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 :

M. Philippe GAUDIN, Directeur de Recherche, INRA - Saint-Pée-sur-Nivelle	Président
M. Angel BORJA, Directeur de Recherche, AZTI - TECNALIA - San Sebastian, Espagne	Rapporteur
M. Olivier LE PAPE, Professeur des Universités, AGROCAMPUS OUEST - Rennes	Rapporteur
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M. Olivier GUYADER, 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 conjonction 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*

Sommaire

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[1].

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[1] Le stock étant défini comme l'ensemble des animaux exploitables (Laurec & Le Guen, 1981).

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[2], 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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[2] 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).

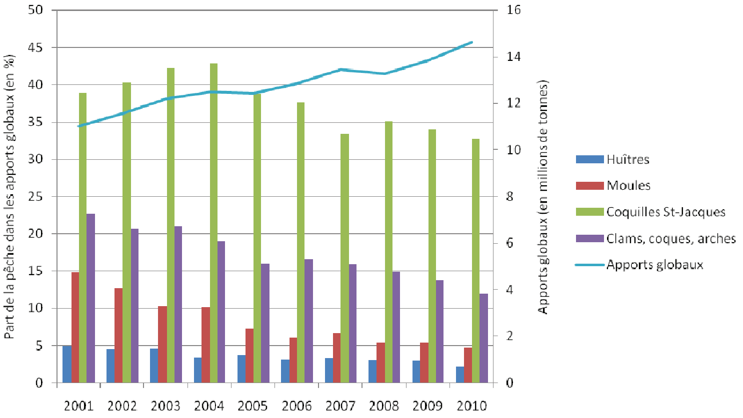

Figure 1. : Évolution de la contribution de la pêche dans les apports globaux (pêche et aquaculture) par groupe d'espèces de bivalves (source : http://www.fao.org/fishery/statistics/fr).

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 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.

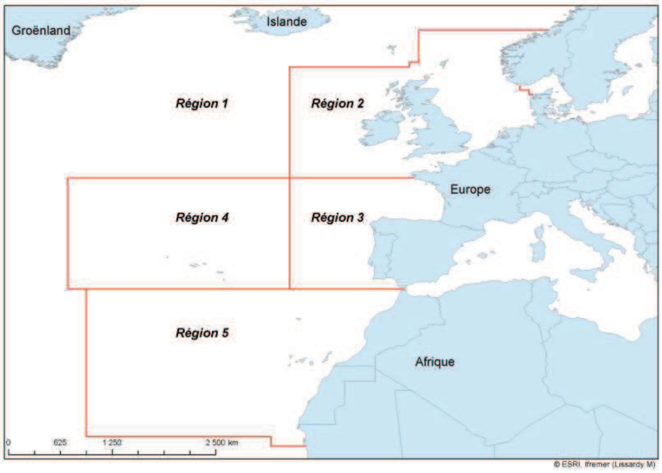

Figure 2. : Localisation des zones concernées par la taille minimale de capture pour la palourde japonaise – zones 1 à 5 excepté Skagerrak/Kattergat.

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[3] (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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[3] 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.

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 restant 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[4] (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.

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[4] Appelé Comité Local des Pêches Maritimes et des Élevages Marins jusqu'en 2012.

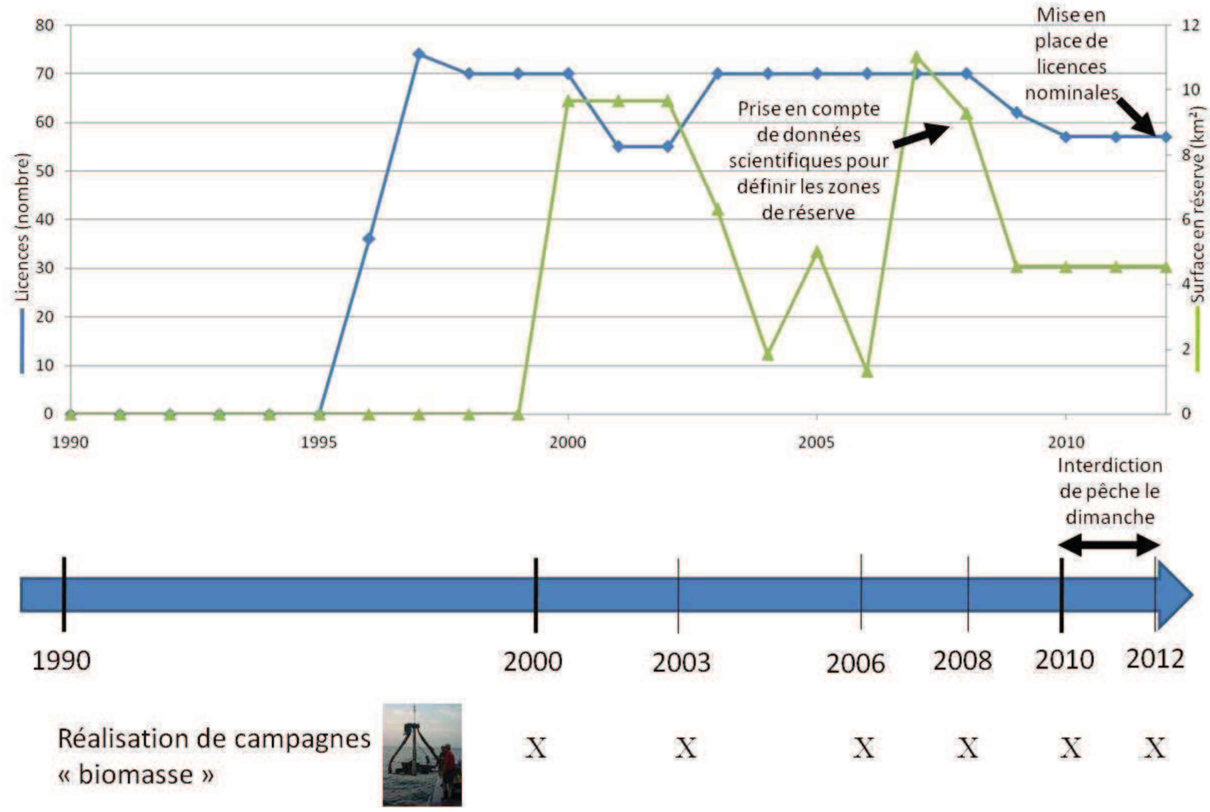
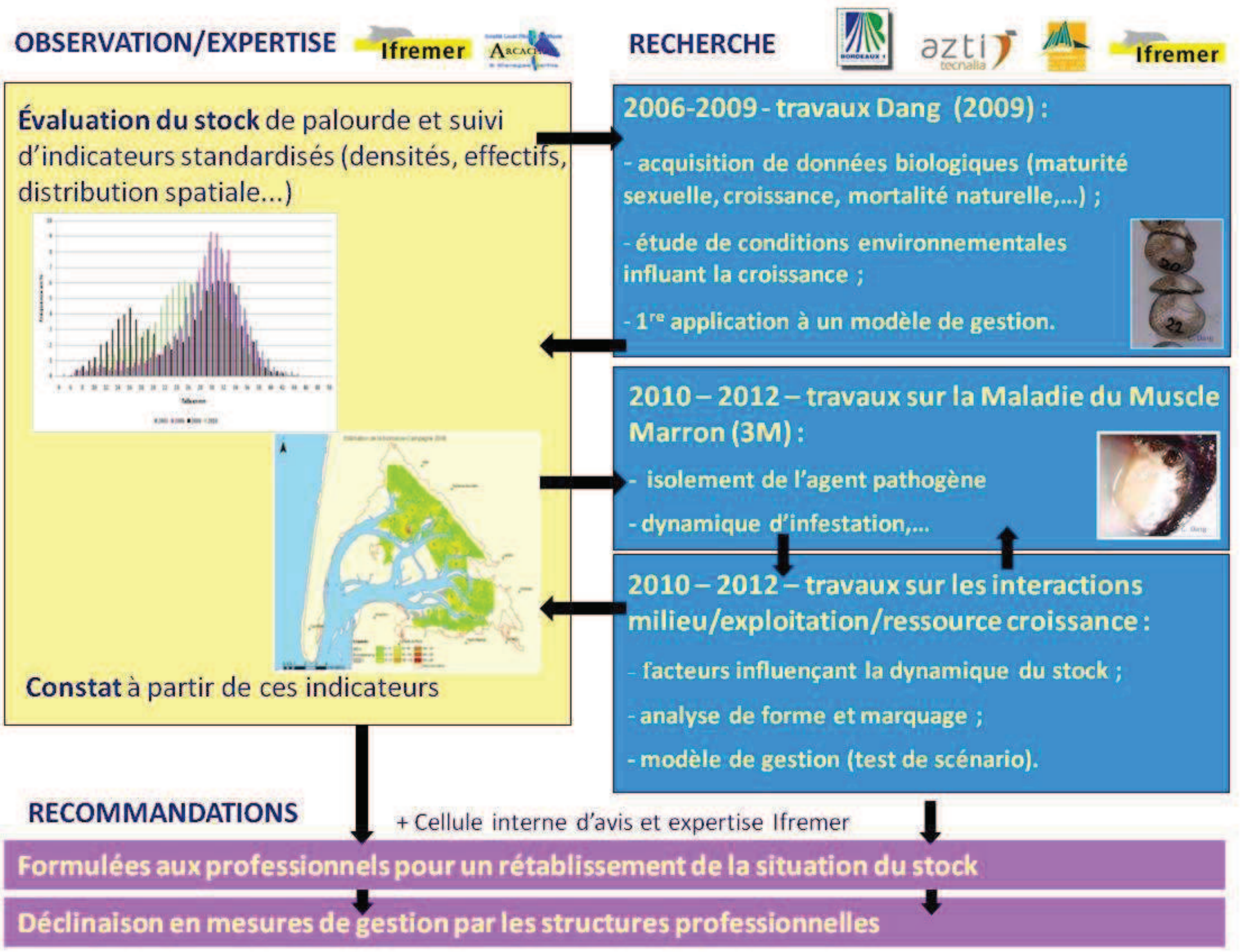


Figure 3. : Synthèse des mesures de gestion appliquées au stock de palourde japonaise du bassin d'Arcachon.

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).



OBSERVATION/EXPERTISE

Évaluation du stock de palourde et suivi d'indicateurs standardisés (densités, effectifs, distribution spatiale...)

Constat à partir de ces indicateurs

RECHERCHE

2006-2009 - travaux Dang (2009) :
- acquisition de données biologiques (maturité sexuelle, croissance, mortalité naturelle,...) ;
- étude de conditions environnementales influant la croissance ;
- 1re application à un modèle de gestion.

2010 – 2012 – travaux sur la Maladie du Muscle Marron (3M) :
- isolement de l'agent pathogène
- dynamique d'infestation,...

2010 – 2012 – travaux sur les interactions milieu/exploitation/ressource croissance :
- facteurs influençant la dynamique du stock ;
- analyse de forme et marquage ;
- modèle de gestion (test de scénario).

RECOMMANDATIONS

+ Cellule interne d'avis et expertise Ifremer

Formulées aux professionnels pour un rétablissement de la situation du stock

Déclinaison en mesures de gestion par les structures professionnelles

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 ?

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.

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[5].

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	*Venerupis* (Chiamenti, 1900)
Espèce	*Venerupis philippinarum* (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).

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[5] 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).

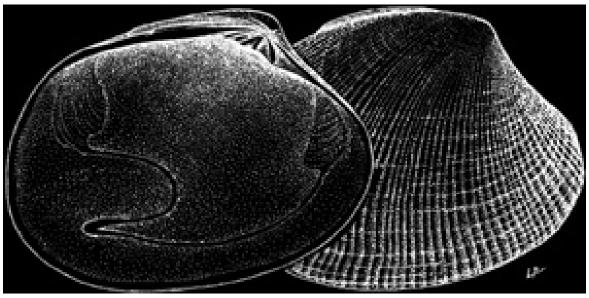

Figure 1.1. : Représentation schématique des valves de la palourde japonaise

(source : http://www.fao.org/fishery/culturedspecies/Ruditapes_philippinarum/fr).

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 20ème 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.

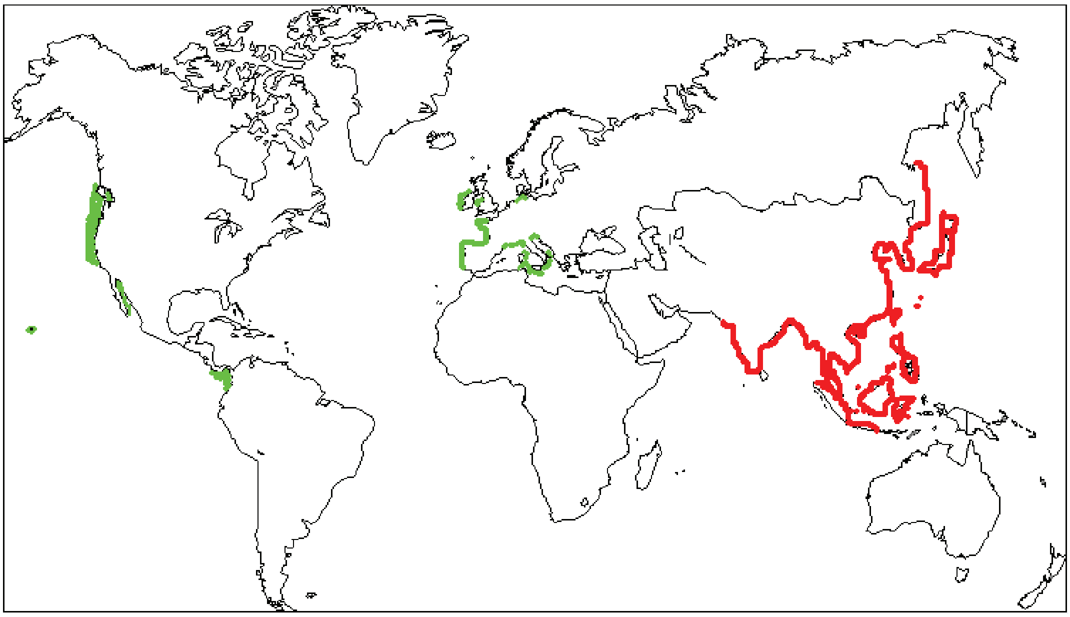

Figure 1.2. : Aire de répartition de la palourde japonaise *Venerupis philippinarum* proposée par Paul-Pont (2010) d’après Flye-Sainte-Marie (2007). En rouge, l’aire originale de répartition. En vert, les zones où des populations introduites se sont développées.

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.).

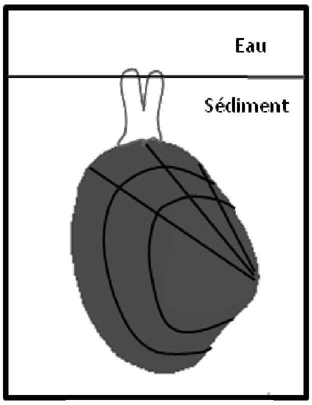

Figure 1.3. : Représentation de la position de vie (hors déplacement) de la palourde dans le sédiment.

1.4. Alimentation

La palourde est déposivore ; 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 particulaires (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 *périostracum*, l'*ostracum* et l'*hypostracum*. La composante organique est limitée au *périsostracum* ; 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.

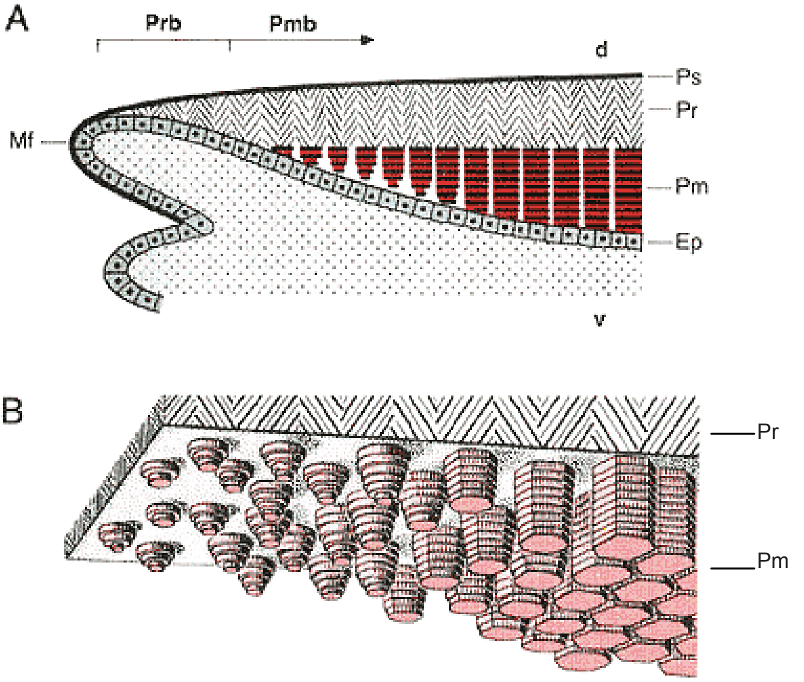

Figure 1.4. : Représentation schématique [(A) en coupe longitudinale (B) en trois dimensions] des zones de croissance d'un bivalve (source : Wehner & Gehring, 1995).

Ps : périostracum ; 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.

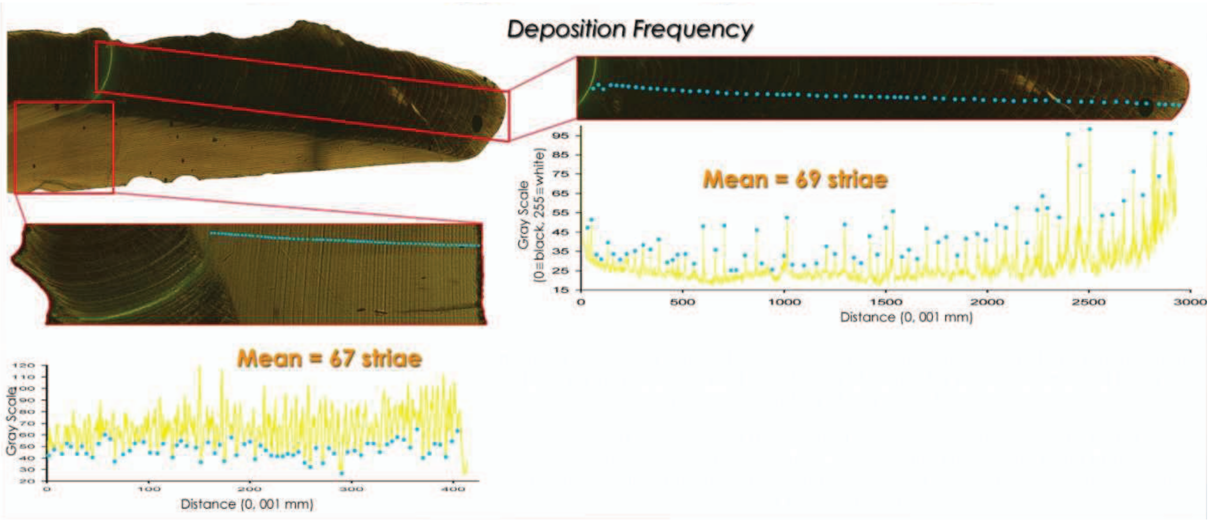

Figure 1.5. : Visualisation de la périodicité tidale de formation des micro-incréments en bordure de valve pour la palourde japonaise à partir d’opération de marquage à la calcéine (source : Caill-Milly et al., 2011).

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 (Goulletquer 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[6]. 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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[6] 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 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.).

	2003	**2006**	**2008**	**2010**
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/m²)	172	152,4	95,2	123
Abondance moyenne (nombre d’individus/m²)	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 km² 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 km² 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 200.10^6 m^3 en période de mortes eaux ; il est compris entre 370 et 400.10^6 m^3 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^3 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).

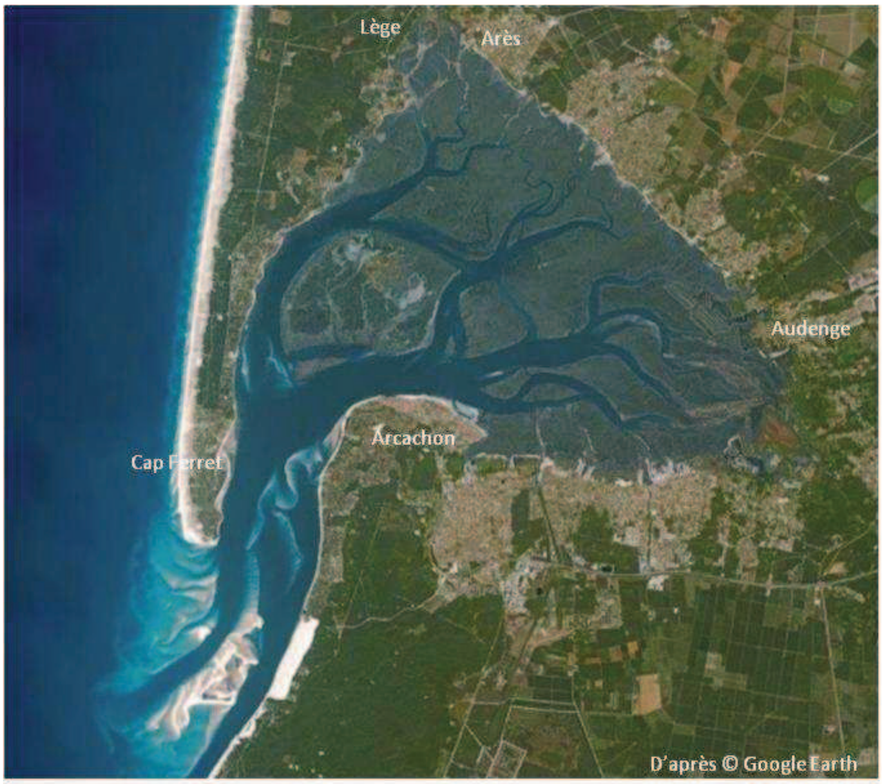

Figure 1.6. : Vue du bassin d'Arcachon.

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.).

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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.).

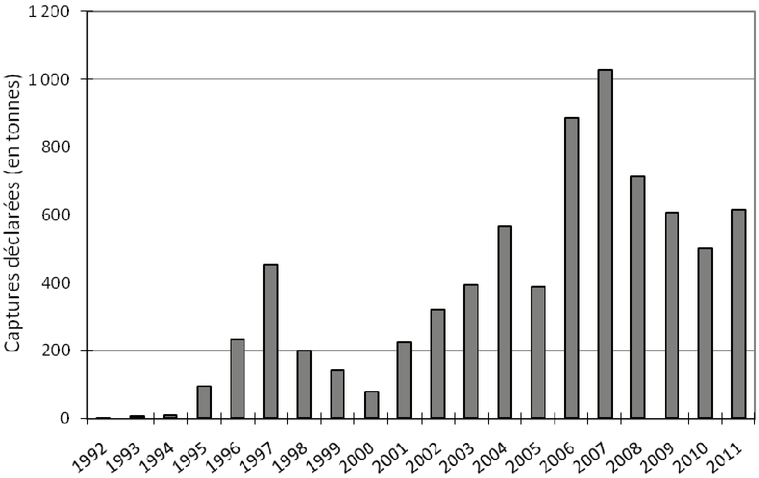

Figure 1.7. : Évolution des captures de palourdes japonaises déclarées par les pêcheurs professionnels pour le bassin d’Arcachon [sources : CRTS, Ifremer, BPA (CRPMEM Aquitaine), valeur estimée pour 1999].

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.).

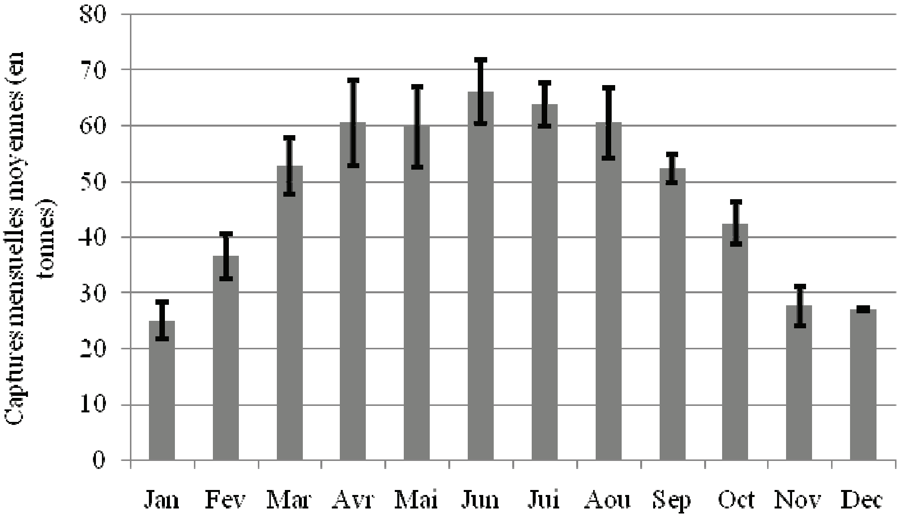

Figure 1.8. : Saisonnalité des apports de palourdes japonaises déclarées par les pêcheurs professionnels pour le bassin d'Arcachon – moyenne et erreur-type calculée sur 2009-2011 [source : BPA (CRPMEM Aquitaine)].

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.

Année	**CPUE moyenne (kg/h) et erreur type entre parenthèse**
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 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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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

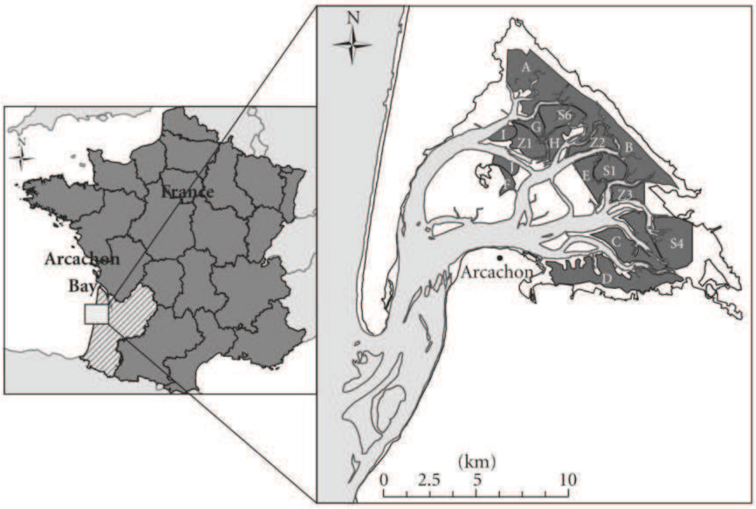


Figure 1: Maps showing the studied site Arcachon Bay (France) and localization of the sampled strata (Sources: ESRI, BD Carthage, Ifremer—M. Lissardy).

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^2 semi sheltered lagoon in the southwest coast of France (Figure 1). Mostly composed of tidal flats (110 km^2 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^2 (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	$= \mathrm{AL}/0.25 \times L^2 \times \pi$	0.65	0.85	0.73	0.02
Circle index ventral view	$= 2 \times \mathrm{AV}/0.25 \times LVent^2 \times \pi$	0.36	0.70	0.48	0.04
Reference Ellipse index lateral view	$= \mathrm{AL}/0.25 \times L^2 \times \pi$	2.63	3.43	2.94	0.10
Reference Ellipse index ventral view	$= 2 \times \mathrm{AV}/0.25 \times LVent^2 \times \pi$	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 0.5 L as diagonals. The second one is twice the area of the valve (ventral view) related to the surface of an ellipse with *LVent* and 0.5 *LVent* 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]).

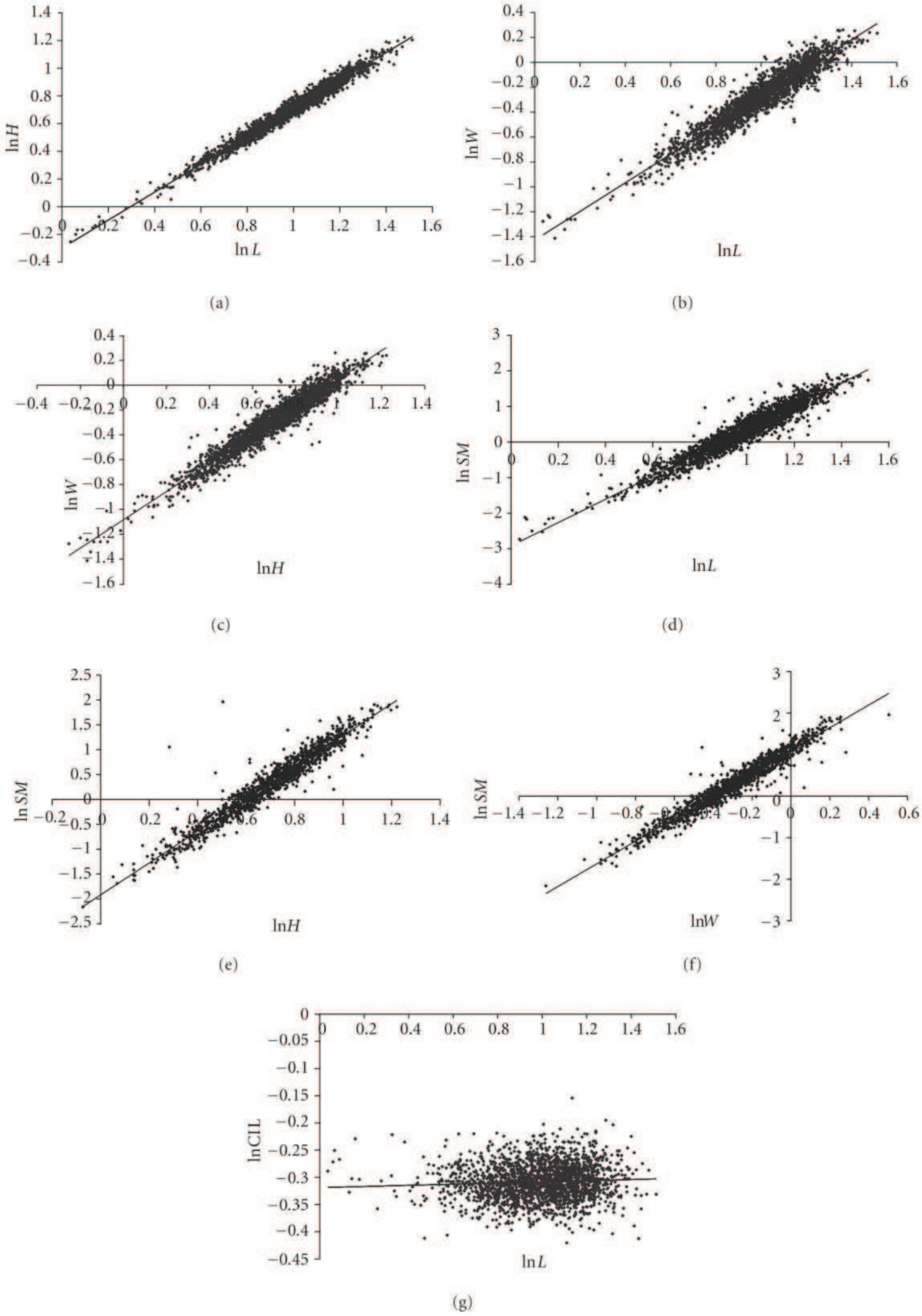
3. Results

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.



(a) (b) (c) (d) (e) (f) (g)

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

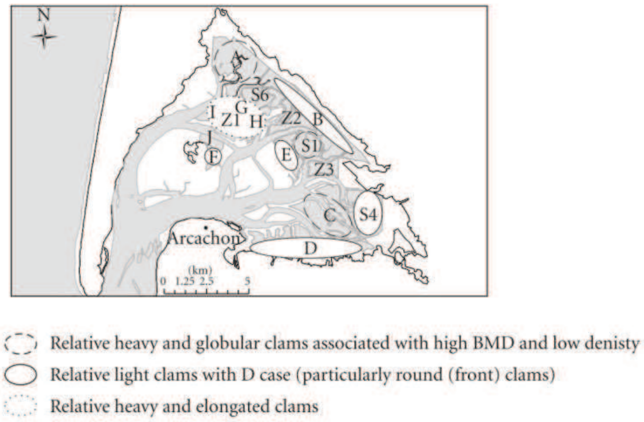
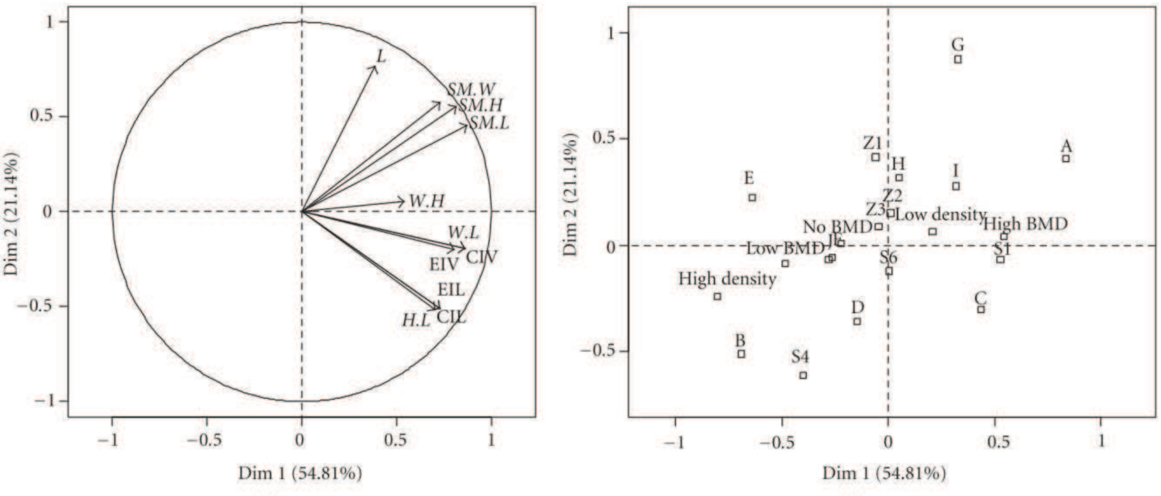


Figure 3: Spatial vizualisation of the allometry patterns related to density and disease.



(a)

(b)

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 (*Mactra 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 Luttikhuizen 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 rhomboides*, 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 rhomboides* [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 taking 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, Luttikhuizen 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).

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.

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

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Abstract:

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

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

Relationships between discriminatory morphometric ratios (describing elongation, valve density and weight related to length) and available environmental conditions (temperature, salinity and chlorophyll a concentrations) were considered using linear multilevel models. They revealed significant relationships with chlorophyll a concentrations and for one ratio with seawater temperature ranging from 12 to 20°C. Four hypotheses are exposited to explain the unexpected relationship identified between morphometric characters and trophic conditions: a negative effect due to high chlorophyll a concentrations; a masked effect of other food resources affecting valve’s growth; an inter-specific competition for food among the filter-feeders populations; effects of other environmental parameters such as sediment type. The observed differences of shape are proposed to respond to a combination of those four hypotheses with varying degrees depending on sites. Finally, consequences on population regulation are addressed.

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

1. Introduction

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

One of the most cultivated and harvested infaunal bivalves in the world, Manila clam (*Venerupis philippinarum*), has been the subject of specific works on relationships between morphometry and environmental factors. They highlighted for this species the leading role played by trophic conditions (Watanabe and Katayama, 2010), currents (Kakino, 1996); offshore or inshore localization (Nakamura et al., 2002). Effect of clams densities was also reported by Bourne and Adkins (1985), Cigarría and Fernandez (1998) and Ohba (1956). Most of those studies rely on conventional shape analysis methods which use distances, ratios, angles between basically landmarks. Very few works implement outline shape analysis such as Fourier series representations (Costa et al., 2008). The majority of those studies concerned Japanese populations. Surprisingly few studies deal with European stocks (Costa et al. 2008) whereas identifying similarities and differences in their responses may be very useful in understanding the mechanisms involved. They could contribute to challenging the conservation of the species by segregating natural processes from anthropogenic impact and be thus useful to identify adequate management measures to local conditions. Contribution of morphological studies on fish stocks management is already effective for some years (Cadrin, 2000; Cadrin and Friedland, 2005); such approaches appear to be more recent on bivalves (Márquez et al., 2010).

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

2. Material and methods

2.1. Study sites

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

“Banc du Guer” is the name given to the natural oyster deposit located at the river mouth of the Léguer river in North Brittany. The estuary is approximately 2.7 km^{-2} and has a mono-channel. An important sandy structure is located at the north-west of the bay (Augris and Simplet, 2012). At the mouth of the river, the bottom is mainly composed of fine shell sand. A facies characterized by heterogeneous mixture that can contain branches and debris of calcareous algae is also observed in this zone. The proportion of gravels tends to increase towards the middle of the bay (Augris and Simplet, 2012). Manila clams are mainly located in substrates composed of sand or mud and gravel. This bay is strongly influenced by tide levels. Currents are stronger outer the bay than inner. Speed tidal currents are comprised between 1.5 and 2 knots. Salinity varies little during the year in the downstream part of the estuary (http://envlit.ifremer.fr).

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

Bellevue is located at the western part of Marennes-Oleron Bay which is a semi-closed bay connected to the Bay of Biscay by the Pertuis d'Antioche in the north and the Pertuis de Maumusson in the south. In this area, sea bottoms are fairly shallow and space dividing due to different islands leads to a complex hydrology (http://envlit.ifremer.fr). To the coast, sedimentation is promoted by the break of the swell. Transit currents move from north to south (through the two Pertuis). Hydrodynamics remains locally dominated by swell action and tidal currents generating strong superficial changes in inter-tidal sand distribution (Le Hir et al., 2010). Those inter-tidal sand areas are limited; they host a large portion of the Manila clam population.

Arcachon Bay is a 156 km² semi-sheltered lagoon mostly composed of intertidal flats (110 km² within the inner lagoon). This mesotidal system is characterized by a sediment composition ranging from mud to muddy sands and colonized by vast *Zoltera noltii* seagrass meadows. Both influenced by external neritic waters and by continental inputs (Dang, 2009), this bay presents a semi-diurnal 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 (Plus et al., 2006). Considering an arc from west to south within the bay, Manila clam population is on the whole located on its east side.

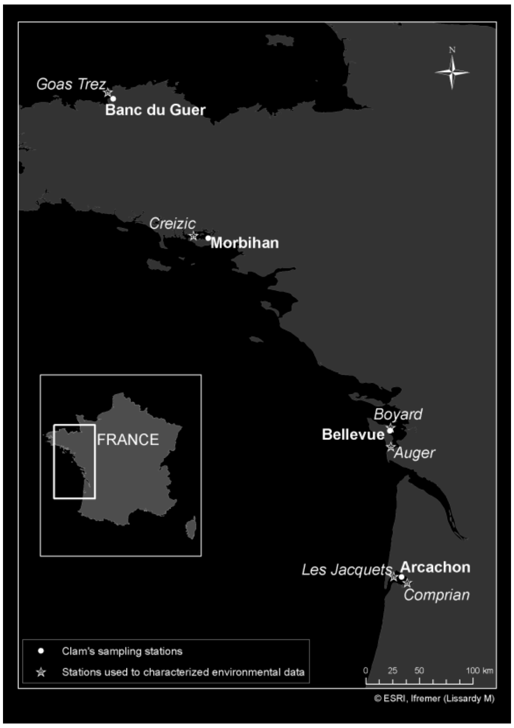

Fig. 1. Maps showing the studied site Arcachon Bay (France) and localization of the sampled strata (Sources: ESRI, BD Carthage, Ifremer – M. Lissardy).

2.2. Sampling collection

R. philippinarum shells were collected between March 2010 and March 2012 (details in Table 1). For Arcachon and Morbihan sites, a Hamon grab was employed at high tides and sediment cores were filtered onboard. For Banc du Guer and Bellevue, the samples were undertaken at low tide by hand within quadrats. For both techniques, the sample consist in sediment cores of 0.25 m² (0.5 m * 0.5 m) and depth is greater than the maximum buried depth known for Manila clam [10-12 cm when temperature is very low, Le Treut (1986)]. Sampled stations were randomly defined for each sites and identified by their geographic coordinates. Brought back to the laboratory, the clams were stored à -20°C until analyzed. To limit potential size dependency (Fan et al., 2007) on the morphometric characteristics, only individuals between 35.0 mm and 37.5 mm in shell length were sub-sampled for each site. The level and the variability of length among the sites are similar (Kruskal-Wallis test: chi-squared = 5.394, df = 3, p-value = 0.1451; Levene test: F value = 0.3296, df = 3, p-value = 0.804).

2.3. Environmental conditions

To consider the hydrological conditions which prevailed for each sites and potentially influenced morphometry characteristics, data from the national base Quadrige[2] were used. The main objectives of this base are to manage and exploit data provided by environmental survey networks undertaken by Ifremer. Sampling is carried out once a week or bi-monthly (depending on the parameters), at the slack of low tide (by strong coefficient) and high tide (by low coefficient) alternatively. For this study, we used both REPHY and ARCHYD networks and selected the parameters seawater temperature, salinity and chlorophyll a concentration (considered as an indicator of trophic resources according to Shibata et al., 1999).

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

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

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) 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 03°32’ W	47°33’ N 02°44’ W	45°56’N 01°13’ W	44°43’ N 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

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

Mean = Mean value; Med = Median value; SD = Standard Deviation, T6 = Percentage of temperature values above 6°C; T12_20 = Percentage of temperature values between 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 (µg l^{-1})	1,3	1,8	3,0	3,1
Chloro a Med (µg l^{-1})	1,1	1,4	2,4	2,5
Chloro a SD (µg l^{-1})	0,9	1,6	2,0	2,3

2.4. Shells preparation and classical morphology descriptors

In laboratory, all the shells were cleaned, dried at 38°C for 48 h and the valves were separated. Then for each clam two high-resolution pictures (lateral and ventral views) of the left valve were undertaken by using the TNPC software (Digital Processing for Calcified Structures, www.TNPC.fr) and image analyses were performed. Six physical parameters were retained and used to express ratios. Those 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 1.10^{-4} millimeter and 0.1 mg are associated to linear and weight measures:

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

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

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 referrers 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 referrers 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 referrers 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 referrers 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 referrers 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 referrers 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 referrers 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 referrers 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.

2.5. Representation of clam shapes using contour detection

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

- detectors based on gradient operators like Prewitt filters (Maini et al., 2006), Sobel filters (Sobel, 1990), Laplacien;
- detectors based on analytic approach like Canny filter (Canny, 1986), Deriche filter (Deriche, 1990);
- and active contours also called "snakes" (Kass et al., 1988).

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

2.6. Statistical analysis

Statistic analysis is used to answer two questions and so statistical analysis is divided in two parts: 1) description of the biometric variables related to the sites and individuals classification; 2) multilevel modeling to highlight the relationships between biometry and environmental parameters. The eight morphometric parameters described above were taken into account (H/L, W/L, W/H, SM/L, SM/H, SM/W, SM/Al, SM/Av). Concerning environmental conditions and level indicators variations, we chose to retain eight metrics, some ones giving an idea of a level value and others of variability (T Med, T SD, T6, T12_20, Sal Med, Sal SD, Chloro a Med, Chloro a SD).

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

Level and variability of length among the sites are similar. Significant differences among the morphometric ratios were tested with Kruskal-Wallis tests (using a type I error rate of 0.05). Morphometric peculiarities of each site were then regarded from a multivariate point of view, using descriptive multivariate statistical analysis. Normality of each ratio at each site was not verified with the original data. For a given parameter, the needed transformations to reach normality differed from one site to another. Moreover, equality of variance-covariance matrix at each site was not satisfied. In those conditions, usual classification methods such as LDA (Linear Discriminant Analysis), QDA (Quadratic Discriminant Analysis) or HLDA (Heteroscedastic Linear Discriminant Analysis) were not well-adapted to our data to confirm the observed variations among sites. We chose to implement Classification Tree (CT) which is a data mining method used to implement supervised classification. The aim is to find rules built from a set of explanatory variables that can separate the values of the target variable. In this sense it has the advantage of not requiring any binding assumption on the variables distribution, except that the target variable, if qualitative, does not contain rare outcomes. The obtained rules which take into account interaction between the variables can be displayed graphically using a binary tree. The hierarchical power of separability of each explanatory variable on the target variable can be interpreted. Statistical evaluation of the quality of the results is possible through several error rates of misclassification.

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

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

Multilevel modeling to highlight the relationships between biometry and environmental parameters

The morphometric ratios identified as the most discriminatory by the previous classification method were considered one by one as dependent variables of the variability of environmental conditions. For each of those variables, a linear multilevel model (LMM, also called mixed effects linear model) was fitted using site and the associated environmental conditions to quantify the dependences. To do this, we follow the sequence of steps proposed by Bliese (2012):

- Step 1 - a "null" mixed model is created taking into account only sites by examining intercept variability among site (random effect). The Intraclass Correlation Coefficient (ICC) is then calculated to determine how much of the total variance between-site variance is. We compare this null model and the model without a random intercept by assessing a model contrasts using Anova function;
- Step 2 - environmental conditions are then added one by one as predictors (fixed effect) to build several multilevel models. Since these models are nested, we used a likelihood ratio test (LRT) to evaluate the significance of adding each environmental and a combination of several ones to the null model. The final LMMs retained are as parsimonious as possible. To evaluate the gain of adding predictors on within and between site variances, we calculate the percentages of variance explained by using the following formula:

  Variance explained = [1 – (Variance with predictors / Variance without predictors)] * 100

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

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

3. Results

3.1 Spatial heterogeneity of morphometric characters

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

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

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

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
H/L	0.65	0.72	0.74	0.74	0.76	0.82	0.03	105.89	$2.2e^{-16}$
W/L	0.24	0.28	0.29	0.29	0.31	0.40	0.02	44.82	$1.012e^{-09}$
W/H	0.33	0.38	0.40	0.40	0.41	0.50	0.03	30.59	$1.039e^{-06}$
SM/L	0.35	0.83	0.95	0.97	1.10	1.57	0.19	59.43	$7.797e^{-13}$
SM/H	0.47	1.15	1.30	1.31	1.46	2.04	0.23	38.53	$2.18e^{-08}$
SM/W	1.14	2.97	3.28	3.29	3.62	4.78	0.52	52.75	$2.076e^{-11}$
SM/Al	0.17	0.41	0.46	0.47	0.52	0.73	0.08	39.87	$1.133e^{-08}$
SM/Av	0.48	1.20	1.32	1.34	1.46	1.95	0.20	64.24	$7.31e^{-14}$

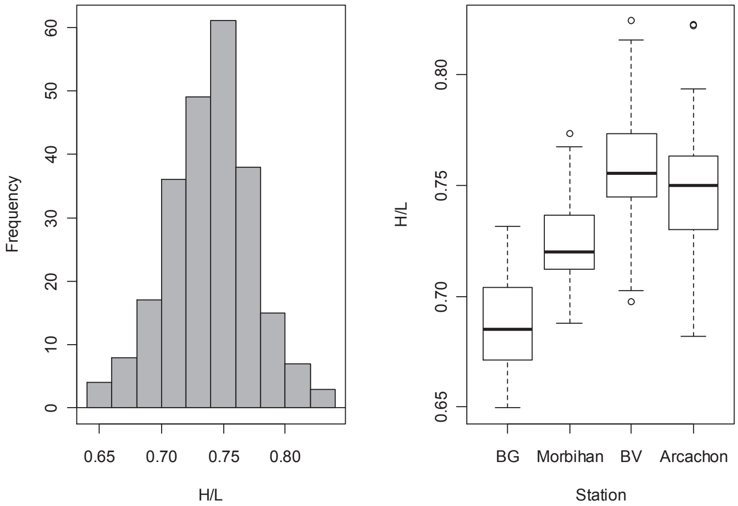

Fig. 2. *H/L* frequency distribution for the entire dataset and box plot according to factor site.

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

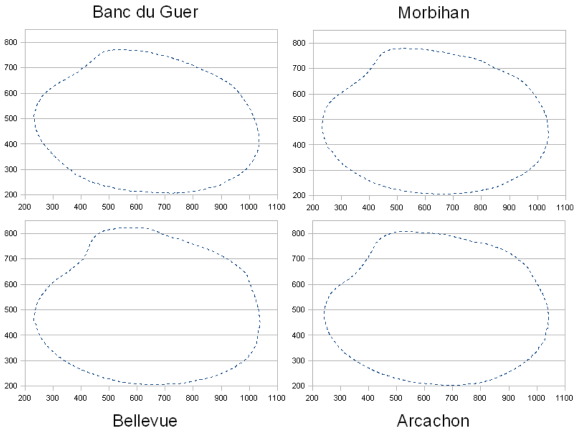

Fig. 3. Representation of active contours (“snakes technique”) detected on four valves considered as typical of each of the four sites valves. (a) Banc du Guer, (b) Morbihan Gulf, (c) Bellevue, (d) Arcachon Bay.

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

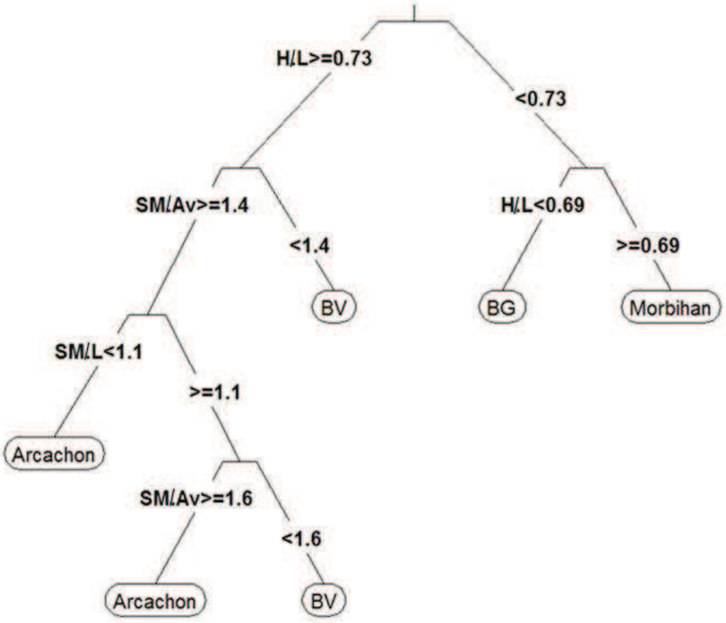

Fig. 4. Plot of the selected classification tree obtained after pruning. Banc du Guer (BG), Morbihan Gulf (Morbihan), Bellevue (BV) and Arcachon Bay (Arcachon).

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

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

3.2. Relationship between environmental conditions and morphometry

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

Once predictors are taken into account, the LMM shows that the three ratios are significantly related to environmental parameters (Table 6). The percentages of between-site intercept variance explained by those predictors are high; they range from 71 % to 88 % depending on ratios. The latter share one common feature: a relationship with trophic condition expressed by Chloro a Med. *SM/Av* displays additional links with temperature descriptors (T20_20) and with Chloro a SD. This last indicator also influences *H/L*. For *H/L*, residuals display a well aligned distribution whereas for the two others ratios, distribution's extremities presents incorrectly adjusted points (Fig. 5).

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

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

	Step 1 – Null model		Step 2 – Final model		
Morphometric ratios	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
H/L	61 %	p-value <.0001***	Chloro a Med Chloro a SD	71 %	p-value = 0.03325 *
SM/Av	27 %	p-value <.0001***	T12_20 Chloro a Med Chloro a SD	88 %	p-value = 0.01651 *
SM/L	27 %	p-value <.0001***	Chloro a Med	85 %	p-value = 0.005284 **

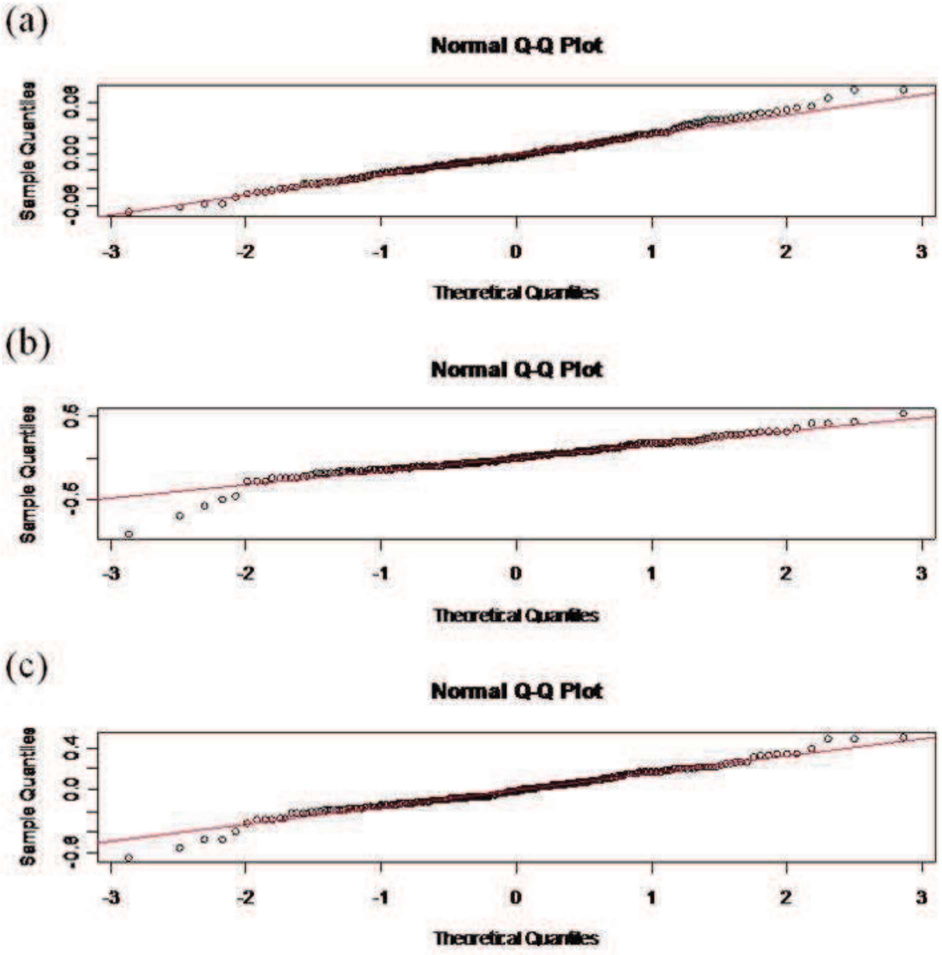

Fig. 5. Normal qqplots regarding the three multilevel linear models respectively built for *H/L* (a), *SM/Av* (b) and *SM/L* (c).

Discussion

Emphasis of a north-south differences regarding morphometric patterns

For the four studied sites, Elongation index appears to be a discriminating criterion (with substantially lower values for Banc du Guer than those obtained for Arcachon and Bellevue). The slender character observed in north Brittany (and to a lesser extent in Morbihan) is in accordance with observations made in north-west of France (Normandy), in Tunisia and in Italy on clams of similar length (respectively by Gérard, 1978; Ben Ouada et al., 1998 and

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

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

Given those results from classical morphometric ratios, complementary approach using contour detection technique might be helpful to consider morphological differences within and between sites. A first implementation of this approach has been conducted on four clams considered as representative of sites. As well as providing illustrations on classical morphometric ratios this technique also seems to reveal different forms of anterior-dorsal valves' margin. On the basis of those preliminary displaying results, it would be interesting to pursue research in this area because prosogyrous shape is known to reflect an adaptation to sediment characteristics for other bivalves' species (Stanley, 1975; Eagar, 1978; Trueman et al., 1966). Rufino et al. (2006) have especially reported the concern to combine various morphometrics approaches (linear, contour analysis and landmarks analysis) on *Chamelea striatula*.

Learning from supervised classification method and reflexions regarding management strategies

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

We can notice that for the sites presenting the highest sample numbers (Arcachon Bay and Bellevue), the interpretation level was much detailed. On the opposite for the sites having smaller sample numbers (Morbihan and Banc du Guer), a loss in the interpretation level occurred. This fact can partly explain that only 55 % of the clams originated from Banc du Guer were correctly classified. In the case of Arcachon which site also displayed a high percentage of incorrectly classified individuals (41 %), we think that this result has to be connected with the spatial morphometric variability recently described by Caill-Milly et al. (2012). Manila clam is characterized by sedentary-life history and aggregated distributions (Kalyagina, 1994). In those conditions, its large spatial extent of the species within the bay (around 46 km², Sanchez et al., 2010) associated with the high morphometric variability should promote spatial regulation at the bay scale. The importance of taking into account spatial dimension into management strategies has been emphasized by Defeo (2003) for sandy beach stocks. A review of successful case studies implying spatial dynamics has also been undertaken by Caddy and Defeo (2003). In practice, such local legislation has been applied in addition to European legislation since 2000 in Arcachon Bay. It concerns protected area surfaces with localizations changing over time. Those protected areas are part of a package of measures designed at a regional scale and implemented in a co-management context. Integration of morphometric considerations based on contour detection techniques might be helpful to reinforce criteria regarding area selection.

An unexpected relationship identified between morphometric characters and trophic conditions

Implementation of LMMs on *H/L*, *SM/Av* and *SM/L* revealed significant relationships with chlorophyll a concentrations and in one case with seawater temperature comprised between 12 and 20°C. As an indicator of valve's density regarding ventral area, *SM/Av* is thus negatively linked with the optimum range of temperature known to intervene on Manila clam's growth (Maître-Allain, 1982). Those results are consistent with shell's hypostracum growth. This inner layer of the valves has been demonstrated to be positively influenced by the maximum seawater temperature and negatively influenced by pressure (Olson et al., 2012). This would suggest that in our case the more the temperature remains within the optimum range for growth, the less the formation of this inner layer is enhanced.

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

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

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

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

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

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

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

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

Several authors established that morphometric characteristics could reveal more or less favorable environmental conditions (Hamai, 1935; Ohba, 1959; Eagar et al., 1984) with, in particular for Manila clam, the demonstration that morphological characters can be used as proxy of nutritional condition (Watanabe and Katayama, 2010). In those conditions, we tend to believe that the observed differences of shape respond to a combination of those four hypotheses with varying degrees depending on sites. Those elements highlighted the complexity of the factors involved in the shell characteristics. Superimpositions of several factors and high difficulties to separate them have already been reported by Orensanz et al. (1991).

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

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

Conclusion

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

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

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

Acknowledgement

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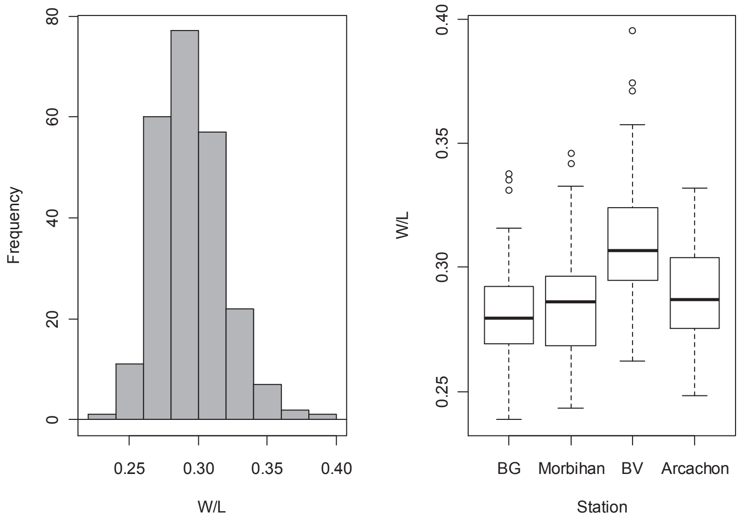
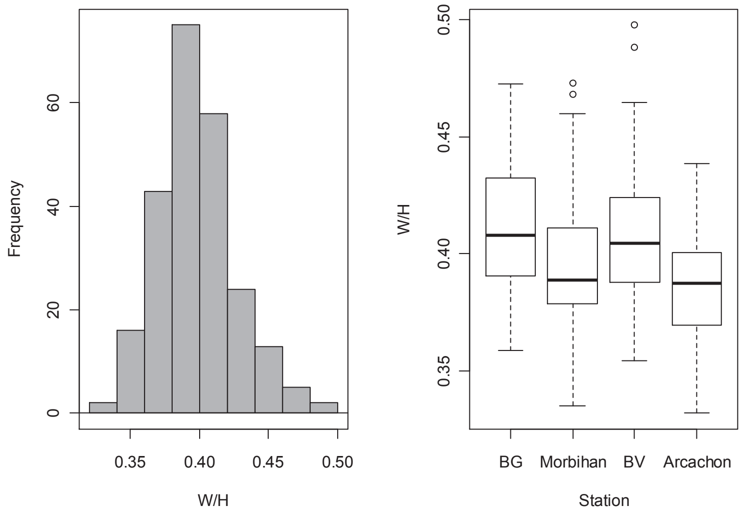
All authors declare no conflicts of interest.

Appendix



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



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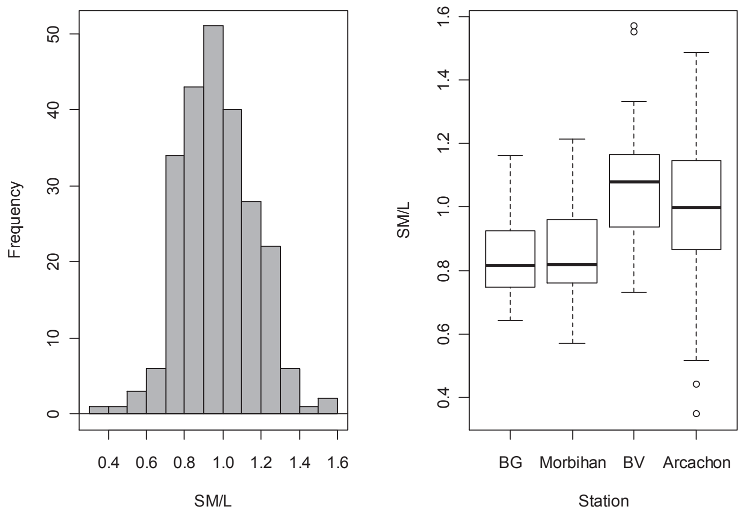

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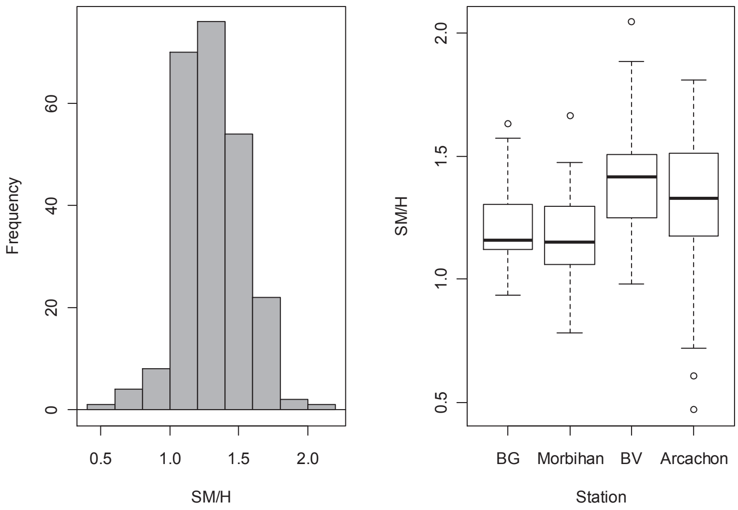

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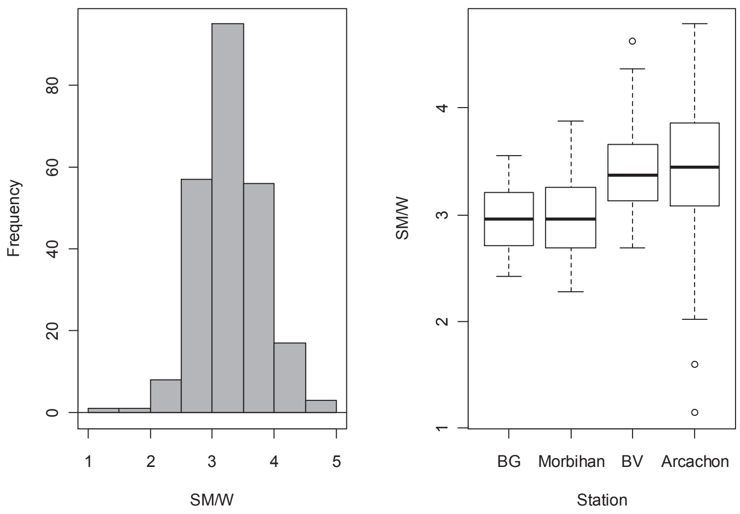

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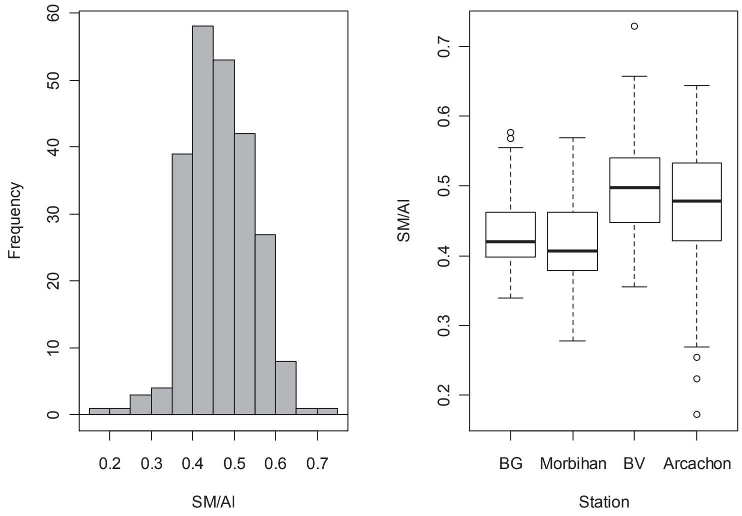
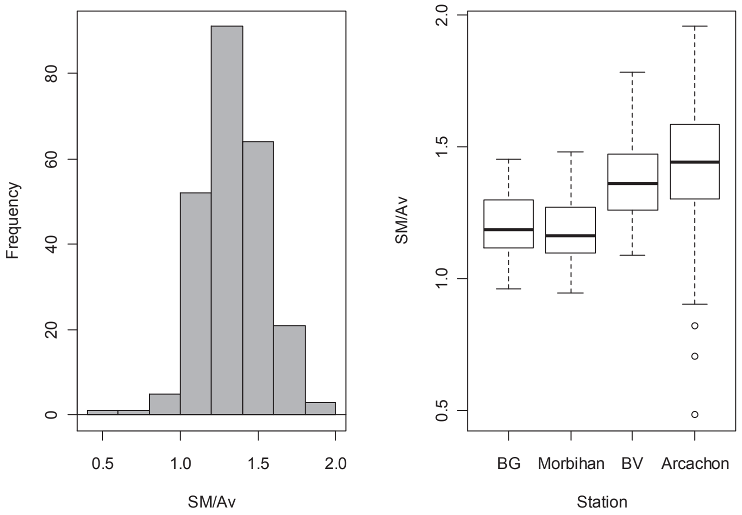


SM/Al frequency distribution for the entire dataset and box plot according to factor site.



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

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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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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Abstract:

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

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

Introduction

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

Upon professional fishermen request and in order to find equilibrium between exploitation and conservation of this aquatic biological resource, a long-term monitoring programme was launched in 2000 to identify important issues in terms of management decisions. The main component of this programme aims at assessing clam biomass through standardized indicators (Bertignac *et al.*, 2001; Caill-Milly *et al.*, 2003, 2006, 2008; Sanchez *et al.*, 2010) and developing a specific management model under the software Vensim ® (Bald *et al.*, 2009; Dang, 2009). This modelling approach belongs to simulation modelling category, built from the dynamic systems (DS) paradigm developed in the 1950s by Forrester (1973). Within the conceptual sub-category, the structure of this model describes the mechanistic relationships among abiotic, biotic, and anthropogenic ecosystem components. The classification of the elements involved in the system relies on determination of the "stocks" (*sensu* Vensim terminology *i.e.* describing the elements in the system e.g. clams, fishermen,…), the "flows" between these stocks (natural mortality/month, quantity of clams passing from a class to another, those elements are defined by time functions) and information that determines the value of the flows (auxiliary variables). The model developed for Manila clam has been constructed with a monthly time step; simulations cover a 10 years period. Specifically intended to address long-term issues, its main objective is to develop a decision tool when different management options exist, based on a modeling principle similar to the one used by Ortiz *et al.* (2002) on Peruvian scallop. It also brings a better understanding of the structural causes impacting the behavior of the system under study.

Up to now, the model is built at the global basin scale and one variable having a potential effect on the biological functions is taken into account, namely the temperature. This factor is indeed considered as the key environmental variable because it regulates not only both **growth** and **survival** of *Ruditapes philippinarum* (Mann, 1979; Bernard, 1983; Goulletquer *et al.*, 1989 in Melià *et al.*, 2004) but also its reproductive behavior (Delgado *et al.*, 2007). In the current version of the model developed for Arcachon Bay by Bald *et al.* (2009), the factor temperature is integrated for its effect on the **reproduction** function (*i.e.* during the **spawning** period or phase). Yet, recent works (on this species or performed to the related species *Ruditapes decussatus*) have underlined that this phase, along with others, can also be influenced by additional factors such as hydrodynamic regime, sediment type, food supply, oxygen (Breber, 1980; Rodriguez-Morosco *et al.*, 1992; Urrutia *et al.*, 1999).

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

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

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

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

Considering now the **growth** function, numerous authors agree with the main role played by the temperature on *Ruditapes species* (Laing *et al.*, 1987; Toba, 1987 in Nakamura *et al.*, 2002; Beiras *et al.*, 1994; Fan *et al.*, 2007). A pattern of growth has even specifically been presented by Maître-Allain (1982) for Manila clam; it stated that no growth occurred under 6°C and that an optimal growth was expected between 12 and 20°C for this species in Thau lagoon. For the Jiaozhou Bay (China), the most suitable range of temperature for shell growth was ascertained between 18 and 23°C (Fan *et al.*, 2007). Nevertheless, numerous studies established also the role of other factors. For example, Yamamoto *et al.* (1956) demonstrated that the growth rate of *Ruditapes philippinarum* in Akkeshi Lake (Japan) was intimately related to the sea temperature and the abundance of plankton. Later on in the lagoon of Thau (France), Maître-Allain (1982) comforted those results by highlighting the link between the increase of the growth rate and the quantity of chlorophyll a, at least up to a threshold. Goulletquer *et al.* (1987) established that the duration of immersion has also a significant effect, at least under ground culture conditions in the Bay of Marenne-Oléron (France).

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

Using a 10 year dataset and complementary multivariate approaches, this paper presents the pathway applied to select few environmental parameters (with temporal lag) of main interest to explain the variability of the stock (data from field campaigns) across the period. With those elements, our study will also allow to address whether more physical or biological factors of physiological relevance (known for their effect on reproduction, growth…as explained above) should be integrated in the model of simulation. Temperature is already integrated in the model only for its effect on reproduction function. To test the relevance of additional effects, we consider temperature conditions during specific periods selected for their importance on the Manila clam life cycle.

Methods

2.1. Study site

Arcachon Bay is a 156 km² semi-sheltered lagoon in the southwest coast of France (Fig. 1). The inner lagoon is composed by 110 km² of tidal flats (mesotidal system) with a sediment composition ranging from mud to muddy sands and colonized by vast *Zoltera noltii* seagrass meadows. The tide is semi-diurnal and the bay is both influenced by oceanic (external neritic waters) and continental (principally from the Eyre River) inputs (Dang, 2009). The characteristics of these water masses as well as the slow renewal of water by tides (Plus *et al.*, 2006) induce salinity and temperature gradients within the bay (Bouchet, 1968).

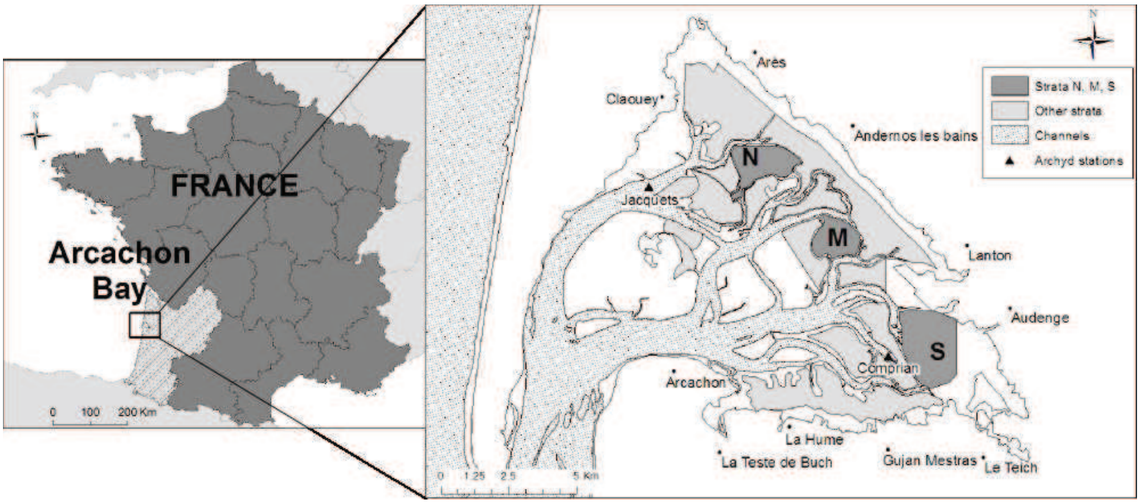

Fig. 1. Study area, selected strata and Archyd stations locations.

2.2. Population descriptors

Concerning the stock status, the present work is based on data collected during late spring field campaigns performed every two or three years in the Arcachon Bassin since the year 2000 (Bertignac *et al.*, 2001; Caill-Milly *et al.*, 2003, 2006, 2008; Sanchez *et al.*, 2010). The sampling gear is a Hamon grab which collects a sediment core of 0.25 m² (0.5 m * 0.5 m) on a 0.2 m depth at the ebb tide. Recommended tool for sampling the benthic macro-infauna from coarse substrata, it is particularly well adapted for the Manila clam, which is usually buried at around 2-5 cm deep depending on their size and with a maximum depth around 10-12 cm when temperature is very low (Le Treut, 1986). The core samples were filtered onboard with running water over a set of three sieves with 2, 1 and 0.5 cm mesh size. All specimens of Veneridae were sorted, identified, counted and measured to the nearest 1 mm using a slide calliper. Apart for year 2000 when each clam was weighted, the other individual weights were estimated using the relation between weight and length determined by Caill-Milly *et al.* (2003) for Arcachon Bay. These campaigns were carried out following a standardized protocol (stratified random sampling) with 16 strata investigated according to a sampling effort of 10 stations per km². Among those, 3 strata (noted N for North, M for Middle and S for South) were selected because on one hand they have been investigated since year 2000 and on the other hand they present different localisations inside the Bay.

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

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^2	Dens_Nb
Density in weight	Average density expressed in weight of Manila clams per m^2	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 *Ruditapes philippinarum*, *Ruditapes decussatus* and *Venerupis aureus* (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

2.3. Environmental parameters

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

Given that the studied population is mainly composed of clams aged from 1 to 3 years old, it was decided to consider these parameters for the 3 years preceding the population descriptors measurements at the year t (*i.e.* year 2000, 2003, 2006, 2008 or 2010). Since the campaigns providing the population descriptors occurred in June for the year t, we look at the environmental conditions prevailing during the last twelve months (*i.e.* from June t-1 to May t). Because temperature is already integrated in the model, more specific temporal aggregations were also considered for this parameter in order to focus on reproduction, growth and mortality potential effects. Those temporal lags are considered on environmental variables to interact with biological phenomena considered as indirect effects and often appearing on a local scale (Wiens, 1989). According to the forecasted effects related to the biological functions described in the introduction, 13 variables were retained; they represent physical environment and food supply conditions (Table 2).

2.4. Multivariate analyses

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

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

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

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

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

Factors	**Variables or built indicators**	**Forecast biological functions influenced**	**Codifications**
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

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
Phytoplancton (assessed by Chloro A)	Quantity of phytoplancton 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 phytoplancton 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

2.4.1. Characterizing the population

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

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

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

To complete the above analyses, two Regularized Canonical Correlation Analyses (RCANCOR1 and RCANCOR2) were applied to the whole stock descriptors (as first set) and respectively to physical environment and trophic conditions (as second set) using the CCA package on R (Gonzalez *et al.*, 2008). The squared canonical correlation measures the proportion of variance of a canonical variate explained by the original variables.

Results

3.1. Synthetic description of the stock

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

To summarize those results about the stock status, the variables integrating the higher part of the variability of the collected data are first those related to the larger clams (Perc35_Nb and Perc35_Wg) and secondly the variable characterizing the proportion of juveniles (Perc17_Nb).

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			

3.2. Correlation between physical factors, food supply and stock

Physical conditions (Fig. 2 and 3)

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

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

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

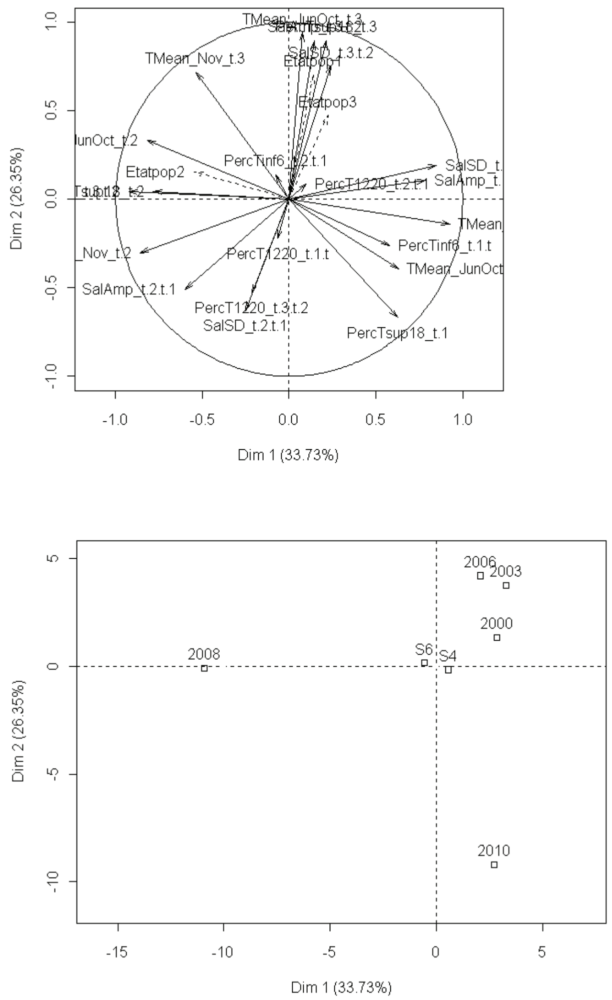

Fig. 2. NPCA2 on physical conditions (plot individuals and variables graphs).

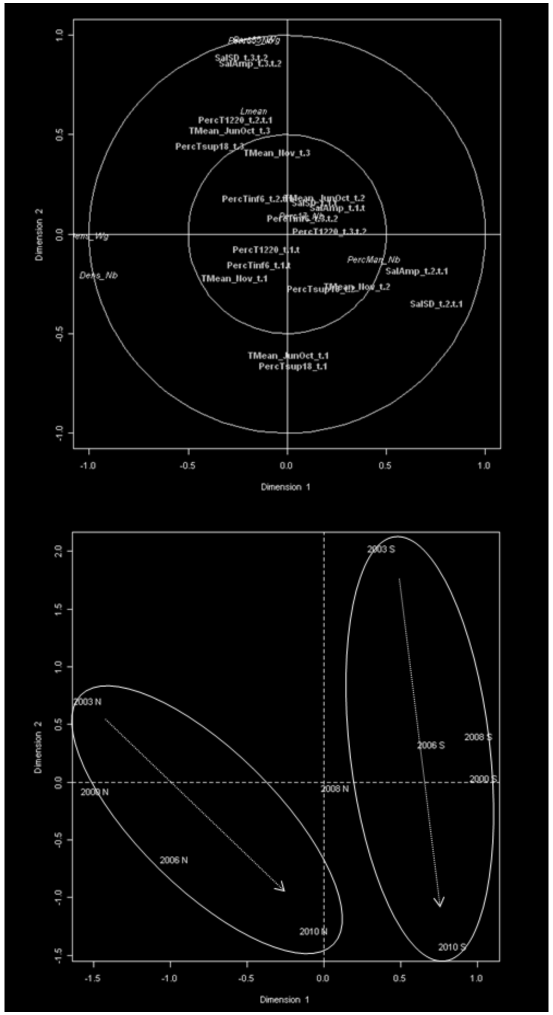

Fig. 3. Variables and units representations on the plane defined by the first two canonical variates of the RCANCOR1 on physical conditions.

Food supply (Fig. 4 and 5)

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

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

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

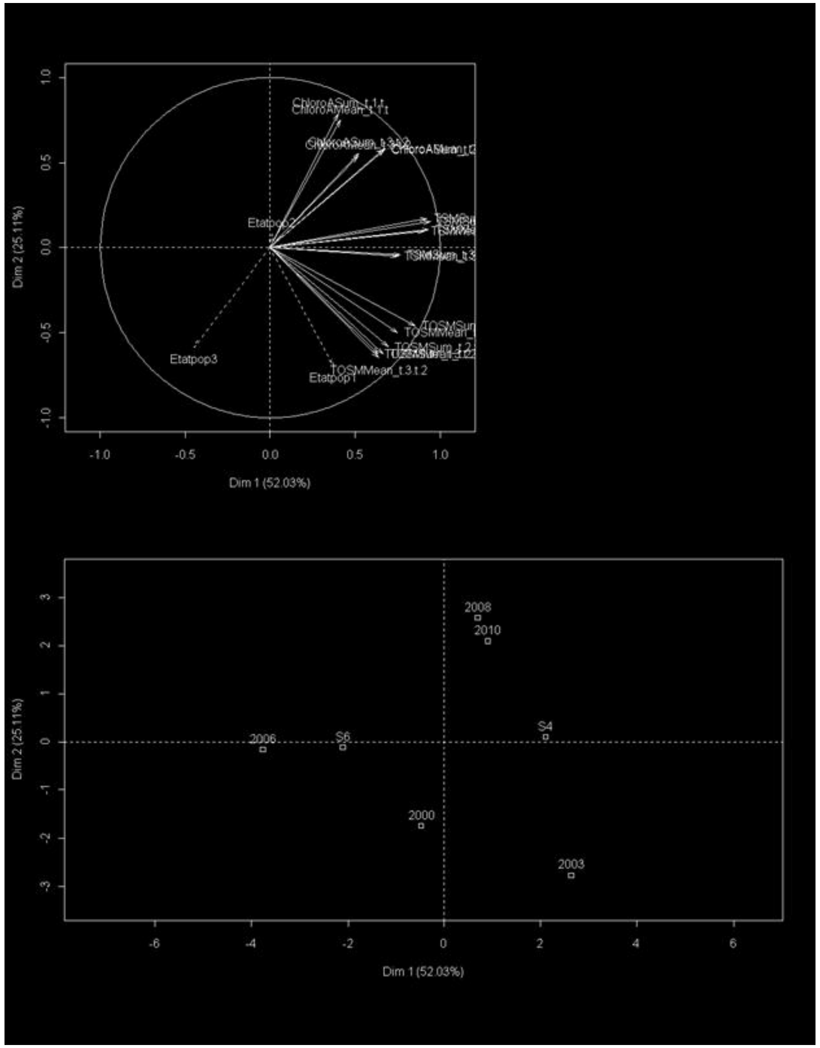

Fig. 4. NPCA3 on trophic conditions (plot individuals and variables graphs).

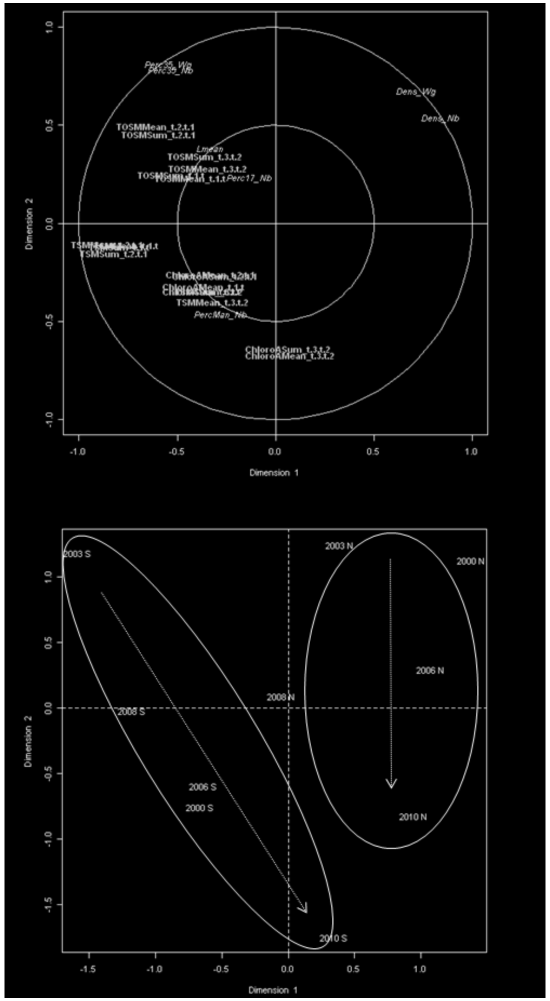

Fig. 5. Variables and units representations on the plane defined by the first two canonical variates of the RCANCOR2 on trophic conditions.

Discussion

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

NPCA were applied on the overall data set mixing environmental variables (respectively for physical environment and trophic conditions) and population characteristics where each statistical unit is a data for one year and one experimental site. Considering separately spatial and temporal information, one can obtain two factors which can be put as supplementary factors in the PCA. These analyses show the correlations between the initial variables and characterize each year and site according to those variables. In addition, each RCANCOR gives one optimal combination of environmental variables and one optimal combination of population parameters in the sense that both are correlated. The statistical units are expressed as spatio-temporal and can then be discussed in two ways: environmental conditions and population characteristics.

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

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

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

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

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

Focusing on the different stock descriptors, the obtained correlations are different considering the sizes of the clams since high relative abundance of large clams are concomitant to low chlorophyll a and high TSOM indicators whereas high proportion of juveniles are related to high chlorophyll a and low TSM values. Those differences can first illustrate qualitative differences in the type of food assimilated by the clams related to their size (*i.e.* a hypothesis of a trophic sources diversification between the young on one hand and the clams older than a year on the other hand). Considerations about the diversity of the Manila clam diet have already been discussed above and much of the feeding items have been demonstrated to come from the POM (Kharlamenko *et al.*, 2001). In the same time, larvae stages are known for consuming diatoms as well as dinoflagellates (Loosanof *et al.*, 1963; Le Treut, 1986). Similarly, our results are consistent with those obtained by Sobral and Widdows (2000) (*i.e.* a lowering of the trophic performances for the related species *Ruditapes decussatus* under high TSM) since the TSM values are must lower for Arcachon Bay. A second hypothesis is related to a possible effect of the TSM going beyond the nutrition function. Since Total Suspended Matter is comprised of sediments, dead or decaying plant and animals parts and still living particles, we can supposed that it can influence clam's gills and/or velum for younger stages. This last disturbance on the larval swimming activity could have happened in our case; such effect of TSM has already been pointed out on Manila clam by Le Treut (1986). A positive or negative effect of inorganic particles in the suspended matter was also reported for mollusks in general by Deslous-Paoli (1987), depending on the concentration and type of mineral composition.

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

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

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

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

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

Spatial-temporal considerations

For Arcachon Bay, a seasonal rhythm and a spatial discretization between the North and the South for the trophic sources was demonstrated by Dang *et al.* (2009). The method we used cannot provide information on temporal variability except annual tendencies for each variable but reveals levels of indicators related to TSM higher in the Southern site than in the Northern one. Relation between environmental conditions and strata is also observed for variation of salinity level. These differences can be related to the freshwater inputs from the Eyre River and/or to a lower renewal of the water mass in the South-East part of the Bay (occurs under North or Western wind conditions as simulated by Plus *et al.*, 2006). However, those relations remain limited in comparison with temporal effects and militate in favor of a homogenization of the environmental studied conditions within the bay. For the rest and from year to year, the temporal pattern is characterized by temperature increase prevailing during the different phases of the reproduction and to a lesser extent, by the augmentation of the chlorophyll a indicators.

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

Consequences on the current model

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

Concerning environmental conditions, temperature is integrated in the model for its effect on the reproduction function (*i.e.* during the spawning period or phase). Our results confirm the importance of this factor especially during the reproduction phase. As the current model already integrates this process, it does not seem necessary to modify the model for this parameter.

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

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

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

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

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

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

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

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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 partie-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 démonter 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 approfondier 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 influer 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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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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Abstract

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

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

Taking into account those new improvements, simulations were firstly conducted from July 2003 and December 2008. For this historical modelization, the model outputs fit well with the real data since the deviation percentages between observed and predicted data met the criterion set to 10%. Then, seven selected management strategies regarding only local regulatory authorities were modeled and forecasts of their impacts on the total biomass were considered from January 2009 to December 2017. A collapse of the stock is predicted if the management alternatives applied in 2008 were maintained. Relevance of combined selected management measures was highlighted to achieve a recovery of the stock. Within the framework of working groups (associating scientists, fishermen and administration representatives), those simulations were presented, discussed and the stakeholders chose to apply from 2008/2009: reduction of the licenses fishing number (two outgoing licenses for one incoming license); protected areas; prohibition to fish one day per week. Those management scenarios were also completed by three additional scenarios to consider potential effects of environmental or market modifications to the stock evolution.

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

Keywords: system dynamic model, co-management, population dynamic, Arcachon Bay, *Venerupis philippinarum*

1. Introduction

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

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

For population dynamics model, several authors (De Leo and Gatto, 2000; Solidoro et al., 2003) have underlined the importance of length class differentiation to take into account differences in vital rates such as fertility, mortality, and respiration (Flye-Sainte-Marie et al., 2007). So in the Stock/Maturation/Mortality block, the Manila clam population in Arcachon Bay is divided into sub-populations according to length classes. Four classes are applied corresponding to: juvenile size class (from 0 to 20 mm); adult under the minimum current harvest size class (from 21 to 34 mm) and two adult size classes above the minimum current harvest size (from 35 to 39 mm and upper 40 mm).The evolution over time of the number of clams in each class is controlled by specific growth, natural and fishing mortalities parameters.

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

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

This paper proposes new improvements of the model developed for Manila clam in Arcachon Bay. Such developments are in accordance with the four main uses of a model reminded by del Granado (2007) namely: increasing the human understanding of the considered system; communicating visually, making prediction and supporting decision-making (Felleman, 1999; Hannon and Ruth, 1994; Shenk and Franklin, 2001).

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

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

2. Material and methods

2. 1. Study site

Arcachon Bay is a 156 km² semi-sheltered lagoon in the southwest coast of France (Fig. 1). Mostly composed of intertidal flats (110 km² within the inner lagoon which are colonized by a vast *Zoltera noltii* seagrass meadows), the composition of this mesotidal system ranges from mud to muddy sands. The tide is semi-diurnal and the bay is both influenced by oceanic (external neritic waters) and continental (principally from the Eyre River) inputs (Dang, 2009). The characteristics of these water masses as well as the slow renewal of water by tides (Plus et al., 2006) both influence salinity and temperature within the bay. Variations of those two parameters are important when considering indicators computed over the last ten years (source Archyd network): seawater temperature ranges from 1.8 to 27.4°C (mean value 15.4°C); salinity ranges from 15.4 to 35.4 (mean value 30.2). As trophic indicators, chlorophyll a concentration varies from 0.4 to 30.8 μgl^{-1} (mean value 2.6 μgl^{-1}).

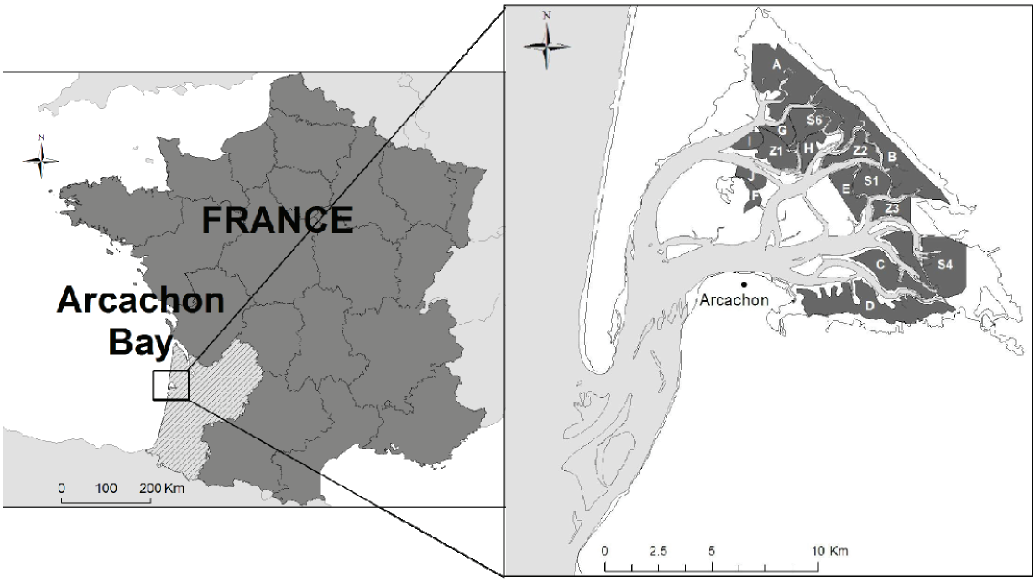


Fig. 1. Maps showing the studied site Arcachon Bay (France) (Sources: ESRI, BD Carthage, Ifremer – M. Lissardy).

2.2. Species description

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

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

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

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

2.3. Fishing activity and its management

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

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

2.4. Recent improvement of the model formulation

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

2.4.1. Integration of newly and specific available life traits data

- Recruitment (Production block)

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

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

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

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

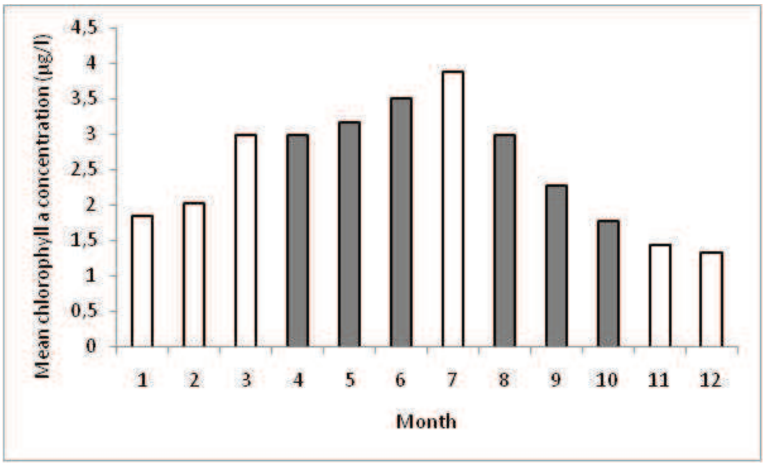


Fig. 2. Mean chlorophyll a concentrations along the year (in gray: spawning periods).

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

- Growth (Stock/Maturation/Mortality)

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

- Natural mortality (Stock/Maturation/Mortality)

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

2.4.2. Adjustment of the fishing activity and its control parameters

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

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

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

$$Fi = NFL \times CVL \times FEi \times 10^6 \times (ABS\text{-}PAS) / (MWi \times ABS)$$

with NFL= Number of Fishing Licenses, CVL = Catches Volume per fishing License each month, FEi = Fishing Effort for class i, ABS = Arcachon Bay Surface, PAS = Protected Area Surface, MWi = Mean Weight for class i. This parameter Fi takes different values along the year according to the beginning (OFM = Open Fishing Month) and the duration of the fishing period (CDS= Capture Duration Season). Units are given in Table A.1.

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

2.5. Calibration, validation and sensitivity of the model

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

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

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

This "historical" modelization ends in December 2008. It traces the stock evolution before testing new management strategies.

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

To assess the sensitivity of the model, uncertainty of three key parameters (natural mortality, recruitment and spawning maximum temperature) were considered. They were chosen for two reasons: a high inter-annual variability and a non-consensus precise threshold of temperature on spawning. Chlorophyll a concentration was not taken into account in this sensitivity analysis. Each parameter is studied separately to test the variability of the estimated biomass using thousand Monte Carlo simulations (Multivariate Sensitivity Analysis) with a random uniform distribution of probability.

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

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

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^{-2})	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

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

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

2.6. Simulations of several management strategies

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

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

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

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

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

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

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

Key: NFL= number of fishing licenses, CVL = catches volume by license (t month^{-1} license^{-1}), CSD = capture season duration (month), PAS = Protected area surface (m^2), ABS = Arcachon Bay Surface (m^2).

	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	↗	↗↗	=	↗	=	=

2.7. Simulations of environmental and market modifications

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

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

3. Results

3.1. Goodness of fit of the model

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

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

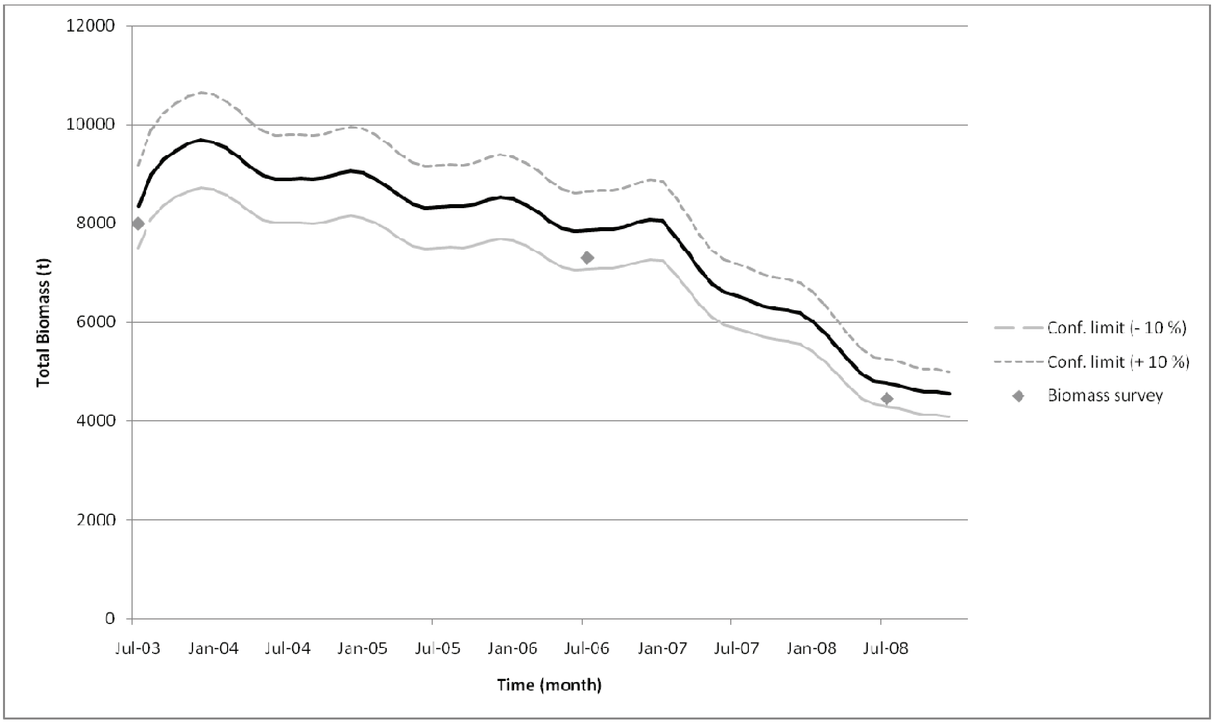


Fig. 3. Total biomass (t) simulated between July 2003 and December 2008 (“historical” modelization).

3.2. Forecasts according to management scenarios

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

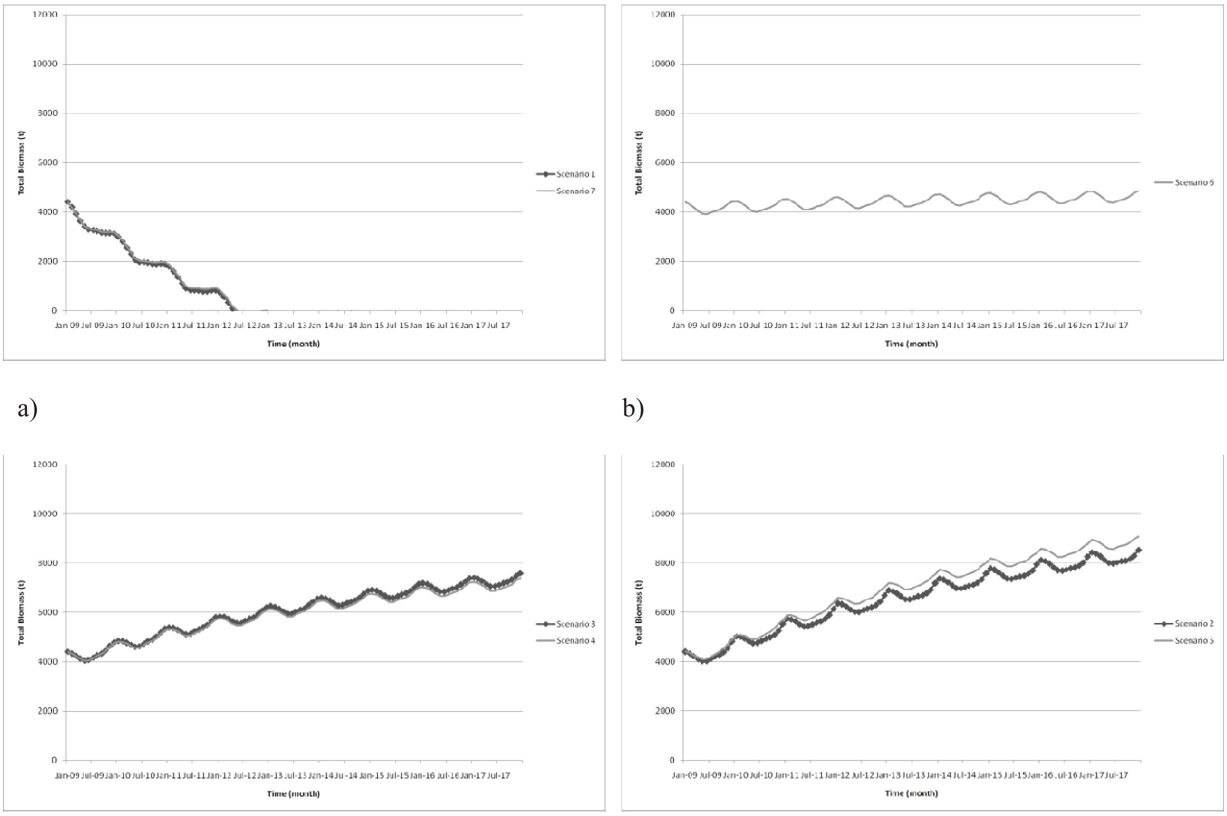
- a first category corresponding to Scenario 1 (status quo) and Scenario 7 is the collapse of the clam stock in less than four years (mid 2012);
- a second category, obtained with Scenario 6 leads to a stabilization of the stock at 2008 level (around 4,500 tons);
- a third category is achieved by Scenario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

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

3.3. Forecasts according to environmental and market modifications

For the three simulations of environmental and market modifications (applied in addition to status quo management measures), the total biomass exhibits a collapse in less than five years after their introduction (Fig. 5). Scenario 9 (temperature modifications) and Scenario 10 (price effect) display the sharpest declines with values close to those of Scenario 1 (Status quo). Whereas temperature is one of the key parameters expected to be affected by climate change, the consequences of its slight increase over 9 years does not cause, owing to its effect on the spawning phase, noticeable impact on the stock.

Concerning trophic resources, an increase of 40% of the mean chlorophyll a concentrations over 3 years enables to defer the decrease of the total biomass but leads to a collapse in 2014.



a) b)

c) d)

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

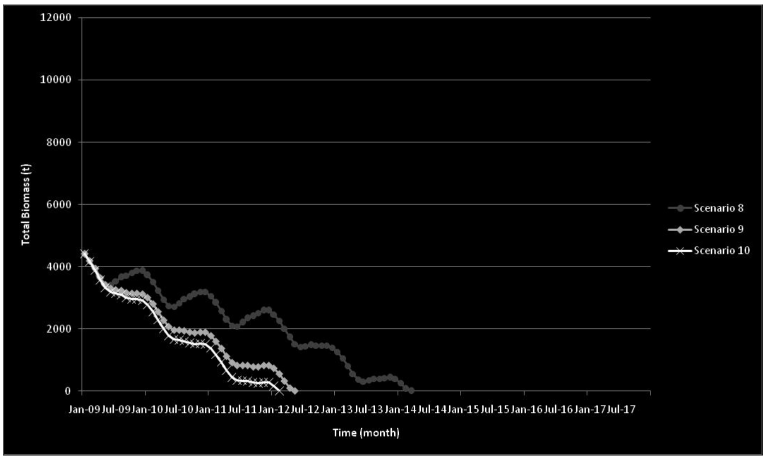


Fig.5. Total biomass (t) forecasts obtained for Scenario 8 to 10 between January 2009 and December 2017.

3.4. Model sensitivity

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

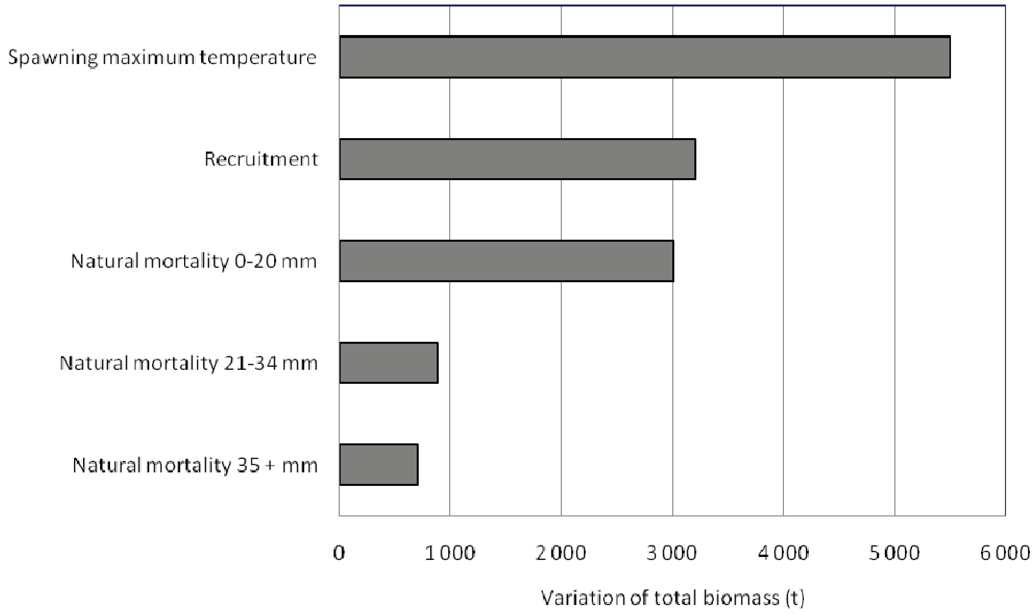


Fig. 6. Differences between the maximum and the minimum values of the total estimated biomass for parameters “natural mortality”, “recruitment” and “spawning maximum temperature” resulting of Monte Carlo simulations.

4. Discussion

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

Integration of specific available life traits data

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

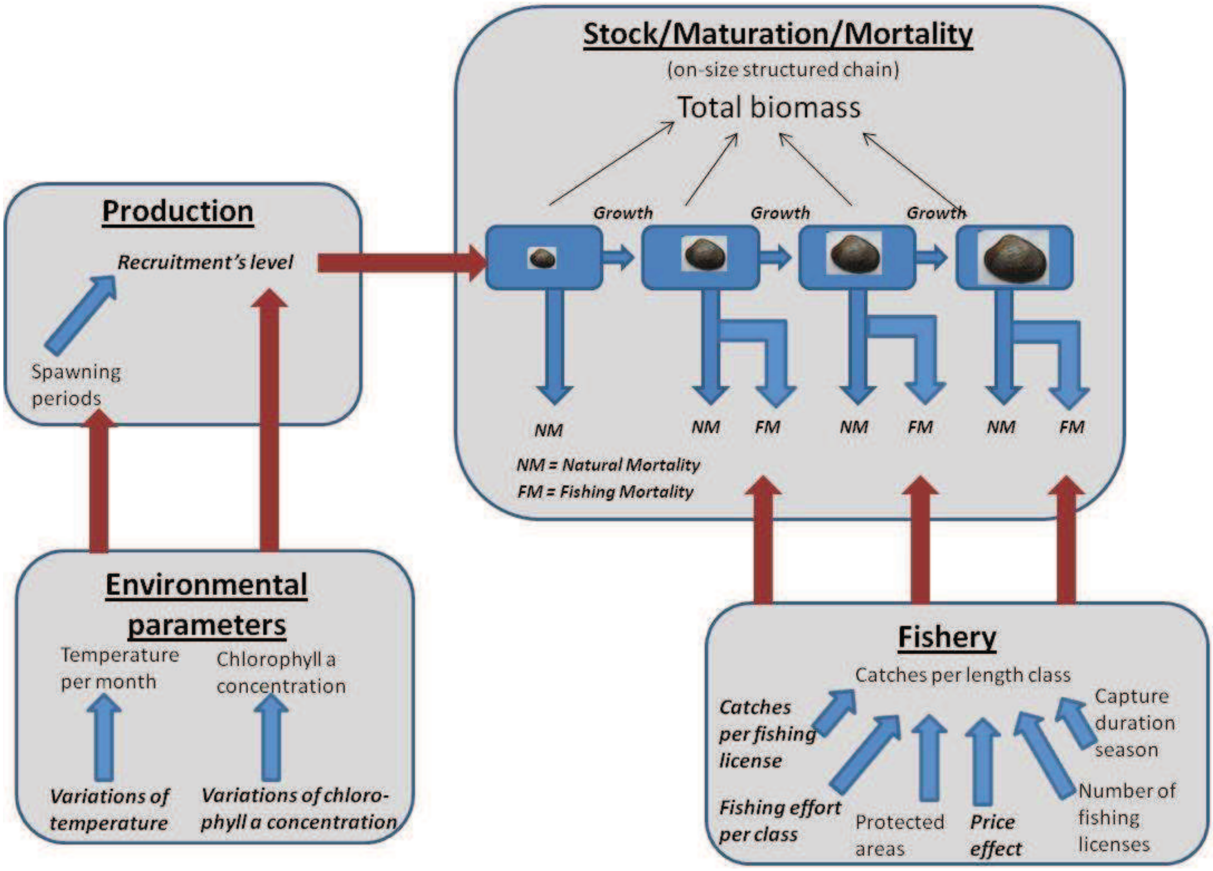


Fig. 7. Scheme of the current Manila clam model illustrating recent improvements (in italic bold) regarding blocks and interactions among blocks.

First of all, environmental drivers on key processes of the population dynamics have been reinforced thanks to new formulations. This evolution mainly concerns the reproduction phase. Until now this phase, which is one of the key processes of population dynamics (Flye-Saint-Marie, 2007) was only controlled by seawater temperature. A preliminary modulation depending on food availability expressed by chlorophyll a levels has been undertaken; such relation needs to be more precisely established. Nevertheless this measurement of photosynthetic pigment water concentration remains relatively easy to acquire and appears to be the most common indicator used for food availability (*e.g.* Shibata et al., 1999). Unlike the older stages (Flye-Sainte-Marie et al., 2003), we have not identified any works questioning the validity of this descriptor as an adequate substitute for food availability in young Manila clams. In those conditions, this formulation corresponds to a more realistic hypothesis since the two modelized environmental parameters (temperature and food supply) are wellknown for influencing the reproductive phase (Delgado et al., 2007; Devauchelle, 1990; Holland and Chew, 1974; Le Pennec and Benninger, 2000; Mann, 1979; Ohba, 1959; Soudant et al., 2004; Toba and Miyama, 1995).

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

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

Considering those changes to the original formulation of the model, we consider that future improvements could mainly concern the question of linkage between the stock and the recruitment. The current biomass surveys led every two years indicate high variability of the recruitment levels at the bay scale (Sanchez et al., 2010) that is in concordance with recent works undertaken by Tezuka et al. (2012). Nevertheless, they do not allow validating of any intraspecific stock/recruitment relation for the investigated population. To identify this relationship for coastal species, Freire and García-Allut (2000) reported the importance of scale considerations or the occurrence of low stock levels to be detected. Moreover, processes involved are complicated because a stronger effect of interspecific stock-recruitment relationship can also occur as was demonstrated for *Donax hanleyanus* by Defeo (1998). In the absence of any evidence, we assess that recruitment fluctuations in response to environmental parameters are much stronger than those linked to density-dependent mechanisms (intra and interspecific). If this hypothesis would be revised, the model structure would allow, for example, considering fertility rates according to size classes since reproductive effort and fecundity are age-related (Gosling, 2003). For the lagoon of Venice, Solidoro et al. (2003) considered that each parental class (minimum length required 18 mm) allows the successful implantation of one hundred juveniles. For Arcachon Bay, a first approach could be undertaken by using the age-related gonadal production established by Urrutia et al. (1999) for *Venerupis decussatus*.

Adjustment of the realized fishing activity and its control parameters

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

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

Performance of the model, sensitivity and used framework

The adequacy of the model to reality was considered by using the acceptable limit of deviation percentage between observed and predicted data sets (Bald et al., 2006, 2009; Borja and Bald, 2000). This methodology was retained because very few datasets were available. As soon as additional datasets are acquired, it would be worth considering the model performance with new indices of performance, such as those implemented by Anastácio et al. (2009) for *Scrobicularia plana*. In particular, the implementation of the Loague and Green's modeling efficiency (EF) would provide an overall indication of the goodness of fit (Mayer and Butler, 1993).

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

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

Towards a co-management approach for this local exploited stock

From the beginning, the model is specifically intended to strengthen the management process by making more complete and more defensible decisions. After the integration of available ecological and fishing data in the model, this tool was thus used for the first time for management purposes in 2008-2009. The simulations were presented and discussed in the framework of working groups (associating scientists, fishermen and administration representatives). The choice of a management strategy involving several management measures (preferred to one strong measure modification) has emerged. Its concerns: reduction of the number of fishing licenses (one input for two outputs); choice of two complementary protected area zones; prohibition to fish on Sundays. Concerning protected area zones, professional retain smaller total surface but chose areas with relative high potential of reproduction assessed by using a 2D hydrologic model. Fig. 8 displays the forecast of the expected total biomass with the retained management measures. It presents a slower decline of the biomass compared to status quo; a reevaluation of the situation and the necessary measures will be conducted in 2012. Whereas the first measure is directly managed by professional organizations, the two others resulted in administrative decisions also enforceable for recreational fishermen.

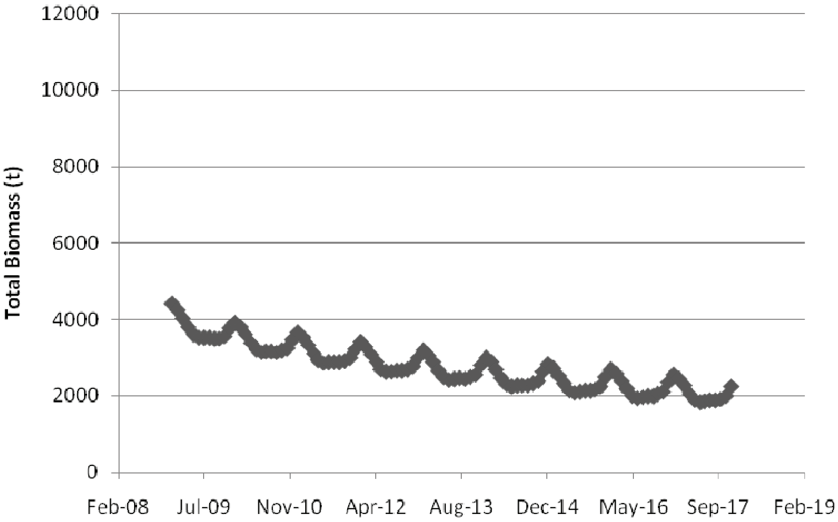


Fig. 8. Total biomass (t) forecast with the management measures chosen by the fishermen.

Similar approaches based on models are conducted *inter alia* on gooseneck barnacle (Bald et al., 2006); Peruvian scallop (Ortiz et al., 2002). In our case its implementation completes the existing collaborations between scientists and fishermen since the field surveys have been conducted by those two entities since 2003. This type of functioning is in line with orientations of the Oregon's Development Fisheries Program (see Harte et al., 2008) because it aims at incorporating design of science and management plans for small-scale fisheries. Integration of different kinds of operational management measures and institutional structures for governance was highlighted by Defeo (2011) as a key issue of successful management of sandy beach fisheries. This approach is wished-for in the case of coastal Galician fisheries (Freire and García-Allut, 2000; Freire et al., 2002); it has been already applied in Southeast Asia coastal fisheries since the 1960s (Pomeroy, 1995).

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

The current parameter shared by the stakeholders and used to compare the different management strategies essentially rests on the total biomass evolution. In order to improve the functioning of this collaborative framework, we expect to encompass at the same time ecological and socio-economic valuations of the measures impact as proposed by Eliott (2012). Socio-objectives are generally poorly defined; a price-effect has been recently integrated in the model to enrich it and to take into account human behavior. Such relation needs to be more precisely established as well as the relation between biomass availability, effort and profitability of the fishery. For example, it would be interesting to introduce modification of CVL level in response to strong decrease of total biomass. Nevertheless this cognitive approach will be likely to be used for reevaluation of the management decision at the end of 2012 once the last biomass survey will have provided an update estimate of the monitored indicators. As well, a reflection on desired breakdown of the licenses between full time and part time activities could be set. They will facilitate communication and management decisions at regional scale as long as they are shared by the different involved entities.

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Appendix

Table Appendix 1: equations' formulation for the modelized 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^{-2} month^{-1})	JP: juveniles production per surface unit and per month (ind m^{-2} month^{-1}) M1: effective per surface unit of the ith class length having died (ind m^{-2} month^{-1}) G2: effective per surface unit of the ith length class having grown to achieve the next length class (ind m^{-2} month^{-1})
	Temporal clam effective evolution per surface unit for a generic ith length class	$LCi = Gi\text{-}1 - Mi - Gi{+}1$ ind m^{-2} month^{-1}	Gi-1: effective per surface unit of the previous length class having grown to achieve the ith class (ind m^{-2} month^{-1}) Mi: effective per surface unit of the ith class length having died (ind m^{-2} month^{-1}) Gi+1: effective per surface unit of the ith length class having grown to achieve the next length class (ind m^{-2} month^{-1})
	Temporal transfert due to growth process of individuals from length class i to length class i+1per surface unit	$Gi = LCi \times GRi$ (ind m^{-2} month^{-1})	GRi: growth rate of the ith length class (dimensionless)
	Temporal stock evolution at the bay scale for a generic ith length class	$SCi = LCi \times MWi \times ABS / 10^6$ (t month^{-1})	MWi: mean weight of the ith length class (g) ABS: Arcachon Bay Surface (m^2)
	Temporal mortality evolution per surface unit for a generic ith length class	$Mi = Zi + Fi$ (ind m^{-2} month^{-1})	Zi: natural mortality of the ith length class (ind m^{-2} month^{-1}) Fi: fishing mortality of the ith length class (ind m^{-2} month^{-1})
	Temporal natural mortality evolution per surface unit for a generic ith length class	$Zi = \exp(a + c \times Li + d \times T + e \times Di)$ (ind m^{-2} month^{-1})	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 ith length class (mm) T: sea water temperature at instant t (°C) Di: density of the ith length class (ind m-^{2})

	Quantity of clams (of all sizes) into the overall bay	Stock = ∑SCi x MWi x ABS/ 10^6 (t)	Variables already presented above
Temperature	Temperature at instant t	T = f x sin(((2 x π)/365) x (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 (Tsmin<T<Tsmax, 1, 0) (dimensionless)	T: temperature (°C) Tsmin: minimum temperature for spawning (°C) Tsmax: maximum temperature for spawning (°C)
	Juveniles production per surface unit and per month	JP = JPm x SP (ind m^{-2} $month^{-1}$)	JPm: juvenile production per spawning month (ind m^{-2} $month^{-1}$)
Fishery	Temporal fishing catches evolution expressed in effective per surface unit for the i^{th} length class	Fi = LCi x FEi x CDS (ind m^{-2} $month^{-1}$)	FEi: fishing effort expressed in percentage of the total fishing effort all length class considered applied to the i^{th} length class (%) CDS: capture duration season (month)
	Total fishing catches expressed in volume	TFC = ∑ Fi x PEE x (1-(PAS/ABS)/100) (t)	PEE: ratio of the total catches related to the total exploitable stock (dimensionless) PAS: Protected area surface (m²)

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^{-2} $month^{-1}$)	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 $length^{3.0469}$ ($r^2 = 0.94$)
ABS: Arcachon Bay Surface	46,4 x 10^6 (m^2)	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^{-1}) d: 0.055 (°C) e: 0.0006 (ind m^{-2})	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^{th} 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

	> 40: 0.61 (ind m^{-2})	
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^2)	Local legislation

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.

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.

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

Méthodes adaptées	Travaux engagés ou en projet	Incidences pour la gestion
Analyse de contours type landmarks couplée à la méthode conventionnelle jusqu'à présent utilisée Attribution des conditions environnementales par palourde (nature du sédiment, temps d'exondation, chlorophylle a,..) Etude des relations entre morphométrie et conditions environnementales	Collaboration initiée dans le cadre de la Fédération de Recherche MIRA* avec le LIUPPA** pour appréhender les techniques de contours (projet financé sur appel d'offres BQR – 2011-2012) à partir de clichés terrain Collaboration avec le LMAP*** sur l'encadrement d'un stage de M2 (juin à septembre 2012) visant à considérer les atouts et inconvénients de la mise en œuvre des méthodes des landmarks et des analyses de Fourier sur des clichés de palourdes	Locale Intégration de critères morphométriques pour le choix des zones de réserves Pertinence de proposer des cribles professionnels de caractéristiques différentes (maille ronde ?...) Nationale Pertinence de proposer des tailles minimales de captures différentes en fonction des gisements telles que pratiquées au Japon,…

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Poursuivre la compréhension des conditions de réalisation de la croissance

Méthodes adaptées	Travaux engagés ou en projet	Incidences pour la gestion
Etude des micro-incréments de la coquille pour déterminer les taux de croissance en fonction de différents paramètres (localisation, température, saison,…)	Réalisation d'expérimentations de marquage à la calcéine (2010-2011) confirmant sa faisabilité technique Mise en relation des données de croissance avec la température et comparaison entre deux sites d'implantation à entreprendre Pour cela, collaborations avec le Pôle de Sclérochronologie de Boulogne engagées ; elles sont à poursuivre en lien avec le rapprochement de la plate-forme de sclérochronologie de l'Inra de Saint-Pée initiée via MIRA	Locale Informations pouvant intervenir dans le choix de périodes de fermeture, voire leur localisation

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
Ajuster le niveau des captures mensuelles au niveau de la biomasse disponible Mieux intégrer les dynamiques d'exploitation en particulier en matière d'évolution de l'effort de pêche Estimer les captures réalisées par la pêche de loisir	Non démarré 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	Locale Réalisme favorable à la communication au sein du groupe de travail palourde Informations pouvant intervenir dans le choix de mesures de gestion adaptées aux différentes sources de mortalité

Intégration de l'incertitude dans la modélisation de processus

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

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

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