and Circle index ventral view (CIV) to compare the valves' forms to circular ones: the first one is the area of the valve (lateral view) related to the surface of a circle with  $L$  as

diameter. The second one is twice the area of the valve (ventral view) related to the surface of a circle with  $LVent$  as diameter. Those two indices are complementary, respectively, to Elongation and Compactness index. For both of them, if the value is close to 1, it means that the shape tends to be circular.

- (iii) Ellipse index lateral view (EIL) and Ellipse index ventral view (EIV) are also considered to compare the valves' forms with elliptical ones. The first one is the area of the valve (lateral view) related to the surface of an ellipse with  $L$  and  $0.5L$  as diagonals. The second one is twice the area of the valve (ventral view) related to the surface of an ellipse with  $LVent$  and  $0.5LVent$  as diagonals. Those indices are also complementary to Elongation and Compactness indices since they provide information on the more or less flattened form of the shell.
- (iv) Three descriptors involving the weight and successively the 3 dimensions ( $L$ ,  $H$ , and  $W$ ) with weight ratio 1, weight ratio 2, and weight ratio 3.

For *Ruditapes philippinarum*, globularity is described as a result of a faster increase of width related to length [7]. In terms of indices retained above, this character can be defined for clams presenting high Compactness, CIV, and EIV indices.

According to Hamai [25], Ohba [3], and Eagar et al. [9], morphometric characteristics could reveal more or less favorable environmental conditions. For Manila clam, a low Elongation index is observed to localities presenting clams with high condition index [23] meaning favorable environmental conditions. Consequently, CIL index close to 1 and EIL index greater than 1 could indicate unfavorable environmental conditions.

Moreover, Watanabe and Katayama [23] linked those morphometrics characteristics to commercial considerations for *Ruditapes philippinarum*: the less palatable individuals are



the ones with fatter and rounder shell shape that is, high value of Elongation index and CIL index close to 1.

In other words, the best shape for ecological and economical purposes needs to be considered as a combination of several characteristics: at least low  $H/L$  ratio combined with low values of CIL and EIL.

#### 2.4. Multivariate Analysis

**2.4.1. Shell Shape Analysis.** In this subsection, all samples were considered. After brief descriptive statistics, linear regressions were performed on the logarithmically transformed data on parameters and shape descriptors versus size. It allows to account for significant shape changes correlated to size and is based on the classical equations for allometry ( $Y = aX^k$ ) proposed by Huxley [26]. Focusing on the coefficient named  $k$  (allometric exponent) provides information about differences of growth rates between the two considered descriptors, in particular when it concerns width versus length it can reflect globularity as defined above. This parameter allows summarizing the growth rate and so it is compared to other areas.

When problems of “bad fitting” (presence of a shift between observed and predicted data) were detected using for example the corresponding residuals of this classical model, an alternative model built on piecewise regressions [27] was tested. It is also called segmented regressions model. It provides regression analysis on both sides of an automatically determined breakpoint. This methodology was used by Katsanevakis et al. [28] for bivalves’ species. The choice of the “best” model was undertaken by using the AIC (Akaike Information Criterion; [29]) score; the lowest AIC score gives the one to select. The breakpoint is a parameter which can be viewed as an indicator of fast ecological changes or linked to marked events [28]. The regression equations before and after this breakpoint illustrate the shift of the shell growth to different morphological patterns during ontogeny.

**2.4.2. Spatial Allometry Patterns.** In this part, clams longer than 30 mm (i.e., 661 clams) were retained to consider spatial variability of allometric descriptors. This choice was decided in order to avoid size effect and to consider whether a link with two of the shape potential drivers (density or the brown muscle disease—coded BMD) could be detectable (since the smallest clam presenting this pathology was 26 mm long). To interpret the allometric variability in terms of density, two classes were defined: below 100 clams  $m^{-2}$  (“low density”); above 100 clams  $m^{-2}$  (“high density”). Concerning pathology, proportion of clams infected by BMD within the sample was coded into 3 classes: no clams infected (“No BMD”); below 3.7% of infected clams (“Low BMD”); above 3.7% of infected clams (“High BMD”). Normalized principal components analysis (NPCA) was conducted in order to consider the relations between the synthetic shape descriptors and spatial considerations (strata encoded by letters, see Figure 1), density and proportion of clams infected by BMD (added as supplementary factors). This methodology is widely used for such investigations [30, 31].

Calculations were carried out under R (<http://cran.r-project.org/web/packages/Rcmdr/index.html>) and the following packages: factomineR for NPCA, stats for linear regressions, and SiZer for piecewise regressions (<http://cran.r-project.org/web/packages/SiZer/index.html>; [32]).

### 3. Results

**3.1. Shell Shape in Arcachon Bay.** The range of studied population length was between 10.4 and 45.0 mm (mean: 27.4 mm; standard deviation: 5.21 mm). Other statistics on the morphometric variables are summarized in Table 1. The mean shell pattern (average values) was described by an Elongation index of 0.75, a Compactness index of 0.28, and a Convexity index of 0.37. By comparison with traditional forms (circular or elliptical), valve shape was better described as circular when it was seen from the side view and elliptical when seen from ventral view. For the three weight ratios, the values were ranging between 0.57 and 2.02 and presented higher variability within the considered population than the other morphometric variables (relative standard deviations around 45%).

**3.2. Allometric Patterns.** Classical linear regressions (Figures 2(a)–2(g); see also Supplementary Materials available online at doi: 10.1155/2012/281206) revealed isometry for pattern such  $H$  related to  $L$  (called  $H$  to  $L$  allometric relation), characterized by an allometric exponent ( $k$ ) equal to 1.00 indicating that an increase of the length did not induce changes of growth rate of the height. For other ( $W$  versus  $L$ ,  $H$  versus  $L$ ,  $SM$  versus  $L$ ,  $SM$  versus  $H$ , and  $SM$  versus  $W$ ) allometric relations,  $k$  exceeded 1.00 which means a positive allometry for these pairs of variables. Higher  $k$  values were obtained for relation involving the weight. No significant relations were obtained for the circle or ellipse indices in relation to the length. For  $H$  to  $L$  allometric relation, classical and piecewise regressions had similar goodness of fit (AIC scores close to  $-2360$ ). For  $SM$  to  $L$  allometric relation, AIC score with classical model amounted to 859, whereas it is established to 854 with piecewise regression, this second modeling was considered to be better adjusted to our data for this ratio. The results of these two piecewise regressions ( $H$  to  $L$ ,  $SM$  to  $L$ ) showed breakpoints corresponding, respectively, to  $L = 15.7$  mm and  $L = 19.6$  mm.

**3.3. Spatial Allometry Patterns, Density, and Disease Effects.** For clams longer than 30 mm, the shape was correctly summarized by the first three dimensions of the NPCA (93.8% of the variance) described in Table 2, hereafter called Character 1, Character 2, and Character 3.

Heavy shells (regarding classical linear dimensions) with high values of width related to length were found in strata A, C, and S1. Those globular shells were associated with low-density levels (average 48 clams  $m^{-2}$ ) and high proportions of clams infected by BMD (average 12% of the sample) (see Figures 3 and 4). Besides, those two factors were significantly discriminated on the first axe which was characterized by the variables  $SM/L$ ,  $SM/H$ ,  $W/L$  ratios, circle and reference ellipse lateral indices.

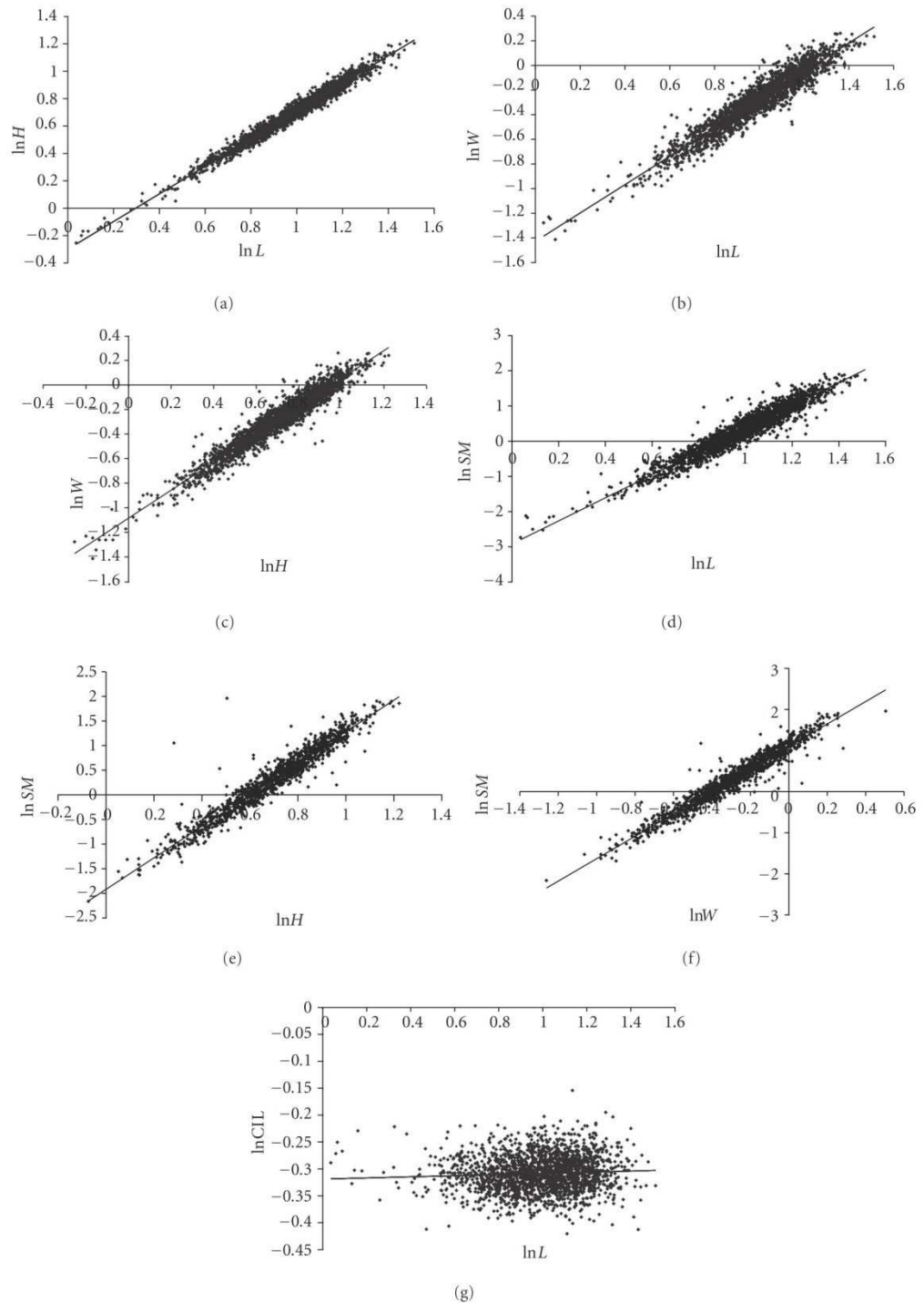
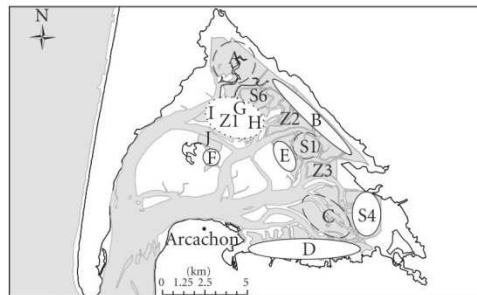


FIGURE 2: Allometric relations for pairs of parameters and shape descriptors (logarithmically transformed data).

TABLE 2: NPCA synthetic descriptors.

Selected principal components	Description	Shape tendency
Character1	Individuals presenting high values for $SM/L$ , $SM/H$ , $W/L$ ratios, high indices related to ventral circle and reference ellipse	Heavy shells regarding linear measures and high values of width related to length-globular individuals
Character2	$L$ , $H/L$ , $EIL$ , $CIL$ and two of the weight ratios ( $SM/H$ and $SM/W$ ): the higher the indices of related mass and length, the less the clam presents a round form (lateral view)	Heavy shells regarding linear dimensions but associated to high values of lengths
Character3	Shells with high $H/L$ ratio and lateral indices, by opposition to low $W/L$ and $W/H$ ratios	Round shells (lateral view) and little width related to length and height



- Relative heavy and globular clams associated with high BMD and low density
- Relative light clams with D case (particularly round (front) clams)
- Relative heavy and elongated clams

FIGURE 3: Spatial visualisation of the allometry patterns related to density and disease.

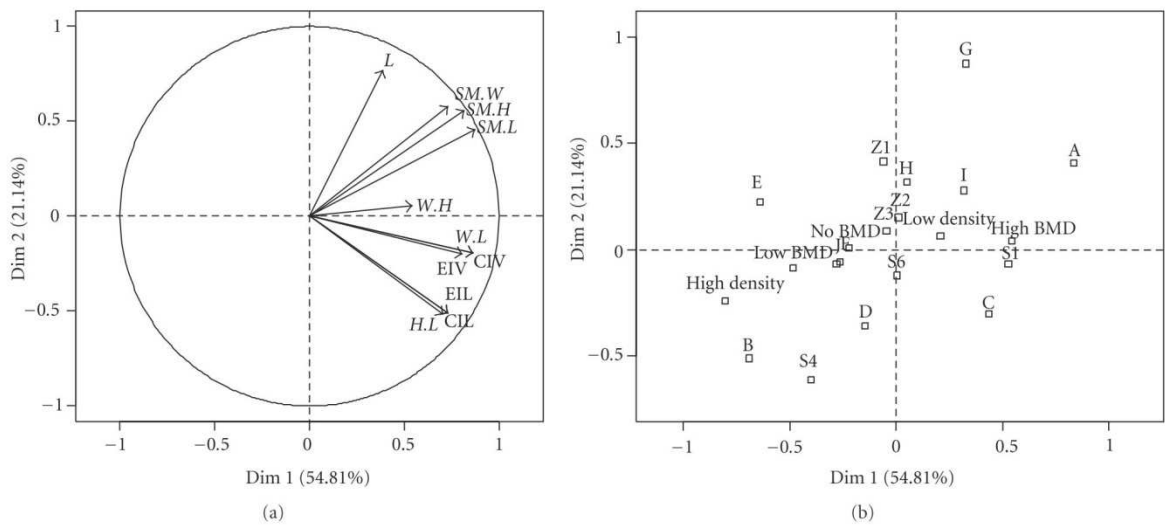


FIGURE 4: NPCA on morphometric variables (individuals and variables graphs) with strata, density, and BMD as supplementary factors.

TABLE 3: Comparison of morphometric results with other sites including Europe.

Site/Area	Mean morphometrics results	Length (S. D.) indications of the studied population (mm)	Sources
Japan	$\overline{H/L}$ from 0.70 to 0.75 $\overline{W/L}$ from 0.40 to 0.45	Range 10.8 (0.60) to 11.5 (0.63)	Deduced from Watanabe and Katayama [23]—Figure 3
China	$\overline{H/L} = 0.69$ $\overline{W/L} = 0.44$	Mean Length 20.35 (1.35)	Deduced from Fan et al. [33]—Table 1
Spain (bottom culture)	$\overline{H/L}$ from 0.58 to 0.73 $\overline{W/L}$ from 0.41 to 0.48	Range 13.7 (0.26) to 26.6 (0.43)	Deduced from Cigarría and Fernández [18]—Table 1
Tunisia	$\overline{H/L} = 0.69$ $\overline{W/L} = 0.44$	Mean Length 35.0 (3.82)	Deduced from Ben Ouada et al. [30]—Table 1
Italy	$\overline{H/L} = 0.71$ $\overline{W/L} = 0.50$	Mean Length 39.2 (5.7)	Deduced from Geri et al. [34]—Table 1
France (Barfleur)	$\overline{H/L}$ from 0.68 to 0.71 $\overline{W/L}$ from 0.40 to 0.48	Range 19 to 33	Deduced from Gérard [7]—Figures 32 and 36

Note: after having checked for valves symmetry on a subsample, the W/L ratio (obtained by TNPC system) for Arcachon was multiplied by two in order to allow for realistic comparison with published ratios.

Heavy shells (regarding classical linear dimensions) but associated to high values of lengths were found in strata G, H, Z1, and Z3.

Those two types of strata differ from strata B, E, and S4 for which individuals presented low weight related to length, height, or width.

Stratum D was illustrated by circular shells (lateral view) and little width related to length and height by opposition to strata F, S1, and Z3.

Spatial visualization of those results revealed a typology defined by 3 main areas which differ in particular by their distance to the ocean connection (Figure 3).

#### 4. Discussion

*4.1. Shell Shape: Profile and Main Characteristics according to Some Populational Descriptors.* This current study investigates the morphometric traits of *Ruditapes philippinarum* within Arcachon Bay using ratios classically employed for calcified structures. Observed values for those ratios (Table 1) establish that this population is characterized by relatively round ( $H/L = 0.75$ ,  $CIL = 0.73$ ) and globular shells ( $W/L = 0.28$ ,  $EIV = 0.95$ ). Those results confirm the professional observations on the existence of a peculiar morphological pattern (so-called globular or “*boudeuses*” clams by French fishermen) which is described by a more compact form as usually observed.

Those conventional morphometric variables allow for comparison between the Arcachon Bay population and other ones from remote sites (deduced from [7, 18, 23, 30, 33, 34]). It emphasizes that shells are characterized by a much less elongated and more globular form than in other sites including Europe (Table 3) highlighting so a less favorable environment for the development of the clam and also individuals less attractive for economical point of view. These results are still consistent if we consider only the smallest

individuals as Cigarría and Fernández [18], Watanabe and Katayama [23] did (data not shown).

Dependence of shell morphology on local environmental conditions has been indicated by Costa et al. [12] reminding inter alia the phenotypic plasticity in valve shape with a reference to the work of Kwon et al. [11] on transplantation results. They correspond more globally to the concept proposed by Lucas [8] in which ecological conditions seem to strongly influence both bivalves’ morphology and physiology. The spatial patterns observed at the bay scale advocate for the existence of specific local environmental conditions that could be related for example to the hypsometric level or to continental input. Unfortunately in this present study, we couldn’t take into account those kinds of factors.

Our study focuses on two factors that may affect the observed shape descriptors within the bay: i/density and ii/presence of an emergent disease, the BMD. Relationships among low density (below 100 clams  $m^{-2}$ ), absence or low presence of BMD (proportion of clams infected by BMD within the sample ranging from 0 to 3.7%) and clams presenting high  $SM/L$ ,  $SM/H$ , and  $W/L$  ratios are highlighted using the observed values in Arcachon Bay.

The question of density dependence of the Manila clam’s shell shape appears to have been considered in the literature but with no consensus. In our study, concomitance between high densities and propensity to be elongated is depicted. This is comparable to the results obtained by Cigarría and Fernández [18] in Eo Estuary (Spain) for this same species but under lowest densities conditions for Arcachon Bay (maximal density in the present work: 358 clams  $m^{-2}$ ; 1000 clams  $m^{-2}$  for Eo estuary). For the Spanish site, this height’s density dependence was interpreted as a consequence of space competition since the height corresponds to the horizontal occupation in the sediment (because of the position of the buried clam). Space competition issue was also reported for *Cerastoderma edule* [35, 36]. Alumno-Bruscia et al. [37] describe as well an elongation of the shell for high population

density for *Mytilus edulis*, while it is interesting to note that they raised the question of a consequence of a real physical interference, food depletion, or a combination of both. With respect to Manila clam, different observations have been made. Clam density was identified among other factors to impact the suitability of lagoon's areas (at local scale) for clam cultivation through a model-based approach [38]. For high densities conditions, Ohba [15] observed an increase of length proportionately less important than the ones in height and width. Bourne and Adkins [16] reported a common happening of stunted clams for wild populations and Mitchell [17] stated for Manila clam that density in the Canadian beach determines the maximum size they will grow before stunting occurs. Otherwise, a competition for space was also suggested between *Ruditapes philippinarum* and three species (*Macra veneriformis*, *Nihonotrypaea japonica*, and *Upogebia major*) by Tamaki et al. [39]. For the Arcachon population, low density levels are associated with heavy and globular character. A common unfavorable environmental factor (see below) could be considered to explain these observations. Because the densities remain much lower than other studied sites, we can address in the same time the question of an environmental reason going beyond density strictly seen as spatial interference as suggested by some authors. A possible limitation of the maximum carrying capacity due to all the filter feeding species and not only within the Manila clam's population could be a hypothesis. On intraspecific competition issues to explain growth deficit, it would also have been interesting to consider the biomass. Insofar as we selected here the individuals above 30 mm, we consider that the biomass and density are well correlated.

To the best of our knowledge, correlation between disease and morphology had not been studied. For the Arcachon population, relationships between high proportion of clams affected by BMD and globular form (associated to heavy clams regarding length and height) have been described. Recently highlighted by Dang et al. [19], this pathology affects the posterior adductor muscle and leads to a progressive calcification of this organ. Valve activity and clam mobility appear to be affected, including valves hermetic ability. Because causal relationship between the globular form and BMD has not been demonstrated, we can wonder if the disease could have impacted the globular form or if unfavorable environmental condition leading to specific shape patterns could have favored the affection development in specific site. The first hypothesis is supported by a significant discrimination of the BMD modalities on the first axe which is characterized by the variables  $SM/L$ ,  $SM/H$ ,  $W/L$  ratios, circle and reference ellipse lateral indices. It implies that the disease would develop a sufficiently long time to modify the shell shape. So far, the only available information is that the smaller infected recorded clam is 26 mm long (de Montaudouin, personal communication). For the second hypothesis, no argument is available up to now. Both of them are in accordance with the description of a decrease of the condition index (for Arcachon Bay) associated to the BMD pathology [40]. It is also consistent with the highlighted correlation between  $H/L$  and to a less extent  $W/L$  with nutritional condition indices described by

Watanabe and Katayama [23]. More generally, the observed globularity is in accordance with phenotypic changes under "unfavorable" conditions described by several authors [3, 9, 25].

Apart from density and disease effects, other factors have been proposed or demonstrated to impact the shell morphology. From an evolutionary point of view, defense against predator is considered as the most important function of the shell as reminded by Tokeshi et al. [41]. Considering different species of bivalves including a related species *Ruditapes variegatus*, these authors pointed out that the larger the shell, the more resistant the shell is regarding breakage by predators. For *M. balthica* in the North Sea, the hypothesis of a selective predation of the more globular shells has been proposed by Luttikhuisen et al. [42]. For avian predators, this form may mean a harder prey to swallow but also promotes a higher salt content which is according to Visser et al. [43] research, energetically costly to excrete. Those biological interpretations are applicable for fast predators but for slower ones, the capacity of moving away and burrowing deeper is considered as prevailing and is easier for flatter shells [42].

The main influence of predation on molluscan shell morphology has also been indicated by Watanabe and Katayama [23], but they attributed preferentially significant local differences in elongation and compactness indices to differences of nutritional conditions as explained above.

Other factors such as current velocity, water depth, or nature of the sediment have also been proposed for their influence on Venerids' shape [7, 44–46]. For Gérard [7], the nature of the sediment is of a great influence on the sharpness of the shell. For *Tapes rhomboïdes*, a related species, globular character was depicted in the Plymouth region (Great Brittany). Originally attributed by Holme [44] to an effect of pressure (related to water depth), this conclusion was challenged by Eagar [45] who focused on other physical conditions (muddy substrates and sheltered localizations). He made the physiological assumption that "obesity" could prevent the shell from sinking within the sediment and could provide stability. On other bivalves species (*Tellina tenuis*, *Donax vittatus*, *Macoma balthica*, and *Cerastoderma edule*), Trueman et al. [47] reported an effect of substrate of particle size and shell shape on the penetration of the bivalves' shells.

Up to now, those environmental factors are incompletely known for Arcachon Bay by comparison with other sites and should require further investigations.

**4.2. Allometric Patterns: Synthetic Descriptors of Main Interest of Growth.** For the first time, our study provides allometric data for the main exploited stock in France (see Table 1 and Figure 2). Allometric coefficient ( $k$ ) is ranging between 1 (isometry for  $H$  to  $L$ ) and 3 (positive allometry with higher coefficient for ratios taking into account the weight). Those values are consistent with other allometric patterns described for *Ruditapes philippinarum* and related species such as *Ruditapes decussatus*, *Ruditapes variegatus*, and *Tapes rhomboïdes* [7, 41, 48, 49]. In particular, considering that age is in turn reflected by the length like Eagar et al. [9] did, our results confirm that the globular character is more pronounced in ageing individuals.



Both linear and piecewise regressions models fit correctly the data for  $H$  to  $L$  and  $SM$  to  $L$  relationships, despite the fact that the piecewise model appears to be better in the case of  $SM$  to  $L$ . Both of them highlight discontinuities in the relative growth curves with marked breakpoints at length 15.7 mm and 19.6 mm. After the growth becomes faster for directions other than length and clams tend to be globular. Katsanevakis et al. [28] estimated that those changes in growth trajectories during ontogeny were worth being taken into account since they can be linked to marked events in the life history or fast ecological changes. For Manila clam, the identified breakpoints correspond to the second year of life of the clam; they match with the supposed size of maturity for this species. According to Holland and Chew [50], sexual maturation begins at 5 mm and spawning at 20 mm for Manila clam.

For *Venerupis senegalensis*, it is interesting to note that Eagar [45] observed a second breakpoint interpreted as a shell-limiting process for  $H$  to  $L$  and  $W$  to  $L$  for length class plotted against length of shell. The physiological explanation proposed by this author was a weaker efficacy of muscles when respiratory and food-collecting capacity per unit tissue decrease while the length increases. Those results were obtained with mean ratios per length classes, ignoring the individual variability information.

Spatial variability is shown and three main morphological groups of adult clams are identified. For those clams, similar shell shape appears to be grouped in the proximate strata G, H, and Z1; they could be seen as clams living in optimal conditions compared to the rest of the bay. The shape tendencies also appear to differ by their distance to the ocean connection (Figure 3). A high intertidal localization (involved in particular in the access time to food supply) could intervene but the necessary data were not considered in this work to address this point. This would be consistent with the observations of stunted clams especially in high intertidal areas and at higher clam densities done by Bourne and Adkins [16].

Morphometric investigations led by Ben Ouada et al. [30] on *Ruditapes decussatus* for sites along the Tunisian coast identified the existence of three phenotypes (globular, slender, truncated) and established a high polymorphism not only at between-population but also at within-population scales. This high variability within population was also genetically demonstrated [51, 52]. Nevertheless, Luttikhuisen et al. [42] established that shell shape variation was not randomly distributed over sites for *Macoma balthica*, and Costa et al. [12] indicated that “contribution of local adaptation to the morphological differentiation of population of clam is still poorly studied phenomenon.”

**4.3. Regulation Considerations.** Currently four conservation measures are applied to regulate the fishing activity (number of licenses, minimum legal harvest size, fishing period, and no-take zones). Among those, the minimum legal harvest size is the only measure defined by European legislation; in practice applicable to the whole catches in Europe. Manila clam in Arcachon Bay presents a growth deficiency above 32 mm [20] and the present study reveals a different

morphology for the shell shape compared to other sites with a propensity to be globular. These characteristics are both driven by environmental factors and exploitation; do they reflect a situation of stress for this species or adaptation? Can they challenge the minimum legal harvest size for the benefit of a local one more adapted to this situation?

### Conflict of Interests

All authors declare no conflict of interests.

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## **Chapitre 3 – Évaluation des facteurs non contrôlés impactant la variabilité de la population**



La réalisation des fonctions biologiques des bivalves est connue pour être fortement influencée par les conditions environnementales (Gosling, 2003). Leurs effets induisent des réponses aux échelles inter et intrasites qui se traduisent par des différences de caractères phénologiques et phénotypiques. La capacité de l'espèce à produire des phénotypes différents en fonction des conditions environnementales dans lesquelles se déroule le développement définit le concept de plasticité phénotypique (Via et al., 1995). Ces variations vont potentiellement concerner les traits biologiques (également appelés traits d'histoire de vie) qui caractérisent le cycle de vie, les potentialités de résistance ou de résilience, la morphologie, la physiologie et le comportement du taxon considéré (Archaimbault et al., 2010).

Dans le cas de ce travail de recherche, nous nous sommes intéressés à la réponse au niveau de la morphologie et de la physiologie pour leur importance dans le cas des populations de bivalves peu mobiles.

### *Morphologie*

L'**Article 1** a mis en évidence l'existence de patrons morphologiques distincts au sein de la population d'Arcachon et a souligné le caractère bombé et rond de face des individus par rapport à d'autres populations de palourde japonaise. Cependant les informations morphométriques de référence disponibles concernent essentiellement des populations d'Asie et du bassin méditerranéen (Nakamura et al., 2002 ; Fan et al., 2007 ; Ben Ouada et al., 1998 , Geri et al., 1996), très peu de travaux se sont intéressés aux populations des côtes atlantiques (Gérard, 1978 ; Cigarría and Fernandez, 1998). Dans ces conditions, l'**Article 2** s'attache à tester l'hypothèse d'une forme spécifique sur le bassin par une étude morphométrique comparative sur quatre gisements de palourde japonaise distribués le long des côtes atlantiques françaises (Banc du Guer, golfe du Morbihan, Bellevue et bassin d'Arcachon). La méthode d'analyse de forme utilisée est identique à celle mise en œuvre dans l'**Article 1**, à savoir la méthode conventionnelle basée sur des ratios de métriques et/ou de poids. Une représentation des contours a également été entreprise sur une sélection d'individus afin de considérer l'intérêt de son couplage à la méthode conventionnelle pour des recherches futures. Pour les bivalves contemporains, les méthodes d'analyse de contours sont rares (Costa et al., 2010). Pour la palourde japonaise, elles sont à l'heure actuelle essentiellement limitées à

l'analyse des harmoniques de Fourier (Costa et al., 2008). Dans le but d'identifier les facteurs environnementaux responsables de cette variabilité phénotypique, les corrélations ont été recherchées entre les caractères morphométriques discriminants les quatre populations et les paramètres décrivant les conditions de température, de salinité et trophiques disponibles via les réseaux de surveillance de l'environnement ([www.envlit.fr](http://www.envlit.fr)).

### *Physiologie*

Concernant les traits d'histoire de vie de la population de palourde japonaise du bassin d'Arcachon, les travaux de Dang (2009) ont permis d'acquérir des connaissances sur le déroulement des fonctions de reproduction, de croissance et sur la mortalité naturelle. Pour certains paramètres de la population, des effets des conditions environnementales et/ou de facteurs infectieux ont déjà pu être mis en évidence. L'ensemble de ces informations qualitatives et quantitatives sont synthétisées dans le Tableau 3.1.

Ces travaux ont mis en exergue le rôle des facteurs pathologies et ressources trophiques sur des paramètres importants (croissance et reproduction) de dynamique de population. Dans le but de poursuivre la compréhension de l'influence environnementale sur les effectifs de la population, nous nous sommes intéressés dans l'**Article 3** à l'étude des relations existantes entre des descripteurs du stock et des paramètres décrivant les conditions physiques et trophiques.

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

Paramètres de dynamique de population	Descripteurs estimés	Relations démontrées avec paramètres environnementaux et/ou facteurs infectieux
Reproduction	Indice de condition (IC) et stades de maturation des gonades décrivant une à deux pontes en fonction des zones et des années  Niveaux de recrutement	Température : pas de relations établies mais description des conditions de température du sédiment au moment de la reproduction en accord avec la littérature  Niveau tidal : augmentation de l'IC avec le niveau tidal  Infection : diminution de l'IC au fur et à mesure du stade de l'infection par la Maladie du Muscle Marron (3M)
Croissance	Paramètres K et Linf de l'équation de Von Bertalanffy	Niveau tidal : diminution du taux de croissance avec le niveau tidal  Ressources trophiques : variabilité intersite de Linf principalement attribuée à la proportion de phytoplancton consommé et dans une moindre mesure à la couverture en herbier.  Facteurs physiques : variabilité intersite de Linf influencée dans une moindre mesure par la température et la salinité.
Mortalité	Coefficient de mortalité naturelle	Infection : contribution importante de la 3M au taux de mortalité naturelle

Tableau 3.1. : Synthèse des paramètres de dynamique de population de la palourde japonaise du bassin d'Arcachon et des relations identifiées avec les conditions environnementales et/ou les facteurs infectieux d'après les travaux de Dang (2009).

Pour ce faire, les descripteurs du stock ont été sélectionnés à partir de données de campagnes d'évaluations standardisées. Les données environnementales proviennent de réseaux de surveillance du milieu marin ([www.envlit.fr](http://www.envlit.fr)). Outre des descripteurs classiques de niveaux et de variations, des agrégations temporelles pour des valeurs définies dans la littérature comme ayant un impact possible sur la dynamique de la population ont été considérées. La sélection des paramètres environnementaux étudiés s'appuie sur la présentation en début d'**Article 3** d'une synthèse bibliographique des facteurs identifiés pour les différentes phases du cycle de vie de l'espèce. Ce choix résulte aussi des données disponibles au sein des réseaux de surveillance.

**Article 2**

Titre : Morphological trends of Manila clam (*Venerupis philippinarum*) as spatial patterns and following environmental variability

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1 **Morphological trends of Manila clam (*Venerupis philippinarum*) as spatial**  
2 **patterns and following environmental variability**

3

4

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20 **Abstract:**

21 For species' dynamics highly influenced by environmental conditions, sustainable  
22 management for conservation and/or exploitation purposes requires the ability to segregate  
23 natural processes from anthropogenic impacts. Identification of phenotypic variations  
24 regarding morphological patterns and understanding the mechanisms involved constitute in  
25 this context useful tools to identify adequate management measures to large and local  
26 conditions. Whereas such approaches are already effective on fish stocks management, they  
27 are more recent on bivalves while these resources are also good candidates.

28 The present paper tests the hypothesis of particular morphological patterns of Manila clam  
29 (*Venerupis philippinarum*) by undertaking a comparative morphometric studies on four  
30 populations of the French Atlantic coasts (Banc du Guer, Morbihan Gulf, Bellevue and  
31 Arcachon Bay). The methodology relies mainly on conventional shape analysis methods with  
32 eight morphometric ratios involving metrics and weight. In addition, a first implementation of  
33 outline description is conducted on selected individuals. This latter seems to reveal different  
34 forms of anterior-dorsal valves' margin whose interest is identified for future researches.  
35 Using supervised classification method, morphometric-latitude trends between northern and  
36 southern sites is for the first time suggested for a Veneridae species.

37 Relationships between discriminatory morphometric ratios (describing elongation, valve  
38 density and weight related to length) and available environmental conditions (temperature,  
39 salinity and chlorophyll a concentrations) were considered using linear multilevel models.  
40 They revealed significant relationships with chlorophyll a concentrations and for one ratio  
41 with seawater temperature ranging from 12 to 20°C. Four hypotheses are exposed to explain  
42 the unexpected relationship identified between morphometric characters and trophic

43 conditions: a negative effect due to high chlorophyll a concentrations; a masked effect of  
44 other food resources affecting valve's growth; an inter-specific competition for food among  
45 the filter-feeders populations; effects of other environmental parameters such as sediment  
46 type. The observed differences of shape are proposed to respond to a combination of those  
47 four hypotheses with varying degrees depending on sites. Finally, consequences on  
48 population regulation are addressed.

49

50 **Keywords: shell shape, linear morphometric methods, contour detection, environmental**  
51 **effect, linear multilevel model, bivalve, Atlantic ocean**

52

53 **1. Introduction**

54 Phenotypic plasticity of bivalves' shell morphometry has largely been reported in the  
55 literature (Brown et al., 1976; Costa et al., 2008; Eagar et al., 1984; Lucas, 1981; Rosenberg,  
56 1972; Seed, 1968; Yonge and Campbell, 1968). Various ecological factors are known to  
57 intervene, sometimes without consensus: latitude (Beukema and Meehan, 1985; Fiori and  
58 Defeo, 2006); depth of distribution (Claxton et al., 1998); tidal excursion or shore level  
59 (Dame, 1972; Franz, 1993); water movements such as waves, turbulences or currents (Akester  
60 and Martel, 2000; Fuiman et al., 1999; Hinch and Bailey, 1988); type of sediment (Claxton et  
61 al., 1998; Eagar et al., 1984); salinity (Mariani et al., 2002); type of natural predator  
62 (Lutthikuizen et al., 2003; Nagarajan et al., 2006); trophic conditions (Tomaru et al., 2002).

63 One of the most cultivated and harvested infaunal bivalves in the world, Manila clam  
64 (*Venerupis philippinarum*), has been the subject of specific works on relationships between  
65 morphometry and environmental factors. They highlighted for this species the leading role  
66 played by trophic conditions (Watanabe and Katayama, 2010), currents (Kakino, 1996);  
67 offshore or inshore localization (Nakamura et al., 2002). Effect of clams densities was also  
68 reported by Bourne and Adkins (1985), Cigarría and Fernandez (1998) and Ohba (1956).  
69 Most of those studies rely on conventional shape analysis methods which use distances,  
70 ratios, angles between basically landmarks. Very few works implement outline shape analysis  
71 such as Fourier series representations (Costa et al., 2008). The majority of those studies  
72 concerned Japanese populations. Surprisingly few studies deal with European stocks (Costa et  
73 al. 2008) whereas identifying similarities and differences in their responses may be very  
74 useful in understanding the mechanisms involved. They could contribute to challenging the  
75 conservation of the species by segregating natural processes from anthropogenic impact and

76 be thus useful to identify adequate management measures to local conditions. Contribution of  
77 morphological studies on fish stocks management is already effective for some years (Cadrin,  
78 2000; Cadrin and Friedland, 2005); such approaches appear to be more recent on bivalves  
79 (Márquez et al., 2010).

80 In this context, the present study focuses on four populations of the French Atlantic coasts to  
81 highlight 1) on whether morphological patterns could be identified and related to spatial  
82 considerations; 2) and finally on the existing relationships between those parameters and  
83 selected environmental parameters. Conventional methods are mainly used; they are  
84 complemented by outline approach.

85

## 86 **2. Material and methods**

### 87 2.1. Study sites

88 Four intertidal sites along the Atlantic French coasts were selected to undertake the  
89 comparative morphometric study: Banc du Guer, Morbihan Gulf, Bellevue and Arcachon Bay  
90 (Fig. 1). Various criteria were taken into account for the choice of the sites: not only the  
91 presence of important Manila clams populations along a latitudinal gradient but also the  
92 availability of standardized environmental data related to the site.

93 “Banc du Guer” is the name given to the natural oyster deposit located at the river mouth of  
94 the Léguer river in North Brittany. The estuary is approximately 2.7 km<sup>2</sup> and has a mono-  
95 channel. An important sandy structure is located at the north-west of the bay (Augris and  
96 Simplet, 2012). At the mouth of the river, the bottom is mainly composed of fine shell sand.  
97 A facies characterized by heterogeneous mixture that can contain branches and debris of

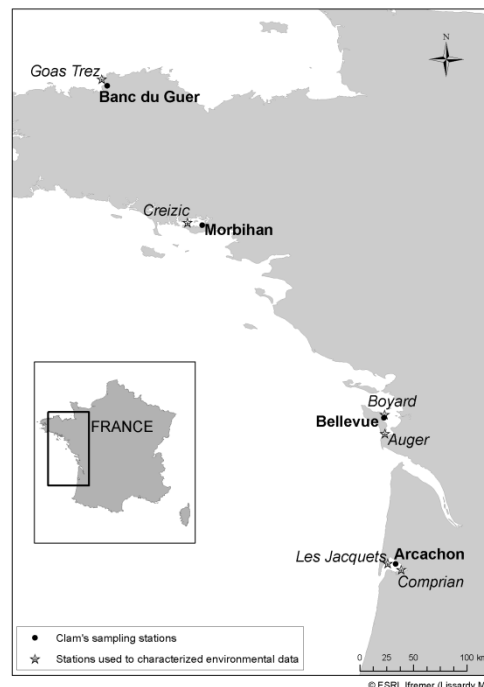
98 calcareous algae is also observed in this zone. The proportion of gravels tends to increase  
99 towards the middle of the bay (Augris and Simplet, 2012). Manila clams are mainly located in  
100 substrates composed of sand or mud and gravel. This bay is strongly influenced by tide levels.  
101 Currents are stronger outer the bay than inner. Speed tidal currents are comprised between 1.5  
102 and 2 knots. Salinity varies little during the year in the downstream part of the estuary  
103 (<http://envlit.ifremer.fr>).

104 The Morbihan Gulf is a macrotidal-dominated system. It has a surface area of 115 km<sup>2</sup> and an  
105 average depth of 4.4 m. This gulf, dotted with islands and islets, is opened to the ocean by a  
106 0.9 km wide bottleneck (Azandegde, 2010) giving its very sheltered character. This narrowing  
107 combined with deep valleys (corresponding to old flooded rivers) defined a complex  
108 hydrodynamics within the gulf. Whereas in the western part it can generate high current  
109 speeds, currents are reduced in the eastern part (Anonyme, 2006). Hydrosedimentary is also  
110 largely controlled by orientation of the islands although rapid changes are described. The  
111 eastern basin is odd that is its sediments are finer and settle on the substrate as silt. Bernard  
112 and Chauvaud (2002) described the sediments of this area as sandy mud and fine sand more  
113 or less silted. Manila clam is exploited in this eastern part; *Zoltera noltii* seagrass meadows  
114 are also listed.

115 Bellevue is located at the western part of Marennes-Oleron Bay which is a semi-closed bay  
116 connected to the Bay of Biscay by the Pertuis d'Antioche in the north and the Pertuis de  
117 Maumusson in the south. In this area, sea bottoms are fairly shallow and space dividing due to  
118 different islands leads to a complex hydrology (<http://envlit.ifremer.fr>). To the coast,  
119 sedimentation is promoted by the break of the swell. Transit currents move from north to  
120 south (through the two Pertuis). Hydrodynamics remains locally dominated by swell action

121 and tidal currents generating strong superficial changes in inter-tidal sand distribution (Le Hir  
122 et al., 2010). Those inter-tidal sand areas are limited; they host a large portion of the Manila  
123 clam population.

124 Arcachon Bay is a 156 km<sup>2</sup> semi-sheltered lagoon mostly composed of intertidal flats  
125 (110 km<sup>2</sup> within the inner lagoon). This mesotidal system is characterized by a sediment  
126 composition ranging from mud to muddy sands and colonized by vast *Zoltera noltii* seagrass  
127 meadows. Both influenced by external neritic waters and by continental inputs (Dang, 2009),  
128 this bay presents a semi-diurnal macrotidal rhythm. Temperature and salinity gradients within  
129 the bay are controlled by the characteristics of these water masses as well as the slow renewal  
130 of water by tides (Plus et al., 2006). Considering an arc from west to south within the bay,  
131 Manila clam population is on the whole located on its east side.



132

133 **Fig. 1.** Maps showing the studied site Arcachon Bay (France) and localization of the sampled strata (Sources:

134 ESRI, BD Carthage, Ifremer – M. Lissardy).



135           2.2. Sampling collection

136 *R. philippinarum* shells were collected between March 2010 and March 2012 (details in  
137 Table 1). For Arcachon and Morbihan sites, a Hamon grab was employed at high tides and  
138 sediment cores were filtered onboard. For Banc du Guer and Bellevue, the samples were  
139 undertaken at low tide by hand within quadrats. For both techniques, the sample consist in  
140 sediment cores of 0.25 m<sup>2</sup> (0.5 m \* 0.5 m) and depth is greater than the maximum buried  
141 depth known for Manila clam [10-12 cm when temperature is very low, Le Treut (1986)].  
142 Sampled stations were randomly defined for each sites and identified by their geographic  
143 coordinates. Brought back to the laboratory, the clams were stored à -20°C until analyzed. To  
144 limit potential size dependency (Fan et al., 2007) on the morphometric characteristics, only  
145 individuals between 35.0 mm and 37.5 mm in shell length were sub-sampled for each site.  
146 The level and the variability of length among the sites are similar (Kruskal-Wallis test: chi-  
147 squared = 5.394, df = 3, p-value = 0.1451; Levene test: F value = 0.3296, df = 3, p-value =  
148 0.804).

149           2.3. Environmental conditions

150 To consider the hydrological conditions which prevailed for each sites and potentially  
151 influenced morphometry characteristics, data from the national base Quadrige<sup>2</sup> were used.  
152 The main objectives of this base are to manage and exploit data provided by environmental  
153 survey networks undertaken by Ifremer. Sampling is carried out once a week or bi-monthly  
154 (depending on the parameters), at the slack of low tide (by strong coefficient) and high tide  
155 (by low coefficient) alternatively. For this study, we used both REPHY and ARCHYD  
156 networks and selected the parameters seawater temperature, salinity and chlorophyll a

157 concentration (considered as an indicator of trophic resources according to Shibata et al.,  
158 1999).

159 To limit inter-annual variability of the environmental parameters for each site, we decided to  
160 consider those parameters for the three years preceding the sampling collections. This three  
161 years period also corresponds roughly to the age of the studied clams (deduced from Le Treut,  
162 1986). Six stations (Goas Trez, Creizic, Boyard, Auger, Les Jacquets, Comprian) were  
163 considered as representative of the four studied sites (Fig. 1). For site presenting two stations,  
164 data were pooled.

165 From these data, two types of complementary metrics were defined. Firstly classical metrics  
166 (mean, median and standard deviation) were calculated. Secondly specific temporal  
167 aggregations were also considered for temperature in order to focus on its potential effects  
168 since numerous authors agree with the main role played by temperature on *Venerupis species*  
169 regarding growth function (Beiras et al., 1994; Fan et al., 2007; Laing et al., 1987; Toba, 1987  
170 in Nakamura et al., 2002). A pattern of growth has specifically been presented by Maître-  
171 Allain (1982) for Manila clam. It stated that no growth occurred under 6°C and that an  
172 optimal growth was expected between 12 and 20°C for this species in Thau lagoon. For the  
173 Jiaozhou Bay (China), the most suitable range of temperature for shell growth was ascertained  
174 between 18 and 23°C (Fan et al., 2007). In our work we referred to the pattern established for  
175 Thau lagoon and calculated (per site) two complementary characteristics: the percentage of  
176 observed values below 6°C and the percentage of observed temperature between 12°C and  
177 20°C. This environmental data set is synthesized in Table 2.

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

178 **Table 1.** Samples locations of *Venerupis philippinarum* characterized by their geographic coordinates, sampling periods, number of sub-sampled (between 35.0 and 37.5 mm)  
 179 individuals, average length and weight (+/- standard deviation) of the sub-sampled clams.

	Banc du Guer	Morbihan Gulf	Bellevue	Arcachon Bay
Geographic coordinates	48°44' N	47°33' N	45°56' N	44°43' N
	03°32' W	02°44' W	01°13' W	01°07' W
Sampling date	August 2011	March 2010	March 2012	May-June 2010
Number of clams between 35.0 and 37.5 mm sub-sampled	31	43	79	85
Mean length of sub-sampled clams (35.0 to 37.5 mm)	36.4	36.2	36.4	36.2
Mean weight of sub-sampled clams (35.0 to 37.5 mm)	3.06	3.09	3.87	3.60

180

181

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

182 **Table 2.** Seawater temperature (T), salinity (Sal) and chlorophyll a concentration (Chloro a) at the four sites.

183 Mean = Mean value; Med = Median value; SD = Standard Deviation, T6 = Percentage of temperature values above 6°C; T12\_20 = Percentage of temperature values between  
184 12°C and 20°C.

	Banc du Guer	Morbihan Gulf	Bellevue	Arcachon Bay
T Mean (°C)	13,6	13,8	14,2	15,2
T Med (°C)	14,0	15,0	14,9	15,5
T SD (°C)	3,8	4,3	4,5	5,6
T6 (%)	< 0,1	2,7	2,3	3,5
T12_20 (%)	60,5	65,3	51,2	38,7
Sal Mean (dimensionless)	34,2	33,2	33,5	30,6
Sal Med (dimensionless)	34,6	34,0	33,6	31,1
Sal SD (dimensionless)	1,3	1,8	1,4	2,3
Chloro a Mean ( $\mu\text{g l}^{-1}$ )	1,3	1,8	3,0	3,1
Chloro a Med ( $\mu\text{g l}^{-1}$ )	1,1	1,4	2,4	2,5
Chloro a SD ( $\mu\text{g l}^{-1}$ )	0,9	1,6	2,0	2,3

185

186

187 2.4. Shells preparation and classical morphology descriptors

188 In laboratory, all the shells were cleaned, dried at 38°C for 48 h and the valves were  
189 separated. Then for each clam two high-resolution pictures (lateral and ventral views) of the  
190 left valve were undertaken by using the TNPC software (Digital Processing for Calcified  
191 Structures, www.TNPC.fr) and image analyses were performed. Six physical parameters were  
192 retained and used to express ratios. Those parameters consist in linear or surface measures  
193 directly obtained from the shape analysis (lateral or ventral views) and weight measure of  
194 each left valve. Respective accuracies of  $1.10^{-4}$  millimeter and 0.1 mg are associated to linear  
195 and weight measures:

- 196 - Length ( $L$ ), defined as the longest distance from front edge to back edge (mm). It is  
197 the reference length obtained from lateral view;
- 198 - Height ( $H$ ), as distance from the umbo to edge (mm) obtained from lateral view;
- 199 - Width ( $W$ ), as longest distance of the valve in a lateral plane across the valve (mm)  
200 obtained from ventral view;
- 201 - Lateral Area ( $Al$ ), defined as the surface of the valve projected on a plan on lateral  
202 view;
- 203 - Ventral Area ( $Av$ ), defined as the surface of the valve projected on a plan on ventral  
204 view;
- 205 - Weight or Shell Mass ( $SM$ ), as dry Mass of the left valve (mg).

206 To describe and compare the morphology of the individuals regarding the sites, eight classical  
207 morphometric variables were retained: three sharpness indices defined as Elongation index  
208 ( $H/L$ ), Compactness index ( $W/L$ ), Convexity index ( $W/H$ ); three Weight linear ratios ( $SM/L$ ,  
209  $SM/H$ ,  $SM/W$ ) and two Weight surface ratios ( $SM/Al$ ,  $SM/Av$ ) (see Table 3 for details).

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

210 **Table 3.** Computations, ranges and interpretations of the morphometric variables used to describe morphological characteristic among sites.

Indicators	Computations (units)	Minimum to maximum (standard deviation)	Interpretations
Elongation index	$H/L$ (dimensionless)	0.65 to 0.82 (0.03)	It refers to the slender character of the valve from lateral view. The smaller the ratio, the more slender the valve is from lateral view.
Compactness index	$W/L$ (dimensionless)	0.24 to 0.40 (0.02)	It refers to the compactness of the valve from ventral view. The higher the ratio, the more dome-shape (curved) the valve is from ventral view.
Convexity index	$W/H$ (dimensionless)	0.33 to 0.50 (0.03)	It also refers to a curved character of the valve but from a front view. The higher the ratio, the more convex the valve is from front view.
Weight linear ratio 1	$SM/L$ $g\ cm^{-1}$	0.35 to 1.57 (0.19)	It refers to the valve weight related to the length. The higher the ratio, the heavier the valve is regarding its length.
Weight linear ratio 2	$SM/H$ $g\ cm^{-1}$	0.47 to 2.04 (0.23)	It refers to the valve weight related to the height. The higher the ratio, the heavier the valve is regarding its height.
Weight linear ratio 3	$SM/W$ $g\ cm^{-1}$	1.14 to 4.78 (0.52)	It refers to the valve weight related to the width. The higher the ratio, the heavier the valve is regarding its width.
Weight surface ratio 1	$SM/Al$ $g\ cm^{-2}$	0.17 to 0.73 (0.08)	It refers to the density of the valve expressed in $g\ cm^{-2}$ and concerns the surface of the valve projected on a plan on lateral view. Bearing in mind that the thickness of the valve is not taken into account, the higher the ratio, the denser per this surface area the valve is.
Weight surface ratio 2	$SM/Av$ $g\ cm^{-2}$	0.48 to 1.95 (0.20)	It refers to the density of the valve expressed in $g\ cm^{-2}$ and concerns the surface of the valve projected on a plan on ventral view. Bearing in mind that the thickness of the valve is not taken into account, the higher the ratio, the denser per this last surface area the valve is.

211 2.5. Representation of clam shapes using contour detection

212 In addition to those classical morphometric descriptors, a first representation of the clam  
213 shapes (in lateral view) was undertaken by using contour detection technique. For each site, a  
214 typical valve presenting morphometric ratios close to the average ratios of the site was  
215 selected. Three classical categories of contour detection techniques can be listed:

216 - detectors based on gradient operators like Prewitt filters (Maini et al., 2006), Sobel  
217 filters (Sobel, 1990), Laplacien;

218 - detectors based on analytic approach like Canny filter (Canny, 1986), Deriche filter  
219 (Deriche, 1990);

220 - and active contours also called "snakes" (Kass et al., 1988).

221 Among them, we focused on active contours. A snake is a set of points placed on the image,  
222 which move towards the shape to be extracted. The motion of each point depends on two  
223 energies. The first one, called internal energy, controls the intrinsic characteristics of the  
224 snake, like elasticity, space between points, and so on ... The second one, called external  
225 energy, defines a kind of force field, based on the initial image and which obliges points to  
226 move towards the shape. The definition of this external force is the real challenge for a good  
227 extraction. More precisely, in our case, we compute it directly from the image. First, we  
228 amplify the difference between the different areas of the image, and attenuate the variations of  
229 pixels intensity and pixels color in a same area. Then we applied a Canny filter, in order to  
230 extract frontiers between areas. In the resulting image, these frontiers are represented by  
231 pixels with a high intensity. Our external force made contour points to move towards these  
232 pixels.

233 2.6. Statistical analysis

234 Statistic analysis is used to answer two questions and so statistical analysis is divided in two  
235 parts: 1) description of the biometric variables related to the sites and individuals  
236 classification; 2) multilevel modeling to highlight the relationships between biometry and  
237 environmental parameters. The eight morphometric parameters described above were taken  
238 into account (H/L, W/L, W/H, SM/L, SM/H, SM/W, SM/Al, SM/Av). Concerning  
239 environmental conditions and level indicators variations, we chose to retain eight metrics,  
240 some ones giving an idea of a level value and others of variability (T Med, T SD, T6, T12\_20,  
241 Sal Med, Sal SD, Chloro a Med, Chloro a SD).

242 *Description of the biometric variables related to the sites and individuals classification*

243 Level and variability of length among the sites are similar. Significant differences among the  
244 morphometric ratios were tested with Kruskal-Wallis tests (using a type I error rate of 0.05).  
245 Morphometric peculiarities of each site were then regarded from a multivariate point of view,  
246 using descriptive multivariate statistical analysis. Normality of each ratio at each site was not  
247 verified with the original data. For a given parameter, the needed transformations to reach  
248 normality differed from one site to another. Moreover, equality of variance-covariance matrix  
249 at each site was not satisfied. In those conditions, usual classification methods such as LDA  
250 (Linear Discriminant Analysis), QDA (Quadratic Discriminant Analysis) or HLDA  
251 (Heteroscedastic Linear Discriminant Analysis) were not well-adapted to our data to confirm  
252 the observed variations among sites. We chose to implement Classification Tree (CT) which  
253 is a data mining method used to implement supervised classification. The aim is to find rules  
254 built from a set of explanatory variables that can separate the values of the target variable. In  
255 this sense it has the advantage of not requiring any binding assumption on the variables



256 distribution, except that the target variable, if qualitative, does not contain rare outcomes. The  
257 obtained rules which take into account interaction between the variables can be displayed  
258 graphically using a binary tree. The hierarchical power of separability of each explanatory  
259 variable on the target variable can be interpreted. Statistical evaluation of the quality of the  
260 results is possible through several error rates of misclassification.

261 Once a decision tree constructed, it is essential to validate its use by estimating the probability  
262 that the predicted class for any data is correct. This estimate depends on the dataset used to  
263 compute it. So, this is a random variable. The methodology used to manipulate such tool  
264 consists of constructing a sequence of nested sub-trees increasingly parameters. We then  
265 selected one of these trees using a 10-folds cross-validation estimate of the misclassification  
266 rate which is an estimate of the probability of misclassifying a new data. This led to select the  
267 tree which has the best predictive power while being parsimonious. This step is called  
268 pruning. It provides a simplification of the classification tree and makes it more easily  
269 interpretable. It avoids over-fitting.

270 The proportion of statistical units whose class is poorly predicted by the tree calculated on the  
271 whole sample is called the resubstitution error rate. The confusion matrix summarizes the  
272 reclassification of the observations, and allows to quickly identify which outcome of the  
273 target variable is poorly predicted by the selected tree.

274 *Multilevel modeling to highlight the relationships between biometry and environmental*  
275 *parameters*

276 The morphometric ratios identified as the most discriminatory by the previous classification  
277 method were considered one by one as dependent variables of the variability of environmental  
278 conditions. For each of those variables, a linear multilevel model (LMM, also called mixed

279 effects linear model) was fitted using site and the associated environmental conditions to  
280 quantify the dependences. To do this, we follow the sequence of steps proposed by Bliese  
281 (2012):

282 - Step 1 - a “null” mixed model is created taking into account only sites by examining  
283 intercept variability among site (random effect). The Intraclass Correlation  
284 Coefficient (ICC) is then calculated to determine how much of the total variance  
285 between-site variance is. We compare this null model and the model without a  
286 random intercept by assessing a model contrasts using Anova function;

287 - Step 2 - environmental conditions are then added one by one as predictors (fixed  
288 effect) to build several multilevel models. Since these models are nested, we used a  
289 likelihood ratio test (LRT) to evaluate the significance of adding each  
290 environmental and a combination of several ones to the null model. The final LMMs  
291 retained are as parsimonious as possible. To evaluate the gain of adding predictors  
292 on within and between site variances, we calculate the percentages of variance  
293 explained by using the following formula:

$$294 \text{ Variance explained} = [1 - (\text{Variance with predictors} / \text{Variance without predictors})]$$
$$295 * 100$$

296 The goodness of fit was then analyzed using associated residuals and a normal  
297 qqplot.

298 Calculations were carried out under R Software. The following packages were used:  
299 FactoMineR for simple descriptive statistics, rpart for classification trees. LMMs were  
300 performed using procedure lmer from lme4 library and nlme library.

301 **3. Results**

302 **3.1 Spatial heterogeneity of morphometric characters**

303 For the 238 samples, the means values of Elongation, Compactness and Convexity indices  
304 were 0.74, 0.29 and 0.40 respectively. By comparison with traditional forms (circular or  
305 elliptical), valve shape is better described as circular when it is seen from the side view and  
306 elliptical when seen from ventral view. The average Weight ratios range from 0.97 to 3.29 g  
307  $\text{cm}^{-1}$  and depend on the linear measure concerned. Weight surface ratios amount to 0.47 g  
308  $\text{cm}^{-1}$  in lateral view and 1.34 g  $\text{cm}^{-2}$  in ventral view. Variations around the average are much  
309 smaller for the three sharpness indices than for the other ratios (Table 4).

310 Distributions of those morphometric parameters seem to display differences among sites with  
311 an apparent north/south difference for some of them (Fig. 2 and Appendix). In particular the  
312 valves from Banc du Guer appear to be the more slender whereas the valves from Arcachon  
313 Bay and Bellevue are rounder from lateral view. Concerning compactness, the individuals  
314 from Bellevue are displaying globally higher ratios. For ratios regarding weight and linear or  
315 surface variables, differences between northern sites (Banc du Guer and Morbihan Gulf) and  
316 southern sites (Bellevue and Arcachon Bay) are observed. For those characters, southern  
317 ratios tend to present higher values than northern ones. Concerning Arcachon Bay a high  
318 variability should be noted for those last ratios.

319 Kruskal-Wallis tests applied to each ratio (test statistics:  $df = 3$ ,  $p\text{-value} < 1.039e^{-06}$ )  
320 confirmed significant differences among sites (Table 4):  $H/L$ ,  $SM/Av$  and  $SM/L$  presented the  
321 higher chi-squared values.

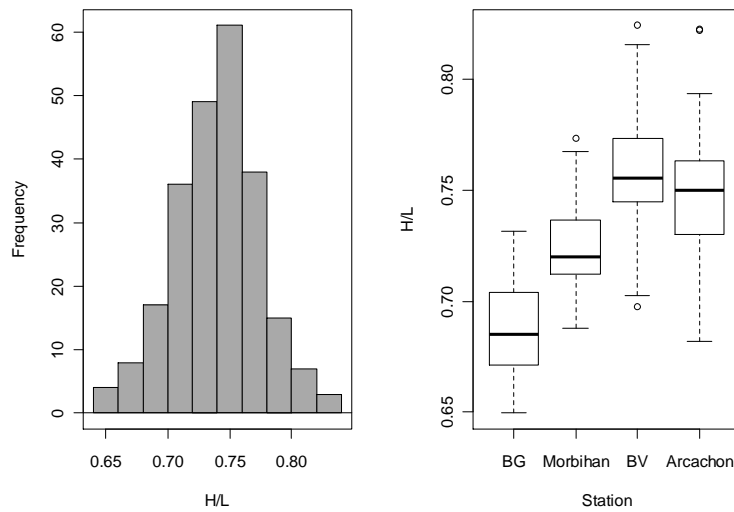
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322 **Table 4.** Morphometric characteristics of global sample (n = 238).

Indicators	Minimum	25%	50%	Mean	75%	Maximum	Sd	Kruskal-Wallis statistics to test spatial differences (factor= station)	
								Chi-squared	p-value
<i>H/L</i>	0.65	0.72	0.74	0.74	0.76	0.82	0.03	105.89	2.2e <sup>-16</sup>
<i>W/L</i>	0.24	0.28	0.29	0.29	0.31	0.40	0.02	44.82	1.012e <sup>-09</sup>
<i>W/H</i>	0.33	0.38	0.40	0.40	0.41	0.50	0.03	30.59	1.039e <sup>-06</sup>
<i>SM/L</i>	0.35	0.83	0.95	0.97	1.10	1.57	0.19	59.43	7.797e <sup>-13</sup>
<i>SM/H</i>	0.47	1.15	1.30	1.31	1.46	2.04	0.23	38.53	2.18e <sup>-08</sup>
<i>SM/W</i>	1.14	2.97	3.28	3.29	3.62	4.78	0.52	52.75	2.076e <sup>-11</sup>
<i>SM/Al</i>	0.17	0.41	0.46	0.47	0.52	0.73	0.08	39.87	1.133e <sup>-08</sup>
<i>SM/Av</i>	0.48	1.20	1.32	1.34	1.46	1.95	0.20	64.24	7.31e <sup>-14</sup>

323

324

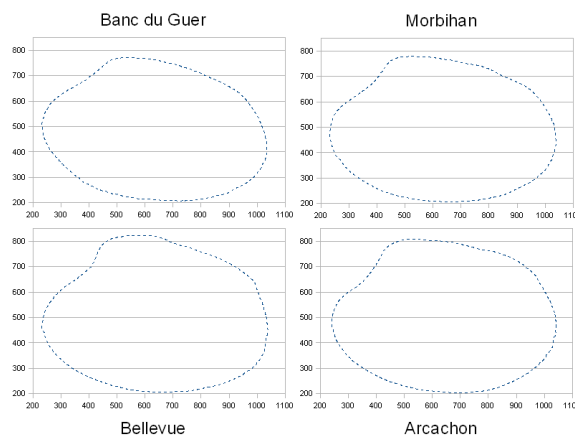


325

326 **Fig. 2.** *H/L* frequency distribution for the entire dataset and box plot according to factor site.

327

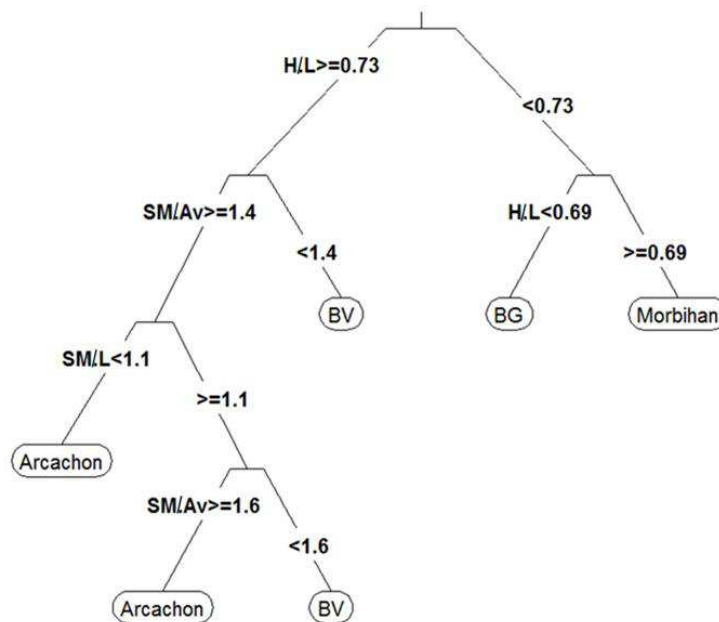
328 Representation of the active contours detected on four valves considered as typical of each of  
 329 the four sites valves (Fig. 3 a to d) completed the description of the shell. It illustrates the  
 330 flattened character (for lateral view) of the shell from Banc du Guer particularly by contrast  
 331 with Bellevue and Arcachon Bay. It should also be noted that this illustration seems to reveal  
 332 on those four valves different types of form concerning the antero-dorsal region,  
 333 characteristic that cannot be detected using conventional descriptors. Arcachon and Bellevue  
 334 sites are believed to exhibit a more curved shape of this region than the two others.



335

336 **Fig. 3.** Representation of active contours (“snakes technique”) detected on four valves considered as typical of  
 337 each of the four sites valves. (a) Banc du Guer, (b) Morbihan Gulf, (c) Bellevue, (d) Arcachon Bay.

338 The selected classification tree is displayed in Figure 4. It confirms the discriminating power  
 339 of the 3 ratios:  $H/L$ ,  $SM/Av$  and  $SM/L$  because their combination led to the best accuracy.  
 340 They illustrate a more or less round shape from lateral view and account for density regarding  
 341 linear or surface measures to discriminate French sites. Banc du Guer and Morbihan sites are  
 342 discriminated only by one character  $H/L$  ratio. This ratio is lower than 0.69 for Banc du Guer  
 343 and is comprised between 0.69 and 0.73 for Morbihan. Arcachon is characterized by  
 344 individuals displaying high values of  $H/L$  ( $> 0.73$ ) and  $SM/Av$  ( $> 1.4$ ). Then they are identified  
 345 either by  $SM/L$  ratio below 1.1 or by  $SM/L$  above 1.1 but associated with  $SM/Av$  higher than  
 346 1.6. Bellevue is also marked by high value of  $H/L$  ( $> 0.73$ ) but then presents two modalities:  
 347 individuals with low  $SM/Av$  ( $< 1.4$ ) or individuals with  $SM/Av$  comprised between 1.4 and 1.6  
 348 associated with high  $SM/L$  ( $> 1.1$ ).



349  
 350 **Fig. 4.** Plot of the selected classification tree obtained after pruning. Banc du Guer (BG), Morbihan Gulf  
 351 (Morbihan), Bellevue (BV) and Arcachon Bay (Arcachon).

352 The misclassification rate is 47 %, which means that the estimate probability that a new  
353 observation is incorrectly classified is 47 %. The resubstitution rate is 38 %, which means that  
354 38 % of the observations are wrongly classified in our dataset.

355 The confusion matrix is presented in Table 5. The proportions of individuals correctly  
356 classified into their original group are higher for Bellevue and Morbihan with respectively  
357 81 % and 72 %. Banc du Guer and Arcachon display lower percentages, 55 % and 41 %  
358 respectively.

### 359 ***3.2. Relationship between environmental conditions and morphometry***

360 For the three considered morphometric ratios ( $H/L$ ,  $SM/Av$  and  $SM/L$ ), the percentage of  
361 variation in individuals' morphometric values as a function of the site to which the clam  
362 belongs is estimated to vary from 27 % to 61 % (Table 6). The higher value of ICC is  
363 obtained for  $H/L$ .

364 Once predictors are taken into account, the LMM shows that the three ratios are significantly  
365 related to environmental parameters (Table 6). The percentages of between-site intercept  
366 variance explained by those predictors are high; they range from 71 % to 88 % depending on  
367 ratios. The latter share one common feature: a relationship with trophic condition expressed  
368 by Chloro a Med.  $SM/Av$  displays additional links with temperature descriptors (T20\_20) and  
369 with Chloro a SD. This last indicator also influences  $H/L$ . For  $H/L$ , residuals display a well  
370 aligned distribution whereas for the two others ratios, distribution's extremities presents  
371 incorrectly adjusted points (Fig. 5).

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372 **Table 5.** Confusion matrix related to the selected classification tree (expressed in %).

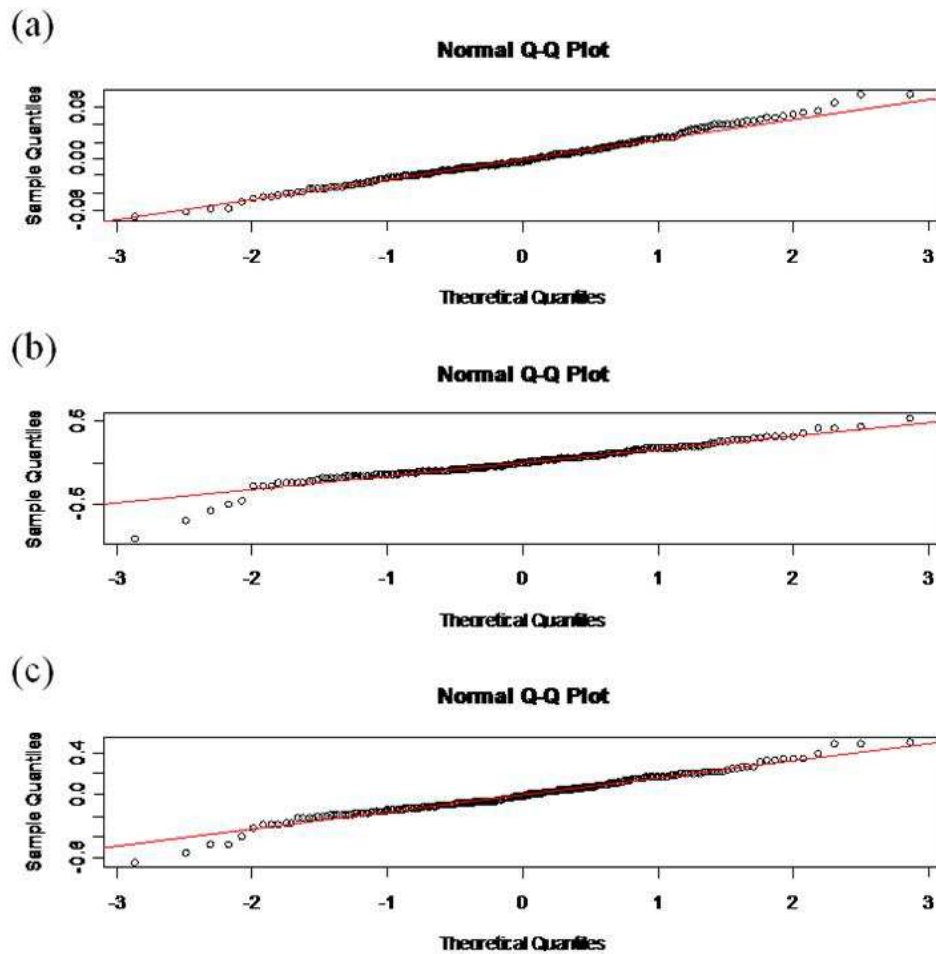
Real/Predicted	Arcachon	BG	BV	Morbihan
Arcachon	15	0	11	9
BG	0	7	0	6
BV	3	0	27	4
Morbihan	1	0	4	13

373

374 **Table 6.** Linear Multilevel Models showing the effect of environmental parameters (related to temperature and chlorophyll a) on discriminatory morphometric ratios identified  
 375 for Manila clams populations using classification techniques (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ).

Morphometric ratios	Step 1 – Null model		Step 2 – Final model		
	Intraclass Correlation Coefficient (ICC)	Significance between null model containing random spatial effect and one without	Significant environmental variables	% of between group intercept variance explained by predictors	Significance between null and final model
<i>H/L</i>	61 %	p-value <.0001***	Chloro a Med Chloro a SD	71 %	p-value = 0.03325 *
<i>SM/Av</i>	27 %	p-value <.0001***	T12_20 Chloro a Med Chloro a SD	88 %	p-value = 0.01651 *
<i>SM/L</i>	27 %	p-value <.0001***	Chloro a Med	85 %	p-value = 0.005284 **





376

377 **Fig. 5.** Normal qqplots regarding the three multilevel linear models respectively built for  $H/L$  (a),  $SM/Av$  (b) and

378  $SM/L$  (c).

379

## 380 Discussion

### 381 *Emphasis of a north-south differences regarding morphometric patterns*

382 For the four studied sites, Elongation index appears to be a discriminating criterion (with

383 substantially lower values for Banc du Guer than those obtained for Arcachon and Bellevue).

384 The slender character observed in north Brittany (and to a lesser extent in Morbihan) is in

385 accordance with observations made in north-west of France (Normandy), in Tunisia and in

386 Italy on clams of similar length (respectively by Gérard, 1978; Ben Ouada et al., 1998 and

387 Geri et al., 1996). For Arcachon Bay, the round character observed from lateral view has  
388 already been described by Caill-Milly et al. (2012). Our results indicate that Bellevue is in the  
389 same case. Concerning compactness, the average ratio for the four sites is 0.29. Whereas this  
390 character does not appear to be discriminating among those sites, this value is high by  
391 comparison with available data in the literature (Ben Ouada et al., 1998; Gérard, 1978; Geri et  
392 al., 1996). For the other ratios, very few comparisons can be undertaken with other sites  
393 because of limited available literature.

394 Within the four studied populations, two morphotypes have been highlighted: a northern  
395 pattern characterized by slender valves and relatively light in weight regarding linear or  
396 surface measures; a southern pattern featuring opposite characters. Whereas no size-latitude  
397 trends (calculated as the geometric mean of shell length and height on a  $\log_2$  scale) has been  
398 highlighted for Veneridae by Berke et al. (2012); this present study advocates, all else being  
399 equal, for a latitude influence on other morphometric descriptors. At finer scale,  
400 discrimination using the classical morphometric variables among the four populations is less  
401 obvious. In *Venerupis decussatus*, high polymorphism has already been demonstrated by Ben  
402 Ouada et al. (1998) not only at between-population but also at within-population scales.  
403 Genetic reasons have also been proposed to explain such variations by Moraga (1984) and  
404 Jarne et al. (1988). Nevertheless, Costa et al. (2008) established that shell morphology was  
405 prevalently subjected to local environmental conditions.

406 Given those results from classical morphometric ratios, complementary approach using  
407 contour detection technique might be helpful to consider morphological differences within  
408 and between sites. A first implementation of this approach has been conducted on four clams  
409 considered as representative of sites. As well as providing illustrations on classical

410 morphometric ratios this technique also seems to reveal different forms of anterior-dorsal  
411 valves' margin. On the basis of those preliminary displaying results, it would be interesting to  
412 pursue research in this area because prosogyrous shape is known to reflect an adaptation to  
413 sediment characteristics for other bivalves' species (Stanley, 1975; Eagar, 1978; Trueman et  
414 al., 1966). Rufino et al. (2006) have especially reported the concern to combine various  
415 morphometrics approaches (linear, contour analysis and landmarks analysis) on *Chamelea*  
416 *striatula*.

417 **Learning from supervised classification method and reflexions regarding management**  
418 **strategies**

419 Implementation of data mining method allowed to avoid violation of assumptions required by  
420 classical classifications methods. CT's application to ecological subject is more recent than  
421 for LDA and QDA which are largely implemented for ecological studies for a long time  
422 (Mercier et al., 2011). In this study, CT permitted to select three morphometric ratios ( $H/L$ ,  
423  $SM/Av$  and  $SM/L$ ) of eight available to discriminate the four sites. This highlighted  
424 combination of few ratios contradicts the conventional wisdom that better accuracy is  
425 obtained when increasing the explicative variables number (Arslan and Secor, 2008). The  
426 resubstitution rate achieved is 38 %. Regarding Mercier et al. (2011) criterion defined for  
427 otolith classifications, this rate is intermediate. This underlines the complexity of the shape  
428 considerations and supports the combination of various morphometrics approaches as  
429 discussed above.

430 We can notice that for the sites presenting the highest sample numbers (Arcachon Bay and  
431 Bellevue), the interpretation level was much detailed. On the opposite for the sites having  
432 smaller sample numbers (Morbihan and Banc du Guer), a loss in the interpretation level

433 occurred. This fact can partly explain that only 55 % of the clams originated from Banc du  
434 Guer were correctly classified. In the case of Arcachon which site also displayed a high  
435 percentage of incorrectly classified individuals (41 %), we think that this result has to be  
436 connected with the spatial morphometric variability recently described by Caill-Milly et al.  
437 (2012). Manila clam is characterized by sedentary-life history and aggregated distributions  
438 (Kalyagina, 1994). In those conditions, its large spatial extent of the species within the bay  
439 (around 46 km<sup>2</sup>, Sanchez et al., 2010) associated with the high morphometric variability  
440 should promote spatial regulation at the bay scale. The importance of taking into account  
441 spatial dimension into management strategies has been emphasized by Defeo (2003) for sandy  
442 beach stocks. A review of successful case studies implying spatial dynamics has also been  
443 undertaken by Caddy and Defeo (2003). In practice, such local legislation has been applied in  
444 addition to European legislation since 2000 in Arcachon Bay. It concerns protected area  
445 surfaces with localizations changing over time. Those protected areas are part of a package of  
446 measures designed at a regional scale and implemented in a co-management context.  
447 Integration of morphometric considerations based on contour detection techniques might be  
448 helpful to reinforce criteria regarding area selection.

449 ***An unexpected relationship identified between morphometric characters and trophic***  
450 ***conditions***

451 Implementation of LMMs on  $H/L$ ,  $SM/Av$  and  $SM/L$  revealed significant relationships with  
452 chlorophyll a concentrations and in one case with seawater temperature comprised between  
453 12 and 20°C. As an indicator of valve's density regarding ventral area,  $SM/Av$  is thus  
454 negatively linked with the optimum range of temperature known to intervene on Manila  
455 clam's growth (Maître-Allain, 1982). Those results are consistent with shell's hypostracum

456 growth. This inner layer of the valves has been demonstrated to be positively influenced by  
457 the maximum seawater temperature and negatively influenced by pressure (Olson et al.,  
458 2012). This would suggest that in our case the more the temperature remains within the  
459 optimum range for growth, the less the formation of this inner layer is enhanced.

460 Regarding trophic conditions, we identified a common relationship for the three considered  
461 ratios. Round shape and heavy valves regarding ventral area and length are correlated to high  
462 median chlorophyll a concentrations. In addition, round shape and heavy valves regarding  
463 ventral area are related to chlorophyll a variations but with opposite effects.

464 This result is surprising since good trophic conditions are expected to stimulate better growth  
465 characterized by slender shape and light weight's valve [Alumno-Bruscia et al. (2001) on  
466 *Mytilus edulis*; Watanabe and Katayama (2010) on *Venerupis philippinarum*].

467 To explain this apparent discrepancy with those previous studies on bivalves, we identified  
468 four hypotheses:

469 1) chlorophyll a is present in too much quantities leading to the opposite effect of  
470 that expected. In the lagoon of Thau (France), Maître-Allain (1982) already highlighted the  
471 existence of a threshold value regarding food supply beyond which the link between the  
472 increase of growth rate and the quantity of chlorophyll a is no more verified. Gills are in this  
473 case supposed to be disrupted by clogging phenomenon. Regarding the measured  
474 concentrations in this study, this may have been the case for the higher values;

475 2) chlorophyll a is insufficient to account for trophic conditions usable by Manila  
476 clam and may mask other important food resources affecting valve's growth. Such  
477 assumption has already been challenged by Flye-Sainte-Marie (2008). As a bottom  
478 suspension-feeding bivalve, Manila clam ingest not only phytoplankton (Kasai et al., 2004;

479 Kanaya et al., 2005; Yokoyama et al., 2005; Spillman et al., 2008) but also filters the  
480 sediment-water interface and can therefore ingest bacteria (Kharlamenko et al., 2001),  
481 diatoms, detritic particulate organic matter, small rotifer (Sorokin and Giovanardi, 1995),  
482 dinoflagellates (Li et al., 2001), microphytobenthos (Kang et al., 2007);

483 3) owing to trophic competition, the quantity of food really available for Manila  
484 clam is limited. For Arcachon this issue is supported by the evolution of other filter-feeders  
485 populations such as *Crepidula fornicata* and wild *Crassostrea gigas* (Dang, 2009), but also  
486 *Mytilus edulis*. Observations of numerous Ascidiacea have also been reported by De  
487 Montaudouin (personal communication). For the other sites, we have not identified such  
488 competition;

489 4) biases due to effect of factors not taken into account in this study. We refer in  
490 particular to crowding, immersion time and/or sediment effects. Competition for space is  
491 unlikely to occur because the natural densities are at a much lower level than the densities  
492 considered to impact in literature (Cigarría and Fernandez, 1998). Unfortunately, we do not  
493 have currently available data on the two other listed factors. Their likely effects must not be  
494 neglected particularly for sediment characteristics which have been proved to strongly impact  
495 other Veneridae species (Stanley, 1975; Eagar, 1978; Trueman et al., 1966). It seems thus  
496 relevant to undertake further researches in this area.

497 Several authors established that morphometric characteristics could reveal more or less  
498 favorable environmental conditions (Hamai, 1935; Ohba, 1959; Eagar et al., 1984) with, in  
499 particular for Manila clam, the demonstration that morphological characters can be used as  
500 proxy of nutritional condition (Watanabe and Katayama, 2010). In those conditions, we tend  
501 to believe that the observed differences of shape respond to a combination of those four  
502 hypotheses with varying degrees depending on sites. Those elements highlighted the

503 complexity of the factors involved in the shell characteristics. Superimpositions of several  
504 factors and high difficulties to separate them have already been reported by Orensanz et al.  
505 (1991).

506 In the present study, clams from the southern sites globally exhibit higher values than  
507 northern ones for both Elongation index and ratios involving weight. Watanabe and Katayama  
508 (2010) demonstrated that high values of Elongation index were associated to low conditions  
509 factors and highlighted correlations between fast growth, thickness of the shell and flatness of  
510 the valves. Referring to those works and notwithstanding that the present study does not take  
511 into account the thickness of the valves, the indicators of density of the valve could thus  
512 reveal that clams from southern sites display slower growth than the northern ones.

513 For Arcachon Bay, Dang et al. (2010) have already described smaller condition index and  
514 inferior growth (from 32 mm) compared to other sites. The hypothesis of less favorable  
515 conditions is thus consistent for this site and it should be possible to use indicators of valve's  
516 density proposed in this article as proxies of this status. For Bellevue absence of similar data  
517 does not allow us to formulate such assumption for the moment.

518

## 519 **Conclusion**

520 This study suggests, for the first time, morphometric-latitude trends for a Veneridae species.  
521 Based on inter-site considerations, it gives a complementary outlook on relationships between  
522 Bivalves and latitude to Berke et al. (2012) research that focused on Bergmann's rule.

523 Conventional morphometric ratios integrating weight density indicators exhibit correlations  
524 with environmental parameters in particular chlorophyll a concentrations and to a less extent  
525 seawater temperature. Combined with the first implementation of outline description, the  
526 highlighted patterns raise the question of combined effect of environmental conditions. They  
527 encourage to further explore those possible relationships notably by taking into account  
528 sediment characteristics.

529 Contribution of local adaptation of morphological differentiation is still currently a poorly  
530 studied phenomenon (Costa et al., 2008). Elucidation of those effects should promote  
531 comprehension of the ecological traits of Manila clams at inter and intrasite scales. It is all the  
532 more relevant that life history traits' differences can address topical ecological applications  
533 including fisheries conservation and management (Blanck and Lamouroux, 2007). Typically  
534 for Manila clam, they should promote adequate spatial management strategies.

535

### 536 **Acknowledgement**

537 We are grateful to Gérard Véron and Ludovic Bouché for providing shell samples from Banc  
538 du Guer and Morbihan Gulf. We thank also Alain Briand, Raphaël Le Guillou and Michel  
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540 Noëlle de Casamajor and Muriel Lissardy for providing respectively environmental data from  
541 Quadrige<sup>2</sup> and localization map. The authors wish also to thank Simplicie Dossou-Gbete for  
542 his advices on statistical classifications procedures.

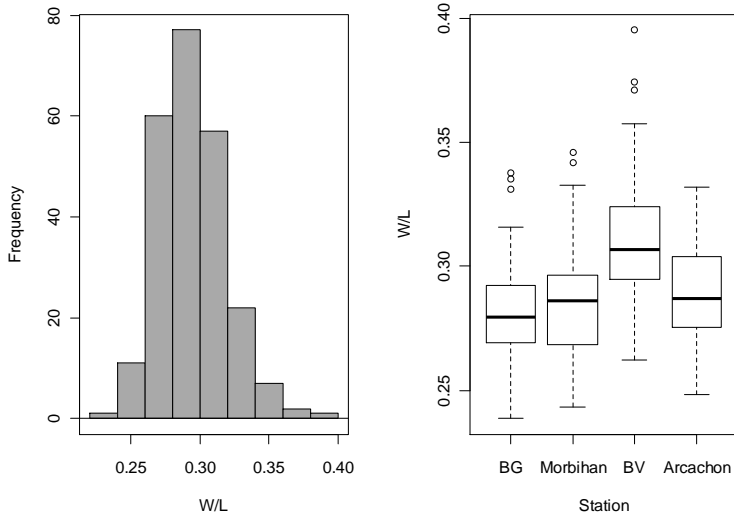
543 All authors declare no conflicts of interest.

544



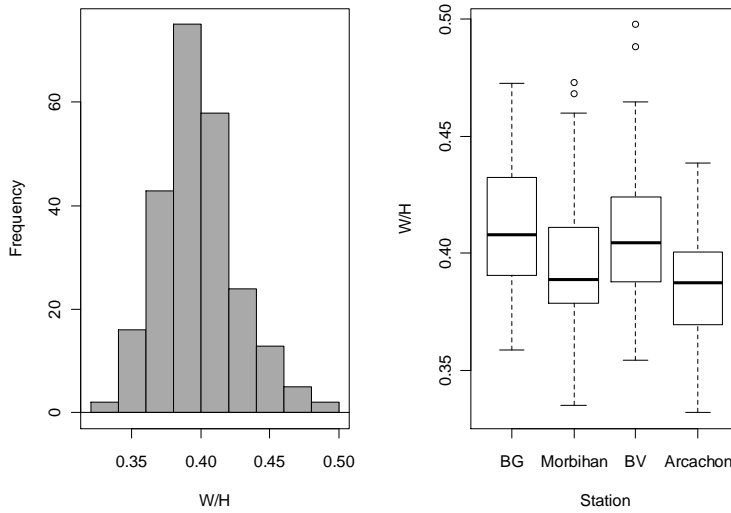
545

546 **Appendix**



547

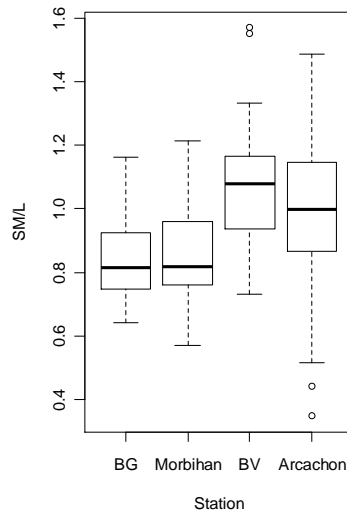
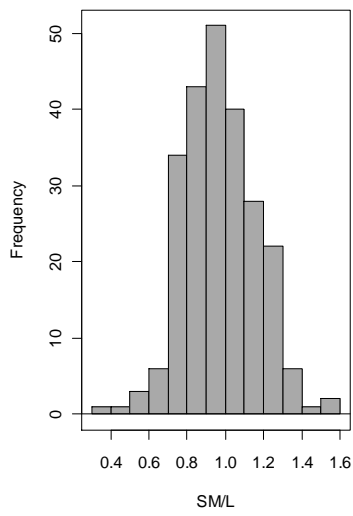
548 *W/L* frequency distribution for the entire dataset and box plot according to factor site.



549

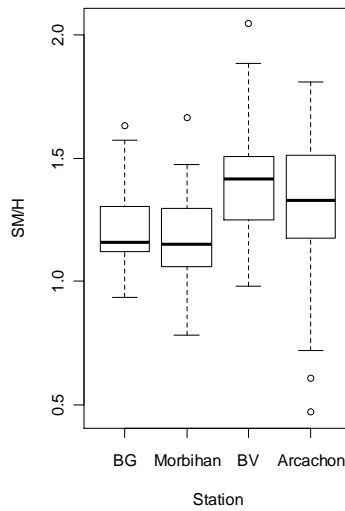
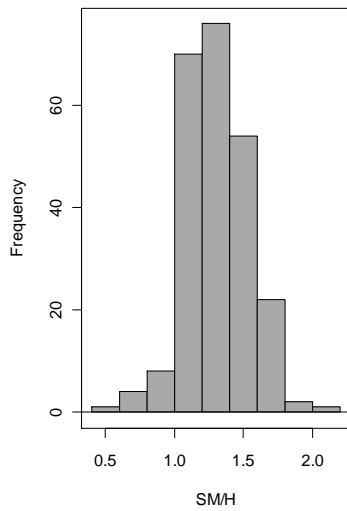
550 *W/H* frequency distribution for the entire dataset and box plot according to factor site.

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population



551

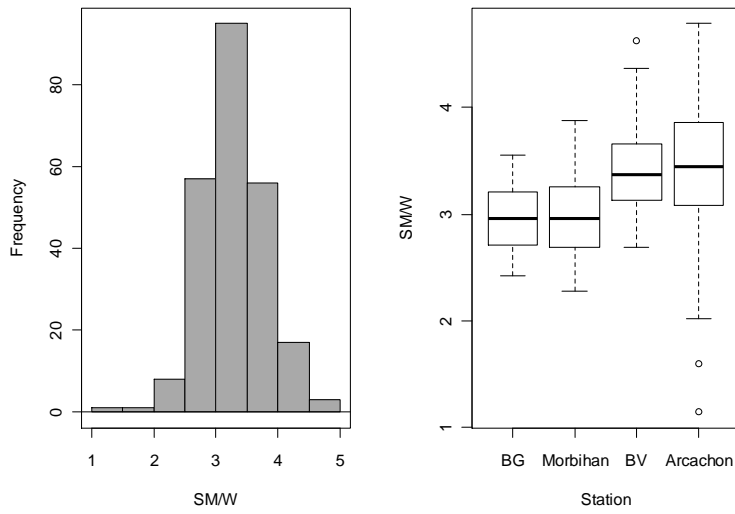
552 *SM/L* frequency distribution for the entire dataset and box plot according to factor site.



553

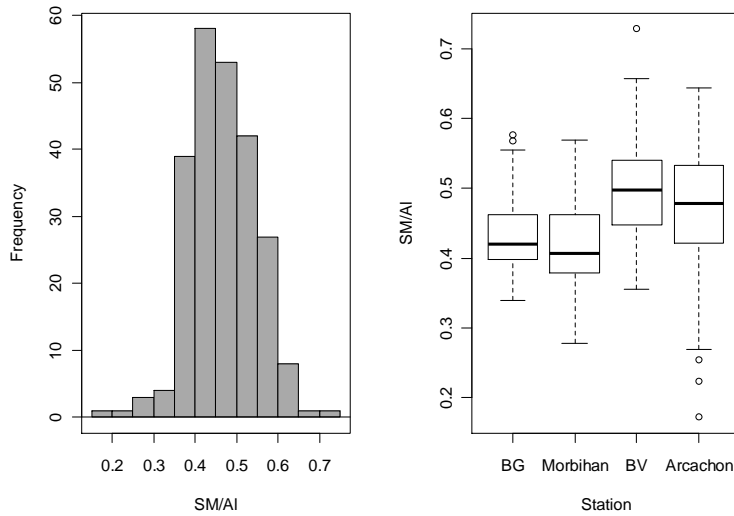
554 *SM/H* frequency distribution for the entire dataset and box plot according to factor site.

Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population



555

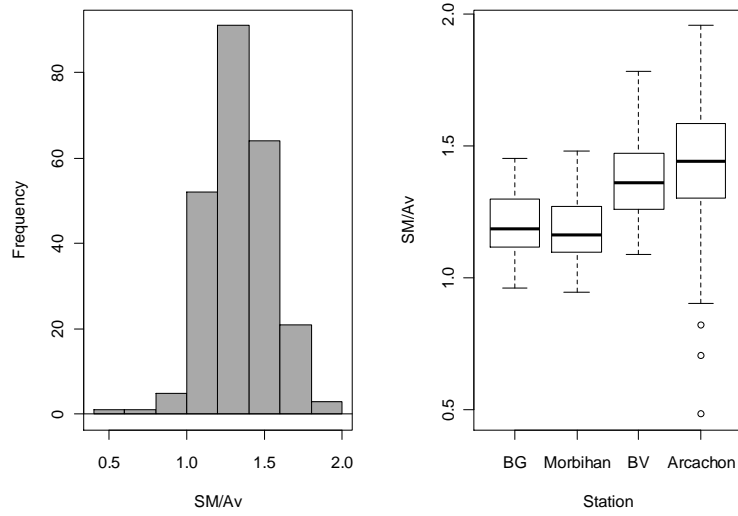
556 *SM/W* frequency distribution for the entire dataset and box plot according to factor site.



557

558 *SM/AI* frequency distribution for the entire dataset and box plot according to factor site.

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population



559

560 *SM/Av* frequency distribution for the entire dataset and box plot according to factor site.

561



**Article 3**

Titre : Detection of interrelations between stock status and environment using complementary multivariate analyses on temporal aggregations of environmental variables - Application to Manila clam (*Ruditapes philippinarum*) of Arcachon Bay (France)

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1 **Detection of interrelations between stock status and environment using**  
2 **complementary multivariate analyses on temporal aggregations of**  
3 **environmental variables -**  
4 **Application to Manila clam (*Ruditapes philippinarum*) of Arcachon Bay**  
5 **(France)**

6  
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19 **Abstract:**

20 Previously introduced for aquaculture purpose, the Manila clam (*Ruditapes*  
21 *philippinarum*) in Arcachon Bay (France) is currently a neonatural resources exploited  
22 by fishermen (professional and recreational). In order to provide scientific elements for  
23 management purpose aiming at reaching equilibrium between exploitation and  
24 conservation of this aquatic biological resource, a monitoring program including a  
25 specific simulation model has been conducted. Up to now, only one environmental  
26 parameter, water temperature, is included in the model for its influence on the  
27 reproduction phase. In order to consider if additional parameters should be integrated in  
28 the model, the study methodology was based on three steps. First step was to consider  
29 the stock status using synthetic descriptors (from field campaigns). Second step was to  
30 construct aggregated environmental parameters on periods expected to be relevant from  
31 biological point of view or according to previous results within the bay (related to  
32 temperature, salinity and trophic conditions from Archyd network, a hydrology follow-  
33 up on stations distributed within the bay). Complementary multivariate approaches  
34 (Normalized PCA and Regularized Canonical Correlation Analysis) were then carried  
35 out in a third step. Food availability appears to be correlated to the maximum of  
36 descriptors. The results show different relationships between juvenile and older stages  
37 for chlorophyll a, Total Suspended Organic Matter and Total Suspended Matter  
38 variables. The analyses also confirmed the role of temperature among the considered  
39 environmental parameters focusing on the reproduction period. Consequently it is  
40 proposed to include food supply as a second environmental parameter in the current  
41 simulation model in order to provide a more realistic and feasible decision-support

42 system. Noting that seawater photosynthetic pigments measurement (chlorophyll a)  
43 appears to be the most common indicator used for food availability; ways of refining the  
44 model are discussed. This methodology is transferable to other bivalve species and other  
45 sites.

46

47 **Introduction**

48 The Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) is indigenous to  
49 the Indo-Pacific region but, largely as a result of human activity, it is now widely  
50 distributed along the Pacific coast of America, the Atlantic coast of Europe, the Adriatic  
51 and Aegean seas (Kim, 1995; Gouletquer, 1997; Jensen *et al.*, 2004, 2005). In  
52 Arcachon Bay, France, the local population of Manila clam is thus neonatural,  
53 originating from venerid culture trials carried out in the 80s (Robert and Deltreil, 1990).  
54 Successful development of this population within the bay and its high market value  
55 have led to the progressive settlement of a fishery from the middle of the 90s. In the  
56 recent years, production by the commercial fisheries is comprised between 500 to 1,000  
57 tons per year and the total biomass is estimated between 4,500 and 8,000 tonnes  
58 (Sanchez *et al.*, 2010). The population of Arcachon Bay represents thus the most  
59 important Manila clam stock for which a sustained monitoring programme exists, the  
60 second one being for the population of Morbihan (Brittany) totalising 1397 tons  
61 (D'Hardivillé *et al.*, 2010). Following European large-scale common conservation  
62 measures (e.g. minimal harvesting size), the management of this local resource benefits  
63 also from regional conservation measures, such as those adopted by the 'Comité  
64 Régional des Pêches Maritimes et des Élevages Marins d'Aquitaine' (upon proposal  
65 from the 'Comité Local des Pêches Maritimes et des Élevages Marins d'Arcachon').

66 Upon professional fishermen request and in order to find equilibrium between  
67 exploitation and conservation of this aquatic biological resource, a long-term  
68 monitoring programme was launched in 2000 to identify important issues in terms of  
69 management decisions. The main component of this programme aims at assessing clam

70 biomass through standardized indicators (Bertignac *et al.*, 2001; Caill-Milly *et al.*, 2003,  
71 2006, 2008; Sanchez *et al.*, 2010) and developing a specific management model under  
72 the software Vensim ® (Bald *et al.*, 2009; Dang, 2009). This modelling approach  
73 belongs to simulation modelling category, built from the dynamic systems (DS)  
74 paradigm developed in the 1950s by Forrester (1973). Within the conceptual sub-  
75 category, the structure of this model describes the mechanistic relationships among  
76 abiotic, biotic, and anthropogenic ecosystem components. The classification of the  
77 elements involved in the system relies on determination of the “stocks” (*sensu* Vensim  
78 terminology *i.e.* describing the elements in the system e.g. clams, fishermen,...), the  
79 “flows” between these stocks (natural mortality/month, quantity of clams passing from  
80 a class to another, those elements are defined by time functions) and information that  
81 determines the value of the flows (auxiliary variables). The model developed for Manila  
82 clam has been constructed with a monthly time step; simulations cover a 10 years  
83 period. Specifically intended to address long-term issues, its main objective is to  
84 develop a decision tool when different management options exist, based on a modeling  
85 principle similar to the one used by Ortiz *et al.* (2002) on Peruvian scallop. It also  
86 brings a better understanding of the structural causes impacting the behavior of the  
87 system under study.

88 Up to now, the model is built at the global basin scale and one variable having a  
89 potential effect on the biological functions is taken into account, namely the  
90 temperature. This factor is indeed considered as the key environmental variable because  
91 it regulates not only both **growth** and **survival** of *Ruditapes philippinarum* (Mann,  
92 1979; Bernard, 1983; Gouletquer *et al.*, 1989 in Melià *et al.*, 2004) but also its

93 reproductive behavior (Delgado *et al.*, 2007). In the current version of the model  
94 developed for Arcachon Bay by Bald *et al.* (2009), the factor temperature is integrated  
95 for its effect on the **reproduction** function (*i.e.* during the **spawning** period or phase).  
96 Yet, recent works (on this species or performed to the related species *Ruditapes*  
97 *decussatus*) have underlined that this phase, along with others, can also be influenced by  
98 additional factors such as hydrodynamic regime, sediment type, food supply, oxygen  
99 (Breber, 1980; Rodriguez-Morosco *et al.*, 1992; Urrutia *et al.*, 1999).

100 When **gametogenesis** phase is considered, three main factors are described in the  
101 literature for their effects: temperature, photoperiod and food availability. Regarding the  
102 temperature, Delgado *et al.* (2007) reproduced in laboratory the thermic conditions of  
103 Galician coastal waters and demonstrated experimentally that the gonadal development  
104 was determined not only by the increase of the absolute value but also by the duration  
105 of exposure. These results are in agreement with those published by Mann (1979) and  
106 by Toba and Miyama (1995) and derived from *in situ*, natural, surveys. However, these  
107 results contrast to those obtained by Devauchelle (1990) with populations of Manila  
108 clam originating from different temperate areas; in this case, the onset of gametogenesis  
109 seemed to be related more to the increase in photoperiod rather than to variations in  
110 water temperature. Oocyte and follicular sizes of littoral species have also been pointed  
111 out by Le Pennec and Benninger (2000) to respond in a flexible way to phytoplankton  
112 availability. The effect of food availability on the gametogenesis of *Ruditapes*  
113 *philippinarum* was also withdrawn by Soudant *et al.* (2004).

114 Dealing now with the **spawning** phase, the existence of a minimal temperature of 14°C  
115 for its activation has been proposed by different authors (Ohba, 1959; Holland and

116 Chew, 1974; Mann, 1979). More recently, Park and Choi (2004) demonstrated that the  
117 spawning pulses of clams were controlled not only by the temperature but also by the  
118 salinity and the abundance of food. Taking into account temperature variability during  
119 spawning in Arcachon Bay, Dang *et al.* (2010) also suggested that factors such as  
120 trophic sources or salinity may act. According to this same author and to Robert *et al.*  
121 (1993), spawning periods for Arcachon Bay range from May to October.

122 For the two phases, **larval development** and its **settlement** (after a pelagic phase of 3  
123 weeks, Le Treut, 1986) most of the literature focused on the influence of the  
124 temperature. For example, Emmett *et al.* (1991) demonstrated that the Manila clam eggs  
125 are supposed to required 1-2 days at the temperature of 13-16°C to hatch, whilst  
126 Robinson and Breese (1984) established that the optimal temperature for larval survival  
127 is about 23-25°C for this species. However, Chicharo and Chicharo (2001)  
128 demonstrated that the early life stage (considered here by its plankton abundance,  
129 benthic recruitment and growth rates) of another Veneridae (especially *Venerupis*  
130 *decussatus*) was not only influenced by the water temperature but also by the advection.  
131 For *Ruditapes philippinarum*, meiofaunal predators (particularly nematodes) were also  
132 proved to impact the larval settlement (Williams, 1980). Beside temperature, Ishii *et al.*  
133 (2001) listed other environmental factors such as winter's lowering, effects of the winter  
134 monsoon, pathogens, predation by crabs, fish and shorebirds.

135 Considering now the **growth** function, numerous authors agree with the main role  
136 played by the temperature on *Ruditapes species* (Laing *et al.*, 1987; Toba, 1987 in  
137 Nakamura *et al.*, 2002; Beiras *et al.*, 1994; Fan *et al.*, 2007). A pattern of growth has  
138 even specifically been presented by Maître-Allain (1982) for Manila clam; it stated that

139 no growth occurred under 6°C and that an optimal growth was expected between 12 and  
140 20°C for this species in Thau lagoon. For the Jiaozhou Bay (China), the most suitable  
141 range of temperature for shell growth was ascertained between 18 and 23°C (Fan *et al.*,  
142 2007). Nevertheless, numerous studies established also the role of other factors. For  
143 example, Yamamoto *et al.* (1956) demonstrated that the growth rate of *Ruditapes*  
144 *philippinarum* in Akkeshi Lake (Japan) was intimately related to the sea temperature  
145 and the abundance of plankton. Later on in the lagoon of Thau (France), Maître-Allain  
146 (1982) comforted those results by highlighting the link between the increase of the  
147 growth rate and the quantity of chlorophyll a, at least up to a threshold. Gouilletquer *et*  
148 *al.* (1987) established that the duration of immersion has also a significant effect, at  
149 least under ground culture conditions in the Bay of Marenne-Oléron (France).

150 Finally, different general studies not devoted to a particular function of the biological  
151 cycle of the Manila clam have also established relations between the metabolic activity  
152 and the salinity (see for example Kim *et al.*, 2001). In controlled condition, Manila clam  
153 displays a significant sensibility to exceptional events with rapid changes in the  
154 salinity's value.

155 Using a 10 year dataset and complementary multivariate approaches, this paper presents  
156 the pathway applied to select few environmental parameters (with temporal lag) of main  
157 interest to explain the variability of the stock (data from field campaigns) across the  
158 period. With those elements, our study will also allow to address whether more physical  
159 or biological factors of physiological relevance (known for their effect on reproduction,  
160 growth...as explained above) should be integrated in the model of simulation.  
161 Temperature is already integrated in the model only for its effect on reproduction

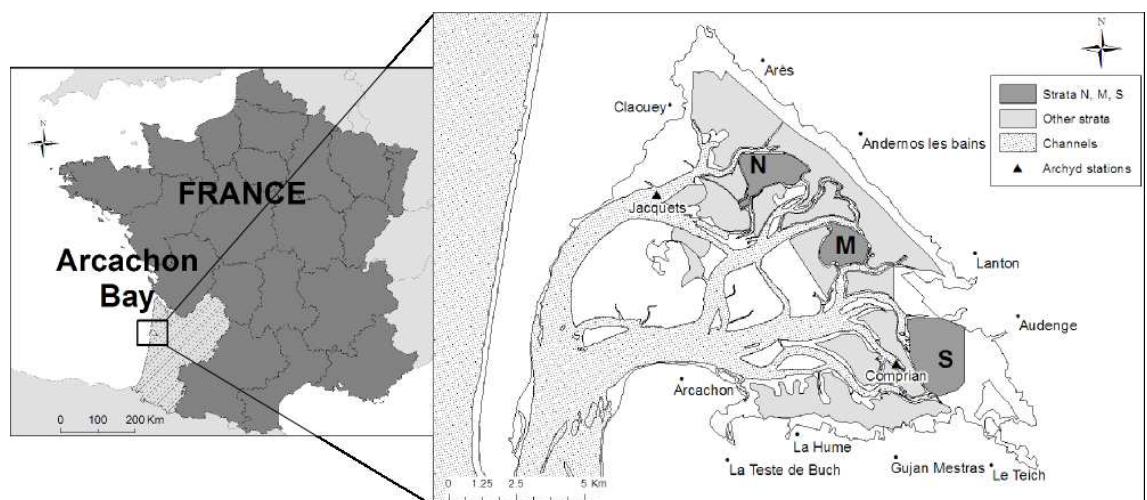
162 function. To test the relevance of additional effects, we consider temperature conditions  
163 during specific periods selected for their importance on the Manila clam life cycle.

164

## 165 **Methods**

### 166 2.1. Study site

167 Arcachon Bay is a 156 km<sup>2</sup> semi-sheltered lagoon in the southwest coast of France  
168 (Fig. 1). The inner lagoon is composed by 110 km<sup>2</sup> of tidal flats (mesotidal system) with  
169 a sediment composition ranging from mud to muddy sands and colonized by vast  
170 *Zoltera noltii* seagrass meadows. The tide is semi-diurnal and the bay is both influenced  
171 by oceanic (external neritic waters) and continental (principally from the Eyre River)  
172 inputs (Dang, 2009). The characteristics of these water masses as well as the slow  
173 renewal of water by tides (Plus *et al.*, 2006) induce salinity and temperature gradients  
174 within the bay (Bouchet, 1968).



175

176 **Fig. 1.** Study area, selected strata and Archyd stations locations.



177 2.2. Population descriptors

178 Concerning the stock status, the present work is based on data collected during late  
179 spring field campaigns performed every two or three years in the Arcachon Bassin since  
180 the year 2000 (Bertignac *et al.*, 2001; Caill-Milly *et al.*, 2003, 2006, 2008; Sanchez *et*  
181 *al.*, 2010). The sampling gear is a Hamon grab which collects a sediment core of 0.25  
182 m<sup>2</sup> (0.5 m \* 0.5 m) on a 0.2 m depth at the ebb tide. Recommended tool for sampling  
183 the benthic macro-infauna from coarse substrata, it is particularly well adapted for the  
184 Manila clam, which is usually buried at around 2-5 cm deep depending on their size and  
185 with a maximum depth around 10-12 cm when temperature is very low (Le Treut,  
186 1986). The core samples were filtered onboard with running water over a set of three  
187 sieves with 2, 1 and 0.5 cm mesh size. All specimens of Veneridae were sorted,  
188 identified, counted and measured to the nearest 1 mm using a slide calliper. Apart for  
189 year 2000 when each clam was weighted, the other individual weights were estimated  
190 using the relation between weight and length determined by Caill-Milly *et al.* (2003) for  
191 Arcachon Bay. These campaigns were carried out following a standardized protocol  
192 (stratified random sampling) with 16 strata investigated according to a sampling effort  
193 of 10 stations per km<sup>2</sup>. Among those, 3 strata (noted N for North, M for Middle and S  
194 for South) were selected because on one hand they have been investigated since year  
195 2000 and on the other hand they present different localisations inside the Bay.

196 To illustrate the stock status, seven descriptors were considered for each stratum and  
197 their values calculated for each campaign for their significance on populational  
198 structure, abundance, recruitment level and potential competition among Veneridae  
199 (Table 1). The strata localisation is presented in Figure 1.

### Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

200 **Table 1.** Descriptors of the stock considered for each campaign.

Descriptor	Description	Codification
Density in number	Average density expressed in number of Manila clams per m <sup>2</sup>	Dens_Nb
Density in weight	Average density expressed in weight of Manila clams per m <sup>2</sup>	Dens_Wg
Percentage of clams above 35 mm in number	Ratio between the quantity of Manila clams above 35 mm (minimum legal size for fishing since 2008) and the quantity of Manila clams all sizes together, quantities are expressed in number	Perc35_Nb
Percentage of clams above 35 mm in weight	Ratio between the quantity of Manila clams above 35 mm (minimal legal size for fishing since 2008) and the quantity of Manila clams all sizes together, quantities are expressed in weight. It indicates the proportion of marketable clams on the global stock expressed in weight.	Perc35_Wg
Percentage of clams under 17 mm in number	Ratio between the quantity of Manila clams under 17 mm and the quantity of Manila clams all sizes together, quantities are expressed in number. It indicates a recruitment level (arrival of juveniles born the year before).	Perc17_Nb
Percentage of Manila clams related to the identified Veneridae	Ratio between the quantity of Manila clams and the quantity of identified Veneridae namely <i>Ruditapes philippinarum</i> , <i>Ruditapes decussatus</i> and <i>Venerupis aureus</i> (potential competition among Veneridae), quantities are expressed in number.	PercMan_Nb
Mean length of the clams	Average mean length of the Manila clams in millimetres.	Lmean

201

202           2.3. Environmental parameters

203    To consider the hydrological conditions which prevailed before and potentially  
204    influenced the state of the stock described through the previous descriptors, data from  
205    the Archyd network were used. This network exists since 1988 and concerns 7 stations  
206    distributed on the whole bay. Sampling is carried out once a week, in the  
207    neighbourhoods of noon, at the slack of low tide (by strong coefficient) and high tide  
208    (by low coefficient) alternatively. Various physical, chemical and biological parameters  
209    are measured: temperature, salinity, suspended matter, oxygen, chlorophyll a and  
210    phaeopigments, silicate, nitrate, ammonium, phosphate (Auby *et al.*, 2010). Considering  
211    the studied strata, 2 stations were considered to be representative: Les Jacquets and  
212    Comprian (Fig. 1).

213    Given that the studied population is mainly composed of clams aged from 1 to 3 years  
214    old, it was decided to consider these parameters for the 3 years preceding the population  
215    descriptors measurements at the year  $t$  (*i.e.* year 2000, 2003, 2006, 2008 or 2010). Since  
216    the campaigns providing the population descriptors occurred in June for the year  $t$ , we  
217    look at the environmental conditions prevailing during the last twelve months (*i.e.* from  
218    June  $t-1$  to May  $t$ ). Because temperature is already integrated in the model, more  
219    specific temporal aggregations were also considered for this parameter in order to focus  
220    on reproduction, growth and mortality potential effects. Those temporal lags are  
221    considered on environmental variables to interact with biological phenomena  
222    considered as indirect effects and often appearing on a local scale (Wiens, 1989).  
223    According to the forecasted effects related to the biological functions described in the

224 introduction, 13 variables were retained; they represent physical environment and food  
225 supply conditions (Table 2).

#### 226 2.4. Multivariate analyses

227 Explanatory multivariate analyses are applied to different data groups such as classical  
228 analysis type PCA on single data table and Regularized Canonical Correlation Analysis  
229 (RCANCOR).

230 Canonical correlation analysis (CANCOR) is a multivariate explanatory statistical  
231 method used to highlight correlations between two data sets of quantitative variables  
232 observed on the same statistical units. The main purpose of CANCOR is the exploration  
233 of sample correlations between these two data sets, whereas PCA deals with one data  
234 set in order to reduce dimensionality through linear combination of initial variables.

235 Classical CANCOR aims to resume on one hand the variables of one dataset (by way of  
236 linear combination) and on the other hand the variables of the other dataset (by way of  
237 linear combinations too) so that these two new information capture the maximum  
238 correlation between the two initial datasets. The intensity of the overall relationships  
239 between the canonical variates is given by the canonical correlation which represents  
240 the bivariate correlation between the two canonical variates. This analysis allows thus to  
241 quantify the relations identified and to classify the degree of influence of the explicative  
242 variables and the initial variables to explain. A regularized version of CANCOR is used  
243 to deal with our dataset which contains more variables than statistical units (Gonzalez *et*  
244 *al.*, 2008).

245 Methods are presented below in the light of each forecasted aims.

Chapitre 3 - Évaluation des facteurs non contrôlés impactant la variabilité de la population

246 **Table 2.** Temporal aggregated variables considering biological relevance to describe the environmental conditions.

<b>Factors</b>	<b>Variables or built indicators</b>	<b>Forecast biological functions influenced</b>	<b>Codifications</b>
Temperature (T)	Mean temperature (in °C) from June to October for years t-3, t-2 and t-1	Reproduction (gametogenesis, spawning, larval settlement)	TMean_JunOct_t.3 TMean_JunOct_t.2 TMean_JunOct_t.1
	Percentage of temperature's values above 18°C from June to October for years t-3, t-2 and t-1	Reproduction (gametogenesis, spawning)	PercTsup18_t.3 PercTsup18_t.2 PercTsup18_t.1
	Mean temperature (in °C) in November for years t-3, t-2 and t-1	Reproduction (larval settlement)	TMean_Nov_t.3 TMean_Nov_t.2 TMean_Nov_t.1
	Percentage of temperature's values under 6°C from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	PercTinf6_t.3.t.2 PercTinf6_t.2.t.1 PercTinf6_t.1.t
	Percentage of temperature's values between 12 and 20°C from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	PercT1220_t.3.t.2 PercT1220_t.2.t.1 PercT1220_t.1.t

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Salinity (Sal)	Relative standard deviation on the mean salinity (in %) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	SalSD_t.3.t.2 SalSD_t.2.t.1 SalSD_t.1.t
	Range between the extreme salinity's values (maximum-minimum) (in Psu) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	SalAmp_t.3.t.2 SalAmp_t.2.t.1 SalAmp_t.1.t
Phytoplankton (assessed by Chloro A)	Quantity of phytoplankton assessed with the sum of the chlorophyll a's values (in mg/l) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	ChloroASum_t.3.t.2 ChloroASum_t.2.t.1 ChloroASum_t.1.t
	Quantity of phytoplankton assessed with the mean chlorophyll a's value (in mg/l) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth	ChloroAMean_t.3.t.2 ChloroAMean_t.2.t.1 ChloroAMean_t.1.t
Total Suspended Matter (TSM) and Total Organic Suspended Matter (TOSM)	Sums of Total Suspended Matter's values and of Total Organic Suspended Matter's values (in mg/l) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth, Mortality	TSMSum_t.3.t.2 TSMSum_t.2.t.1 TSMSum_t.1.t  TOSMSum_t.3.t.2 TOSMSum_t.2.t.1 TOSMSum_t.1.t
	Means Total Suspended Matter's values and Total Organic Suspended Matter's values (in mg/l) from June to May for years t-3/t-2, t-2/t-1 and t-1/t	Growth, Mortality	TSMMean_t.3.t.2 TSMMean_t.2.t.1 TSMMean_t.1.t  TOSMMean_t.3.t.2 TOSMMean_t.2.t.1 TOSMMean_t.1.t

247 2.4.1. Characterizing the population

248 A normalized PCA (NPCA1) is implemented on the variables describing the stock (cf.  
249 § 2.2) in order to not only identify the linear relations among the descriptors but also to  
250 summarize those seven descriptors with a less numerous quantity of variables and more  
251 synthetic: the principal components (also called dimensions in the following). The aim  
252 is then to use these new variables to link them to those describing the physical  
253 environment and the trophic conditions. This reduction of the observed variables allows  
254 to work with a more meaningful and manageable number of factors without excessive  
255 loss of information (Appeldoorn, 1983).

256 2.4.2. Describing the relationships between the environmental conditions and the  
257 stock's descriptors

258 A normalized PCA on the variables describing the physical environment (cf. § 2.3.) and  
259 a normalized PCA on the variables describing the trophic conditions were applied  
260 (NPCA2 and NPCA3 respectively). For both of them, the first principal components  
261 coming from NPCA1 were added as supplementary variable (restricted to strata N and S  
262 because of availability of environmental measures) as long as the aim was to explain  
263 them. This first approach permits to highlight relationships between exogenous  
264 variables related to the environment and the descriptors of the stock but focuses mainly  
265 on relationships among environmental variables. Time and spatial considerations are  
266 taken within the analysis with years and strata as supplementary factors.

267 To complete the above analyses, two Regularized Canonical Correlation Analyses  
268 (RCANCOR1 and RCANCOR2) were applied to the whole stock descriptors (as first  
269 set) and respectively to physical environment and trophic conditions (as second set)

270 using the CCA package on R (Gonzalez *et al.*, 2008). The squared canonical correlation  
271 measures the proportion of variance of a canonical variate explained by the original  
272 variables.

273

## 274 **Results**

### 275 3.1. Synthetic description of the stock

276 The stock is correctly described by the first 3 dimensions of the NPCA1 (87.0 % of the  
277 variance), hereafter called Etatpop1, Etatpop2 and Etatpop3 (Table 3). The first  
278 dimension, Etatpop1 (36.0 % of the variability) characterizes the relative abundance of  
279 Manila clam longer than 35 mm (expressed in number of individuals and weight), the  
280 mean length of the clams and the density in number (all sizes considered). A high  
281 abundance of large individuals is correlated to a low density (in number) for all sizes  
282 taken together. The second dimension, Etatpop2 (27.6 % of the variability) represents  
283 the percentage of juvenile clams (i.e. < 17 mm), the mean length and the percentage of  
284 *R. philippinarum* related to the identified Veneridae: the higher the part of the Manila  
285 clam, the smaller the percentage of juveniles. The last dimension considered, Etatpop3  
286 (23.4 % of the variability) illustrates the density expressed both in number and weight.

287 To summarize those results about the stock status, the variables integrating the higher  
288 part of the variability of the collected data are first those related to the larger clams  
289 (Perc35\_Nb and Perc35\_Wg) and secondly the variable characterizing the proportion of  
290 juveniles (Perc17\_Nb).



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291 **Table 3.** Stock descriptors PCA results to identify synthetic variables.

Number	Eigenvalue	Percentage of variance	Identified stock descriptors		Synthetic variables identified as
			With negative coordinates	With positive coordinates	
1	2.52	36.0	Dens_Nb	Perc35_Wg, Perc35_Nb, Lmean	Etatpop1
2	1.93	27.6	Lmean, PercMan_Nb	Perc17_Nb	Etatpop2
3	1.64	23.4		Dens_Nb, Dens_Wg	Etatpop3
4	0.68	9.7			
5	0.20	2.8			
6	0.03	0.4			
7	0.01	0.1			

292

293 3.2. Correlation between physical factors, food supply and stock

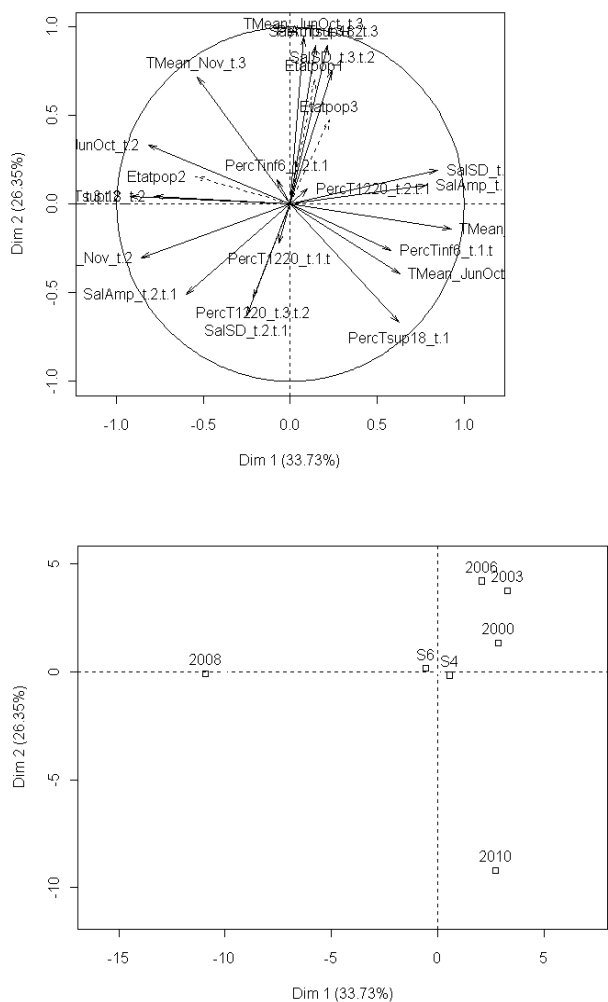
294 Physical conditions (Fig. 2 and 3)

295 Results of NPCA2 show that only Etatpop1 is linked to the physical conditions  
296 displayed on the second axis: i/ high T between June and November and high  
297 proportion of values above 18°C for year t-3, ii/ large variations in salinity between  
298 June and May t-3/t-2. NPCA2 also points out relationships between two factors -  
299 temperature and salinity- and a discrimination of the different years but failed to  
300 discriminate the strata.

301 In addition, RCANCOR1 shows strong negative correlation between total abundance  
302 (Dens\_Wg and Dens\_Nb) and high salinity variations for year t-2/t-1 (thanks to the  
303 interpretation of the first canonical variate which canonical correlation = 0.99). The  
304 second canonical variate (canonical correlation = 0.99) summarizes the links between  
305 proportions of larger clams (above 35 mm), high salinity variations for year t-3/t-2 and  
306 low temperature conditions for year t-1.

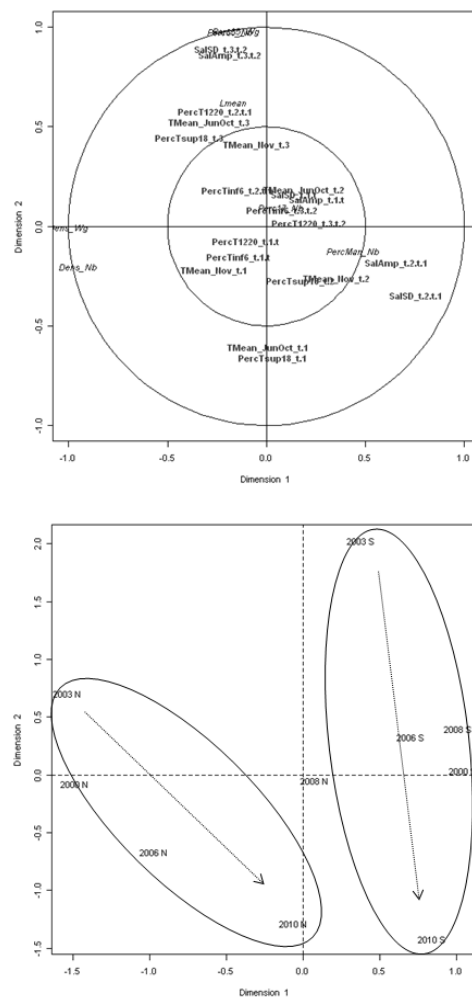
307 Focusing on stock, strata S and N mainly differ in terms of abundance and physical  
308 conditions: N is generally characterized by strong abundances contrary to S which is  
309 illustrated by stronger variations of salinity. Considering more precisely the evolution of  
310 these strata over time, we can notice that: i/ stratum N had strongly changed from a high  
311 total abundance to a mean one and from high abundance of clams above 35 mm to low  
312 one, ii/ stratum S stays relatively low in terms of total abundance and presents a strong  
313 diminution in terms of abundance of clams above 35 mm, iii/ those phenomena are  
314 concomitant to an increase of the temperature conditions between June and October  
315 from 2000 to 2010 on both strata. Environmental and stock indicators tend to be the  
316 same in 2010 for both strata.

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317

318 **Fig. 2.** NPCA2 on physical conditions (plot individuals and variables graphs).



320

322 **Fig. 3.** Variables and units representations on the plane defined by the first two  
323 canonical variates of the RCANCOR1 on physical conditions.

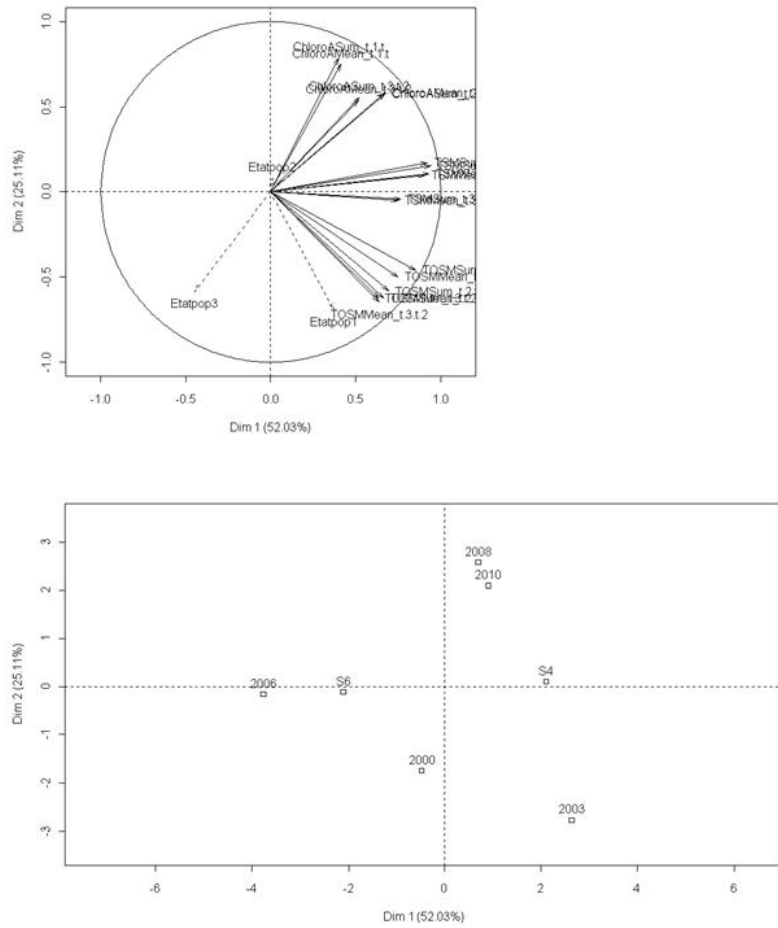
322 Food supply (Fig. 4 and 5)

323 Results of NPCA3 show that all the three Etatpop (*i.e.* 1, 2 & 3) appeared to be linked to  
324 food supply indicators. Etatpop1 and Etatpop3 were particularly elevated when TSOM  
325 was higher and Chloro A lower. By contrast, high values of Etatpop2 occurred for low  
326 values of Chloro A and TSM during year t-3. NPCA3 also pointed out discrimination of  
327 years thanks to all the different indicators used to describe food supply and  
328 distinguished strata but only for TSM.

329 In addition, RCANCOR2 shows strong negative correlation between total abundance  
330 (Dens\_Wg and Dens\_Nb) and high TSM for years t-2/t-1 and t-1/t (thanks to the  
331 interpretation of the first canonical variate which canonical correlation = 0.99). The  
332 second canonical variate (canonical correlation = 0.99) summarizes the links between  
333 proportions of larger clams (above 35 mm) with low concentrations of Chloro A for  
334 year t-3/t-2.

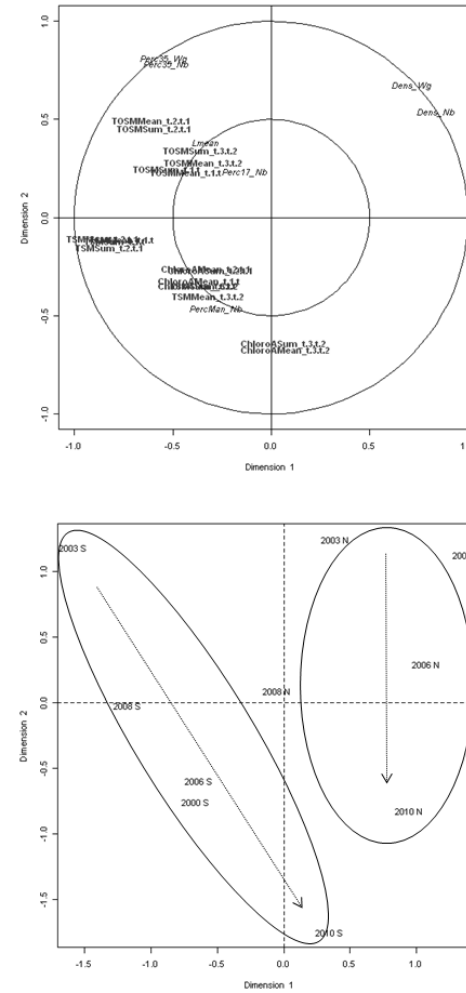
335 Focusing on stock and in addition to RCANCOR1 which already gives results on the  
336 characteristics of the stock, RCANCOR2 highlights that strata S and N also differ in  
337 terms of trophic conditions: N is generally characterized by low indicators of TSM and  
338 TSOM by contrast to S. Considering more precisely the evolution of these strata over  
339 time, we can notice that both strata have evolved from a situation of low chlorophyll a  
340 concentrations to higher values and tend to present similar conditions in 2010 with a  
341 lower extent for N.

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342

343 **Fig. 4.** NPCA3 on trophic conditions (plot individuals and variables graphs).



345

347 **Fig. 5.** Variables and units representations on the plane defined by the first two  
348 canonical variates of the RCANCOR2 on trophic conditions.

347 **Discussion**

348 The construction of indicators on periods (not annual) allows to consider the potential  
349 effect of various factors closer to biological reality, *i.e.* with a link to life cycle and life  
350 history pattern of this bivalve, beginning with spawning, larval dynamics including  
351 settlement and development of adult stock. Temporal aggregation of data has already  
352 been undertaken by Melià *et al.* (2004) for studying seeding conditions; in the present  
353 study, the aggregations are implemented for their biological relevance for a larger  
354 number of variables. Coupled with extensive and complementary statistical analyses  
355 (NPCA and RCANCOR), this methodology aims to discriminate the main parameters  
356 correlated with the descriptors of the state of the stock but cannot be used to assess  
357 which environmental factor has the greatest impact on stock dynamics. Appeldoorn  
358 (1983) has previously underlined the advantages of the PCA to study effects of  
359 environmental conditions on growth variables especially because it produces  
360 meaningful and easily interpretable variables. He also highlighted that variable  
361 integration effects can incorporate some factors not specifically measured. Considering  
362 macrobenthos-environment relationship, Van der Meer (1991) demonstrated the  
363 informative and easy interpretable statistics and figures obtained with canonical  
364 correlation analysis.

365 NPCA were applied on the overall data set mixing environmental variables  
366 (respectively for physical environment and trophic conditions) and population  
367 characteristics where each statistical unit is a data for one year and one experimental  
368 site. Considering separately spatial and temporal information, one can obtain two  
369 factors which can be put as supplementary factors in the PCA. These analyses show the

370 correlations between the initial variables and characterize each year and site according  
371 to those variables. In addition, each RCANCOR gives one optimal combination of  
372 environmental variables and one optimal combination of population parameters in the  
373 sense that both are correlated. The statistical units are expressed as spatio-temporal and  
374 can then be discussed in two ways: environmental conditions and population  
375 characteristics.

376 This methodology is transferable to other bivalve species and other sites.

377 **A strong link highlighted between food availability and the state of the stock**

378 Among the environmental parameters, the one correlates to the maximum of descriptors  
379 is the food availability namely “chlorophyll a” concentration. Manila clam is an  
380 infaunal suspension-feeder with a dietary regime dominated by phytoplankton (Kasai *et*  
381 *al.*, 2004; Kanaya *et al.*, 2005; Yokoyama *et al.*, 2005; Spillman *et al.*, 2008). The  
382 action of phytoplankton species on the growth of *Ruditapes decussatus*, a related  
383 species in *in situ* conditions has already been demonstrated by Lelong and Riva (1976)  
384 and since we considered chlorophyll a as an indicator of the living phytoplankton (by  
385 opposition to the pheopigments concentration indicating degenerating forms), our  
386 results are consistent with those results.

387 The isotopic study performed by Dang (2009) on Manila clam in the Arcachon Bay  
388 confirmed this major diet but also highlighted the contribution of other trophic sources  
389 such as *Zostera noltii* leaf detritus and SOM. The high complexity of the diet of Manila  
390 clam was furthermore stressed by Flye-Sainte-Marie (2008); as a bottom suspension-  
391 feeding bivalve, it filters the sediment-water interface and can ingest bacteria

392 (Kharlamenko *et al.*, 2001), diatoms, detritic particulate organic matter, small rotifer  
393 (Sorokin and Giovanardi, 1995), dinoflagellates (Li *et al.*, 2001) but also  
394 microphytobenthos. The present study is limited by the fact that only chlorophyll a,  
395 TSM and TOSM (see Table 2) are considered to detect relationships between those  
396 trophic conditions and the stock descriptors. Nevertheless, the fact that half of the data  
397 used in the Archyd network was recorded at low tides provides indications on a limited  
398 water column.

399 Focusing on the different stock descriptors, the obtained correlations are different  
400 considering the sizes of the clams since high relative abundance of large clams are  
401 concomitant to low chlorophyll a and high TSOM indicators whereas high proportion of  
402 juveniles are related to high chlorophyll a and low TSM values. Those differences can  
403 first illustrate qualitative differences in the type of food assimilated by the clams related  
404 to their size (*i.e.* a hypothesis of a trophic sources diversification between the young on  
405 one hand and the clams older than a year on the other hand). Considerations about the  
406 diversity of the Manila clam diet have already been discussed above and much of the  
407 feeding items have been demonstrated to come from the POM (Kharlamenko *et al.*,  
408 2001). In the same time, larvae stages are known for consuming diatoms as well as  
409 dinoflagellates (Loosanof *et al.*, 1963; Le Treut, 1986). Similarly, our results are  
410 consistent with those obtained by Sobral and Widdows (2000) (*i.e.* a lowering of the  
411 trophic performances for the related species *Ruditapes decussatus* under high TSM)  
412 since the TSM values are must lower for Arcachon Bay. A second hypothesis is related  
413 to a possible effect of the TSM going beyond the nutrition function. Since Total  
414 Suspended Matter is comprised of sediments, dead or decaying plant and animals parts



415 and still living particles, we can supposed that it can influence clam's gills and/or velum  
416 for younger stages. This last disturbance on the larval swimming activity could have  
417 happened in our case; such effect of TSM has already been pointed out on Manila clam  
418 by Le Treut (1986). A positive or negative effect of inorganic particles in the suspended  
419 matter was also reported for mollusks in general by Deslous-Paoli (1987), depending on  
420 the concentration and type of mineral composition.

421 **Confirmed links between temperature and stock's descriptors and highlighted**  
422 **links for salinity's case**

423 Temperature is the second factor presenting correlations with the descriptors of the  
424 stock. Those correlations concern at the same time high temperatures between May and  
425 November year t-3 and high proportion of temperature above 18°C with the relative  
426 high abundance of large clams and density.

427 As reviewed in the introduction, this factor is known for its influence on many  
428 biological functions of the life cycle of Manila clam (reproduction, growth, survival...)  
429 and has been largely reported (Mann, 1979; Bernard, 1983; Gouletquer *et al.*, 1989 in  
430 Melià *et al.*, 2004; Delgado *et al.*, 2007). Our results emphasize here the role of  
431 temperature mainly on the reproduction period and to a lesser extent to the growth.  
432 They were obtained with a three years period whereas no interrelation was found  
433 between Etatpop2 and high temperatures between May and November the year before.  
434 A hypothesis could be that high temperatures may have promoted not only the  
435 reproduction period but also the velocity of growth for the young individuals leading to  
436 a size exceeding quickly 17 mm.

437 The lack of results for temperatures theory known to have a positive effect on growth  
438 (range 12-20°C) however suggests that this effect does not extend to older clams. Using  
439 the Scope For Growth index, Nam Han *et al.* (2008) reported highest SFG values at  
440 20°C both for small and large clams.

441 The last variable identified concerns the salinity with high variations of salinity linked  
442 to high proportions of large clams and again with an important delay (June t-3 to May  
443 t-2). The biological relevance of this result is not clear except that even if *Ruditapes*  
444 *philippinarum* is an euryhaline organism [observed minimum salinity in nature reported  
445 by Gosling (2003) is 12‰]; Ishii *et al.* (2005) demonstrated for the Ariake Bay in Japan  
446 that its larvae were concentrated in the higher salinity water (similar salinity ranges to  
447 Arcachon). Also, a bimonthly survey led by Calvez and Guillou (1998) showed no  
448 effect of this factor on winter juvenile mortalities.

#### 449 **Spatial-temporal considerations**

450 For Arcachon Bay, a seasonal rhythm and a spatial discretization between the North and  
451 the South for the trophic sources was demonstrated by Dang *et al.* (2009). The method  
452 we used cannot provide information on temporal variability except annual tendencies  
453 for each variable but reveals levels of indicators related to TSM higher in the Southern  
454 site than in the Northern one. Relation between environmental conditions and strata is  
455 also observed for variation of salinity level. These differences can be related to the  
456 freshwater inputs from the Eyre River and/or to a lower renewal of the water mass in the  
457 South-East part of the Bay (occurs under North or Western wind conditions as  
458 simulated by Plus *et al.*, 2006). However, those relations remain limited in comparison  
459 with temporal effects and militate in favor of a homogenization of the environmental

460 studied conditions within the bay. For the rest and from year to year, the temporal  
461 pattern is characterized by temperature increase prevailing during the different phases of  
462 the reproduction and to a lesser extent, by the augmentation of the chlorophyll a  
463 indicators.

464 On broad temporal scale, the North stratum is characterized by high abundances of  
465 clams associated to weak variations of salinity and low values for TSM whereas the  
466 South stratum exhibits low abundances of clams associated to high variations of salinity  
467 and high quantities of TSM. On a finest temporal scale, both strata evolve in a same  
468 way according to abundances of larger clams (above 35 mm), variation of salinity,  
469 temperature and level of chlorophyll a to reach in 2010 a environment presenting: low  
470 rate of larger clams, lower variations of salinity, higher temperature levels during  
471 reproduction period and higher quantities of chlorophyll a. The gaps between those two  
472 strata are less important in 2010 which tends to limit the impact of spatial variability on  
473 the stock dynamics.

#### 474 **Consequences on the current model**

475 The current version of the model developed for Arcachon Bay by Bald *et al.* (2009) is  
476 implemented with a monthly time step and is built at the global basin scale. According  
477 to our results, there is no need to refine or enlarge this spatio-temporal scale.  
478 Predictability and space-time scaling seems to be adequate for management purposes.

479 Concerning environmental conditions, temperature is integrated in the model for its  
480 effect on the reproduction function (*i.e.* during the spawning period or phase). Our

481 results confirm the importance of this factor especially during the reproduction phase.  
482 As the current model already integrates this process, it does not seem necessary to  
483 modify the model for this parameter.

484 Then, regarding the relationships obtained, it seems necessary to add a second  
485 environmental factor, the food supply. The measurement of photosynthetic pigment  
486 (chlorophyll a) water concentration appears to be the most common indicator used for  
487 food availability (*e.g.* Shibata *et al.*, 1999). However, recent works (on clams longer  
488 than 26 mm) suggest that chlorophyll a concentrations are not the adequate substitute  
489 for food availability for Manila clam (Flye-Sainte-Marie *et al.*, 2003). Nevertheless,  
490 integration of the different trophic sources by the clam depending on its size are not  
491 “done” yet (estimation of the food resources available to suspension feeding bivalves is  
492 recognized as a major problem in modeling bivalve energetic, see *e.g.* Bayne, 1998;  
493 Grant and Bacher, 1998). Therefore, it is proposed to use chlorophyll a concentration  
494 which remains relatively easy to acquire and to associate variability to this parameter  
495 into the model. A method is described by Husson (2001) for parameters that are known  
496 to be effective but remain difficult to assess. This change will transform the current  
497 model from deterministic to stochastic. Such approach has already been developed on  
498 Manila clam by Melià *et al.* (2004) on body growth and survival submodels. By  
499 incorporating some kind of uncertainty in the forecasts, it has the advantage of being  
500 effective for the development of risk-averse management policies.

501 Temperature and food supply remain the most common external factors related to  
502 growth whatever approach led (regression models, the best-fit of empirical curves  
503 against data, energetic budget approaches). The energy balance models developed on

504 Manila clam (Solidoro *et al.*, 2000; Flye-Sainte-Marie *et al.*, 2003; Flye-Sainte-Marie,  
505 2008) are among the most recent; similar works developed by Grant (1996) on *Mytilus*  
506 *edulis* reached to the same conclusions. It appears that the cases in which food resources  
507 did not appear significant concerned eutrophic areas (Solidoro *et al.*, 2000; Melià *et al.*,  
508 2004).

509 The fact that these parameters influence the recruitment, one of the strongest process  
510 controlling the dynamic of the Manila clam population (Dang, 2009), advocates also for  
511 this choice.

512 Since the results dealing with salinity are not obvious to explain, it does not seem  
513 appropriate to include this third parameter in the model. This decision avoid falling into  
514 model over-parameterization by looking for a model based on phenomenological  
515 description of clam demography rather than on a detailed interpretation of metabolic  
516 processes as advised by Melià *et al.* (2004).

517 The ultimate purpose of this work is to consider the opportunity to refine the existing  
518 model of management developed by Bald *et al.* (2009) in order to provide the more  
519 realistic and feasible decision-support system. Thus, simulations for different scenarios  
520 will rely on a biological functioning modelling which will be the strongest as possible  
521 (*i.e.* taking into account the main sources of variability of environmental origin). This  
522 recognition of essential missing knowledge and the connection between the natural and  
523 the human environment are some of the key features of Integrated Assessment approach  
524 (Jakeman *et al.*, 2008). The follow-up of the stock operated through regular field  
525 campaigns will still be essential to dispose of reference points over time.

526 As discussed above with the food supply's case, the final choice will depend on the data  
527 availability and on the benefit they will convey to the model (equilibrium between  
528 model complexity and tuning). The regular check of this model also allows integrating  
529 changes that could appear over time. It is all the more important that a limitation of the  
530 trophic resources inside the bay is raised because of the evolution of other filter-feeders  
531 populations such as *Crepidula fornicata* and wild *Crassostrea gigas* (Dang, 2009), but  
532 also *Mytilus edulis*. Observations of numerous Ascidiacea have also been reported by  
533 De Montaudouin (personal communication). The issue of the level of larviphagy on  
534 *Ruditapes philippinarum* generated by species such as *Mytilus edulis* (Lehane and  
535 Davenport, 2004) could also be addressed.

536

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542 All authors declare no conflicts of interest.



## **Chapitre 4 – Développement du modèle de simulation et son application comme outil d'aide à la gestion**





Prédire l'évolution d'un stock nécessite la connaissance du passé, l'identification d'un mode de fonctionnement (ou d'une « loi ») et la déduction de conséquences selon le principe que des causes semblables produisent des effets semblables (El Dajani, 2002). Pour la gestion d'une population naturelle, les outils de simulation reproduisent l'interaction dynamique entre les processus biologiques et physiques et le processus de détermination de l'action en fonction de l'état courant du système (Goffinet, 2003). Les modèles sont ainsi des entités mathématiques se substituant à la réalité (Laurec & Le Guen, 1981).

Dans le cas des populations exploitées, une composante humaine assurant une fonction de gestion est à intégrer pour rendre compte de son effet sur le système. Parce qu'elles permettent d'anticiper, les techniques liées à la prédiction constituent aujourd'hui un outil d'aide à la décision de première importance. Ils permettent aux décideurs de disposer de projections pertinentes de la situation présente et de tester des politiques de gestion sous forme de scénarios réalistes (Goffinet, 2003). Contrairement à ce qui est souvent affiché à l'origine de leur développement, ces outils pour l'halieutique ne sont pas directement manipulés par les gestionnaires, ils sont utilisés par les chercheurs et contribuent à affiner l'expertise au sein de diverses instances de gestion des ressources contribuant ainsi aux démarches de cogestion. Structurant l'information parfois massive, ces techniques constituent également des vecteurs de communication (support de communication et/ou transfert de connaissances) au sein des parties prenantes. L'ensemble des fonctions apportées par ces outils est synthétisé par del Granado (2007) par les termes : accroissement de la compréhension du système considéré par l'homme, source de communication visuelle, outil de prédiction et outil d'aide à la décision.

Dans le domaine de l'halieutique, les réactions de la population en réponse à son exploitation et à son environnement peuvent être décrites soit à l'aide de modèles globaux, également appelés modèles synthétiques ou empiriques, soit grâce à des modèles analytiques, également appelés modèles structuraux ou mécanistes (Laurec & Le Guen, 1981 ; Goffinet, 2003). Dans le premier cas, l'évolution du stock, c'est-à-dire sa dynamique, est considérée comme une réponse à une pression (de pêche pour l'essentiel) sans que l'on cherche à établir d'équations décrivant les processus intermédiaires impliqués. Dans le second cas, l'approche analytique vise à démontrer le mécanisme de fonctionnement du stock, à reconnaître un certain nombre de

rouages fondamentaux et à préciser leur articulation (Laurec & Le Guen, 1981). Les processus sont ainsi décrits à partir des connaissances (biologiques, physiques, sociales, ...) mobilisées et intégrés de manière hiérarchisée au sein d'un même système. Pour construire ces modèles intégrateurs, six approches de modélisation sont identifiées par Ekasingh et al. (2005) : les systèmes experts, les modèles à base d'agents, les systèmes dynamiques, les réseaux Bayésiens, les modèles couplés complexes et les méta-modèles. Les indicateurs produits par ces modèles peuvent être des niveaux moyens simples. Dans ce cas, l'état instantané du système détermine univoquement son état à l'instant suivant (Lesne, 2008) ; on parle alors de modèles déterministes. Les indicateurs peuvent également être produits sous la forme de distribution de valeurs possibles ou plus ou moins probables ; on parle alors de modèles stochastiques (Jørgensen, 2008). On observe actuellement une tendance à l'intégration de composantes stochastiques au sein de modèles à l'origine déterministes afin de disposer d'outil de simulation plus robuste (Munro et al., 2010). La méthode mathématique la plus commune pour développer des modèles déterministes repose sur l'utilisation d'équations différentielles. Elles permettent de décrire les interactions entre les variables et de rendre compte des flux qui sont l'évolution de grandeurs dans le temps ou dans l'espace (Cetin, 2007).

Dans le cas de la population de palourde japonaise du bassin d'Arcachon, un modèle a été développé par Bald et al. (2009) avec pour objectif de permettre l'analyse et la comparaison des effets sur le stock de différentes mesures de gestion. Il s'agit par conséquent d'un outil d'aide à la décision. Le choix s'est porté sur un modèle analytique afin de rendre compte des mécanismes régissant la dynamique de la population. L'ensemble du cycle vital de l'espèce est considéré. Cela permet non seulement de prendre en compte l'exploitation réelle des individus en dessous de la taille légale de capture, mais aussi d'intégrer des effets de facteurs naturels sur l'ensemble des stades biologiques.

Afin de tenir compte des différences de paramètres fondamentaux entre les diverses catégories d'individus au sein de la population (tels que taux de croissance, taux de mortalité naturelle ou par pêche,...), le modèle développé est un modèle démographique structuré en classes de taille. L'importance de la prise en compte de ces différences de paramètres au sein d'une même population a été relevée par plusieurs auteurs (De Leo & Gatto, 2000 ; Solidoro et al., 2003). La structuration en âge n'a pas été retenue lors du développement du modèle en

raison de sa détermination difficile à partir de la lecture classique des stries de croissance externes marquées sur la coquille. En conditions défavorables ou au moment de la reproduction, des stries surnuméraires ont en effet été décrites pour cette espèce et pour la palourde européenne dans la littérature (Garcia, 1993 ; Kanazawa & Sato, 2008). C'est pour cette raison que la lecture des micro-incréments internes de la coquille est entreprise (Caill-Milly et al., 2011) pour approfondir les conditions de réalisation de la croissance.

L'approche utilisée en termes de modélisation est la théorie des systèmes dynamiques qui est un paradigme développé depuis les années 1950 sous l'impulsion des travaux de Forrester (1973) ; il repose sur l'utilisation d'équations différentielles. Le modèle est par ailleurs de type déterministe.

Le paramétrage initial du modèle a été réalisé en utilisant des données biologiques disponibles dans la littérature, en injectant des données sur les traits biologiques de l'espèce pour le bassin d'Arcachon (Dang, 2009), ou à défaut par une procédure itérative amenant à la stabilisation de la population.

Nous avons poursuivi le développement du modèle pour trois raisons :

- la valorisation de données acquises pendant les travaux de Dang (2009) mais non pleinement exploitées pour le paramétrage du modèle ;
- la nécessité d'intégrer l'effet des conditions trophiques sur l'évolution de la population au vue des relations fortes mises en évidence entre les descripteurs du stock et des conditions trophiques intra-bassin (**Article 3**) ;
- la possibilité de préciser les données de captures par la pêche professionnelle injectées dans le modèle et de renforcer la considération d'éléments économiques pouvant influencer sur les stratégies d'exploitation.

Les implémentations réalisées sur les trois développements précités sont présentées dans l'**Article 4**, ainsi qu'une première analyse de sensibilité sur des paramètres du modèle. Elles permettent de réduire des faiblesses du modèle identifiées dans l'article de Bald et al. (2009). L'utilisation du modèle de simulation dans le cadre du processus de cogestion associant pêcheurs professionnels, scientifiques et administration autour de la question de la gestion durable de cette ressource est également décrite dans l'**Article 4**.



**Article 4**

Titre : From system dynamic modeling to co-management initiative reinforcement – an applied case with an exploited marine bivalve population (*Venerupis philippinarum*) in a mesotidal coastal lagoon

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1 **From system dynamic modeling to co-management initiative reinforcement**  
2 **– an applied case with an exploited marine bivalve population (*Venerupis***  
3 ***philippinarum*) in a mesotidal coastal lagoon**

4  
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21 **Abstract**

22 Effective planning strategies regarding the Manila clam (*Venerupis philippinarum*) resource  
23 in Arcachon Bay rely on a gradually set up co-management approach implying scientific  
24 advices and involving fishermen with an administration support. In order to strengthen this  
25 management process, a specific compartmental single-species model has been developed to  
26 assess different management strategies. Based upon an on-size structure of the population and  
27 built from the dynamic systems paradigm, the modelling approach belongs in the simulation  
28 modelling category and involves selected parameters for their impact on the population  
29 dynamics.

30 Both the integration of newly and specific available life traits data, and the adjustment of the  
31 fishing activity and its control parameters, allow the revision of the first version including  
32 model parameters and integration of new formulations. Effect of food availability, production  
33 of newly settled juveniles, growth rates, and price, accounted for the bulk of the undertaken  
34 improvements. In addition, a sensitivity analysis regarding uncertainty on selected parameters  
35 was conducted to provide information about parameters that most influence the system.

36 Taking into account those new improvements, simulations were firstly conducted from July  
37 2003 and December 2008. For this historical modelization, the model outputs fit well with the  
38 real data since the deviation percentages between observed and predicted data met the  
39 criterion set to 10%. Then, seven selected management strategies regarding only local  
40 regulatory authorities were modeled and forecasts of their impacts on the total biomass were  
41 considered from January 2009 to December 2017. A collapse of the stock is predicted if the  
42 management alternatives applied in 2008 were maintained. Relevance of combined selected  
43 management measures was highlighted to achieve a recovery of the stock. Within the  
44 framework of working groups (associating scientists, fishermen and administration

45 representatives), those simulations were presented, discussed and the stakeholders chose to  
46 apply from 2008/2009: reduction of the licenses fishing number (two outgoing licenses for  
47 one incoming license); protected areas; prohibition to fish one day per week. Those  
48 management scenarios were also completed by three additional scenarios to consider potential  
49 effects of environmental or market modifications to the stock evolution.

50 Bearing in mind that this tool is implemented to increase the human understanding of the  
51 considered system, communicate visually, make predictions, and support decision-making  
52 assumptions, further improvements are finally discussed. In particular for future research, it is  
53 expected to deeply encompass ecological and socio-economic valuations of the measures of  
54 impact. As long as those objectives are shared by the different involved entities at the regional  
55 scale, communication and management decisions should be facilitated.

56

57

58 Keywords: system dynamic model, co-management, population dynamic, Arcachon Bay,

59 *Venerupis philippinarum*

60

61

62 **1. Introduction**

63 Management of coastal zones is considered globally as an important issue (Pastres et al.,  
64 2001) as soon as it implies multiple–conflicting goals involving socio-economic and  
65 ecological considerations (Freire et al., 2002). This is particularly true for areas providing  
66 bivalves resources because they frequently allow the development of flourishing activities  
67 either for fishing or farming (Vincenzi et al., 2006). Design and implementation of adaptive  
68 management system policies are vital to conciliate socio-economic activity and long-term  
69 sustainability of the natural environment (De Leo and Levin, 1997). For this purpose, models  
70 constitute useful tools for guiding management of coastal waters, including monitoring  
71 exploited species, which are one of the economic dimensions of the coastal zone system.

72 Several models have thus been designed to reinforce management of exploited species (Dalla  
73 Riva et al., 2009; Ferriera et al., 2009; Grant et al., 2007; Marshall and Crowder, 1996;  
74 Solidoro et al., 2003). The model developed for Manila clam by Bald et al. (2009) aims at the  
75 same purposes and is a compartmental single-species model driven by selected parameters  
76 based upon an on-size structure of the population and some dynamics of the species. This  
77 modelling approach belongs to simulation modelling category, built from the dynamic  
78 systems paradigm developed in the 1950s by Forrester (1973). That is, the interactions among  
79 variables and the evolution over time of the level variables are mathematically represented by  
80 differential equations. The process being modelled is structured into basic components' parts  
81 corresponding to four related so-called blocks: Production; Stock/Maturation/Mortality;  
82 Temperature and Fishery (see Bald et al., 2009).

83 For population dynamics model, several authors (De Leo and Gatto, 2000; Solidoro et al.,  
84 2003) have underlined the importance of length class differentiation to take into account

85 differences in vital rates such as fertility, mortality, and respiration (Flye-Sainte-Marie et al.,  
86 2007). So in the Stock/Maturation/Mortality block, the Manila clam population in Arcachon  
87 Bay is divided into sub-populations according to length classes. Four classes are applied  
88 corresponding to: juvenile size class (from 0 to 20 mm); adult under the minimum current  
89 harvest size class (from 21 to 34 mm) and two adult size classes above the minimum current  
90 harvest size (from 35 to 39 mm and upper 40 mm). The evolution over time of the number of  
91 clams in each class is controlled by specific growth, natural and fishing mortalities  
92 parameters.

93 The production of juveniles (Production block) is defined by a quantity of recruits arriving in  
94 the system during spawning period, which is controlled by seawater temperature conditions  
95 (Temperature block). The influence of seawater temperature during the spawning phase, has  
96 largely been described by Holland and Chew (1974), Mann (1979), Ohba (1959), Park and  
97 Choi (2004). Temperature, is also known for its effect on larval development and settlement  
98 (after a pelagic phase of 3 weeks, Le Treut, 1986) as demonstrated by Robinson and Breese  
99 (1984) and Emmett et al. (1991). Seawater temperature is simulated using the sinusoidal  
100 function proposed by Melià et al. (2004) adjusted to the Arcachon bay conditions (Bald et al.,  
101 2009).

102 Inside the fishery block, the fishing mortality is controlled by the following parameters:  
103 fishing effort per clam length class, capture duration season, number of delivered fishing  
104 licenses, catches volume per license and protected area surface. To convert the volume of  
105 catches per length class to effective per length class, the length-weight relationship for the  
106 Manila clam population established by Cail-Milly et al. (2003) was used.

107 This paper proposes new improvements of the model developed for Manila clam in Arcachon  
108 Bay. Such developments are in accordance with the four main uses of a model reminded by

109 del Granado (2007) namely: increasing the human understanding of the considered system;  
110 communicating visually, making prediction and supporting decision-making (Felleman, 1999;  
111 Hannon and Ruth, 1994; Shenk and Franklin, 2001).

112 As recommended by Bald et al. (2009), revision of the first version of the model parameters  
113 has to be undertaken as soon as more ecological data on the Manila clam are available and as  
114 on-going studies in the Arcachon Bay are completed. Six weaknesses in the model were  
115 pointed out by Bald et al. (2009). New information allowed for clarification of the following  
116 four: effect of food availability, production of newly settled juveniles, growth rates and  
117 indirectly on natural predation.

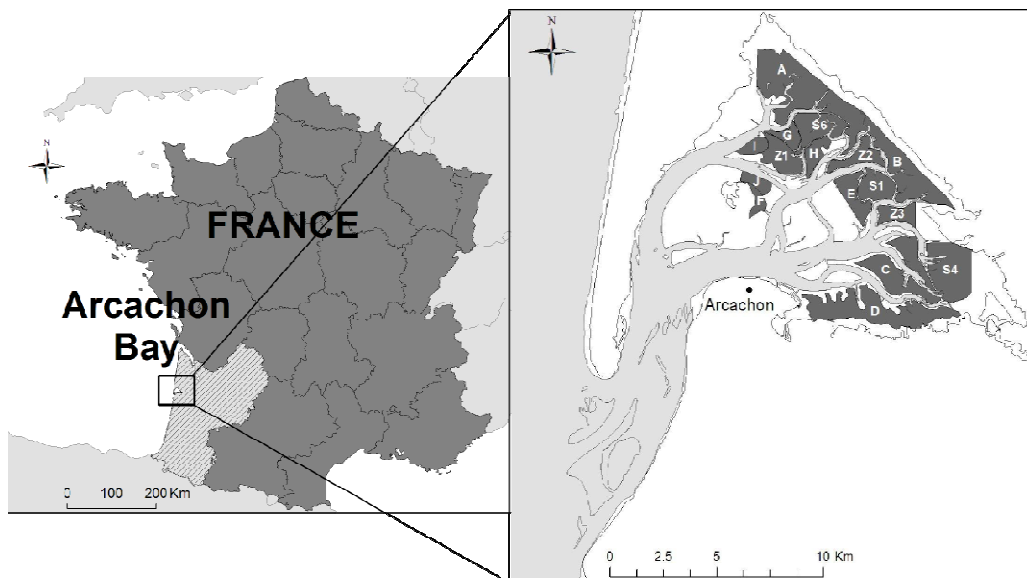
118 In this context the present paper 1) briefly re-visits the model structure and its initial  
119 calibration; 2) provides the latest developments accountable not only with stock and  
120 environmental conditions, but also with a more realistic harvesting activity and with economic  
121 considerations; 3) integrates a sensitivity analysis regarding uncertainty on a selection of  
122 parameters and 4) describes how this simulation tool is nowadays integrated in a co-  
123 management process.

## 124 **2. Material and methods**

### 125 2. 1. Study site

126 Arcachon Bay is a 156 km<sup>2</sup> semi-sheltered lagoon in the southwest coast of France (Fig. 1).  
127 Mostly composed of intertidal flats (110 km<sup>2</sup> within the inner lagoon which are colonized by a  
128 vast *Zostera noltii* seagrass meadows), the composition of this mesotidal system ranges from  
129 mud to muddy sands. The tide is semi-diurnal and the bay is both influenced by oceanic  
130 (external neritic waters) and continental (principally from the Eyre River) inputs (Dang,

131 2009). The characteristics of these water masses as well as the slow renewal of water by tides  
132 (Plus et al., 2006) both influence salinity and temperature within the bay. Variations of those  
133 two parameters are important when considering indicators computed over the last ten years  
134 (source Archyd network): seawater temperature ranges from 1.8 to 27.4°C (mean value  
135 15.4°C); salinity ranges from 15.4 to 35.4 (mean value 30.2). As trophic indicators,  
136 chlorophyll a concentration varies from 0.4 to 30.8  $\mu\text{g l}^{-1}$  (mean value 2.6  $\mu\text{g l}^{-1}$ ).



137

138 **Fig. 1.** Maps showing the studied site Arcachon Bay (France) (Sources: ESRI, BD Carthage, Ifremer – M.  
139 Lissardy).

140

## 141 2.2. Species description

142 Manila clam (*Venerupis philippinarum*) is an infaunal species inhabiting various substrates  
143 (sandy, sandy-muddy and muddy bottoms). As a suspension-feeding bivalve, its dietary  
144 regime is dominated by phytoplankton (Kanaya et al., 2005; Kasai et al., 2004; Spillman et  
145 al., 2008; Yokoyama et al., 2005). Length class differentiation within the population relies on  
146 the valve's length, which is defined as the longest distance from front edge to back edge  
147 (mm). For bivalves, fecundity is age-related (Gosling, 2003); for the Manila clam, sexual  
148 maturity is considered effective for clams above 20 mm length (Holland and Chew, 1974).

149 Most often, two spawning periods occur during a year in Arcachon bay. They range from  
150 April to June and August to October and are controlled by seawater temperature when it raises  
151 between 15°C and 22°C (Dang et al., 2010).

152 Metamorphosis and settlement occur generally after a 2-3 week period of pelagic larval stage.  
153 Then spatial distribution is of aggregative type, limited lateral displacements of individuals  
154 are reported to reach six meters per month (Tamura, 1970 in Le Treut, 1986). Manila clam  
155 maximum lifespan is unknown (Dee Boersma et al., 2006); Gillespie et al. (1999) indicate that  
156 it rarely exceeds 10 years of age in fished populations.

157 Among the factors influencing natural mortality, we can list the classical ones: natural  
158 predation (*Carcinus maenas*, *Ocenebra erinacea*, birds...), diseases (Brown Muscle  
159 Disease,...) and aging. Pollution could also intervene to increase this mortality.

### 160 2.3. Fishing activity and its management

161 Fishermen go on fishing areas by boat and exploitation takes place at low tide. Clams are  
162 extracted by hand. They sometimes scrape the sediment with a small tool. Fishing data from  
163 national and regional databases are used to consider the exploitation.

164 Whereas the minimum legal harvest size (35 mm since 2008, 40 mm before) is set by  
165 European legislation (EC Regulation CE n°40/2008), local legislation may concern in  
166 addition various measures such as protected areas, fixed number of licenses and limited  
167 fishing periods. They vary over time and are considered in the next sections. Those local  
168 measures are under the responsibility of professional organizations (like Comité Régional des  
169 Pêches Maritimes et des Élevages Marins d'Aquitaine) and can also involve governmental  
170 authorities.

171 2.4. Recent improvement of the model formulation

172 The process being modelled is structured into four basic components' parts (so-called blocks):  
173 Production; Stock/Maturation/Mortality; Temperature and Fishery. Equations' formulations  
174 for each process and their initial parametrization are presented and detailed in Appendix  
175 (Table Appendix 1 and Table Appendix 2 edited and updated from Bald et al., 2009). We are  
176 reminded that the population is divided into length classes and that the chosen endpoints of  
177 those classes depend on biological and exploitation considerations. Two types of  
178 improvements were applied to the initial model.

179 2.4.1. Integration of newly and specific available life traits data

180 - Recruitment (Production block)

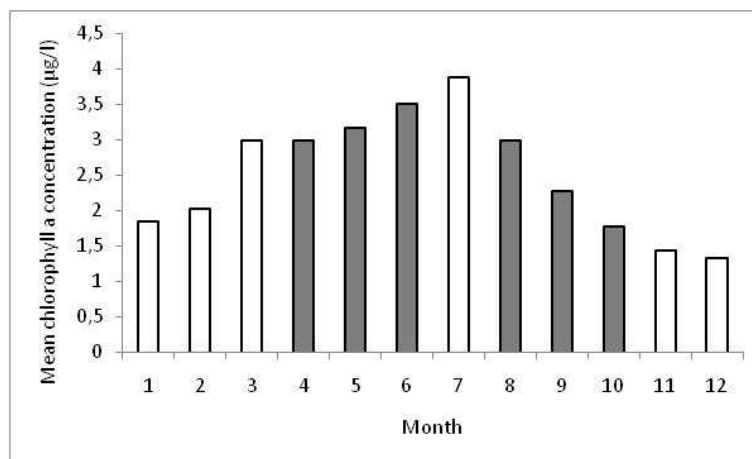
181 In a first step, recruitment level was reviewed to decrease the use of iterative modeling and to  
182 rely on a more realistic value. Since Berthou et al. (1997) considered that the number of  
183 recruits is furnished by the abundance of individuals below 17 mm, data from standardized  
184 campaigns (Sanchez et al., 2010) were used to estimate the clam's recruitment per surface  
185 unit. So a production of 1.21 recruits per m<sup>2</sup> was estimated and fixed as an input into the  
186 production block for the spawning period. This value is underestimated due to the fact that it  
187 includes the natural mortality for the individuals between 0 and 17 mm since the spawning.

188 In a second step, a reassessment of this recruitment level had to be performed according to the  
189 above consideration and to reinforce the environmental effect on this life period.

190 Particularly, concerning reproduction phase (from gametogenesis to spawning), temperature,  
191 photoperiod and food availability are the three main factors highlighted for their effects in the  
192 literature (Delgado and Pérez Camacho, 2007; Devauchelle, 1990; Holland and Chew, 1974;  
193 Le Pennec and Benninger, 2000; Mann, 1979; Ohba, 1959; Soudant et al., 2004; Toba and



194 Miyama, 1995). Reduced impact, a possible effect of salinity has also been described by Park  
 195 and Choi (2004) and Dang et al. (2010). For larval development and associated settlement,  
 196 most of the literature focused on the influence of temperature (Emmett et al., 1991; Robinson  
 197 and Breese, 1984) even if winter's lowering, winter monsoon, pathogens and predation have  
 198 also been listed for their effects (Ishii et al., 2001; Williams, 1980). The interaction between  
 199 stock status and the environment for Arcachon Bay was highlighted by Caill-Milly et al.  
 200 (2010), emphasizing the importance of temperature and especially on the reproduction phase  
 201 (already taken into account in the model). To complete, parameters were added to the initial  
 202 sinusoidal curve modeling temperature evolution to precise temporal events: temperature  
 203 variation to test hypothesis of increase or decrease of the mean temperature and temporal  
 204 characteristic of this event (beginning, duration and end). Food supply appears to be a second  
 205 environmental factor to include in the model with different effect according to the considered  
 206 stage and particularly for young stages. Hypothesis was made that proportions of recruits are  
 207 related to chlorophyll a values. Considering the evolution of the mean chlorophyll a  
 208 concentration along the year (Fig.2), one can notice an increase of this food resource during  
 209 the first spawning period (April to June) and a decrease for the second spawning period  
 210 (August to October).



211

212 **Fig. 2.** Mean chlorophyll a concentrations along the year (in gray: spawning periods).

213 In this paper, we used this trend on chlorophyll a to modulate the trend of the recruit's level  
214 and added a parameter, chlorophyll a evolution, to test hypothesis of its proportional impact  
215 on the quantity of recruits (created values are precised in section 2.7.).

216 - Growth (Stock/Maturation/Mortality)

217 Using experimental data, Dang et al. (2010) defined the Von Bertalanffy Growth Function  
218 (VBGF) parameters related to Arcachon Bay. Those recent ecological data led to the  
219 reassessment of realistic growth rates estimates: 0.361, 0.245, 0.227 (dimensionless)  
220 respectively for length classes 0-20, 21-34 and 35-39 mm.

221 - Natural mortality (Stock/Maturation/Mortality)

222 A recent direct assessment of this source of mortality could be drawn from enclosure field  
223 experiments undertaken by Dang et al (2010) within Arcachon Bay between December 2005  
224 and November 2007. They were established at 6.9%, 3.9%, 1.8% and 1.2% respectively for  
225 length classes 0-20, 21-34, 35-39 and > 40 mm (deduced from Dang et al., 2010).

#### 226 2.4.2. Adjustment of the fishing activity and its control parameters

227 Whereas few data were available to describe the fishing activity (Fishery block) when the  
228 model was firstly developed, additional data can now be used to precise the activity. This  
229 information concerns annual fishing declarations of Manila clam within Arcachon Bay and  
230 was extracted from two databases considered as the most reliable according to the chosen  
231 periods: between 2003 and 2008, the national statistic database of the “Système  
232 d’Informations Halieutiques”; from 2009 on, the “Base Pêche Aquitaine”. Combined with the  
233 annual number of active fishing licenses (coded NFL and equal to: 70 from 2003 to 2008; 62  
234 in 2009 and 57 in 2010), the total annual volumes of catches declared by the fishermen allow  
235 the calculation of mean catches volume per fishing license each month (coded CVL).

236 Concerning the fishing mortality per length class and because clams below the legal harvest  
237 size are known to be exploited (anonymous catches reports and authority controls), fishing  
238 effort was reallocated on the whole length classes in the following way: for 21-34, 35-39 and  
239 > 40 mm length classes, they have respectively been estimated to 40%, 50% and 10% to take  
240 into account a higher fishing pressure on clams below the minimum legal size which seems to  
241 be more realistic.

242 This new information led to the reformulation of the temporal fishing catches evolution  
243 denoted  $F_i$  for the  $i^{\text{th}}$  length class, which is expressed in effective per surface unit, units ind  
244  $\text{m}^{-2} \text{month}^{-1}$ , according to the following equation:

$$245 \quad F_i = \text{NFL} \times \text{CVL} \times \text{FE}_i \times 10^6 \times (\text{ABS-PAS}) / (\text{MW}_i \times \text{ABS})$$

246 with NFL= Number of Fishing Licenses, CVL = Catches Volume per fishing License  
247 each month,  $\text{FE}_i$  = Fishing Effort for class  $i$ , ABS = Arcachon Bay Surface, PAS = Protected  
248 Area Surface,  $\text{MW}_i$  = Mean Weight for class  $i$ . This parameter  $F_i$  takes different values along  
249 the year according to the beginning (OFM = Open Fishing Month) and the duration of the  
250 fishing period (CDS= Capture Duration Season). Units are given in Table A.1.

251 Along with the parameters already taken into account for fishery's description, a lack of  
252 socio-economic drivers' consideration was highlighted during working groups (involving  
253 scientists and fishermen). In particular, reactions to selling price variations were pointed out  
254 to be included. According to fishermen expected behavior, a price effect was considered with  
255 a linear response of CVL to price (see section 2.7. for details).

## 256 2.5. Calibration, validation and sensitivity of the model

257 Starting in July 2003, which corresponds to the first available dataset on size distribution of  
258 the population within the bay (Caill-Milly et al., 2003), the model was calibrated with recent  
259 populational, ecological and fishery data obtained by Caill-Milly et al. (2003, 2006, 2008) and

260 Dang et al. (2009, 2010). The parameters differing from the initial model formulation (see  
261 Table A.2) are:

- 262 - production of 1.21 recruits per  $m^{-2}$ ;
- 263 - growth rates 0.361, 0.245, 0.227 for length classes 0-20, 21-34 and 35-39 mm;
- 264 - the natural mortalities 6.9%, 3.9%, 1.8% and 1.2% for length classes 0-20, 21-34,  
265 35-39 and  $> 40$  mm;
- 266 - catches volumes per fishing license estimated at  $0.6 \text{ t month}^{-1} \text{ license}^{-1}$  between  
267 2003 and 2006, and  $1.22 \text{ t month}^{-1} \text{ license}^{-1}$  for 2007 and 2008;
- 268 - fishing efforts 40%, 50% and 10% for length classes 21-34, 35-39 and  $> 40$  mm.

269

270 This “historical” modelization ends in December 2008. It traces the stock evolution before  
271 testing new management strategies.

272 Model’s validation was performed using the subsequent stock assessments (2003, 2006,  
273 2008). Those observed data were compared to the predicted data given by the model. The  
274 model efficiency, that is the calibration step, was evaluated by the percentage of deviation  
275 between observed and predicted data sets. The criterion of a maximum deviation percentage  
276 (set to 10%) was retained according to previous works (Bald et al., 2006, 2009; Bald and  
277 Borja, 2002).

278 To assess the sensitivity of the model, uncertainty of three key parameters (natural mortality,  
279 recruitment and spawning maximum temperature) were considered. They were chosen for two  
280 reasons: a high inter-annual variability and a non-consensus precise threshold of temperature  
281 on spawning. Chlorophyll a concentration was not taken into account in this sensitivity  
282 analysis. Each parameter is studied separately to test the variability of the estimated biomass

283 using thousand Monte Carlo simulations (Multivariate Sensitivity Analysis) with a random  
 284 uniform distribution of probability.

285 In the case of natural mortality, the standard deviation of calculated values established from  
 286 Dang (2009) was employed as the uncertainty measure ( $\pm 3.3$ ,  $\pm 1.5$  and  $\pm 1.1\%$  for the  
 287 0-20 mm, 20-35 mm and 35-40 mm length classes respectively). Concerning the settlement of  
 288 new recruits in Arcachon Bay, Sanchez et al. (2010) estimated a fluctuation between 4 and  
 289 20% of the total population from 2003 to 2010, which represents a 16% of variation. This  
 290 percentage of variation was employed as uncertainty measure for this parameter. Finally in  
 291 the case of spawning maximum temperature, few works established a threshold (Delgado and  
 292 Pérez-Camacho, 2007; Obha, 1959; Toba and Miyama, 1995), which challenged us to  
 293 consider a possible difference of  $+ 0.5^{\circ}\text{C}$  (Table 1).

294 **Table 1.** Parameters' uncertainty applied in the model to assess the sensitivity analysis using Monte Carlo  
 295 simulations.  
 296

Parameters	Uncertainty applied	References
Natural mortality (%)	0-20 mm: 6.9 +/- 3.3 21-34: 3.9 +/- 1,5 35-40 mm: 1.8 +/- 1.1	Dang et al., 2010
Recruitment (ind m <sup>-2</sup> )	1.21 +/- 0.12	Determined from Sanchez et al. (2010) on the entire population
Spawning maximum temperature (°C)	22 +/- 0.5	Delgado and Pérez-Camacho, 2007; Obha, 1959; Toba and Miyama, 1995

297

298 This approach looks like the One-Factor-At-A-Time analysis where the initial values of the  
 299 parameters are modified using percentages chosen here to account for ecological reality. The  
 300 range of the two extremes of the obtained subsequent total biomass estimates for each  
 301 parameter is then computed. Related to the corresponding relative variation of the input  
 302 parameter, it provides information about the parameters that most influence the system.

303 All the simulations were performed using the object-oriented modelling framework Vensim ®  
304 DSS. This software, developed for over twenty years, is widely used to construct simulation  
305 models of business, scientific, environmental, and social systems. Specific dynamic models  
306 regarding exploited marine resources (by fishing and aquaculture) have been developed under  
307 Vensim, Stella, Simile, Extend softwares (Dalla Riva et al., 2009; Ferriera et al., 2009; Grant  
308 et al., 2007; Solidoro et al., 2003).

## 309 2.6. Simulations of several management strategies

310 Since the aim of the model was to be used as a decision-support tool, working groups  
311 associating scientists and fishermen was held in 2008, to define management alternatives  
312 regarding only local regulatory authorities.

313 Forecasts from January 2009 to December 2017 resulting of the introduction of different  
314 management options are undertaken. The seven scenarios related to management strategies  
315 and retained for this paper are the following (see also Table 2):

- 316 - Scenario 1 (status quo) corresponds to maintenance of the management measures  
317 in similar levels than those applied in 2008 ( $CVL = 1.22 \text{ t month}^{-1} \text{ license}^{-1}$ ,  $CDS =$   
318  $12 \text{ months}$ ,  $PAS/ABS = 18.5$ );
- 319 - Scenario 2 reduces both the catches per fishing license ( $CVL = 0.6 \text{ t month}^{-1}$   
320  $\text{license}^{-1}$ ), the capture duration season ( $CDS = 10.3 \text{ months}$ ) and increases the  
321 protected area surface ( $PAS/ABS = 22$ );
- 322 - Scenario 3 reduces the catches per fishing license ( $CVL = 0.6 \text{ t month}^{-1} \text{ license}^{-1}$ )  
323 and extended slightly more the protected area surface ( $PAS/ABS = 24$ );
- 324 - Scenario 4 simulates a decrease of the catches per fishing license ( $CVL = 0.6 \text{ t}$   
325  $\text{month}^{-1} \text{ license}^{-1}$ ) concomitant to a strong reduction of the fishing licenses'  
326 number ( $NFL = 55$ );

- 327 - Scenario 5 considers both reductions of the catches per fishing license  
 328 (CVL = 0.6 t month<sup>-1</sup> license<sup>-1</sup>), capture duration season (CDS = 11 months) and  
 329 number of fishing licenses (NFL = 60) associated to an increase of the protected  
 330 area surface (PAS/ABS = 22);
- 331 - Scenario 6 sets a limit to the catches per fishing licenses (CVL) equal to 0.6 t  
 332 month<sup>-1</sup> license<sup>-1</sup> (quota);
- 333 - Scenario 7 defines this limit of CVL to 1.20 t month<sup>-1</sup> license<sup>-1</sup> (quota).

334

335 When a parameter is not detailed above, this means that the applied value is still the same as  
 336 in the “historical” modelization.

337 To undertake comparisons between those management scenarios, evolution of the total  
 338 biomass trend is compared between the chosen scenarios and the continuation of the active  
 339 management measures in 2008 (status quo - Scenario 1).

340 **Table 2.** Description of the seven management scenarios retained by the working group associating scientists  
 341 and fishermen and integrated in the model from 2009 to 2019. Relatives differences of each management  
 342 measures applied in Scenarios 2 to 7 are compared to Scenario 1 (status quo) management measures values using  
 343 the following codification = no changes, ↗ increase comprised between 1 and 20%, ↗↗ increase (strictly)  
 344 superior to 20%, ↘ decrease comprised between 1 and 20%, ↘↘ decrease (strictly) superior to 20%.

345

346 Key: NFL= number of fishing licenses, CVL = catches volume by license (t month<sup>-1</sup> license<sup>-1</sup>), CSD = capture  
 347 season duration (month), PAS = Protected area surface (m<sup>2</sup>), ABS = Arcachon Bay Surface (m<sup>2</sup>).

348

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6	Scenario 7
NFL	70	=	=	↘↘	↘	=	=
CVL	1.22	↘↘	↘↘	↘↘	↘↘	↘↘	↘
CDS	12	↘	=	=	↘	=	=
PAS/ABS	18.5	↗	↗↗	=	↗	=	=

349

350

351

352 2.7. Simulations of environmental and market modifications

353 Three other scenarios were defined to consider the potential effects of environmental or  
354 market modifications to the stock evolution in addition to status quo management measures.  
355 For those scenarios, management measures applied are the same as those retained for  
356 Scenario 1 (status quo) on which the additional hypotheses were applied from 2009:

- 357 - Scenario 8 corresponds to the implementation of the recruits' production  
358 modulation according to chlorophyll a concentrations during spawning months  
359 (respectively 1.30, 1.40, 1.51, 1.30, 1.01 and 0.73 recruits per m<sup>2</sup> for April, May,  
360 June, August, September and October) with a simulated increase of the mean  
361 chlorophyll a concentrations over 3 years (2009-2011). This last increase was set  
362 to 40% according to the mean percentage of variation of the chlorophyll a  
363 concentration for spawning period observed from 2000 to 2010;
- 364 - Scenario 9 simulates an increase of the seawater temperature. To define this  
365 augmentation and given the lack of projections regarding this parameter at a  
366 regional scale, we considered benchmarks related to air temperature modeled for  
367 scenario B1 [(Special Report on Emission Scenarios, Nakicenovic et al. (2000)].  
368 Between 2021 and 2050 and for south-western France, the mean value of air  
369 temperature is projected to rise to between 10% and 15% (Peings et al., 2012). In  
370 those conditions, we decided to test an increase of 0.06°C per year corresponding  
371 to 0.4% of the current mean seawater temperature parameterized within the model  
372 (15.85°C). This modification was applied between 2009 and 2017;
- 373 - Scenario 10 considers the increase of 10% of the CVL in response to the  
374 augmentation of the selling price from 3.5 €/kg to 4.5 €/kg. Those values were  
375 mainly based on interviews with fishermen.

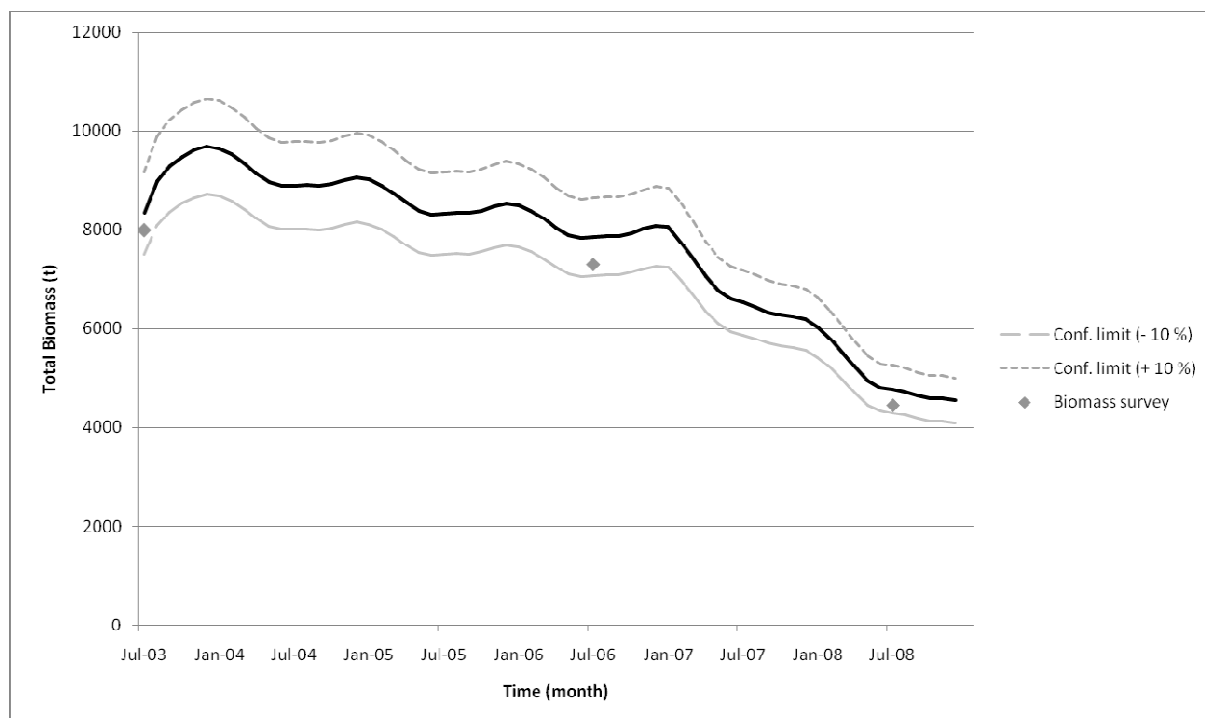


376 **3. Results**

377 3.1. Goodness of fit of the model

378 Between July 2003 and December 2008, the model output is illustrated in Fig. 3. It presents a  
 379 short period characterized by an increase of the total biomass up to 9,687 tons at the end of  
 380 2003 and promptly after a decrease of this biomass to reach 4,546 tons at the end of the year  
 381 2008.

382 For this historical modelization, the model outputs fit well with the real data since the  
 383 percentage of deviation between observed and predicted data are respectively 4% in 2003, 8%  
 384 in 2006, 7% in 2008 (Fig. 3). Those values met the criterion of a maximum deviation  
 385 percentage set to 10%.



386  
 387 **Fig. 3.** Total biomass (t) simulated between July 2003 and December 2008 (“historical” modelization).  
 388

389           3.2. Forecasts according to management scenarios

390   Once the seven management scenarios are applied, the different evolutions of the total  
391   biomass according to the applied management strategies (from January 2009 to December  
392   2017) can be summarized in four following categories (worst to best, see Fig. 4a to d):

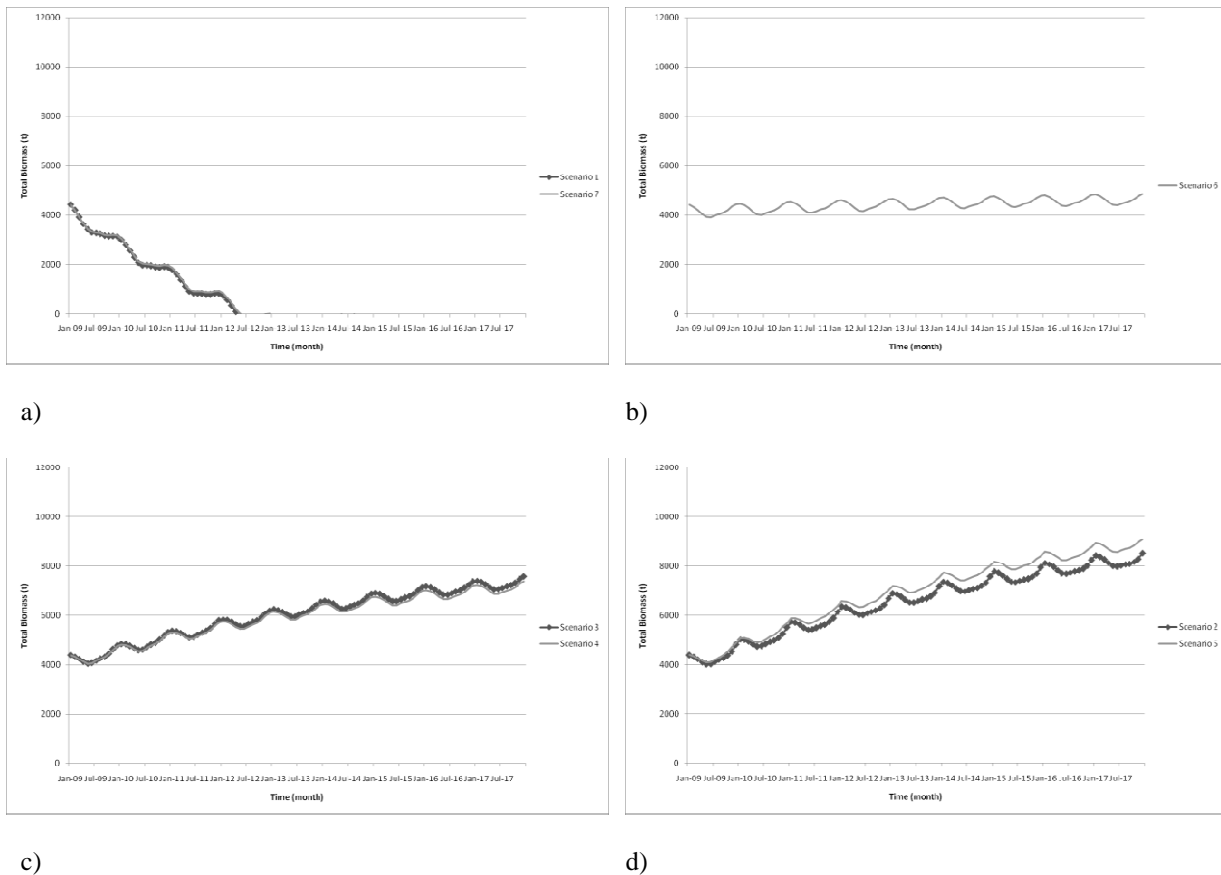
- 393       - a first category corresponding to Scenario 1 (status quo) and Scenario 7 is the  
394       collapse of the clam stock in less than four years (mid 2012);
- 395       - a second category, obtained with Scenario 6 leads to a stabilization of the stock at  
396       2008 level (around 4,500 tons);
- 397       - a third category is achieved by Scenario 4 and Scenario 3. The total biomass  
398       exhibits a regular increase and almost reaches 7,500 tons for both cases at the end  
399       of the simulation period;
- 400       - the last category is obtained for Scenario 2 and Scenario 5. These scenarios allow  
401       the recovery of the stock to respectively 8,500 and 9,000 tons, which roughly  
402       correspond to the initial stock level.

403   Those results highlight the relevance of combining selected management measures to achieve  
404   a recovery of the stock.

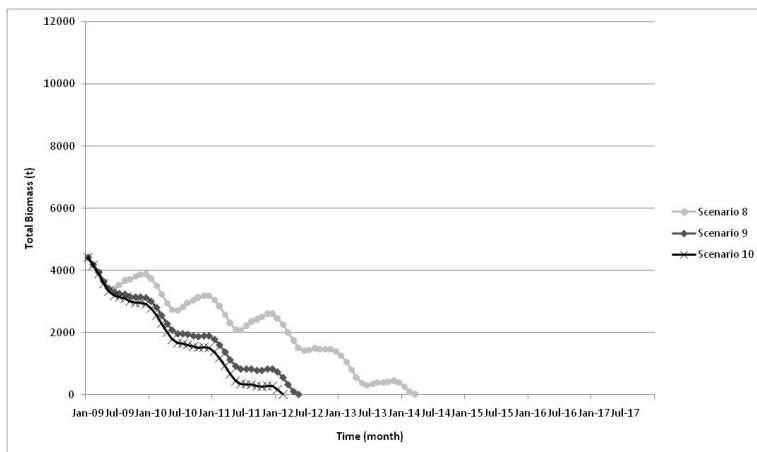
405           3.3. Forecasts according to environmental and market modifications

406   For the three simulations of environmental and market modifications (applied in addition to  
407   status quo management measures), the total biomass exhibits a collapse in less than five years  
408   after their introduction (Fig. 5). Scenario 9 (temperature modifications) and Scenario 10 (price  
409   effect) display the sharpest declines with values close to those of Scenario 1 (Status quo).  
410   Whereas temperature is one of the key parameters expected to be affected by climate change,

411 the consequences of its slight increase over 9 years does not cause, owing to its effect on the  
 412 spawning phase, noticeable impact on the stock.  
 413 Concerning trophic resources, an increase of 40% of the mean chlorophyll a concentrations  
 414 over 3 years enables to defer the decrease of the total biomass but leads to a collapse in 2014.



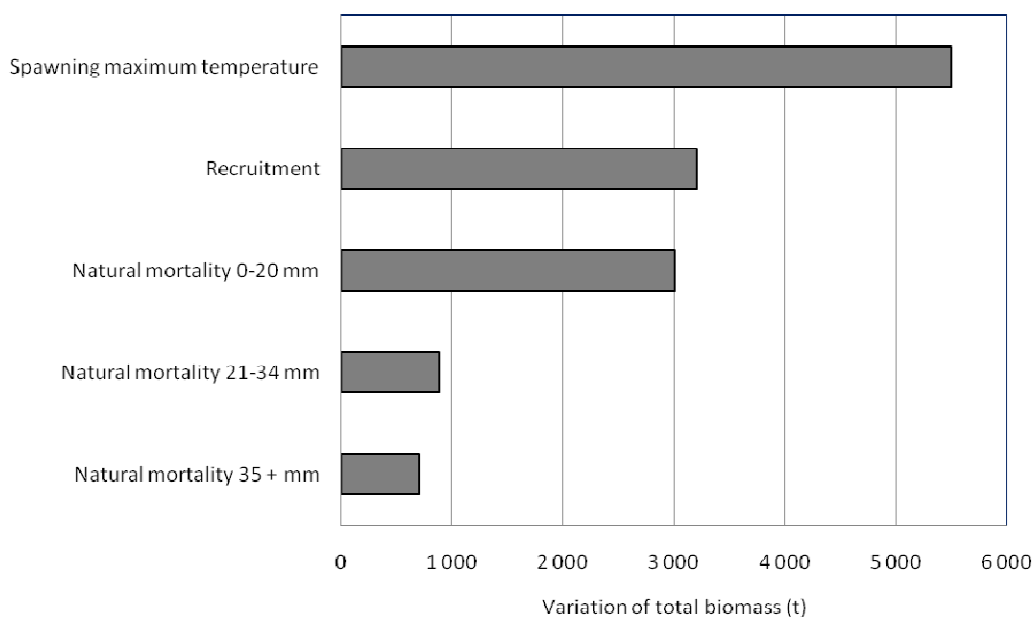
415 **Fig. 4a to d.** Total biomass (t) forecasts obtained for Scenario 1 to 7 between January 2009 and December 2017.  
 416 They are grouped by category: a) Scenarios 1 and 7; b) Scenario 6; c) Scenarios 3 and 4; d) Scenarios 2 and 5.



417 **Fig.5.** Total biomass (t) forecasts obtained for Scenario 8 to 10 between January 2009 and December 2017.

418 3.4. Model sensitivity

419 The results of the test on sensitivity are given in Fig. 6. Each bar represents the difference  
 420 between the maximum and the minimum values of the resulting total biomass estimates. The  
 421 model appears to be more sensitive to the environmental parameter (spawning maximum  
 422 temperature) and to younger stages (recruitment and natural mortality 0-20 mm) in a lesser  
 423 extent. For older stages, the simulated variations do not exceed 1,000 tones. A 2% variation in  
 424 seawater temperature (around 22°C) leads to a biomass variation equal to 5,500 tones. A 10%  
 425 variation in recruitment level (around 1.21 recruits per m<sup>-2</sup>) leads to a biomass variation equal  
 426 to 3,200 tones. Concerning natural mortality, the respective variations for the length classes  
 427 0-20, 21-34 and 35-39 mm were 61%, 38% and 61%. They led to the following biomass  
 428 variations: 3,000 tones, 875 tones and 700 tones.



429  
 430 **Fig. 6.** Differences between the maximum and the minimum values of the total estimated biomass for parameters  
 431 “natural mortality”, “recruitment” and “spawning maximum temperature” resulting of Monte Carlo simulations.

432  
 433

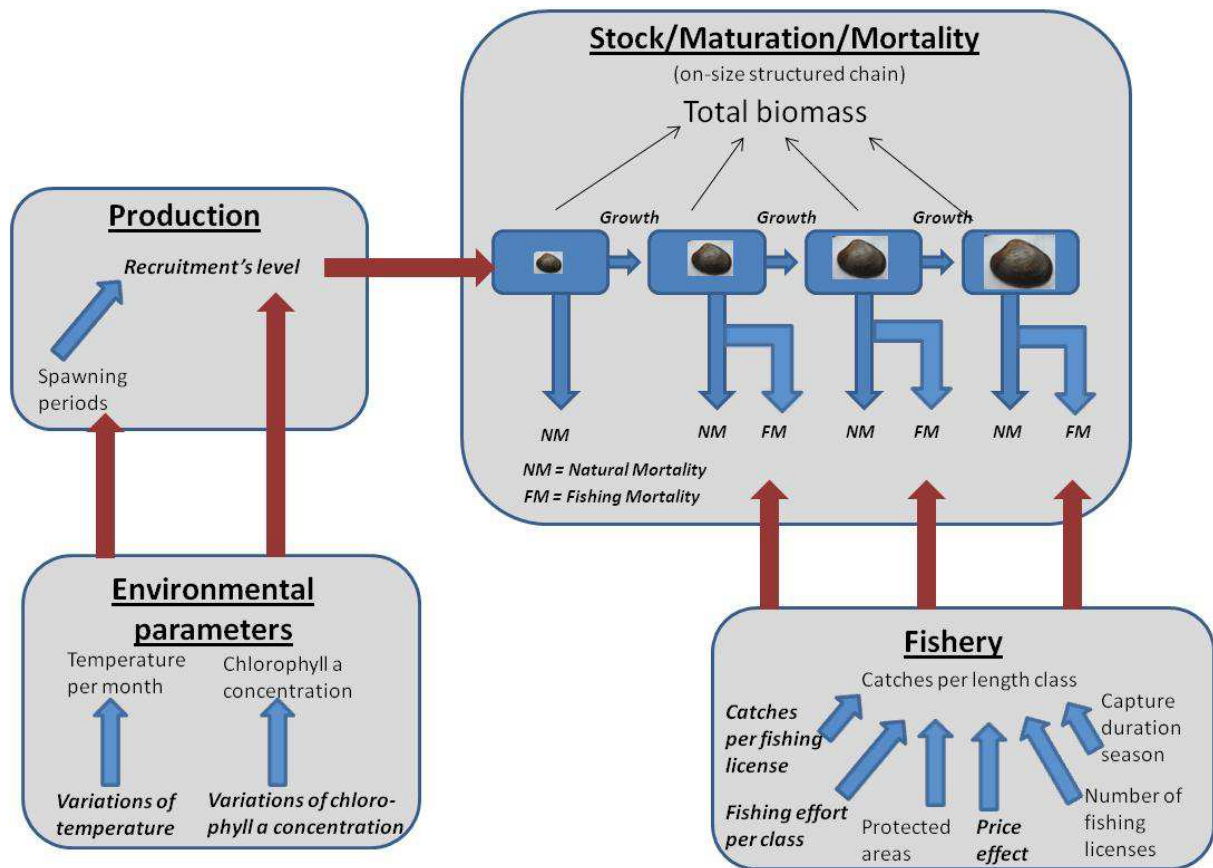
434 **4. Discussion**

435 The development of this simulation model responds to the need for a user-friendly tool to  
436 consider repercussions of alternative management strategies. The aim is to facilitate a crucial  
437 socio-economic harvesting activity on the Manila clam (second most important shellfish  
438 activity related to the bay behind oyster cultures) and long term sustainability of an exploited  
439 natural resource. Most of the existing management models dealing with clams necessitate the  
440 assessment of a large number of parameters (Cossarini et al., 2009; Pastres et al., 2001;  
441 Solidoro et al., 2000). Our present model necessitates fewer parameters and relies on a  
442 “system dynamic” approach implemented in order to understand and conceptualize the  
443 complex system regarding both the surrounding environment and human activity (Costanza  
444 and Ruth, 1998). Taking into account the initial assumptions listed in Bald et al. (2009), major  
445 developments and improvements have been undertaken. They are synthesized in Fig. 7  
446 regarding blocks and interactions among blocks.

447 **Integration of specific available life traits data**

448 Initial model's parameterization relied mainly on different bibliographic sources related to  
449 population dynamics of the Manila clam (Beninger and Lucas, 1984; Melià et al., 2004;  
450 Rodríguez-Moscoso et al., 1992; Solidoro et al., 2000, 2003) together with data related to  
451 Arcachon Bay (Caill-Milly et al., 2003 and G. Trut, unpublished data). Recent ecological data  
452 available at the bay scale led to the revision of previous model's assumptions.

453



454

455 **Fig. 7.** Scheme of the current Manila clam model illustrating recent improvements (in italic bold) regarding  
 456 blocks and interactions among blocks.

457

458 First of all, environmental drivers on key processes of the population dynamics have been  
 459 reinforced thanks to new formulations. This evolution mainly concerns the reproduction  
 460 phase. Until now this phase, which is one of the key processes of population dynamics (Flye-  
 461 Saint-Marie, 2007) was only controlled by seawater temperature. A preliminary modulation  
 462 depending on food availability expressed by chlorophyll a levels has been undertaken; such  
 463 relation needs to be more precisely established. Nevertheless this measurement of  
 464 photosynthetic pigment water concentration remains relatively easy to acquire and appears to  
 465 be the most common indicator used for food availability (*e.g.* Shibata et al., 1999). Unlike the  
 466 older stages (Flye-Sainte-Marie et al., 2003), we have not identified any works questioning  
 467 the validity of this descriptor as an adequate substitute for food availability in young Manila  
 468 clams. In those conditions, this formulation corresponds to a more realistic hypothesis since

469 the two modeled environmental parameters (temperature and food supply) are wellknown  
470 for influencing the reproductive phase (Delgado et al., 2007; Devauchelle, 1990; Holland and  
471 Chew, 1974; Le Pennec and Benninger, 2000; Mann, 1979; Ohba, 1959; Soudant et al., 2004;  
472 Toba and Miyama, 1995).

473 A second important process for population dynamics, growth, could also have been  
474 determined by this integration of specific environmental drivers. The reason being that  
475 numerous authors agree with the main role played by the temperature on *Venerupis species*  
476 (Beiras et al., 1994; Fan et al., 2007; Laing et al., 1987; Toba, 1987 in Nakamura et al., 2002),  
477 but also food supply (Maître-Allain, 1982; Yamamoto et al., 1956) and even duration of  
478 immersion (Gouletquer et al., 1987). Nevertheless, two reasons led to the application of minor  
479 changes in the formulation of the growth process. First, the highlighted interrelations between  
480 the studied stock status and temperature do not concern growth but mainly the reproductive  
481 phase (Caill-Milly et al., 2010). Secondly, the possible effects involved (direct and indirect  
482 through the link between temperature and trophic resources) are highly complex and the  
483 current constitution of the model did not allow considering them suitably. Numerous  
484 references have already addressed the problem of model complexity (Costanza and Sklar,  
485 1985; Håkanson, 1999; Jørgensen, 1988) since the right balance must be struck between  
486 simplicity and complexity. On one hand a simplistic model may not account for important  
487 ecological processes and may reduce descriptive and realistic model properties (Cetin, 2007).  
488 On the other hand, a highly complex model may reduce predictive accuracy, be difficult to  
489 run, and produce a high number of errors (Håkanson, 1999; Tsang, 1991). High dependence  
490 on assumptions, parameters values, and environmental forcing functions was also mentioned  
491 by Murray and Parslow (1999). We assume that ecological processes involved in the growth  
492 phase are insufficiently controlled at the moment.

493 Concerning natural mortality, the previous formulation relied on an empirical equation  
494 proposed by Solidoro et al. (2000, 2003). A recent direct assessment of this source of  
495 mortality has been drawn from enclosure field experiments undertaken by Dang et al. (2010)  
496 within Arcachon Bay between December 2005 and November 2007. In addition to being  
497 reliable data for the considered stock, their variations with age (related to mean size) are  
498 coherent with the models proposed by Caddy (1991) and Appeldoorn (1988) to reproduce  
499 mortality at age. Moreover, those values are used to account for the natural predation of  
500 Manila clams, which is considered to be important in Arcachon Bay (Robert and Deltreil,  
501 1990).

502 Considering those changes to the original formulation of the model, we consider that future  
503 improvements could mainly concern the question of linkage between the stock and the  
504 recruitment. The current biomass surveys led every two years indicate high variability of the  
505 recruitment levels at the bay scale (Sanchez et al., 2010) that is in concordance with recent  
506 works undertaken by Tezuka et al. (2012). Nevertheless, they do not allow validating of any  
507 intraspecific stock/recruitment relation for the investigated population. To identify this  
508 relationship for coastal species, Freire and García-Allut (2000) reported the importance of  
509 scale considerations or the occurrence of low stock levels to be detected. Moreover, processes  
510 involved are complicated because a stronger effect of interspecific stock-recruitment  
511 relationship can also occur as was demonstrated for *Donax hanleyanus* by Defeo (1998). In  
512 the absence of any evidence, we assess that recruitment fluctuations in response to  
513 environmental parameters are much stronger than those linked to density-dependent  
514 mechanisms (intra and interspecific). If this hypothesis would be revised, the model structure  
515 would allow, for example, considering fertility rates according to size classes since  
516 reproductive effort and fecundity are age-related (Gosling, 2003). For the lagoon of Venice,



517 Solidoro et al. (2003) considered that each parental class (minimum length required 18 mm)  
518 allows the successful implantation of one hundred juveniles. For Arcachon Bay, a first  
519 approach could be undertaken by using the age-related gonadal production established by  
520 Urrutia et al. (1999) for *Venerupis decussatus*.

#### 521 **Adjustment of the realized fishing activity and its control parameters**

522 Using data from two databases (“Système d’Informations Halieutiques” and “Base Pêche  
523 Aquitaine”), considered as the most reliable for professional fishing activities, new  
524 formulations of the monthly catches volume per fishing license has been integrated. In  
525 addition, the fishing effort according to the different length classes has been reallocated  
526 relying on more realistic field information. Those evolutions allowed reformulating the  
527 temporal fishing catches evolution expressed in effective per surface unit for the each length  
528 class (units ind m<sup>-2</sup> month<sup>-1</sup>). The fishery block was also completed by a first possibility to  
529 simulate a price effect on the fishing strategies.

530 The current fishing activity modelled within the model remains the professional one.  
531 Nevertheless, Manila clams are still caught by recreational fishermen. An upcoming  
532 assessment of this leisure activity will be undertaken in the upcoming months under a  
533 coordination of the French Agency for Marine Protected Areas. If the recreational activity is  
534 not negligible, future model’s improvements should incorporate this factor of changes within  
535 the model.

#### 536 **Performance of the model, sensitivity and used framework**

537 The adequacy of the model to reality was considered by using the acceptable limit of  
538 deviation percentage between observed and predicted data sets (Bald et al., 2006, 2009; Borja  
539 and Bald, 2000). This methodology was retained because very few datasets were available. As

540 soon as additional datasets are acquired, it would be worth considering the model  
541 performance with new indices of performance, such as those implemented by Anastácio et al.  
542 (2009) for *Scrobicularia plana*. In particular, the implementation of the Loague and Green's  
543 modeling efficiency (EF) would provide an overall indication of the goodness of fit (Mayer  
544 and Butler, 1993).

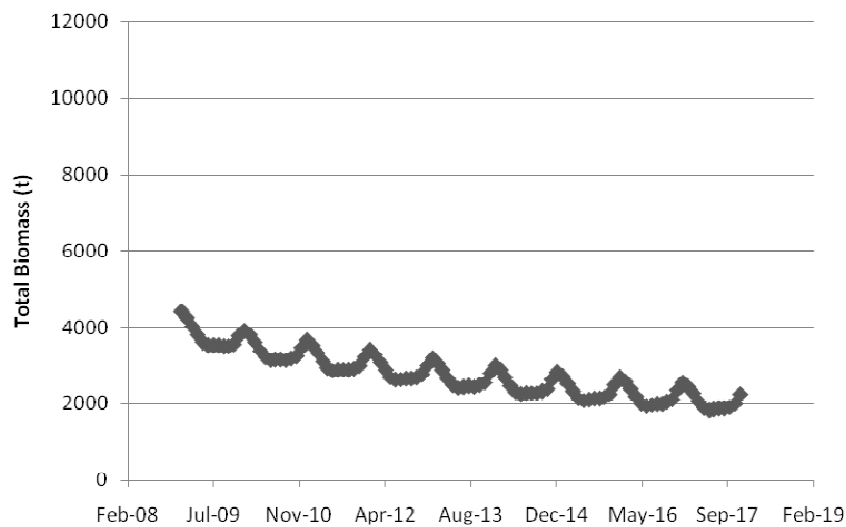
545 Temperature conditions related to spawning periods appear to give the biggest sensitivity for  
546 the total biomass. This reflects the importance of the parameters controlling the number of  
547 recruits on the modeled dynamics.

548 The improvement of the model has been conducted step by step and the latest formulation  
549 both reinforces environmental and socio-economic considerations within the model.  
550 Cumulative effects of those drivers can therefore be regarded (Scenarios 8 to 10). Although  
551 limitations on the modeling of biological process have been identified, they mainly concern  
552 the complex effects of temperature and food supply on growth. Bearing those limitations in  
553 mind, we consider that the model remains reliable to look at different management strategies  
554 under current environmental conditions but is not well suited to consider strong  
555 environmental shifts such as those considered in the worst climate change case scenarios.

#### 556 **Towards a co-management approach for this local exploited stock**

557 From the beginning, the model is specifically intended to strengthen the management process  
558 by making more complete and more defensible decisions. After the integration of available  
559 ecological and fishing data in the model, this tool was thus used for the first time for  
560 management purposes in 2008-2009. The simulations were presented and discussed in the  
561 framework of working groups (associating scientists, fishermen and administration  
562 representatives). The choice of a management strategy involving several management

563 measures (preferred to one strong measure modification) has emerged. Its concerns: reduction  
564 of the number of fishing licenses (one input for two outputs); choice of two complementary  
565 protected area zones; prohibition to fish on Sundays. Concerning protected area zones,  
566 professional retain smaller total surface but chose areas with relative high potential of  
567 reproduction assessed by using a 2D hydrologic model. Fig. 8 displays the forecast of the  
568 expected total biomass with the retained management measures. It presents a slower decline  
569 of the biomass compared to status quo; a reevaluation of the situation and the necessary  
570 measures will be conducted in 2012. Whereas the first measure is directly managed by  
571 professional organizations, the two others resulted in administrative decisions also  
572 enforceable for recreational fishermen.



573

574 **Fig. 8.** Total biomass (t) forecast with the management measures chosen by the fishermen.

575

576 Similar approaches based on models are conducted *inter alia* on gooseneck barnacle (Bald et  
577 al., 2006); Peruvian scallop (Ortiz et al., 2002). In our case its implementation completes the  
578 existing collaborations between scientists and fishermen since the field surveys have been  
579 conducted by those two entities since 2003. This type of functioning is in line with  
580 orientations of the Oregon's Development Fisheries Program (see Harte et al., 2008) because

581 it aims at incorporating design of science and management plans for small-scale fisheries.  
582 Integration of different kinds of operational management measures and institutional structures  
583 for governance was highlighted by Defeo (2011) as a key issue of successful management of  
584 sandy beach fisheries. This approach is wished-for in the case of coastal Galician fisheries  
585 (Freire and García-Allut, 2000; Freire et al., 2002); it has been already applied in Southeast  
586 Asia coastal fisheries since the 1960s (Pomeroy, 1995).

587 Effective decision-making regarding Manila clam resources in Arcachon Bay thus rely on  
588 scientific advices and involve fishermen with administrative support. Gradually set up, one of  
589 its key features of this co-management approach (*i.e.* fishers and managers working together  
590 to improve the regulatory process, Gutiérrez et al., 2011) is that fishermen form a group and  
591 manage the fishery resources in a collective manner (Uchida and Wilen, 2004). According to  
592 Nielsen and Vedsmand (1999) co-management classification, the type of co-management in  
593 use for Manila clams in Arcachon Bay is between the cooperative and the delegated type. The  
594 role of fishermen participating in planning, formulation, monitoring, control, and management  
595 plans' surveillance was mentioned by Castilla and Defeo (2005). To assess the efficiency of  
596 the management choices on Arcachon Bay, evolution of standardized population indicators is  
597 monitored. The favorable evolution of the total biomass and the positive effect of the  
598 protected areas observed in 2010 (Sanchez et al., 2010) have to be confirmed or not in 2012.

599 The current parameter shared by the stakeholders and used to compare the different  
600 management strategies essentially rests on the total biomass evolution. In order to improve the  
601 functioning of this collaborative framework, we expect to encompass at the same time  
602 ecological and socio-economic valuations of the measures impact as proposed by Elliott  
603 (2012). Socio-objectives are generally poorly defined; a price-effect has been recently  
604 integrated in the model to enrich it and to take into account human behavior. Such relation

605 needs to be more precisely established as well as the relation between biomass availability,  
606 effort and profitability of the fishery. For example, it would be interesting to introduce  
607 modification of CVL level in response to strong decrease of total biomass. Nevertheless this  
608 cognitive approach will be likely to be used for reevaluation of the management decision at  
609 the end of 2012 once the last biomass survey will have provided an update estimate of the  
610 monitored indicators. As well, a reflection on desired breakdown of the licenses between full  
611 time and part time activities could be set. They will facilitate communication and  
612 management decisions at regional scale as long as they are shared by the different involved  
613 entities.

614

#### 615 **Acknowledgements**

616 We are greatly indebted to Alice Khayati and Céline Laffitte for their valuable help  
617 concerning management description at the bay scale. We also thank Candice Millard for  
618 English editing and Muriel Lissardy for providing localization map.

619

620 All authors declare no conflicts of interest.

621

622 **Appendix**

623 Table Appendix 1: equations' formulation for the modeled process (time step is month), edited and updated from Bald et al. (2009).

Block	Process	Equation formulation (units)	Variables (units)
Stock/Maturation/ Mortality	Temporal clam effective evolution per surface unit for the first length class	$LC1 = JP - M1 - G2$ (ind m <sup>-2</sup> month <sup>-1</sup> )	JP: juveniles production per surface unit and per month (ind m <sup>-2</sup> month <sup>-1</sup> ) M1: effective per surface unit of the 1 <sup>th</sup> class length having died (ind m <sup>-2</sup> month <sup>-1</sup> ) G2: effective per surface unit of the 1 <sup>th</sup> length class having grown to achieve the next length class (ind m <sup>-2</sup> month <sup>-1</sup> )
	Temporal clam effective evolution per surface unit for a generic i <sup>th</sup> length class	$LCi = Gi-1 - Mi - Gi+1$ ind m <sup>-2</sup> month <sup>-1</sup>	Gi-1: effective per surface unit of the previous length class having grown to achieve the i <sup>th</sup> class (ind m <sup>-2</sup> month <sup>-1</sup> ) Mi: effective per surface unit of the i <sup>th</sup> class length having died (ind m <sup>-2</sup> month <sup>-1</sup> ) Gi+1: effective per surface unit of the i <sup>th</sup> length class having grown to achieve the next length class (ind m <sup>-2</sup> month <sup>-1</sup> )
	Temporal transfert due to growth process of individuals from length class i to length class i+1 per surface unit	$Gi = LCi \times GRi$ (ind m <sup>-2</sup> month <sup>-1</sup> )	GRi: growth rate of the i <sup>th</sup> length class (dimensionless)
	Temporal stock evolution at the bay scale for a generic i <sup>th</sup> length class	$SCi = LCi \times MWi \times ABS / 10^6$ (t month <sup>-1</sup> )	MWi: mean weight of the i <sup>th</sup> length class (g) ABS: Arcachon Bay Surface (m <sup>2</sup> )
	Temporal mortality evolution per surface unit for a generic i <sup>th</sup> length class	$Mi = Zi + Fi$ (ind m <sup>-2</sup> month <sup>-1</sup> )	Zi: natural mortality of the i <sup>th</sup> length class (ind m <sup>-2</sup> month <sup>-1</sup> ) Fi: fishing mortality of the i <sup>th</sup> length class (ind m <sup>-2</sup> month <sup>-1</sup> )
	Temporal natural mortality evolution per surface unit for a generic i <sup>th</sup> length class	$Zi = \exp(a + c \times Li + d \times T + e \times Di)$ (ind m <sup>-2</sup> month <sup>-1</sup> )	a, c, d and e: coefficients of the equation relating natural mortality with length of individuals, sea water temperature and density Li: mean length for the i <sup>th</sup> length class (mm) T: sea water temperature at instant t (°C) Di: density of the i <sup>th</sup> length class (ind m <sup>-2</sup> )

## Chapitre 4 – Développement du modèle de simulation et son application comme outil d'aide à la gestion

	Quantity of clams (of all sizes) into the overall bay	$Stock = \sum SC_i \times MW_i \times ABS / 10^6$ (t)	Variables already presented above
Temperature	Temperature at instant t	$T = f \times \sin(((2 \times \pi) / 365) \times (t - h)) + g$	f, h and g: coefficients of the sea water temperature with f : half of the maximum temperature variation (°C) h: phase (days) g: mean annual temperature (°C)
Production	Spawning occurrence for a given month	SP = If then else ( $T_{smin} < T < T_{smax}$ , 1, 0) (dimensionless)	T: temperature (°C) T <sub>smin</sub> : minimum temperature for spawning (°C) T <sub>smax</sub> : maximum temperature for spawning (°C)
	Juveniles production per surface unit and per month	JP = JP <sub>m</sub> x SP (ind m <sup>-2</sup> month <sup>-1</sup> )	JP <sub>m</sub> : juvenile production per spawning month (ind m <sup>-2</sup> month <sup>-1</sup> )
Fishery	Temporal fishing catches evolution expressed in effective per surface unit for the i <sup>th</sup> length class	$F_i = LC_i \times FE_i \times CDS$ (ind m <sup>-2</sup> month <sup>-1</sup> )	FE <sub>i</sub> : fishing effort expressed in percentage of the total fishing effort all length class considered applied to the i <sup>th</sup> length class (%) CDS: capture duration season (month)
	Total fishing catches expressed in volume	$TFC = \sum F_i \times PEE \times (1 - (PAS/ABS)/100)$ (t)	PEE: ratio of the total catches related to the total exploitable stock (dimensionless) PAS: Protected area surface (m <sup>2</sup> )

625 Table Appendix 2: initial parametrization of the equations edited and updated from Bald et al. (2009).

Parameters' sets	Values (units)	Methodology and References
JPm: juveniles production per spawning month	3.3 (ind m <sup>-2</sup> month <sup>-1</sup> )	Determined by iterative modeling until achieving stability of the population because of unavailable adequate published information
GR1 to GR4: growth rates of the length class 1 to 4	[0-20]: 0.39 [21 – 34]: 0.091 [35 – 39]: 0.08 > 40: / (dimensionless)	Following the growth model developed by Melià et al (2004), calculation of the proportion of individuals for each length class that grow and pass to the next class from data obtained by Caill-Milly et al. (2003) and tuned by iterative simulations until achieving stability of the population
MW1 to MW4: mean weight of the length class 1 to 4	[0-20]: 0.99 [21 – 34]: 6.62 [35 – 39]: 11.66 > 40: 18.29 (g)	Calculated from relation length-weight displayed by Caill-Milly et al. (2003) Weight = 0.2162 x length <sup>3.0469</sup> (r <sup>2</sup> = 0.94)
ABS: Arcachon Bay Surface	46,4 x 10 <sup>6</sup> (m <sup>2</sup> )	Surface of the inter-tidal flats colonized by Manila clam within the bay (Caill-Milly et al., 2003)
a, c, d and e: coefficients of the equation relating natural mortality with length of individuals, sea water temperature and density	a: - 7.3 c: 0.041 (mm <sup>-1</sup> ) d: 0.055 (°C) e: 0.0006 (ind m <sup>-2</sup> )	Adapted from empirical equation developed for Venice Lagoon (Italy) by Solidoro et al. (2000, 2003) with a determined by iterative modeling until achieving stability of the population
Li: Mean length for the i <sup>th</sup> length class	[0-20]: 14.84 [21 – 34]: 29.31 [35 – 39]: 36.39 > 40: 41.35 (mm)	Calculated from Caill-Milly et al., 2003
Di: density of the ith length class	[0-20]: 1.70 [21 – 34]: 17.78 [35 – 39]: 4.23	Calculated from Caill-Milly et al., 2003



## Chapitre 4 – Développement du modèle de simulation et son application comme outil d'aide à la gestion

	> 40: 0.61 (ind m <sup>-2</sup> )	
f, h and g: coefficients of the sea water temperature with f: (°C) phase (days) g: mean annual temperature (°C) f : half of the maximum temperature variation	f: 6.5 (°C) h: - 115 (days) g: 15.8 (°C)	Singular value decomposition applied to the sea water temperature data set provided by Gilles Trut (Ifremer, unpublished data) and the fitted model by Bald et al. (2009) h adjusted to present the lower mean error between those two sets of data
Tsmin: minimum temperature for spawning	15 (°C)	Literature (Beninger and Lucas, 1984; Rodríguez-Moscoso et al., 1992; Solidoro et al., 2003)
Tsmax: maximum temperature for spawning	22 (°C)	Literature (Rodríguez-Moscoso et al., 1992; Solidoro et al., 2003)
FE1 to FE4: fishing effort expressed in percentage of the total fishing effort all length class considered applied to class 1 to 4	[0-20]: 0 [21 – 34]: 0 [35 – 39]: 0.7 > 40: 0.3 (dimensionless)	Estimated from Caill-Milly, pers. commun.
CDS: capture duration season	12 (month)	Local legislation
PEE: ratio of the total catches related to the total exploitable stock	0.21(dimensionless)	From Caill-Milly et al., 2003
PAS: Protected area surface	(m <sup>2</sup> )	Local legislation

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## **Conclusion générale et perspectives**

## Conclusion générale et perspectives

La présente thèse a été mise en place pour poursuivre la compréhension des traits d'histoire de vie écologique de la population et intégrer ces connaissances dans le modèle de simulation utilisé à des fins de gestion.

### **Rappels des principaux résultats**

#### *Morphologie et croissance*

L'analyse de forme conventionnelle basée sur des mesures métriques et pondérales a permis d'établir, pour la population de palourde japonaise (*Venerupis philippinarum*) du bassin d'Arcachon, des relations d'allométrie entre des paires de descripteurs. Ils concernent la longueur, la hauteur, l'épaisseur et le poids de la valve ; les relations démontrées sont essentiellement de type allométrie positive. Un changement significatif de morphologie a été mis en évidence à partir d'une longueur voisine de 16-20 mm qui correspond à la deuxième année de vie [en référence aux travaux de Dang (2009)]. À partir de cette taille, les taux de croissance de la hauteur et du poids de la valve sont donc plus importants que celui de la longueur.

L'étude de la variabilité phénotypique intra-site a conduit à identifier trois patrons morphologiques au sein du bassin d'Arcachon. Pour ces mêmes paramètres, la variabilité phénotypique inter-site, considérée en comparant la population de palourde du bassin d'Arcachon avec celles de Bellevue, du golfe du Morbihan et du Banc du Guer, a mis en évidence une différence entre les sites du nord (Banc du Guer et golfe du Morbihan) et les sites du sud (Bellevue et bassin d'Arcachon). Les trois ratios morphométriques considérés comme discriminants pour ces populations sont l'indice d'élongation, un indice de densité de la valve et l'indice faisant intervenir le poids de la valve sur sa longueur (H/L, SM/Av et SM/L).

Les résultats obtenus sur la morphologie convergent pour indiquer que certaines zones intra-bassin paraissent défavorables pour le développement des individus. À l'inverse, ils identifient la zone située dans la partie centre nord comme favorable à leur bon développement. Ils indiquent par ailleurs que la seule prise en compte de la longueur masque des variations de formes de la coquille non seulement au sein de la population mais également lors de comparaison de différentes populations.

## Conclusion générale et perspectives

### *Facteurs identifiés pour leurs effets sur les traits de vie de l'espèce*

Parmi les facteurs susceptibles d'influencer la variabilité morphologique et la physiologie de l'espèce, ce travail de recherche s'est intéressé à une pathologie émergente, à la densité de palourdes japonaises et aux conditions environnementales (décrites par la température, la salinité et les conditions trophiques).

L'occurrence du caractère globuleux dans le bassin d'Arcachon est associée à de faibles densités et à de fortes proportions d'individus affectés par la maladie du muscle marron. Il ne semble donc pas y avoir de relation densité-dépendante pour la forme à l'échelle du bassin. À notre connaissance, pour cette espèce, aucune relation entre morphologie et pathologie n'avait jusqu'à présent été mise en évidence dans la littérature.

Prenant en compte un effet site sur la morphologie des individus, les relations entre les conditions environnementales et les morphotypes révèlent une corrélation significative entre les trois ratios morphométriques discriminants (H/L, SM/Av et SM/L) et les conditions trophiques approchées par la concentration en chlorophylle a. Par ailleurs, un lien entre l'indice de densité de la valve et le pourcentage de températures comprises entre 12 et 20°C est également démontré. L'interprétation de ces résultats illustre la complexité des facteurs intervenant sur la morphologie des individus à la fois à l'échelle intra et inter-sites et ouvre sur l'effet potentiel d'autres facteurs (tels que la nature du substrat, le niveau hypsométrique) ou plus généralement de la notion de conditions favorables de l'habitat et qui ne sont pas considérés dans le cadre de ce travail. Cette hypothèse est renforcée par les résultats préliminaires apportés par l'analyse de contour sur une sélection d'individus. La mise en œuvre de cette technique complémentaire aux méthodes conventionnelles semble en effet montrer une différence de forme au niveau de la marge antéro-dorsale de la valve. Cette zone est identifiée dans la littérature pour son rôle sur la stabilité du bivalve au sein du substrat.

La synthèse bibliographique sur l'effet des facteurs environnementaux couplée aux connaissances sur la phénologie intra-bassin de l'espèce ont permis de s'intéresser à des agrégations temporelles de paramètres décrivant les conditions physiques et trophiques et influençant potentiellement la dynamique de population. Les corrélations mises en évidence entre ces descripteurs du milieu et des descripteurs d'état du stock ont confirmé l'importance de la température notamment pendant la période de reproduction entre mai et novembre. Il ressort également des analyses de très nombreux liens impliquant un rôle des ressources trophiques.

## Conclusion générale et perspectives

Leurs natures varient en fonction des deux stades considérés (juvéniles et adultes) et conduisent à émettre deux hypothèses : des régimes alimentaires différents liées à l'âge et/ou des perturbations d'autres fonctions (respiration et/ou locomotion) par les particules en suspension.

L'ensemble de ces résultats conduit à considérer que les ressources trophiques doivent être intégrées dans les processus décrivant la dynamique du stock au côté du rôle joué par la température.

### *Evolution du modèle de simulation et son application dans un contexte de cogestion*

Les modifications majeures apportées au modèle de simulation initialement développé ont porté sur : l'intégration de l'effet des ressources trophiques dans les processus décrits ; la révision de la production de juvéniles et des taux de croissance par classe de taille ; la précision de données de captures par la pêche professionnelle et l'ajout d'un effet prix sur les stratégies de pêche. En parallèle à la validation du modèle, l'analyse de sensibilité entreprise a mis en évidence la sensibilité du modèle aux paramètres environnementaux et aux variables relatives aux stades les plus jeunes. Ces résultats confortent le bienfondé du renforcement de la formalisation des processus faisant intervenir les paramètres environnementaux sur la période de recrutement. Il constitue un compromis entre compréhension de la complexité du système et réalisme des processus jugés comme primordiaux et retenus dans la modélisation.

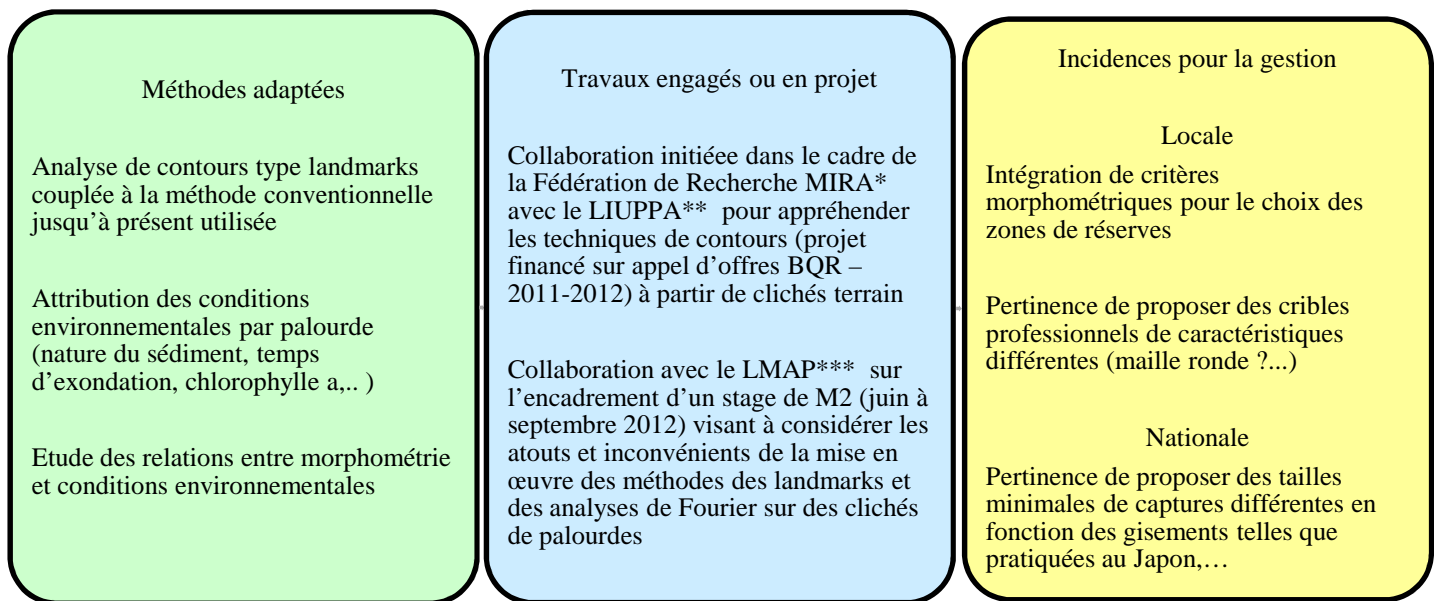
Deux principales faiblesses sont identifiées dans le modèle. D'une part, le modèle n'est pas forcément bien adapté pour rendre compte de l'effet d'évènements extrêmes car ils impliquent des valeurs de paramètres se situant en dehors des gammes de valeurs utilisées pour construire le modèle. Ces valeurs « hors normes » peuvent toutefois être utilisées dans des analyses de sensibilité pour considérer le comportement du modèle. D'autre part, les captures mensuelles par pêcheur sont supposées indépendantes de la valeur de la biomasse exploitable. La spécification de la fonction de capture pourrait être améliorée en prenant mieux en compte les stratégies de pêche. Ces dernières sont actuellement uniquement appréhendées via l'effet prix.

Dans un contexte de cogestion, l'outil a été utilisé pour réaliser des projections sur le devenir des populations en fonction de différentes mesures de gestion. Les différences de tendances d'évolution de la biomasse en réponse à ces dispositifs d'action ont servi aux gestionnaires pour la définition des mesures de gestion actuellement en vigueur. Le modèle a renforcé la démarche participative engagée.

## Perspectives

Les travaux réalisés dans le cadre de cette thèse ouvrent sur différentes pistes de recherche qui sont détaillées ci-après pour ce qui est des méthodes envisagées, des collaborations et de leurs incidences en matière de gestion.

### *Poursuivre la compréhension des liens entre signaux morphométriques et environnement*

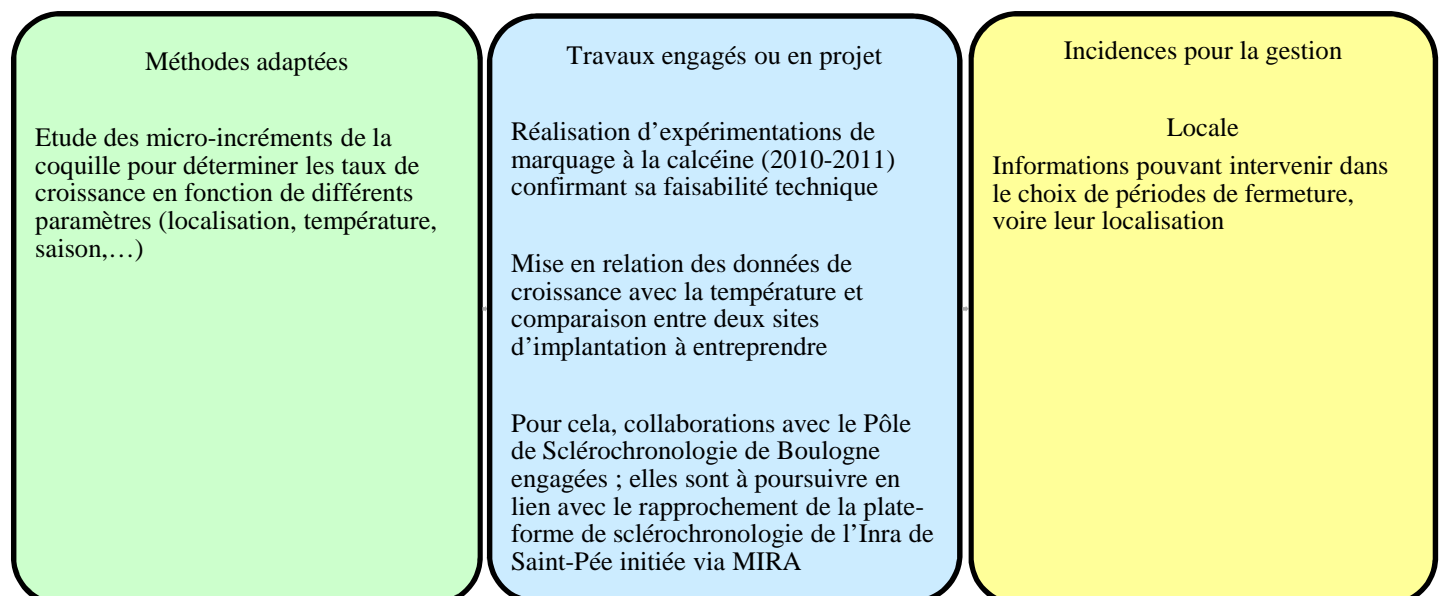


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### *Poursuivre la compréhension des conditions de réalisation de la croissance*



## Conclusion générale et perspectives

*Affiner le réalisme de la prise en compte de l'exploitation par la pêche (tout type de prélèvement, stratégies de pêche,...)*

Méthodes adaptées	Travaux engagés ou en projet	Incidences pour la gestion
<p>Ajuster le niveau des captures mensuelles au niveau de la biomasse disponible</p> <p>Mieux intégrer les dynamiques d'exploitation en particulier en matière d'évolution de l'effort de pêche</p> <p>Estimer les captures réalisées par la pêche de loisir</p>	<p>Non démarré</p> <p>Intégration du bassin d'Arcachon en tant que site pilote dans l'étude nationale pêche à pied récréative déposée en septembre 2012 à l'appel d'offres LIFE + sous la coordination de l'Agence des Aires Marines Protégées</p>	<p>Incidences pour la gestion</p> <p>Locale</p> <p>Réalisme favorable à la communication au sein du groupe de travail palourde</p> <p>Informations pouvant intervenir dans le choix de mesures de gestion adaptées aux différentes sources de mortalité</p>

*Intégration de l'incertitude dans la modélisation de processus*

Méthodes adaptées	Travaux engagés ou en projet	Incidences pour la gestion
<p>Analyses de Monte-Carlo jusqu'à la modélisation de processus spécifiques selon une approche stochastique (Husson, 2001 ; Fulton et al., 2011)</p>	<p>Démarrage de l'approche par analyses de Monte-Carlo pour des paramètres environnementaux et populationnels</p> <p>Étendre cette démarche à des paramètres décrivant les captures</p> <p>Parmi les paramètres les plus influençant (environnement, population, exploitation), intégrer la modélisation de l'incertitude</p>	<p>Incidences pour la gestion</p> <p>Locale</p> <p>Intégrer une approche des risques dans le processus de gestion</p>

*Affiner l'estimation du recrutement actuellement modulé par la température et la chlorophylle a*

Méthodes adaptées	Travaux engagés ou en projet	Incidences pour la gestion
<p>Tester la densité-dépendance entre niveau de recrutement et population en place</p> <p>Si relation établie, modéliser une relation entre adultes et juvéniles</p> <p>Si relation non établie, chercher à mieux comprendre les facteurs environnementaux influant ce recrutement</p>	<p>Non démarré</p> <p>Possibilité d'étendre le dénombrement par FlowCam (prélèvements Ifremer Arcachon) aux larves de palourde ?</p> <p>Utilisation de relations liant production de gonade ou nombre d'oeufs à la taille de l'animal</p> <p>Utilisation de mesures du réseau Archyd ou simulations issues du modèle Mars 3D</p>	<p>Incidences pour la gestion</p> <p>Locale</p> <p>Mieux dissocier les effets de la pêche et de l'environnement sur le stock de géniteurs et par voie de conséquence sur les juvéniles</p>



## Conclusion générale et perspectives

## **Références bibliographiques**

Hors celles de l'article publié (article 1 du Chapitre 2) déjà présentées

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