



HAL
open science

Rôle de l'espèce ingénieure *Upogebia pusilla* dans le fonctionnement biogéochimique des écosystèmes intertidaux à herbier (*Zostera noltei*) du bassin d'Arcachon

Ludovic Pascal

► **To cite this version:**

Ludovic Pascal. Rôle de l'espèce ingénieure *Upogebia pusilla* dans le fonctionnement biogéochimique des écosystèmes intertidaux à herbier (*Zostera noltei*) du bassin d'Arcachon. Biodiversité et Ecologie. Université de Bordeaux, 2017. Français. NNT : 2017BORD0017 . tel-01583030

HAL Id: tel-01583030

<https://theses.hal.science/tel-01583030v1>

Submitted on 6 Sep 2017

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THÈSE PRÉSENTÉE
POUR OBTENIR LE GRADE DE
DOCTEUR DE
L'UNIVERSITÉ DE BORDEAUX

ÉCOLE DOCTORALE SCIENCES ET ENVIRONNEMENTS

SPÉCIALITÉ : Biogéochimie et écosystèmes

Par Ludovic PASCAL

**Rôle de l'espèce ingénieure *Upogebia pusilla* dans le
fonctionnement biogéochimique des écosystèmes
intertidaux à herbier (*Zostera noltei*) du bassin d'Arcachon**

Sous la direction de : Olivier MAIRE
Co-directeur : Antoine GRÉMARE (HDR)

Soutenue le 19 Avril 2017

Membres du jury :

M. GARABETIAN, Frédéric	Professeur, Université de Bordeaux	Président
M. CHAUVAUD, Laurent	Directeur de recherche, CNRS	Rapporteur
M. GRENZ, Christian	Directeur de recherche, CNRS	Rapporteur
Mme. ROSSI, Francesca	Chargée de recherche, CNRS	Examinatrice
M. ARCHAMBAULT, Philippe	Professeur, Université Laval (Canada)	Examineur
M. DEFLANDRE, Bruno	Maître de conférences, Université de Bordeaux	Invité
M. de MONTAUDOUIN, Xavier	Professeur, Université de Bordeaux	Invité

Rôle de l'espèce ingénieure *Upogebia pusilla* dans le fonctionnement biogéochimique des écosystèmes intertidaux à herbier (*Zostera noltei*) du bassin d'Arcachon

Résumé : Dans le bassin d'Arcachon, le crustacé thalassinidé *Upogebia pusilla* habite préférentiellement les vasières intertidales colonisées par les zostères naines (*Zostera noltei*) où il trouve la stabilité sédimentaire indispensable à l'établissement durable de son terrier. Du fait de la profondeur de ce dernier (> 30 cm) et de sa grande mobilité, cette espèce ingénieure a souvent été négligée dans les études antérieures ayant pour objectif de mieux comprendre le rôle des communautés macro-benthiques dans le fonctionnement des herbiers de phanérogames et les conséquences de leur régression rapide. Ce manuscrit présente une étude intégrée du rôle d'*U. pusilla* dans le fonctionnement de son écosystème en s'attachant particulièrement à caractériser et quantifier les relations entre (1) ses différentes activités (fouissage, ventilation, locomotion, ...), (2) les modes de bioturbation qui en résultent et (3) leurs impacts respectifs sur la dynamique biogéochimique sédimentaire. Ce travail montre qu'*U. pusilla* engendre un remaniement et une bioirrigation intenses de la matrice sédimentaire qui l'entoure. Sa présence stimule ainsi fortement la reminéralisation de la matière organique sédimentée et les échanges de solutés à travers l'interface eau-sédiment. Bien que l'influence d'*U. pusilla* sur ces processus écologiques et biogéochimiques soit très dépendante des conditions environnementales (e.g., saisonnalité, prévalence parasitaire), l'ensemble de mes résultats suggère que le déclin progressif de ses populations, conséquence directe de la dégradation de son habitat, est susceptible de fortement altérer le fonctionnement global des écosystèmes du bassin d'Arcachon.

Mots clés : Bioturbation, Remaniement sédimentaire, Bioirrigation, Flux benthiques, Comportement, Parasitisme, Saisonnalité, Analyse d'image

Role of the engineer species *Upogebia pusilla* in the biogeochemical functioning of intertidal seagrass (*Zostera noltei*) ecosystems in Arcachon bay

Abstract: In Arcachon bay, the endobenthic thalassinid crustacean *Upogebia pusilla* is tightly associated with the intertidal dwarf grass *Zostera noltei* providing the sediment stability required for the construction of (semi-)permanent burrows. Because of the depth and complex architecture of their burrow (> 30 cm), this high mobile engineer species have been largely ignored in previous studies aiming at better understanding the role of macrobenthic communities in the functioning of seagrass ecosystems and the consequences of their rapid decline. This manuscript presents an integrated study regarding the role played by *U. pusilla* in the functioning of its ecosystem, with particular emphasis on the characterisation and quantification of the relationships between (1) its different activities (burrowing, ventilating, walking...), (2) both bioturbation modes and rates and (3) their respective impacts on the sedimentary biogeochemical dynamics. This work shows that mud shrimp activity leads to high mixing and bioirrigation of the surrounding sediment matrix, thus strongly enhancing organic matter mineralisation processes and solute exchanges across the sediment-water interface. Although the influence of *U. pusilla* on ecological and biogeochemical processes largely depends on environmental conditions (e.g., seasonality and parasitism), altogether my results suggest that the gradual decline of its population in Arcachon bay, as a direct consequence of benthic habitat degradation, may greatly alter the overall functioning of this vulnerable marine ecosystem.

Keywords: Bioturbation, Sediment reworking, Bioirrigation, Benthic fluxes, Behaviour, Parasitism, Seasonality, Image analysis

Remerciements

Je tiens tout d'abord à exprimer ma profonde gratitude à **Olivier Maire** et **Antoine Grémare**, mes deux directeurs de thèse sans qui ce travail n'existerait tout simplement pas. Olivier, merci pour la confiance que tu m'as accordée, pour ton soutien et ta disponibilité. Sache que je mesure la chance que j'ai de t'avoir eu comme directeur de thèse. Antoine, même si nous nous sommes moins vu pendant « la phase expérimentale » de ma thèse, je ne vous remercierai jamais assez pour le soutien que vous m'avez apporté pour la rédaction de ce manuscrit. Je vous présente d'ailleurs mes excuses pour les entraînements de ping-pong que je vous ai fait rater. Encore merci à vous deux, pour tout ce que vous m'avez appris, je vous en serai toujours reconnaissant.

Je souhaite remercier tout particulièrement deux personnes avec qui j'ai eu le plaisir et l'honneur de travailler. **Bruno Deflandre**, je voudrais te dire un grand merci pour tout ce que tu as fait pour moi... D'abord professionnellement, pour m'avoir initié à la biogéochimie, et particulièrement à l'art des incubations et des titrations Winkler (avec un CV = 0). Ensuite personnellement, pour les parties de squash toujours serrées, les dégustations de vins et de whisky, ... (je n'y suis pas vraiment sujet, mais si je devais énumérer toute la liste, je crois bien que j'en aurais le vertige). Surtout, merci pour ton soutien pendant mes périodes de doutes. **Xavier de Montaudouin**, merci de m'avoir ouvert les portes du monde des parasites et de celui, peut-être encore plus mystérieux, des ANCOVAs. Merci, d'avoir pris le temps de répondre à (toutes !!!) mes questions. Merci pour ta patience et ta gentillesse.

Je voudrais aussi remercier tous ceux qui ont participé de près ou de loin à mon travail. Merci **Alicia Romero-Ramirez** pour ton aide et d'avoir toujours tenu les délais même quand je te demandais une optimisation du logiciel « pour hier ». Merci **Guillaume Bernard** pour ton aide et m'avoir initié à l'utilisation des PERMANOVAs (un monde tout aussi mystérieux que celui des ANCOVAs). Merci **Nicolas Lavesque** d'avoir identifié ce « petit truc orange dans l'eau du terrier ». Merci **Sabrina Bichon** de m'avoir formé à l'analyse des sels nuts, et à l'utilisation du CHN. Merci aux membres de l'atelier, **Henri Bouillard** et **Christian Portier** d'avoir su fabriquer mes concepts quelques fois loufoques et de m'avoir tant de fois dépanné avec les problèmes de mésocosme. Merci à **Nicolas Savoye**, de m'avoir initié à l'analyse isotopique. Et enfin, merci à **Francis Prince**, capitaine du PLANULA IV et aux nombreux matelots qui se sont succédés.

Remerciements

Je remercie également les stagiaires ayant participé à ce travail : **Elisa Teisseire, Anaïs Richard, Juliana Vongue, Pierre Ramond, et Ilan Pérez.**

Ensuite je souhaite remercier **Laurent Chauvaud** et **Christian Grenz** d'avoir accepté d'évaluer mon travail de thèse. Je remercie également **Francesca Rossi, Philippe Archambault** et **Frédéric Garabetian** d'avoir bien voulu en être les examinateurs.

Un grand nombre de personnes a contribué à rendre ces trois années ($\frac{1}{2}$) inoubliables, et il est clair que ce travail de thèse aurait été tout autre sans leur amitié. Un grand merci à mes collègues de bureau et en tout premier lieu **Antoine Nowaczyk** ! Merci pour ces parties de pêche au rendement extraordinaire ! Merci pour ton humour, bref, ... Merci pour tout ! Merci à **Sonia Gasmi** avec qui j'ai partagé mon bureau pendant 2 années et qui a été, avec Antoine, une excellente partenaire de lancer de boules de papier. Je te souhaite bon courage pour la fin de ta thèse. I don't forget **Lúisa Magalhães** (the Portuguese typewriter) thank you for your kindness and friendliness. Et enfin, la dernière arrivée, **Annabelle Dairain**, dont l'étendu de ses connaissances me surprendra toujours. Bon courage pour la fin de ta thèse et « T'inquiète, ça va l'faire ! ».

Alicia, Nicolas, Guillaume et **Cerise Daffe**, je tiens à nouveau à vous remercier mais cette fois ci pour vos qualités humaines. **Sophie Gentes**, merci pour ta gentillesse (même si tu as abîmé mon vélo ;)).

Il est difficile de penser à tout le monde en écrivant ces remerciements et j'espère que ceux que je n'ai pas listé ici m'en excuseront, ce n'est pas pour autant que je les oublie.

Un grand merci à toute ma famille qui, malgré la distance, a toujours été là pour moi. Merci pour votre patience et votre compréhension. C'est grâce à vous tous que j'en suis là et je ne vous remercierai jamais assez pour tout ce que vous m'avez donné !

Enfin, merci à toi Sophie, pour ton soutien, ton réconfort et ton amour, ... J'espère être à la hauteur de tout ce que tu m'apportes.

A ma famille,

Financements

Pour réaliser ce travail, j'ai bénéficié d'une allocation de recherche de trois ans du Ministère de l'Enseignement Supérieur et de la Recherche. Les différentes études que j'ai conduites se sont directement inscrites dans le cadre du projet « UPOBA » (EC2CO-DRIL). Elles ont également bénéficié d'équipements acquis pendant les projets IZOFLUX (ANR blanc) et BIOMIN (LEFE-CYBER et EC2CO).

Préambule

Au sein du laboratoire Environnements et Paléoenvironnements Océaniques et Continentaux (UMR 5805 EPOC), où j'ai réalisé ma thèse de doctorat, une attention particulière est portée, depuis plusieurs années, à la régression de l'herbier de zostères naines (*Zostera noltei*) du bassin d'Arcachon, considéré comme le plus vaste herbier intertidal de phanérogames marines d'Europe (Auby et Labourg, 1996). En effet, depuis la publication de Plus et al., (2010) qui a rapporté une régression drastique de 22,8 km² (soit 33 %) en 20 ans, de nombreuses études ont été menées pour identifier les causes et les conséquences de ce déclin rapide. Les derniers rapports IFREMER (Auby et al., 2016, 2011), dans lesquels le laboratoire EPOC a été largement impliqué, recensent les principales causes de cette régression qui semblent essentiellement résulter des effets conjugués de vagues de chaleurs ayant touchées la région Aquitaine entre 2003 et 2006 et de la présence de contaminants (*e.g.*, herbicides) dans l'eau. Actuellement, une thèse de doctorat adossée au projet ZODARSED (LabEx COTE) tente de mieux comprendre les causes physiques (*i.e.*, hydrodynamiques) de la régression des herbiers et de démêler les causes et les conséquences physiques de cette régression.

Les conséquences de la réduction de la surface occupée par l'herbier ainsi que de sa densité ont été étudiées au cours de plusieurs travaux de thèses qui ont porté sur l'hydrodynamisme, la biogéochimie sédimentaire et la diversité biologique. Les résultats obtenus ont permis de mettre en évidence de multiples effets de la régression de l'herbier de *Z. noltei* sur l'environnement littoral du bassin d'Arcachon. Ainsi, le déclin de l'herbier favorise les phénomènes de resuspension sédimentaire. En diminuant la pénétration de la lumière dans la colonne d'eau, ce processus impacte négativement la production des phanérogames (Ganthy, 2011). Cette régression provoque également de profonds changements sur la dynamique biogéochimique sédimentaire. Elle favorise notamment le relargage par le sédiment de nutriments stockés dans les eaux interstitielles et en particulier d'ammonium et de phosphore (Delgard, 2013). La diversité et l'abondance de la macrofaune benthique sont également négativement affectées par la régression des herbiers (Do, 2012). De plus, le système racinaire et rhizomial exerçant un rôle structurant et stabilisateur de la matrice sédimentaire, sa régression affecte l'ensemble des processus sédimentaires et notamment la bioturbation, ce qui se traduit par une augmentation de l'amplitude et de la variabilité spatiale de l'intensité du remaniement sédimentaire (Bernard, 2013). Ces études

ont largement participé à l'amélioration des connaissances du fonctionnement des écosystèmes à zostères du bassin d'Arcachon et ont ainsi permis de mieux comprendre les conséquences écologiques et biogéochimiques potentielles de la régression des herbiers marins. Cependant, au-delà de la disparition progressive de l'herbier *per se* et de ses répercussions directes sur les processus hydrodynamiques, biogéochimiques et biologiques, les sédiments végétalisés abritent également des espèces ingénieures qui leur sont étroitement voire exclusivement associées. La régression de l'herbier pourrait donc avoir des répercussions plus larges que celles envisagées jusqu'à présent et impacter de manière indirecte de nombreux processus régulés par ces espèces ingénieures.

Dans ce contexte, l'objectif général de mon travail de doctorat consistait à évaluer le rôle d'une espèce ingénieure (*Upogebia pusilla*) dans le fonctionnement écologique et biogéochimique des écosystèmes intertidaux à herbier du bassin d'Arcachon afin d'appréhender d'une manière plus fine les conséquences potentielles de la régression de l'herbier

Table des matières

Introduction

1	La bioturbation des sédiments marins côtiers.....	3
1.1.	La bioturbation : un processus clef dans le fonctionnement des écosystèmes benthiques.....	3
1.1.1.	Définition.....	3
1.1.2.	Le remaniement sédimentaire.....	3
1.1.3.	La bioirrigation.....	6
1.1.4.	Rôle de la bioturbation dans les processus de diagénèse précoce.....	7
2	Les crustacés décapodes thalassinidés.....	9
2.1	Taxinomie.....	9
2.2	Distribution.....	11
2.3	Morphologies des terriers.....	15
2.4	Les thalassinidés : Les plus grands bioturbateurs des écosystèmes marins ?	18
2.4.1	Modification des propriétés physiques de l'habitat sédimentaire par l'activité de bioturbation des thalassinidés.....	22
2.4.2	Modification de la biogéochimie sédimentaire par l'activité des thalassinidés	24
2.4.3	Le contrôle des assemblages de macrofaune par les thalassinidés.....	27
2.5	Les principaux facteurs influençant l'activité des thalassinidés	28
2.5.1	La température.....	28
2.5.2	L'hypoxie	29
2.5.3	Le parasitisme.....	29
3	Site d'étude : Le bassin d'Arcachon.....	32
3.1	Présentation du bassin d'Arcachon	32
3.2	La régression de l'herbier de <i>Zostera noltei</i>	35
3.3	Objectifs du travail.....	37
3.4	Organisation du manuscrit.....	38

Chapitre 1 : Activité d'*Upogebia pusilla*

Behaviour, sediment reworking and oxygen dynamics in the Gebiidean mud shrimp <i>Upogebia pusilla</i>	43
Abstract	44
1. Introduction	45
2 Materials and methods.....	47
2.1 Animals collection and maintenance.....	47
2.2 Sediment reworking and burrow characteristics	47
2.3 Behaviour	49
2.4 Oxygen dynamics.....	50
2.5 Data analysis.....	51
3 Results	51
3.1 Burrow characteristics.....	51
3.2 Behaviours.....	54
3.3 Sediment reworking	57
3.4 Oxygen dynamics.....	60
4 Discussion.....	63
4.1 Behaviour	63
4.2 Sediment reworking	65
4.3 Oxygen dynamics.....	69

Chapitre 2 : Influence d'*Upogebia pusilla* sur les flux biogéochimiques à l'interface eau-sédiment

Influence of the mud shrimp <i>Upogebia pusilla</i> (Decapoda: Gebiidea) on solute and porewater exchanges in an intertidal seagrass (<i>Zostera noltei</i>) meadow of Arcachon Bay: an experimental assessment.	73
Abstract	74
1 Introduction	75
2 Materials and methods.....	77
2.1 Study site	77
2.2 Sampling and experimental design.....	78
2.3 Sediment characteristics	78
2.4 Benthic solute exchanges	79
2.5 Measurements of porewater exchange rates.....	81
2.6 Data treatments.....	82

3	Results	83
3.1	Sediment characteristics	83
3.2	General observations	83
3.3	Oxygen fluxes.....	84
3.4	Nutrients fluxes	88
3.5	Porewater exchange rates	89
4	Discussion.....	91
4.1	Sediment porewater exchanges	91
4.2	Oxygen uptake.....	94
4.3	Nutrient fluxes.....	98
5	Conclusion.....	100

Chapitre 3 : Influence de l'ectoparasite *Gyge branchialis* sur *Upogebia pusilla*

Partie A

	Dynamics of the <i>Upogebia pusilla</i>-<i>Gyge branchialis</i> marine host-parasite system	105
	Abstract	106
1	Introduction	107
2	Materials and Methods	109
2.1	Study site and sampling.....	109
2.2	<i>Upogebia pusilla</i> and <i>Gyge branchialis</i> analyses	110
2.3	Data analysis.....	111
2.3.1	<i>Upogebia pusilla</i> growth	111
2.3.2	Infestation by <i>Gyge branchialis</i>	111
3	Results	112
3.1	Population dynamics of <i>Upogebia pusilla</i>	112
3.2	Infestation by <i>Gyge branchialis</i> : spatial survey	114
3.3	Infestation by <i>Gyge branchialis</i> : temporal survey	118
4	Discussion.....	120
4.1	Early infestation of <i>Upogebia pusilla</i>	120
4.2	Influence of <i>Gyge branchialis</i> on <i>Upogebia pusilla</i> reproduction.....	122
4.3	Influence of <i>Gyge branchialis</i> on <i>Upogebia pusilla</i> total length and individual dry weight.....	123
5	Conclusion.....	125

Partie B

Parasitism of engineer species: a key factor of marine ecosystem functioning	127
Abstract	128
1 Introduction	129
2 Materials and methods.....	130
2.1 Field sampling and experimental design.....	130
2.2 Behaviour monitoring.....	131
2.3 Quantification of bioturbation rates	132
2.3.1 Sediment reworking.....	132
2.3.2 Bioirrigation	132
2.4 Assessment of ecosystem functioning.....	134
2.5 Data treatments.....	135
3 Results	135
3.1 Behaviour	135
3.2 Bioturbation.....	137
3.2.1 Sediment reworking.....	137
3.2.2 Bioirrigation	140
3.3 Ecosystem functioning	140
4 Discussion.....	143
4.1 Influence of the parasite at the organism-level	144
4.2 Consequences on ecosystem functions.....	144

Synthèse et perspectives

1 Comportement de l'espèce ingénieure <i>Upogebia pusilla</i>	152
1.1 Objectifs et principaux résultats acquis.....	152
1.2 Perspectives.....	154
2 La bioturbation induite par <i>Upogebia pusilla</i>	156
2.1 Objectifs	156
2.2 Le remaniement sédimentaire	156
2.2.1 Principaux résultats acquis	156
2.2.2 Perspectives	159
2.3 La bioirrigation d' <i>Upogebia pusilla</i>	160
2.3.1 Principaux résultats acquis	160
2.3.2 Perspectives	161

3	Influence d' <i>Upogebia pusilla</i> sur la dynamique biogéochimique du sédiment	163
3.1	Objectifs et principaux résultats	163
4.3	Perspectives	165
5	Rôle indirect du parasitisme dans le fonctionnement des écosystèmes côtiers <i>via</i> son influence sur une espèce ingénieure	167
6	Conclusion générale : rôle d' <i>Upogebia pusilla</i> dans le fonctionnement écologique et biogéochimique des sédiments végétalisés du bassin d'Arcachon.....	169
	Références bibliographiques	175

Données supplémentaires

Annexe I : Positive interaction between seagrass (<i>Zostera noltei</i>) and burrowing mud shrimp (<i>Upogebia pusilla</i>), a preliminary field study	209
Annexe II : Moulages de terrier <i>in-situ</i>	225
Annexe III : Relations biométriques.....	227
Annexe IV : Romero-Ramirez et al. 2016.....	229
Annexe V : Lavesque et al. 2016.....	267

Liste des figures

Introduction

- Figure I.1 :** Les quatre types majeurs (*i.e.*, groupes fonctionnels) de remaniement sédimentaire effectués par la macrofaune benthique dans les écosystèmes marins. (A) biodiffuseurs, (B) convoyeur vers le haut, (C) convoyeur vers le bas et (D) régénérateur (D'après Kristensen et al., 2012).....5
- Figure I.2 :** Stratification théorique des accepteurs d'électrons dans les sédiments marins sans et avec bioturbation. Modifié d'après Aller (1982)8
- Figure I.3 :** Morphologie général d'un crustacé thalassinidé. Le céphalothorax supportant 5 paires de périoïpodes et l'abdomen supportant une paire de pléopodes par segment (5 paires), un telson et deux paires d'uropodes et. (Modifié d'après Liu, 2015)10
- Figure I.4 :** Distribution mondiale des groupes majeurs de thalassinidés et répartition du nombre d'espèces de thalassinidés en fonction de la latitude. Modifié d'après Dworschak, 2000 et Pillay et Branch, 201112
- Figure I.5 :** Mécanismes potentiels des effets négatifs des thalassinidés sur les herbiers de phanérogames (Modifié d'après Dewitt, 2009)14
- Figure I.6 :** Photographie de moulage de terrier d'*Upogebia pusilla* (A ; photo L. Pascal) et de *Callianassa subterranea* (B ; photo Nickell et Atkinson, 1995).16
- Figure I.7 :** Topographie du sédiment de surface en présence de *Callianassa truncata* (insert) dans la baie de Campese (Italie). D'après Ziebis et al., (1996)19
- Figure I.8 :** Influence des thalassinidés sur le fonctionnement des écosystèmes benthiques (Modifié d'après Pillay et Branch, 2011 et Volkenborn, 2012)22
- Figure I.9 :** Schématisation de l'influence des thalassinidés sur la consommation d'oxygène et le cycle de l'azote. L'épaisseur des flèches est proportionnelle à l'intensité des processus ou des flux (Modifié d'après d'Andrea et DeWitt, 2009)27
- Figure I.10 :** Mécanismes potentiels des effets de la bioturbation des thalassinidés sur la macrofaune benthique (Modifié d'après Pillay et al., 2007)28

- Figure I.11** : Un individu d'*Upogebia pusilla* infesté au niveau de la cavité branchiale par un couple de Bopyridea *Gyge branchialis* (insert). Dans l'insert, le mâle nain (flèche blanche) est fixé sur la face ventrale de la femelle au niveau de ses ouvertures génitales.31
- Figure I.12** : Localisation du bassin d'Arcachon sur la côte Atlantique française (insert) et emplacement des stations échantillonnées durant mes travaux de thèse. En *bleu* l'océan et la zone subtidale, en *marron* la zone intertidale et en *blanc* le continent. Identification des stations d'Ouest en Est : *REO* : « La réousse », *CLA* : « Le cla », *DRO* : « Drôle », *HOS* : « Les hosses », *GRA* : « Graveyron », *MOU* : « Les mousettes », *NEG* : « La nègue », *TES* : « Le tes », *GER* : « Germanan », *GAR* : « Garrèche », *BOU* : « Bourut », *TEY* : « le teychan », *ARO* : « Arouillet », *SAL* : « Salos », *PAS* : « Passant ». Le site « La nègue » correspond au site d'échantillonnage pour les expériences *ex-situ* effectuées durant ma thèses de doctorat.....33
- Figure I.13** : Un individu *Upogebia pusilla* à proximité d'une ouverture de son terrier (diamètre d'environ 1,5 cm) à la surface d'un sédiment colonisé par l'herbier de *Zostera noltei* (l'organisme a été volontairement extrait de son terrier).....34
- Figure I.14** : Surface colonisée par l'herbier de *Zostera noltei* en 2005 et en 2007 avec les différentes classes de taux de recouvrement du sédiment par les feuilles de *Z. noltei* (D'après Auby et al., 2011).....36

Chapitre 1 : Activité d'*Upogebia pusilla*

- Figure 1.1** : Schematic view of a representative burrow at D4. Green line: Former sediment-water interface evidenced by luminophore layer, dotted line: burrow length, T_{RS} : average thickness of the reworked sediment layer surrounding the burrow, H: average height of expelled sediment used to estimate the volume of expelled sediment on the sediment water-interface (V_{ES}), Red dotted arrows (P1, P2 and P3) represent the three patterns of sediment reworking observed in *Upogebia pusilla*, see text for details. *: position of the micro optical oxygen sensor.48
- Figure 1.2** : Average (\pm SE) proportions of time allocated to each behaviour during winter (black bars, n = 4), spring (white bars, n = 5) and summer (light grey bars, n = 5) experiments. Different letters indicate significant (PERMANOVA and pair-wise test, $p < 0.05$) between seasons differences.56

- Figure 1.3 :** Relationships between experiment duration and: (A) the thickness of reworked sediment (T_{RS}), (B) the cumulative volume of reworked sediment (B_{RS}), and (C) the cumulative volume of expelled sediment (V_{ES}). Relationship between the cumulative volume of reworked sediment (B_{RS}) and the cumulative volume of sediment expelled at the water-sediment interface (V_{ES}) at D4 (D).58
- Figure 1.4 :** Relationship between estimated and measured total volume of reworked sediment. Measured total volume of reworked sediment corresponds to the sum of the volume of expelled sediment (V_{ES}) and the volume of reworked sediment surrounding the burrow (B_{RS}) which are computed using Eq. (2) and Eq. (3), respectively. Estimated total volume of reworked sediment corresponds to the estimation of volume of reworked sediment using the model output from multiple linear regressions. See text for details about the model.....58
- Figure 1.5 :** Relationships between experiment duration and: (A) average (\pm SE) vertical biodiffusion (D_{bv}), and (B) vertical bioadvection (V_{bv}) coefficients during winter, spring, and summer experiments ($n = 10$ in all cases).60
- Figure 1.6 :** O_2 dynamics in the overlying water. (A) Representative example of the effect of *Upogebia pusilla* activity on temporal changes (min) of O_2 saturation (%) in the overlying water. Red colour depicted temporal changes during “Burrowing”, blue colour depicted temporal changes during “Ventilation”, green colour depicted temporal changes during “Walking”, and black colour depicted temporal changes during “Resting”. (B) Relationship between the time-duration before a ventilation event and the magnitude of O_2 decrease during this event. See text for details about the relationship62
- Figure 1.7 :** O_2 dynamics in the burrow water. (A, B and C) Example of behaviour-specific O_2 saturation pattern in the burrow lumen when the mud shrimp was (A and B) far and (C) close from the micro-optode. Red colour depicted temporal changes during “Burrowing”, blue colour depicted temporal changes during “Ventilating”, green colour depicted temporal changes during “Walking” and black colour depicted temporal changes during “Resting”. (D) Relationship between O_2 saturation at the onset of a ventilation event and the mud shrimp distance from the sensor. See text for details about the relationship.....63

Chapitre 2 : Influence d'*Upogebia pusilla* sur les flux biogéochimique à l'interface eau-sédiment

- Figure 2.1 :** *Sampling site.* Location of Arcachon Bay on the French Atlantic coast (A) and of the study site (44° 40.782' N, 1° 08.321' W) in the central part of Arcachon Bay (B). *Zostera noltei* meadows are presented in gray (from Plus et al. 2010).....77
- Figure 2.2 :** *Sediment oxygen uptake.* Representative examples of temporal changes in O₂ concentration in *With-* (solid line) and *Without-* (long dashes) *Upogebia* treatment cores.84
- Figure 2.3 :** Oxygen and nutrient fluxes. Average (\pm SE) of: (A) O₂ uptakes: TOU (solid bars), mud shrimp uptake (white bars), (B) ammonium releases: NH₄⁺ benthic flux (solid bars), mud shrimp release (white bars), (C) nitrate and (D) silicate fluxes across the sediment–water interface. Black bars correspond to measurements carried out within cores *Without-Upogebia*. Light gray bars correspond to measurements carried out within cores *With-Upogebia*. White bars correspond to measurements carried out on individual mud shrimp. Different letters indicate significant (overall $\alpha=0.05$) differences between combinations of seasons and treatments. Lower case letter: two-way ANOVA, higher case letter: one-way ANOVA.....86
- Figure 2.4 :** *Porewater exchange rates.* (A) Representative examples of temporal changes in the moving averages (over 1min) of uranine concentration during core incubations in *Without-* (long dashes) and *With-* (solid line) *Upogebia* treatment cores. (B) Average (\pm SE) porewater exchange rates (Q) measured in *Without-* (black bars) and *With-* (White bars) *Upogebia* treatment cores. Different letters indicate significant (overall $\alpha=0.05$) differences between combinations of seasons and treatments.90

Chapitre 3 : Influence de l'ectoparasite *Gyge branchialis* sur *Upogebia pusilla*

Partie A

- Figure 3A.1 :** Location of the sampled stations in Arcachon Bay and related prevalences of infections of *Upogebia pusilla* by *Gyge branchialis* as recorded during the spatial survey. Dark grey: Land, light grey: intertidal area and white: water. BOU : Bourrut; CLA : Le Cla; GAR : Garrèche ; HOS : Les Hosses; MOU : Les Moussettes; NEG : La Nègue; PAS : Passant; REO : La Réousse; TES : Le Tes; TEY : Le Teychan109
- Figure 3A.2 :** Temporal survey: Growth curve of *Upogebia pusilla* as fitted using Von Bertalanffy Growth Function (VBGF) ($k = 3.96 \text{ yr}^{-1}$; $L_{\infty} = 49.9 \text{ mm}$)114
- Figure 3A.3 :** Spatial and temporal surveys: Prevalence of *Gyge branchialis* in *Upogebia pusilla* in relation with total carapace length based on spatial (A) and temporal (B) survey. Different shades of grey refer to the 4 groups discriminated by hierarchical clustering analysis.....115
- Figure 3A.4 :** Spatial and temporal surveys: Relationships between *Gyge branchialis* (males and females) lengths and *Upogebia pusilla* total length as recorded during the spatial (A) and the temporal (B) surveys116
- Figure 3A.5 :** Spatial and temporal surveys: Effect of parasitism on *Upogebia pusilla* total length (A and B) and dry weight (C and D) (\pm SE) according to spatial (A and C) and temporal (B and D) surveys117
- Figure 3A.6 :** Temporal and spatial surveys: relationships linking TL and DW in infested and non-infested mud shrimp recorded during the spatial (A) and the temporal (B) surveys118

Partie B

- Figure 3B.1 :** Average (\pm SD) proportions of time allocated to each behaviour in *Parasitized-* and *Healthy-*treatments during summer. * indicates significant differences in time devoted to each behaviour in *Parasitized-* as compared to *Healthy-*treatments (one-way PERMANOVAs and pair-wise test, $p < 0.05$).....136

Figure 3B.2 : Average (\pm SD) sediment reworking coefficients. (A) Vertical biodiffusion (D_{bv} , solid bars, left scale) and bioadvection (V_{bv} , hatched bars, right scale) coefficients and (B) orthogonal to the burrow wall biodiffusion coefficient (D_{bw}) during winter and summer. Different letters indicate significant differences between combinations of seasons and treatments (two-way PERMANOVAs and pair-wise test, $p < 0.05$). Lower case: D_b ; Higher case: V_{bv}138

Figure 3B.3 : Average (\pm SD) bioirrigation rates (Q in mL h^{-1}) during winter and summer. Different letters indicate significant differences between combinations of seasons and treatments (two-way PERMANOVAs and pair-wise test, $p < 0.05$).....140

Figure 3B.4 : Average (\pm SD) of (A) O_2 uptakes: TOU (solid bars) and mud shrimp respiration (hatched bars), (B) NH_4^+ releases: NH_4^+ benthic fluxes (solid bars) and mud shrimp excretion (hatched bars), (C) NO_3^- and (D) dSi fluxes across the sediment-water interface. Different letters (higher case letter: mud shrimp respiration or excretion, lower case letter: benthic fluxes) indicate significant differences between combinations of treatments and seasons (two-way PERMANOVAs and pair-wise test, $p < 0.05$).....142

Synthèse et perspectives

Figure S.1 : Représentation schématique de l'articulation des principaux résultats obtenus durant mes travaux de thèse (bulle à fond blanc) et des principales perspectives qui en découlent (bulles à fond bleu).....171

Données supplémentaires

Figure AI.1 : Location of the sampling sites in Arcachon Bay (ARO: Arouillet; BOU : Bourrut; CLA : Le Cla; DRO: Drole; GAR : Garrèche; GER: Germanan; GRA: Graveyron; HOS : Les Hosses; MOU : Les Moussettes; NEG : La Nègue; PAS : Passant; REO : La Réousse; SAL: Salos; TES : Le Tes; TEY : Le Teychan) and the reference point (REF) from which the distance from the sea was measured. *Light grey*: ocean and subtidal area; *Dark grey*: intertidal area; *White*: land.....210

Figure AI.2 : Biplot showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ration of *Upogebia pusilla* specimens, *U. pusilla* specimens minus isotopic fractionation, sediment surface, sediment column. Data for phytoplankton, microphytobenthos, macroalgues, degraded seagrass, seagrass +

epiphyte, and continental particulate organic matter in Arcachon Bay came from Dubois et al. 2012 and FELIBA project (V. DAVID & N. SAVOYE, unpublished data).....	217
Figure AIV.1 : AVIExplore graphical user interface: (1) AVIExplore – Mobile module, (2) AVIExplore – Fixed module, (3) AVIExplore – ScriptEdit module, (4) summary of system characteristics, (5) extension files for future versions, and (6) software manual and information.....	234
Figure AIV.2 : Internal structure of AVIExplore. Origin, work and secondary work images are 24 bit bitmaps for color images and video frames. Gray images are 8 bit images. Regions of interest (ROIs) and masks are structures saved in external files, wich can be loaded on demand. Op: operation	236
Figure AIV.3 : External files generated by AVIExplore. Continuous arrows refer to files that must to be loaded by the user. Dashed arrows refer to files automatically loaded by the software.....	237
Figure AIV.4 : AVIExplore – Mobile, AVIExplore – Fixed and AVIExplore – ScriptEdit module’s general graphic user interface: (1) video display window, (2) strip menu, (3) video time scrollbar, and (4) area differing between modules.....	237
Figure AIV.5 : Interactions between different modules and modes of AVIExplore.....	238
Figure AIV.6 : A: AVIExplore – Mobile: Typical flowchart of a video obtained with a mobile device, B: AVIExplore – Fixed: Typical flowchart of a video obtained with a fixed device.....	240
Figure AIV.7 : Coral mapping case study: dissimilarities of Grey-Level Co-occurrence Matrix for each image of the video. Numbered vertical dashed lines indicate different images which are shown on the right. 1 and 2: images of the water-sediment interface, 3: image of the water-sediment interface at high altitude and 4: image of the water column.	246
Figure AIV.8 : Coral mapping case study: results of the execution of the two scripts on a single image. (A) Original image showing the delimitation of ROI in yellow, (B) image with white overlay covering apparently dead and living corals, and (C) image with a red overlay covering only apparently living corals.....	247

Figure AIV.9 : Coral mapping case study: Mapping of (A) apparently dead and living corals, and (B) apparently living corals.....248

Figure AIV.10 : Mud shrimp case study: (A) Example of an image extracted from the video with an ROI corresponding to the delimitation of the visible part of the burrow, (B) Automatic and (C) Visual assessment of the temporal changes in the occurrence of the three monitored behaviors: ‘Resting/ventilating’, ‘Burrowing’ and ‘Walking’250

Figure AIV.11 : Mud shrimp case study: Combination of AVIExplore extracted features to assess the three different behaviors of *Upogebia pusilla*.....251

Figure AIV.12 : Passive suspension-feeder case study: (A) Reference image showing the disposition of the 15 studied worms with their retracted gill-crowns, (B) Localization of the 15 ROIs around the shadow of the top extremity of the tubes where extended gill-crowns (10 worms) can be observed, (C) Temporal changes in individual filtering activities.....254

Figure AIV.13 : Passive suspension-feeder case study: (A) Temporal changes in the number of worms filtering (B) Temporal changes in individual cumulated filtering activities. .255

Figure AV.2 : Adult males of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) from Arcachon Bay (Arcachon Marine Station collection: A: male, BL = 7.89 mm; B-D: male, BL = 7.52 mm). (A) lateral view. SP1: first sternal process; SP6: sixth sternal process; GA: genital appendage; (B) right thoracopod 3 endopod, inner view; (C) telson, ventral view; (D) right uropod, ventral view. Scale bars: 0.5 mm.....272

Figure AV.3 : Living male specimen of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) from Arcachon Bay (BL = 7.52 mm) (Arcachon Marine Station collection, same specimen as in Fig. 2 B-D). (A) lateral view; (B) anterior part.274

Figure AV.1 : Sampling site (“Le Navire Brûlé”) of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) in Arcachon Bay (SW France).....278

Liste des tableaux

Introduction

Tableau I.1 : Classification phylogénétique actuelle tel que décrite par Bracken et al., (2009) et Robles et al., (2009) des différents groupes classés parmi les clades des Gebiidea et des Axiidea.....11

Tableau I.2 : Résultat du test de corrélation multiple (Forward stepwise regression) des variables environnementales impliquées dans la prédiction de la densité d'*Upogebia pusilla*. L'absence de coefficient indique que la variable n'est pas incluse dans le modèle. L'astérisque (*) indique un effet significatif.35

Chapitre 1 : Activité d'*Upogebia pusilla*

Table 1.1 : Mean values of main burrow characteristics (length, depth, number of openings and number of turning chambers) recorded immediately after luminophore input (D0) and the 4 (D4) and 30 days (D30) later.....52

Table 1.2 : Results from PERMANOVA and PERMDISP analyses for differences in burrow length, burrow depth, number of burrow openings, number of turning chambers, mean thickness of the reworked sediment layer surrounding the burrow (T_{RS}), volume of reworked sediment surrounding the burrow (B_{RS}) and volume of sediment expelled at the sediment-water interface (V_{ES}), among Seasons and Experiment durations. *: PERMDISP, $p < 0.05$53

Table 1.3 : Description, average bout-duration (\pm SD) and interval-duration (average \pm SD) of each behaviour during winter ($n = 4$), spring ($n = 5$) and summer ($n = 5$) experiments. * indicates significant between seasons differences (one-way PERMANOVA, $p < 0.05$)55

Chapitre 2 : Influence d'*Upogebia pusilla* sur les flux biogéochimiques à l'interface eau-sédiment

Table 2.1 : <i>Sediment characteristics</i> . Average depth-integrated values (20 cm depth) of median grain size (D ₅₀), porosity (Φ), permeability (k), and organic carbon content (OC) of the sediment of the study site in winter, spring and summer. The variation coefficients associated with vertical variability are given in brackets.	83
Table 2.2 : <i>Data treatment</i> . ANOVA results of Treatment and Season effects on benthic solute fluxes, mud shrimp O ₂ uptake, mud shrimp NH ₄ ⁺ excretion and porewater exchanges (Q). p values in bold indicate significant factor effects	87
Table 2.3 : <i>Porewater exchange rates</i> . Available literature data for benthic macrofauna.	93
Table 2.4 : <i>Benthic solute fluxes</i> . Available TOU, NH ₄ ⁺ and NO ₃ ⁻ flux data for benthic macrofauna.....	97

Chapitre 3 : Influence de l'ectoparasite *Gyge branchialis* sur *Upogebia pusilla*

Partie A

Table 3A.1 : Spatial and temporal surveys: Counts and proportions (between brackets) of females, males and feminized males in relation with the presence/absence of the parasite	113
Table 3A.2 : Comparative results concerning ecological and biological traits of different <i>Upogebia</i> species. Md: grain-size median; CL: Cephalo-thoracic length; <i>G.b.</i> : <i>Gyge branchialis</i> ; <i>G.o.</i> : <i>Gyge ovalis</i> ; <i>O.g.</i> : <i>Orthione griffenis</i> ; N: number of analysed individuals; S: Sea.....	121

Partie B

Table 3B.1 : Average (± SD) bout-duration and interval-duration of each behaviour in <i>Parasitized</i> - and <i>Healthy</i> -treatment during summer. * indicates significant difference between seasons (one-way PERMANOVAs, p < 0.05)	137
---	-----

Table 3B.2 : Average (\pm SD) of burrow characteristic (burrow length, burrow depth, number of burrow opening, number of turning chambers and burrow diameter) and sediment reworking (T_{RS} : mean thickness of the reworked sediment layer surrounding the burrow, B_{RS} : volume of reworked sediment surrounding the burrow and V_{ES} : volume of sediment expelled onto the sediment) just after, 4 days and 30 days after luminophore input in *Parasitized-* (p) and in *Healthy-* (h) treatments. * Indicates significant differences between States within Season (three-way PERMANOVAs and pair-wise test, $p < 0.05$)
139

Table 3B.3 : Average (\pm SD) sediment reworking rates (biodiffusion, D_b and bioadvection, V_b), bioirrigation rate (Q) and oxygen (TOU) and nutrients benthic fluxes (NH_4^+ , NO_3^- and dSi) in *Without-Upogebia-*, *Healthy-* and *Parasitized-*treatments. The column entitled “Population” correspond to the average values expected for a natural population with 21 % of infested mud shrimp (Pascal et al. 2016a). The difference (in italic) of the values calculated for a natural population relatively to a healthy population has been computed. Note that Q has been standardized for a mud shrimp density of 144 ind m^{-2} as for flux measurements.....148

Données supplémentaires

Table AI.1 : Mean (\pm SD) values of *Upogebia pusilla* and environmental variables in each station. The variation coefficients associated with vertical variability are given in brackets214

Table AI.2 : ANOVA results of station effects on *Upogebia pusilla* mean density, individual total length (TL) and individual dry weight (DW).215

Table AI.3 : Stepwise multiple linear regression results of environmental variables involved in the prediction of *Upogebia pusilla* mean density, individual total length (TL) and individual dry weight (DW). The absence of coefficient indicates that variable is not included in the model. * indicates significant factor effect216

Table AII.1 : Mesures de l'étendu horizontale, de la profondeur, de nombre de sortie et de chambre de retournement et diamètre moyen du tube et des chambres de retournement effectuées sur des moulages de terrier d'*Upogebia pusilla*. La ligne grisée (moulage

numéro 5) correspond à un moulage de terrier d'un juvénile. Les valeurs correspondantes n'ont pas été prises en compte dans le calcul des valeurs moyennes.226

Table AIII.1 : Biometry relationships for *U. pusilla* according to sex categories. Different lines in sex category indicate significant between sex categories differences (ANCOVA, $p < 0.05$) in the considered biometric relationship. AFDW: Ash-free Dry Weight of total shrimp (g); CL: Cephalo-thoracic carapace Length (mm); DW: total shrimp Dry Weight (g); DW2pr: Dry Weight of 2 Productylus; MM: Male; FF: Female; FM: Feminized Male; FW: total Fresh Weight (g); Lpl: Length of pleopod (mm); Lpr: Length of productylus (mm); TL: Total Length (mm); Wpr: Width of productylus (mm)228

Table AIV.1 : Format of Geolocalization File: (1) Explanation, (2) Example.....239

Table AIV.2 : List of extracted features by the AVIExplore - Mobile module. In (1-6) i, j are the horizontal and vertical coordinates in the Greylevel Co-occurrence Matrix, P is the cell value.241

Table AIV.3 : List of parameters to select for analyzing when using the AVIExplore - Fixed module.....243

Table AIV.4 : Coral mapping case study: Details of the two scripts used to: detect, quantify the surface, visualize and save each analyzed image. For (A) apparently living and dead corals, and (B) apparently living corals.246

Table AIV.5 : Mud shrimp case study: Frequency of occurrence of the different types of discrepancies between the visual and the automated analysis.252

Introduction

1 La bioturbation des sédiments marins côtiers

1.1. La bioturbation : un processus clef dans le fonctionnement des écosystèmes

benthiques.

1.1.1. Définition

Le terme bioturbation fait référence à « l'ensemble des processus de transports résultant d'une activité biologique qui affecte directement ou indirectement la matrice sédimentaire. Ces processus de transports incluent à la fois le remaniement sédimentaire et la bioirrigation » (Kristensen et al., 2012). Bien qu'il n'utilise pas exactement ce terme dans sa monographie « *The formation of Vegetable Mould Through the Action of Worms With Observation of Their Habits* », Charles Darwin est considéré comme le précurseur de l'étude de la bioturbation (Darwin, 1881). Il a en effet consacré son dernier ouvrage scientifique à l'étude de la bioturbation du sol. Dans celui-ci, il décrit avec un niveau de détails sans précédent la façon dont des vers de terre participent à la formation des sols, à leur fertilité ainsi qu'aux processus d'érosion et de sédimentation. L'engouement pour l'étude de la bioturbation n'a cependant pas été immédiat. Il aura en effet fallu attendre environ un siècle pour que les scientifiques se rendent compte que les organismes fouisseurs « bioturbent » une très grande partie de la surface de la Terre, y compris le fond des océans (Kristensen et al., 2012; Meysman et al., 2006). Les connaissances sur les processus de bioturbation se sont donc considérablement améliorées lors des dernières décennies. Il est maintenant largement admis que la bioturbation joue un rôle central dans l'écologie des sédiments meubles marins (Rhoads et Young, 1970; Cadée, 2001; Reise, 2002; Lohrer et al., 2004).

1.1.2. Le remaniement sédimentaire

Le remaniement sédimentaire correspond aux transports de particules. Il résulte de l'activité des organismes benthiques, à savoir principalement de la construction et de la maintenance de structures biogéniques (*e.g.*, terriers, tubes, chambres de nutrition), de la locomotion et de la nutrition. A travers ces activités, les organismes benthiques transforment la matrice sédimentaire aussi bien à l'interface eau-sédiment qu'en profondeur. Sous l'action de ces organismes, le sédiment est déstabilisé et décompacté, ce qui entraîne en général une augmentation de sa porosité et de sa perméabilité (Aller, 1980; Aller, 1988; Huettel et Gust, 1992; Volkenborn et al., 2007a; Volkenborn et al., 2009). Le remaniement sédimentaire induit

également des modifications de la topographie ainsi que de la texture de la surface du sédiment ce qui contribue à augmenter sa rugosité (Grigg et al., 2007; Maire et al., 2007a; Rowden et al., 1998). La création et l'entretien de cette rugosité modifient les conditions hydrodynamiques et la cohésion entre les particules sédimentaires, paramètres qui contrôlent les processus d'érosion et d'accrétion du sédiment (Orvain et al., 2012).

Chaque espèce génère un mode de remaniement sédimentaire qui lui est propre et qui dépend notamment de ses caractéristiques éthologiques. La notion de groupe fonctionnel a été introduite de manière à catégoriser les grands types de remaniement sédimentaire en fonction des modes de nutriments, de locomotions et d'autres aspects du mode de vie tel que la construction de terrier. De cette manière, les organismes sont ainsi classiquement répartis en quatre groupes fonctionnels (**Figure I.1**) (François et al., 1997; Kristensen et al., 2012) :

(1) Les **biodiffuseurs** sont des organismes dont l'activité entraîne un transport particulaire continu, dans toutes les directions et sur des distances très courtes, pouvant être assimilé à de la diffusion moléculaire. Ce mode de remaniement sédimentaire peut être divisé en trois sous-groupes : (i) les *biodiffuseurs épigés* qui vivent à la surface du sédiment et déplacent uniquement les particules se situant à l'interface eau-sédiment (*e.g.*, les décapodes *Scopimera* spp. ou *Uca* spp. qui, lorsqu'ils se nourrissent à la surface du sédiment peut remanier 13 g de sédiment sec par jour (Penha-Lopes et al., 2009)), (ii) les *biodiffuseurs superficiels* qui sont des organismes endogés vivant dans la partie supérieure de la colonne sédimentaire (~5 cm) (*e.g.*, le bivalve *Abra ovata* qui remanie les 5 premiers centimètres du sédiment à un taux relativement important, pouvant atteindre $51,6 \text{ cm}^2 \text{ an}^{-1}$ (Maire et al., 2007b)) et (iii) les *biodiffuseurs à galeries* qui sont des organismes construisant un réseau de galeries, dans les 10 à 30 premiers centimètres de la colonne sédimentaire, connectées à la surface (*e.g.*, le polychète *Hediste diversicolor* qui remanie le sédiment autour de son terrier à un taux pouvant atteindre $1,7 \text{ cm}^2 \text{ j}^{-1}$ (Lindqvist et al., 2013)).

(2) Les **convoyeurs vers le haut** sont des organismes positionnés verticalement qui se nourrissent en profondeur dans le sédiment. Les particules ingérées sont ensuite transportées *via* le tube digestif de manière non-locale. Il en résulte à la fois (i) un transport actif de particules depuis la zone de nutrition vers une couche supérieure du sédiment et (ii) un transport passif dû à un affaissement de la colonne sédimentaire au niveau de la cavité créée lors de l'ingestion de particules par l'organisme. Lorsque ces organismes sont en contact avec la surface du sédiment, ils provoquent l'éjection de particule à l'interface eau-sédiment (*e.g.*,

la population d'*Arenicola marina* de la mer de Wadden qui dépose en moyenne $400 \text{ cm}^3 \text{ m}^{-2} \text{ an}^{-1}$ de particule sur l'interface eau-sédiment (Cadée, 1976)).

(3) Les **convoyeurs vers le bas** sont des organismes également positionnés verticalement mais qui se nourrissent à la surface du sédiment. Ces organismes génèrent un remaniement sédimentaire de l'interface benthique où ils sélectionnent les particules ingérées qui sont ensuite transportées de manière non-locale et éjectées sous forme de fèces dans des couches plus profondes du sédiment. Lors de la construction ou de la maintenance de leurs structures biologiques, les organismes appartenant à ce groupe peuvent induire un déplacement non-sélectif de particules vers la surface du sédiment (*e.g.*, le polychète *Cirriformia grandis* qui sélectionne préférentiellement les particules comprises entre 32 et 63 μm et les transporte à plus de 5 cm sous la surface (Shull et Yasuda, 2001))

(4) Les **régénérateurs** sont des organismes qui transportent des particules de la colonne sédimentaire vers la surface du sédiment lors de la construction ou de l'entretien de leurs terriers temporaires. Un transport passif inverse intervient lorsque le courant fait tomber les particules de surface à l'intérieur du terrier ou lorsque celui-ci est détruit (*e.g.*, les décapodes appartenant au genre *Uca* qui construisent des terriers de plus de 10 cm de profondeur et dont un seul individu peut excaver jusqu'à 20 g j^{-1} de sédiment sec (Penha-Lopes et al., 2009)).

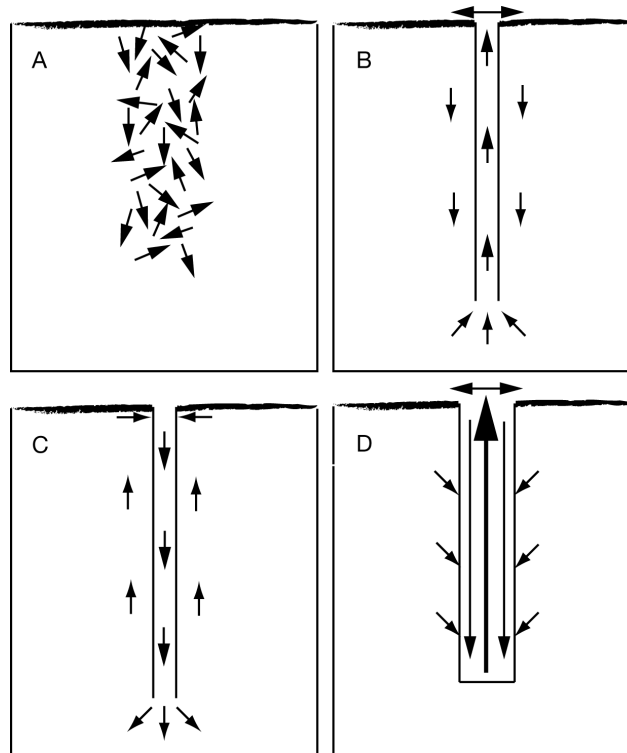


Figure I.1 : Les quatre types majeurs (*i.e.*, groupes fonctionnels) de remaniement sédimentaire effectués par la macrofaune benthique dans les écosystèmes marins. (A) biodiffuseurs, (B) convoyeur vers le haut, (C) convoyeur vers le bas et (D) régénérateur (D'après Kristensen et al., 2012)

La diversité fonctionnelle (*i.e.*, le nombre de groupes fonctionnels différents présents sur un site d'intérêt) est maintenant reconnue comme un paramètre primordial dans le contrôle de l'intensité de la bioturbation (Mermillod-Blondin et al., 2005). Cependant, la classification d'un organisme dans une de ces catégories n'est pas toujours évidente. Un même organisme peut, en effet, présenter simultanément ou successivement plusieurs activités résultant chacune en des modes de bioturbation différents. Par exemple, la construction de terrier par les crabes violonistes (*Uca* spp.) amènerait à les classer parmi les régénérateurs alors que leur activité de nutrition à la surface du sédiment suggère plutôt de les classer parmi les biodiffuseurs épigés. Dans ce type de cas, c'est l'activité dominante qui est considérée pour classer l'espèce dans un groupe fonctionnel. Des espèces appartenant au même genre peuvent également avoir des modes de remaniement sédimentaire différents (Maire et al., 2006). La classification d'un organisme au sein d'un (ou plusieurs) groupe fonctionnel nécessite donc des connaissances précises de l'éthologie de l'espèce en question. L'assimilation d'une espèce à un groupe fonctionnel par analogie morphologique ou spécifique n'est pas satisfaisante et ce tout particulièrement lorsque l'objectif est de déterminer le potentiel de bioturbation d'une communauté (Solan et al., 2004a) qui somme les potentiels de bioturbation des espèces composant cette communauté, eux-mêmes dérivés de la classification de ces espèces dans les différents groupes fonctionnels (*e.g.*, Queirós et al., 2013). Il est donc essentiel d'étudier de manière précise le comportement et le mode de transport des particules sédimentaires pour chaque espèce avant de les classer parmi un ou plusieurs groupes fonctionnels. *C'est pourquoi l'étude comportementale d'Upogebia pusilla a constitué un objectif central de mon travail de thèse.*

1.1.3. La bioirrigation

Un des principaux défis pour les organismes endogés est de survivre dans un habitat où la disponibilité en oxygène est limitée. En effet, dans un sédiment cohésif riche en matière organique, l'oxygène pénètre typiquement dans les premiers millimètres de la colonne sédimentaire. Ainsi, pour pouvoir vivre dans des sédiments majoritairement anoxiques, les organismes fouisseurs doivent constamment maintenir une connexion avec l'eau surnageante qui est plus riche en oxygène. Dans ce but, certains organismes utilisent des structures morphologiques spécialisées (*e.g.*, le siphon inhalant des mollusques bivalves) alors que d'autres (*e.g.*, polychètes et crustacés) construisent et maintiennent des structures biogéniques à l'intérieur de la colonne sédimentaire. Ces structures augmentent significativement la surface de l'interface eau-sédiment ce qui favorise l'irrigation passive (*i.e.*, par diffusion) du sédiment. Leur ventilation (*i.e.*, la génération d'un flux d'eau au sein de la structure)

augmente activement les échanges d'eau entre l'eau interstitielle et l'eau surnageante (*i.e.*, la bioirrigation). En ventilant leurs structures, les organismes endogés modifient, en effet, (1) les gradients de solutés entre l'eau interstitielle et l'eau du terrier, moteur des transports diffusifs (Aller, 2014) et (2) le niveau de pression hydraulique à proximité de l'organisme ce qui engendre un transport advectif d'eau dans toutes les directions vers ou à partir de l'organisme (Volkenborn et al., 2012; Wethey et al., 2008; Woodin et al., 2010). L'intensité de ces transports dépend également des propriétés physiques du sédiment (comme la porosité et la perméabilité) qui sont elles-mêmes affectées par le remaniement sédimentaire. Les augmentations de la porosité et de la perméabilité facilitent en effet les échanges entre la colonne sédimentaire et la colonne d'eau (Huettel et Gust, 1992; Volkenborn et al., 2007a; Volkenborn et al., 2009).

La modification de la topographie de la surface du sédiment par les organismes benthiques (*cf.* paragraphe 1.1.2. Le remaniement sédimentaire) affecte également les échanges entre l'eau interstitielle et l'eau surnageante. La présence de monticules ou de cônes de nutrition et les mouvements de l'eau surnageante génèrent en effet des variations de pression le long de l'interface eau-sédiment qui favorisent la pénétration d'eau dans la colonne sédimentaire (*i.e.*, bioirrigation passive (Røy et al., 2005, 2002; Volkenborn et al., 2007b)).

1.1.4. Rôle de la bioturbation dans les processus de diagénèse précoce

Dans les sédiments marins côtiers, la minéralisation de la matière organique dépend largement des métabolismes microbiens (Glud et al., 2003) lesquels sont tributaires de la disponibilité en ressources (*i.e.*, matière organique) et des conditions abiotiques (*i.e.*, potentiel redox et température). L'absence de bioturbation conduit à la création d'un sédiment dit « laminé » présentant des strates horizontales bien distinctes. L'apport de matière organique depuis la colonne d'eau est la principale ressource pour les microorganismes hétérotrophes du sédiment. Dans ces conditions, la voie de minéralisation de la matière organique est contrôlée par des transports diffusifs résultant en une stratification verticale des accepteurs finaux d'électrons (**Figure I.2**). Typiquement, cette séquence suit l'ordre suivant (de la surface vers le fond) qui est fonction du rendement d'énergie libre de réaction redox : O_2 , NO_3^- , MnO_2 , Fe_2O_3 , SO_4^{2-} , CO_2 (Froelich et al., 1979).

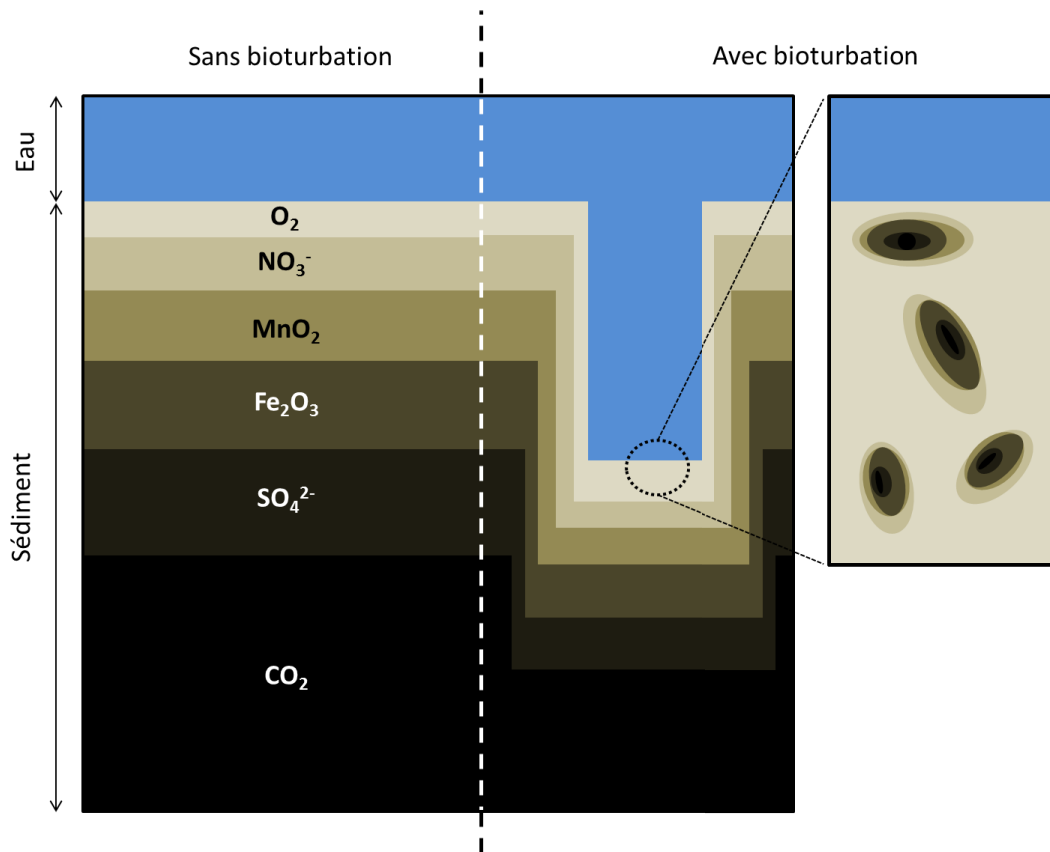


Figure I.2 : Stratification théorique des accepteurs d'électrons dans les sédiments marins sans et avec bioturbation. Modifié d'après Aller (1982)

En mélangeant des particules de sédiment, les organismes bioturbateurs déplacent la matière organique qui leur est associée. De la matière organique labile se trouve ainsi transportée en profondeur dans la colonne sédimentaire et réciproquement, de la matière organique réfractaire est déposée à la surface du sédiment. De cette manière, les organismes bioturbateurs modifient la disponibilité des ressources pour les microorganismes. Le remaniement sédimentaire induit également la compaction du sédiment lors de la construction de structure, et sa décompaction lorsqu'il est excavé. La modification de ces propriétés physiques du sédiment joue un rôle majeur dans le fonctionnement des écosystèmes benthiques puisqu'elle facilite ou restreint le transport des solutés oxydants nécessaires au métabolisme des microorganismes. D'autre part, la ventilation des structures biogéniques favorise l'approvisionnement en oxygène de la colonne sédimentaire transformant ainsi la simple zonation verticale de la distribution spatiale des accepteurs finaux d'électrons en un réseau tridimensionnel bien plus complexe. Les organismes bioturbateurs introduisent ainsi un degré important d'hétérogénéité spatiale et augmentent le nombre de micro-niches écologiques (*e.g.*, terriers oxydés dans un sédiment anoxique ou au contraire fèces anoxiques dans un terrier oxygène) (**Figure I.2**).

Parce que l'oxygène est l'accepteur final d'électron le plus favorable énergétiquement (Glud, 2008), les augmentations associées des ressources disponibles et de la concentration en oxygène stimulent l'activité de minéralisation aérobie de la matière organique par les microorganismes (Mermillod-Blondin et Rosenberg, 2006). De plus, l'oxygène sert d'oxydant aux métabolites réduits produits par des processus anaérobies de minéralisation de la matière organique (*e.g.*, NH_4^+ , H_2S et CH_4) ce qui (1) diminue la concentration de ces composés réduits et (2) augmente la concentration de leurs formes oxydées (NO_x , SO_4^{2-} , CO_2 , respectivement) et favorise ainsi les processus de minéralisation anaérobies. Par conséquent, la bioturbation a une forte influence sur les taux et les voies de minéralisation de la matière organique et diminue ainsi le stockage de la matière organique dans les sédiments.

2 Les crustacés décapodes thalassinidés

2.1 Taxinomie

Les espèces appartenant au groupe des Euarthropoda, Crustacea, Malacostraca, Decapoda, Thalassinidea sont des organismes endogés dont la morphologie générale se rapproche de celle du groupe des Malacostraca, Decapoda, Caridea qui englobe les organismes ordinairement désignés par le terme « crevette » (**Figure I.3**). De ce fait, les thalassinidés sont communément appelés « crevettes de vase », « crevettes fouisseuses » ou encore, et plus localement, « machottes ». Dans la littérature anglo-saxonne, ces organismes sont regroupés sous les termes « mud shrimp », « mud prawn », « ghost shrimp », « sand prawn » ou, plus rarement et principalement en Australie, « marine yabby ».

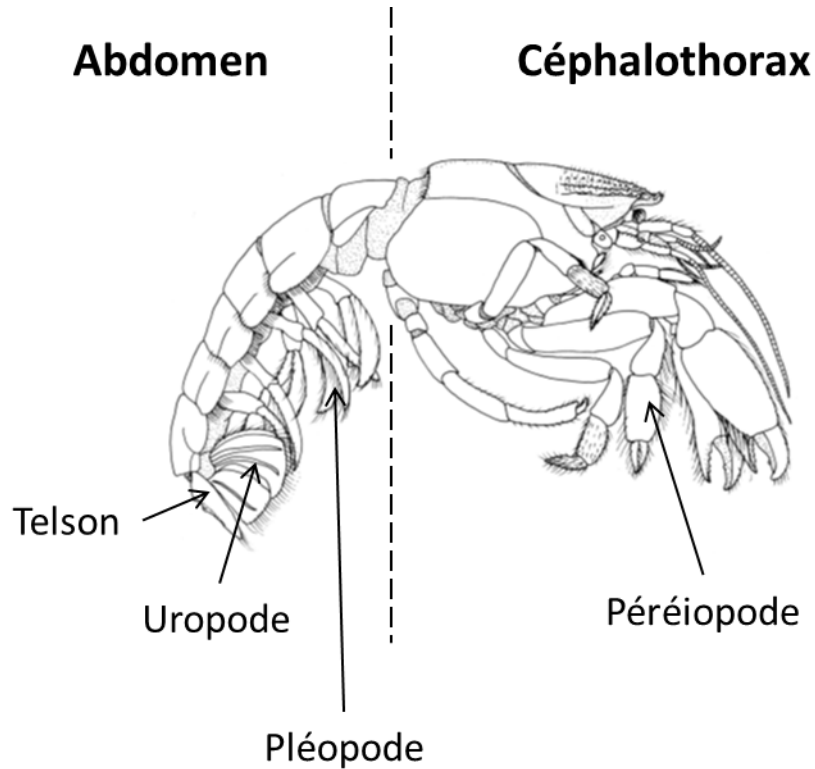


Figure I.3 : Morphologie général d'un crustacé thalassinidé. Le céphalothorax supportant 5 paires de péréiopodes et l'abdomen supportant une paire de pléopodes par segment (5 paires), un telson et deux paires d'uropodes et. (Modifié d'après Liu, 2015)

Le groupe des Thalassinidea tel que décrit par Felder (2001) est composé de 11 familles, 96 genres et regroupe approximativement 550 espèces. Cependant, ce groupe est actuellement considéré comme paraphylétique et a désormais été remplacé dans la classification phylogénétique récente par deux clades distincts (*i.e.*, Gebiidea et Axiidea) (Robles et al., 2009). Cette nouvelle classification est synthétisée dans le **Tableau I.1**.

Tableau I.1 : Classification phylogénétique actuelle tel que décrite par Bracken et al., (2009) et Robles et al., (2009) des différents groupes classés parmi les clades des Gebiidea et des Axiidea

« Thalassinidea »	
Gebiidea	Axiidea
Laomediidae <i>Jaxea, Laomedia</i>	Axiidae <i>Calaxius, Calocarides, Calocaris, Calastacus, Eiconaxius</i>
Thalassinidae <i>Thalassina</i>	Callianassidae <i>Biffarius, Callianassa, Callichirus, Calliax, Corallianassa, Corallichirus, Eucalliax, Glypturus, Lepidophtalmus, Neocallichirus, Neotrypaea, Nihonotrypaea, Pestarella, Sergio</i>
Upogebiidae <i>Acutigebia, Aethogebia, Austinogebia, Potamogebia, Upogebia</i>	
Axianassidae <i>Axianassa</i>	Callianadeidae <i>Callianidea, Crosniera, Thomassina</i>
	Ctenochelidae <i>Ctenochelas</i>
	Micheleidae <i>Meticonaxius, Michelea</i>
	Strahlaxiidae <i>Neaxius, Strahlaxius</i>

Cependant, parce que (1) les Gebiidea et les Axiidea ont des traits fonctionnels très similaires et que (2) le terme « Thalassinidea » est largement établi dans la littérature, j'ai choisi d'utiliser ce dernier (ou plus particulièrement le terme français « thalassinidé ») dans mon manuscrit de thèse puisqu'il permet de faire référence à l'ensemble des crevettes de vase, tout en reconnaissant que ce groupe est paraphylétique.

2.2 Distribution

Les thalassinidés sont distribués dans tous les écosystèmes intertidaux et subtidaux à sédiment meuble à l'exception des zones polaires. Leur diversité spécifique augmente graduellement des pôles vers les tropiques et atteint son maximum dans la zone tropicale (**Figure I.4**). Ces espèces colonisent en général les environnements côtiers dont la bathymétrie est comprise entre 0 et 200 m de profondeur. Néanmoins, deux espèces du clade des Axiidae ont été retrouvées à plus de 2000 m de profondeur (Dworschak, 2000). Les espèces appartenant aux clades des Callianassidae, Upogebiidae et Thalassinidae colonisent préférentiellement des zones peu profondes, intertidales et subtidales ne dépassant pas les 20

m de profondeur (Dworschak, 2000). La plupart de ces espèces colonisent des sédiments nus mais certains thalassinidés, essentiellement suspensivores, semblent étroitement associés aux herbiers de phanérogames.

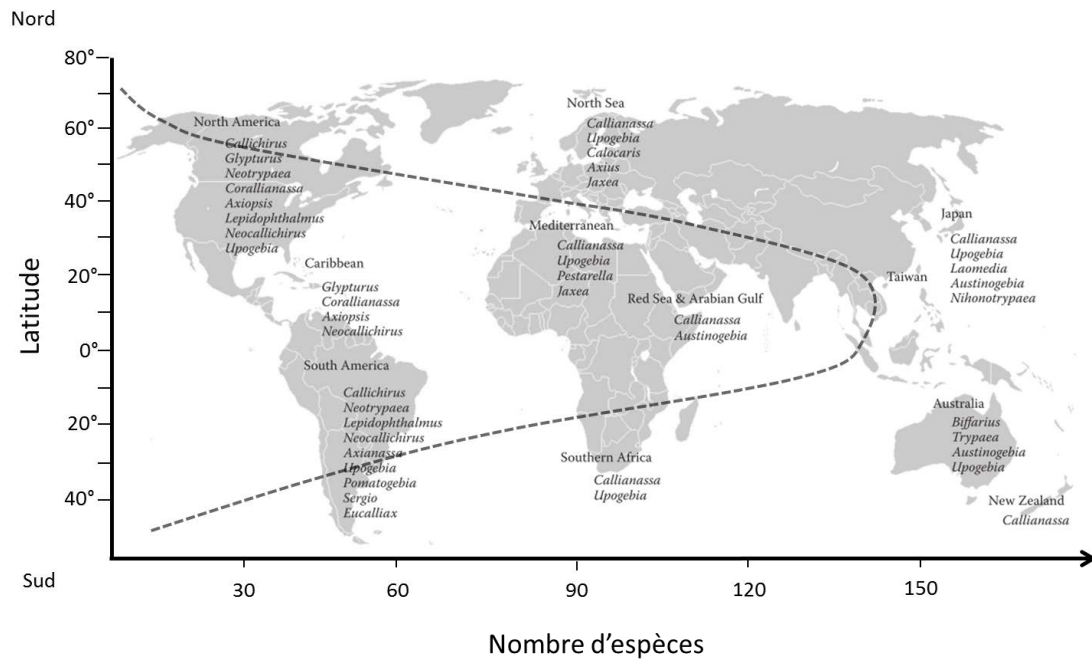


Figure I.4 : Distribution mondiale des groupes majeurs de thalassinidés et répartition du nombre d'espèces de thalassinidés en fonction de la latitude. Modifié d'après Dworschak, 2000 et Pillay et Branch, 2011.

Les herbiers de phanérogames sont constitués des seules plantes à fleurs adaptées à la vie marine en immersion. Les herbiers jouent un rôle structurant important pour les communautés benthiques mais également dans les transferts de matière organique et d'énergie entre les écosystèmes (Hemminga et Duarte, 2000). Alors que leurs racines et rhizomes stabilisent le sédiment, leurs feuilles qui constituent la canopée modifient l'hydrodynamisme local en formant des zones à faible énergie (Ganthy et al., 2015) permettant de piéger la matière organique en suspension. Ils fournissent également un abri contre la prédation et une zone riche en nourriture à une faune et une flore des plus diversifiées au monde (Hemminga et Duarte, 2000). Les herbiers servent en outre de zone de nurserie pour de nombreux organismes (Heck et al., 2003). La majorité des études traitant des interactions entre organismes bioturbateurs et herbiers de phanérogames met en évidence des mécanismes d'exclusion mutuelle répertoriés sous le terme de « guerre biomécanique » (« biomechanical warfare ») (van Wesenbeeck et al., 2007). En effet, les herbiers contraignent l'installation des grands organismes bioturbateurs en stabilisant et en compactant le sédiment. Ce mécanisme empêche leur pénétration dans le sédiment et/ou limite leur mobilité dans la

colonne sédimentaire (Brenchley, 1982; Philippart, 1994). A l'inverse, les organismes bioturbateurs déstabilisent le sédiment et favorisent les phénomènes de resuspension (*cf.* paragraphe 1.1.2. Le remaniement sédimentaire). Ce processus diminue la clarté de l'eau et limite ainsi les apports radiatifs nécessaires à la photosynthèse des plantes en : augmentant la turbidité de l'eau et en recouvrant les jeunes pousses de sédiment (Philippart, 1994; van Wesenbeeck et al., 2007). L'activité de fouissage des organismes bioturbateurs est également susceptible d'endommager le système racinaire et rhizomial ainsi que d'enfouir leurs graines à des profondeurs non favorables à leur germination (Brenchley, 1982; Dumbauld et Wyllie-Echeverria, 2003; Valdemarsen et al., 2011; van Wesenbeeck et al., 2007). Ce dernier point est cependant à nuancer puisque qu'il a été montré que l'enfouissement des graines d'herbiers par *Hediste diversicolor*, *Arenicola marina* et *Marenzelleria viridis* pourrait également favoriser : (1) leur survie en réduisant la pression de prédation et (2) leur germination via les processus de digestion ou d'usure contre les particules sédimentaires (Delefosse et Kristensen, 2012). La présence de petits individus bioturbateurs (adultes ou juvéniles) est par ailleurs susceptible de favoriser la croissance des herbiers en diminuant la teneur en composés réduits toxiques sans causer de dommage aux racines (Suykerbuyk et al., 2012).

Ces processus d'exclusion mutuelle sont particulièrement intenses entre les thalassinidés et les herbiers de phanérogames. Suchanek (1983) a par exemple montré à partir d'observations *in-situ* que le taux de recouvrement de l'herbier de *Thalassia testudinum* était négativement corrélé avec la densité de quatre espèces appartenant au clade des Callianassidae. La survie de cet herbier était aussi réduite lorsqu'il était transplanté dans une zone de fortes densités de Callianassidae, suggérant que ces derniers étaient capables d'exclure les herbiers de leur habitat naturel. Siebert et Branch (2006) ont réalisé la même expérience en transplantant l'herbier de *Zostera capensis* dans une zone colonisée par *Callianassa kraussi*. Dans cette expérience, la transplantation de *C. kraussi* élimine l'herbier et réciproquement, la transplantation d'herbier induit une réduction du nombre de *C. kraussi*. L'ensemble des effets négatifs des thalassinidés sur les herbiers de phanérogames est synthétisé dans la **Figure I.5**.

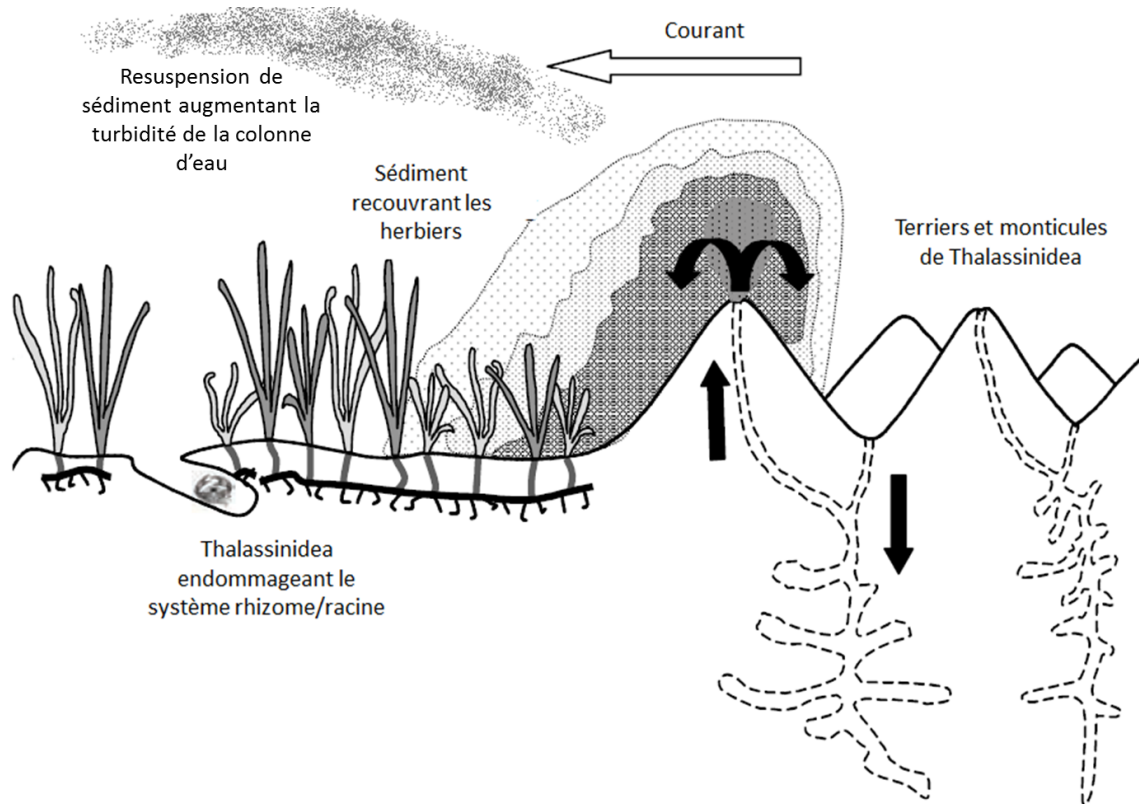


Figure I.5 : Mécanismes potentiels des effets négatifs des thalassinidés sur les herbiers de phanérogames (Modifié d'après Dewitt, 2009)

Ainsi, il a longtemps été admis que les thalassinidés et les herbiers présentent systématiquement des relations d'exclusion mutuelle. Il s'avère en réalité que la nature de ces interactions dépend étroitement de la biologie de l'espèce de thalassinidé impliquée et tout particulièrement de son régime trophique. Par exemple, Siebert et Branch (2006) ont montré une forte interaction négative entre *Z. capensis* et le thalassinidé déposivore *C. kraussi* mais à l'inverse une corrélation positive entre ces zostères et le suspensivore *Upogebia africana*. Les interactions différentes entre ces deux thalassinidés et l'herbier sont dues au fait que *C. kraussi* modifie plus intensément la structure du sédiment qu'*U. africana*. Il n'est toutefois pas impossible que *C. kraussi* exclue également *U. africana* qui trouve refuge au sein de l'herbier. Cependant, ces auteurs observent lors de leurs expériences que lorsque *U. africana* est transplantée dans un herbier elle devient bien plus abondante que dans les sédiments vaseux qu'elle colonise habituellement. La corrélation positive entre l'herbier et *U. africana* ne serait donc pas une conséquence de l'exclusion de *C. kraussi* dans les herbiers, mais plutôt due au fait que l'herbier fournit à *U. africana* un sédiment stable et probablement une plus grande quantité de matière organique en suspension. Ces conditions sont en effet optimales

pour construire un terrier quasi-permanent et pour optimiser l'acquisition de ressources trophiques par un organisme suspensivore.

2.3 Morphologies des terriers

La plupart des thalassinidés sont des organismes endogés qui vivent dans des terriers plus ou moins complexes, considérés comme permanents (*i.e.*, la structure du terrier varie peu au cours du temps) ou semi-permanents (*i.e.*, des extensions au terrier sont fréquemment construites et des anciennes galeries abandonnées). Leurs morphologies sont extrêmement diverses et dépendent notamment du régime trophique de l'occupant. Les organismes considérés comme suspensivores, dont la plupart des espèces appartiennent au groupe des Upogebidae, construisent des terriers relativement simples, le plus souvent en forme de « U » (Atkinson et Taylor, 2005) (**Figure I.6A**). Cette morphologie facilite la création d'un courant unidirectionnel par l'organisme pour faire pénétrer dans son terrier la matière organique présente à l'interface benthique dont il se nourrit (Abed-Navandi et al., 2005; Dworschak, 1987a; Dworschak et al., 2006). Chez certaines espèces, ces terriers présentent une extension verticale partant de la base du « U » leur conférant une forme générale dite en « Y » (**Figure I.6A**). Cette seconde galerie peut servir à stocker provisoirement du sédiment ou des débris (*e.g.*, coquilles, racines/rhizomes) excavés lors de la maintenance ou de l'extension du terrier. Elle peut également avoir un rôle de refuge en cas de perturbation (*e.g.*, dessiccation pour les espèces intertidales) ou de risque de prédation (Atkinson et Taylor, 2005). Certaines sections du tube ont un diamètre supérieur à la largeur du corps de l'organisme ce qui lui permet de se retourner plus facilement dans son terrier. Ces zones appelées « chambres de retournement » sont disposées le long du terrier, en particulier au niveau des zones d'inflexion (*i.e.*, partie coudée en bas des tubes verticaux formant le « U ») et de bifurcation (*e.g.*, liaison entre la base du « U » et l'extension verticale) (Dworschak 1983; Astall et al., 1997, L.P. observations personnelles). Quelle que soit l'espèce considérée, le nombre de chambres de retournement dépend directement de la longueur et de la profondeur du terrier (Dworschak, 1983, L.P. observations personnelles).

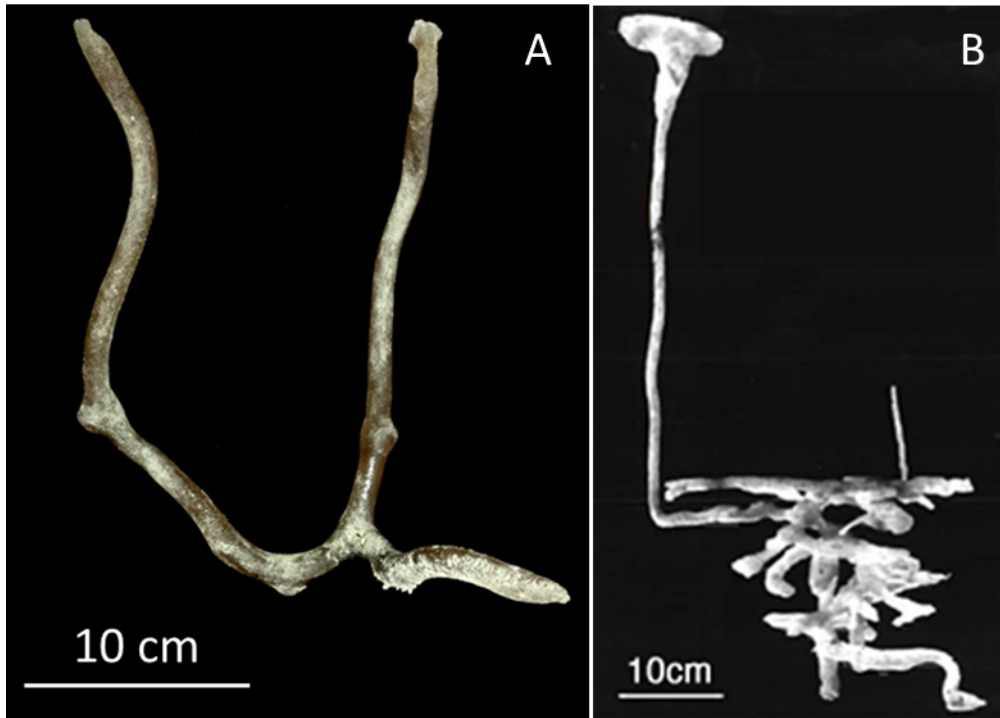


Figure I.6 : Photographie de moulage de terrier d'*Upogebia pusilla* (A ; photo L. Pascal) et de *Callianassa subterranea* (B ; photo Nickell et Atkinson, 1995).

Les terriers les plus complexes sont très souvent caractéristiques d'un régime trophique de type dépositore, particulièrement répandu chez les organismes du groupe des Callianassidae. Ces organismes construisent des terriers présentant une première section composée d'une unique galerie ouverte à la surface du sédiment et s'enfonçant verticalement à plusieurs dizaines de centimètres en profondeur, puis se divisant en plusieurs branches plus ou moins courtes et tortueuses (Nickell et Atkinson, 1995) (**Figure I.6B**). Cette seconde section très ramifiée est le résultat d'une activité de fouissage intense liée à la recherche de nourriture (Atkinson et Taylor, 2005). Certaines de ces branches peuvent également servir de zone de « culture¹ » au sein desquelles certaines espèces, telle que *Neaxius acanthus* (famille des Strahlaxiidae), stockent des débris de phanérogames ou d'algues afin de stimuler la croissance de microorganismes (bactérie et/ou meiofaune) qui seront eux-mêmes consommés par la suite (Dworschak, 1987a; Coelho et al., 2000; Atkinson et Taylor, 2005; Kneer et al., 2008).

Il est néanmoins important de noter que la plupart des thalassinidés, comme de nombreuses autres espèces d'organismes macrobenthiques (Riisgård et Kamermans, 2001; Maire et al., 2006), n'ont pas un mode d'alimentation strict et qu'ils peuvent rapidement

¹ « culture » est une traduction explicite et imparfaite du terme anglais « gardening »

passer d'un mode à un autre (dépositore → suspensore, et *vice-versa*) en fonction de la quantité et de la qualité de la nourriture disponible (Nickell et Atkinson, 1995). *U. pusilla* qui est considérée comme une espèce principalement suspensore peut par exemple, lorsque la quantité de matière organique présente dans l'eau est faible, mettre en suspension du matériel déposé dans le terrier, ou se nourrir directement par ingestion de sédiment collecté sur la paroi de ce même terrier (Dworschak, 1987a). Le lien entre morphologie du terrier et régime trophique peut être alors plus complexe à établir. Certaines espèces vont même jusqu'à construire des terriers avec des sections spécifiquement adaptées aux différents modes de prélèvement de la nourriture. Ainsi, le terrier de l'espèce *Jaxea nocturna* (clades des Laomediidae) présente systématiquement une première section superficielle en forme de « U » dédiée à un mode de nutrition de type suspensore, lorsque la quantité de matière organique présente dans l'eau surnageante est suffisante. En profondeur, une seconde section composée de nombreuses branches rend compte au contraire d'une activité de type dépositore adoptée par l'organisme lorsque la quantité de nourriture en suspension descend sous un seuil critique (Nickell et Atkinson, 1995).

De la même manière que l'architecture générale, les dimensions des terriers varient largement en fonction du régime trophique. Ainsi, les espèces suspensores du genre *Upogebia* (e.g., *Upogebia omissa*, *U. pusilla* et *U. stellata*) construisent en moyenne des terriers de 20 à 30 cm de profondeur, correspondant à une augmentation de 290 % la surface d'échange entre l'eau et le sédiment (Dworschak, 1983; Nickell et Atkinson, 1995; Coelho et al., 2000). Les terriers d'*U. major* peuvent cependant être beaucoup plus profonds et atteindre plus de 200 cm de profondeur (Kinoshita, 2002). De manière générale, les terriers sont généralement plus profonds chez les dépositores. Ils s'étendent ainsi fréquemment verticalement sur plus de 70 cm chez *Callianassa subterranea* (Nickell et Atkinson, 1995) et peuvent même atteindre 250 cm de profondeur chez *C. truncata* et *C. louisianensis* (Phillips, 1971; Ziebis et al., 1996). L'augmentation de la surface d'échange eau-sédiment peut alors être supérieure à 400 % (Ziebis et al., 1996). Les dimensions des terriers de thalassinidés varient également en fonction de nombreux facteurs environnementaux. Les terriers sont, par exemple, généralement plus profonds et plus étendus dans les sédiments vaseux que sableux (Rowden et Jones, 1995). La compétition interspécifique pour les ressources favorise par ailleurs la construction de structures plus profondes (Peterson, 1977).

2.4 Les thalassinidés : Les plus grands bioturbateurs des écosystèmes marins ?

Lors de la construction et de la maintenance de leurs terriers, les thalassinidés déplacent de grands volumes de sédiment qui sont rapidement éjectés à l'interface benthique, bien qu'une partie puisse être compactée le long des parois ou stockée provisoirement dans une galerie particulière. Le sédiment excavé étant systématiquement décompacté, mélangé et fluidifié par les activités de fouissage et de transport, une part plus ou moins importante du volume éjecté (qui dépend directement de la taille des particules, de leur cohésion ainsi que de l'hydrodynamisme à l'interface eau-sédiment), est mise en suspension et emportée à distance par les courants. La partie restante s'accumule autour des ouvertures du terrier et forme progressivement des monticules qui peuvent atteindre plusieurs centimètres de hauteur. De telles structures mesurent en moyenne 5 cm de haut chez *C. subterranea* (Rowden et al., 1998) et jusqu'à 9 cm chez *C. truncata* (Ziebis et al., 1996, voir **Figure I.7**). La mesure du volume ou de la masse de sédiment éjecté à l'interface (dénommé « sediment turnover » dans la littérature) est l'unique manière utilisée, jusqu'à présent, pour quantifier le remaniement sédimentaire chez les thalassinidés. Plusieurs méthodes ont été développées et mises en œuvre pour estimer ces taux. Swinbanks et Luternauer (1987) ont par exemple calculé, en utilisant une méthode de nivelage *in situ*, un taux de $18 \text{ mL ind}^{-1} \text{ j}^{-1}$ pour *Neotrypaea californiensis* alors que Suchanek (1983) en piégeant le sédiment éjecté hors du terrier d'individus du genre *Callianassa* spp. a estimé un taux de $0.004 \text{ kg (sec) m}^{-2} \text{ j}^{-1}$. La diversité des méthodes utilisées rend cependant la comparaison entre études et espèces particulièrement compliquée. Pour cette raison, Rowden et Jones (1993) ont proposé de standardiser la méthode de quantification en : (1) utilisant les méthodes de piégeage considérées comme plus pratiques à mettre en œuvre et plus précises, et (2) exprimant la quantité de sédiment en poids sec plutôt qu'en volume. Par la suite, Stamhuis et al., (1997) puis Rowden et al. (1998) ont estimé des taux allant de 11 à $20.6 \text{ kg (sec) m}^{-2} \text{ an}^{-1}$ pour *Callianassa subterranea*, et Berkenbusch et Rowden (1999) des taux allant jusqu'à $96 \text{ kg (sec) m}^{-2} \text{ an}^{-1}$ pour *C. filholi*. A ma connaissance, il n'existe aucun taux de « sediment turnover » estimé pour les thalassinidés suspensivores. Le paradigme actuel est que, du fait de leur régime trophique, les thalassinidés suspensivores expulseraient moins de sédiment hors de leur terrier que les déposivores (voir la revue par Pillay et Branch (2011), paragraphe « Thalassinidean-macrofauna interactions »).

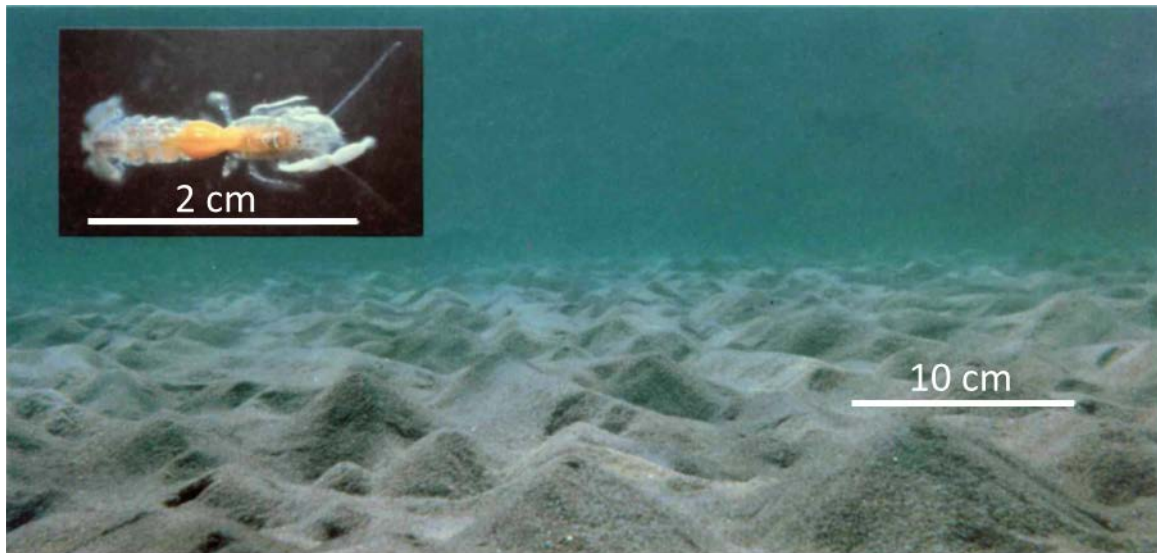


Figure I.7 : Topographie du sédiment de surface en présence de *Callinassa truncata* (insert) dans la baie de Campese (Italie). D'après Ziebis et al., (1996)

Il est également important de noter que la mesure du « sediment turnover » considère uniquement les déplacements de sédiment verticaux depuis les couches profondes vers la surface sédimentaire. Elle néglige ainsi totalement l'ensemble des processus de transport particulaire limités aux couches de subsurface. Pourtant, ces derniers sont susceptibles de représenter une proportion non-négligeable (voire potentiellement dominante) du remaniement sédimentaire total engendré par les thalassinidés puisque Dworschak (1983) a estimé chez *U. pusilla*, en comparant le volume du terrier à celui du sédiment expulsé à la surface, que seulement 50 % du volume du terrier était finalement éjecté à la surface. Afin de mieux comprendre le rôle des thalassinidés, *via* leur activité de bioturbation, dans le fonctionnement des écosystèmes marins, il semble particulièrement important de caractériser et de quantifier la totalité du remaniement sédimentaire incluant donc l'ensemble des processus de transport particulaires de subsurface. *Ainsi, un des objectifs de ma thèse a été de caractériser et de quantifier le remaniement sédimentaire total engendré par U. pusilla en portant une attention toute particulière au remaniement sédimentaire intervenant sous l'interface eau-sédiment.*

Pour survivre dans un environnement particulièrement pauvre en oxygène, les thalassinidés, comme tous les organismes endogés, ventilent leurs terriers. Le temps consacré à la ventilation et la fréquence de ces événements varient selon le régime trophique de l'organisme. En effet, les organismes dépositores ventilent leur terrier pour maintenir un niveau d'oxygène adéquat pour la respiration et évacuer les déchets métaboliques qui s'accumulent progressivement alors que les suspensivores utilisent également ce

comportement pour s'alimenter en filtrant la matière en suspension. De ce fait, les thalassinidés suspensivores ventilent plus fréquemment leur terrier et y consacrent plus de temps que les déposivores (Stamhuis et al., 1996). *U. pusilla* (suspensivore) ventile par exemple son terrier en moyenne toutes les 10 min et y consacre 50 % de son temps (Dworschak, 1981) alors que *C. subterranea* (déposivore) ventile son terrier toutes les 40 min (Forster et Graf, 1995) et y consacre seulement 8 % de son temps (Stamhuis et al., 1996). De telles différences se traduisent par des taux de ventilation bien plus élevés chez les thalassinidés suspensivores (atteignant 900 mL h⁻¹ chez *U. pusilla*, Dworschak, 1981) que les déposivores (compris entre 29 et 63 mL h⁻¹ chez *C. japonica*, Koike et Mukai, 1983). L'activité de ventilation stimule la bioirrigation du sédiment en favorisant les échanges entre l'eau interstitielle et l'eau surnageante (cf. paragraphe 1.1.3. La bioirrigation). Bien que la littérature soit relativement riche en ce qui concerne des taux de ventilation des terriers (e.g., Dworschak, 1981; Aller et al., 1983; Koike et Mukai, 1983; Forster et Graf, 1995; Astall et al., 1997), il n'existe, à ma connaissance, aucun véritable taux de bioirrigation mesuré en milieu contrôlé chez les thalassinidés. Toutefois, Webb et Eyre (2004) ont mesuré *in situ* un taux de bioirrigation de 367 L m⁻² d⁻¹ en présence de *Trypaea australiensis*. Cette valeur fait partie des plus élevées jamais mesurées pour des organismes reconnus comme de grands bioirrigateurs tel qu'*Arenicola marina* et *Hediste (Nereis) spp.* (Kristensen, 2001; Rao et al., 2014). Compte tenu du fait que *T. australiensis* est un organisme déposivore, le taux de bioirrigation du sédiment en présence d'un thalassinidé suspensivore devrait *a priori* être encore supérieur. Il est toutefois important de noter que l'intensité de bioirrigation est tributaire des propriétés physiques du sédiment (cf. paragraphe 1.1.3 Bioirrigation). *Un des objectifs de ma thèse a été d'évaluer l'influence d'*U. pusilla* sur la bioirrigation d'un sédiment faiblement perméable.* Au vu de l'ensemble de ces données, il apparaît de façon claire que les thalassinidés ont, à l'échelle de l'individu, un fort potentiel de bioturbation. Cependant, l'impact à l'échelle d'un écosystème dépend également des densités auxquelles ces organismes sont retrouvés. *Un autre objectif de ma thèse a donc consisté à déterminer la distribution spatiale et les densités d'*U. pusilla* à l'échelle du bassin d'Arcachon. Ce point s'avère indispensable pour extrapoler les résultats obtenus (en laboratoire) à l'échelle de l'écosystème.*

Les thalassinidés font partie des organismes les plus communs parmi la macrofaune des écosystèmes côtiers et estuariens (Dworschak, 2000) dans lesquels ils sont souvent retrouvés en (très) forte densité. Par exemple, la densité de *Callinassa truncata* estimée dans la baie de Campese en Italie (**Figure I.7**) est de 120 individus m⁻² (Ziebis et al., 1996). En

moyenne, 75 individus de *T. australiensis* ont été recensés au mètre carré par Contessa et Bird (2004) sur la côte Sud de l'Australie, 161 ind. m⁻² d'*U. pugettensis* dans la baie de Yaquina (Oregon, USA) par D'Andrea et DeWitt (2009) et plus de 650 ind. m⁻² de *Lepidophthalmus sinuensis* sur la côte caribéenne colombienne (Nates et Felder, 1998). Dworschak (1987b) a mis en évidence un lien entre la densité d'*U. pusilla* et la taille des individus avec des densités atteignant un maximum de 2420 ind. m⁻² pour des organismes de petite taille (longueur totale allant de 12 mm à 37 mm) contre 92 ind. m⁻² pour de plus gros organismes dont la longueur totale variait entre 46 et 52 mm. De telles densités, associées à une activité de bioturbation intense ont conduit Cadée (2001) à considérer les thalassinidés comme faisant partie des organismes bioturbateurs les plus importants des sédiments meubles marins.

Via leur activité de bioturbation, les thalassinidés influencent en effet fortement les caractéristiques de leur habitat sédimentaire. Une telle modification affecte aussi bien les communautés benthiques qui lui sont associées que les processus biogéochimiques sédimentaires entraînant des boucles de rétroactions complexes. L'influence des thalassinidés sur le fonctionnement des écosystèmes est schématisée dans la **Figure I.8** et est détaillée point par point dans les paragraphes suivants.

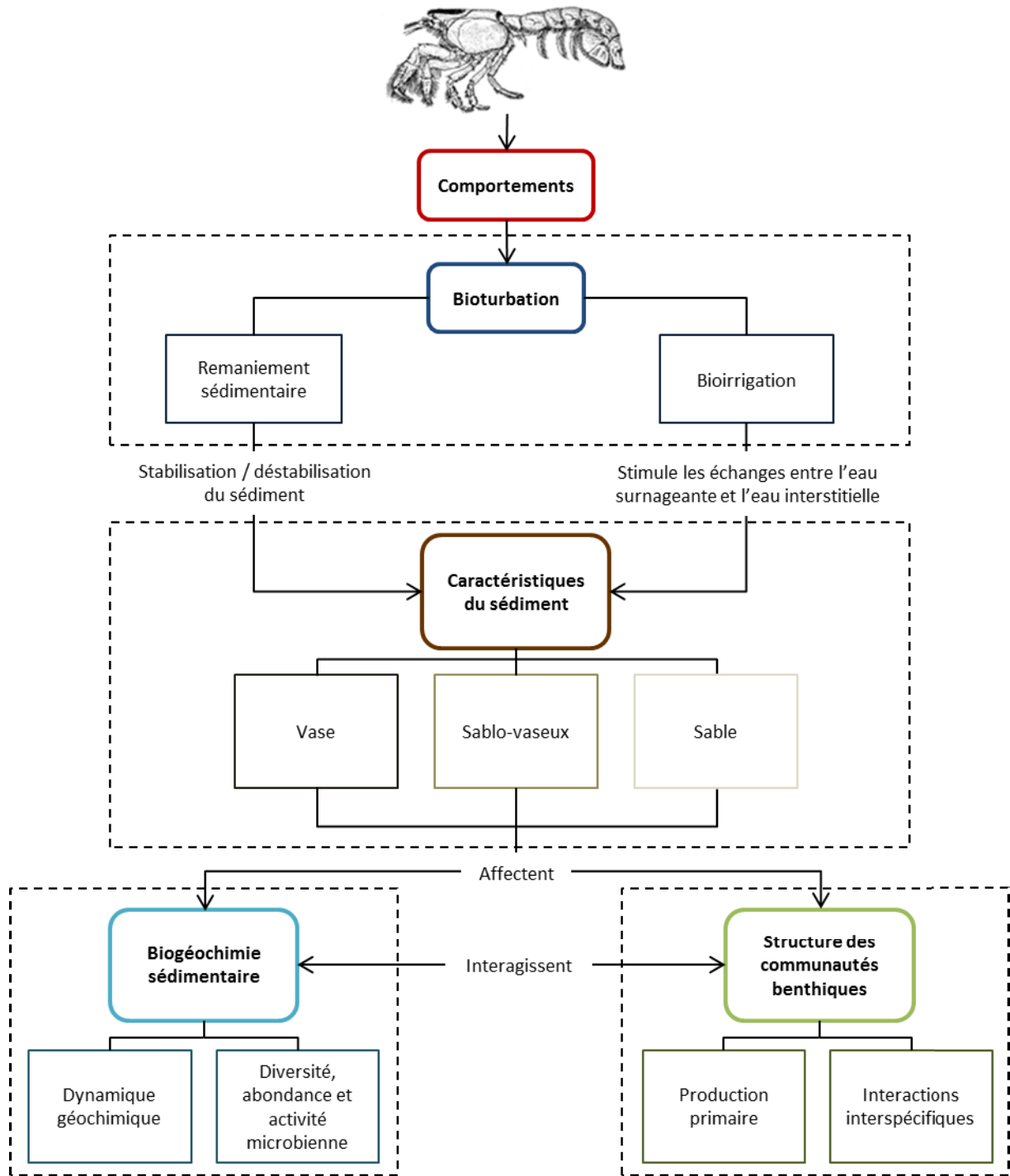


Figure I.8 : Influence des thalassinidés sur le fonctionnement des écosystèmes benthiques (Modifié d'après Pillay et Branch, 2011 et Volkenborn, 2012)

2.4.1 Modification des propriétés physiques de l'habitat sédimentaire par l'activité de bioturbation des thalassinidés

La bioturbation des thalassinidés a d'importantes répercussions sur les propriétés physiques du sédiment, aussi bien à proximité immédiate de l'interface eau-sédiment qu'en profondeur (Ziebis et al., 1996; Rowden et al., 1998; Siebert et Branch, 2005a; Waldbusser et

Marinelli, 2006; Pillay et al., 2007a; D'Andrea et DeWitt, 2009). A la surface du sédiment, les monticules qui se forment lors des activités de fouissage et de nutrition des organismes augmentent la rugosité du sédiment (Zo exprimé en cm). En mer du Nord, Rowden et al. (1998) ont ainsi estimé une multiplication par un facteur 1000 de la rugosité sédimentaire qui passait de 0.0007 cm en hiver à 0.79 cm en été lorsque *Callianassa subterranea* est active. Cette forte rugosité, associée à la fluidité du sédiment expulsé hors du terrier (*cf.* paragraphe 1.1.2. Le remaniement sédimentaire), favorise la mise en suspension du sédiment qui peut entraîner un export de 7 kg (poids sec) de sédiment m⁻² mois⁻¹ en présence de *C. subterranea* en été (Rowden et al., 1998). Puisque les particules fines sont plus sujettes à la resuspension, l'érosion de la surface du sédiment favorise l'accumulation des particules les plus grossières et denses (Rowden et al., 1998) et peut ainsi augmenter significativement la perméabilité et la porosité des premiers centimètres de la colonne sédimentaire (Ziebis et al., 1996).

De nombreuses espèces de thalassinidés effectuent un tri des particules sédimentaires en sélectionnant préférentiellement les plus fines pour se nourrir. Par exemple, *Trypaea australiensis* sélectionne les particules de sédiment < 63 µm (Stapleton et al., 2001) alors que l'estomac de *C. subterranea* contient majoritairement des particules < 30 µm (Stamhuis et Videler, 1998). Ces particules sont ensuite expulsées hors du terrier sous forme de fèces. En conséquence, les terriers de nombreuses espèces de thalassinidés dépositores, appartenant notamment au genre des *Callianassa*, sont appauvris en particules fines par rapport au reste de la matrice sédimentaire (Suchanek, 1983). Les parois des terriers des espèces suspensivores, appartenant notamment au groupe des *Upogebidae*, sont au contraire enrichies en particules fines (Swinbanks et Murray, 1981). Dans ce dernier cas, il est toutefois souvent difficile de déterminer si cette sélection résulte d'avantage d'un tri actif de l'organisme que du piégeage des particules fines par le mucus recouvrant la paroi du terrier (Posey et al., 1991; D'Andrea et DeWitt, 2009). Néanmoins, quelle qu'en soit la cause, la présence de ces crevettes fouisseuses modifie profondément les caractéristiques granulométriques des zones sédimentaires colonisées par l'organisme. La porosité et la perméabilité de la colonne sédimentaire sont, de fait, aussi largement influencées par les activités de ces crustacés. Dans un sédiment classique, l'augmentation de la pression avec la profondeur dans la colonne sédimentaire tend à augmenter la compaction et à diminuer la porosité et la perméabilité du sédiment. En présence d'organismes bioturbateurs, et particulièrement des thalassinidés, ce gradient peut être fortement altéré *via* la décompaction du sédiment lors de son excavation et la diminution de la proportion en particules fines contenues dans le sédiment. De telles modifications altèrent la structure cohésive de la matrice sédimentaire en augmentant l'espace

libre entre les particules et donc le volume d'eau interstitielle. Katrak et Bird (2003) ont ainsi démontré expérimentalement une augmentation significative d'environ 15 % de la porosité du sédiment lorsque celui-ci est colonisé par *Trypaea australiensis*. De leur côté, Ziebis et al. (1996) ont estimé que la sélection de particules de sédiment d'une certaine taille est responsable de l'augmentation de la perméabilité de la colonne sédimentaire colonisée par *Callianassa truncata*. Au contraire, la sélection de particules fines observée majoritairement chez les espèces suspensivores contribue à diminuer la perméabilité des substrats meubles (Waldbusser et Marinelli, 2006). Les modifications des propriétés physiques du sédiment ne se limitent pas toujours aux zones situées à proximité immédiate des terriers. Elles peuvent s'étendre à l'ensemble de l'habitat sédimentaire lorsque les densités sont relativement élevées. Dans une étude à long terme effectuée au Japon, Flach et Tamaki (2001) ont ainsi observé que l'accroissement de la population de *Nihonotrypaea harmandi* a provoqué une réduction de la teneur en particules fines du sédiment à l'échelle de la baie de Tomioka (Japon).

De telles modifications des propriétés physiques du sédiment influencent la facilité avec laquelle s'effectue le transport de l'eau interstitielle et de ses solutés ainsi que l'intensité des échanges à l'interface eau-sédiment, ce qui impacte considérablement la dynamique biogéochimique du compartiment benthique (Ziebis et al., 1996). Ces différents aspects sont détaillés dans le paragraphe suivant.

2.4.2 Modification de la biogéochimie sédimentaire par l'activité des thalassinidés

Une des premières conséquences de la modification de la taille des particules sédimentaires est un changement de la teneur du sédiment en matière organique. Cet effet peut correspondre à un enrichissement, ou bien au contraire à un appauvrissement, selon l'éthologie des espèces considérées. Les sédiments fins présentent une teneur en matière organique plus importante que les sédiments plus grossiers (Dale, 1974; Hargrad, 1972; Longbottom, 1970; Mayer, 1994a, 1994b). Ainsi, les sédiments (sous la surface) colonisés par *Trypaea australiensis*, qui éjecte hors de son terrier les particules les plus fines sans le consolider à l'aide de mucus et/ou de débris végétaux, sont 13 % plus pauvres en matière organique que les sédiments non colonisés par cette espèce (Webb et Eyre, 2004). La présence d'autres thalassinidés tend, au contraire, à augmenter la quantité de matière organique contenue en profondeur dans le sédiment. Ceci est notamment le cas de nombreuses espèces telles que *Corallianassa longiventris* et *Pestarella tyrrhena*, qui incorporent des phyto-débris dans la paroi de leurs terriers ou dans des chambres spécifiques

où elles « cultivent² » les micro-organismes dont elles se nourrissent, doublant ainsi la teneur en carbone de la paroi du terrier par rapport au sédiment de surface (Abed-Navandi et al., 2005). *Neaxius acanthus* se nourrit quant à elle directement de ces phyto-débris incorporés à la paroi de son terrier et induit une augmentation par un facteur 5 de la teneur en matière organique de cette paroi par rapport au sédiment avoisinant (Vonk et al., 2008). Certaines espèces déposent enfin du mucus sur la paroi de leur terrier pour le stabiliser. C'est par exemple le cas d'*U. pugettensis* qui, *via* ce comportement, double la teneur en matière organique du sédiment (D'Andrea et DeWitt, 2009).

Deux des implications biogéochimiques les plus importantes de la bioirrigation sont : (1) l'apport d'oxygène dans un sédiment majoritairement anoxique, et (2) la diminution des concentrations des solutés nocifs (*e.g.*, métabolites réduits). Cependant, la vision traditionnelle qui définit les terriers ventilés comme une simple extension de la surface du sédiment, au travers de laquelle des échanges diffusifs et advectifs ont lieu, est fortement réductrice. En effet, du fait de l'intermittence des activités de ventilation des thalassinidés (Forster et Graf, 1995) et du volume d'eau restreint contenu à l'intérieur du terrier, le sédiment à proximité de celui-ci fait face à des alternances de conditions oxiques et anoxique sur des échelles de temps relativement courtes (10 à 90 min selon Volkenborn et al., 2012). A proximité du terrier, le sédiment est par conséquent soumis à des conditions géochimiques bien plus dynamiques que le sédiment de surface (Volkenborn et al., 2012). Le volume de sédiment subissant ces oscillations géochimiques dépend de sa perméabilité (Mermillod-Blondin et Rosenberg, 2006; Volkenborn et al., 2012). Dans les systèmes peu perméables (*i.e.*, vases) le volume de sédiment impacté est relativement faible et se limite à quelques millimètres autour de la paroi du terrier. Au contraire, dans les sédiments perméables (*i.e.*, sables) les transports de solutés sont facilités et peuvent s'exercer sur de plus grandes distances, si bien qu'un volume plus important de sédiment subit ces oscillations.

L'hétérogénéité spatiale et temporelle des propriétés sédimentaires entourant les terriers de thalassinidés a des effets significatifs sur l'abondance et la diversité des microorganismes associés. Les fortes teneurs en matière organique au niveau des parois du terrier favorisent leur colonisation par des microorganismes (Kinoshita et al., 2008, 2003) qui y sont 4 à 10 fois plus abondants qu'à la surface du sédiment (Dobbs et Guckert, 1988; Dworschak, 2001; Papaspyrou et al., 2005). La composition des communautés microbiennes

² « cultivent » est une traduction explicite et imparfaite du terme anglais « gardening »

varie quant à elle en fonction de la disponibilité en matière organique (Papasprou et al., 2005) et de la stabilité des conditions géochimiques (Bertics et Ziebis, 2009; Volkenborn et al., 2012). De manière générale, les communautés bactériennes colonisant les parois des terriers des thalassinidés sont à la fois différentes et plus diversifiées que celles retrouvées à la surface du sédiment à proximité immédiate de l'ouverture de ce terrier ainsi que dans le sédiment environnant (Papasprou et al., 2005; Bertics et Ziebis, 2009). L'influence de l'activité des thalassinidés sur les communautés bactériennes ne s'arrête pas aux parois de leurs terriers mais affecte également la composition des communautés présentes à la surface du sédiment (Laverock et al., 2010). Leur bioturbation impacte tout autant l'activité de ces microorganismes que la composition de leurs communautés. La dégradation microbienne de la matière organique est effectivement plus importante au niveau des parois des terriers qu'à la surface du sédiment et que dans les sédiments non colonisés par les thalassinidés (Bird et al., 2000; Kinoshita et al., 2008; Sasaki et al., 2014). De telles modifications de communautés, d'abondances et d'activités des micro-organismes dues à la bioturbation des thalassinidés ont de grandes répercussions sur les échanges d'oxygène et de sels nutritifs à l'interface eau-sédiment et influencent donc considérablement le fonctionnement des écosystèmes marins.

La quantification des flux d'oxygène et de nutriments entre la colonne sédimentaire et la colonne d'eau (*i.e.*, le couplage benthique-pélagique) est particulièrement importante dans l'étude du fonctionnement des écosystèmes côtiers. En effet, elle permet d'évaluer le recyclage de la matière organique qui sédimente sur l'interface eau-sédiment ou qui est produite localement. De nombreuses études ont montré une augmentation de la consommation d'oxygène par le sédiment en présence de thalassinidés. La consommation d'oxygène totale est par exemple multipliée par 1,7 en présence de *Pestarella tyrrhena* (Papasprou et al., 2004) et jusqu'à 5,5 en présence d'*Upogebia pugettensis* (D'Andrea et DeWitt, 2009) par rapport à des sédiments sans thalassinidés. Les effets sur le cycle de l'azote sont particulièrement marqués avec une forte augmentation des taux d'ammonification (*e.g.*, 7 fois plus élevés en présence d'*Upogebia pugettensis* ; D'Andrea et DeWitt, 2009), de nitrification (*e.g.*, 1.7 fois plus élevés en présence de *Trypaea australiensis* ; Jordan et al., 2009) et de dénitrification (*e.g.* 2,9 fois plus élevés en présence d'*Upogebia deltaura* ; Howe et al., 2004). Les thalassinidés exercent une telle influence sur les processus biogéochimiques, *via* leurs impacts sur les communautés microbiennes, qu'ils sont considérés comme des « ingénieurs géochimiques des écosystèmes » (D'Andrea et DeWitt, 2009) (**Figure I.9**). *Un des objectifs de ma thèse consistait par conséquent à évaluer l'influence d'Upogebia pusilla sur l'intensité des*

échanges d'oxygène et de sels nutritifs à l'interface eau-sédiment d'un herbier de zostère intertidal.

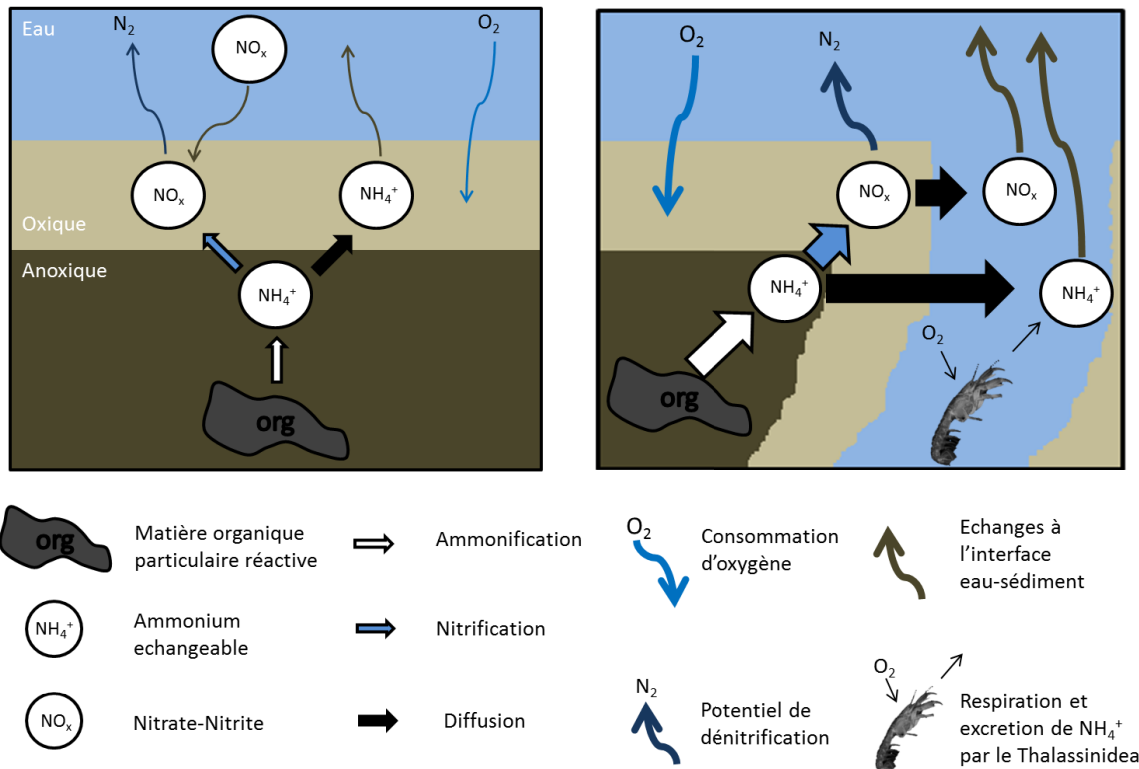


Figure I.9 : Schématisation de l'influence des thalassinidés sur la consommation d'oxygène et le cycle de l'azote. L'épaisseur des flèches est proportionnelle à l'intensité des processus ou des flux (Modifié d'après d'Andrea et DeWitt, 2009)

2.4.3 Le contrôle des assemblages de macrofaune par les thalassinidés.

Bien que ce point ne soit pas en lien direct avec mon travail de thèse, il me semble important d'effectuer un bref état des connaissances actuelles sur ce sujet afin de mieux appréhender l'importance du rôle joué par les thalassinidés dans le fonctionnement global des écosystèmes qu'ils colonisent. Plusieurs études ont montré que les thalassinidés exercent une influence considérable sur la composition des communautés de macrofaunes. Il a en effet été observé des modifications drastiques des communautés de macrofaunes en lien avec une augmentation des effectifs de thalassinidés (Tamaki, 1994; Flach et Tamaki, 2001; Amaro et al., 2007; Pillay et al., 2008). Il existe à ce jour un consensus sur trois scénarios expliquant l'impact des thalassinidés sur l'assemblage de macrofaune (**Figure I.10**, Pillay et al., 2007a): (1) Le remaniement sédimentaire des thalassinidés provoque l'enfouissement de la macrofaune causant la mort de ces organismes, leur migration ou une augmentation de leur coût métabolique, (2) l'activité des thalassinidés augmente l'érodabilité du sédiment provoquant ainsi la saturation des appareils de filtration des organismes suspensivores, et

enfin (3) la quantité de biofilm est diminuée en présence de thalassinidés ce qui réduit d'autant la disponibilité en nourriture pour les organismes brouteurs.

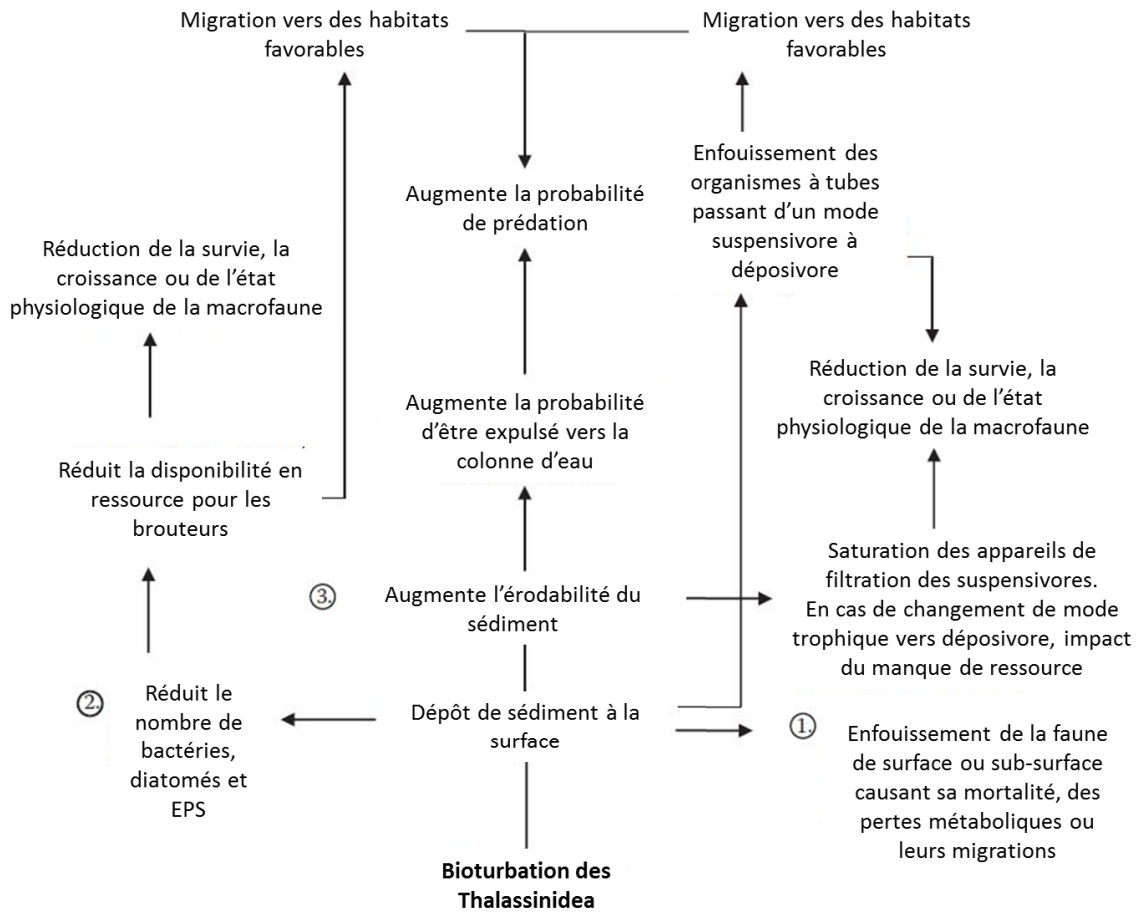


Figure I.10 : Mécanismes potentiels des effets de la bioturbation des thalassinidés sur la macrofaune benthique (Modifié d'après Pillay et al., 2007)

2.5 Les principaux facteurs influençant l'activité des thalassinidés

2.5.1 La température

La température est considérée comme un des facteurs environnementaux majeurs affectant la biologie des organismes marins. Elle contrôle en effet les distributions géographique et bathymétrique des espèces (Bhaud et al., 1995; Pörtner, 2002) mais aussi, plus largement, la dynamique des écosystèmes benthiques (Kinne, 1970). Elle est par exemple déterminante dans les cycles de reproduction et dans d'autres processus physiologiques comme le métabolisme et la croissance (Kinne, 1970). Des activités, telles que le fouissage, la ventilation, la locomotion et la nutrition sont par conséquent directement affectées par la température (Riisgård et al., 1992; Riisgård et Banta, 1998). Peu d'études se sont intéressées au comportement des thalassinidés, mais il y transparaît que ces organismes sont actifs plus

de 60 % du temps (Gagnon et al., 2013; Kneer et al., 2008; Stamhuis et al., 1996). Aucune étude n'a toutefois mesuré directement l'effet des variations de la température sur le comportement de ces organismes. Certains résultats suggèrent néanmoins, mais seulement indirectement, que l'activité de fouissage est impactée par les fluctuations de température. La taille des terriers de plusieurs thalassinidés est par exemple positivement corrélée à la température de l'eau (Berkenbusch et Rowden, 2000; Butler et Bird, 2008). Le taux de « sediment turnover » augmente par ailleurs fortement avec la température (Rowden et al., 1998; Berkenbusch et Rowden, 1999). A ma connaissance il n'existe aucune étude mettant précisément en évidence l'influence de la température sur l'activité de ventilation chez un thalassinidé. *Durant mes travaux de thèse, j'ai donc porté une attention toute particulière aux variations saisonnières de température. J'ai étudié leurs influences d'une manière intégrée allant du comportement d'Upogebia pusilla jusqu'à son influence sur les flux biogéochimiques benthiques.*

2.5.2 L'hypoxie

Les thalassinidés ont une grande capacité d'adaptation aux conditions hypoxiques grâce à leur taux métaboliques relativement bas, un métabolisme anaérobie efficace et la capacité d'augmenter l'affinité de leur hémocyanine avec l'oxygène (Leiva et al., 2015). Astell et al. (1997) ont cependant montré que lors d'épisodes hypoxiques, *U. deltaura* et *U. stellata* modifient leurs comportements et ventilent plus fréquemment leur terrier. Une fois passée une concentration critique située entre 50 et 30 Torr, ces deux espèces voient le battement de leurs scaphognathites diminuer. L'activité générale de ces organismes semble également diminuer lors d'épisodes hypoxiques. Hill (1981) a en effet observé chez trois espèces du genre *Upogebia* que, lorsque la concentration d'oxygène dans le terrier passe sous une concentration critique, ces organismes se déplacent vers la surface du sédiment et restent à proximité de l'ouverture de leur terrier.

2.5.3 Le parasitisme

Comme la plupart des êtres vivants terrestres (Combes, 2001), les thalassinidés sont susceptibles d'être parasités par plusieurs organismes. La présence de nombreux parasites a en effet été constaté sur et dans ces crustacés : des ectoparasites tels que des bopyres (Isopode) qui sont systématiquement fixés dans l'une des deux cavités branchiales (Dworschak, 1988; Griffen, 2009; Smith et al., 2008; Tucker, 1930) et des endoparasites tels que des métacercaires de trématodes et des acanthocéphales (Dworschak, 1988). Des espèces commensales tel que des polychètes du genre *Hesperonoe* et des bivalves du genre

Peregrinamor ont également été observées fixées sur la partie abdominale de thalassinidés (Kato et Itani, 1995; Sato et al., 2001).

Au cours de mon travail de thèse, il s'est avéré que de nombreuses crevettes fouisseuses échantillonnées étaient infestées par un bopyre. Ce parasite a un cycle de vie composé de deux hôtes (Bonnier, 1900; Bourdon, 1968; Williams et An, 2009). La larve planctonique *cryptoniscus* pénètre dans la cavité branchiale d'un thalassinidé où elle est protégée par le branchiostegite. Une fois fixée, la larve perce la cuticule de son hôte pour se nourrir de son hémolymphe (Bonnier, 1900). La première larve à s'être fixée dans la cavité branchiale se transforme en femelle fonctionnelle et grandit rapidement jusqu'à provoquer un gonflement de la cavité branchiale (**Figure I.11**). La seconde larve à pénétrer cette même cavité se transforme quant à elle en mâle fonctionnel nain qui se fixe sur la femelle (**Figure I.11, insert**). La reproduction sexuée se déroulant dans la cavité branchiale du thalassinidé le définit, de fait, comme hôte définitif. Après fécondation, la larve épiscardium est relâchée dans l'eau où elle infeste un copépode et se transforme en larve *cryptoniscus* avant d'infester son hôte définitif. Les Bopyroidea affectent considérablement l'état physiologique de leur hôte. Le Bopyridea *Orthione griffenis* a par exemple un effet négatif sur la croissance d'*U. pugettensis*, induisant un déficit en taille et en poids à son hôte (Smith et al., 2008). Il provoque également la féminisation des mâles de ce même hôte (Griffen, 2009). La capacité de reproduction des individus infestés est ainsi fortement altérée (Dumbauld et al., 2011) ce qui peut provoquer, lorsque la prévalence de ce parasite augmente, une forte chute de la densité de crevettes fouisseuses, voire leur quasi-disparition (Dumbauld et al., 2011). L'influence du parasite sur son hôte semble cependant dépendre des conditions environnementales et notamment de la disponibilité en matière organique (Nanri et al., 2010). De plus, dans certaines études, l'influence du bopyre sur le sexe de son hôte apparaît négligeable par rapport à celle d'un contaminant (Ubaldo et al., 2014). En l'état actuel des connaissances, il est donc difficile d'établir un schéma général de l'influence des bopyres sur les thalassinidés. Il semble par conséquent intéressant d'étudier cette relation hôte-parasite dans un nouvel écosystème. *Un des objectifs de ma thèse a donc consisté à étudier la dynamique de cette relation ainsi que ses conséquences sur l'état physiologique de l'hôte.*



Figure I.11 : Un individu d'*Upogebia pusilla* infesté au niveau de la cavité branchiale par un couple de Bopyridea *Gyge branchialis* (insert). Dans l'insert, le mâle nain (flèche blanche) est fixé sur la face ventrale de la femelle au niveau de ses ouvertures génitales.

Malgré le caractère ingénieur des thalassinidés, à ma connaissance aucune étude ne s'est intéressée aux conséquences de cette relation hôte-parasite sur le fonctionnement des écosystèmes. Il a pourtant été montré chez d'autres crustacés décapodes que les parasites Bopyridea affectent négativement leur niveau d'activité. Par exemple, la crevette pistolet *Synalpheus elizabethae* se déplace et se toilette deux fois moins lorsqu'elle est infestée par un *Bopyrion* sp. que lorsqu'elle est saine (McGrew et Hultgren, 2011). De la même manière, la crevette *Palaemonetes pugio* parasitée par *Probopyrus pandalicola* présente un niveau d'activité jusqu'à 4 fois inférieur à celui d'une crevette saine (Bass et Weis, 1999). Cette réduction résulte du fardeau énergétique que représente le parasite puisque sa demande métabolique s'ajoute à celle de son hôte. Il a d'ailleurs été estimé que *P. pandalicola* ingère quotidiennement jusqu'à 25 % du volume total de l'hémolymphe de *P. pugio* (Walker, 1977), induisant ainsi une demande énergétique qui représente jusqu'à 10 % des besoins quotidiens de l'hôte (Anderson, 1977). Dans le cas des thalassinidés, la relation hôte-parasite pourrait avoir d'importantes répercussions sur le fonctionnement des écosystèmes si le bopyre affecte un trait impliqué dans un processus responsable du caractère ingénieur de l'hôte (Thomas et

al., 1999). Il a en effet été montré que l'infection d'une coque par des trématodes avait un impact négatif sur sa capacité de fouissage et de locomotion, réduisant ainsi l'intensité de bioturbation du sédiment ce qui conduit à une augmentation : (1) de la densité des espèces de polychètes et de gastéropodes associées, ainsi que (2) de la diversité spécifique des sédiments colonisés (Mouritsen et Poulin, 2005; Mouritsen et Poulin, 2010). *Un des objectifs de mon travail de thèse a consisté à évaluer l'influence de l'infestation d'un bopyre sur le comportement de son hôte Upogebia pusilla ainsi que sur les processus sédimentaires et les flux biogéochimiques à l'interface eau-sédiment régulés par ce même hôte.*

3 Site d'étude : Le bassin d'Arcachon

3.1 Présentation du bassin d'Arcachon

Le bassin d'Arcachon est une lagune semi-fermée de forme triangulaire d'une superficie totale de 174 km² (**Figure I.12**). Cette lagune se situe au Sud de la côte Atlantique française et constitue la seule échancrure du littoral sableux aquitain. Elle est soumise à une marée semi-diurne d'amplitude comprise entre 1.1 et 4.9 m dont le courant transite par un système de passes ouvertes sur l'océan, de 2 à 3 km de large sur 12 km de long. Les apports d'eau douce continentale proviennent majoritairement du delta de la Leyre, qui se situe dans la partie Est du bassin et, dans une moindre mesure, du canal du Porge à la pointe Nord de la lagune. Du fait de cette double influence (*i.e.*, marine et continentale), trois masses d'eau aux caractéristiques thermiques et halines spécifiques sont distinguées : les eaux néritiques externes, moyennes et internes (Boucher, 1968). La zone intertidale représente environ les deux tiers de la superficie totale du bassin (117 km²) et est constituée de sédiment allant de la vase au sable. Le tiers restant représente les réseaux de chenaux (57 km²) dont la profondeur ne dépasse pas 25 m. Une grande proportion de la zone intertidale est recouverte par des herbiers à *Zostera noltei* (environ 70 km²) ; herbier considéré comme le plus vaste d'Europe (Auby et Labourg, 1996).

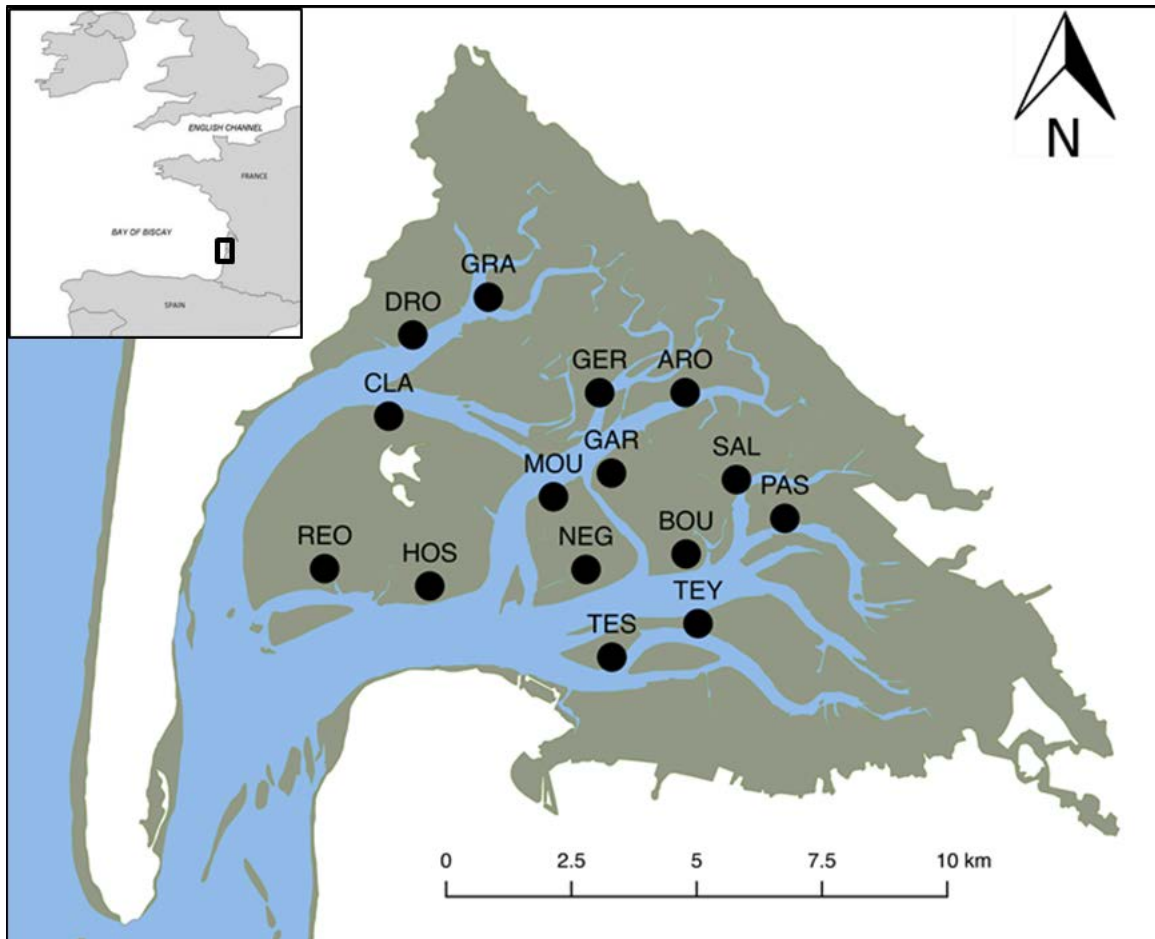


Figure I.12 : Localisation du bassin d’Arcachon sur la côte Atlantique française (insert) et emplacement des stations échantillonnées durant mes travaux de thèse. En *bleu* l’océan et la zone subtidale, en *marron* la zone intertidale et en *blanc* le continent. Identification des stations d’Ouest en Est : *REO* : « La réousse », *CLA* : « Le cla », *DRO* : « Drôle », *HOS* : « Les hosses », *GRA* : « Graveyron », *MOU* : « Les mousettes », *NEG* : « La nègue », *TES* : « Le tes », *GER* : « Germanan », *GAR* : « Garrèche », *BOU* : « Bourut », *TEY* : « le teychan », *ARO* : « Arouillet », *SAL* : « Salos », *PAS* : « Passant ». Le site « La nègue » correspond au site d’échantillonnage pour les expériences *ex-situ* effectuées durant ma thèse de doctorat.

Dans la zone intertidale, l’influence de facteurs identifiés comme : (1) les caractéristiques des masses d’eaux, (2) la bathymétrie et (3) la présence d’herbiers à *Z. noltei* structurent la répartition spatiale des différentes communautés benthiques (Blanchet et al., 2004). Comme la plupart des herbiers (Boström et Bonsdorff, 1997; Hemminga et Duarte, 2000; Boström et al., 2006), celui du bassin d’Arcachon abrite une faune particulièrement diversifiée (Blanchet et al., 2004).

Les études faunistiques visant à déterminer la diversité et l’abondance spécifique des sédiments marins, et en particulier celles de la faune endogée, mettent classiquement en œuvre des méthodologies utilisant des bennes et/ou carottiers. Ces équipements échantillonnent une zone allant de quelques centimètres au-dessus de l’interface eau-sédiment

jusqu'à une profondeur d'environ 20 cm dans la colonne sédimentaire. Cette zone échantillonnée correspond à celle colonisée par la majorité des organismes benthiques (Barnes et Barnes, 2012). Certains organismes vivent cependant à des profondeurs plus importantes. Leur présence est souvent ignorée lorsqu'aucune trace de leur activité (*e.g.*, fèces, zone de nutrition) n'est visible à la surface du sédiment. Dans les environnements à herbier, leur présence est d'autant plus ignorée que les herbiers et les organismes bioturbateurs présentent souvent des mécanismes d'exclusion mutuelle (*cf.* paragraphe 2.2. Distribution). Pourtant, dans le bassin d'Arcachon, le thalassinidé *Upogebia pusilla* (**Figure I.13**) (qui semble être l'unique représentant des thalassinidés colonisant les vasières intertidales de cette lagune bassin) colonise préférentiellement les zones à herbiers de *Z. noltei* et est quasi-absent dans les sédiments nus.



Figure I.13 : Un individu *Upogebia pusilla* à proximité d'une ouverture de son terrier (diamètre d'environ 1,5 cm) à la surface d'un sédiment colonisé par l'herbier de *Zostera noltei* (l'organisme a été volontairement extrait de son terrier).

Un échantillonnage sur 15 stations (**Figure I.12**), que j'ai effectué en amont de mon travail de thèse, m'a en effet permis d'établir l'existence d'une corrélation positive entre la densité d'*U. pusilla* et la biomasse de l'herbier de zostères naines (**Tableau I.2**, voir **Annexe I** pour plus de détails). Compte tenu de la forte influence des thalassinidés sur les caractéristiques et les processus biogéochimiques sédimentaires et, plus généralement, sur le fonctionnement global des écosystèmes benthiques, négliger le thalassinidé *U. pusilla* est susceptible de fortement altérer notre vision du fonctionnement des écosystèmes à herbiers. Il

semble donc particulièrement important et intéressant d'étudier son rôle dans le fonctionnement écologique et biogéochimique de l'écosystème benthique du bassin d'Arcachon.

Tableau I.2 : Résultat du test de corrélation multiple (Forward stepwise regression) des variables environnementales impliquées dans la prédiction de la densité d'*Upogebia pusilla*. L'absence de coefficient indique que la variable n'est pas incluse dans le modèle. L'astérisque (*) indique un effet significatif.

Variable dépendante	Densité		
Régression linéaire multiple			
R ²	0.56		
F	17.719		
p value	< 0.001*		
Corrélation des variables environnementales			
	Coefficient	F	p value
<i>Constante</i>	0.0315	--	--
<i>D₅₀</i>	--	2.213	0.159
<i>C/N</i>	--	0.302	0.591
<i>Porosité</i>	--	3.469	0.053
<i>Biomasse herbier</i>	0.118	17.719	< 0.001*
<i>Altitude</i>	--	0.0176	0.896
<i>Distance à l'océan</i>	--	3.337	0.056

3.2 La régression de l'herbier de *Zostera noltei*

L'herbier de *Zostera noltei* occupe les zones intertidales du bassin d'Arcachon depuis le XVIII^{ème} siècle au moins, période à laquelle cet herbier a été répertorié pour la première fois (Masse, 1708). Comme de nombreux herbiers dans le monde (Orth et al., 2006; Waycott et al., 2009), celui du bassin d'Arcachon connaît une forte régression depuis une vingtaine d'années. Plus et al. (2010) ont observé une diminution de 33 % de la surface occupée par cet herbier entre 1989 et 2007. Le déclin, dans un premier temps modéré jusqu'en 2005, s'est drastiquement accéléré entre 2005 et 2007 (Plus et al., 2010) laissant certaines vasières à nues (**Figure I.14**). Au-delà de la réduction de la surface et de la densité des herbiers *per se*, ce déclin est également susceptible d'induire la régression, voire la perte, des populations d'*Upogebia pusilla* associées.

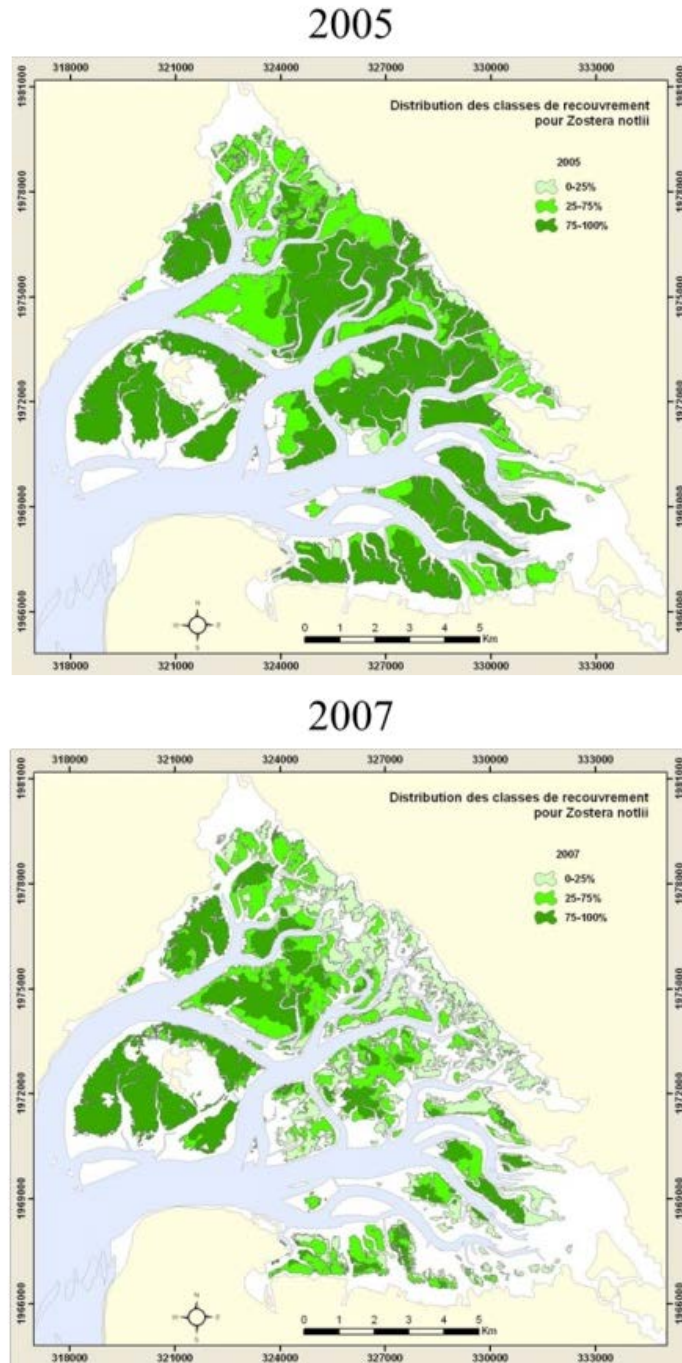


Figure I.14 : Surface colonisée par l’herbier de *Zostera noltei* en 2005 et en 2007 avec les différentes classes de taux de recouvrement du sédiment par les feuilles de *Z. noltei* (D’après Auby et al., 2011)

Les conséquences d’une telle perte sont potentiellement néfastes mais restent à ce jour très difficiles à appréhender. Les études ayant pour but d’évaluer les conséquences de la régression des herbiers sur le fonctionnement des écosystèmes sont en effet souvent basées sur la comparaison entre des sédiments végétalisés et des sédiments nus adjacents (Bernard et al., 2014; Delgard et al., 2013, 2016). Pour obtenir un résultat précis, cette méthodologie nécessite de prendre en compte la totalité des organismes qui jouent un rôle dans le processus

étudié. Ceci est particulièrement important pour les organismes colonisant préférentiellement l'un ou l'autre type de sédiment. Or, de la même manière que celles portant sur la diversité des organismes endogés (*cf.* paragraphe 3.1. Présentation du bassin d'Arcachon), la résolution vertical de ces études ne permet pas la prise en compte d'*U. pusilla*. Notre compréhension des conséquences de la régression des herbiers sur le fonctionnement des écosystèmes est par conséquent très certainement biaisée du fait des différences de densités d'*U. pusilla* très nettes entre ces deux types de sédiments.

3.3 Objectifs du travail

L'objectif général de mon travail de thèse consistait à mieux comprendre le rôle et l'importance d'*Upogebia pusilla* dans le fonctionnement des écosystèmes à *Zostera noltei* du bassin d'Arcachon, avec une attention particulière portée aux variations saisonnières ainsi qu'à l'influence du parasitisme. Ce travail permettra à terme d'évaluer plus précisément les conséquences de la régression de l'herbier de zostères naines sur le fonctionnement écologique et biogéochimique des écosystèmes benthiques du bassin d'Arcachon.

Dans ce contexte général, mon travail de thèse comportait trois objectifs spécifiques:

- Etudier le comportement et le remaniement sédimentaire d'*U. pusilla*.
- Déterminer l'influence d'*U. pusilla* sur la dynamique biogéochimique des sédiments à herbiers
- Evaluer l'influence du parasite *Gyge branchialis* sur l'état physiologique d'*U. pusilla* et les conséquences de cette infestation sur la dynamique biogéochimique des sédiments à herbiers

3.4 Organisation du manuscrit

Ce mémoire, construit sous la forme d'articles scientifiques est organisé en trois chapitres suivis d'une conclusion générale.

Chapitre I : Activité d'*Upogebia pusilla*

Ce chapitre porte sur l'étude expérimentale du comportement d'*Upogebia pusilla* et établit un lien direct entre le comportement de cet organisme, son activité de remaniement sédimentaire et la dynamique de l'oxygène autour de son terrier. Ce premier chapitre fait l'objet d'un article scientifique actuellement soumis à la revue *Marine Ecology Progress Series*.

Article n°1 : L. Pascal, O. Maire, B. Deflandre, A. Romero-Ramirez, A. Grémare (soumis pour publication) **Behaviour, sediment reworking and oxygen dynamics in the Gebiidean mud shrimp *Upogebia pusilla*** ; *Marine Ecology Progress Series*

Chapitre II : Influence d'*Upogebia pusilla* sur les flux biogéochimiques à l'interface eau-sédiment

Ce chapitre porte sur l'étude expérimentale du rôle d'*Upogebia pusilla* dans le fonctionnement biogéochimique des écosystèmes intertidaux végétalisés du bassin d'Arcachon. Ce deuxième chapitre fait l'objet d'un article scientifique paru en 2016 dans la revue *Journal of Experimental Marine Biology and Ecology*.

Article n°2 : L. Pascal, O. Maire, N. Volkenborn, P. Lecroart, S. Bichon, X. de Montaudouin, A. Grémare, B. Deflandre (2016) **Influence of the mud shrimp *Upogebia pusilla* (Decapoda : Gebiidea) on solute and porewater exchanges in an intertidal seagrass (*Zostera noltei*) meadow of Arcachon Bay: An experimental assessment** ; *Journal of Experimental Marine Biology and Ecology*, 477:69-79, doi : 10.1016/j.jembe.2016.01.008

Chapitre III : Influence de l'ectoparasite *Gyge branchialis* sur *Upogebia pusilla*

PARTIE A

Les travaux présentés dans ce chapitre sont consacrés à la caractérisation des effets de l'ectoparasite *Gyge branchialis* sur les processus biogéochimiques contrôlés par *Upogebia pusilla*. Ce type d'étude nécessite d'une part, une estimation de la prévalence d'une telle infestation et de ses effets physiologiques sur l'hôte (*U. pusilla*), et, d'autre part, une série d'expériences dédiées. La première partie de ce chapitre est donc consacrée à l'étude des effets physiologiques de *G. branchialis* sur *U. pusilla* qui a fait l'objet d'un article scientifique paru en 2016 dans la revue *Marine Biology*.

Article n°3 : L. Pascal, X. de Montaudouin, A. Grémare, O. Maire (2016) **Dynamics of the *Upogebia pusilla*-*Gyge branchialis* marine host-parasite system** ; *Marine Biology*, 163 : 195, doi : 10.1007/s00227-016-2969-9

PARTIE B

La seconde partie de ce chapitre concerne les expériences menées sur des individus infestés par *Gyge branchialis*, visant à déterminer l'influence de ce parasite sur le comportement de son hôte et les conséquences sur les processus biogéochimiques contrôlés par *Upogebia pusilla*. Cette partie fait l'objet d'un article scientifique qui sera prochainement soumis.

Article n°4 : L. Pascal, A. Grémare, X. de Montaudouin, B. Deflandre, A. Romero-Ramirez, O. Maire (à soumettre) **Parasitism of engineer species: a key factor controlling marine ecosystem functioning**

Conclusion générale

Cette dernière partie présente une synthèse de l'ensemble des résultats obtenus lors de ce travail ainsi que les principales perspectives qui en découlent.

Chapitre 1 :

*Activité d'*Upogebia pusilla**

**Behaviour, sediment reworking and oxygen dynamics in the
Gebiidean mud shrimp *Upogebia pusilla***

Ludovic Pascal^{1,2}, Olivier Maire^{1,2}, Bruno Deflandre^{1,2}, Alicia Romero-Ramirez^{1,2} and
Antoine Grémare^{1,2}

¹Univ. Bordeaux, EPOC, UMR 5805, F-33600 Pessac, France

²CNRS, EPOC, UMR 5805, F-33600 Pessac, France

Article soumis à la revue Marine Ecology Progress Series

Abstract

Thalassinidean mud shrimp are among the most influential bioturbating species in coastal soft sediments. However, little is still known about their behaviour and resulting sedimentary and biogeochemical processes taking place below the sediment-water interface. In this study, we examine how the different behaviours of the mud shrimp *Upogebia pusilla* affects both sediment reworking and oxygen dynamics at and below the sediment-water interface. We identified four main types of behaviours: “Resting”, “Walking”, “Ventilating” and “Burrowing”. According to studied season, 36 to 78% of its time was devoted to the last two behaviours. We observed three patterns of sediment reworking: (1) at the sediment-water interface through the frequent expulsion of excavated sediment (2) below the sediment surface by introducing and then moving downward surficial particles within the burrow, and (3) within the burrow by compacting excavated sediment against burrow walls. Overall, sediment reworking was mostly cued by the “Burrowing” behaviour and processes taking place below the sediment surface accounted on average for about 75% of total sediment reworking. Activity and sediment reworking were higher during summer, intermediate during spring and lower during winter, which suggests a major effect of temperature. Oxygen dynamics in the overlying water was closely related to the “Ventilating” behaviour, which caused sudden drop in oxygen saturation. Conversely, the decreases in oxygen saturation within the burrow were behaviour-specific (*i.e.*, more marked during “Burrowing”) and the onset of “Ventilating”, which induces marked increases in oxygen saturation, appeared associated with an oxygen saturation level between 10 and 25%.

1. Introduction

Due to their relative large body size, high densities (up to 650 ind. m⁻²; Nates and Felder 1998) and intense burrowing activity, endobenthic shrimp-like crustaceans (*i.e.*, mud shrimp), formerly classed as Thalassinidea but now separated in the two clades Gebiidea and Axiidea (Bracken et al. 2009, Robles et al. 2009), are considered among the most influential engineers in marine soft-bottom ecosystems. These organisms dig permanent or semi-permanent complex burrows constituted of several branches, which extend deep (*i.e.*, up to 2 m) in the sediment column and connect to the overlying water by several distant openings (Kinoshita 2002). Burrow construction and maintenance strongly increase the surface of the sediment-water interface and result in the continual excavation of large amount of deep sediment, which are expelled at the sediment-water interface (Rowden et al. 1998). Mud shrimp probably induce the highest turnover rates in marine sedimentary environments (Cadée 2001). They profoundly affect sediment physical (*e.g.*, granulometry, porosity and permeability), chemical (*e.g.*, organic carbon content, oxygen concentration) and biological (*e.g.*, structure and diversity of both prokaryotic and eukaryotic benthic communities) properties (Aller and Dodge, 1974; Berkenbusch and Rowden, 2000; Bird et al., 2000; Laverock et al., 2011; Pillay et al., 2007b). Living deep in the sediment column, far below the surficial oxic layer, mud shrimp frequently ventilate their burrow to fulfil their metabolic requirements and remove toxic metabolites that progressively accumulate in burrow water. The highest ventilation rate (*i.e.*, up to 900 mL h⁻¹) in Thalassinidean has been reported in *Upogebia pusilla* (Dworschak 1981). Although the typical “open-ended” morphology of mud shrimp burrows limits pressure gradients and lateral porewater advection, ventilation strongly enhances sediment irrigation (Webb and Eyre, 2004) and thereby increases oxygen availability within the sediment. In a previous study, we have estimated that *U. pusilla* contributes to increase porewater flow and solute exchanges across the sediment-water interface of intertidal seagrass meadows in Arcachon Bay by a factor up to 5 (Pascal et al., 2016b).

Because of their considerable importance in the functioning of coastal ecosystems worldwide, engineering activities of burrowing mud shrimp have been extensively studied over the last decades (see review by Pillay and Branch 2011). All the methodologies developed so far to assess sediment reworking rates generated by burrowing mud shrimp were, however, based on the quantification of the volume of sediment expelled at the

sediment surface and thereby neglect subsurface processes (Rowden and Jones, 1993). Yet, the sediment surrounding mud shrimp burrow walls is enriched in organic matter and frequently reworked (Kinoshita et al., 2008; Suchanek, 1983). Such a bias clearly limits our current understanding of the impact of mud shrimp populations on organic matter remineralisation, and on the overall biogeochemical functioning of soft-bottom ecosystems. This could be especially exacerbated when mud shrimp are the main contributors to sediment reworking, which is most often the case in seagrass beds from which most of other large infaunal organisms are excluded by the dense network of roots and rhizomes (Bernard et al., 2014; Brenchley, 1982; Philippart, 1994; Valdemarsen et al., 2011; van Wesenbeeck et al., 2007).

Only a few experimental studies have dealt with the assessments of mud shrimp behaviours and time allocation patterns (Anderson et al., 1991; Gagnon et al., 2013; Kneer et al., 2008; Stamhuis et al., 1996). This largely results from the difficulty in observing the sediment column without disturbing the behaviour of benthic macrofauna. Experimental techniques based on image analysis procedures have been developed during the last two decades to assess the activities of benthic macrofauna at the sediment-water interface (Grémare et al., 2004; Hollertz and Duchêne, 2001; Jordana et al., 2000). These techniques have later been coupled with the use of specific (thin) aquaria to characterize and quantify the activity of benthic fauna within the sediment column (Maire et al., 2010, 2007a) during laboratory experiments. Coupled with the use of luminophores (*i.e.*, inert fluorescent particles) they have allowed the assessment of the influence of environmental parameters on both macrofauna behaviour and associated sediment reworking (Bernard et al., 2016; Maire et al., 2007a). Maire et al. (2007a, 2010) for example highlighted that sediment reworking induced by infaunal deposit-feeding bivalves is largely modulated by a set of abiotic (including temperature and food availability) and biotic (including threat by predators) factors.

The present study aimed at applying a similar approach, coupled with the use of high frequency oxygen micro-sensors, for assessing the behaviour, sediment reworking and oxygen dynamics in the mud shrimp *Upogebia pusilla*, which is a dominant species within the seagrass beds of Arcachon Bay. Based on a set of laboratory experiments carried out during three seasons, its main objectives were to: (1) characterize the different behaviours of this species, (2) quantify sediment reworking both at the sediment-water interface and within the

sediment column, and (3) establish a link between behaviours and both sediment reworking and oxygen dynamics in the overlying and burrow waters.

2 Materials and methods

2.1 Animals collection and maintenance

Three sets of controlled laboratory experiments were carried out in winter (January), spring (April) and summer (August) 2014. During each season, 30 adult specimens of the mud shrimp *Upogebia pusilla* were collected at low tide in an intertidal *Zostera noltei* meadow (44° 40.782' N, 1° 08.321' W) of Arcachon Bay (Southwest coast of France) using a bait piston pump. Mud shrimp were immediately isolated in individual containers. Back at the laboratory, they were measured (Total Length from the tip of the rostrum to the tip of the telson, ± 1 mm) and weighted (Blotted Wet Weight, ± 0.1 mg). During each season, 10 undamaged and bopyrid-free mud shrimp (4.6 ± 0.4 cm in TL and 1.9 ± 0.3 g in BW) were selected and individually introduced in a thin aquarium (25 (L) \times 1.9 (W) \times 50 (H) cm) previously filled with a 30 cm layer of sieved (500 μ m mesh) sediment collected at the sampling site (D_{50} : 159 μ m, organic carbon: 0.35 % DW). Experiments started 48 h after mud shrimp introduction, which allowed for the construction of a whole (*i.e.*, open-ended) burrow during all seasons. All aquaria were kept in a dark thermo-regulated room (at 12, 16 and 22 °C in January, April and August, respectively, corresponding to the measured seawater temperature during field sampling) during the whole duration of experiments (a month) and fuelled with a continuous seawater flow (~ 0.25 L min^{-1} , same temperature as above).

2.2 Sediment reworking and burrow characteristics

Sediment reworking was first quantified during a 30 days period using luminophores (*i.e.*, inert particle tracers fluorescing under UV light). Fifteen gDW of luminophores (100 - 160 μ m size range) were homogeneously spread at the sediment surface. Both sides of each aquarium were then photographed with a digital camera (D100, Nikon ®, 3008 \times 2000 pixels) under UV light ($\lambda = 380$ nm) immediately following luminophores input (D0) and after 3, 6, 12, 24, 48, 72, 96, 120, 144, 168, 192, 216, 240, 288, 336, 408, 480 and 720 h. Two vertically adjacent pictures (27 \times 18 cm each) were taken for each side of the aquarium and assembled afterwards as a single image (27 \times 35 cm in size, 92 μm^2 pixel^{-1} in resolution). Composite

images were saved in JPEG format and analysed as described in Maire et al. (2006), allowing for the assessment of 1D luminophore vertical concentration profiles. Vertical biodiffusion (D_{bv}) and bioadvection (V_{bv}) coefficients were then estimated by fitting a biodiffusion-bioadvection transport model to these vertical profiles (Gerino et al., 1998; Meysman et al., 2003):

$$\frac{\partial^2 C}{\partial t} = D_{bv} \frac{\partial^2 C}{\partial z^2} - v_{bv} \frac{\partial C}{\partial z} \quad (1)$$

where C is the luminophore concentration (%), t is the time (year) and z is the vertical depth in the sediment column (cm). D_{bv} and V_{bv} were estimated by convergent iterations and weighted least-squared regressions of model prediction on observed luminophore profiles (see Maire et al. 2006 for further details). The volume of sediment expelled at the sediment-water interface (V_{ES} , cm^3) was also estimated by measuring the average height of sediment over the original sediment-water interface (\bar{H} , **Figure 1.1**) and using the following equation:

$$V_{ES} = \bar{H} \times L \times W \quad (2)$$

where L and W are the length of and the width of the aquarium, respectively.

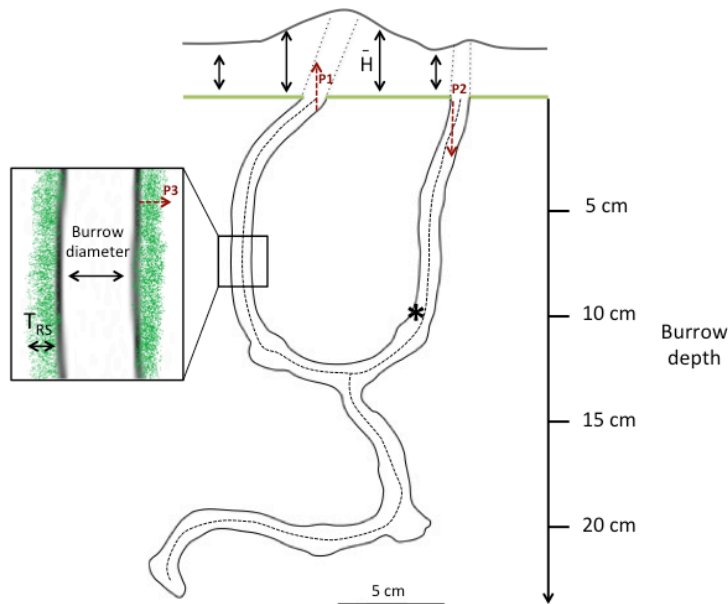


Figure 1.1 : Schematic view of a representative burrow at D4. Green line: Former sediment-water interface evidenced by luminophore layer, dotted line: burrow length, T_{RS} : average thickness of the reworked sediment layer surrounding the burrow, \bar{H} : average height of expelled sediment used to estimate the volume of expelled sediment on the sediment water-interface (V_{ES}), Red dotted arrows (P1, P2 and P3) represent the three patterns of sediment reworking observed in *Upogebia pusilla*, see text for details. *: position of the micro optical oxygen sensor.

The average thickness of the reworked layer surrounding burrows (T_{RS} , cm) was estimated by measuring the distance between the burrow wall and the most distant luminophore along five different sections randomly distributed within the burrow (**Figure 1.1**). The average volume of reworked sediment surrounding the burrow (B_{RS} , cm³) was then computed using the following equation:

$$B_{RS} = [L_b \times \pi(r_b + T_{RS})^2] - [L_b \times \pi r_b^2] \quad (3)$$

where L_b is the total burrow length (cm), r_b is the mean burrow radius (cm) and T_{RS} is the mean thickness of the reworked sediment layer surrounding the burrow (cm).

The component of sediment reworking occurring perpendicularly to burrow wall was modelled after 4 days of incubation using a simple biodiffusive model (Cochran, 1985):

$$\frac{\partial^2 C}{\partial t} = D_{bw} \frac{\partial^2 C}{\partial x^2} \quad (4)$$

Where C is the luminophore concentration (%), t is the time (year) and x is the orthogonal distance from the burrow wall (cm). This was achieved on three aquaria per season. Selected aquaria were those with the longest proportion of visible burrow wall and thus those allowing for the best assessments of decrease in luminophore concentration with increasing orthogonal distances from burrow wall.

Burrow length and maximal depth within the sediment column (cm) as well as the number of openings and turning chambers were also measured at D0, and after 4 (D4) and 30 days (D30) of incubation (**Figure 1.1**).

2.3 Behaviour

Mud shrimp behaviours were recorded for a 3-day time period starting one day after luminophores input. Behaviours were recorded using an automated image acquisition system composed of a video sensor (μ Eye UI-1480SE, IDS Imaging®, 2560 × 1920 pixels) connected to a microcomputer and driven by the AviExplore software (Romero-Ramirez et al., 2016). This sensor was positioned in front of the aquarium side displaying the longest visible part of the burrow lumen. Images were acquired in total darkness under infrared light ($\lambda > 700$ nm) during 72 h with an acquisition frequency of 0.1 Hz. Collected images with a surface resolution of 98 μm^2 pixel⁻¹ were assembled in a time-lapse AVI video file. Time-

lapse sequences were then visually inspected, which allowed for the identification of the main behaviours and the assessments of: (1) the proportion of time allocated to each behaviour, (2) the average bout-duration of each behaviour, and (3) the average time between two bouts of the same behaviour. Despite the small thickness of our aquaria, mud shrimp could sometimes remain hidden in parts of their burrow, which was covered by a thin layer of sediment. In order not to bias the estimates of the relative proportions of time devoted to the different behaviours (Stamhuis et al. 1996), only records during which mud shrimp were visible more than 90 % of the time were considered for analysis. Accordingly, the behaviours of only 4, 5 and 5 mud shrimps were investigated during winter, spring and summer, respectively. Overall, this corresponded to 840 h of monitoring.

2.4 Oxygen dynamics

During summer experiments, the O₂ saturation within the burrow was recorded during a 72 h time-period starting immediately after the end of the sediment reworking experiment. O₂ saturations were measured at a frequency of 1 Hz, simultaneously with a second sequence of behaviour monitoring as previously described. A micro-optode (OXF1100, Pyroscience) was positioned using a micromanipulator in the lumen of the “U” part of the burrow (*i.e.*, ~10 cm deep in the sediment column; 2 mm from the burrow wall, **Figure 1.1**). A mini-optode (OXROB10, Pyroscience) was placed in the overlying water at ~10 cm above the sediment surface to check for the full oxygenation of the water column. Both sensors were connected to a Firesting oxygen meter (Pyroscience) driven by the Firesting logger software (Ver. 2.364). A two-point linear calibration of both sensors was initially achieved between the O₂ concentration of the overlying water measured by Winkler titration (Grasshoff et al., 1999) and a zero O₂ concentration in a sodium ascorbate solution. After 72 h of continuous recording, the micro-optode was carefully removed from the sediment and the aquarium was hermetically sealed with a PVC lid. The mini-optode was then inserted into the lid and repositioned in the overlying water at ~10 cm above the sediment surface. The overlying water was continuously stirred with a Teflon-coated magnetic disc at ~100 rpm during incubations. Measurements were stopped as soon as the O₂ level in the overlying water fell below 70 % of its initial value.

2.5 Data analysis

For each behaviour, the significance of between seasons differences in: (1) proportion of allocated time, (2) bout-duration, and (3) between bout interval-duration were assessed using One-Way PERmutation Multivariate ANalyses Of VARIances (PERMANOVAs). Since all records lasted exactly the same time, these analyses were performed on raw duration data. The effect of seasons on D_{bw} was assessed using a One-Way PERMANOVA. The effects of experiment duration and season on burrow characteristics and sediment reworking parameters were assessed using Two-Way PERMANOVAs. The design consisted in two fixed factors (Experiment duration and Season) with a third random factor (Replicate) nested within Season (Bernard et al., 2016; Braeckman et al., 2011). In case of significant interaction between fixed factors, pairwise test were performed to characterise their modalities. The effects of the tested factors on the dispersion (*i.e.*, among experiment variability) of each variable were checked using the PERMDISP procedure (Anderson 2006) (same distance and same design as described above). All PERMANOVAs and associated tests were performed on untransformed data using Euclidean distance and the PRIMER v6 package with the PERMANOVA+ add-on software (Anderson et al., 2008; Clarke and Warwick, 2001).

The relationships between: (1) B_{RS} and V_{ES} , (2) the duration of the time period preceding each ventilation event and the magnitude of the decrease in O_2 concentration in the overlying water column during this event, and (3) the O_2 saturation in the burrow at the onset of ventilation and the distance of the mud shrimp from the micro-optode were tested using simple linear regression models. The relationship between the cumulative amount of: (1) different types of activity, and (2) total reworked sediment was assessed using a (forward stepwise) multiple linear regression model. All regression analyses were performed using the SIGMAPLOT, v12.5 software.

3 Results

3.1 Burrow characteristics

Mud shrimp built a complete open-ended burrow within less than 24 hours during winter and less than 12 hours during spring and summer. All initial U-shape burrows progressively evolved into Y-shape burrows during spring and summer *versus* only 30 % during winter. Mud shrimp burrows were between 16 and 155 cm long with a maximal depth

between 7 and 30 cm within the sediment column. They had 2 to 3 openings and a rather constant diameter close to 1.5 cm with 2 to 8 turning chambers (**Table 1.1**) located 10 to 20 cm apart. Burrow depth and the number of openings significantly differed between experiment durations but not between seasons (**Table 1.2**). Both parameters tended to increase with experiment durations (**Table 1.1**). Burrow length and the number of turning chambers significantly differed between seasons and experiment durations with a significant interaction between these two factors (**Table 1.2**) due to a more pronounced increase in the values of these two parameters with experiment durations during summer and a lower one during winter (**Table 1.1**).

Table 1.1 : Mean values of main burrow characteristics (length, depth, number of openings and number of turning chambers) recorded immediately after luminophore input (D0) and the 4 (D4) and 30 days (D30) later.

Time / Season	<i>n</i>	Length (cm)	Depth (cm)	Number of openings	Number of turning chambers
D0					
Winter	10	34.5 ± 7.3	14.0 ± 3.3	2.0 ± 0.0	2.2 ± 0.5
Spring	10	39.9 ± 13.4	16.5 ± 5.9	2.0 ± 0.0	2.9 ± 0.5
Summer	10	42.3 ± 13.1	15.7 ± 4.9	2.0 ± 0.0	2.8 ± 0.8
D4					
Winter	10	35.9 ± 9.4	14.3 ± 3.3	2.0 ± 0.0	2.2 ± 0.5
Spring	10	44.5 ± 17.6	17.9 ± 7.3	2.0 ± 0.0	2.9 ± 0.5
Summer	10	52.3 ± 9.9	19.3 ± 5.4	2.0 ± 0.0	2.8 ± 0.8
D30					
Winter	10	47.1 ± 16.8	15.5 ± 3.8	2.6 ± 0.6	3.8 ± 1.5
Spring	10	76.8 ± 26.0	22.4 ± 8.2	2.5 ± 0.5	4.4 ± 1.3
Summer	10	96.7 ± 27.5	26.7 ± 8.9	2.3 ± 0.5	5.1 ± 1.2

Table 1.2 : Results from PERMANOVA and PERMDISP analyses for differences in burrow length, burrow depth, number of burrow openings, number of turning chambers, mean thickness of the reworked sediment layer surrounding the burrow (T_{RS}), volume of reworked sediment surrounding the burrow (B_{RS}) and volume of sediment expelled at the sediment-water interface (V_{ES}), among Seasons and Experiment durations. *: PERMDISP, $p < 0.05$

Factors		Burrow length	Burrow depth	Number of burrow openings	Number of turning chambers	T_{RS}	B_{RS}	V_{ES}	D_{bv}	V_{bv}
<i>Seasons</i>	df	2	2	2	2	2	2	2	2	2
	MS	4478.8	234.63	0.0333	6.7111	0.184	131880	83391	1.618E7	6.832E5
	Pseudo-F	7.047*	2.727*	0.443	4.387	43.979	42.573*	54.447*	78.580	12.052*
	p(perm)	0.005	0.097	0.883	0.023	0.001	0.001	0.001	0.001	0.001
<i>Durations</i>	df	2	2	2	2	15	15	15	15	15
	MS	10595	287.09	0.9	22.411	2.285	485960	410850	2.208E5	24467
	Pseudo-F	82.991*	29.399*	11.951*	42.315*	1192.700*	255.160*	296.570*	2.182	1.942*
	p(perm)	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.013	0.034
<i>Replicate(Seasons)</i>	df	27	27	27	27	27	27	27	27	27
	MS	635.52	86.038	0.0753	1.530	0.004	3097.7	1531.6	2.0479E5	56379
	Pseudo-F	4.978*	8.811*	1.000*	2.888*	2.184	1.627	1.106	2.024	4.475
	p(perm)	0.001	0.001	0.483	0.003	0.003	0.058	0.378	0.004	0.001
<i>Season x Durations</i>	df	4	4	4	4	30	30	30	30	30
	MS	1408.2	61.061	0.033	1.478	0.0462	49489	49748	1.115E5	14616
	Pseudo-F	11.030*	6.253*	0.443*	2.790	24.131*	25.985*	35.911*	1.102	1.160
	p(perm)	0.001	0.002	0.8	0.049	0.001	0.001	0.001	0.338	0.274
<i>Residuals</i>	df	54	54	54	54	300	300	300	300	300
	MS	127.7	9.7651	0.0753	0.5296	0.0019	1904.5	1385.3	1.012E5	12599

3.2 Behaviours

Four main behaviours were identified, namely “Walking”, “Ventilating”, “Burrowing” and “Resting” (**Table 1.3**). During “Walking”, mud shrimp alternatively walked and turned in their burrow without transporting sediment. During “Ventilating”, mud shrimp generated a unidirectional water flow by beating their four pairs of pleopods. “Ventilating” behaviour was further divided into two subclasses, namely: (1) “Flushing” during which mud shrimp quickly (*i.e.*, < 1 min on average) renewed their burrow water, usually immediately following a period of intense burrowing; and (2) “Pumping” which consisted in a regular beating movement of pleopods inducing a constant water flow through the burrow, without sediment transport towards the sediment-water interface. These two behaviours could easily be discriminated based on: (1) the pleopod beat frequency, and (2) the ejection of unconsolidated sediment in the overlying water. “Burrowing” consisted in digging and carrying sediment. During “Resting”, no visible displacement was observed, although mud shrimp periodically bended their abdomen under their cephalothorax.

Table 1.3 : Description, average bout-duration (\pm SD) and interval-duration (\pm SD) of each behaviour during winter (n = 4), spring (n = 5) and summer (n = 5) experiments. * indicates significant between seasons differences (one-way PERMANOVA, $p < 0.05$)

Behaviour	Description	Bout-duration (min)			Interval-duration (min)		
		Winter	Spring	Summer	Winter	Spring	Summer
Walking^a	Walking or turning through the burrow without sediment transport	* 1.8 \pm 0.2	2.0 \pm 0.5	1.0 \pm 0.4	42.5 \pm 18.7	80.4 \pm 26.6	80.4 \pm 37.3
Ventilating^b	Movements of the four pairs of pleopods	5.7 \pm 2.2	7.9 \pm 4.5	6.9 \pm 1.5	* 42.4 \pm 24.3	17.7 \pm 5.2	9.5 \pm 2.3
- <i>Flushing</i>	<i>Strong ventilation causing the ejection of sediment out of the burrow</i>	* 0.7 \pm 0.1	0.8 \pm 0.1	0.9 \pm 0.1	512.6 \pm 448.0	159.4 \pm 143.1	69.8 \pm 32.0
- <i>Pumping</i>	<i>Movement of the pleopods without sediment transport</i>	6.2 \pm 2.2	9.9 \pm 6.0	8.3 \pm 1.5	* 46.9 \pm 24.8	23.1 \pm 7.6	12.1 \pm 3.2
Burrowing^c	Sediment transport	* 12.7 \pm 3.0	9.2 \pm 3.1	7.1 \pm 1.3	* 46.1 \pm 28.5	21.9 \pm 9.7	12.7 \pm 2.9
Resting^d	Stay stationary	* 16.9 \pm 5.2	17.1 \pm 5.5	7.7 \pm 1.7	18.6 \pm 3.7	28.8 \pm 13.4	31.8 \pm 5.8

Corresponding behaviour patterns in Anderson et al. (1991) ^aLocomotory, ^bIrrigation, ^cBurrowing, ^dStationary

Corresponding behavioural classes in Stamhuis et al. (1996) ^aWander, ^bVentilate, ^cBurrow, ^dRest

Corresponding behaviour patterns in Gagnon et al. (2013) ^aOther activities, ^bIrrigation of burrow, ^cSediment to surface, Transport and digging + manipulation, ^dIn sight inactive

For each behaviour, the proportions of allocated time significantly differed between seasons (**Figure 1.2**, One-Way PERMANOVA, $p < 0.001$ in all cases). Mud shrimp significantly spent more time both “Ventilating” and “Burrowing” as seawater temperature raised whereas the time allocated to “Resting” was reduced. Moreover, the way mud shrimp seasonally changed their time allocation differed between behaviours. Changes in the proportion of time allocated to “Ventilating” mainly resulted from changes in the mean interval duration between successive ventilation bouts, whereas the mean duration of each ventilation bout did not significantly differ between seasons (**Table 1.3**). Conversely, changes in the proportions of time allocated to “Burrowing” resulted from significant changes in both bout and between bout-interval durations (**Table 1.3**). Changes in the proportion of time allocated to “Resting” resulted from significant differences between bout-durations whereas between bout-interval durations did not significantly differed between seasons mostly due to a high variability during spring (**Table 1.3**).

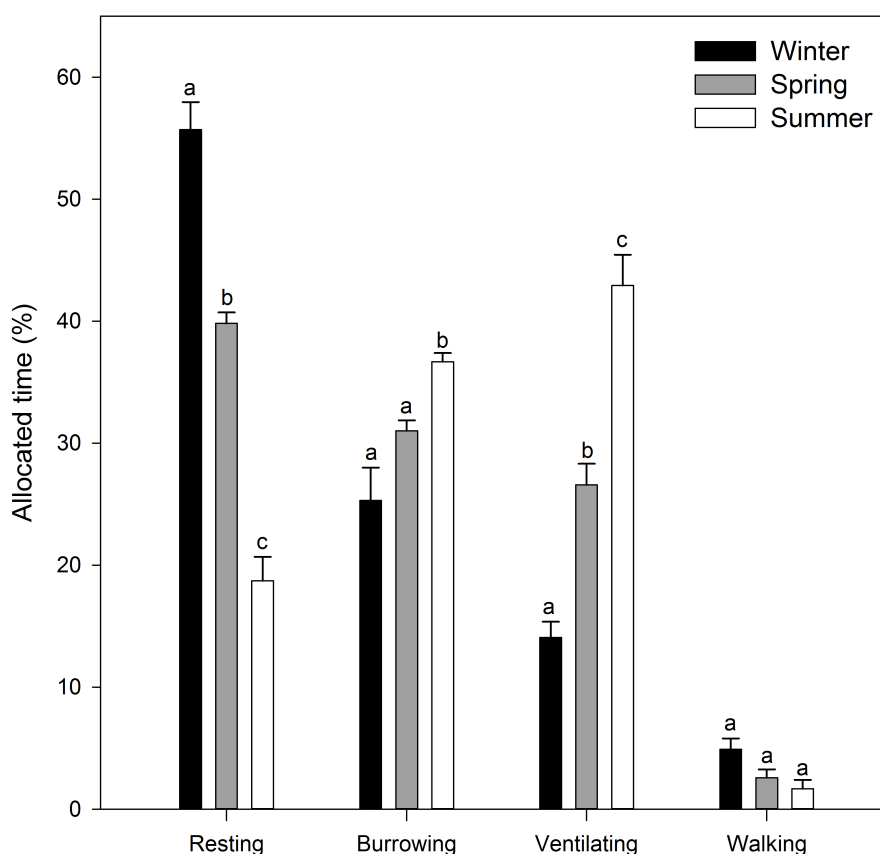


Figure 1.2 Average (\pm SE) proportions of time allocated to each behaviour during winter (black bars, $n = 4$), spring (white bars, $n = 5$) and summer (light grey bars, $n = 5$) experiments. Different letters indicate significant (PERMANOVA and pair-wise test, $p < 0.05$) between seasons differences.

3.3 Sediment reworking

The thickness of the reworked sediment layer surrounding the burrow (T_{RS}), the cumulative volume of reworked sediment surrounding the burrow (B_{RS}) and the cumulative volume of sediment expelled at the water-sediment interface (V_{ES}) all significantly differed between experiment durations and seasons with significant interactions between these two factors (**Table 1.2**). T_{RS} sharply increased until D4 and then remained relatively constant until the end of the experiment (**Figure 1.3A**). This initial increase was more pronounced during summer than during spring and winter. B_{RS} also sharply increased during the first 4 days of the experiments but did not stabilize after then due to continuous increases in burrow lengths (**Figure 1.3B**). Here again the initial increase was more pronounced during summer than during spring and winter. Conversely, V_{ES} tended to increase constantly with experiment durations but at a higher rate during summer versus an intermediate and a lower one during spring and winter, respectively (**Figure 1.3C**). At D4, B_{RS} and V_{ES} correlated positively (simple linear regression, $F = 48.868$, $p < 0.001$; **Figure 1.3D**). B_{RS} then represented 79.5, 72.1 and 72.3 % of total cumulative reworked sediment (*i.e.*, $B_{RS} + V_{ES}$) during winter, spring and summer, respectively. Overall, changes in the total volume of reworked sediment were best described by the amount of time allocated to “Burrowing” (multiple linear regression, $F = 67.347$, $p < 0.001$; **Figure 1.4**). Associated model was:

$$y = 0.00909x - 2.014 \quad (5)$$

where y represents the total volume of reworked sediment and x the amount of time (min) allocated to “Burrowing”.

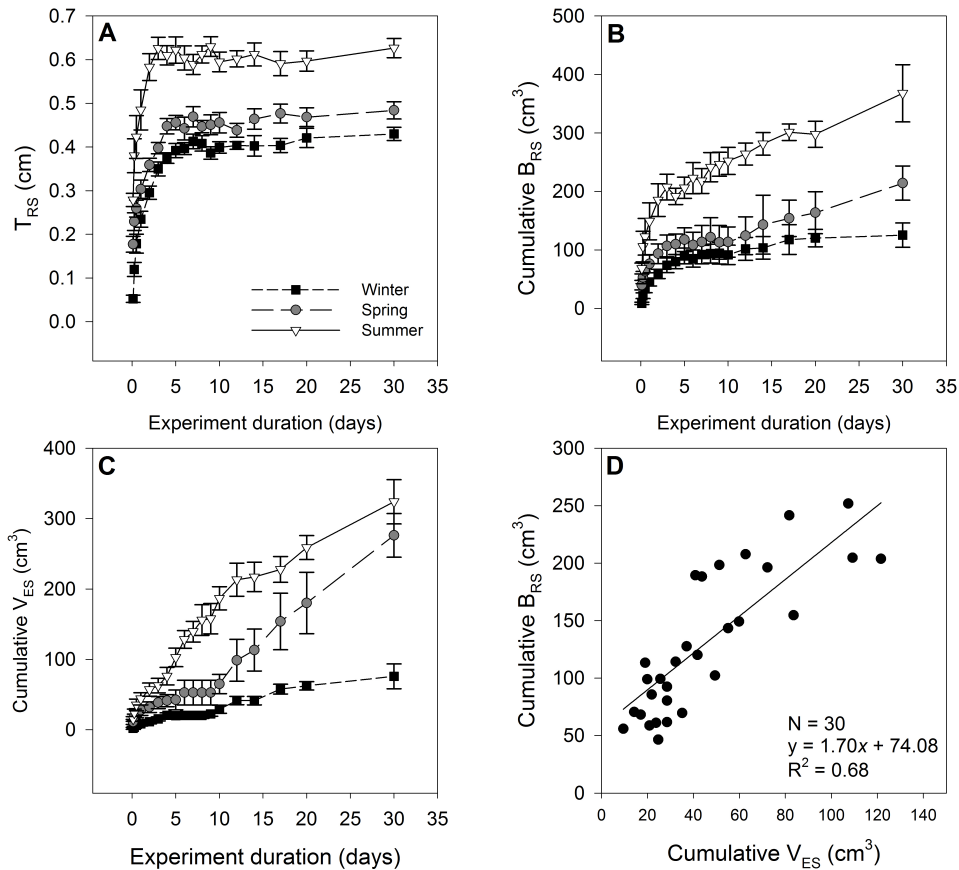


Figure 1.3 : Relationships between experiment duration and: (A) the thickness of reworked sediment (T_{RS}), (B) the cumulative volume of reworked sediment (B_{RS}), and (C) the cumulative volume of expelled sediment (V_{ES}). Relationship between the cumulative volume of reworked sediment (B_{RS}) and the cumulative volume of sediment expelled at the water-sediment interface (V_{ES}) at D4 (D).

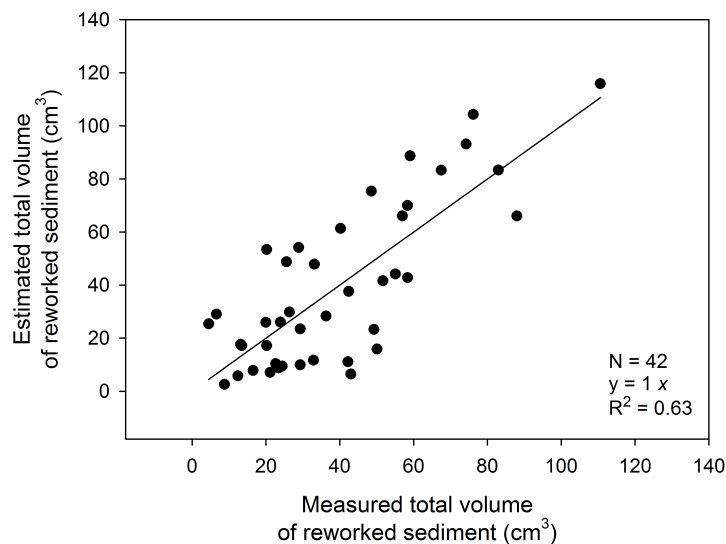


Figure 1.4 : Relationship between estimated and measured total volume of reworked sediment. Measured total volume of reworked sediment corresponds to the sum of the volume of expelled sediment (V_{ES}) and the volume of reworked sediment surrounding the burrow (B_{RS}) which are computed using Eq. (2) and Eq. (3), respectively. Estimated total volume of reworked sediment corresponds to the estimation of volume of reworked sediment using the model output from multiple linear regressions. See text for details about the model.

Vertical biodiffusion (D_{bv}) and bioadvection (V_{bv}) coefficients significantly differed between experiment durations and seasons (**Table 1.2**) without significant interactions between these two factors. Changes in D_{bv} with experiment durations showed similar patterns during all 3 seasons (**Figure 1.5A**). D_{bv} increased during the first days of the experiment to reach maximal values (90.2 ± 44.0 , 347.7 ± 114.1 and $1181.7 \pm 189.8 \text{ cm}^2 \text{ y}^{-1}$, during winter, spring and summer, respectively) around D4. D_{bv} then consistently decreased until the end of the experiment. The lack of interaction between seasons and experimental durations in affecting V_{bv} likely resulted from the very high variability in V_{bv} during the very first days of the experiments. Indeed, the relationships between V_{bv} and experiment durations seemed to show different patterns between seasons (**Figure 1.5B**). During summer, V_{bv} increased during the first days of the experiment to reach a maximal value of $234.7 \pm 111.8 \text{ cm y}^{-1}$ at D3. V_{bv} then decreased to $144.5 \pm 10.3 \text{ cm y}^{-1}$ at D17 before remaining almost constant until the end of the experiment. In spring, V_{bv} reached its maximal value ($101.2 \pm 10.1 \text{ cm y}^{-1}$) only at D17 and then slightly decreased until the end of the experiment. In winter, V_{bv} remained nil until D10. It then steadily increased to reach its maximal value ($46.6 \pm 18.5 \text{ cm y}^{-1}$) at D30. Overall, mean D_{bv} and V_{bv} were always higher in summer than in spring and in spring than in winter.

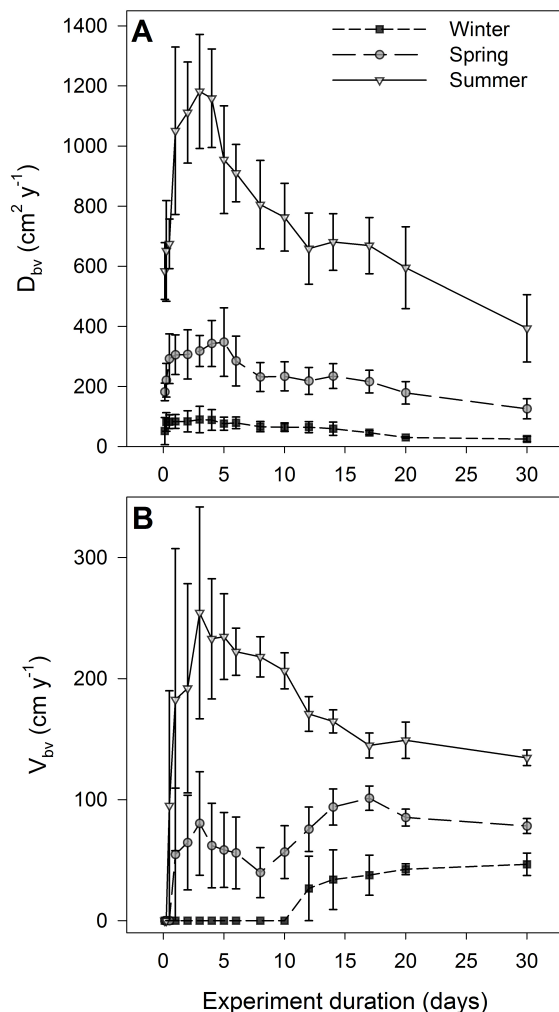


Figure 1.5 : Relationships between experiment duration and: (A) average (\pm SE) vertical biodiffusion (D_{bv}), and (B) vertical bioadvection (V_{bv}) coefficients during winter, spring, and summer experiments ($n = 10$ in all cases).

Biodiffusion coefficients associated with the component of sediment reworking occurring around burrow wall (D_{bw}) significantly differed between seasons (One-Way PERMANOVA, $F = 38.745$, $p = 0.004$). Average D_{bw} were higher during summer, intermediate during spring and lower during winter (7.9 ± 1.4 , 3.6 ± 0.9 and $1.1 \pm 0.0 \text{ cm}^2 \text{ y}^{-1}$, respectively).

3.4 Oxygen dynamics

In summer, all temporal changes in O_2 saturation in the overlying water column showed a typical pattern in stair-shape (**Figure 1.6A**). Stair-shape curves consisted in a succession of periods of relatively low oxygen decline ($-0.08 \pm 0.04 \text{ \% min}^{-1}$) interspersed by periods of relatively rapid oxygen decline ($-0.33 \pm 0.09 \text{ \% min}^{-1}$). Periods of relatively low

decline lasted on average 11.8 ± 5.2 min during which mud shrimp were “Burrowing”, “Walking” or “Resting” while periods of rapid decline lasted on average 2.9 ± 1.3 min during which mud shrimp were always “Ventilating”. The duration of ventilation by the mud shrimp (as assessed by video observations) sometimes lasted longer than the period of oxygen decline *per se* as observed on the third and the sixth steps in **Figure 1.6A**. Overall, there was a significant correlation (simple linear regression, $F = 69.261$, $p < 0.001$) between the duration of the time preceding a sharp decrease in O_2 saturation and the magnitude of this decrease (**Figure 1.6B**).

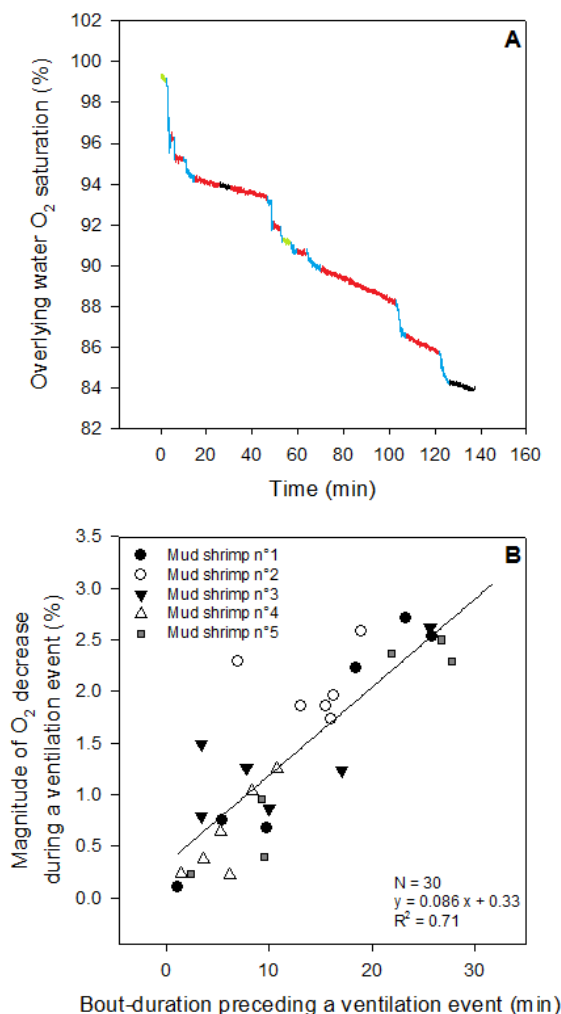


Figure 1.6 : O₂ dynamics in the overlying water. (A) Representative example of the effect of *Upogebia pusilla* activity on temporal changes (min) of O₂ saturation (%) in the overlying water. Red colour depicted temporal changes during “Burrowing”, blue colour depicted temporal changes during “Ventilation”, green colour depicted temporal changes during “Walking”, and black colour depicted temporal changes during “Resting”. (B) Relationship between the time-duration before a ventilation event and the magnitude of O₂ decrease during this event. See text for details about the relationship

O₂ saturation in the burrow lumen varied between 95 and 10 % (**Figure 1.7A, B and C**). The direction and intensity of these changes were tightly related to mud shrimp behaviours (**Figure 1.7A, B and C**). Slow O₂ saturation decreases ($-0.9 \pm 0.3 \text{ \% min}^{-1}$) were detected when mud shrimp were “Resting” or “Walking” (**Figure 1.7A, C**). Rapid O₂ saturation decreases ($-6.7 \pm 3.4 \text{ \% min}^{-1}$) were detected when mud shrimp were “Burrowing” (**Figure 1.7B, C**). Conversely, sharp increases in O₂ saturation ($27.4 \pm 4.3 \text{ \% min}^{-1}$) were always associated with “Ventilating” (**Figure 1.7A, B and C**). The mean ventilation duration necessary for O₂ saturation to reach its maximum value during a single ventilation event was $2.9 \pm 0.7 \text{ min}$. There was a significant positive correlation (simple linear regression, $F =$

165.364, $p < 0.001$) between the distances of the mud-shrimp from the sensor and the values of O_2 saturation at the onset of ventilation (**Figure 1.7D**). When mud shrimp were close to the sensor, the onset of “Ventilating” corresponded to an O_2 saturation between 12 and 25 %.

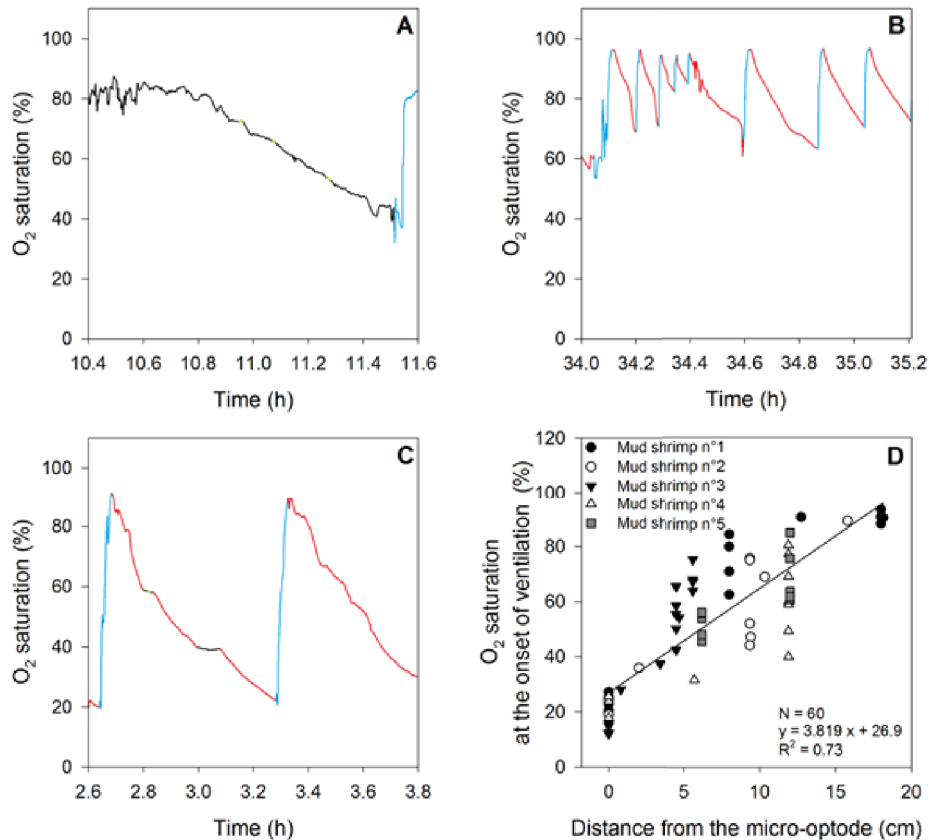


Figure 1.7 : O_2 dynamics in the burrow water. (A, B and C) Example of behaviour-specific O_2 saturation pattern in the burrow lumen when the mud shrimp was (A and B) far and (C) close from the micro-optode. Red colour depicted temporal changes during “Burrowing”, blue colour depicted temporal changes during “Ventilating”, green colour depicted temporal changes during “Walking” and black colour depicted temporal changes during “Resting”. (D) Relationship between O_2 saturation at the onset of a ventilation event and the mud shrimp distance from the sensor. See text for details about the relationship

4 Discussion

4.1 Behaviour

To our knowledge, the only literature data regarding mud shrimp behaviours have been collected on deposit-feeding species (Anderson et al., 1991; Gagnon et al., 2013; Stamhuis et al., 1996). Despite the fact that *Upogebia pusilla* is a suspension-feeder (Dworschak, 1987a), the four behaviours identified during the present study are equivalent to

those described during these three studies for *Calocaris macandreae*, *Callinassa subterranea* and *Calocaris templemani*, respectively (**Table 1.3**).

The averages proportion of time allocated to active behaviours (*i.e.*, “Burrowing”, “Ventilating” and “Walking”) by *U. pusilla* were 43, 60 and 82% during winter, spring and summer, respectively. This can be compared with the values of 66% reported during springtime for another coastal mud shrimp *C. subterranea* (Stamhuis et al. 1996), which suggests that this proportion is not related to feeding modes. The main difference in the time allocation between the two species was associated to “Ventilating” and “Walking”. During spring, *U. pusilla* spent 26.6% of its time ventilating *versus* only 9.9% for *C. subterranea* (Stamhuis et al. 1996). Conversely, during the same season, *U. pusilla* spent only 2.6% of its time “Walking” *versus* 14.8% for *C. subterranea* (Stamhuis et al. 1996). Such differences may relate to the trophic mode since: (1) “Ventilating” may occur more frequently in suspension feeders because it is related both to respiration and nutrition, and (2) conversely to suspension-feeders, deposit-feeders rely on “Walking” to forage for food within their burrow.

The proportions of time allocated to “Burrowing” during spring by *U. pusilla* (31.0%, present study) and *C. subterranea* (33.3%, Stamhuis et al. 1996) were almost equivalent. This may seem odd since deposit-feeders are relying on “Burrowing” both for feeding and burrow maintenance, which led to the paradigm according to which the amounts of sediment expelled at the sediment-water interface should be lower in suspension- than in deposit-feeding mud shrimp (Pillay and Branch, 2011; Posey et al., 1991). However, our own results: (1) showed that “Burrowing” is mostly responsible for sediment reworking by *U. pusilla*, and (2) do not support the occurrence of significant differences in the volume of sediment reworked by suspension- and deposit-feeding mud shrimp (see below the “sediment reworking” section of the discussion). Overall, this is in good agreement with the equality in the proportion of time allocated to “burrowing” by *U. pusilla* and *C. subterranea*.

To our knowledge, this study is the first one assessing seasonal changes in between-behaviours time allocation in a mud shrimp. Between winter and summer, the proportion of time allocated by *U. pusilla* to an active behaviour increased by a factor 2.5. More specifically, the proportions of time allocated to “Burrowing” and “Ventilating” increased by a factor 1.4 and 3, respectively. Because of the 10°C difference between summer and winter temperature, these values also constitute Q_{10} and can thus be compared with the value of 2.8 reported for oxygen consumption rates in the mud shrimp *Callinassa kraussi* (within a 14-

21°C temperature range, Hanekom and Baird 1987). They can also be compared with the Q_{10} values of 3.8 and 2.8 recorded between the same two seasons for the components of Total Oxygen Uptake and pore water exchange rates due to the presence of *U. pusilla* (data from Pascal et al. 2016b). Interestingly, the increases in the proportions of time devoted to “Burrowing” and “Ventilating” during summer resulted from a decrease in “Burrowing” bout-durations and increases in both “Burrowing” and “Ventilating” bout frequencies. Since our results suggest that the level of O_2 saturation triggering ventilation is constant (see also the “Oxygen dynamics” section below), this is here again consistent with a direct effect of temperature on mud shrimp behaviour. During summertime, oxygen consumptions by the mud shrimp and associated microbial communities indeed increase, which tends to: (1) reduce the time of “Burrowing” required to reach this threshold and thereby the duration of “Burrowing” bouts, and (2) increase the frequency of both “Ventilating” and “Burrowing” bouts. Temperature thus clearly appears as the main factor driving between-season differences in between-behaviour time allocation.

4.2 Sediment reworking

Our results clearly show the occurrence of three distinct patterns in the sediment reworking induced by *Upogebia pusilla*, which transports sediment (**Figure 1.1**): (1) outside its burrow by expelling excavated sediment at the sediment-water interface (P2, Dworschak 1983, LP personal observations) (P1), (2) below the sediment surface by introducing and then moving downward surficial particles within the burrow and (3) within its burrow by compacting excavated sediment against burrow walls (P3). P1 and P2 are mostly vertical, whereas P3 occurs perpendicularly to burrow walls (*i.e.*, mostly horizontally due to the general morphology of the burrow, **Figure 1.1**). Previous studies assessing sediment reworking by mud shrimp have only considered P1 through the assessment of sediment turnover rates (Berkenbusch and Rowden, 1999; Pillay et al., 2012; Rowden et al., 1998; Suchanek, 1983). During the present study, we also modelled the resultant of P1 and P2 using a 1D biodiffusion-bioadvection model (Maire et al., 2016). We also assessed P3 by experimentally measuring T_{RS} and B_{RS} , and using a simple biodiffusive model to determine D_{bw} . During all three seasons, there was a rapid limitation of T_{RS} , which stabilized after *ca.* 4-5 days. This probably resulted from the quick burying of luminophores below the new sediment water interface (*i.e.*, through P1), which rapidly precludes them to be introduced in

mud shrimp burrows (LP personal observation). This restricted the validity of our estimations of B_{RS} to the periods of initial increases in T_{RS} (*i.e.*, until D4).

During this period of time, V_{ES} (P1) accounted on average for only about 25 % of the total (*i.e.*, P1+P3) volume of reworked sediment. Using a different approach, Dworschak (1983) estimated this proportion to be 50 % in *U. pusilla*. This highlights the necessity of considering the components of sediment reworking by *U. pusilla* taking place below the sediment-water interface when assessing the role of this mud shrimp in sedimentary processes. This statement is likely to hold for other mud shrimp and especially other suspension-feeding upogebiids, which build (semi)permanent burrows that only require to be consolidated (Dworschak 1983, Nickell & Atkinson 1995). Average V_{ES} recorded during the present study at D30 were between 76 (winter) and 324 cm³ (summer). They were converted in sediment turnover rates (*sensu* Rowden & Jones 1993 and Moyo et al. 2017) between 3.3 and 14.0 g dry weight d⁻¹ assuming a sediment density of 1.3 gDW.cm³. These results were then up scaled to a one-year time period, using an average density of 2.7 ind. m⁻² (as measured at the scale of a vegetated intertidal mudflat in Arcachon Bay; L.P. unpublished) and the recorded seasonal changes in seawater temperature (<http://somlit.epoc.u-bordeaux1.fr>), leading to a value of 9.6 kgDW m⁻² y⁻¹. Similar estimates have already been obtained for *Callianassa subteranea* (11 kg m⁻² y⁻¹ according to Rowden et al. 1998 and 15 kg m⁻² y⁻¹ according to Stamhuis et al. 1997). It is worth noticing that all three estimates were based on laboratory experiments during which mud shrimp were restricted within experimental enclosures. This probably less affected *U. pusilla* since its burrow is (semi)permanent (Dworschak 1983) in comparison to *C. subteranea*, which continuously add new branches to its burrow (Nickell and Atkinson 1995, Atkinson and Taylor 2005). The most comparable value (*i.e.*, 96 kg m⁻² y⁻¹) has thus probably been measured *in-situ* for the deposit-feeding mud shrimp *Callianassa filholi* with an average density of 16.4 ind.m⁻² (Berkenbusch and Rowden 1999). After standardising for density, this resulted in values of 3.6 and 5.8 kg ind.⁻¹ y⁻¹ for *U. pusilla* and *C. filholi*, respectively. Due to: (1) the level of uncertainty associated with these computations, (2) possible (even if minor) underestimation for *U. pusilla*, and (3) possible heterogeneities between *ex-* and *in-situ* experiments, our conclusion is that these figures are not far enough to support the occurrence of significant differences in P1 between the two species and furthermore between suspension- and deposit-feeding mud shrimp.

The results from the multiple linear regression model linking the total volumes of reworked sediments (*i.e.*, P1 + P3) and the proportions of time allocated to the 4 different behaviours revealed the existence of a strong positive correlation between the proportion of time allocated to “Burrowing” and the total volumes of reworked sediment (**Figure 1.4**). This suggests that, in *U. pusilla*, “Burrowing” is the behaviour that is mostly inducing sediment reworking.

Besides those direct assessments, we also used: (1) a 1D vertical biodiffusion-bioadvection model, as already achieved by Maire et al (2016), to derive the coefficients (D_{bv} and V_{bv}) associated with the vertical component of sediment reworking, and (2) a biodiffusive model to derive the coefficient (D_{bw}) associated with P3. Overall, there was a good agreement between changes in D_{bv} and B_{RS} . In both cases, values were indeed higher during summer, intermediate during spring and lower during winter experiments. Moreover, and especially during summer, D_{bv} and B_{RS} showed related patterns with respect to experiment durations with: (1) sharp initial increases in both cases, and (2) a decrease in D_{bv} and a slower increase in B_{RS} after D4. The initial increase in D_{bv} resulted from both: (1) the gradual transport of luminophores at depth, and (2) a sharp increase in T_{RS} . After D4, (1) the luminophore surface layer tended to become buried under the sediment expelled from the burrow (P1), (2) luminophore maximal penetration depth (*i.e.*, the bottom of the burrow) was reached (P2), and (3) T_{RS} became constant resulting in a diminution of the increase in B_{RS} with experiment duration (P3). All 3 processes accounted for a decrease in D_{bv} with experiment duration. The high variability in V_{bv} detected until D10 during the summer and, to a lower extent, the spring experiments (**Figure 1.5B**) resulted from the time duration necessary to integrate inter-individual differences in the timing of sediment expulsion at the sediment-water interface. After D10, there was also a good agreement between changes in V_{bv} and V_{ES} , which were higher during summer, intermediate during spring and lower during winter. Moreover, these two parameters showed related temporal patterns after D10. In summer, V_{ES} increase was reduced after D10 accounting for a decrease in V_{bv} with experiment duration. Conversely, during spring, V_{ES} increased stronger after than before D10 resulting in an increase in V_{bv} followed by a stabilisation. During winter, V_{bv} and V_{ES} also followed the same temporal pattern with respect to experimental duration.

Comparing D_{bv} and V_{bv} with literature data proved difficult because of: (1) the large variety of models used to assess vertical sediment reworking (*e.g.*, Gerino et al. 1998; Maire et al. 2006; Bernard et al. 2012; Lindqvist et al. 2013), and (2) differences in the dimensions

of experimental enclosures. It has for example been shown that the inclusion of a bioadvective term in a bioturbation model results in a lower D_{bv} as compared to those derived from a simple biodiffusive model (Gerino et al., 1994). The geometry of experimental enclosures may also interfere since the small thickness of our aquaria may have biased our estimates of vertical sediment reworking (e.g., through overestimations of burrow depth and of the thickness of the layer of expelled sediment) as compared to large cylindrical cores. Nevertheless, the large discrepancy between our D_{bv} and V_{bv} and literature data suggests that *U. pusilla* is a highly efficient sediment reworking species. Our D_{bv} were indeed up to 1000-fold higher than those previously reported for the Amphipod *Corophium volutator* (De Backer et al., 2011; Mermillod-Blondin et al., 2005) and the Polychaete *Hediste diversicolor* (Lindqvist et al. 2013) using cylindrical cores and up to 20-fold higher than those measured for the three Bivalves *Abra segmentum (ovata)*, *A. nitida* and *A. alba* using thin aquaria (Maire et al. 2006, Bernard et al. 2016). These comparisons are consistent with the results of Maire et al. (2016) who recently found a 10-fold higher D_{bv} coefficient in *U. pusilla* as compared to *H. diversicolor* using cylindrical cores. Similarly, our V_{bv} coefficients are up to 45-fold higher than those previously reported for the Oligochaete *Lumbriculus variegatus* (Blankson et al., 2017).

Although sediment reworking has been mostly investigated through its vertical component (e.g. Gerino et al. 1994; Gerino et al. 1998; François et al. 2002; Maire et al. 2008), its horizontal component can be as relevant (Bernard et al. 2012) or even an order of magnitude higher (Wheatcroft, 1991) depending on species. In *U. pusilla*, this component is mostly associated to P3 because of the general shape of the burrow. During the present study, D_{bw} were assessed at D4, when T_{RS} reached their maximum values. Based on the comparison between D_{bv} and D_{bw} , the horizontal component of sediment reworking by *U. pusilla* appears ca. 100-folds lower than the vertical one. This result may seem surprising first but it is consistent with the difference between the thickness of the sediment layer reworked along the burrow wall and burrow depth.

As for all other sediment reworking proxies, D_{bw} were higher during summer, intermediate during spring and lower during winter experiments, which is coherent with the positive relationship found between mud shrimp activity (and especially “Burrowing”) and the total volume of reworked sediment. These results are also fully consistent with previous findings for other thalassinids. Rowden et al. (1998) for example reported higher sediment expulsion rates in *C. subterranea* during summer than during winter (0.06 to 0.4 kgDW m⁻²

m⁻¹ during winter vs. 1.3 to 2.8 kgDW m⁻² m⁻¹ during summer), whereas Berkenbusch & Rowden (1999) found a strong correlation between sediment turnover rate by *C. filholi* and seawater temperature. Overall, this suggests that temperature is one of the main environmental factors controlling mud shrimp activity and sediment reworking.

4.3 Oxygen dynamics

The short-term dynamics of O₂ saturation in the overlying water clearly shows a cyclical pattern constituted by the alternation between periods of low decrease and events of sharp decreases in O₂ saturation. This pattern is clearly controlled by the “Ventilating” behaviour of the mud shrimp since drops in O₂ saturation occurred only during ventilation events (**Figure 1.6**). This confirms the intermittent ventilation behaviour of mud shrimp (Forster and Graf, 1995; Kristensen and Kostka, 2005; Stamhuis et al., 1996; Volkenborn et al., 2012). The analysis of the time series of O₂ saturation allowed us to estimate the interval between (*i.e.*, 11.8 minutes) and the duration (*i.e.*, 2.9 minutes) of each drop. These values are similar to those already reported by Dworschak (1981) for *Upogebia pusilla* using a similar approach. Moreover, our estimation of the duration of O₂ drop is also consistent with those already measured for several deposit-feeding mud shrimp (Forster and Graf 1995, Stamhuis et al. 1996, Volkenborn et al. 2012). Interestingly, the average duration of a ventilation event (as determined from video observation during summer experiment) was 6.9 minutes, while the average time duration between two consecutive ventilation events was only 9.5 minutes (**Table 1.3**). In spite of the tight association between ventilation events, it thus appears that *U. pusilla* tended to ventilate during a longer period than required to fully oxygenate their burrow as observed on the third and sixth O₂ drops in **Figure 1.6A**. A possible explanation lies in the fact that this species is a suspension-feeder, which also uses ventilation for a feeding purpose. It would now be interesting to carry out a similar experiment on a deposit-feeding mud shrimp to further test this hypothesis.

O₂ saturation within the burrow showed a clear cyclical pattern as already observed for other mud shrimp such as *C. subterranea* (Forster and Graf 1995) and *N. californiensis* (Volkenborn et al. 2012). We found a significant negative relationship between O₂ saturation measured by the optode within the burrow at the onset of a ventilation event and the distance of the mud shrimp to this sensor (**Figure 1.7D**). If we assume that the mud shrimp initiate a ventilation event at a given O₂ saturation, this suggests that the spatial distribution of O₂ content in the burrow is not uniform. More specifically, this result supports the fact that O₂

saturation would be minimal close to the mud shrimp and would increase with increasing distance from the mud shrimp. There are some rationales to support this assumption: (1) the mud shrimp is respiring and thus consuming O₂ (Koike and Mukai 1983, Forster and Graf 1995) and (2) its activity contribute to release reduced compounds, which are readily oxidized in the oxygenated burrow water (Aller et al., 1983; Kristensen, 2000; Kristensen and Kostka, 2005). According to these hypotheses, the O₂ saturation threshold at which *U. pusilla* is starting ventilating would be between 12 and 25%. This range is coherent with the minimal O₂ saturation levels (*i.e.*, 12, 20 and 30 %) observed within the burrow water of *C. japonica* (Koike & Mukai 1983), *N. californiensis* (Volkenborn et al. 2012) and *U. major* (Koike & Mukai 1983), respectively.

Temporal changes in O₂ saturation within the burrow were clearly relying on the behaviour of the mud shrimp (**Figure 1.7**). When mud shrimp were “Resting” or “Walking”, O₂ decreases were similar and remained very low. They were probably mainly resulting from: (1) mud shrimp respiration, (2) microbial community respiration and (3) diffusive transport of O₂ from the burrow lumen to the sediment. Since thalassinid mud shrimp show very low metabolic rates (Atkinson and Taylor 2005), microbial community respiration and diffusive transport of O₂ through the burrow wall may account for the main part of oxygen consumption during these periods. Conversely, O₂ saturation tended to drop quickly when mud shrimp were “Burrowing” due to the increase in mud shrimp metabolism and the release of reduced compounds previously trapped within the sediment column that are quickly re-oxidized through a series of coupled oxidation-reduction reactions (Aller et al. 1983, Kristensen 2000, Kristensen & Kostka 2005).

Chapitre 2 :

Influence d'*Upogebia pusilla* sur les flux biogéochimiques à l'interface

eau-sédiment

Influence of the mud shrimp *Upogebia pusilla* (Decapoda: Gebiidea) on solute and porewater exchanges in an intertidal seagrass (*Zostera noltei*) meadow of Arcachon Bay: an experimental assessment

Ludovic Pascal^{1,2}, Olivier Maire^{1,2}, Nils Volkenborn³, Pascal Lecroart^{1,2}, Sabrina Bichon^{1,2}, Xavier de Montaudouin^{1,2}, Antoine Grémare^{1,2} and Bruno Deflandre^{1,2}

¹Univ. Bordeaux, EPOC, UMR 5805, F-33400 Talence, France

²CNRS, EPOC, UMR 5805, F-33400 Talence, France

³School of Marine and Atmospheric Sciences, Stony Brook University, Stony Brook, NY 11794, USA

*Article publié dans la revue Journal of Experimental Marine Biologie and Ecology*³

477:69-79,2016 ;doi : 10.1016/j.jembe.2016.01.008

³ Ce manuscrit correspond à la version acceptée de l'article et présente des différences mineures par rapport à la version éditée. Cette dernière est disponible sur le site de l'éditeur : <http://www.sciencedirect.com/science/article/pii/S0022098116300090>

Abstract

The aim of the present study was to investigate the influence of the mud shrimp *Upogebia pusilla* on porewater and solute exchanges in an intertidal *Zostera noltei* meadow of Arcachon Bay. Laboratory experiments carried out during three seasons showed that *U. pusilla* strongly enhanced sediment porewater exchange rates (averaging 26, 45 and 71 L m⁻² d⁻¹ in winter, spring and summer, respectively) in comparison to uninhabited sediments for which these rates were moderate (averaging 9, 9 and 16 L m⁻² d⁻¹ in winter, spring and summer, respectively). Total Oxygen Uptakes (TOU) were increased by factors around 2.5 during the three studied seasons whilst oxygen consumption by the shrimp accounted for 64, 28 and 21 % of TOU in winter, spring and summer, respectively. *U. pusilla* also significantly enhanced the uptake of nitrate (up to 13.8-fold in summer) and the release of ammonium (up to 3.0-fold in summer) and silicate (up to 3.8-fold in spring) by the sediment. Overall, our results highlight the key role of *U. pusilla* in controlling oxygen and nutrient fluxes in Arcachon Bay. Because *U. pusilla* populations are predominantly found in the sediments of *Z. noltei* meadows, the full assessment of the functional effects resulting from the decline of this meadow should include the effects associated to the disappearance of *U. pusilla* as well.

1 Introduction

With an average net primary production reaching $817 \text{ gC m}^{-2} \text{ yr}^{-1}$, seagrass meadows are among the most productive marine ecosystems (Mateo et al., 2006). Their dense canopies strongly attenuate tidal, wind and wave-driven current velocities, thereby simultaneously enhancing the deposition of fine organic-rich particles and preventing sediment resuspension (Hemminga and Duarte, 2000). The sequestration of considerable amount of organic matter (*i.e.*, 15 % of carbon storage of the world ocean) allows them to directly or indirectly sustain complex trophic networks (Boström and Bonsdorff, 1997). Seagrasses host diverse macrobenthic communities (Blanchet et al., 2004; Boström et al., 2006), which play a key role in the functioning of coastal benthic ecosystems (Duffy, 2006).

The light requirements of seagrasses limit their development to coastal shallow water areas such as lagoons, where they are exposed to a large variety of natural and anthropogenic disturbances which has induced a fast and intense global loss over the last decades (Waycott et al., 2009). About 25 % of marine phanerogam species together with the ecological services they provide are currently considered as extremely threatened (Short et al., 2011). Recent studies have shown that the alteration of seagrass habitats consistently induces a significant loss of benthic biodiversity (Calizza et al., 2013; Pillay et al., 2010) and deeply affects biogeochemical exchanges at the sediment-water interface (Delgard et al., 2013; Duarte et al., 2005). However, most investigations focusing on benthic communities associated with seagrasses and their impact on biogeochemical processes have been carried out using either sediment cores or benthic chambers. They have therefore most often been dealing with the upper twenty centimeters of the sediment column only (*i.e.*, the typical penetration depth of sediment cores), where the majority of infaunal organisms are indeed present (Barnes and Barnes, 2012; Bernard et al., 2014; Blanchet et al., 2004). Conversely, the impact of deep and mobile burrowing species, which live in burrows deeper than 20 cm, has been largely neglected. This has not often been considered a major problem since seagrasses and large bioturbating organisms usually tend to exclude each other (Brenchley, 1982; Philippart, 1994; Valdemarsen et al., 2011; van Wesenbeeck et al., 2007). However, the nature of specific interactions between seagrasses and burrowing mud shrimp is not always negative and seems tightly dependent on their feeding behavior. Callianassids, which are primarily deposit-feeders, predominantly inhabit unvegetated areas where they can easily and continually burrow within the sediment column (Siebert and Branch, 2006). Conversely, a few

suspension-feeding species belonging to the Upogebiidae group seem to preferentially colonize seagrass meadows as below-ground plant systems provide the sediment stability required for the construction of their permanent or semi-permanent burrows (Siebert and Branch, 2006). This is typically the case in Arcachon Bay where the suspension-feeding mud shrimp *Upogebia pusilla* preferentially inhabits intertidal seagrass meadows (Pascal et al. in prep., see “Annexe I”). Due to their positioning deep in the sediment and their mobility, these mud shrimp easily escape traditional sampling gears (*e.g.*, grabs and hand sediment corers), which are designed to only collect the upper 10-20 cm of the sediment column (Blanchet et al. 2004). Moreover, given the presence of multiple (*i.e.*, typically between 2 and 4) openings per burrow and the relatively long distance between them (Dworschak 1983), the deployments of *in situ* incubation chambers may most often fail to capture their impact on solute exchanges as well, unless a specific design is set up to account for the presence of mud shrimp (Webb and Eyre 2004).

Mud shrimp are among the most efficient bioturbators inhabiting marine soft sediments (see review by Pillay and Branch (2011)). They dig large galleries deep in the sediment, rework large amount of deposited material, and largely increase the exchange surface between the sediment column and the overlying water (Coelho et al. 2000). Moreover, they strongly enhance sediment-water exchange rates through the frequent ventilation of their burrow (Webb and Eyre 2004). As stated above, and in spite of their potential impact, the influence of mud shrimp on the biogeochemical dynamics of vegetated sediments is currently largely ignored. Moreover, our understanding of the functional consequences of seagrass regression, which is most often based on comparisons between vegetated and adjacent bare sediments (Bernard et al., 2014; Delgard et al., 2013; Pillay et al., 2010), is also likely biased (and probably underestimated) because of differences in densities of mud shrimp within these two sediment types.

Although difficult to assess *in-situ*, the contribution of mud shrimp to ecosystem functioning can be tackled through *ex-situ* manipulative experiments. This approach is particularly suitable to study the effect of a single species (such as a mud shrimp) on ecosystem processes (such as porewater and solute exchanges at the sediment water interface). Thus, the present study aimed at quantifying the impact of the presence of the mud shrimp *Upogebia pusilla* on porewater exchange rates and benthic fluxes of O₂, NH₄⁺, NO₃⁻ and dSi within an intertidal flat colonized by the dwarf-grass *Zostera noltei*. This was achieved through seasonally replicated *ex-situ* experiments.

2 Materials and methods

2.1 Study site

Sediment cores and mud shrimp were collected in Arcachon Bay, which is located along the French Atlantic coast (**Figure 2.1**). This shallow semi-enclosed macrotidal embayment (174 km²) is characterized by a semi-diurnal tide with an amplitude between 1.1 and 4.9 m. Its intertidal area (115 km²) consists of soft sediments, ranging from sand to mud. It is partially covered by a *Zostera noltei* (dwarf grass) meadow. The decline of seagrasses has been especially severe in Arcachon Bay where the intertidal *Z. noltei* meadow, initially the largest in Europe, has lost a third of its total surface between 1989 and 2007 (Plus et al. 2010). During the same time period, the regression of the eelgrass (*Zostera marina*) meadow has been even worse, with a loss of three quarters of its initial surface (Plus et al. 2010). In Arcachon Bay, dwarf grass meadows are preferentially inhabited by the deep burrow-dwelling Gebiidean Crustacean *Upogebia pusilla* (Pascal et al. in prep., see “Annexe I”), which is likely to have declined as well because of such a tight association. The study site, a vegetated intertidal mudflat located in the middle part of the bay (44° 40.782' N, 1° 08.321' W), has suffered from seagrass regression since 2005. Sediment leaf coverage currently averages 71 % during summertime (Pascal, L. unpublished data). This *Zostera* meadow is still supporting an important population of *U. pusilla* (23 ind. m⁻² ; Pascal et al. in prep) whereas this mud shrimp is absent from bare sediments (Pascal et al. in prep.).

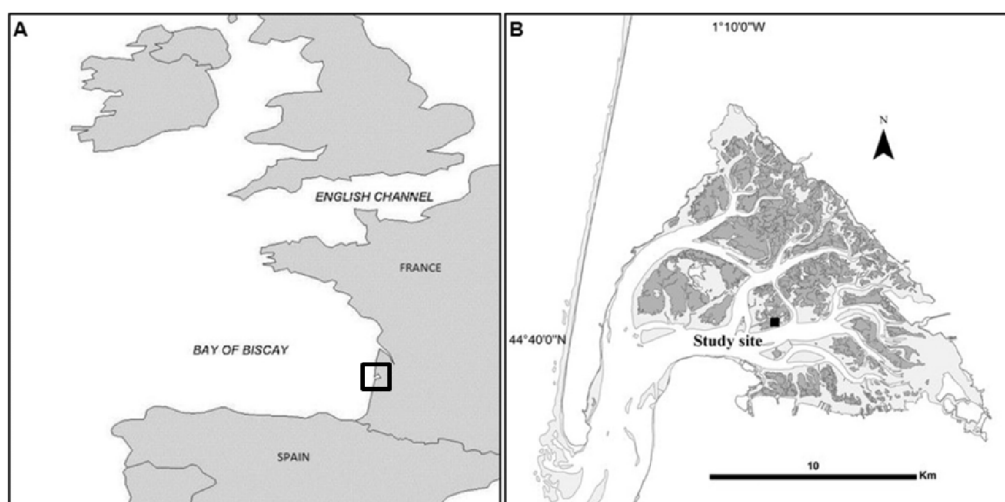


Figure 2.1 : *Sampling site.* Location of Arcachon Bay on the French Atlantic coast (A) and of the study site (44° 40.782' N, 1° 08.321' W) in the central part of Arcachon Bay (B). *Zostera noltei* meadows are presented in gray (from Plus et al. 2010).

2.2 Sampling and experimental design

Experiments were carried out during three seasons (spring: April 2012, winter: February 2013 and summer: September 2013) encompassing the yearly amplitude of seawater temperature at the study site. Two days prior each experiment, one small (3 cm inner diameter, 10 cm long) and nine large (9.4 cm inner diameter, 25 cm long) sediment cores were collected by hand, using transparent acrylic tubing (15 and 40 cm long, respectively), at low tide within an homogeneous patch of *Z. noltei*. These cores never contained any adult specimens of *U. pusilla*, which were collected at the same time using a bait piston pump and then isolated in individual containers to avoid aggression. Sediment cores and mud shrimp were immediately brought back to the laboratory. Mud shrimp were measured (total length from the tip of the rostrum to the tip of the telson) and weighed (Blotted Wet Weight, ± 0.1 mg). Four healthy specimens of the same length (4.9 ± 0.2 cm) and weight (1.7 ± 0.1 gBWW) were selected and immediately introduced in four randomly selected field-collected large sediment cores (“*With-Upogebia* treatment”). Mud shrimp density in experimental cores (144 ind. m^{-2}) was higher than at the study site (see above) but (1) cores with a larger diameter were not suitable for the purpose of this study and (2) such a density is in the range of those available in the literature (e.g., Dworschak 1987b; D’Andrea and DeWitt 2009). Four field-collected large sediment cores were kept without mud shrimp (“*Without-Upogebia* treatment”). All sediment cores were placed in a dark thermo-regulated room at *in situ* temperature for seven days, allowing for mud shrimp acclimation. During that time, a continuous flow ($\sim 0.25 \text{ L min}^{-1}$) of filtered water ($0.2 \mu\text{m}$) was set up for each sediment core to ensure a good oxygenation of the overlying water ($\sim 0.7 \text{ L}$ per core). Seawater temperatures and salinities were kept constant at $10 \text{ }^\circ\text{C}$ and 32 , $13 \text{ }^\circ\text{C}$ and 30 and $19 \text{ }^\circ\text{C}$ and 32 during the whole duration of winter, spring and summer experiments, respectively, which corresponded to average field values.

2.3 Sediment characteristics

Except for permeability, sediment characteristics were assessed on sediment cores collected as described above in April 2012 (spring), February 2013 (winter) and September 2013 (summer). Sediment permeability was assessed on sediment samples collected in February (winter), April (spring) and September (summer) 2014.

The sediment grain size of the 20 first centimeters of the sediment column of a large sediment core was assessed by sieving pre-weighted dried sediment over a column with decreasing mesh size (1000, 500, 250, 125 and 63 μm). Median grain diameters (D_{50}) were computed using GRADISTAT v4.0 (Blott and Pye, 2001).

Sediment porosity (Φ) was assessed by slicing a large sediment core every 5 mm from the top to 2 cm depth, every 10 mm between 2 and 10 cm depth and every 50 mm between 10 and 20 cm depth. Each sediment slice was weighed and immediately frozen. The loss of water was measured after freeze-drying and corrected for sea salt content.

Sediment permeability was measured in small sediment cores by the “constant head method”, which consists in measuring the flow of water through the sediment matrix at a given hydraulic pressure (Klute and Dirksen, 1986). The hydraulic conductivity (K in m s^{-1}) was calculated using equation (1):

$$K = (V \times L) / (h \times A \times t) \quad (1)$$

Where V is the volume of water collected (m^3) over a given time period T (s), L is the sediment core length (m), h is the height of the water column (pressure head, m), A is the surface area of the sediment-water interface (m^2) and t is the duration of water collecting.

Sediment permeability (k in m^2) was then calculated using equation (2):

$$k = (K \times m) / (d \times g) \quad (2)$$

Where K is the hydraulic conductivity (m s^{-1}), m is the porewater viscosity ($\text{g m}^{-1} \text{s}^{-1}$), d is the water density (g m^{-3}) and g is the gravity ($= 9.81 \text{ m s}^{-2}$).

Organic carbon content (OC) was measured on the homogenized, freeze-dried samples used for porosity calculation (see above), with an automatic CN analyzer (ThermoFinnigan Flash EA1112 Series) after acidification with 2M HCl (overnight at 50°C) to remove carbonates.

2.4 Benthic solute exchanges

Benthic solute exchanges were measured in the dark within each of the four *With-Upogebia* treatments and the four *Without-Upogebia* treatments cores (see section 2.2). When starting measurements, the water flow was turned off, and 35 mL of the overlying water were

sampled for initial measurements of dissolved oxygen (O_2), ammonium (NH_4^+), nitrate (NO_3^-) and dissolved silicate (dSi) concentrations. Sediment cores were then hermetically sealed with a PVC lid. O_2 concentration was continuously measured in each sediment core using a mini-optode (OXROB10, Pyroscience) connected to a Firesting Oxygen Meter (Pyroscience) and piloted by a laptop. Linear calibration was achieved between the oxygen concentration of the overlying water measured by Winkler titration (Grasshoff et al. 1999) and zero oxygen in a sodium ascorbate solution. Sensors were inserted into the lid and placed 5 cm above the sediment surface. The overlying water was continuously stirred with a Teflon-coated magnetic bar at ~100 rpm during the incubations. Incubation duration was adjusted so that O_2 concentration in the overlying water never fell below 70 % of its initial value. Incubations typically lasted between 4 and 6 hours in *Without-Upogebia* treatments cores versus 1 and 3.5 hours in *With-Upogebia* treatments cores. At the end of core incubations, samples of overlying water were collected for final nutrient measurements (see above). Sediment cores were then opened and left overnight with a continuous oxygenated water flow before starting sequential replications ($n = 5$).

Water samples were analyzed for NO_3^- (Wood et al., 1967), NH_4^+ (Aminot et al., 1997) and dSi (Truesdale and Smith, 1976) using a Quattro-SEAL auto analyzer. In all treatments, benthic O_2 and nutrients fluxes were calculated from the difference between initial and final concentrations, assuming a constant solute exchange relative to time. Fluxes were computed using equation (3):

$$F = [(C_f - C_i) \times V] / (t \times S) \quad (3)$$

Where V is the volume (m^3) of overlying water, S is the surface (m^2) of the water-sediment interface, C_i and C_f are the initial and final concentrations of solutes in the overlying water ($mmol L^{-1}$) and t is the incubation period (day). According to equation (3) a positive flux (F , $mmol m^{-2} d^{-1}$) is directed from the sediment to the overlying water.

To assess the contribution of the own respiration (*i.e.*, oxygen uptake) and excretion (*i.e.*, NH_4^+ release) of the mud shrimp to Total Oxygen Uptake (TOU) by the sediment and NH_4^+ fluxes, mud shrimp were removed from their burrow at the end of each experiment and individually placed in transparent acrylic tubes completely filled with 0.7 L of filtered (0.2 μm) and autoclaved seawater in a temperature controlled room. Tubes containing the same volume of filtered and autoclaved seawater were used as controls. Two hours later, the tubes

were sealed and O₂ concentration was then continuously recorded with mini-optodes as described above, whilst water was sampled at the start (*i.e.*, as soon as tubes were sealed) and at the end of these incubations for further NH₄⁺ analyses. Tubes were then opened and left two hours with a continuous oxygenated water flow before starting sequential replications (n = 3). Ammonium excretion could not be measured during winter experiments because of a storage failure of water samples. Individual respiration and excretion rates were both expressed in: (1) mmol m⁻² d⁻¹ to assess the contribution of the shrimp to TOUs and NH₄⁺ fluxes at the sediment-water interface, and (2) in μmol ind⁻¹ d⁻¹ to be easily compared with literature values. Since there were no significant temporal changes in O₂ and NH₄⁺ concentrations within controls, mud shrimp respiration and excretion rates were not corrected. To our knowledge, this procedure is the only one currently used for mud shrimp (Papasprou et al., 2004; Paterson and Thorne, 1995; Thompson and Pritchard, 1969). Although caution was taken to keep mud shrimp: (1) in total darkness, and (2) undisturbed during two hours before the beginning of the measurements, we cannot nevertheless exclude that it may have led to an overestimation of their oxygen uptake.

2.5 Measurements of porewater exchange rates

Porewater exchange rates were defined as the exchange of water between sediment porewater and overlying water. They were measured according to Na et al. (2008). Immediately after benthic solute exchanges measurements, a fluororimetric probe (Cyclops ©-7, Turner Design, λ_{excitation} = 490 nm; λ_{measured} = 514 nm) was gently positioned in the overlying water of each sediment core at ~7 cm above the sediment surface. Uranine (sodium fluorescein, C₂₀H₁₀Na₂O₅) was used as transport tracer to quantify the volumetric exchange of water and dissolved solutes across the sediment-water interface (Na et al. 2008). At the start of each experiment, 1.6 mL of an uranine stock solution (3.7 mg L⁻¹) was added in each core to reach an initial concentration of 10 μg L⁻¹. The decrease in uranine concentration was then continuously (1 Hz) measured during 36 hours. Constant aeration by air bubbling allowed keeping the dissolved tracer homogeneously distributed and the overlying water saturated with oxygen during the whole experiment. The porewater exchange rate (Q), standardized for mud shrimp density (see section 2.2), was estimated by fitting a simplified version of the mathematical model developed by Meysman et al. (2007) to the moving averages (over 1 minute) of the tracer data:

$$C_{ow}(t) = \frac{A}{B} C_{ow}^0 + \left(1 - \frac{A}{B}\right) C_{ow}^0 e^{-Bt} \quad (4)$$

$$A = \frac{Q}{V_{pw} + M_s K_{ad}}, B = \frac{Q}{V_{ow}} \left(1 + \frac{V_{ow}}{V_{pw} + M_s K_{ad}}\right) \quad (5)$$

Where C_{ow} is the concentration of the dissolved tracer in overlying water ($\mu\text{g L}^{-1}$), V_{ow} and V_{pw} the volumes (mL) of overlying water and of porewater, M_s the sediment wet weight (gWW) and K_{ad} the mean adsorption rate of uranine onto sediment particles.

The volumes of overlying water and porewater were determined by measuring the heights of the overlying water and of the sediment column before the introduction of the mud shrimp. An uranine adsorption coefficient of $K_{ad}=0.25$ mL per g of dry sediment was determined from a series of batch experiments assuming that adsorption rates were similar along the burrow walls and at the sediment-water interface. Porewater exchange rates (Q) were estimated using Matlab (ver. 9, Mathworks) by convergent iterations and weighted least-squares regression of model predictions on temporal uranine concentration decline. The first thirty minutes of the experiments were not considered for the calculation of porewater exchange rates since we hypothesized that the strong initial decrease in uranine concentration resulted partly from: (1) the mixing between overlying and burrow waters, and (2) the rapid adsorption of uranine onto organic particles at the sediment surface and along the burrow wall.

2.6 Data treatments

The influence of *Upogebia pusilla* on porewater and solute exchanges was assessed by calculating the ratio between *With-Upogebia* treatment and *Without-Upogebia* treatment at each season. Differences in solute (O_2 and nutrients) exchanges rates between treatments and seasons were assessed using a two-way ANOVA on the means ($n = 4$ per treatment) of the 5 sequential replicate of each experimental cores. Whenever appropriate, *a posteriori* multiple comparison *t* tests corrected using the Holm-Sidak procedure were used to assess differences among treatments and seasons. Differences in shrimp respiration (means of sequential incubations) in different seasons were tested using a one-way ANOVA followed by *a posteriori* *t* tests corrected using the Holm-Sidak procedure (see above) for O_2 consumption and NH_4^+ excretion. Differences in porewater exchange rates between treatments and seasonal experiments were assessed using two-way ANOVA followed by *a posteriori* *t* test corrected using the Holm-Sidak procedure (see above) directly on the results of each experimental cores

(n = 4 per treatment). In all cases, statistical analyses were performed on untransformed data; data normality was tested using Shapiro-Wilk test and variance homogeneity was tested using Bartlett's test.

3 Results

3.1 Sediment characteristics

All sediments consisted of muddy sand (78 % sand, 22 % mud on average) with an almost constant (*i.e.*, close to 141 μm) D_{50} (**Table 2.1**). There were only minor seasonal changes in both porosity and permeability (*i.e.*, 0.42-0.45, and $7.5\text{-}7.9 \cdot 10^{-13} \text{ m}^2$, respectively (**Table 2.1**). To estimate the volume of sediment porewater in equations (4) and (5) a mean porosity value of 0.43 was used. OC ranged from 0.23 (summer) to 0.32 % DW (winter).

Table 2.1 : *Sediment characteristics*. Average depth-integrated values (20 cm depth) of median grain size (D_{50}), porosity (Φ), permeability (k), and organic carbon content (OC) of the sediment of the study site in winter, spring and summer. The variation coefficients associated with vertical variability are given in brackets.

Date	D50 (μm)	Φ (Volume ratio)	k (m^2)	OC (%DW)
Winter	141	0.45 (6.6 %)	7.5×10^{-13}	0.32 (10.3 %)
Spring	141	0.43 (0.7 %)	7.7×10^{-13}	0.31 (9.3 %)
Summer	141	0.42 (1.2 %)	7.9×10^{-13}	0.23 (9.5 %)

3.2 General observations

All mud shrimp started digging a blind-ended burrow as soon as introduced in experimental cores. Within 24 hours, they built a complete U or Y-shape open-ended burrow (*i.e.* with two well visible openings at the sediment surface). Since mud shrimp consistently buried along the wall of the transparent enclosures, it was possible to determine with a ruler (precision $\pm 1\text{mm}$) the vertical extension of burrows, which ranged between 18.3 and 24.7 cm depth. The thickness of the layer of sediment expelled from the burrow during their whole week of acclimation was around 5 cm. During the experiments, mud shrimp continued to rework sediment within their burrow, and to periodically ventilate them. At the end of the whole experimental process (*i.e.* two weeks starting from sampling), seagrasses were still

healthy both in *With-* and *Without-Upogebia* treatments although they were partially covered by sediment expelled from burrows in the cores with *Upogebia*.

3.3 Oxygen fluxes

Representative examples of temporal changes in O_2 concentrations recorded in the overlying water of the *With-* and *Without-Upogebia* treatment cores are presented in **Figure 2.2**. In *Without-Upogebia* treatment cores, O_2 concentration decreased linearly over time. Conversely, in *With-Upogebia* treatment cores, O_2 concentration decreased non-linearly over time with a succession of periods of: (1) low and rather constant oxygen consumption lasting for 10 min. on average (as computed by randomly selecting 3 of these periods for each of the 12 studied individual mud shrimp), and (2) rapid decline in O_2 concentration indicative of high O_2 consumption lasting on average for 3 min. (as computed by randomly selecting 3 of these periods for each of the 12 studied individual mud shrimp). Visual observations showed that these last periods corresponded to intermittent pumping activity.

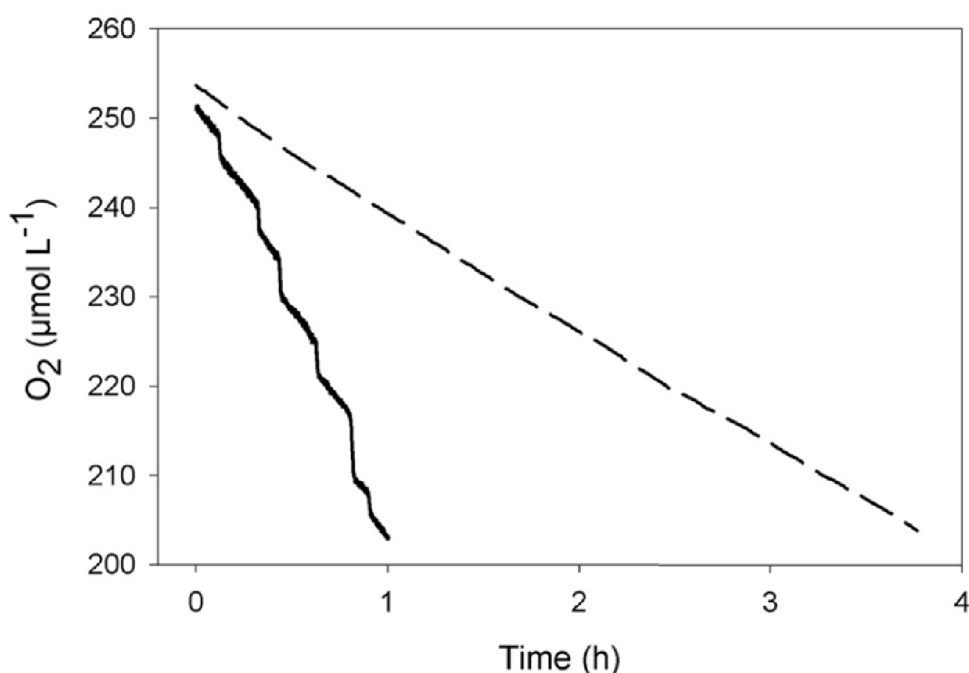


Figure 2.2 : *Sediment oxygen uptake.* Representative examples of temporal changes in O_2 concentration in *With-* (solid line) and *Without-* (long dashes) *Upogebia* treatment cores.

Average TOU significantly differed between *With-* and *Without-Upogebia* treatment cores and between seasons with a significant interaction between these two factors (**Figure 2.3A, Table 2.2**). Average TOU significantly differed between seasons in *Without-Upogebia* treatment cores with lower values during winter than during spring and summer. In *With-*

Upogebia treatment cores, they were significantly lower during winter than during spring and during spring than during summer. Average TOU were significantly higher in the *With-Upogebia* than in the *Without-Upogebia* treatment cores during winter (33.5 ± 4.5 vs. 14.1 ± 1.1 $\text{mmol m}^{-2} \text{d}^{-1}$), during spring (68.1 ± 4.2 vs. 25.0 ± 1.4 $\text{mmol m}^{-2} \text{d}^{-1}$) and during summer (125.7 ± 8.0 vs. 51.8 ± 5.4 $\text{mmol m}^{-2} \text{d}^{-1}$). In all seasons cores containing shrimp always exhibited higher TOU than cores without shrimp with multiplying factors between 2.4 (winter and summer) and 2.7 (spring).

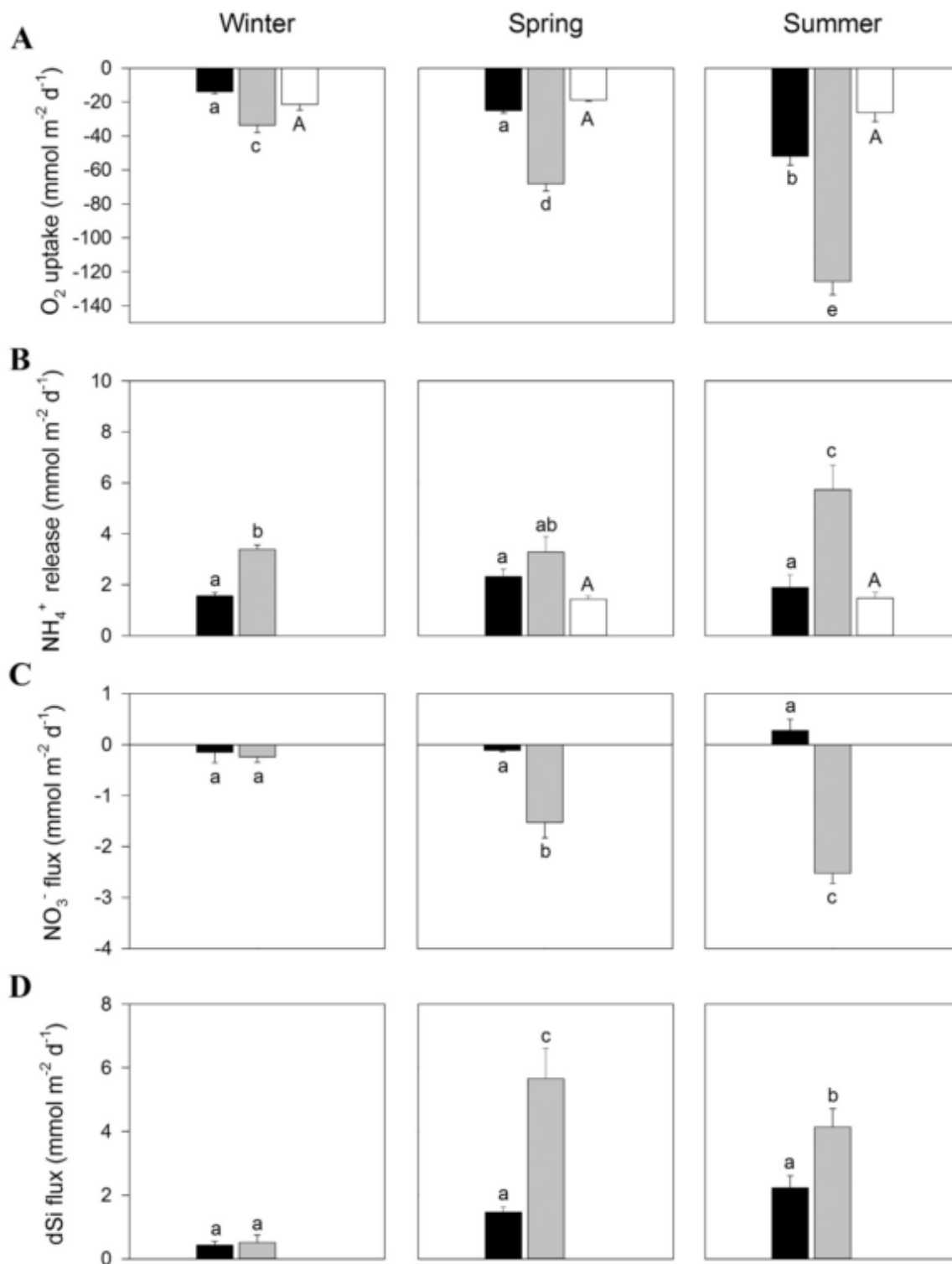


Figure 2.3 : Oxygen and nutrient fluxes. Average (\pm SE) of: (A) O₂ uptakes: TOU (solid bars), mud shrimp uptake (white bars), (B) ammonium releases: NH₄⁺ benthic flux (solid bars), mud shrimp release (white bars), (C) nitrate and (D) silicate fluxes across the sediment–water interface. Black bars correspond to measurements carried out within cores *Without-Upogebia*. Light gray bars correspond to measurements carried out within cores *With-Upogebia*. White bars correspond to measurements carried out on individual mud shrimp. Different letters indicate significant (overall $\alpha=0.05$) differences between combinations of seasons and treatments. Lower case letter: two-way ANOVA, higher case letter: one-way ANOVA

Table 2.2 : *Data treatment.* ANOVA results of Treatment and Season effects on benthic solute fluxes, mud shrimp O₂ uptake, mud shrimp NH₄⁺ excretion and porewater exchanges (Q). p values in bold indicate significant factor effects

Source	df	MS	F	p value
Two-way ANOVA				
TOU				
Season	2	8714.311	99.138	<0.001
Treatment	1	13304.150	151.355	<0.001
Treatment x Season	2	1491.270	16.965	<0.001
Residual	20	87.901		
NH₄⁺ flux				
Season	2	3.725	3.025	0.072
Treatment	1	29.545	23.996	<0.001
Treatment x Season	2	4.734	3.845	0.040
Residual	20	1.231		
NO₃⁻ flux				
Season	2	1.811	10.103	<0.001
Treatment	1	13.253	73.952	<0.001
Treatment x Season	2	3.659	20.418	<0.001
Residual	20	0.179		
dSi flux				
Season	2	27.519	21.675	<0.001
Treatment	1	32.928	25.936	<0.001
Treatment x Season	2	12.718	10.017	<0.001
Residual	20	1.270		
Q				
Season	2	96.514	8.409	0.003
Treatment	1	536.817	46.772	<0.001
Treatment x season	2	46.721	4.071	0.037
Residual	20	11.477		
One-way ANOVA				
Respiration				
Season	2	69.473	1.577	0.250
Residual	11	44.057		
Excretion				
Season	1	0.003	0.019	0.894
Residual	7	0.148		

Average *Upogebia* individual oxygen uptake rates did not significantly differ between seasons with corresponding values of 148 ± 24 , 130 ± 6 , 166 ± 23 $\mu\text{mol ind}^{-1} \text{d}^{-1}$ during winter, spring and summer, respectively (**Table 2.2**). Given the density of mud shrimp within the cores with *Upogebia*, these values corresponded to 21.4 ± 2.4 , 18.7 ± 0.8 and 26.3 ± 5.1 $\text{mmol m}^{-2} \text{d}^{-1}$ (**Figure 2.3A**), which respectively accounted for 64, 28 and 21 % of TOU in the *With-Upogebia* treatment cores.

3.4 Nutrients fluxes

Average NH_4^+ fluxes were always positive indicating a consistent net release from the sediment to the overlying water column (**Figure 2.3B**). Overall, average NH_4^+ fluxes significantly differed between *With-* and *Without-Upogebia* treatment cores, but not between seasons (**Table 2.2**). In addition there was a significant interaction between these two factors. Average NH_4^+ fluxes in *Without-Upogebia* treatment cores were low (*i.e.*, between 1.6 ± 0.1 and 2.3 ± 0.3 $\text{mmol m}^{-2} \text{d}^{-1}$ during winter, spring and summer) and did not significantly differ between seasons. Average NH_4^+ fluxes in *With-Upogebia* treatment cores were significantly higher during summer (5.7 ± 0.8 $\text{mmol m}^{-2} \text{d}^{-1}$) than during winter and spring (3.4 ± 0.2 and 3.3 ± 0.6 $\text{mmol m}^{-2} \text{d}^{-1}$, respectively). Average NH_4^+ fluxes were significantly higher in *With-* than *Without-Upogebia* treatment cores during both summer and winter. Corresponding multiplying factors were 3.0 and 2.1, respectively. Average individual NH_4^+ release rates did not significantly differ between spring and summer with corresponding values of 10 ± 1 $\mu\text{mol ind}^{-1} \text{d}^{-1}$ in spring and 10 ± 2 $\mu\text{mol ind}^{-1} \text{d}^{-1}$ in summer, respectively (**Table 2.2**). Given the density of mud shrimp within the *With-Upogebia* treatment cores, these values corresponded to 1.4 ± 0.2 $\text{mmol m}^{-2} \text{d}^{-1}$ and 1.5 ± 0.2 $\text{mmol m}^{-2} \text{d}^{-1}$ (**Figure 2.3B**) accounting for 44 and 26 % of the NH_4^+ release in the *With-Upogebia* treatment cores, respectively.

Except for the *Without-Upogebia* treatment cores during summer, average NO_3^- fluxes were always directed toward the sediment (**Figure 2.3C**). They significantly differed between *With-* and *Without-Upogebia* treatment cores and between seasons with a significant interaction between these two factors (**Table 2.2**). In *Without-Upogebia* treatment cores, NO_3^- fluxes were barely detectable (*i.e.*, < 0.3 $\text{mmol m}^{-2} \text{d}^{-1}$) and did not significantly differ between seasons. In *With-Upogebia* treatment cores, NO_3^- uptakes were significantly higher during summer (2.5 ± 0.2 $\text{mmol m}^{-2} \text{d}^{-1}$) than during spring (1.5 ± 0.3 $\text{mmol m}^{-2} \text{d}^{-1}$), and during spring than during winter (0.2 ± 0.1 $\text{mmol m}^{-2} \text{d}^{-1}$). The impact of the presence of the

mud shrimp was higher in spring (increased by a factor 13.8) and summer (inversion of the flux) than during winter (increased by a factor 1.6).

Average dSi fluxes were always positive, indicating a net release from the sediment to the water column (**Figure 2.3D**). They significantly differed between *With-* and *Without-Upogebia* treatment cores and between seasons with a significant interaction between these two factors (**Table 2.2**). In *Without-Upogebia* treatment cores, average dSi fluxes were low (*i.e.*, between 0.4 ± 0.1 and 2.2 ± 0.4 mmol m⁻² d⁻¹ during winter and spring, respectively) and did not significantly differ between seasons. In *With-Upogebia* treatment cores, average dSi fluxes were significantly higher during spring (5.7 ± 1.0 mmol m⁻² d⁻¹) than during summer (4.1 ± 0.6 mmol m⁻² d⁻¹) and during summer than during winter (0.5 ± 0.2 mmol m⁻² d⁻¹). Average dSi fluxes were significantly higher in *With-* than *Without-Upogebia* during both spring and summer. Corresponding multiplying factors were of 3.8 and 1.9, respectively.

3.5 Porewater exchange rates

Representative examples of the temporal declines in uranine concentration in the overlying water of the incubation cores are presented in **Figure 2.4A**. The lowest diminutions in uranine concentrations were recorded in *Without-Upogebia* treatment cores (-8 ± 2 % during winter, -10 ± 3 % during spring and -21 ± 1 % during summer on average after 36 h). Conversely, the *With-Upogebia* treatment cores showed rapid and intense decreases in uranine concentrations over time (-39 ± 9 % during winter, -47 ± 5 % during spring and -62 ± 6 % during summer on average after 36 h).

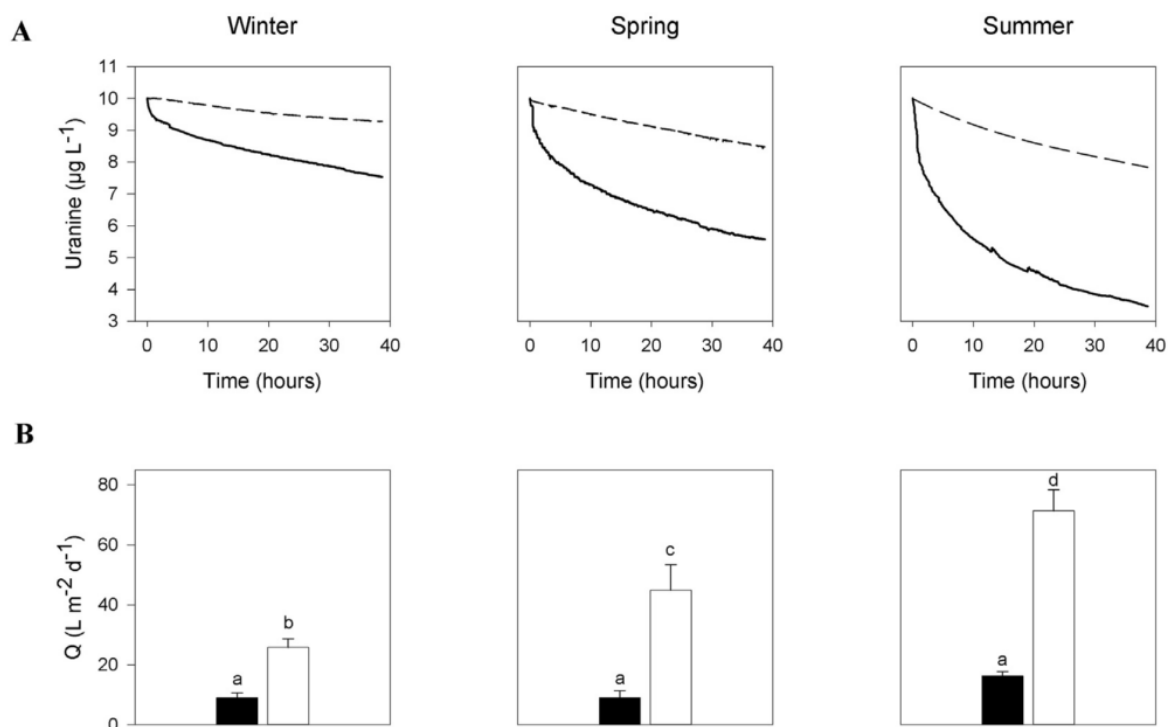


Figure 2.4 : Porewater exchange rates. (A) Representative examples of temporal changes in the moving averages (over 1min) of uranine concentration during core incubations in *Without-* (long dashes) and *With-* (solid line) Upogebia treatment cores. (B) Average (\pm SE) porewater exchange rates (Q) measured in *Without-* (black bars) and *With-* (White bars) Upogebia treatment cores. Different letters indicate significant (overall $\alpha=0.05$) differences between combinations of seasons and treatments.

Porewater exchange rates (Q) significantly differed between treatments and seasons with a significant interaction between these two factors (**Table 2.2**). In *Without-Upogebia*, they were low (9.0 ± 1.4 , 9.0 ± 2.4 and $16.3 \pm 1.4 \text{ L m}^{-2} \text{d}^{-1}$ in winter, spring and summer, respectively) and did not significantly differ between seasons (**Figure 2.4B**). In *With-Upogebia* treatment cores, they were significantly lower in winter ($25.7 \pm 2.8 \text{ L m}^{-2} \text{d}^{-1}$) than in spring ($44.9 \pm 8.7 \text{ L m}^{-2} \text{d}^{-1}$), and in spring than in summer ($71.3 \pm 7.0 \text{ L m}^{-2} \text{d}^{-1}$). Assuming a sediment column height of 28.7 cm and a porosity of 0.43, this resulted in overall sediment porewater turnover times of 4.8, 2.7 and 1.7 d in winter, spring and summer, respectively. During all three seasons, average porewater exchange rates were significantly higher in *With-* than *Without-Upogebia* treatment cores. Corresponding multiplying factors were of 2.9, 5.0 and 4.4 during winter, spring and summer, respectively.

4 Discussion

4.1 Sediment porewater exchanges

In the absence of *U. pusilla*, porewater exchange rates were low and did not significantly differ between seasons. Together with sediment reworking, bioirrigation is one of the two processes constitutive of bioturbation (Kristensen et al. 2012). In this sense, our results are complementary to those of Bernard et al. (2014) who recently reported low sediment reworking rates in intertidal *Zostera noltei* bed of Arcachon Bay in the absence of *U. pusilla*. Although sediment reworking and bioirrigation are mainly induced by different biological activities (*i.e.*, locomotion, feeding and burrowing vs. ventilation), they are both directly related to the traits (*i.e.* body size, burrowing depth and feeding modes) of benthic organisms to disturb the sediment matrix (Kristensen et al. 2012). The importance of large macrofauna for bioturbation has been explicitly stressed (Solan et al., 2004a). This is particularly relevant in seagrass meadows since phanerogams and most of large burrowing organisms classically negatively interact, leading to mutual exclusion and spatial segregation (Brenchley, 1982; Suchanek, 1983). Therefore, the low porewater exchange rates recorded during the present study in cores without *Upogebia* are fully coherent with the composition and lifestyle characteristics of the macrobenthic infaunal community associated with the rhizosphere of seagrasses, which is dominated by small bodied species living at (*e.g.* *Melinna palmata*) or immediately below (*e.g.*, *Aphelochaeta marioni*, *Tubificoides benedii* and *Heteromastus filiformis*) the water-sediment interface (Bernard et al. 2014). Moreover, the porewater exchange rates measured in cores without *Upogebia* did not significantly differ between seasons, which suggest that they may have been limited by the same factor (*i.e.*, macrofauna composition) during all three seasons. Overall, and together with those of Bernard et al. (2014), our results confirm that, in the absence of *U. pusilla*, intertidal seagrass meadows in Arcachon Bay are relatively little bioturbated with both limited sediment reworking and porewater exchanges across the sediment-water interface.

The comparison of the porewater exchange rates measured in cores with *Upogebia* with literature data proves difficult because most of existing studies have been assessing water fluxes through the burrows (see Astall et al. 1997 for review). Available sediment porewater exchange rates are listed in **Table 2.3**. They are limited to two polychaetes (*Arenicola marina* and *Marenzelleria viridis*) and one single deposit-feeding mud shrimp (*Trypea australiensis*). The porewater exchange rates in the presence of the mostly suspension feeding mud shrimp

U. pusilla recorded during the present study are about 5 times lower than those recorded for the deposit-feeding mud shrimp *Trypaea australiensis* (Webb and Eyre 2004). This result is surprising since ventilation activity in burrow-dwelling invertebrates is typically lower in deposit- than in suspension-feeders as the formers only irrigate their burrows for respiration versus both respiration and feeding for the latter (Papaspyrou et al. 2004). It has for example been estimated that the deposit-feeding mud shrimp *Callianassa subterranea* allocates only 8 % of its time to ventilation (Stamhuis et al. 1996) versus 50 % in *U. pusilla* (Dworschak 1981). Such a discrepancy between our sediment exchange rates and those of Webb and Eyre (2004) may be linked to methodological considerations: (1) Webb and Eyre (2004) used a model, which did not take into account the adsorption of their tracer (CsCl) on sediment, which may have led to an overestimation of porewater exchange rates; (2) they performed their experiments *in-situ* and reported a clear effect of the rising tide on porewater exchange rates whereas our experiments were carried out *ex-situ* under static conditions, which precludes such an effect; (3) conversely to Webb and Eyre (2004) we noticed a quick decline in tracer concentration during the first half hour of incubation (which we mainly) attributed to the equilibration between the overlying and burrow waters and excluded this time period when modeling pore water exchanges, which could also have contributed to our measurements of lower porewater exchange rates. Besides these methodological considerations, data in **Table 2.3** also suggest a correlation between sediment porewater exchanges and sediment types with lower values associated with fine sands and the highest one with medium-coarse sand. Sediment compaction and cohesiveness are strongly enhanced by seagrasses (van Wesenbeeck et al. 2007). Seagrass meadows are the preferred habitat of the mud shrimp and the low permeability of the sediment ($k = 7.5-8 \times 10^{-13} \text{ m}^2$) may focus water flow through their burrows and the adjacent surrounding sediment and hence limit porewater exchange rates.

Table 2.3 : Porewater exchange rates. Available literature data for benthic macrofauna.

Species	Density (m ⁻²)	Biomasse (gWW m ⁻²)	Sediment type	Porewater exchange rates (L m ⁻² d ⁻¹)	Multiplying factor	Sources
<i>Trypaea australiensis</i>	24	--	Medium-coarse sand	367.2	5	Webb and Eyre 2004
<i>Marenzelleria viridis</i>	1200	240	Sand	276	--	Quintana et al. 2011
<i>Arenicola marina</i>	120	--	Fine sand	45.7 < <i>x</i> < 73.1	1.5 < <i>x</i> < 5.1	Rao et al. 2014
<i>Upogebia pusilla</i>	144	245	Fine sand	25.7 < <i>x</i> < 71.3	2.9 < <i>x</i> < 5	This study

The impact of the mud shrimp on porewater exchange rates varied seasonally with corresponding multiplying factors between 2.9 (winter) and 5 (spring). These results are not surprising given: (1) the large body size, high densities, burrowing depth and intense ventilation activity of *U. pusilla* (Dworschak 1981), and (2) the positive effect of temperature on nutrition and bioirrigation (Hymel and Plante, 2000; Rao et al., 2014). The impacts of the presence of *U. pusilla* (present study) and *T. australiensis* (Webb and Eyre 2004) on porewater exchange rates were close despite potential differences in their ventilation activity (see above). It is, however, here again difficult to draw any sound ecological conclusion from such a similarity because of differences in methodological approaches. New comparative studies using strictly similar methodologies are thus clearly needed to better constrain the effect of environmental (*e.g.*, sediment characteristics) and biological (*e.g.*, feeding types of mud shrimp) factors on sediment porewater exchange rates.

4.2 Oxygen uptake

The average TOU measured in cores without *Upogebia* significantly differed between seasons. They were between 13.8 mmol m⁻² d⁻¹ (winter) and 52.0 mmol m⁻² d⁻¹ (summer), which is in good agreement with those (between 15 and 73 mmol m⁻² d⁻¹) reported in muddy sands colonized by seagrasses (Asmus et al., 2000; Holmer et al., 1999; Jensen et al., 1998). They were however much lower than those previously reported in two healthy *Z. noltei* meadows (leaf coverage > 75 %, Auby et al. 2011) located respectively in the central part (from 86.4 mmol m⁻² d⁻¹ in winter to 252 mmol m⁻² d⁻¹ in summer; Welsh et al. 2000) and in the inner part (from 20.2 mmol m⁻² d⁻¹ in winter to 139.2 mmol m⁻² d⁻¹ in summer; Delgard et al. 2016) of Arcachon Bay. Such discrepancies can be attributed to: (1) differences in vegetation densities and associated respiration rates (Delgard et al., 2016), and (2) sedimentary organic carbon contents (*i.e.*, 0.2 % DW during the present study versus 2.2 % DW in Delgard et al. 2016 and Bernard et al. 2014). Porewater exchange rates measured in cores without *Upogebia* indeed did not significantly differ between seasons, and seasonal changes in TOU in the absence of mud shrimp may thus be mainly attributed to higher seagrass biomass during spring and summer (Auby and Labourg, 1996) and associated: (1) higher respiration rates and (2) stimulation of benthic microbial activity resulting from the exudation of labile organic matter by roots (Kaldy et al., 2006).

In cores with *Upogebia*, the short-term dynamics of oxygen exchanges at the sediment-water interface was mainly controlled by the ventilation activity of the mud shrimp

as illustrated by the continuous measurement of oxygen concentration in the overlying water of experimental cores (**Figure 2.2**). Periods of relatively slow oxygen consumption were indeed periodically interrupted by strong and rapid oxygen decrease resulting in a typical stair-shape curve. Visual observation of the cores showed that these sudden oxygen drops occurred during ventilation periods when mud shrimp increased their pumping activity to flush their burrow. During the present study, the burrow was flushed on average every 10 min and the mean duration of each flushing event was 3 min as already reported by Dworschak (1981) for the same species in the Adriatic Sea. The interval between two consecutive flushing events was much shorter than in the deposit-feeding mud shrimp *C. subterranea* (40 min on average according to Forster and Graf 1995) but longer than in the deposit feeding species *Neotrypaea californiensis* (3-7 min, Volkenborn et al. 2012). Conversely, the mean duration of each flushing event seems to consistently last about 3 min in all burrowing mud shrimp whatever their feeding modes (Astall et al., 1997; Dworschak, 1981; Forster and Graf, 1995; Stamhuis et al., 1996; Volkenborn et al., 2012).

The average TOU measured in cores with *Upogebia* significantly differed between seasons. They were between $33.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ (winter) and $125.7 \text{ mmol m}^{-2} \text{ d}^{-1}$ (summer), which is in the range of those previously reported for other benthic macrofauna in sediments ranging from silt to coarse sand (**Table 2.4**). Overall, the presence of the mud shrimp resulted in a 2.4 (winter) to 2.7 (spring) increase in TOU, which is in the range of literature data regarding other benthic macrofauna (**Table 2.4**). Seasonal changes in TOU in cores with *Upogebia* may be attributed to: (1) higher seagrass biomasses during spring and summer (see above), (2) an increase in mud shrimp oxygen uptake with temperature, and (3) the increase in porewater exchange rates during spring and even more during summer and the resulting stimulation of benthic microbial activity resulting from the supply of oxygen in otherwise hypoxic area of the sediment. During the present study, the average oxygen uptake by the mud shrimp was $2.6 \text{ } \mu\text{mol O}_2 \text{ gBWW}^{-1} \text{ h}^{-1}$, which tends to be similar to those measured in other burrowing shrimp such as *P. tyrrhena* ($3.1 \text{ } \mu\text{mol O}_2 \text{ gBWW}^{-1} \text{ h}^{-1}$, Papaspyrou et al. 2004), *U. pugettensis* ($2.6 \text{ } \mu\text{mol O}_2 \text{ gBWW}^{-1} \text{ h}^{-1}$; Thompson and Pritchard 1969) and *Trypaea australiensis* ($1.5 \text{ } \mu\text{mol O}_2 \text{ gBWW}^{-1} \text{ h}^{-1}$; Paterson and Thorne 1995). During winter, the sum of average TOU in cores without *Upogebia* and direct oxygen uptake by the mud shrimp accounted for the totality of average TOU in cores with *Upogebia* versus only 64 and 62 % during spring and summer, respectively. Moreover, direct oxygen uptake by the mud shrimp accounted for the totality of its contribution to TOU in cores with *Upogebia* during winter

versus only 43 and 36 % during spring and summer respectively. These results are in good agreement with the higher impact of the mud shrimp on sediment porewater exchange rates during spring and summer (see section 4.1). They underline the importance of indirect effects (*i.e.*, stimulation of microbial organic mineralization processes) associated with the presence of the mud shrimp during spring and summer.

Table 2.4 : *Benthic solute fluxes.* Available TOU, NH₄⁺ and NO₃⁻ flux data for benthic macrofauna.

Species	Sediment type	Density (m ⁻²)	Biomass (gWW m ⁻²)	Flux (mmol m ⁻² d ⁻¹)	Multiplying factor	Source
TOU						
<i>Trypaea australiensis</i>	Medium-Coarse sand	24	--	40.6	1.8	Webb and Eyre 2004
<i>Pestarella tyrrhene</i>	Fine sand	200	180	52.1	1.7	Papaspyrou et al. 2004
<i>Upogebia pugettensis</i>	Fine sand	111	170*	225.7	5.5	D'Andrea and DeWitt 2009
<i>Trypaea australiensis</i>	Coarse sand	80	242	14.8	3.0	Jordan et al. 2009
<i>Nereis sp.</i>	Silt and fine mud	1500	--	98.4	--	Nizzoli et al. 2007
<i>Arenicola marina</i>	Fine sand	120	--	23.0 < x < 50.2	1.1 < x < 5.1	Rao et al. 2014
<i>Upogebia pusilla</i>	Fine sand	144	245	33.5 < x < 125.7	2.4 < x < 2.7	This study
NH₄⁺						
<i>Trypaea australiensis</i>	Medium-Coarse sand	24	--	2.9	Reverse	Webb and Eyre 2004
<i>Pestarella tyrrhene</i>	Fine sand	200	180	3.0	Reverse	Papaspyrou et al. 2004
<i>Upogebia pugettensis</i>	Fine sand	111	170*	16.4	5.5	D'Andrea and DeWitt 2009
<i>Trypaea australiensis</i>	Coarse sand	80	242	4.5	15.1	Jordan et al. 2009
<i>Nereis sp.</i>	Silt and fine mud	1500	--	20.8	--	Nizzoli et al. 2007
<i>Arenicola marina</i>	Fine sand	120	--	7.2 < x < 22.6	1.3 < x < 7.8	Rao et al. 2014
<i>Upogebia pusilla</i>	Fine sand	144	245	3.3 < x < 5.7	1.4 < x < 3.0	This study
NO₃⁻						
<i>Trypaea australiensis</i>	Medium-Coarse sand	24	--	0.55	0.7	Webb and Eyre 2004
<i>Pestarella tyrrhene</i>	Fine sand	200	180	4.0	0.7	Papaspyrou et al. 2004
<i>Upogebia pugettensis</i>	Fine sand	111	170*	11.4	Reverse	D'Andrea and DeWitt 2009
<i>Trypaea australiensis</i>	Coarse sand	80	242	1.37	1.9	Jordan et al. 2009
<i>Nereis sp.</i>	Silt and fine mud	1500	--	-13.5	--	Nizzoli et al. 2007
<i>Arenicola marina</i>	Fine sand	120	--	-0.7 < x < -2.2	0.8 < x < 9	Rao et al. 2014
<i>Upogebia pusilla</i>	Fine sand	144	245	-0.2 < x < -2.5	1.6 < x < Reverse	This study

* Indicates g Dry Weight m⁻². Reverse indicates an inversion of the direction of the flux

4.3 Nutrient fluxes

As opposed to NO_3^- and NH_4^+ , dSi is not directly involved in the remineralization of organic matter. dSi fluxes across the sediment-water interface are typically cued by: (1) the amount of biogenic siliceous material present at this interface (Gallinari et al., 2008); (2) bacterial degradation of the organic matrix protecting diatom frustules (Bidle and Azam, 1999); (3) temperature, which directly controls the kinetic of hydrolytic and geochemical reactions and subsequently both Si dissolution rate and solubility (Loucaides et al., 2011); and (4) bioirrigation which accelerate the exchanges of dSi through porewater (Ullman and Aller, 1989).

During the present study, dSi effluxes measured in cores without *Upogebia* were between 0.4 mmol (winter) and 2.2 mmol m⁻² d⁻¹ (summer). These values are in the same range as those reported in temperate coastal environments (Asmus et al., 2000; Ní Longphuirt et al., 2009). Although, average dSi fluxes in cores without *Upogebia* did not significantly differ between seasons, there was a trend toward lower values during winter. Since porewater exchange rates in cores without *Upogebia* did not differ between seasons (see section 4.1), this trend appears consistent with a seasonal trend in seawater temperature. Average dSi fluxes in cores with *Upogebia* significantly differed between seasons. Moreover, they were significantly higher than in cores without *Upogebia* during both spring and summer. As for sediment porewater exchange rates, the impact of the presence of the mud shrimp on these fluxes was higher during spring than during summer. This suggests that together with seawater temperature, the ventilation activity of mud shrimp is a key factor in controlling seasonal changes in dSi fluxes.

As stated above NO_3^- and NH_4^+ are directly involved in the remineralization of organic matter and tightly interact through several processes including ammonification, nitrification, denitrification, dissimilatory nitrate reduction to ammonium (DNRA) and anaerobic ammonium oxydation (anammox). Seasonal changes in their fluxes should thus be discussed simultaneously. In cores without *Upogebia*, average NO_3^- and NH_4^+ fluxes both did not differ between seasons. Average NO_3^- fluxes always remained close to zero indicating that the production and consumption processes of NO_3^- within the sediment offset each other. Conversely, NH_4^+ fluxes measured in cores without *Upogebia* were consistently positive indicating that the production of NH_4^+ through ammonification was higher than its uptakes by

nitrifying bacteria and seagrasses. Here again, these results contradict those of Welsh et al. (2000) who consistently reported a net consumption of NH_4^+ by the sediment in another *Z. noltei* meadow of Arcachon Bay. As previously discussed for oxygen uptake, this discrepancy can be directly linked with differences in seagrass cover since NH_4^+ is their main source of inorganic nitrogen (Lee et al., 2007).

Average NO_3^- and NH_4^+ fluxes in cores with *Upogebia* were between -0.2 and -2.5 $\text{mmol m}^{-2} \text{d}^{-1}$, and 3.3 and 5.7 $\text{mmol m}^{-2} \text{d}^{-1}$, respectively and both differed between seasons. Average NH_4^+ flux values are in good agreement with those previously reported for other mud shrimp but are much lower than those reported for the polychaetes *Hediste* sp. and *Arenicola marina* (**Table 2.4**). Conversely, we consistently reported during the present study negative NO_3^- fluxes as reported for the polychaetes *Hediste* sp. and *A. marina*, whereas previous studies regarding mud shrimp reported positive ones (**Table 2.4**). As previously suggested to account for the low values of sediment porewater exchange rates in the presence of *U. pusilla* as compared to other mud shrimp, these differences may also be linked to the low permeability of seagrass sediment which may contribute to limit the thickness of the oxic sediment layer surrounding burrow. Indeed, Nielsen et al. (2004) clearly showed that nitrification and nitrate reduction are two spatially separated processes since nitrifying bacteria are restricted to the oxic sediment layer whilst nitrate reduction is strictly anaerobic. Therefore, nitrate production through nitrification occurring in the thin oxic layer surrounding the burrows of *U. pusilla* would not be sufficient to sustain the denitrification occurring in the sediment zone at the immediate vicinity of the oxic-anoxic boundary (Kristensen and Kostka 2005).

NH_4^+ release and NO_3^- uptake showed the same seasonal pattern with highest values during summer and lowest ones during winter. Moreover, the sum of the average NH_4^+ flux in cores without *Upogebia* during winter and NH_4^+ release by individual mud shrimp (assuming an NH_4^+ excretion rates similar to those recorded during spring and summer which are in the range of previously reported rates for other mud shrimp (Jordan et al., 2009; Papaspyrou et al., 2004) accounted for 90 % of the average NH_4^+ flux in cores with *Upogebia*, versus only 58 % during summer. During winter, the impact of the mud shrimp on NH_4^+ fluxes was mostly (82 %) direct (*i.e.*, resulting from its own excretion), whereas 62 % of the impact of the presence of the mud shrimp was indirect during summer. These results are almost similar to those obtained for TOU together with the fact that: (1) average NO_3^- uptake and (2) sediment porewater exchange rates were highest during summer. This suggests that NO_3^- and

NH_4^+ fluxes are tightly controlled during this season by the positive effect of the ventilation activity of the mud shrimp on nitrogen removal processes. Numerous studies have shown that the coupled nitrification-denitrification is usually strongly enhanced in the presence of burrow-dwelling macrofauna due to ventilation activity (see Laverock et al. 2011 for review). However, the NO_3^- uptake here suggests that other processes *e.g.*, anammox, may have contributed to N removal in the cores with *Upogebia*. Interestingly, a recent study has evidenced the role of anammox as a N removal mechanism from muddy and sandy intertidal sediments in Arcachon Bay (Fernandes et al., 2015).

During spring, average NO_3^- fluxes in cores with *Upogebia* were intermediary so as sediment porewater exchange rates. They could thus be considered as cued by the same factors as during summer. Conversely, average NH_4^+ fluxes did not significantly differ from those recorded during winter in spite of significantly higher sediment porewater exchange rates. This suggests the occurrence of another process responsible for the consumption of NH_4^+ in the sediment during spring. The fact that, during this season, the sum of average NH_4^+ fluxes in cores without *Upogebia* and NH_4^+ release by individual mud shrimp would be higher (*i.e.*, 115 %) than the average NH_4^+ flux in cores with *Upogebia* further support this hypothesis. As mentioned above: (1) spring in Arcachon Bay corresponds to the period of maximum growth for *Z. noltei* (Auby and Labourg 1996), and (2) NH_4^+ is the main source of inorganic nitrogen for seagrasses (Lee et al. 2007). Our interpretation is that average NH_4^+ fluxes in cores with *Upogebia* during spring were reduced due to the increased NH_4^+ uptake by growing seagrasses. The lack of any seasonal significant difference in average NH_4^+ fluxes in cores without *Upogebia* may have partly resulted from a lack of statistical power. In this context, it may prove interesting to carry out future experiments: (1) with a higher number of replicates for cores without *Upogebia*, and (2) under different light conditions (*i.e.*, including light periods) because of the potential interactions of NH_4^+ fluxes with the metabolism of *Z. noltei*.

5 Conclusion

The degradation of *Z. noltei* meadows in Arcachon Bay over the last decades has had direct consequences on the ecological and biogeochemical functioning of benthic ecosystems (Bernard et al., 2014; Delgard et al., 2013). This degradation may also significantly affect the population of the mud shrimp *U. pusilla*, which predominantly inhabits seagrass meadows

(Pascal et al. in prep., see “Annexe I”). Up to now, experimental studies comparing oxygen and nutrient fluxes at the sediment-water interface within seagrass meadows and bare sediments have used methodologies which do not account for the presence of mud shrimp within seagrass meadows. However, our comparison of TOU in both *With-* and *Without-Upogebia* treatment cores together with the standardization of their differences to the density at the study site shows 1.3 to 1.4-fold higher TOU in the presence of mud shrimp which could be compared to 1.9 to 3.4-fold higher TOU in vegetated than in bare sediment during spring and summer depending on shoot density (Delgard et al., 2016). Finally, it should be stressed that: (1) seagrasses and suspension-feeding Gebiidean mud shrimp are co-occurring in several other intertidal mud flats (Dworschak, 1987b; Siebert and Branch, 2005b), and (2) the assessment of the functional consequences of the decline of seagrass meadow should include those related to the associated decline of mud shrimp in these systems as well.

Chapitre 3 :

Influence de l'ectoparasite *Gyge branchialis* sur *Upogebia pusilla*

Dynamics of the *Upogebia pusilla*-*Gyge branchialis* marine host-parasite system

Ludovic Pascal^{1,2}, Xavier de Montaudouin^{1,2}, Antoine Grémare^{1,2} and Olivier Maire^{1,2}

¹Univ. Bordeaux, EPOC, UMR 5805, F-33400 Talence, France

²CNRS, EPOC, UMR 5805, F-33400 Talence, France

*Article publié dans la revue Marine Biology*⁴

163:195,2016 ; doi : 10.1007/s00227-016-2969-9

⁴ Ce manuscrit correspond à la version acceptée de l'article et présente des différences mineures par rapport à la version éditée. Cette dernière est disponible sur le site de l'éditeur : <http://link.springer.com/article/10.1007%2Fs00227-016-2969-9>

Abstract

The influence of burrowing invertebrates on the functioning of soft-bottom ecosystems is tightly dependent on their physiological state, which may itself be strongly affected by parasite infestation. However, the dynamics, prevalence and physiological consequences of parasitism remain poorly known in many species, such as sediment-dwelling crustaceans. During the present study, we investigated the effects of the ectoparasite (bopyrid) isopod *Gyge branchialis* on the fitness of the gebiidean mud shrimp *Upogebia pusilla*. A spatial survey conducted in June 2013 at 10 stations scattered across intertidal seagrass meadows of Arcachon Bay (44°40' N, 1°10' W) showed that on average 16 % of mud shrimp were infested by *G. branchialis*. Moreover, a temporal survey carried out at one of these stations over the year 2014 revealed that prevalence remained relatively high throughout the year, ranging from 10 % to 33 %. This interaction has various physiological consequences for *U. pusilla*. In particular, infested mud shrimp consistently exhibited a significant deficit in total length and individual dry weight as compared to non-infested specimens. Moreover, 89 % of infested males were feminized (*i.e.*, developed female secondary sexual characters) whereas infested females were never ovigerous. Our results demonstrate that *G. branchialis* strongly impair *U. pusilla* fitness including its ability to reproduce. Accordingly, through their (1) potential impact on mud shrimp abundances and (2) alteration of their physiological state, high bopyrid infestation could profoundly alter the bioturbation activity of mud shrimp populations and overall their influence on the functioning of soft-bottom ecosystems in Arcachon Bay.

1 Introduction

Upogebid mud shrimp may largely dominate coastal soft-substrate faunal biomasses (Dworschak, 1988; Nel and Branch, 2013; Sasaki et al., 2014) but are surprisingly rarely mentioned in most of field studies describing macrobenthic communities. The main reason for that is the difficulty in sampling these highly mobile burrowers, which can dig burrows down to 2 m deep in the sediment (Sasaki et al. 2014). Such an underestimation of mud shrimp importance not only biases the assessment of macrobenthic diversity, but it also limits our understanding of ecosystem functioning. Mud shrimp are indeed a major component of benthic food webs (Tunberg, 1986). These large sediment-dwellers are also very efficient bioturbators, which largely control sediment properties (*e.g.*, porosity, stability, oxygenation and organic content) and sedimentary processes (*e.g.*, remineralisation and nutrient cycling) (D'Andrea and DeWitt, 2009; Papaspyrou et al., 2004; Pascal et al., 2016b; Pillay and Branch, 2011). The preservation of their populations and the services they provide currently constitutes a major ecological concern even though their presence in high densities may also occasionally enter in conflict with human activities (Hong and Lee, 2014).

Many natural and anthropogenic environmental factors can affect mud shrimp behaviour and population dynamics, such as food availability (Hanekom and Erasmus, 1988), hypoxia (Astall et al. 1997) and predation (Dumbauld et al., 2008) including human harvesting for baits (Nel and Branch, 2013). Mud shrimp symbionts are another key factor structuring mud shrimp populations (Dumbauld et al. 2011; see symbiont list in Campos et al. 2009); however, the most studied relationship by far is the one involving ectoparasitism by bopyrid isopods (Astall et al., 1996; Bonnier, 1900; Tucker, 1930; Ubaldo et al., 2014). These parasites typically experience a two-host life cycle (Bonnier, 1900; Bourdon, 1968; Williams and An, 2009). The first planktonic larva (cryptoniscus) infesting an individual mud shrimp settles in the gill chamber where it is protected by the branchiostegite. It then perforates the host cuticle to feed on the haemolymph. Sex determination in the bopyrid is under epigenetic control, in that the cryptoniscus larva is first an unfunctional male and later becomes a functional female. This female then grows rapidly until it occupies the whole gill chamber, thereby swelling the branchiostegite (Bonnier 1900). The second larva that penetrates into an infested gill chamber transforms into a functional dwarf male and settles on the female. Bopyrid reproduction takes place in the gill chamber, thus defining mud shrimp as the definitive host. After fecundation, epicaridium larvae are released in the water column where they infest the intermediate host, a copepod (ectoparasitism). The parasites then evolve in

microniscus larvae and eventually in cryptoniscus larvae, which are released in the water column before infesting another mud shrimp.

The family of Upogebiidae consists of 13 genera and 170 species, including 118 species in the sole genus *Upogebia* (Hong and Lee 2014). Accordingly, a total of 605 bopyrid species are known (Williams and Boyko, 2012). Only a few *Upogebia*-bopyrid associations have been studied so far. Although they may at first seem similar in terms of functioning, these host-parasite systems in fact differ according to many features. Species like *U. pusilla* typically inhabit muddy bottoms (Dworschak, 1987b), whereas others like *U. yokoyai* or *U. deltaura* are predominantly found in coarser sediments (Kinoshita et al., 2010; Tunberg, 1986). The sex-ratios of the mud shrimp population vary according to species, locations and time periods (Dworschak, 1988). The effects of bopyrid parasites on their host strongly vary as well. In some host-parasite systems, males host are feminized (Griffen, 2009) but not in others (Pinn et al., 2001; Ubaldo et al., 2014). Along the same line, some authors consider the effects of the parasite on its host as insignificant (Tucker, 1930), whereas others conversely report substantial negative effects on growth, fecundity and other physiological processes (Dumbauld et al., 2011).

In Arcachon Bay, a recent study has shown that *U. pusilla* exerts a major influence on several benthic biogeochemical processes (*i.e.*, bioirrigation and organic matter mineralization) within seagrass meadows (Pascal et al., 2016b). This work was exclusively conducted on non-infested adult mud shrimp, which resulted in the elimination of a large number of bopyrid (identified as *Gyge branchialis*) infested individuals from the prior study (L.P. personal observation). We therefore became interested in assessing the effect of parasitism on the biogeochemical processes mediated by *U. pusilla*, which required both dedicated laboratory experiments (Pascal et al. in prep, see “Chapitre 3 – Partie B”) and an upscaling at the scale of the whole Bay. This latter goal necessitated baseline survey data on *U. pusilla* demographics, prevalence of bopyrid infestation and physiological effect of infestation on mud shrimp. As mentioned above, it was not possible to derive these pieces of information from the literature due to the low number of existing studies and the occurrence of major disparities in their results. The present study therefore aimed to assess the spatial and temporal patterns of prevalence of *G. branchialis* infestation and its effect on mud shrimp individuals both in terms of reproductive effort and somatic characteristics (*i.e.*, length and biomass).

2 Materials and Methods

2.1 Study site and sampling

Arcachon Bay is a macrotidal coastal lagoon (tide range = 0.9-4.9 m) located on the French Atlantic coast (44°40' N, 1°10' W) (**Figure 3A.1**). This 156 km² ecosystem is connected to the Atlantic Ocean by a narrow channel. Most (*i.e.*, 61 km² in 2005) of the intertidal area (115 km²) is covered by the currently largest *Zostera noltei* European intertidal seagrass bed (Auby and Labourg 1996; Plus et al. 2010). Water temperature seasonally fluctuates between 6 and 25 °C and salinity between 27 and 36 (Auby et al. 2011).

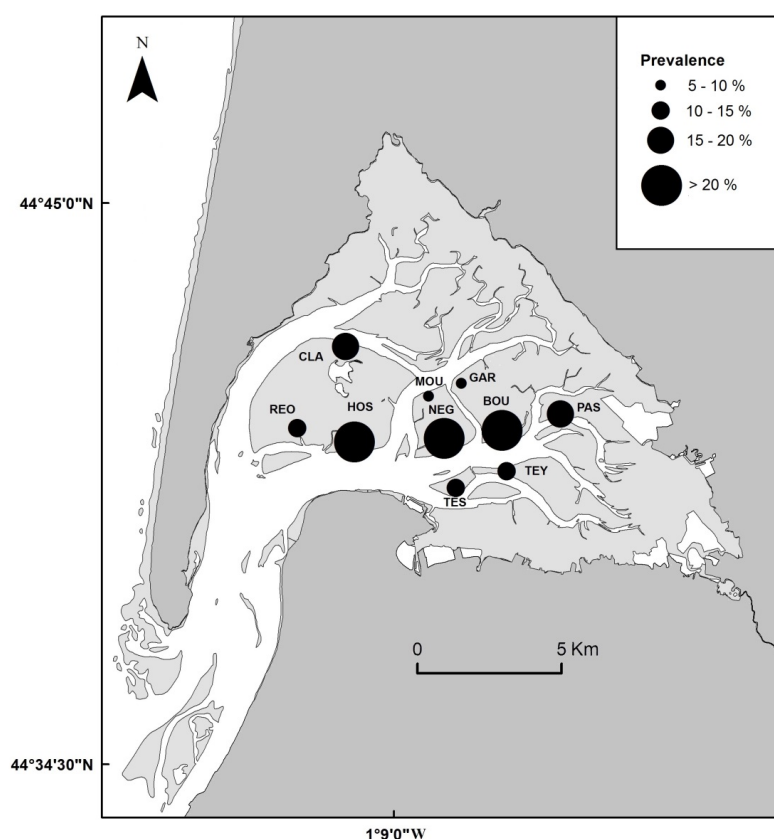


Figure 3A.1 : Location of the sampled stations in Arcachon Bay and related prevalences of infections of *Upogebia pusilla* by *Gyge branchialis* as recorded during the spatial survey. Dark grey: Land, light grey: intertidal area and white: water. BOU : Bourrut; CLA : Le Cla; GAR : Garrèche ; HOS : Les Hosses; MOU : Les Moussettes; NEG : La Nègue; PAS : Passant; REO : La Réousse; TES : Le Tes; TEY : Le Teychan

Upogebia pusilla is a common mud shrimp in Arcachon Bay. About 50 mud shrimps were first sampled in June 2013 at each of ten stations (spatial survey) (**Figure 3A.1**). A single station (“La Nègue”, **Figure 3A.1**) showing both a high bopyrid prevalence and high

mud shrimp abundance was then selected for investigating the temporal dynamics of the host-parasite system (temporal survey). On average, 50 mud shrimps were collected on 12 sampling dates (*i.e.*, *ca.* monthly) during year 2014 at this station. All samplings were carried out using a bait piston pump. Mud shrimp were immediately isolated in individual plastic bags to avoid aggression and appendage loss. They were brought back to the laboratory, where they were anesthetized by cold (15 min at -18 °C) before being preserved in 4 % formaldehyde.

2.2 *Upogebia pusilla* and *Gyge branchialis* analyses

Total length (TL) was measured from the tip of the rostrum to the tip of the telson and rounded down to the last millimetre. Sex was determined based on the presence or absence of gonopore and pleopod 1. In *U. pusilla*, females are characterized by the presence of a gonopore on each coxa of pereopod 3 and the presence of pleopod 1. Conversely, these two characters are missing in males. Feminized males combine the absence of gonopore on pereopod 3 (like a male) and the presence of pleopod 1 (like a female) (Pinn et al. 2001; Ubaldo et al. 2014). The presence of eggs on pleopods was also recorded. Both branchiostegites were removed under a stereomicroscope to check for the presence of bopyrids on the gill. Several biometrical analyses were performed for each sex on a selection of collected mud shrimp. Carapace length, length of pleopod 1, length and width of productyle of cheliped were measured to the nearest μm under a stereomicroscope, using NIS-elements 0.4.00.00 software. Chelipeds were also weighed ($\text{DW} \pm 0.1 \text{ mg}$) to (1) assess the relationships between cheliped weight and body length for each sex, and (2) add this value to individual dry weight when mud shrimp had lost one or both chelipeds before analysis. Individual dry weights (including eggs, but excluding *G. branchialis*) were assessed ($\pm 0.1 \text{ mg}$) after 48 h at 60 °C. Few individuals were also weighed for wet weight and for ash free dry weight (4 h at 450 °C) ($\pm 0.1 \text{ mg}$ in both cases).

Each *G. branchialis* female was observed under a stereomicroscope to detect the presence of a dwarf male. Whenever present, both female and male parasites were removed from the gill cavity to be measured (total length, $\pm 1 \mu\text{m}$) and checked for the presence of eggs in females.

2.3 Data analysis

2.3.1 *Upogebia pusilla* growth

At each sampling date and exclusively with non-infested mud shrimp, cohorts were determined from the TL histogram using a modal progression analysis (Bhattacharya, 1967) subroutine (Gayanilo et al., 2005). Each representative component, with a separation index greater than 2, was assumed to constitute a single cohort (FISAT software). Growth parameters of the Von Bertalanffy Growth Function (VBGF) were estimated from TL-at-age data produced by linking mean individual dry weights (IDW) (Gayanilo et al. 2005).

2.3.2 Infestation by *Gyge branchialis*

The proportions of feminized males were compared in infested and non-infested males using a chi-squared test. The relationships between *U. pusilla* TL and *G. branchialis* female or male lengths were tested using simple linear regression models. A chi-squared test was used to determine whether or not one of the two gills was preferentially infested. All these tests were performed independently on the results of the spatial and temporal surveys. The effects of *G. branchialis* on *U. pusilla* TL and IDW were first tested using Student *t* test for paired (*i.e.*, stations or sampling dates) samples. The interactions between differences in TL and IDW in infested and non-infested mud shrimp were then further assessed by using two different approaches. The first one consisted in inferring deficit in IDW for each infested mud shrimp based on its TL. This procedure was based on the comparison between the actual IDW of infested mud shrimp and the IDW derived from the relationship linking TL and IDW in non-infested mud shrimp (Smith et al., 2008). It assumes that infested mud shrimp do not reduce their TL while moulting. The second approach consisted in comparing the relationships linking TL and IDW in infested and non-infested mud shrimp by carrying out ANCOVAs using log-transformed *U. pusilla* IDW as the dependent variable, *U. pusilla* TL as the independent variable and infestation as covariate. These two approaches were carried out independently on data collected during the spatial and temporal surveys. We used a hierarchical clustering under constraint (*i.e.*, no grouping of non-successive size classes) to detect a trend in bopyrid prevalence relative to mud shrimp TL. This approach was applied separately to the results of the spatial and temporal survey. More specifically, we *a priori* defined 2 mm *U. pusilla* TL intervals and grouped (Euclidean distance, average link) them based on the prevalence of *G. branchialis* with the additional constraint that each group should only be composed of adjacent size classes. The relationships between *U. pusilla* TL

(independent variable) and *G. branchialis* length (dependent variable) were compared between male and female *G. branchialis* by carrying out two ANCOVAs based on the spatial and temporal surveys, respectively.

3 Results

3.1 Population dynamics of *Upogebia pusilla*

Overall, we investigated 657 and 669 mud shrimps during the spatial and temporal surveys, respectively. The average proportion of females recorded during these two surveys was 65 % in both cases (**Table 3A.1**). During the temporal survey, the proportion of females varied between 35 (in May) and 80 % (in February and September). It did not show any clear seasonal trend. Females carried eggs from May to August (data not shown). One single ovigerous female was found in May. The proportion of ovigerous females increased rapidly to reach 70 % of the female population in June and a maximum of 78 % in July. It then quickly decreased so that no ovigerous female was found in September. The mean TL of ovigerous females was 46 mm. The TL of the smallest sampled ovigerous female was 36 mm. Based on the growth parameters derived using VBGF (**Figure 3A.2**), it was estimated that the asymptotic TL was reached within less than a year.

Table 3A.1 : Spatial and temporal surveys: Counts and proportions (between brackets) of females, males and feminized males in relation with the presence/absence of the parasite

State	Spatial				Temporal			
	Female	Male	Feminized male	Total	Female	Male	Feminized male	Total
Non-infested	382 (58 %)	157 (24 %)	14 (2 %)	553 (84 %)	348 (52 %)	174 (26 %)	7 (1 %)	529 (79 %)
Infested	48 (7 %)	6 (1 %)	50 (8 %)	104 (16 %)	87 (13 %)	13 (2 %)	40 (6 %)	140 (21 %)
Total	430 (65 %)	163 (25 %)	64 (10 %)	657	435 (65 %)	187 (28 %)	47 (7 %)	669

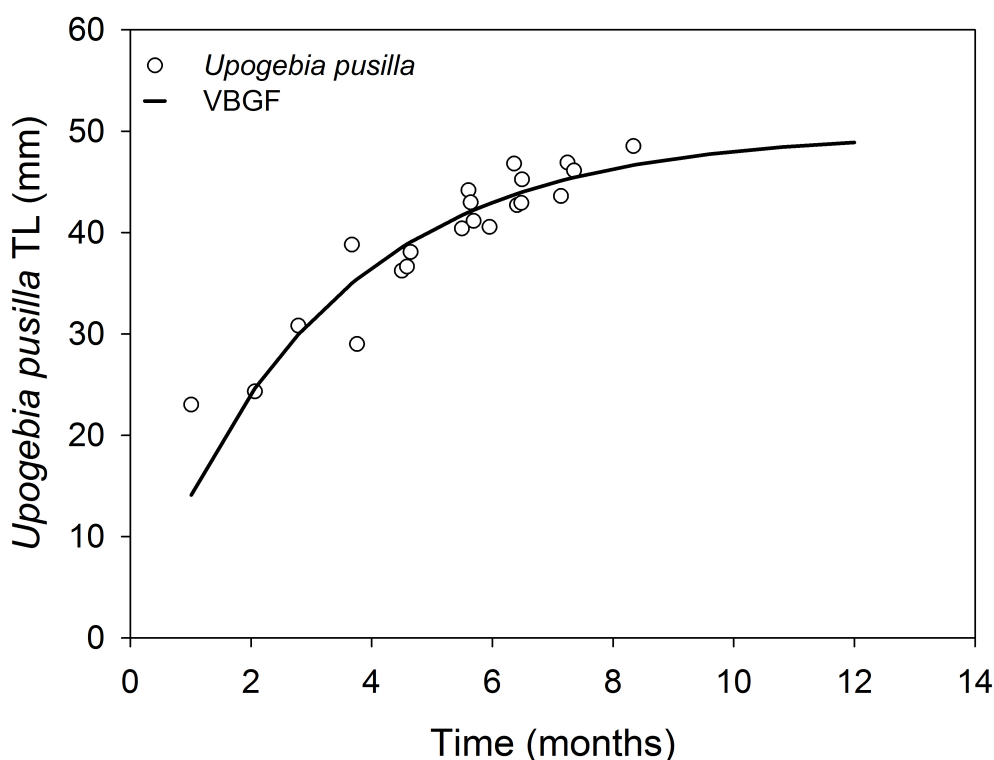


Figure 3A.2 : Temporal survey: Growth curve of *Upogebia pusilla* as fitted using Von Bertalanffy Growth Function (VBGF) ($k = 3.96 \text{ yr}^{-1}$; $L_{\infty} = 49.9 \text{ mm}$)

3.2 Infestation by *Gyge branchialis*: spatial survey

The bopyrid *G. branchialis* infested *U. pusilla* at all sampled stations (**Figure 3A.1**) with prevalence ranging from 6 to 26 % (with an overall average value of 16 %). Prevalence vs. total TL displayed a dome-shaped curve (**Figure 3A.3A**). The clustering method discriminated four TL groups: (1) [20-30 mm] with a mean parasite prevalence of 9 %, (2) [30-38 mm] with a mean parasite prevalence of 22 %, (3) [39-43 mm] with a mean prevalence of 34 % and (4) [44-52 mm] with a mean parasite prevalence of 5 %. The non-infested mud shrimp population was dominated by females, followed by males and a minority of feminized males (**Table 3A.1**). The infested population was equally dominated by feminized males and females, followed by a minority of males (**Table 3A.1**). The percentage of feminized males was significantly higher (Chi-squared test, $X^2 = 59.317$, $p < 0.001$) in infested than in non-infested males (**Table 3A.1**), corresponding to 89 % of the infested male population versus only 4 % of the non-infested male population. In addition, 11 % of the female population were infested versus only 4 % of the male population (excluding feminized males). Feminized males represented 28 % of the male population and 78 % of feminized males were infested.

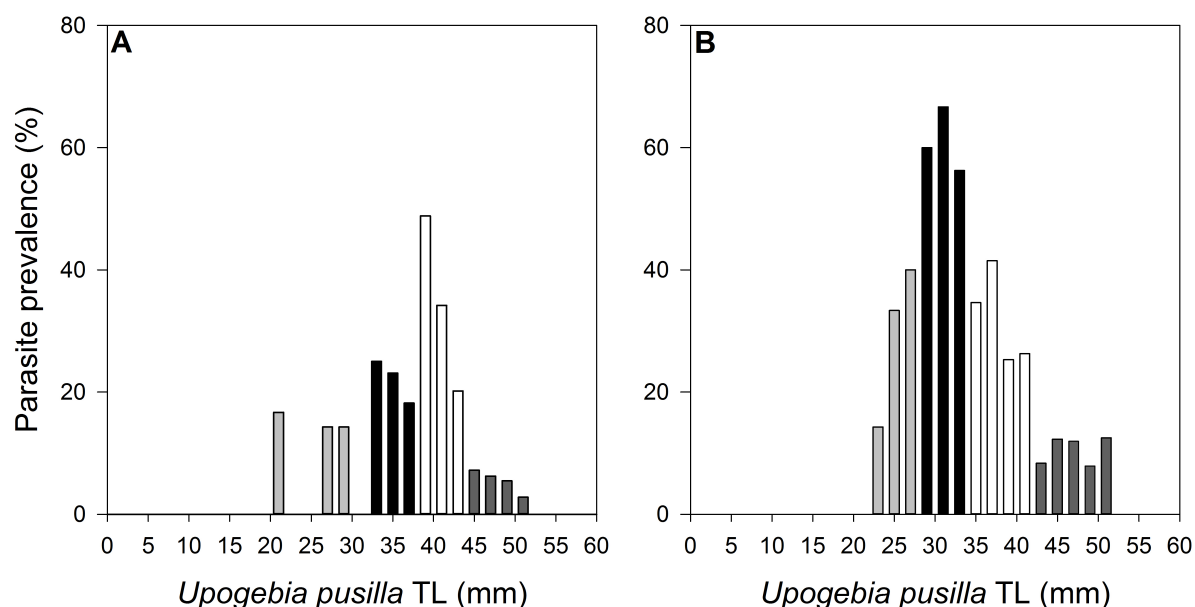


Figure 3A.3 : Spatial and temporal surveys: Prevalence of *Gyge branchialis* in *Upogebia pusilla* in relation with total carapace length based on spatial (A) and temporal (B) survey. Different shades of grey refer to the 4 groups discriminated by hierarchical clustering analysis

The length of *G. branchialis* females ranged between 4 and 14 mm. It correlated positively with *U. pusilla* TL (N = 66, $r = 0.80$, $p < 0.001$) (**Figure 3A.4A**). The length of *G. branchialis* males ranged between 1 and 6 mm. It also correlated positively with *U. pusilla* TL (N = 52, $r = 0.45$, $p < 0.001$) (**Figure 3A.4A**). Ovigerous *G. branchialis* females were found at all stations with a percentage of ovigerous females ranging between 17 and 94 %. *G. branchialis* did not significantly preferentially infest either right (5 % of all *U. pusilla*) or left gill chambers (7 % of all *U. pusilla*) (Chi-squared test, $X^2 = 1.939$, $p = 0.16$). No double infestation was observed.

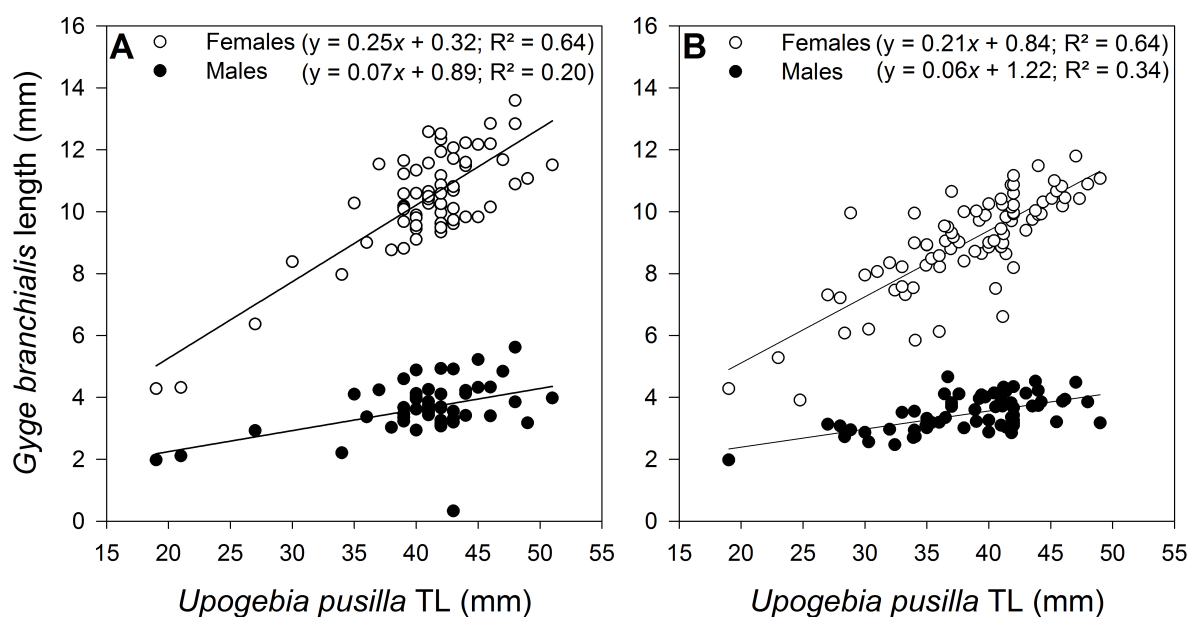


Figure 3A.4 : Spatial and temporal surveys: Relationships between *Gyge branchialis* (males and females) lengths and *Upogebia pusilla* total length as recorded during the spatial (A) and the temporal (B) surveys

Differences in mean TL between infested and non-infested mud shrimp were significant (Student t test for paired sample, $N = 10$, $t = 3.90$, $p = 0.004$). Mean relative differences in TL at the ten sampled stations were between 2 and 17 % (**Figure 3A.5A**) with an average of 7 %. Differences in mean IDW were also significant (Student t test for paired sample, $N = 10$, $t = 10.23$, $p < 0.001$) and corresponding relative mean differences were between 17 and 45 % with an average of 34 % (**Figure 3A.5C**). When standardized for TL, the average deficit in IDW due to parasitism was estimated to be only 9.9 %. The significance of this deficit was further supported by the occurrence of a significant (ANCOVA, $F = 19.57$, $p < 0.001$) difference in the relationships linking TL and IDW in infested ($N = 111$) and non-infested ($N = 546$) mud shrimp (**Figure 3A.6A**).

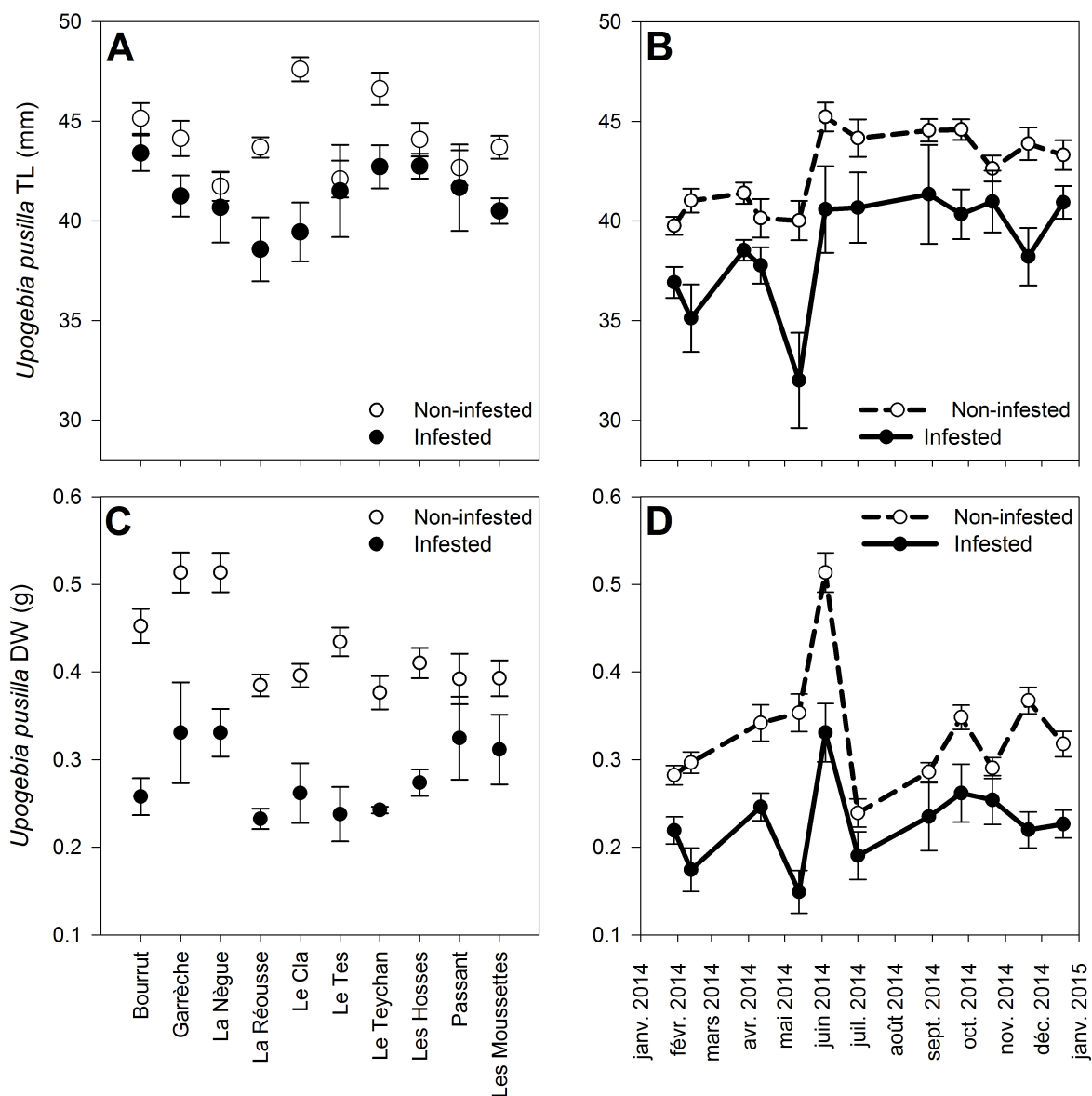


Figure 3A.5 : Spatial and temporal surveys: Effect of parasitism on *Upogebia pusilla* total length (A and B) and dry weight (C and D) (\pm SE) according to spatial (A and C) and temporal (B and D) surveys

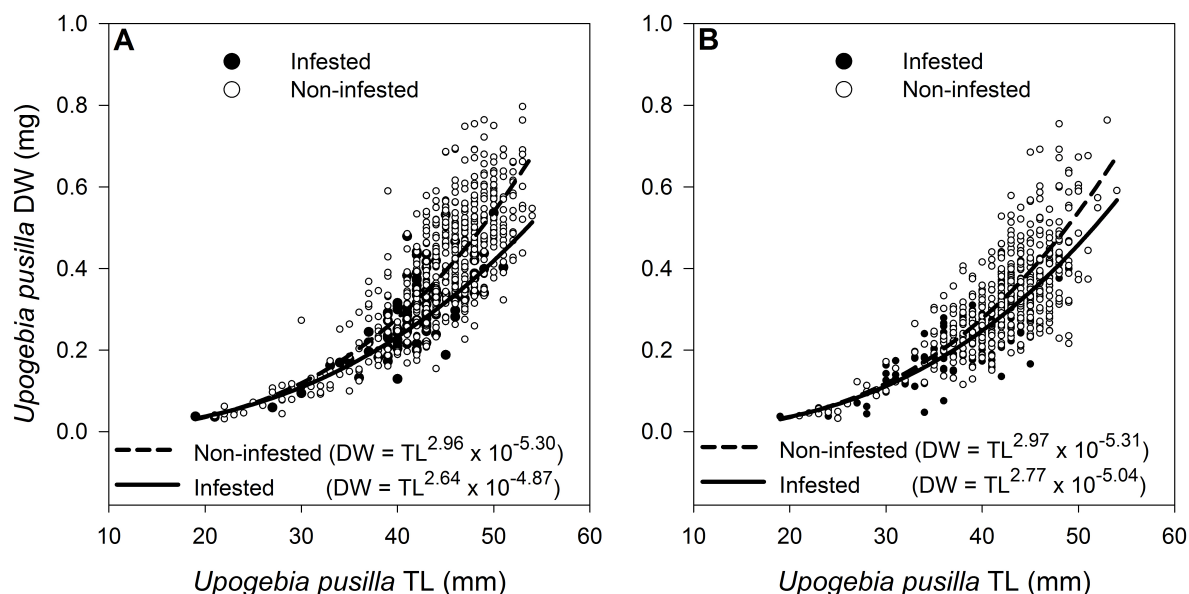


Figure 3A.6 : Temporal and spatial surveys: relationships linking TL and DW in infested and non-infested mud shrimp recorded during the spatial (A) and the temporal (B) surveys

3.3 Infestation by *Gyge branchialis*: temporal survey

The population monitored during the temporal survey was largely dominated by females, followed by males and feminized males (**Table 3A.1**). Parasite prevalence was between 10 and 33 % and did not show any clear seasonal trend. The overall annual parasite prevalence was 21 %. The non-infested population was dominated by females, followed by males and a minority of feminized males (**Table 3A.1**). The infested population was dominated by females, followed by feminized males and a minority of males (**Table 3A.1**). The percentage of feminized males was significantly higher (Chi-squared test, $X^2 = 66.159$, $p < 0.001$) in infested than in non-infested males (**Table 3A.1**), corresponding to 70 % of the infested male population versus only 8 % of the non-infested male population. In addition, 20 % of the female population were infested versus 7 % of the male population (excluding feminized males). The percentage of feminized males was 20 % of the male population but 85 % of these feminized males were infested.

The smallest sampled *U. pusilla* individual (19 mm in TL) was infested. Prevalence vs. TL displayed a dome-shaped curve (**Figure 3A.3B**). The clustering method discriminated four TL groups (**Figure 3A.3B**): (1) [20-28 mm] with a mean parasite prevalence of 22 %, (2) [29-34 mm] with a mean parasite prevalence of 61 %, (3) [35-42 mm] with a mean prevalence of 32 % and (4) [43-55 mm] with a mean parasite prevalence of 8 %.

The length of *G. branchialis* females ranged between 4 and 12 mm and correlated positively with *U. pusilla* TL (N = 83, $r = 0.80$, $p < 0.001$) (**Figure 3A.4B**). The length of *G. branchialis* males ranged between 2 and 5 mm and also correlated positively with *U. pusilla* TL (N = 64, $r = 0.59$, $p < 0.001$) (**Figure 3A.4B**). The relationships linking *U. pusilla* TL and *G. branchialis* length significantly differed between females and males *G. branchialis* (F = 1208.8, and F = 1410.1, for the spatial and temporal surveys, respectively, $p < 0.001$ in both cases). Oviparous *G. branchialis* females were found all year long with a percentage of oviparous females ranging between 33 and 100 % of the total number of females *G. branchialis*, without any clear seasonal trend (data not shown). *G. branchialis* did not differentially infest right (12 % of all *U. pusilla*) versus left gill chambers (10 % of all *U. pusilla*) (Chi-squared test, $X^2 = 2.553$, $p = 0.11$). Only two double infestations were observed, corresponding to 0.3 % of the *U. pusilla* population. The prevalence of double infestation was significantly lower (Chi-squared test, $X^2 = 10.464$, $p < 0.001$) than what expected assuming that double infestation results from two events affecting independently the two gills (*i.e.*, 2.4 %).

Differences in mean TL between infested and non-infested mud shrimp were significant (Student *t* test for paired sample, N = 12, $t = 7.05$, $p < 0.001$). Mean relative differences in TL on the 12 sampling dates were between 4 and 20 % with an average of 10 % (**Figure 3A.5B**). Differences in mean IDW were also significant (Student *t* test for paired sample, N = 11 due to missing data in March, $t = 6.11$, $p < 0.001$) and corresponding relative mean differences were between 13 and 58 % with an overall average of 30 % (**Figure 3A.5D**). In both infested and non-infested mud shrimp, there was a sharp decrease in individual dry weight between June and July, with a rapid recovery within the two following months (**Figure 3A.5B**). When standardized for TL, the average deficit in IDW due to parasitism was estimated to be only 4.4 %. The significance of this deficit was further supported by the occurrence of a significant (ANCOVA, F = 18.86, $p < 0.001$) difference in the relationships linking TL and IDW in infested (N = 129) and non-infested (N = 469) mud shrimp (**Figure 3A.6B**).

4 Discussion

4.1 Early infestation of *Upogebia pusilla*

Based on our own results and literature data, we can propose the following phenology for the *Upogebia pusilla*-*Gyge branchialis* system. Female mud shrimp brood their eggs for about 8 weeks (Tunberg 1986) before releasing them as larvae in the water column between August and October. Larvae then grow for one month (Dworschak 1988) so that benthic recruitment occurs between September and November. The new recruits then probably become quickly infested; the strongest rationale for this being the positive relationships linking *U. pusilla* TL and *G. branchialis* length recorded during both surveys. As an example, during the temporal survey, *U. pusilla* individuals with TL > 45 mm harboured only *G. branchialis* females with TL > 8 mm, whereas *U. pusilla* individuals with TL < 30 mm harboured only *G. branchialis* females with TL < 8 mm (**Figure 3A.4**). This suggests that most infestation occurs during the first 3 months following recruitment (*i.e.*, during winter), which is indeed possible since *G. branchialis* females are ovigerous all year long. This hypothesis is also consistent with the work by Tucker (1930) who stated that infestation of *U. pusilla* by *G. branchialis* is possible when individuals are young (*i.e.*, when the cuticle is thin) and ecdysis is more frequent (*i.e.*, higher vulnerability). More specifically, this author specified that infestation starts when TL is 17 mm (which corresponds to an age of *ca.* two months after recruitment according to our VBGF results). The TL of the smallest mud shrimp collected during the present study was 19 mm (*i.e.*, CL = 6 mm, see **Annexe III appendix 3A.1** for biometrical relationships) and it was infested. This minimal size is intermediate between the values reported by Hughes (1940) (CL = 3 mm) and Dworschak (1988) (CL = 8 mm) (**Table 3A.2**). It also supports an early infestation of *U. pusilla* by *G. branchialis*.

Table 3A.2 : Comparative results concerning ecological and biological traits of different *Upogebia* species. Md: grain-size median; CL: Cephalo-thoracic length; *G.b.*: *Gyge branchialis*; *G.o.*: *Gyge ovalis*; *O.g.*: *Orthonie griffenis*; N: number of analysed individuals; S: Sea

Host	Site	Sediment	Length	% ♀	Ovigerous period	Smallest ovigerous female CL	Parasite	Prevalence (%)	Smallest infested host CL	N	Comment on some parasite effects	Ref
<i>U. pusilla</i>	Adriatic S.	Md = 23-88	♂ > ♀	36-72	03-09	9	<i>G.b.</i>	0-5 ♀ 2-7 ♂	8*	631		Dworschak 1988
	Aegean S.	Md = 147-208	♂ > ♀	39	04-08	12				383		Kevrekidis et al. 1997
	Mediterranean S.			67-75			<i>G.b.</i>	9 ♀ 12 ♂		?	- Negligible feminisation of males, not related to parasite	Tucker 1930
	Mediterranean S.						<i>G.b.</i>		3	35	- Increased fat in infested males	Hughes 1940
	NE Atlantic	Md = 140	♀ > ♂	65	06-08	14	<i>G.b.</i>	13 ♀ 8 ♂	6*	1326	- Feminisation of infested males - Smaller individuals display higher prevalence - Weight loss when infested. - infested females are not ovigerous	This study
<i>U. yokoyai</i>	NW. Pacific	97% sands		70		8	<i>G.o.</i>	2 ♀ 4 ♂	15	163		Kinoshita et al. 2010
<i>U. stellata</i>	Ireland S.		♀ > ♂				<i>G.b.</i>	0		91	- A single intersex individual (no parasite)	Pinn et al. 2001
<i>U. deltaura</i>	North S.	Sandy	♀ = ♂	55	05-08			0		410		Tunberg 1986
<i>U. major</i>	Seto S.			32-40			<i>G.o.</i>	24 ♀ 16 ♂		2500	- Being infested doesn't predict intersex. - Smaller individuals display higher prevalence	Ubaldo et al. 2014
<i>U. pugettensis</i>	NE Pacific	Md = 68-225					<i>O.g.</i>	24 ♀ 6 ♂	10	411	- No evidence of feminisation - Larger individuals display higher prevalence - Parasite negatively affects host energetic state	Repetto and Griffen 2011
	NE Pacific			30-90			<i>O.g.</i>	5-80 ♀ 5-10 ♂	12	640	-Feminisation of infested males - Larger individuals display higher prevalence	Griffen 2009
	NE Pacific				10-11		<i>O.g.</i>	Up to 90%		1350	-No effect on size, sex or survival but effect on fecundity	Dumbauld et al. 2011
	NE Pacific			52			<i>O.g.</i>	42 ♀ 27 ♂	12	197	- Weight loss when infested. - No evidence of feminization	Smith et al. 2008

*Calculated from total length found in the original publication (see **Annexe III Appendix 3A.1** for equation). In bold: the present study

4.2 Influence of *Gyge branchialis* on *Upogebia pusilla* reproduction

Upogebia pusilla females were ovigerous during summer (June to August), which is consistent with results from previous studies (Dworschak 1988; Kevrekidis et al. 1997; **Table 3A.2**), including those carried out on other *Upogebia* species (Tunberg 1986) with the exception of *U. pugettensis* in the NE Pacific where females are ovigerous in October-November (Dumbauld et al. 2011). As already shown by Dumbauld et al. (2011), no ovigerous females were infested suggesting that infested females lose their reproductive capacity. Other bopyrids do indeed hamper host reproduction (Griffen 2009); one invoked mechanism being the consumption of the amount of energy that can be devoted to reproduction by non-infested mud shrimp (Smith et al. 2008). A majority of infested *U. pusilla* were females. However, the proportion of females did not significantly differ within the infested and non-infested populations, thereby suggesting that prevalence was not influenced by the sex of *U. pusilla*. This result is in slight contradiction with previous studies reporting higher infestation rates in *Upogebia* spp. females (Smith et al. 2008; Griffen 2009; Repetto and Griffen 2011; Ubaldo et al. 2014; **Table 3A.2**) and relating to the fact that females tend to produce more lipids than males and thus could provide the bopyrid with an access to food sources enhancing its growth, reproduction and survival (Smith et al. 2008). It is worth noting that the smallest ovigerous female collected during the present study was *ca.* 4 month old. Assuming that most of the infestation of *U. pusilla* occurs before it is 3 month old (see above), this suggests that infested females never had the opportunity to reproduce. Therefore, one can state that the parasitism by *G. branchialis* induces a diminution by 7 % of the female adult mud shrimp population contributing to reproductive effort.

About 25 % of the adult male population were infested as well and almost all infested males were feminized. Male feminization therefore probably quickly follows infestation, which is further supported by the fact that the smallest feminized males were only 27-mm long (corresponding to *ca.* three-month old individuals based on our VBGF) versus 19 mm (corresponding to *ca.* two-month old individuals based on our VBGF) for the smallest infested mud shrimp. Our results clearly show that a larger proportion of males were feminized in infested than in non-infested population. This is in contradiction with a previous work by Tucker (1930) in the Mediterranean Sea who stated that feminisation was negligible and not related to parasitism (**Table 3A.2**). A similar contradiction can be found for *U. pugettensis* in the North-East Pacific since Smith et al. (2008) and then Repetto and Griffen

(2011) did not observe feminization whereas Griffen (2009) conversely did (**Table 3A.2**). The effects of bopyrids on the feminization of their hosts may therefore interact with other environmental factors (Ubaldo et al. 2014), especially those related to nutrition, which may contribute to the explanation of such discrepancies (Nanri et al., 2010). Sex determination in crustaceans is indeed controlled by hormone production by the androgenic gland (Ford, 2008), which is itself related to nutrition. In case of nutritional deficit, androgenic gland production may therefore decrease and feminization (*i.e.*, apparition of female sexual secondary characters) may occur (Nanri et al. 2010). As far as the present study is concerned, it is not fully clear whether feminized males were castrated or not because their gonad integrity was not checked. For instance, in *U. major*, morphological disorders in males occur independently of gonadal development and do not affect sexual reproduction (Nanri et al. 2010).

4.3 Influence of *Gyge branchialis* on *Upogebia pusilla* total length and individual dry weight

During the present study, we reported average relative differences in mean IDW of non-infested versus infested *U. pusilla* of 34 and 30 % during the spatial and temporal surveys respectively. These differences clearly result from two distinct mechanisms, namely: (1) the fact that TL tends to be smaller in infested than in non-infested mud shrimp, and (2) the fact that the relationships linking TL and IDW differ in infested and non-infested mud shrimp. The frequency histograms of prevalence relative to TL derived from both surveys were typically dome-shaped and revealed a tendency toward higher prevalence in mud shrimp with intermediate TL. This pattern slightly differs from the one (*i.e.*, a monotonous decrease of prevalence with TL) reported by Ubaldo et al. (2014) for *U. major* infested by *G. ovalis*, which is also characterized by an early infestation. The pattern found during the present study may however be compatible as well with such an infestation and result from several non-exclusive causes including (1) parasite-dependent mortality, (2) a deleterious effect of the parasite on the growth of its host, and (3) parasite loss (Ubaldo et al. 2014). It is clearly difficult to unravel the effects of these possible causes. However, during the present study, we observed only very occasionally mud shrimp showing signs of a recent release of the parasite and suspected that in some cases this release was artefactual and due to our sampling procedure since the parasite was recovered close to the mud shrimp (LP personal

observation). We therefore do not believe that parasite loss is a major process within the *U. pusilla*-*G. branchialis* system.

Nevertheless, there were clearly less infested mud shrimp both within small and large size classes (**Figure 3A.3**), which is susceptible to induce inverse effects regarding differences in the average relative TL of infested and non-infested mud shrimp (**Figure 3A.5B**). The sign of the above-mentioned differences simply reflects the fact that, during both the spatial and the temporal surveys, the effect of the diminution of prevalence in large mud shrimp was dominant over the effect of the diminution of prevalence in small ones. When standardized for TL, mean relative differences in IDW of non-infested and infested mud shrimp reduced to 9.9 and 4.4 % during the spatial and temporal surveys, respectively. It should be pointed out that large individual variabilities are associated with these two figures because their computation involves: (1) a curve adjustment, and (2) the computation of a difference between two IDW. During both surveys, we nevertheless also recorded significant differences between non-infested and infested mud shrimp in the relationships linking TL and IDW, which further support the occurrence of an effect of parasitism on IDW irrespective of TL standardization. We found only a single reference mentioning the magnitude (*i.e.*, 7.8 %) of such an effect in another mud shrimp (*i.e.*, *U. pugettensis*) infested by another bopyrid (*i.e.*, *Orthonoe griffenis*) (Smith et al. 2008). Because of the above-mentioned restrictions, caution should clearly be taken in comparing these values beyond their order of magnitude.

A classical question in this type of study deals with the causality linking infestation and the physiological state of parasitized individuals. That is to say: is the mud shrimp IDW deficit a consequence and/or a cause of their infestation? While, it is not possible to be fully conclusive, there are several lines of evidence suggesting that the *U. pusilla* deficit in IDW is probably mainly resulting from its infestation by *G. branchialis*. This hypothesis is first supported by the increase in the magnitude of the deficit in IDW of infested mud shrimp with increasing TL (**Figure 3A.6**) as evidenced by the analysis of the *U. pusilla* TL-IDW relationships originating from both the spatial and temporal surveys. Moreover, due to the weak swimming abilities of parasite larvae, infestation intensity is often cued by local hydrodynamics surrounding the host (De Montaudouin et al., 1998) and even more specifically with their ventilation rates (Mikheev et al., 2014). These last authors for example clearly showed that the infestation of the salmonid fish *Onchorhynchus mykiss* by *Diplostomum pseudopathaceum* correlated positively with the ventilation rates of the former. Such a dependency of infestation on ventilation is probably even more marked in endobenthic

species, such as *U. pusilla*, living deep in the sediment column and thus far from the potential sources of cryptoniscus larvae. Ventilation rates are typically higher in individuals in healthy versus poor physiological states, which together with the above-mentioned relationship led Mouritsen et al. (2003) to account for the positive correlation linking the condition index of the New Zealand cockle *Austrovenus stutchburyi* and the intensity of its infection by the trematode *Curtuteria australis*. As far as our *U. pusilla* population is concerned, Pascal et al. (see “Chapitre 3 – Partie B”) recorded a threefold decrease in ventilation rates in infested mud shrimp relatively to non-infested ones. Assuming that (1) ventilation rates are also a key factor in controlling infestation rates of *U. pusilla*, and (2) ventilation rates correlate positively with the physiological state of *U. pusilla*, it is therefore unlikely that infestation by *G. branchialis* would preferentially take place in mud shrimp already showing a deficit in IDW.

5 Conclusion

This study provides essential information regarding the *Upogebia pusilla*-*Gyge branchialis* host-parasite system in Arcachon Bay. For example, and based on both a spatial and a temporal survey, our results show relatively high prevalence all over the year. Moreover, infestation significantly alters the physiological state of mud shrimp since infested individuals exhibited a significant deficit in total length and individual dry weight as compared to non-infested ones. Infestation also negatively affects the reproductive capacity of mud shrimp with almost all infested males being feminized and infested females never being ovigerous. Overall, our results therefore suggest that infestation by *G. branchialis* constitutes a key factor in regulating both mud shrimp population dynamics and individual functional capacities. Since *U. pusilla* populations are suspected to play a key role in the biogeochemistry of soft bottoms in Arcachon Bay, the functional impacts of their infestation by *G. branchialis* should now further be investigated.

Parasitism of engineer species: a key factor of marine ecosystem functioning

Ludovic Pascal^{1,2,*}, Antoine Grémare^{1,2}, Xavier de Montaudouin^{1,2}, Bruno Deflandre^{1,2}, Alicia Romero-Ramirez^{1,2} and Olivier Maire^{1,2}

¹ Univ. Bordeaux, EPOC, UMR 5805, F-33400 Talence, France

² CNRS, EPOC, UMR 5805, F-33400 Talence, France

Cet article sera prochainement soumis

Abstract

Thalassinid crustaceans are among the most influential ecosystem engineers in marine soft-bottom communities. They are also common host of bopyrid isopods, which have severe detrimental consequences on their physiology and population dynamics. In this study, we explored the potential implications of such a host-parasite association on sediment bioturbation and biogeochemical processes. Mesocosm experiments revealed that burrowing and ventilation activities of *Upogebia pusilla* were significantly altered when infested by the bopyrid *Gyge branchialis*, leading to strong reductions of (1) sediment reworking and bioirrigation rates and (2) solute exchanges at the sediment-water interface. Given the worldwide distribution of sediment-dwelling mud shrimp and their key role in bioturbation processes, parasite-mediated alterations of their engineering behaviour may have profound and broad ecological consequences for the functioning of marine coastal ecosystems.

1 Introduction

Over the last decades, a great deal of attention has been devoted to the mechanisms underpinning the relationship between the structure and composition of biological communities and ecosystem functioning (Hooper et al., 2005; Loreau, 2000; Loreau et al., 2001; Naeem et al., 2000). Across numerous field and experimental studies, the diversity of functional traits, rather than species richness *per se*, has been recognized as one of the most influential determinant of ecosystem function (Covich et al., 2004; Hooper et al., 2005; Petchey and Gaston, 2002; Stachowicz et al., 2007). Nevertheless, community contribution to ecosystem properties is not merely dependent on species functional characteristics but also deeply influenced by the combination of species, including the functional identity of dominant species as well as interspecific interactions (Mermillod-Blondin et al., 2005; Norling et al., 2007; Wohlgemuth et al., 2016).

Through the physical, chemical and biological modification of their surrounding environment, engineer species are known to disproportionately contribute to ecosystem processes (*e.g.* sediment bioturbation), thereby being of primary importance in ecosystem functioning (*e.g.* organic matter mineralisation) (Hastings et al., 2007; Jones et al., 1997; Kristensen, 2008; Lohrer et al., 2004). The identification of environmental factors affecting the engineering activity of such species is thus mandatory to better understand their role in ecosystem functioning and to accurately predict the ecological consequences of environmental change. Among biotic factors that can influence ecosystem engineers, parasitism appears to be especially substantial (Hatcher et al., 2012). Indeed, numerous studies have documented parasites importance in structuring communities through their effect on host mortality (Bick, 1994) and/or on ability to reproduce (Lajtner et al., 2008; Schulte-Oehlmann et al., 1997), which can lead to major reduction in host abundance (Meißner and Bick, 1997) and even local extinction (Dumbauld et al., 2011; Jensen and Mouritsen, 1992). However, parasites do not necessarily drive obvious numerical change in their host population, but can also induce more subtle modifications of their host phenotype, such as alteration of physiology (Mischler et al., 2016), or behaviour (Bernot and Lamberti, 2008; Mouritsen and Poulin, 2005; Sato et al., 2012). By modifying the behaviour of its host, a parasite can thus alter its functional role *via* trait-mediated effects (Werner and Peacor, 2003) rather than density-mediated effects. However, the ecological consequences of phenotypic alteration of engineer species induced by parasite remains very poorly documented (Hatcher et al., 2012; Thomas et al., 2005, 1999).

To assess how parasite could affect ecosystem functioning, we performed *ex-situ* experiments involving the thalassinidean crustacean *Upogebia pusilla* and the bopyrid ectoparasite *Gyge branchialis*. Thalassinidean crustaceans (*sensu* Felder, 2001) are large burrowing shrimp-like organisms living in complex and deep burrow that can reach several meters (Kinoshita, 2002). Due to their high density (up to 650 ind m⁻²; Nates and Felder, 1998) and intense burrowing activity (Cadée, 2001), they are considered to be among the most influential ecosystem engineers in marine soft-sediment (Pillay and Branch, 2011). It is, for instance, the case for the mud shrimp *Upogebia pusilla*, which dominates bioturbation processes (*sensu* Kristensen et al., 2012) and strongly stimulates oxygen and nutrients benthic fluxes of intertidal mud flat in Arcachon Bay (Pascal et al., 2016b; submitted, see “Chapitre 1”). This species is strongly infested by the bopyrid *Gyge branchialis*, where yearly parasite prevalence average 21 % in Arcachon Bay (Pascal et al., 2016a). Bopyrids are common ectoparasites of thalassinidean mud shrimp (Campos et al., 2009), where they settle in one of the two gills chamber. Because these parasites feed on their host inner fluid, they have profound effects on their fitness. In particular, there are evidences that in this association the bopyrid parasite strongly impairs its host length and dry weight as well as its ability to reproduce (Pascal et al., 2016a). Given the detrimental impact of this parasite on its host fitness it is realistic to consider that infestation by *G. branchialis* could constitute a key factor in regulating individual engineering traits. We hypothesise that infestation of *U. pusilla* by *G. branchialis* alters the functioning of intertidal mud flat. In other words, we predict that parasitized mud shrimp would exhibit reduced activity (burrowing, ventilating, locomotion) intensities resulting in lower bioturbation rates compared to healthy individuals. Accordingly, if the bioturbation activity of parasitized mud shrimp is significantly altered, we expect a lower influence on ecosystem functions such as organic matter mineralisation and nutrients turnover.

2 Materials and methods

2.1 Field sampling and experimental design

Laboratory experiments were carried out in winter (January) and summer (August) 2014. At each season, 50 adult specimens of the mud shrimp *Upogebia pusilla* were collected using a bait piston pump at low tide within an intertidal *Zostera noltei* meadow in Arcachon Bay (44°40.782’N, 1°08.321’W; see Pascal et al., 2016b for site details, “Chapitre 2”).

Among them, 18 undamaged females of the same length (4.6 ± 0.1 cm) (mean \pm SD), including nine parasitized specimens, were selected and kept isolated in individual containers before being used in the experiments. At the same time as animal sampling, 12 sediment cores (9.4 cm inner diameter, 25 cm long) were collected by hand, using transparent acrylic tubing.

Two sets of experiments were performed simultaneously to assess the influence of parasite infestation on mud shrimp behaviour, bioturbation processes and sediment biogeochemical dynamics. In the first set of experiments, five healthy (*i.e.* bopyrid-free) mud shrimp (“*Healthy-treatment*”) and five parasitized (*i.e.* bopyrid-infested) mud shrimp (“*Parasitized-treatment*”) were individually introduced in ten thin aquaria (25 (L) \times 1.9 (W) \times 50 (H) cm) previously filled with a 30 cm layer of sieved (1 mm mesh) sediment from the sampling site. Three thin aquaria were kept without mud shrimp as control. In the second set of experiments, four healthy (“*Healthy-treatment*”) and four parasitized mud shrimp (“*Parasitized-treatment*”) were individually introduced in field-collected sediment cores. Four sediment cores were kept intact as control (“*Without-Upogebia-treatment*”). All experimental enclosures were then placed in a dark thermo-regulated room and fuelled with a continuous seawater flow (~ 0.25 L min⁻¹) to ensure a good oxygenation of the overlying water. Seawater temperature and salinities were kept constant during the whole duration of the experiments at 12 °C and 30 in January and 22 °C and 30 in August, corresponding to field values recorded during animal sampling.

2.2 Behaviour monitoring

Behavioural recordings were performed using an automated image acquisition system composed of a video sensor (μ Eye UI-1480SE, IDS Imaging®, 2560 \times 1920 pixels) connected to a computer running AviExplore software (Romero-Ramirez et al., 2016). The sensor was placed in front of one side of each aquarium. Experiments were carried out in total darkness under infrared light ($\lambda > 700$ nm) to avoid any potential light disturbance. Recordings started as soon as a complete (*i.e.* open-ended) burrow was built. Each experiment lasted 72 h and image frequency acquisition was 0.1 Hz. Time-lapse sequences were then visually inspected. Only records where mud shrimp were visible for more than 90% of the time were converted into ethograms from which (1) the proportion of time (%) devoted to each behaviour as defined in Pascal et al., (submitted, see “Chapitre 1”) as well as (2) specific average bout-duration (min) and (3) interval-duration (min) were extracted.

2.3 Quantification of bioturbation rates

2.3.1 Sediment reworking

Sediment reworking is defined as sediment particles transport directly or indirectly resulting from mud shrimp behaviours. Sediment reworking rates were quantified using inert fluorescent particles (*i.e.* luminophores) (Maire et al., 2008). At the beginning of the experiment, 15 g of luminophores (100-160 μm size range, 2.5 g cm^{-3} density) were homogeneously spread at the sediment-water interface of each aquarium. Each side of the aquaria was photographed with a digital camera (D100, Nikon®, 3008×2000 pixels) four and thirty days after luminophores input, which correspond to the necessary duration for healthy mud shrimp to rework the whole length of its burrow wall at both season (Pascal et al. submitted, see “Chapitre 1”). Saved JPEG images were then analysed using specifically dedicated software as described in Maire et al., (2006), allowing for the assessment of luminophores vertical profiles. Biodiffusion (D_{bv} , corresponding to diffusion like sediment particles mixing within the sediment column) and bioadvection (V_{bv} , resulting from the ejection of sediment onto the sediment-water interface) coefficients were then estimated by fitting observed depth profiles with a biodiffusion-bioadvection transport model (Gerino et al., 1998; Meysman et al., 2003):

$$\frac{\partial^2 C}{\partial t} = D_{bv} \frac{\partial^2 C}{\partial z^2} - v_{bv} \frac{\partial C}{\partial z} \quad (1)$$

where C is the luminophore concentration (%), t is the time (year) and z is the depth. D_{bv} ($\text{cm}^2 \text{y}^{-1}$) and V_{bv} (cm y^{-1}) are biodiffusion and bioadvection coefficient estimated by convergent iterations and weighted least-squared regressions of model prediction on observed luminophores profiles (see Maire et al., 2006 for further details).

The component of sediment reworking occurring perpendicularly to burrow wall was modelled after 4 days of incubation using a simple biodiffusive model (Cochran, 1985):

$$\frac{\partial^2 c}{\partial t} = D_{bw} \frac{\partial^2 c}{\partial x^2} \quad (2)$$

Where C is the luminophore concentration (%), t is the time (year) and x is the orthogonal distance from the burrow wall (cm). D_{bw} ($\text{cm}^2 \text{y}^{-1}$) is biodiffusion coefficient estimated as mentioned above. This was achieved on four aquaria per season and per treatment. Selected aquaria were those with the longest proportion of visible burrow lumen allowing for the best

assessments of decrease in luminophore concentration with increasing orthogonal distances from burrow wall.

The total length and the vertical extension of burrows (cm) as well as the number of openings and turning chambers were respectively measured and counted at the commencement of experiments (T0) and after 4 (T4) and 30 days (T30). Additionally, two other sediment reworking proxies were assessed from thin aquarium images at T0, T4 and T30. (1) The volume of sediment expelled onto the sediment surface (V_{ES} , cm³) was estimated from the following equation:

$$V_{ES} = \bar{h} \times L \times W \quad (3)$$

where \bar{h} is the average height of sediment that overlaid the original sediment-water interface (cm), L is the aquarium length (25 cm) and W is the aquarium width (1.9 cm).

(2) The mean thickness of the reworked layer surrounding burrows was estimated by measuring the distance between burrow walls and the most distant luminophores within 5 different areas distributed along the burrow. The volume of reworked sediment surrounding the burrow (B_{RS} , cm³) was then estimated from the following equation:

$$B_{RS} = [L_b \times \pi(r_b + t_{RS})^2] - [L_b \times \pi r_b^2] \quad (4)$$

where L_b is the total burrow length (cm), r_b is the mean burrow radius (cm) and T_{RS} is the mean thickness of the reworked sediment layer surrounding the burrow (cm).

2.3.2 Bioirrigation

The bioirrigation is defined as the biologically induced transport of water and associated solutes across the sediment-water interface and within the sediment column (Kristensen et al., 2012). At the beginning of each experiment, a fluorescent soluble tracer (Uranine), allowing for the quantification of dissolved solutes transport across the sediment-water interface, was added in the overlying water of each core. Fluororimetric probes (Cyclops ©-7, Turner Design, $\lambda_{excitation}=490$ nm; $\lambda_{measured}=514$ nm) positioned in the overlying water of each core were used to continuously (1 Hz) measure the decrease in Uranine concentration during 48 hours. The overlying water was kept oxygen saturated with constant air bubbling, which also allowed for a gentle stirring and homogenization of the overlying water without sediment resuspension.

The bioirrigation rate (Q) was estimated by fitting a simplified version of the mathematical model developed by Meysman et al. (2007) to the moving averages (over one minute) of the tracer data:

$$C_{ow}(t) = \frac{A}{B} C_{ow}^0 + \left(1 - \frac{A}{B}\right) C_{ow}^0 e^{-Bt} \quad (5)$$

$$A = \frac{Q}{V_{pw} + M_s K_{ad}}, \quad B = \frac{Q}{V_{ow}} \left(1 + \frac{V_{ow}}{V_{pw} + M_s K_{ad}}\right) \quad (6)$$

where C_{ow} is the concentration of the dissolved tracer in overlying water ($\mu\text{g L}^{-1}$), V_{ow} and V_{pw} the volumes (mL) of overlying water and of porewater, M_s the sediment wet weight (g_{ww}) and K_{ad} the mean adsorption rate of Uranine onto sediment particles. According to Pascal et al. (2016b) a K_{ad} of $0.25 \text{ mL g dry weight}^{-1}$ was used. Q (mL h^{-1}) were estimated using Matlab (ver.9, Mathworks) by convergent iterations and weighted least-squares regression of model predictions on temporal Uranine concentration decline.

2.4 Assessment of ecosystem functioning

Ecosystem functioning is defined as the flow of energy and matter through biological organisation levels (Hooper et al., 2005). In this study, measurements of biogeochemical fluxes across the sediment-water interface (*i.e.* benthic-pelagic coupling) were used as a proxy of ecosystem functioning. Benthic solute exchanges were quantified using the incubation method. When starting incubations, the overlying water was sampled for initial measurements of oxygen (O_2), ammonium (NH_4^+), nitrate (NO_3^-) and dissolved silicate (dSi) concentrations. Experimental enclosures were then hermetically sealed with a PVC lid and the overlying water was continuously stirred with a magnetic bar spinning at ~ 100 rpm. The total duration of each incubation was adjusted so that O_2 concentration in the overlying water did not decrease below 70 % of its initial value. This was achieved using a mini-optode (OXROB10, Pyroscience®) introduced in the overlying water through the lid allowing for the real time measurement of O_2 concentration. At the end of the incubations, the overlying water was sampled for final nutrient measurements. Sediment cores were then left open overnight with a continuous oxygenated water flow before starting sequential replications ($n = 5$).

Water samples were analysed for NO_3^- (Wood et al., 1967), NH_4^+ (Aminot et al., 1997) and dSi (Truesdale and Smith, 1976) using a Quattro-Seal auto-analyser. In all treatments, benthic solute fluxes were calculated using equation (4):

$$F = [(C_f - C_i) \times V] / (t \times S) \quad (7)$$

where V is the volume (m^3) of overlying water, S is the surface (m^2) of the section of the sediment core, C_i and C_f are the initial and final concentrations of solutes in the overlying water (mmol L^{-1}) and t is the incubation duration (day). According to equation (4) a positive flux (F , $\text{mmol m}^{-2} \text{d}^{-1}$) is directed from the sediment to the overlying water and *vice-versa*.

To assess the contribution of the own respiration (*i.e.* oxygen uptake) and excretion (*i.e.* NH_4^+ release) of *Upogebia pusilla* to O_2 and NH_4^+ fluxes, mud shrimp were removed from their burrow at the end of each experiment and individually placed in experimental enclosures completely filled with 0.7 L of filtered ($0.2 \mu\text{m}$) and autoclaved seawater. Incubations were performed as detailed above. Between each sequential replication ($n = 5$) enclosures were left open two hours with a continuous oxygenated flow of filtered seawater.

2.5 Data treatments

All data presented in this study are averages (\pm SE). Differences in allocated time, bout- and interval-duration of each behaviour between *Healthy* and *Parasitized*-treatments were assessed using one-way PERMANOVA on the sum of images corresponding to each behaviour. Differences in D_{bv} , V_{bv} , D_{bw} , Q , oxygen and nutrients fluxes, individual respiration and excretion and porewater exchange rates between treatments and seasons were assessed using a two-way PERMANOVAs. In case of significant interaction between fixed factors, pairwise test were performed to characterise their modalities. All PERMANOVAs and associated tests were performed on untransformed data using Euclidean distance and the PRIMER® v6 package with the PERMANOVA+ add-on software (Clarke & Warwick 2001; Anderson *et al.* 2008).

3 Results

3.1 Behaviour

In winter, parasitized mud shrimp were not visible within their burrow more than 90% of the time. Consequently, their behaviour was characterized strictly based on summer experiments. As previously described by Pascal *et al.* (submitted, see “Chapitre 1”), in non-parasitized *Upogebia pusilla*, four distinct behavioural states, namely “Resting”,

“Burrowing”, “Ventilating” and “Walking”, were identified in parasitized mud shrimp. However, the proportion of time devoted to each of them (but walking) was significantly affected by a bopyrid infestation (**Table 3B.1**). Hence, parasitized individuals significantly spent more time to “Resting” than healthy ones (multiplying factor of 3.1) whilst they significantly reduced the proportion of time allocated to “Burrowing” and “Ventilating” by factors of 1.8 and 2.3, respectively (**Figure 3B.1**). Interestingly, the strategy of time reallocation caused by parasitic infestation differed between specific behaviours. Indeed, the proportion of time allocated to “Burrowing” and “Ventilating” in parasitized specimens was directly reduced by increasing the mean interval duration between two successive periods of specific activities (*i.e.* the mean duration of “Burrowing” and “Ventilating” events remained the same between treatments) (**Table 3B.1**). Conversely, the higher proportion of time devoted to “Resting” in infested organisms resulted from both an increase of the mean duration of “Resting” periods and a decrease of the mean interval duration between them.

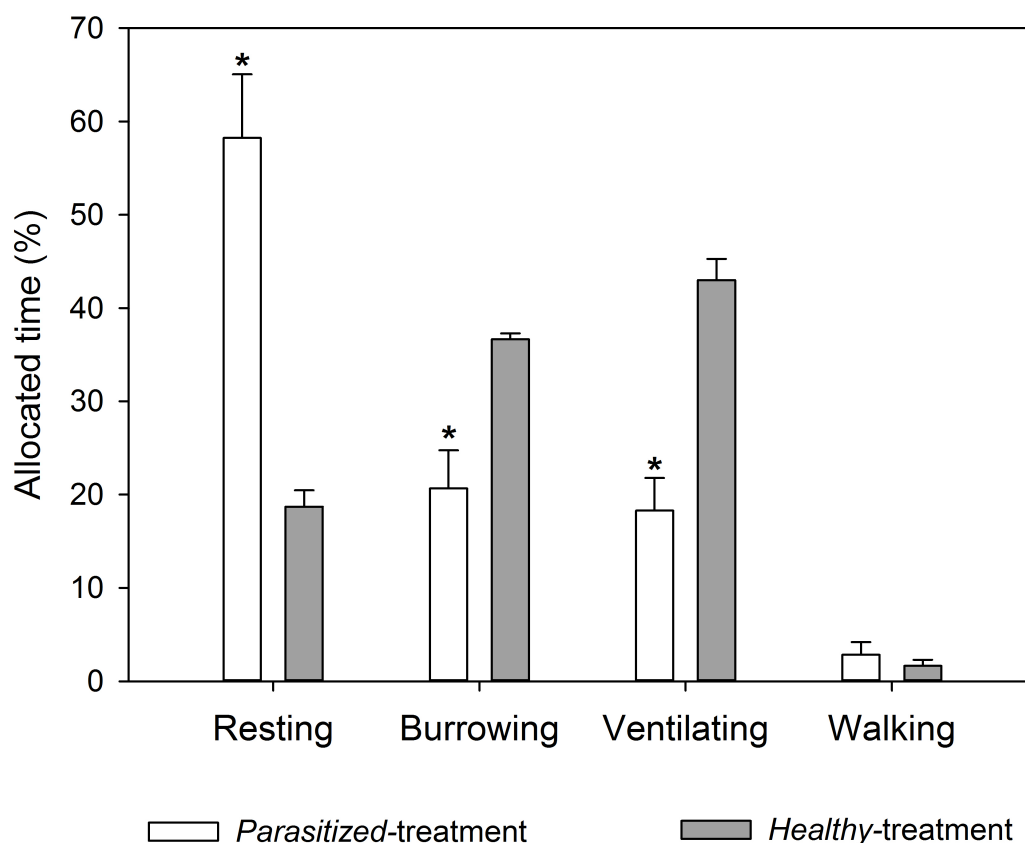


Figure 3B.1 : Average (\pm SE) proportions of time allocated to each behaviour in *Parasitized*- and *Healthy*-treatments during summer. * indicates significant differences in time devoted to each behaviour in *Parasitized*- as compared to *Healthy*-treatments (one-way PERMANOVAs and pair-wise test, $p < 0.05$)

Table 3B.1 : Average (\pm SE) bout-duration and interval-duration of each behaviour in *Parasitized*- and *Healthy*-treatment during summer. * indicates significant difference between seasons (one-way PERMANOVAs, $p < 0.05$)

Behaviour	Bout-duration (min)		Interval-duration (min)	
	Parasitized	Healthy	Parasitized	Healthy
Resting	* 16.0 \pm 3.4	7.7 \pm 0.8	* 15.7 \pm 3.3	31.8 \pm 2.6
Burrowing	6.7 \pm 1.1	7.1 \pm 0.6	* 21.3 \pm 3.9	12.7 \pm 1.3
Ventilating	4.8 \pm 1.3	6.9 \pm 0.7	* 27.5 \pm 7.9	9.5 \pm 1.0
Walking	1.4 \pm 0.3	1.0 \pm 0.2	66.4 \pm 23.4	80.4 \pm 16.8

3.2 Bioturbation

3.2.1 Sediment reworking

During winter, one parasitized mud shrimp did not build a complete open-ended burrow, so that only four parasitized individuals were used for the comparison of (1) burrow characteristics and (2) sediment reworking rates between *Healthy*- and *Parasitized*-treatments. At the two studied seasons, general burrow characteristics did not profoundly differ between treatments although the mean burrow length was significantly shorter in parasitized mud shrimp during summer (**Table 3B.2**). The thickness of the reworked sediment layer surrounding the burrow (T_{RS}) was also consistently thinner in the *Parasitized*-treatment (**Table 3B.2**). The volumes of sediment reworked by parasitized mud shrimp were thus significantly lower (**Figure 3B.2**). This is overall confirmed by the calculation of biodiffusive and bioadvective coefficients, which moreover showed a significant interaction between treatments and seasons for all of them (two-way PERMANOVAs, $F = 11.853, 95.229$ and 6.607 , respectively; $p = 0.001, 0.001$ and 0.014 , respectively). All coefficients were significantly lower during winter than during summer for the three treatments (**Figure 3B.2**). D_{bv} coefficients were significantly lower in *Parasitized*- than in *Healthy*-treatment at the two seasons (with multiplying factors of 4.6 and 4.5 during winter and summer, respectively) whereas the reduction of V_{bv} and D_{bw} was only significant in summer with respective corresponding multiplying factors of 5.5 and 3.1 (**Figure 3B.2A and B**).

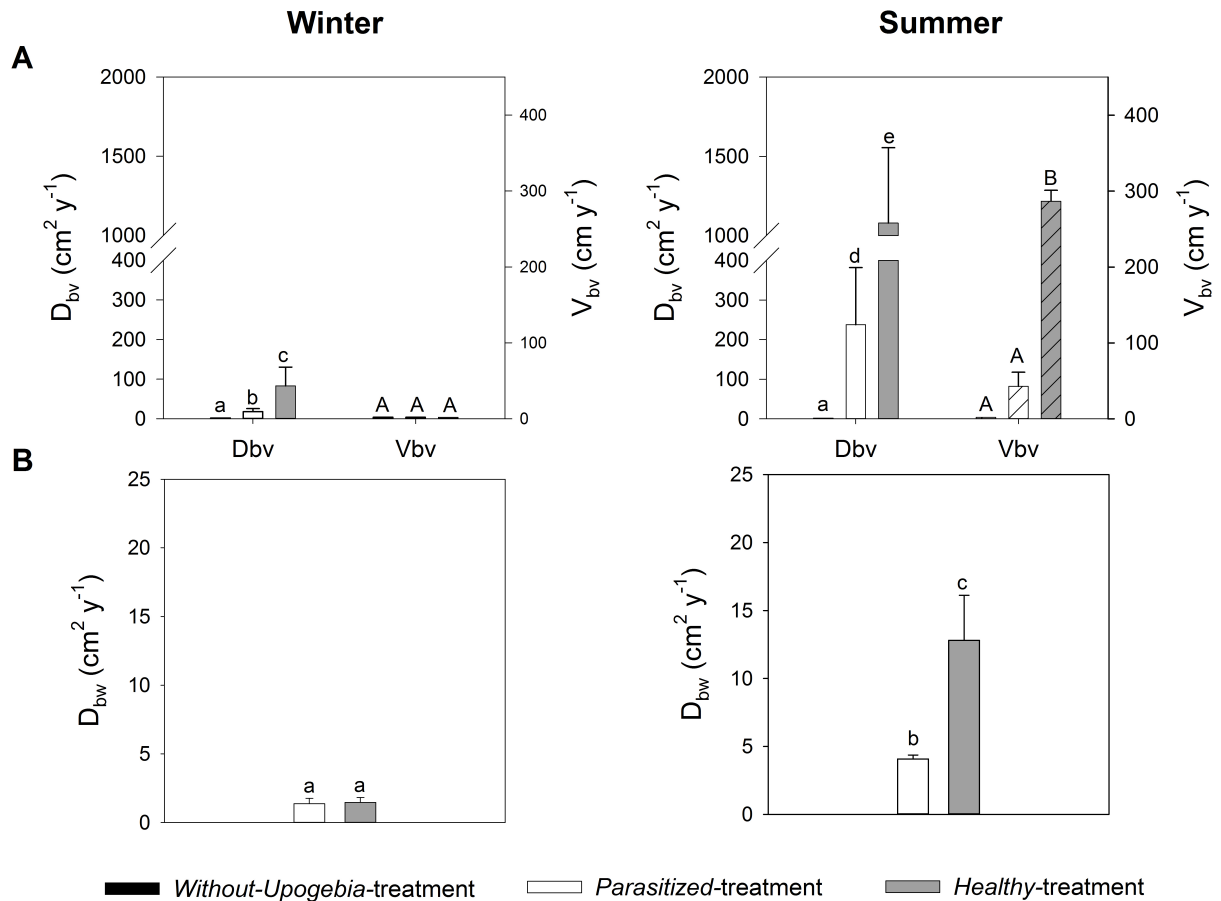


Figure 3B.2 : Average (\pm SE) sediment reworking coefficients. (A) Vertical biodiffusion (D_{bv} , solid bars, left scale) and bioadvection (V_{bv} , hatched bars, right scale) coefficients and (B) orthogonal to the burrow wall biodiffusion coefficient (D_{bw}) during winter and summer. Different letters indicate significant differences between combinations of seasons and treatments (two-way PERMANOVAs and pair-wise test, $p < 0.05$). Lower case: D_b ; Higher case: V_{bv}

Table 3B.2 : Average (\pm SE) of burrow characteristic (burrow length, burrow depth, number of burrow opening and number of turning chambers) and sediment reworking (T_{RS} : mean thickness of the reworked sediment layer surrounding the burrow, B_{RS} : volume of reworked sediment surrounding the burrow and V_{ES} : volume of sediment expelled onto the sediment) just after, 4 days and 30 days after luminophore input in *Parasitized-* (p) and in *Healthy-* (h) treatments. * Indicates significant differences between States within Season (three-way PERMANOVAs and pair-wise test, $p < 0.05$)

Season	Treatment	N	Burrow length (cm)	Burrow depth (cm)	Number of burrow opening	Number of turning chamber	T_{RS} (cm)	B_{RS} (cm ³)	V_{ES} (cm ³)
T0									
Winter	p	4	34.3 \pm 1.3	14.8 \pm 1.1	2.0 \pm 0.0	2.8 \pm 0.5	--	--	--
	h	5	32.5 \pm 2.5	13.1 \pm 1.3	2.0 \pm 0.0	2.0 \pm 0.0	--	--	--
Summer	p	5	32.0 \pm 1.8	16.8 \pm 3.0	2.0 \pm 0.0	2.9 \pm 0.3	--	--	--
	h	5	41.5 \pm 7.6	14.9 \pm 2.1	2.0 \pm 0.0	2.8 \pm 0.4	--	--	--
T4									
Winter	p	4	34.7 \pm 1.2	15.3 \pm 1.2	2.0 \pm 0.0	3.0 \pm 0.5	0.2 \pm 0.0	72.5 \pm 5.3	14.3 \pm 5.6
	h	5	33.2 \pm 3.0 *	13.2 \pm 1.4	2.0 \pm 0.0	2.0 \pm 0.0	0.4 \pm 0.0 *	84.9 \pm 4.0 *	23.6 \pm 3.3 *
Summer	p	5	32.1 \pm 1.8	17.4 \pm 3.1	2.1 \pm 0.2	3.1 \pm 0.4	0.3 \pm 0.0	108.8 \pm 4.7	25.0 \pm 8.0
	h	5	50.3 \pm 5.1	17.1 \pm 1.6	2.0 \pm 0.0	3.0 \pm 0.0	0.6 \pm 0.1	210.2 \pm 18.0	96.0 \pm 11.1
T30									
Winter	p	4	40.0 \pm 3.1	15.5 \pm 0.7	2.0 \pm 0.0	3.3 \pm 0.5	0.3 \pm 0.1	129.2 \pm 12.3	48.8 \pm 9.9
	h	5	41.3 \pm 4.8 *	14.3 \pm 1.0	2.5 \pm 0.3	3.0 \pm 0.6 *	0.4 \pm 0.0 *	133.3 \pm 20.8 *	70.8 \pm 9.9 *
Summer	p	5	60.4 \pm 13.9	20.2 \pm 4.2	2.2 \pm 0.2	3.5 \pm 0.2	0.4 \pm 0.0	144.5 \pm 11.6	100.5 \pm 38.9
	h	5	96.1 \pm 15.8	23.5 \pm 4.7	2.6 \pm 0.3	5.4 \pm 0.7	0.7 \pm 0.0	427.0 \pm 58.0	304.2 \pm 15.2

3.2.2 Bioirrigation

There was a significant interaction between treatments and seasons for the bioirrigation rate (Q) (two-way PERMANOVA, $F = 88.006$, $p = 0.001$) (**Figure 3B.3**). Values of Q coefficients in *Without-Upogebia*-treatment did not significantly differ between seasons and were always significantly different from the treatments containing mud shrimp (**Figure 3B.3**). They were 1.7 and 2.3-fold lower than in *Parasitized*-treatment and 3.6 and 6.7-fold lower than in *Healthy*-treatment during winter and summer, respectively. Q coefficient was always significantly lower in *Parasitized* - than in *Healthy*-treatment (**Figure 3B.3**) with corresponding multiplying factors of 2.2 and 2.9 during winter and summer, respectively. Overall, in treatment containing mud shrimp Q coefficients were always significantly higher during summer than during winter (**Figure 3B.3**).

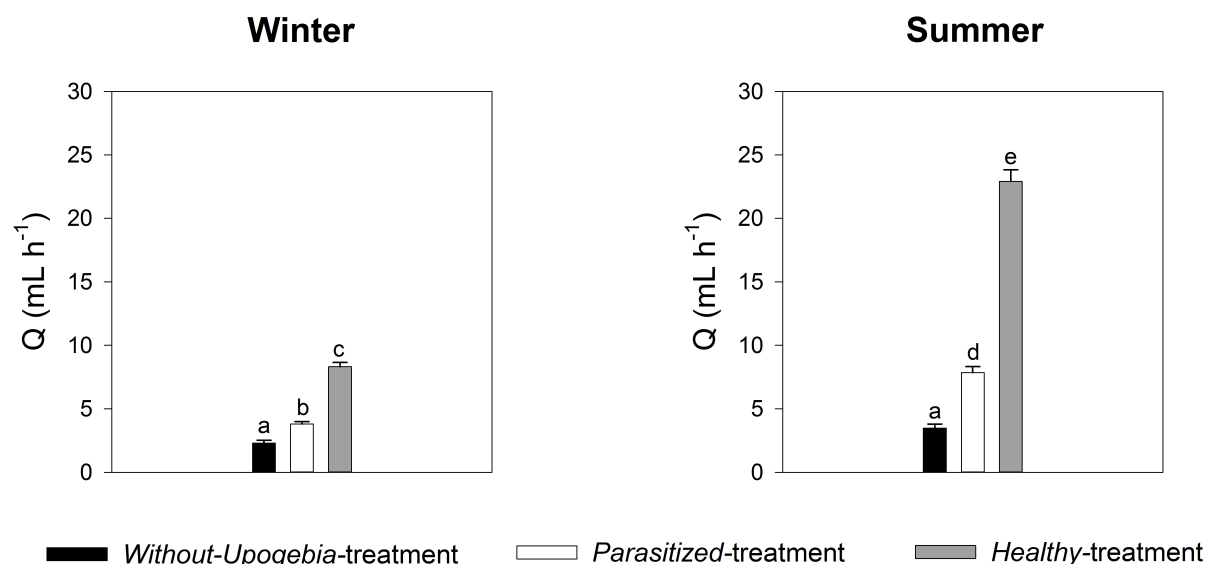


Figure 3B.3 : Average (\pm SE) bioirrigation rates (Q in mL h⁻¹) during winter and summer. Different letters indicate significant differences between combinations of seasons and treatments (two-way PERMANOVAs and pair-wise test, $p < 0.05$).

3.3 Ecosystem functioning

There was a significant interaction between seasons and treatments for the total oxygen uptake (TOU) (two-way PERMANOVA, $F = 6.165$, $p = 0.008$) (**Figure 3B.4A**). In all treatments, average TOUs were significantly higher in summer than in winter (**Figure 3B.4A**). At the two seasons, TOUs were significantly higher in the presence than in the absence of *Upogebia pusilla* (**Figure 3B.4A**). However, they were significantly lower in the *Parasitized*-treatment (1.4 and 1.5-fold lower in winter and summer, respectively). Respiration rates of *Upogebia* specimens significantly differed between seasons but not

between treatments (two-way PERMANOVAs, $F = 7.907$, $p = 0.016$). During winter, they reached 146.1 ± 17.7 and $138.6 \pm 10.5 \mu\text{mol ind}^{-1} \text{d}^{-1}$, for healthy and parasitized mud shrimp respectively and up to 194.7 ± 14.4 and $189.0 \pm 24.8 \mu\text{mol ind}^{-1} \text{d}^{-1}$ during summer. Given the mud shrimp density within experimental enclosures (144 ind. m^{-2}), winter values corresponded to 21.1 ± 2.6 and $20.0 \pm 1.8 \text{ mmol m}^{-2} \text{d}^{-1}$ (**Figure 3B.4A**), which accounted for 37.7 and 50.0% of the TOU in the *Healthy*- and *Parasitized*-treatment, respectively. Similarly, summer values corresponded to 28.0 ± 2.1 and $27.2 \pm 2.1 \text{ mmol m}^{-2} \text{d}^{-1}$, which accounted for 25.1 and 35.5% of the TOU in *Healthy*- and *Parasitized*-treatments, respectively. The sum of TOU in enclosure without *Upogebia* and direct oxygen uptake by the parasitized mud shrimp (*i.e.* respiration) always accounted for the totality of TOU in *Parasitized*-treatment. On the other hand, sum of TOU in enclosure without *Upogebia* and healthy mud shrimp respiration accounted for 75 and 65% of TOU in *Healthy*-treatment during winter and summer, respectively.

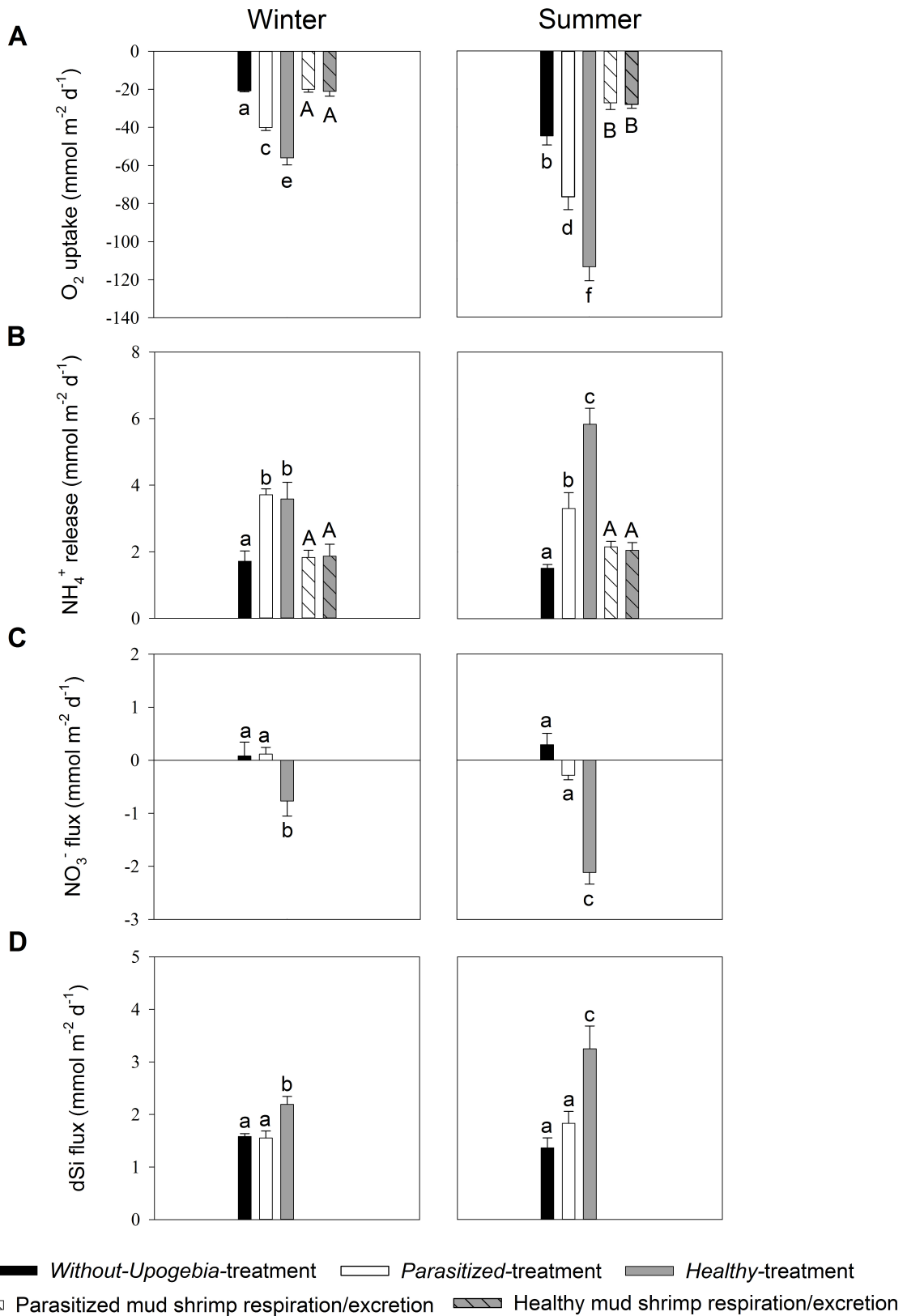


Figure 3B.4 : Average (\pm SE) of (A) O₂ uptakes: TOU (solid bars) and mud shrimp respiration (hatched bars), (B) NH₄⁺ releases: NH₄⁺ benthic fluxes (solid bars) and mud shrimp excretion (hatched bars), (C) NO₃⁻ and (D) dSi fluxes across the sediment-water interface. Different letters (higher case letter: mud shrimp respiration or excretion, lower case letter: benthic fluxes) indicate significant differences between combinations of treatments and seasons (two-way PERMANOVAs and pair-wise test, $p < 0.05$)

NH_4^+ fluxes were consistently directed towards the overlying water in all treatments (**Figure 3B.4B**). There was a significant interaction between treatments and seasons (two-way PERMANOVA, $F = 7.753$, $p = 0.004$). NH_4^+ fluxes in *Without-Upogebia*-treatment did not significantly differ between seasons and were always significantly different from the treatments containing mud shrimp (**Figure 3B.4B**). They were 2.2 and 2.2-fold lower than in *Parasitized*-treatment and 2.1 and 3.9-fold lower than in *Healthy*-treatment during winter and summer, respectively. NH_4^+ fluxes were only higher during summer than during winter for *Healthy*-treatment. NH_4^+ fluxes did not significantly differ between treatment containing mud shrimp during winter but was 1.8-fold higher in *Healthy*- than in *Parasitized*-treatment during summer (**Figure 3B.4B**). Excretion rates of *Upogebia* specimens did not significantly differ between seasons and treatments (two-way ANOVAs, $F = 1.036$ and 0.016 , $p = 0.329$ and 0.900 , respectively). During winter, they were 13.0 ± 2.5 and $12.7 \pm 1.5 \mu\text{mol ind}^{-1} \text{d}^{-1}$, for healthy and parasitized mud shrimp respectively and 14.3 ± 1.6 and $15.0 \pm 1.2 \mu\text{mol ind}^{-1} \text{d}^{-1}$ during summer, respectively. Given the mud shrimp density within experimental enclosures, winter values corresponded to 1.9 ± 0.4 and $1.8 \pm 0.2 \text{mmol m}^{-2} \text{d}^{-1}$ (**Figure 3B.4B**), which accounted for 52.1 and 49.3% of the NH_4^+ in the *Healthy*- and *Parasitized*-treatment, respectively. Similarly, summer values corresponded to 2.1 ± 0.3 and $2.2 \pm 0.2 \text{mmol m}^{-2} \text{d}^{-1}$, which accounted for 35.3 and 65.6% of the TOU in the *Healthy*- and *Parasitized*-treatment, respectively. The sum of NH_4^+ flux in enclosure without *Upogebia* and healthy mud shrimp excretion always accounted for the totality of NH_4^+ flux in *Parasitized*-treatment. On the other hand, sum of NH_4^+ in enclosure without *Upogebia* and healthy mud shrimp excretion accounted for the totality and 61% of NH_4^+ flux in *Healthy*-treatment during winter and summer, respectively.

There was a significant interaction between treatments and seasons for the NO_3^- fluxes (two-way PERMANOVA, $F = 6.978$, $p = 0.009$). NO_3^- fluxes in *Without-Upogebia*- and *Parasitized*-treatments always were barely detectable and did not significantly differ between them and between seasons (**Figure 3B.4C**). NO_3^- fluxes in *Healthy*-treatment were directed toward the sediment column and were always significantly different from the two other treatments (**Figure 3B.4C**). During summer, when NO_3^- fluxes in *Parasitized*- and *Healthy*-treatments were both directed toward the sediment column, a multiplying factor of 4.9 between these two treatments has been calculated.

dSi fluxes were always directed towards the overlying water (**Figure 3B.4D**). They significantly differed between treatments and seasons with a significant interaction between

these two factors (two-way PERMANOVA, $F = 3.880$, $p = 0.032$). dSi fluxes in *Without-Upogebia*- and *Parasitized*-treatments did not significantly differ from one another and between seasons. dSi fluxes in *Healthy*-treatment were significantly higher in summer than in winter and were 1.4 and 1.8-fold higher than in *Parasitized*-treatment during winter and summer, respectively.

4 Discussion

Parasitism can have detrimental effects on their host physiological state by affecting their growth, reproduction, behaviour and even their survival (Hatcher et al., 2012; Mouritsen and Poulin, 2002). Depending on the functional identity and activity of host species, parasite infection could have broad implications in ecosystem processes and properties. Recent studies have suggested that infection of engineer species could also have a determinant role in community structure. For instance, Mouritsen and Poulin (2005, 2010) showed that infection of the cockles (*Austrovenus stutchburyi*) foot tissue by trematodes reduced its burrowing and movement ability, thereby reducing the bioturbation intensity and affecting overall the structure of the associated benthic community. However, very few studies have documented the effects of parasitism of engineer species on ecosystem functioning (Mouritsen and Poulin, 2010; Thomas et al., 1998), which still remain poorly understood. In this study, we quantified the indirect implications of the bopyrid ectoparasit *Gyge branchialis* on benthic ecosystem functioning through its influence on the engineering behaviour of its host, the burrowing mud shrimp *Upogebia pusilla*.

4.1 Influence of the parasite at the organism-level

During winter, parasitized specimens of *Upogebia pusilla* were not visible enough from the side of the thin aquaria to allow for an accurate estimation of average time budget. However, since the visibility of the burrow lumen in experimental enclosures was directly related to burrowing activity, the reduced visibility of parasitized specimens somehow suggested that they were less active than healthy ones.

During summer, the proportion of time allocated to each behaviour could be quantified and compared between *Healthy*- and *Parasitized*-treatments. Hence, the proportion of time devoted to both “Burrowing” and “Ventilating” activities were significantly reduced by the presence of *Gyge branchialis* whilst the duration of periods of total immobility

increased. There are several well-documented examples of parasite-induced modification of host behaviour (Moore, 2002; Mouritsen and Poulin, 2005; Poulin, 1994; Reisinger and Lodge, 2016; Sato et al., 2012; Thomas et al., 1998). Most of these studies focused on the behavioural consequences of Helminth parasites infestation in the second intermediate host, probably because behaviour alteration could be expected since these parasites are transmitted through predation (Poulin, 1994). Since *U. pusilla* is the definitive host of *G. branchialis* (the bopyrid sexually reproduce in its mud shrimp host) it is unlikely that the bopyrid parasite intentionally alters its host behaviour in a way that enhance its susceptibility to be preyed, as it will be prejudicial for the parasite itself. The few studies that have focused on bopyrid infestation effects on their host activity have also shown strong reduced activity level in parasitized shrimp (activity level was between 2.2 and 8.5-folds lower in parasitized *Palaemonetes pugio* as compared to healthy ones (Bass and Weis, 1999) and 2-folds lower in parasitized *Synalpheus elizabethae* as compared to healthy ones (McGrew and Hultgren, 2011)). Such an effect is not surprising given that other studies have shown a detrimental impact of bopyrid parasite on its host metabolism rate (Anderson, 1977, 1975; Hughes, 1940; Nelson et al., 1986). However, it is worth mentioning that during our study, reduced metabolic rate in parasitized mud shrimp did not affect host respiration and excretion (**Figure 3B.4A and B**) which is consistent with the findings of Nelson et al. (1986). These authors found that despite the energy burden of the bopyrid *Argeia pauperata*, the respiration rate of the grass shrimp *Crangon franciscorum* was not affected by the parasite. Therefore, the energy demand of the parasite is most likely drawing on the energy that would normally be devoted to the mud shrimp activity and particularly to “Burrowing” and “Ventilating”.

4.2 Consequences on ecosystem functions

The reduced activity-level in parasitized mud shrimp resulted in low bioturbation levels as indicated by significant lower sediment reworking and bioirrigation rates in parasitized relatively to healthy mud shrimp both during winter and summer experiments (**Figure 3B.2 and 3**). Sediment reworking rates measured in *Without-Upogebia* treatment were nil during both seasons, indicating that luminophores displacement in *Healthy-* and *Parasitized-*treatments was only due to mud shrimp behaviour. It is worth noting that the sediment of *Without-Upogebia* treatment in sediment reworking experiments did not contain any macrofauna specimens since the sediment was sieved. It is thus difficult to draw any sound ecological conclusion from the differences between treatments with and without mud

shrimp. Conversely, sediment of this treatment in bioirrigation experiments was kept intact and thus contained macrofauna specimens. Although sediment reworking and bioirrigation are induced by different behaviour (burrowing *versus* ventilating), they are both directly related to the organism traits (Kristensen et al., 2012). In this sense, the relative slight differences in bioirrigation rate between *Without-Upogebia*- and *Parasitized*-treatment observed during winter and summer (as compared to the one between *Without-Upogebia*- and *Healthy*-treatment) can be extrapolated to the sediment reworking rate. Therefore, our results suggest that parasitized mud shrimp only marginally contribute to sediment bioturbation whereas healthy mud shrimp largely contribute to its increase during summer.

Our results demonstrate that reduced bioturbation activity caused by bopyrid infestation led to a lower influence of the mud shrimp on organic matter mineralisation and nutrients turnover. Bioturbation positively impact organic matter mineralisation efficiency by active transport of organic particles and injection of oxygen into the sediment (Kristensen, 2000; Meysman et al., 2006). By doing so, bioturbating species modulate resources availability (*i.e.* organic matter) and abiotic conditions (*i.e.* redox potential) for microorganisms, which in turn affect microbial-mediated biogeochemical activity (Kristensen et al., 2012). Our results support this rational since healthy mud shrimp significantly enhanced oxygen and nutrient fluxes at the sediment-water interface (**Figure 3B.4**). Moreover, (1) mud shrimp respiration only accounted for 60 and 42% of its contribution to TOU in *Healthy*-treatment during winter and summer, respectively and (2) mud shrimp excretion accounted for the 98 and 48% of its contribution to NH_4^+ flux in *Healthy*-treatment during winter and summer, respectively. The NO_3^- uptake observed during the two seasons (**Figure 3B.4**) suggested that the presence of healthy mud shrimp enhance N removal processes (*e.g.* denitrification, anammox). Conversely, parasitized mud shrimp have reduced ability to maintain and ventilate their burrow as compared to healthy ones (**Figure 3B.1, 2 and 3**), which limit oxygen availability within the sediment and, thereby, reduce organic matter mineralisation capacity of the sediment. Furthermore, our results suggest that the impact of parasitized mud shrimp on TOU and NH_4^+ fluxes was mostly direct (*i.e.*, results from mud shrimp own respiration and excretion) and weakly contribute to indirect effects (*i.e.*, stimulation of microbial organic matter mineralization processes, **Figure 3B.4**). NO_3^- fluxes in the presence of parasitized mud shrimp were consistently close to zero (*i.e.*, production and consumption processes offset each other) and did not differ from the ones without mud shrimp (**Figure 3B.4**), suggesting that parasitized mud shrimp do not affect NO_3^- production

or consumption processes. As opposed to TOU, NH_4^+ and NO_3^- , dSi is not directly involved in organic matter mineralisation. Bioturbating activity may however affect dSi flux across the sediment-water interface by accelerating dSi exchange through porewater (Ullman and Aller, 1989) and destabilising porewater gradient, which may enhance silicate dissolution rates (Reimers and Wakefield, 1989). Therefore the absence of significant difference in dSi flux between *Parasitized*- and *Without-Upogebia*-treatments (**Figure 3B.4**) confirms that parasitized mud shrimp do not significantly contribute to sediment bioturbation (see above) unlike healthy ones.

In conclusion, our experiments revealed that bopyrid infestation affect mud shrimp behaviour, which have strong cascading effect on microbial driven biogeochemical activity, resulting in lower benthic oxygen and nutrients fluxes across the sediment surface. Since engineer species are defined as organisms that influence resource flows to other species (Jones et al., 1994), our results strongly suggest that bopyrid infestation attenuate engineering effects of *U. pusilla* individuals. At the natural population scale and considering a parasite prevalence of 21% (Pascal et al., 2016a), the present study demonstrates that *G. branchialis* indirectly influences ecosystem functioning in Arcachon Bay. For instance, in an *U. pusilla* natural population in summer as compared to a population containing only healthy specimens, sediment reworking rates were between 16.4 and 17.2% lower, bioirrigation rate decrease of 13.8%, leading to a reduction of 6.6 % of the TOU (**Table 3B.3**). Given (1) that burrowing organisms (Meysman et al., 2006; Kristensen et al., 2012) and particularly Thalassinidean mud shrimp (see review by Pillay and Branch, 2011) are considered as ecosystem engineer and (2) the ubiquity of parasites (Combes, 2001), the results reported in this study can be applied over large coastal areas where burrowing organisms occur. Finally, beyond the indirect effect of bopyrid parasite on sedimentary processes documented here, such infestation might have far-reaching effects on higher trophic level since Thalassinidean mud shrimp are suspected to modulate energy flow to nektonic species (Pillay et al., 2008, 2012). While the influence of none letal parasites on ecosystem functioning have been largely overlooked, this study proves that more subtle effects of parasites play a substantial role in ecosystem functioning.

Table 3B.3 : Average (\pm SE) sediment reworking rates (bioturbation, D_b and bioadvection, V_b), bioirrigation rate (Q) and oxygen (TOU) and nutrients benthic fluxes (NH_4^+ , NO_3^- and dSi) in *Without-Upogebia*-, *Healthy*- and *Parasitized*-treatments. The column entitled “Population” correspond to the average values expected for a natural population with 21 % of infested mud shrimp (Pascal et al. 2016a). The difference (in italic) of the values calculated for a natural population relatively to a healthy population has been computed. Note that Q has been standardized for a mud shrimp density of 144 ind m^{-2} as for flux measurements

	<i>Without-Upogebia</i>	<i>Healthy</i>	<i>Parasitized</i>	Population	Difference (%)
Winter					
D_b ($\text{cm}^2 \text{y}^{-1}$)	0.0 \pm 0.0	83.0 \pm 21.2	18.0 \pm 3.5	69.4	16.4
V_b (cm y^{-1})	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0	0.0
Q ($\text{L m}^{-2} \text{d}^{-1}$)	7.9 \pm 0.9	28.7 \pm 1.2	13.2 \pm 0.6	25.4	11.3
TOU ($\text{mmol m}^{-2} \text{d}^{-1}$)	21.0 \pm 0.3	56 \pm 3.3	40 \pm 1.3	52.6	6.0
NH_4^+ ($\text{mmol m}^{-2} \text{d}^{-1}$)	1.7 \pm 0.2	3.6 \pm 0.4	3.6 \pm 0.2	3.6	0.0
NO_3^- ($\text{mmol m}^{-2} \text{d}^{-1}$)	0.1 \pm 0.2	-0.8 \pm 0.3	0.1 \pm 0.1	-0.6	23.6
dSi ($\text{mmol m}^{-2} \text{d}^{-1}$)	1.6 \pm 0.1	2.2 \pm 0.1	1.6 \pm 0.1	2.1	5.7
Summer					
D_b ($\text{cm}^2 \text{y}^{-1}$)	0.0 \pm 0.0	1079.5 \pm 212.6	237.8 \pm 64.5	902.7	16.4
V_b (cm y^{-1})	0.0 \pm 0.0	235.6 \pm 60.1	42.8 \pm 18.7	195.1	17.2
Q ($\text{L m}^{-2} \text{d}^{-1}$)	12.0 \pm 1.2	79.2 \pm 3.2	27.1 \pm 1.7	68.3	13.8
TOU ($\text{mmol m}^{-2} \text{d}^{-1}$)	44.6 \pm 9.6	111.5 \pm 6.6	76.7 \pm 6.1	104.2	6.6
NH_4^+ ($\text{mmol m}^{-2} \text{d}^{-1}$)	1.5 \pm 0.1	5.8 \pm 0.4	3.3 \pm 0.4	5.3	9.1
NO_3^- ($\text{mmol m}^{-2} \text{d}^{-1}$)	0.3 \pm 0.2	-2.0 \pm 0.2	-0.4 \pm 0.1	-1.7	16.8
dSi ($\text{mmol m}^{-2} \text{d}^{-1}$)	1.1 \pm 0.1	3.3 \pm 0.6	1.8 \pm 0.2	3.0	9.5

Synthèse et perspectives

De mon point de vue, la principale originalité de mon travail de thèse réside dans le fait qu'il constitue une étude intégrée du rôle d'une espèce clé, *Upogebia pusilla*, dans le fonctionnement de son écosystème (*i.e.*, les herbiers intertidaux de phanérogames marines). Pour ce faire, mon travail a explicitement associé : (1) l'étude comportementale de cet organisme, (2) la caractérisation et la quantification des processus de bioturbation, incluant le remaniement sédimentaire et la bioirrigation, engendrés par ses différents comportements (fouissage, locomotion, ventilation), et (3) l'évaluation des effets de cette bioturbation intense sur la dynamique biogéochimique du compartiment benthique et les échanges de solutés à travers l'interface eau-sédiment. L'influence de la saisonnalité et du parasitisme sur ces différentes interactions a également été évaluée.

Mon manuscrit comprend quatre articles scientifiques consacrés respectivement à l'étude : (1) du lien entre le comportement d'*U. pusilla*, le remaniement sédimentaire qui en résulte et ses conséquences sur la dynamique de l'oxygène dissous au sein et autour de son terrier, (2) de l'influence de l'activité de cette espèce sur la bioirrigation du sédiment et les flux d'oxygène et de nutriments à l'interface eau-sédiment, (3) de l'interaction hôte-parasite entre *U. pusilla* et *Gyge branchialis* ainsi que des effets de cet ectoparasite sur l'état physiologique de son hôte et (4) des conséquences de cette interaction sur le fonctionnement des écosystèmes à herbier du bassin d'Arcachon. Le premier article a récemment été soumis à la revue *Marine Ecology Progress Series*. Les deux suivants ont respectivement été publiés en 2016 dans les revues *Journal of Experimental Marine Biology and Ecology* et *Marine Biology*. Le quatrième sera prochainement soumis pour publication.

La synthèse qui va suivre a pour objectif de rappeler les principaux résultats obtenus et de présenter les principales perspectives qui en découlent. Elle est structurée en cinq paragraphes consacrés respectivement au/à :

- Comportement d'*Upogebia pusilla*
- L'activité de bioturbation d'*Upogebia pusilla*
- L'influence d'*Upogebia pusilla* sur la dynamique biogéochimique sédimentaire
- Rôle indirect du parasitisme dans le fonctionnement des écosystèmes côtiers *via* son influence sur le comportement des espèces ingénieures
- Une conclusion générale sur le rôle des crustacés thalassinidés dans le fonctionnement écologique et biogéochimique des herbiers de phanérogames marines et plus généralement des écosystèmes côtiers.

1 Comportement de l'espèce ingénieuse *Upogebia pusilla*.

1.1 Objectifs et principaux résultats acquis

Les objectifs spécifiques de la partie de mon travail de thèse portant sur l'analyse comportementale visaient tout d'abord à établir l'éthogramme de cette espèce. Cela a consisté à identifier finement (*i.e.*, avec une haute résolution temporelle) l'ensemble des comportements d'*U. pusilla* et à quantifier précisément la proportion de temps qui leur était respectivement allouée. Il s'agissait ensuite d'estimer les effets des principaux facteurs environnementaux, à la fois abiotiques (*i.e.*, ceux en lien avec la saisonnalité) et biotiques (*i.e.*, en lien avec le parasitisme) sur le comportement d'*U. pusilla*. Cependant, le comportement des thalassinidés est particulièrement difficile à étudier en raison du mode de vie cryptique de ces organismes et de leur grande mobilité. C'est probablement pour cette raison que les études comportementales préalables les concernant se sont essentiellement concentrées sur les activités de ventilation et d'expulsion de sédiment hors du terrier, toutes deux observables depuis la surface du sédiment. Le principal défi pour atteindre ces objectifs consistait donc à pénétrer au sein même de la colonne sédimentaire pour observer *U. pusilla* dans son terrier mais en s'assurant de ne pas engendrer de perturbations qui pourraient altérer son comportement. Des techniques expérimentales innovantes basées sur l'utilisation d'aquariums plats couplées à de l'analyse d'image ont été développées ces dernières années au sein du laboratoire EPOC. Ces techniques ont démontré leur efficacité pour étudier le comportement d'organismes endogés tel que les bivalves *Abra* spp. (*e.g.*, Grémare et al., 2004; Maire et al., 2007b; Bernard et al., 2016). Cependant, *U. pusilla* est un organisme bien plus gros et bien plus mobile que ces bivalves. Au début de ma thèse j'ai donc mis au point des enceintes expérimentales adaptées à la taille d'*U. pusilla* et aux dimensions de son terrier (*i.e.*, des aquariums suffisamment profonds pour permettre aux individus de se déplacer mais également suffisamment étroits pour pouvoir les observer à l'intérieur de leur terrier). Les dimensions suivantes : 25 (largeur) × 1.9 (épaisseur) × 50 (hauteur) cm ont été retenues. Enfin, j'ai déterminé, à partir d'une série de séquences vidéo haute fréquence (24 Hz), la fréquence et la durée d'acquisition minimales requises pour identifier et quantifier la totalité des comportements d'*U. pusilla*, sans perdre d'information. L'acquisition d'image (0,1 Hz pendant 72 h) a été réalisée dans l'obscurité, sous lumière infra-rouge, afin de ne pas altérer le comportement des individus étudiés.

A partir de l'analyse d'enregistrements vidéo (1488 heures au total) permettant d'observer précisément le comportement de 24 individus au sein de leur terrier, quatre grands types de comportements ont pu être identifiés :

- La locomotion : correspond au déplacement et retournement de l'individu dans son terrier sans qu'il ne transporte de sédiment.
- La ventilation : correspond à l'irrigation du terrier. L'eau du terrier chargée en solutés réduits est remplacée périodiquement par de l'eau surnageante riche en oxygène. Le courant d'eau entrant est créé par le battement régulier des pléopodes.
- Le fouissage : l'individu interagit directement avec la matrice sédimentaire lors de la construction et de la maintenance de son terrier. Il peut ainsi creuser, mélanger et compacter du sédiment le long de la paroi du terrier, en transporter d'une galerie à une autre ou bien encore le déposer à l'extérieur de son terrier.
- Le repos : l'organisme reste quasiment immobile. Aucun mouvement n'est détecté à l'exception des mouvements des antennes.

La quantification du temps alloué à chaque comportement a montré que les deux principaux chez *U. pusilla* sont la ventilation (de 14,1 à 42,9 % du temps total d'enregistrement) et le fouissage (de 20,7 à 36,7 % du temps). Chez les individus sains, il a pu être mis en évidence que la proportion de temps allouée à ces deux comportements est soumise à des variations saisonnières significatives. Ainsi, le temps dédié à la ventilation est 3,6 fois plus important en été qu'en hiver. De même, le temps consacré au fouissage est multiplié par 1,5 entre ces deux saisons. L'augmentation de la proportion de temps alloué à la ventilation résulte d'une diminution de l'intervalle entre deux périodes de ventilation successives qui passe de 42 min en moyenne en hiver à seulement 10 min en moyenne en été. La durée moyenne d'une séquence de ventilation reste par contre relativement constante (~ 7 min) quelle que soit la saison. La durée de l'intervalle moyen entre deux périodes successives de fouissage diminue également entre l'hiver (~ 46 min) et l'été (~ 13 min) de même que la durée moyenne d'une séquence (de 13 min en hiver contre seulement 7 min en été). Réciproquement, la proportion moyenne du temps alloué au repos diminue par un facteur 2.9 entre l'hiver et l'été. Cette diminution résulte simultanément d'une réduction de la durée des périodes d'immobilité qui passe de 17 min en moyenne en hiver à 8 min en moyenne en été et de l'intervalle entre deux périodes successives (19 min en moyenne en hiver contre 32 min en

moyenne en été). Le comportement de locomotion ne représente quant à lui que 2 % du temps total et n'est pas significativement influencé par la saisonnalité.

Si le comportement des crevettes de vase parasitées par *Gyge branchialis* a pu être étudié de manière précise en été (voir ci-dessous), cela n'a en revanche pas pu être le cas en hiver. En effet, lors des expériences hivernales, l'activité de fouissage des individus parasités était trop faible pour qu'une proportion satisfaisante de l'intérieur du terrier soit visible depuis les deux faces des aquariums plats. Cette observation tend néanmoins à confirmer l'hypothèse d'une réduction importante de l'activité de fouissage des individus parasités puisque dans les mêmes conditions les individus sains étaient parvenus à creuser des terriers suffisamment bien développés pour que l'intérieur des galeries soit visible. L'étude comportementale effectuée durant la saison estivale confirme cette hypothèse. Ces résultats montrent, en effet, une réduction moyenne par un facteur 3,1 de l'activité des individus parasités par rapport aux individus sains. Cette diminution d'activité se traduit par des proportions de temps allouées aux comportements de fouissage et de ventilation, respectivement, 1,8 et 2,3 fois inférieures en moyenne chez les individus parasités que chez les individus sains.

1.2 Perspectives

L'étude comportementale d'*U. pusilla* a été réalisée en utilisant des techniques d'imagerie. Cette technologie non invasive a aussi l'avantage de permettre l'enregistrement d'une grande quantité d'information (*i.e.*, hautes résolutions spatiale et temporelle) qui peut être analysée et ré-analysée *a posteriori*. Ce point est particulièrement intéressant pour limiter l'investissement humain sur de telles expériences et ainsi pouvoir effectuer des études comportementales en continu sur plusieurs jours voir semaines ou mois. L'analyse des séquences d'images enregistrées reste cependant assez fastidieuse et *pro parte* subjective. Une première étape de semi-automatisation a été franchie au cours de mon travail de thèse grâce à une collaboration avec l'équipe de développeurs du laboratoire EPOC. Un module permettant l'identification et la quantification semi-automatique des comportements chez les crustacés fouisseurs est désormais fonctionnel et disponible (Romero-Ramirez et al., 2016, **Annexe IV**). Des optimisations sont cependant nécessaires pour atteindre un meilleur taux d'identification des différents comportements et finalement passer à une automatisation complète de l'analyse comportementale chez les thalassinidés.

Au cours de ce travail, j'ai également étudié l'influence des variations saisonnières et du parasitisme sur le comportement d'*U. pusilla* en déterminant des proportions de temps allouées à chaque comportement à différentes saisons. Une voie restant à explorer est la mesure de l'intensité de l'activité pour chaque comportement. Cela nécessitera en outre d'identifier des proxy quantitatifs de chaque comportement. Par exemple, l'intensité de l'activité de ventilation pourrait être quantifiée via la mesure de la fréquence de battement des pléopodes. Il me paraîtrait aussi particulièrement intéressant de considérer d'autres facteurs environnementaux susceptibles d'affecter le comportement des thalassinidés. Nickell et Atkinson (1995) ont par exemple mis en évidence des changements de régimes trophiques en fonction de la disponibilité en matière organique. Il me semblerait donc pertinent de tester l'influence de la quantité et de la qualité de la matière organique disponible sur le mode de nutrition (et le comportement associé) des crevettes de vase.

En vu de passer à des expérimentations en milieu naturel, il semble aussi très important de prendre en compte l'effet des interactions interspécifiques sur le comportement des thalassinidés qui s'avèrent être des organismes territoriaux et assez agressifs. Lors des échantillonnages des crevettes de vase, la présence d'*Heteromysis microps* une espèce commensale de son terrier a été observée (Lavesque et al., 2016, **Annexe V**). La présence de cette espèce peut potentiellement influencer le comportement d'*U. pusilla*. Récemment, Moyo et al. (2017) ont en effet mis en évidence que la présence d'un symbiote (*Betaeus jucundus*) dans le terrier de *Callichirus kraussi* provoque une augmentation jusqu'à 50 % du temps alloué à l'excavation de sédiment et réduit jusqu'à 30 % le temps consacré à la ventilation du terrier. Ces auteurs estiment que cette interaction est susceptible d'influencer le rôle de ce thalassinidé dans le fonctionnement de l'écosystème qu'il colonise. De la même manière, la présence d'un prédateur tel que la raie *Raja clavata* (Saglam et Bascinar, 2008) peut modifier le comportement de ces crustacés endogés et leur activité de bioturbation. Un tel effet a déjà été rapporté chez le bivalve *Macoma balthica* en présence du prédateur *Crangon crangon* (Maire et al., 2010).

Une des difficultés rencontrées lors de cette partie de ma thèse sur l'analyse comportementale est liée à la dépendance de la technique d'imagerie utilisée à la visibilité de l'organisme dans son terrier. En effet, il est rare d'avoir accès à la totalité de la lumière du terrier et les résultats peuvent être fortement biaisés si l'organisme est trop souvent caché (> 15 % du temps). Afin de s'affranchir de ce facteur limitant, une méthode prometteuse consiste à mesurer les variations de pression engendrées par les activités hydrauliques des organismes

dans le sédiment (Wethey et Woodin, 2005). Cette méthode a déjà montré son efficacité pour différencier plusieurs types de comportements chez le thalassinidé *Neotrypaea californiensis* (Volkenborn et al., 2012). Le laboratoire EPOC s'est doté d'un équipement de ce type. Les premiers tests ont montré que la perméabilité du sédiment colonisé par *U. pusilla* permettait l'utilisation de tels capteurs et qu'il était possible de distinguer 4 patrons de variations de pression liés à ses différents comportements. Une étape de validation, couplant l'utilisation des capteurs de pression et les techniques d'analyse d'image utilisées lors de mon travail de thèse, est maintenant nécessaire pour relier explicitement activité comportementale et patron de variation de pression. *In fine*, cette méthode pourrait permettre de mesurer *in-situ* avec une très haute résolution spatiale et temporelle tous types d'activité biologique engendrant des variations de pression au sein de la matrice sédimentaire.

2 La bioturbation induite par *Upogebia pusilla*

2.1 Objectifs

Les objectifs spécifiques de la partie de mon travail consacrée à l'étude de la bioturbation d'*Upogebia pusilla* consistaient à étudier les processus de remaniement sédimentaire et de bioirrigation engendrés par ses activités. Il fallait dans un premier temps caractériser et quantifier ces deux processus. Il paraissait ensuite important de quantifier les variations saisonnières du taux de bioturbation d'*U. pusilla* ainsi que l'impact du parasitisme. Il s'agissait, enfin, de relier précisément les deux composantes de la bioturbation aux comportements qui les génèrent. L'étude du remaniement sédimentaire et de la bioirrigation a été réalisée en utilisant des méthodes expérimentales spécifiques détaillées ci-dessous dans deux sous-paragraphes distincts.

2.2 Le remaniement sédimentaire

2.2.1 Principaux résultats acquis

Chez les thalassinidés le remaniement sédimentaire avait jusqu'alors été évalué à partir d'une approche dite de mesure du « sediment turnover » qui consiste à estimer la quantité de sédiment expulsé à l'extérieur du terrier au cours d'un intervalle de temps donné. Mon travail sur le comportement d'*U. pusilla* a permis de mettre en évidence l'importance du comportement de fouissage intervenant au sein de la matrice sédimentaire mais n'induisant pas forcément d'éjection de sédiment à l'extérieur du terrier. Une grande partie du sédiment

remanié lors de la construction et la maintenance du terrier est en fait simplement déplacée puis compactée contre la paroi du terrier. Ce remaniement de subsurface est susceptible d'avoir une influence majeure sur le devenir de la matière organique particulaire présente autour de la paroi du terrier en l'exposant à des conditions oxiques ou, au contraire, en déplaçant dans des zones anoxiques la matière organique labile introduite au sein des galeries. Il paraissait ainsi indispensable de caractériser et de quantifier précisément ce remaniement sédimentaire de subsurface. La première partie de mon travail a donc consisté à mettre en place un dispositif expérimental permettant d'accéder à une vision globale du transport particulaire induit par *U. pusilla*. Afin de lier explicitement le remaniement sédimentaire avec un ou plusieurs comportements décrits ci-dessus, ce dispositif devait également permettre l'analyse comportementale. L'utilisation combinée de luminophores, d'aquariums plats et de techniques d'analyse d'image avait déjà été utilisée pour relier le comportement d'organismes endogés aux processus de remaniement sédimentaire qui en résultent (Maire et al., 2007a). Les dimensions du terrier d'*U. pusilla* étant particulièrement grandes par rapport aux structures biologiques classiquement étudiées (e.g., Maire et al., 2006; Bernard et al., 2016), il était nécessaire de trouver le meilleur compromis entre la résolution des images et la superficie de la zone étudiée. Le champ de prise de vue devait en effet nécessairement comprendre la totalité du terrier ainsi que les monticules de sédiment formés à proximité de ses ouvertures. A l'instar du protocole développé par Maire et al. (2007c) pour étudier l'activité de l'annélide polychète dépositivore tentaculaire *Eupolyornia nebulosa*, la solution adoptée a consisté à juxtaposer puis à fusionner les images de deux zones adjacentes prises à un intervalle de temps très court.

L'analyse des images de 30 aquariums, chacun suivis pendant 30 jours, a permis de caractériser les différents patrons de remaniement sédimentaire et de les quantifier. Trois patrons ont pu être identifiés : un premier à la surface du sédiment *via* l'expulsion hors du terrier de sédiment excavé (P1), un deuxième sous l'interface eau-sédiment *via* l'introduction dans le terrier et le transport vers le bas de particules sédimentaire issues de la surface (P2), et enfin, un troisième à l'intérieur du terrier *via* la compaction et décompaction de sédiment contre la paroi (P3). Deux méthodes ont été mises en œuvre pour quantifier ces différentes composantes du remaniement sédimentaire. Le remaniement sédimentaire associés aux patrons P1 et P3 a tout d'abord été quantifié en effectuant des mesures directement sur les images afin d'estimer les volumes de sédiment remaniés par *U. pusilla* au-dessus et en-dessous de l'interface eau-sédiment. J'ai ainsi pu estimer qu'en moyenne, le remaniement

sédimentaire qui a lieu sous la surface du sédiment correspond à 75 % du remaniement sédimentaire total. Il apparaît ainsi de manière claire que les méthodes jusqu'ici utilisées chez les thalassinidés (qui mesurent en fait seulement P1) sous-estiment fortement le remaniement sédimentaire total induit par ces organismes, pourtant déjà considérés comme les bioturbateurs les plus efficaces (Cadée, 2001).

La deuxième méthode de quantification du remaniement sédimentaire a consisté à estimer indirectement (*via* la modélisation d'un profil de concentrations de luminophores) des coefficients de remaniement sédimentaire. Les composantes verticales des patrons P1 et P2 ont été modélisées en utilisant un modèle de transport bioadvection-biodiffusif. Ce modèle a permis d'obtenir à la fois un coefficient de bioadvection (V_{bv}) correspondant à la vitesse de dépôt de sédiment expulsé hors du terrier sur la surface du sédiment (P1) et un coefficient de biodiffusion (D_{bv}) correspondant au transport vertical de luminophores de la surface vers le fond du terrier (P2). Bien qu'il soit délicat de comparer des coefficients de remaniement sédimentaire obtenus à partir de méthodologies différentes, il apparaît que les V_{bv} et D_{bv} mesurés lors de mon travail se situent parmi les plus élevés jamais enregistrés pour des invertébrés benthiques. Ces résultats suggèrent qu'*U. pusilla* est une espèce qui remanie le sédiment de manière particulièrement intense. Le troisième patron (P3), qui correspond à un transport perpendiculaire par rapport à la paroi du terrier, a quant à lui une résultante principalement horizontale du fait de la morphologie générale du terrier en forme de « U ». Ce patron a été modélisé en utilisant un modèle de transport biodiffusif simple permettant d'obtenir un coefficient de biodiffusion (D_{bw}). Il apparaît que le D_{bw} est approximativement 100 fois inférieur au D_{bv} . En d'autres termes, le remaniement sédimentaire vertical est largement supérieur à celui intervenant horizontalement. Ce résultat peut paraître surprenant au premier abord mais il est cohérent avec la différence de dimension entre l'épaisseur de la couche remaniée le long de la paroi du terrier (qui est typiquement de l'ordre du demi-centimètre) et la profondeur du terrier (qui elle est d'une vingtaine ou trentaine de centimètre). Quels que soit la méthode utilisée, les volumes estimés et les coefficients de remaniement sédimentaire obtenus étaient plus importants en été, intermédiaires au printemps et plus faibles en hiver. Des expériences identiques ont été effectuées sur des individus parasités et ont montré des taux de remaniement sédimentaire de 4,5 à 5,5 fois inférieurs par rapport aux individus sains.

Afin d'établir un lien explicite entre le comportement d'*U. pusilla* et le remaniement sédimentaire induit, des expériences d'études comportementales ont été effectuées

simultanément avec celles consacrées à l'étude du remaniement sédimentaire. L'utilisation d'un modèle de régression multiple m'a ainsi permis de mettre en évidence une corrélation positive entre la proportion de temps allouée au comportement de fouissage et le volume total de sédiment remanié. Ce résultat suggère que chez *U. pusilla*, le remaniement sédimentaire résulte principalement du comportement de fouissage.

2.2.2 Perspectives

La principale perspective découlant de ce travail consiste à étudier le remaniement sédimentaire d'*U. pusilla* à partir d'expériences conduites *in situ*. Ceci a déjà été effectué en utilisant des enceintes expérimentales positionnées dans le sédiment (e.g., Bernard et al., 2014) ou bien un profileur sédimentaire (SPI, e.g., Solan et al., 2004b). Cependant ces méthodologies devraient là encore être adaptées aux dimensions du terrier d'*U. pusilla*.

En attendant, il serait intéressant d'étudier le remaniement sédimentaire d'*U. pusilla* en trois dimensions. En effet, l'utilisation d'aquariums plats limite l'évolution de l'organisme dans un espace à deux dimensions alors qu'en milieu naturel, *U. pusilla* évolue dans un espace à trois dimensions. De ce fait, il est probable que les coefficients de remaniement sédimentaire obtenus par modélisation et plus particulièrement ceux concernant les composantes verticales (*i.e.*, P1 et P2) soient surestimés. Afin d'obtenir des résultats le plus proche possible de la réalité, l'organisme étudié devrait pouvoir évoluer dans un espace en trois dimensions. Ce type d'étude est envisageable en utilisant des méthodes de tomographie assistée par ordinateur (CAT-scan) comme réalisé par Rosenberg et al. (2008). Cela suppose toutefois de pouvoir adapter cette technique aux dimensions du terrier d'*U. pusilla*, aussi bien au niveau de l'échantillonnage (*i.e.*, disposer d'une enceinte suffisamment grande pour prélever le terrier entier mais aussi d'avoir les moyens d'extraire la grande quantité de sédiment entourant le terrier) qu'au niveau de la mesure (*i.e.*, disposer d'un appareil permettant de scanner la totalité de l'échantillon). Cela pose également la question du type de traceur à utiliser afin qu'il puisse être différencier des particules les plus denses tels que les débris coquillés.

D'autre part, dans cette étude le remaniement sédimentaire d'*U. pusilla* a été étudiée après la construction d'un terrier complet (*i.e.*, avec deux ouvertures à la surface du sédiment). Il serait maintenant intéressant d'étudier le remaniement sédimentaire lors de la construction du terrier. Il est vrai que ce processus est certainement relativement court de par la nature permanente ou semi-permanente des terriers de thalassinidés, cependant, il n'est pas

irréaliste que ces terriers présents en zones intertidales ou peu profonde puissent périodiquement s’effondrer suite à une perturbation environnementale (e.g., fort courant, tentative de prédation) ce qui nécessite sa reconstruction immédiate.

Les résultats obtenus lors de ce travail, et particulièrement ceux correspondant au volume de sédiment expulsé hors du terrier soulèvent la question du devenir de ce sédiment. En effet, il est extrêmement rare d’observer des monticules de sédiment associés aux terriers d’*U. pusilla* à marée basse dans le bassin d’Arcachon. Cette observation suggère que la force des courants de marée y est suffisante pour remettre en suspension la totalité du sédiment expulsé hors du terrier. Une perspective intéressante de mon travail consisterait par conséquent à étudier l’influence d’*U. pusilla* sur l’érodabilité du sédiment et son rôle dans la remise en suspension de sédiment à l’échelle de la lagune. Dans ce but, une collaboration avec le Dr. Francis Orvain a été initiée. Une expérience d’érodabilité en canal a été effectuée durant l’été 2016 et les premiers résultats devraient être rapidement disponibles.

2.3 La bioirrigation d’*Upogebia pusilla*.

2.3.1 Principaux résultats acquis

A ma connaissance, cette étude est la première à mesurer l’intensité de la bioirrigation au sein d’un herbier de phanérogames marines. Elle est également la première à mesurer *ex-situ* des taux d’irrigation du sédiment (i.e., transport d’eau interstitielle et solutés dissous) en présence d’un thalassinidé. Pour ce dernier point, elle se démarque donc des études antérieures qui se sont essentiellement concentrées à mesurer des taux de ventilations (i.e., volume d’eau surnageante transporté par l’organisme dans son terrier) (Dworschak, 1981; Koike et Mukai, 1983; Astall et al., 1997). Afin de quantifier la bioirrigation du sédiment, j’ai mesuré la vitesse de dissipation d’un traceur soluble fluorescent (l’uranine) dans l’eau surnageante d’une enceinte expérimentale. Cette méthode a l’avantage d’être non destructrice et non invasive. Elle permet de ce fait d’accéder à une vision dynamique du processus de bioirrigation. Cette approche m’a en outre permis de détecter deux phases dans la dynamique de décroissance du traceur dans l’eau surnageante. Une première décroissance très rapide, d’une durée d’environ 30 minutes, suivie d’une deuxième décroissance plus lente durant le reste de l’expérience. La première phase de décroissance a été attribuée principalement au mélange entre l’eau surnageante et celle du terrier. Comme ce mélange ne correspond pas à proprement parler à de la bioirrigation, la période d’environ 30 minutes correspondante n’a

pas été prise en compte dans la mesure du taux de bioirrigation. Ce taux a ensuite été estimé en ajustant un modèle aux données de concentration du traceur.

Au total, 48 incubations de 72 h chacune ont permis d'évaluer l'influence d'*Upogebia pusilla* sur la bioirrigation du sédiment. Les résultats obtenus montrent que le taux de bioirrigation des sédiments végétalisés du bassin d'Arcachon est 2,9 à 5 fois plus élevé en présence d'*U. pusilla* selon la saison. La variation saisonnière qui semble principalement liée à la température est significative. L'infestation par *Gyge branchialis* affecte aussi significativement son taux de bioirrigation qui est en moyenne 2,2 fois moins important en hiver et 2,9 fois moins important en été pour les individus infectés que pour les individus sains.

Il n'a pas été possible d'établir un lien explicite entre le comportement d'*U. pusilla* et sa bioirrigation. La taille des sondes à fluorescence utilisées pour quantifier la bioirrigation ne permettait pas en effet de combiner leur utilisation à celle des aquariums plats. Par conséquent, seul un lien qualitatif a pu être mis en évidence. Pour ce faire, j'ai utilisé une optode à oxygène beaucoup plus fine qui pouvait être introduite dans un aquarium plat ce qui m'a permis d'enregistrer simultanément le comportement d'*U. pusilla* et le niveau de saturation en oxygène dans l'eau surnageante. Les courbes décrivant les variations temporelles des concentrations en oxygène au cours du temps présentent une forme typique en escalier avec l'alternance de périodes de faible et de forte consommation d'oxygène. La synchronisation des données comportementales à celles des teneurs en oxygène montre que les fortes diminutions de la concentration en oxygène dissous sont systématiquement et uniquement associées à un événement de ventilation. Cette observation confirme que chez *U. pusilla* le processus de bioirrigation est principalement lié au comportement de ventilation même si une activité de fouissage intense qui conduit à l'accumulation de produits réduits dans le terrier stimule le déclenchement d'une période de ventilation et donc indirectement un épisode de bioirrigation lui-même ayant une incidence forte sur la dynamique biogéochimique sédimentaire (cf. paragraphe 3 L'influence d'*Upogebia pusilla* sur la dynamique biogéochimique du sédiment).

2.3.2 Perspectives

Il est important de noter que toutes les mesures de bioirrigation réalisées au cours de mon travail l'ont été avec un type de sédiment unique, celui de la station référence (« La Nègue »). Or dans le bassin d'Arcachon par exemple, il s'avère qu'*U. pusilla* est capable de

coloniser un large spectre de faciès sédimentaires intertidaux, depuis des vases assez fines en fond de bassin jusqu'à des sédiments vaseux très ensablés à proximité des passes. La condition *sine qua non* pour la présence des crevettes étant que la matrice sédimentaire soit suffisamment stable pour permettre l'élaboration d'un terrier profond sur du long terme. De manière générale, mais particulièrement dans les vases les plus fines, cette stabilité est conditionnée dans le bassin d'Arcachon par la présence des phanérogames et le développement d'un système rhizomial et racinaire dense. L'intensité de la bioirrigation étant fortement dépendante des caractéristiques du sédiment (*i.e.*, granulométrie, porosité, tortuosité et surtout perméabilité), il serait intéressant d'effectuer des mesures similaires de transport des solutés dissous le long d'un spectre granulométrique (et donc de porosité et de perméabilité) le plus large possible afin de mieux comprendre la relation entre caractéristiques du sédiment, atténuation des pressions hydrauliques générées par l'activité de ventilation et flux à travers la paroi du terrier et à l'interface sédiment-eau. Ce travail paraît indispensable pour une extrapolation à l'échelle de l'écosystème des mesures d'activités et de bioturbation (*e.g.*, évaluation du potentiel bioirrigateur) d'un organisme modèle réalisées en laboratoire.

La méthode utilisée dans mon travail de thèse a l'avantage de donner une idée précise de la vitesse à laquelle les échanges entre l'eau surnageante et l'eau interstitielle se font. Cependant elle ne permet pas de savoir jusqu'à quelle profondeur et sur quelle distance ont lieu ces échanges. Ce point est particulièrement important puisqu'en plus d'apporter de l'oxygène dans des zones qui en étaient dépourvues, la bioirrigation provoque également le transport de composés dissous réduits (*e.g.*, NH_4^+ , dSi) vers la surface du sédiment (Chennu et al., 2015; Rao et al., 2014; Wethey et al., 2008). Ces nutriments deviennent ensuite disponibles pour des organismes photosynthétiques à la surface du sédiment augmentant ainsi leur productivité (Chennu et al., 2015). Par conséquent, la bioirrigation peut indirectement induire une augmentation des ressources organiques à la surface du sédiment. Il serait par conséquent très intéressant d'étudier sur quelles distances s'exerce l'influence hydraulique d'*U. pusilla*. En utilisant une optode planaire et l'oxygène comme traceur, Volkenborn et al. (2012) ont observé qu'en fonction de la perméabilité du sédiment l'oxygène pouvait pénétrer de quelques millimètres à plusieurs centimètres dans le sédiment autour du terrier de *Neotrypaea californiensis*. L'utilisation de capteur de pression a montré que l'activité hydraulique d'*Arenicola marina* était détectable jusqu'à 50 cm de son point d'origine (Wethey et al., 2008). Delefosse et al. (2015) ont développé une méthode permettant d'observer en trois dimensions l'influence d'organismes sur l'irrigation du sédiment. Cette

méthode utilise un système hybride d'imagerie médicale (PET/CT) permettant d'obtenir une description à la fois qualitative et quantitative de la bioirrigation. L'utilisation d'une de ces méthodes permettrait d'évaluer la zone d'influence (hydraulique) d'*U. pusilla*.

Comme pour le comportement et le remaniement sédimentaire, l'objectif final est de pouvoir mesurer la bioirrigation induite par *U. pusilla* en milieu naturel. Ceci pourrait être envisagé à l'aide de chambres benthiques conçu spécifiquement pour prendre en compte les dimensions d'un terrier. Une telle approche a déjà été utilisée pour étudier *in-situ* l'influence de *Trypaea australiensis* sur l'irrigation du sédiment (Webb et Eyre, 2004). Cependant leur protocole expérimental, combinant l'utilisation d'une cloche benthique et le suivi de la concentration d'un traceur dissous injecté dans cette enceinte expérimentale, ne permet pas d'identifier spécifiquement l'influence du thalassinidé sur l'irrigation du sédiment par rapport à celle d'autres facteurs environnementaux (e.g., courant de marée). L'utilisation de capteurs de pression pourrait également donner des informations clés sur l'influence d'*U. pusilla* sur les transports advectifs d'eau interstitielle. Cela consisterait à mesurer les variations de pression en différents points du sédiment autour des terriers afin de créer une carte 3D isobarique et d'évaluer la progression de la pression induite par la ventilation de l'organisme dans son terrier. Le transport advectif d'eau interstitielle serait ensuite déterminé à partir d'un modèle issu de la régression entre les mesures de pressions, leurs distances par rapport à la structure biogénique d'intérêt (zone de ventilation privilégiée) et caractéristiques physiques du sédiment.

3 Influence d'*Upogebia pusilla* sur la dynamique biogéochimique du sédiment

3.1 Objectifs et principaux résultats

Le premier objectif spécifique de la composante de mon travail portant sur la dynamique biogéochimique du sédiment consistait tout d'abord à quantifier l'influence d'*Upogebia pusilla* sur les échanges d'oxygène, la reminéralisation de la matière organique et les flux de nutriments au travers de l'interface eau-sédiment. Il était ensuite important d'évaluer la variabilité saisonnière de ces interactions ainsi que l'influence du parasitisme sur ces différents processus et flux biogéochimiques. Un dernier objectif consistait à étudier plus finement la dynamique de l'oxygène au sein du terrier d'*U. pusilla* et de la relier explicitement aux différents comportements de cette espèce. Pour ce faire, j'ai utilisé des

aquariums plats et positionné une micro-optode à l'intérieur du terrier. La principale difficulté a consisté à positionner le capteur sans endommager la structure du terrier ni entraver les déplacements d'*U. pusilla*. J'ai pour cela utilisé un micromanipulateur qui m'a permis de positionner délicatement la partie sensible du capteur à l'intérieur du terrier et à exactement 2 mm de sa paroi. Une fois le capteur installé, une caméra a été placée face à l'aquarium pour évaluer de manière synchrone la dynamique temporelle du niveau de saturation en oxygène dans le terrier et le comportement d'*U. pusilla*.

Avec un total de 48 enceintes expérimentales chacune incubée 5 fois, mes résultats montrent de manière générale que les flux d'oxygène et de nutriments sont tous stimulés par l'activité de bioturbation d'*U. pusilla*. La consommation totale d'oxygène par le sédiment (TOU) est de 2,4 à 2,7 fois plus importante en présence qu'en l'absence d'*U. pusilla*. En hiver la respiration par *U. pusilla* représente la totalité de cette augmentation contre seulement 43 % au printemps et 36 % en été. Ce résultat met en évidence l'importance de l'influence de l'activité de bioturbation d'*U. pusilla* sur la dégradation de la matière organique effectuée par les microorganismes au printemps et en été. De la même manière, le relargage d'ammonium par le sédiment est de 2,1 à 3 fois plus important en présence qu'en l'absence d'*U. pusilla*. Ce résultat indique (1) une stimulation des processus d'ammonification, et (2) une augmentation de la libération de l'ammonium piégé dans l'eau interstitielle *via* les activités de ventilation et de fouissage du crustacé. L'impact le plus important de la bioturbation d'*U. pusilla* porte certainement sur le flux de nitrate. Lorsqu'*U. pusilla* est absente, les processus de production et de consommation des nitrates sont d'égale intensité résultant en un flux net quasi-nul. En revanche, les processus de consommation de nitrate (*e.g.*, dénitrification ou potentiellement DNRA) par les microorganismes sont fortement stimulés par la présence des crevettes de vase comme l'indique la consommation de nitrate jusqu'à 13,8 fois plus importante en présence qu'en l'absence d'*U. pusilla*. Enfin, le relargage de silice par le sédiment est également largement stimulé (multiplié par un facteur 2.9 à 5) par la bioturbation d'*U. pusilla*.

La totalité des flux étudiés présentent des variations saisonnières significatives. En présence d'*U. pusilla*, le TOU est par exemple 3,8 fois plus important en été qu'en hiver. Ce même facteur multiplicatif est de 1,7 pour le flux d'ammonium, de 12,5 pour le flux de nitrates, et de 8,2 pour les flux de silice. La présence du parasite *Gyge branchialis* affecte également l'influence d'*U. pusilla* sur les échanges de matière et d'énergie à l'interface sédiment-eau. En effet, lorsque parasitée par un bopyre, la crevette de vase ne stimule ni le flux de nitrate ni celui de silice qui sont similaires à ceux observés dans un sédiment où elle

est absente. Seuls le TOU et le relargage d'ammonium sont alors significativement impacté (augmentation par un facteur 1,9 et 2,2, respectivement). Cependant, ces stimulations sont principalement directes (*i.e. via* sa propre respiration et excrétion) et n'influence donc probablement pas l'activité microbienne contrairement aux individus sains.

A partir de l'analyse couplée des enregistrements vidéo et de micro-optode (360 heures d'enregistrement au total), l'impact de chaque comportement sur la dynamique de l'oxygène dissous au sein du terrier a pu être étudié. Ainsi, le comportement de fouissage et dans une moindre mesure celui de locomotion induisent une décroissance de la saturation en oxygène au sein des galeries du terrier. Cette décroissance est due à la consommation d'oxygène par les microorganismes et, lors des phases de fouissage, à l'oxydation des composés réduits qui étaient stockés dans le sédiment. Seul le comportement de ventilation conduit rapidement à une augmentation de la saturation en oxygène de l'eau du terrier. L'alternance de ces différents comportements conduit à une forte variabilité spatiale et temporelle des teneurs en oxygène dissous au sein (1) de l'eau du terrier et (2) de l'eau interstitielle située à proximité de ce dernier (*via* les processus de bioirrigation). Mes résultats ont montré qu'une valeur seuil comprise entre 12 et 25 % de saturation en oxygène dans l'eau du terrier au niveau de l'organisme déclenche un comportement de ventilation.

4.3 Perspectives

Les résultats obtenus lors de ce travail, et particulièrement ceux concernant le flux de nitrate, s'avèrent différents de ceux obtenus lors d'études précédentes conduites sur d'autres espèces de thalassinidés. Ces dernières ont en effet toutes rapporté une production de nitrate par le sédiment (Papasprou et al., 2004; Webb et Eyre, 2004; D'Andrea et DeWitt, 2009). Il est classiquement reconnu que l'activité des thalassinidés stimule le processus de dénitrification via l'augmentation des apports de NO_3^- issu de la nitrification (*i.e.*, stimulation du couplage nitrification-dénitrification) (Howe et al., 2004; Jordan et al., 2009; Laverock et al., 2011). La stimulation de ce processus ne permet cependant pas d'expliquer la consommation du nitrate observée lors de mon travail. En effet, la consommation de nitrate par le sédiment dans le bassin d'Arcachon indique que le processus de nitrification ne suffit pas pour soutenir à lui seul les processus d'élimination d'azote (*e.g.*, dénitrification et anammox). Cette production insuffisante de nitrate peut être expliquée par la présence de l'herbier qui, par le développement d'un réseau de racines et de rhizomes dense, stabilise le sédiment et réduit sa perméabilité. En limitant de ce fait la circulation de l'eau interstitielle,

les phanérogames limitent l'épaisseur de la couche oxique du sédiment pouvant supporter le processus de nitrification. Il serait, par conséquent, intéressant d'étudier l'organisation, la diversité et l'activité des communautés microbiennes associés aux sédiments colonisés à la fois par l'herbier de zostère naine et par *U. pusilla*. Mes résultats laissent en effet envisager une organisation et/ou un fonctionnement des communautés microbiennes particulier dans ce type d'environnement. Il serait également intéressant de déterminer quels processus d'élimination d'azote ont lieu à proximité des terriers d'*U. pusilla* via, par exemple, l'utilisation de techniques d'« isotope pairing » (e.g., Howe et al., 2004; Jordan et al., 2009).

D'autres part, l'ensemble de mes expériences d'incubations ont été conduites avec du sédiment naturel colonisé par un herbier de zostère naine mais à l'obscurité. Il me paraîtrait maintenant intéressant d'effectuer des incubations en conditions de lumière contrôlées pour évaluer l'influence d'*U. pusilla* sur les flux benthiques lorsque l'herbier est photosynthétiquement actif et à différent niveaux d'activité.

De manière générale, il est important de noter que ces résultats portant sur l'influence d'*Upogebia pusilla* sur la bioirrigation du sédiment et les flux d'oxygène et de nutriments à l'interface benthique correspondent à une densité unique de 144 ind. m⁻². Cette densité est du même ordre de grandeur que celle évaluée pour des populations d'*U. pusilla* en Adriatique (Dworschak, 1987b) et d'*U. pugettensis* dans la baie d'Oregon (D'Andrea et DeWitt, 2009). Elle est par contre supérieure à la densité maximale observée dans le bassin d'Arcachon (37 ind. m⁻²). Il serait en conséquence intéressant d'effectuer des expériences semblables à celles présentées dans ce travail mais en utilisant des enceintes expérimentales plus grandes qui permettraient de tester l'influence de la densité des crustacés sur les flux benthiques.

De la même manière, ces expériences ont été réalisées en utilisant, indépendamment de leur sexe, des organismes adultes d'une longueur totale comprise entre 40 et 50 mm. Cette gamme de taille d'individus adultes est la plus fréquente dans le bassin d'Arcachon puisqu'elle représente plus de 70 % des individus échantillonnés durant ma thèse. Il serait toutefois judicieux (dans un but d'extrapolation à l'échelle des populations) d'évaluer l'importance de la taille mais aussi du sexe d'*U. pusilla* dans les processus de bioturbation ainsi que dans l'intensité des échanges de solutés entre eau interstitielle et surnageante. J'ai effectué une expérience de ce type en fin de thèse et les résultats seront prochainement analysés.

In fine, et comme pour l'ensemble des expériences effectuées durant ma thèse, il serait intéressant d'aborder le transfert vers l'*in-situ*. En raison des dimensions d'un terrier de thalassinidé et de la présence de multiples ouvertures, les techniques classiques de mesure des flux biogéochimiques totaux consistant à positionner une chambre benthique à la surface du sédiment sont difficilement utilisables. En pratique, du fait des dimensions des terriers des thalassinidés, il est en effet difficile de s'assurer de la bonne étanchéité du système. Les techniques d'Eddy corrélation (Berg et al., 2003) permettraient de mesurer les flux d'oxygène à l'interface eau sédiment à la fois *in-situ* et à une échelle spatiale suffisamment grande pour tenir compte de l'impact des populations d'*U. pusilla*. Cet instrument a l'avantage d'être non invasif. Le laboratoire EPOC s'est doté d'un tel instrument, il est donc envisageable de le déployer pour effectuer ce type de mesures.

5 Rôle indirect du parasitisme dans le fonctionnement des écosystèmes côtiers *via* son influence sur une espèce ingénieure

L'ensemble des résultats portant sur l'effet du parasitisme par *Gyge branchialis* montre un impact significatif de ce parasite sur son hôte *Upogebia pusilla*. En effet, l'infestation par ce parasite provoque une modification du comportement du crustacé et affecte négativement l'intensité de son activité de bioturbation. Les répercussions de cette baisse d'activité sont considérables puisque les échanges d'oxygène et de nutriments au travers de l'interface eau-sédiment diminuent alors drastiquement. L'évaluation de l'influence de ce parasite sur le fonctionnement global de l'écosystème a nécessité en amont une étude permettant d'acquérir une vue d'ensemble de l'état des populations d'*U. pusilla* dans le bassin d'Arcachon et du niveau de prévalence de *G. branchialis*. Cette étape s'avère indispensable pour passer du niveau de l'organisme à celui de l'écosystème. Il a ainsi été montré qu'à l'échelle du bassin d'Arcachon, 21 % des individus d'*U. pusilla* étaient infestés par le bopyre. Sur la base de cette prévalence moyenne, j'ai pu estimer que la diminution des taux de remaniement sédimentaire et de bioirrigation de la population d'*U. pusilla* en lien avec le parasitisme pouvait atteindre 16,4 et 13,8 %, respectivement. La diminution de la consommation totale d'oxygène par le sédiment (proxy du taux de reminéralisation) a quant à elle été évaluée à 6,6 %. La capacité de reproduction d'*U. pusilla* est elle aussi considérablement affectée par ce parasite. 89 % des mâles infestés étaient en effet féminisés et aucune femelle infestée n'était ovigère. L'ensemble de mes résultats met ainsi en évidence le fait que *G. branchialis* conditionne fortement le niveau d'influence d'*U. pusilla* sur le

fonctionnement des écosystèmes benthiques et cela de deux manières différentes. Premièrement, le coût énergétique résultant de la nutrition du parasite au détriment de son hôte et la limitation de la capacité de reproduction de ce dernier résultant d'un effet de castration amène *G. branchialis* à contrôler indirectement à la fois la taille et la dynamique de la population de son hôte. Deuxièmement, en altérant le comportement de son hôte, *G. branchialis* limite l'intensité de son activité de bioturbation et par conséquent l'influence de cette dernière sur la dynamique biogéochimique sédimentaire et le couplage pélagos-benthos. Le parasitisme des espèces ingénieuses apparaît donc comme un facteur clé du fonctionnement des écosystèmes benthiques.

Dans le prolongement direct de mon travail, il serait important de mieux comprendre comment, d'un point de vue physiologique, la présence du bopyre conduit à la stérilisation des femelles et, même si cela a été étudié chez d'autres espèces, à la castration et féminisation des mâles. Afin de clarifier l'effet du bopyre sur la capacité des individus infestés à se reproduire, il s'agirait essentiellement d'étudier l'intégrité des gonades des organismes mâles et femelles infestés par ce parasite. D'autre part, il a été rapporté plusieurs types de parasite chez *Upogebia pusilla* (Dworschak, 1988), dont la plupart sont des endoparasites. Contrairement à *Gyge branchialis* qui est un ectoparasite bien visible, les endoparasites (tels que les métacercaires de trématodes) sont difficilement décelables sans effectuer d'étude précise qui consiste bien souvent à disséquer (et donc à tuer) l'organisme. Il serait par conséquent très intéressant de déterminer si d'autres organismes (bivalves, annélides, plathelminthes, ...) parasitent effectivement *U. pusilla* dans le bassin d'Arcachon et le cas échéant d'évaluer leurs influences individuelles ou combinées sur le comportement d'*U. pusilla*.

De manière plus générale, mes résultats mettent en évidence l'importance des effets « cachés » du parasitisme *via* la réduction du niveau d'activité d'une espèce ingénieuse qui lui sert d'hôte sur le fonctionnement des écosystèmes. Compte tenu de l'ubiquité à la fois des espèces ingénieuses et des parasites dans les environnements côtiers, il semble particulièrement important de multiplier ce genre d'étude sur les conséquences fonctionnelles des relations espèces ingénieuses-parasites.

6 Conclusion générale : rôle d'*Upogebia pusilla* dans le fonctionnement écologique et biogéochimique des sédiments végétalisés du bassin d'Arcachon

L'ensemble de mes résultats montre clairement qu'*Upogebia pusilla* est une espèce bioturbatrice très efficace qui influence fortement la dynamique biogéochimique à l'interface eau-sédiment. Il convient cependant de replacer ces résultats dans le contexte général de ma thèse qui consistait à évaluer le rôle d'*U. pusilla* dans le fonctionnement écologique et biogéochimique des écosystèmes végétalisés du bassin d'Arcachon. Lors d'une étude visant à étudier le remaniement sédimentaire des 20 premiers centimètres (*i.e.* sans prendre en compte *U. pusilla*) d'un sédiment colonisé par *Zostera noltei*, Bernard et al. (2014) ont estimé un coefficient de biodiffusion (D_b) compris entre 0,4 et 18,1 $\text{cm}^2 \text{an}^{-1}$. Bien qu'ils ne soient pas directement comparables du fait des différents modèles utilisés et des différentes méthodologies employées, les importantes différences observées entre ces coefficients de biodiffusion et ceux estimés pour *U. pusilla* (qui peuvent atteindre 1158 $\text{cm}^2 \text{an}^{-1}$) suggèrent que cette crevette de vase est l'espèce dominante de ces habitats en terme de remaniement sédimentaire. D'autre part, toujours sans considérer *U. pusilla*, Delgard et al. (2016) avaient considéré que la macrofaune benthique n'influçait que faiblement les variations saisonnières de consommation d'oxygène par le sédiment. Mes résultats suggèrent au contraire que : (1) la présence d'*U. pusilla* stimule fortement la consommation d'oxygène par le sédiment et, (2) son influence sur les TOUs présente une forte dynamique saisonnière. Compte tenu du lien positif entre l'herbier de zostère naine et *U. pusilla* (Annexe I), la régression de l'herbier a donc incontestablement des répercussions bien plus importantes et bien plus complexes que celles estimées jusqu'à présent *via* la disparition de l'espèce ingénieure *U. pusilla* qui lui est étroitement associée.

Il est cependant important de garder à l'esprit que les résultats présentés dans ce travail ont été obtenus expérimentalement et ne reflète donc certainement que de manière imparfaite les processus ayant réellement lieu en milieu naturel. De nombreuses perspectives ont été avancées dans cette synthèse et sont présentées dans un schéma bilan (**Figure S.1**). La plupart consistent en des extensions (ajout de facteurs environnementaux supplémentaires) ou des améliorations (optimisation ou changement des méthodes utilisées) des expérimentations *ex-situ* permettant à la fois de mieux appréhender l'activité d'*U. pusilla* mais aussi d'évaluer au mieux l'influence des différents facteurs environnementaux sur cette activité. L'ensemble

de ses perspectives « intermédiaires » (**Figure S.1**) permettra *in fine* de passer à des expérimentations *in-situ* qui permettront de déterminer avec précision l'importance du rôle joué par *U. pusilla* dans le fonctionnement écologique et biogéochimique des écosystèmes végétalisés du bassin d'Arcachon.

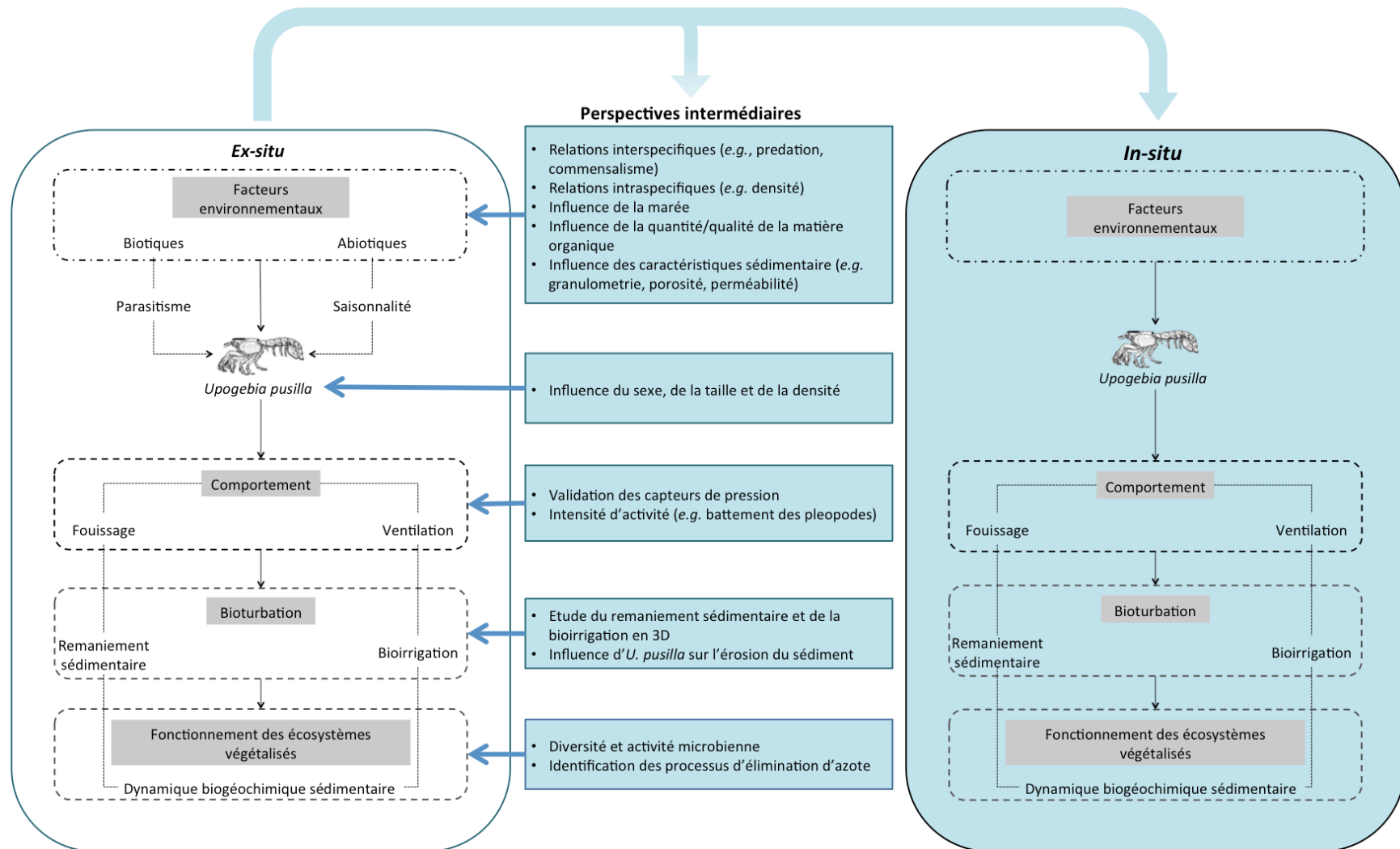


Figure S.1 : Représentation schématique de l'articulation des principaux résultats obtenus durant mes travaux de thèse (bulle à fond blanc) et des principales perspectives qui en découlent (bulles à fond bleu).

Bibliographie générale

Références bibliographiques

A

- Abed-Navandi, D., Koller, H., Dworschak, P.C., 2005. Nutritional ecology of thalassinidean shrimps constructing burrows with debris chambers: The distribution and use of macronutrients and micronutrients. *Mar. Biol. Res.* 1, 202–215. doi:10.1080/17451000510019123
- Aller, R.C., 2014. Sedimentary Diagenesis, Depositional Environments, and Benthic Fluxes, in: Holland, H.D., Turekian, K.K. (Eds.), *Treatise on Geochemistry*. Elsevier Ltd., Oxford, pp. 293–334. doi:10.1016/B978-0-08-095975-7.00611-2
- Aller, R.C., 1988. Benthic Fauna and Biogeochemical Processes in Marine Sediments: The Role of Burrow Structures. Blackburn, T.H., Sørensen, J.(Eds) *Nitrogen Cycl. Costal Mar. Environ.* Wiley Sons, Chichester 301–338.
- Aller, R.C., 1982. The Effects of Macrobenthos on Chemical Properties of Marine Sediment and Overlying Water. Springer US, pp. 53–102. doi:10.1007/978-1-4757-1317-6_2
- Aller, R.C., 1980. Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironment. *Geochim. Cosmochim. Acta* 44, 1955–1965. doi:10.1016/0016-7037(80)90195-7
- Aller, R.C., Dodge, R.E., 1974. Animal-Sediment Relations in a Tropical Lagoon: Discovery Bay, Jamaica. *J. Mar. Res.* 32, 209–232.
- Aller, R.C., Yingst, J.Y., Ullman, W.J., 1983. Comparative biogeochemistry of water in intertidal *Onuphis* (Polychaeta) and *Upogebia* (Crustacea) burrows: temporal patterns and causes. *J. Mar. Res.* 41, 571–604. doi:10.1357/002224083788519722
- Amaro, T.P.F., Duineveld, G.C.A., Bergman, M.J.N., Witbaard, R., Scheffer, M., 2007. The consequences of changes in abundance of *Callianassa subterranea* and *Amphiura filiformis* on sediment erosion at the Frisian Front (south-eastern North Sea). *Hydrobiologia* 589, 273–285. doi:10.1007/s10750-007-0750-2
- Aminot, A., Kirkwood, D.S., Kérouel, R., 1997. Determination of ammonia in seawater by the

- indophenol-blue method: Evaluation of the ICES NUTS I/C 5 questionnaire. *Mar. Chem.* 56, 59–75. doi:10.1016/S0304-4203(96)00080-1
- Anderson, G., 1977. The effects of parasitism on energy flow through laboratory shrimp populations. *Mar. Biol.* 42, 239–251. doi:10.1007/BF00397748
- Anderson, G., 1975. Metabolic response of the caridean shrimp *Palaemonetes pugio* to infection by the adult epibranchial isopod parasite *Probopyrus pandalicola*. *Comp. Biochem. Physiol. -- Part A Physiol.* 52, 201–207. doi:10.1016/S0300-9629(75)80153-8
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. 214.
- Anderson, S.J., Atkinson, R.J.A., Taylor, A.C., 1991. Behavioural and respiratory adaptations of the mud-burrowing shrimp *Calocaris Macandreae* Bell (Thalassinidea: Crustacea) to the burrow environment. *Ophelia* 34, 143–156. doi:10.1080/00785326.1991.10429702
- Asmus, R.M., Sprung, M., Asmus, H., 2000. Nutrient fluxes in intertidal communities of a South European lagoon (Ria Formosa) – similarities and differences with a northern Wadden Sea bay (Sylt-Romo Bay). *Hydrobiologia* 436, 217–235.
- Astall, C.M., Taylor, A.C., Atkinson, R.J.A., 1997. Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of Upogebiid mud-shrimp (Crustacea: Thalassinidea). *Estuar. Coast. Shelf Sci.* 155–168. doi:10.1006/ecss.1996.0207
- Astall, C.M., Taylor, A.C., Atkinson, R.J.A., 1996. Notes on Some Branchial Isopods Parasitic on Upogebiid Mud-Shrimps (Decapoda: Thalassinidea). *J. Mar. Biol. Assoc. UK* 76, 821–824. doi:10.1017/S0025315400031489
- Atkinson, R.J.A.J.A., Taylor, A.C.A., 2005. Aspects of the physiology, biology and ecology of thalassinidean shrimps in relation to their burrow environment, in: *Oceanography and Marine Biology, Oceanography and Marine Biology - An Annual Review*. CRC Press, pp. 211–278. doi:doi:10.1201/9781420037449.ch5
- Auby, I., Bost, C.A., Budzinski, H., Belles, A., Couzi, L., Steinmetz, J., 2011. Régression des herbiers de zostères dans le Bassin d’Arcachon : état des lieux et recherche des causes Régression des herbiers de zostères dans le Bassin d’Arcachon : état des lieux et recherche des causes. *IFREMER* 155 <http://archimer.ifremer.fr/doc/00054/16507/>.
-

Auby, I., Labourg, P.-J., 1996. Seasonal dynamics of *Zostera noltii* hornem. In the bay of Arcachon (France). J. Sea Res. 35, 269–277. doi:10.1016/S1385-1101(96)90754-6

Auby, I., Rigouin, L., Trut, G., Oger-Jeanneret, H., Ganthy, F., Trut, F., Gouriou, L., Bujan, S., Devaux, L., Gouillieux, B., Dalloyau, S., Feigné, C., 2016. Suivi stationnel (2006-2015) des herbiers de zostères (*Zostera noltei* et *Zostera marina*) et calcul de l'indicateur « Angiospermes » (2015) dans la masse d'eau côtière FRFC06 – Arcachon amont - - Bassin Hydrographique Adour-Garonne. IFREMER 50p.

B

Barnes, R.S.K., Barnes, M.K.S., 2012. Shore height and differentials between macrobenthic assemblages in vegetated and unvegetated areas of an intertidal sandflat. Estuar. Coast. Shelf Sci. 106, 112–120. doi:10.1016/j.ecss.2012.05.011

Bass, C.S., Weis, J.S., 1999. Behavioral changes in the grass shrimp, *Palaemonetes pugio* (Holthuis), induced by the parasitic isopod, *Probopyrus pandalicola* (Packard). J. Exp. Mar. Bio. Ecol. 241, 223–233. doi:10.1016/S0022-0981(99)00084-2

Berg, P., Røy, H., Janssen, F., Meyer, V., Jørgensen, B., Huettel, M., de Beer, D., 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. Mar. Ecol. Prog. Ser. 261, 75–83. doi:10.3354/meps261075

Berkenbusch, K., Rowden, A.A., 2000. Latitudinal variation in the reproductive biology of the burrowing ghost shrimp *Callinassa filholi* (Decapoda: Thalassinidea). Mar. Biol. 136, 497–504. doi:10.1007/s002270050709

Berkenbusch, K., Rowden, A.A., 1999. Factors influencing sediment turnover by the burrowing ghost shrimp *Callinassa filholi* (Decapoda: Thalassinidea). J. Exp. Mar. Bio. Ecol. 238, 283–292.

Bernard, G., 2013. Mesures expérimentales et modélisation du remaniement sédimentaire dans le bassin d'Arcachon. Ph.D. Thesis (226 p) Université Bordeaux 1.

Bernard, G., Delgard, M.-L., Maire, O., Ciutat, A., Lecroart, P., Deflandre, B., Duchêne, J., Grémare, A., 2014. Comparative study of sediment particle mixing in a *Zostera noltei* meadow and a bare sediment mudflat. Mar. Ecol. Prog. Ser. 514, 71–86. doi:10.3354/meps10961

- Bernard, G., Duchêne, J.-C., Romero-Ramirez, A., Lecroart, P., Maire, O., Ciutat, A., Deflandre, B., Grémare, A., 2016. Experimental Assessment of the Effects of Temperature and Food Availability on Particle Mixing by the Bivalve *Abra alba* Using New Image Analysis Techniques. PLoS One 11, e0154270. doi:10.1371/journal.pone.0154270
- Bernard, G., Grémare, A., Maire, O., Lecroart, P., Meysman, F., Ciutat, A., Deflandre, B., Duchêne, J.-C., 2012. Experimental assessment of particle mixing fingerprints in the deposit-feeding bivalve *Abra alba* (Wood). J. Mar. Res. 70, 689–718. doi:10.1357/002224012806290705
- Bernot, R.J., Lamberti, G.A., 2008. Indirect effects of a parasite on a benthic community: an experiment with trematodes, snails and periphyton. Freshw. Biol. 53, 322–329. doi:10.1111/j.1365-2427.2007.01896.x
- Bertics, V.J., Ziebis, W., 2009. Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. ISME J. 3, 1269–85. doi:10.1038/ismej.2009.62
- Bhattacharya, C.G., 1967. A simple method of resolution of a distribution into gaussian components. Biometrics 23, 115–135. doi:10.2307/2528285
- Bhaud, M., Cha, J.H., Duchêne, J.C., Nozais, C., 1995. Influence of temperature on the marine fauna: What can be expected from a climatic change. J. Therm. Biol. 20, 91–104. doi:10.1016/0306-4565(94)00031-D
- Bick, A., 1994. *Corophium volutator* (Corophiidae: Amphipoda) as an intermediate host of larval digenea - an ecological analysis in a coastal region of the southern Baltic. Ophelia 40, 27–36.
- Bidle, K.D., Azam, F., 1999. Accelerated dissolution of diatom silica by marine bacterial assemblages. Nature 397, 508–512. doi:10.1038/17351
- Bird, F.L., Boon, P.I., Nichols, P.D., 2000. Physicochemical and Microbial Properties of Burrows of the Deposit-feeding Thalassinidean Ghost Shrimp *Biffarius arenosus* (Decapoda: Callianassidae). Estuar. Coast. Shelf Sci. 51, 279–291. doi:10.1006/ecss.2000.0676
- Blanchet, H., de Montaudouin, X., Lucas, A., Chardy, P., 2004. Heterogeneity of macrozoobenthic assemblages within a *Zostera noltii* seagrass bed: diversity, abundance, biomass and structuring factors. Estuar. Coast. Shelf Sci. 61, 111–123. doi:10.1016/j.ecss.2004.04.008

- Blankson, E.R., Deb Adhikary, N.R., Klerks, P.L., 2017. The effect of lead contamination on bioturbation by *Lumbriculus variegatus* in a freshwater microcosm. *Chemosphere* 167, 19–27. doi:10.1016/j.chemosphere.2016.09.128
- Blott, S.J., Pye, K., 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surf. Process. Landforms* 26, 1237–1248. doi:10.1002/esp.261
- Bonnier, J., 1900. Contribution a l'étude des Épicarides, les Bopyridae. Detached from Travaux de la station zoologique de Wimereux, T.VIII. s.n., Paris. doi:10.5962/bhl.title.10522
- Boström, C., Bonsdorff, E., 1997. Community structure and spatial variation of benthic invertebrates associated with *Zostera marina* (L.) beds in the northern Baltic Sea. *J. Sea Res.* 37, 153–166. doi:10.1016/S1385-1101(96)00007-X
- Boström, C., Jackson, E.L., Simenstad, C.A., 2006. Seagrass landscapes and their effects on associated fauna: A review. *Estuar. Coast. Shelf Sci.* 68, 383–403. doi:10.1016/j.ecss.2006.01.026
- Boucher, J.M., 1968. Etude océanographique des chenaux du bassin d'Arcachon. Université Bordeaux 1.
- Bourdon, R., 1968. Les Bopyridae de mers europeenes. Muséum national d'histoire naturelle, Paris.
- Bracken, H.D., Toon, A., Felder, D.L., Martin, J.W., Finley, M., Rasmussen, J., Palero, F., Crandall, K.A., 2009. The decapod tree of life: Compiling the Data and Moving toward a Consensus of Decapod Evolution. *Arthropod Syst. Phylogeny* 67, 99–116.
- Braeckman, U., Provoost, P., Moens, T., 2011. Biological vs. physical mixing effects on benthic food web dynamics. *PLoS One* 6, e18078. doi:10.1371/journal.pone.0018078
- Brenchley, G.A., 1982. Mechanisms of spatial competition in marine soft-bottom communities. *J. Exp. Mar. Bio. Ecol.* 60, 17–33. doi:10.1016/0022-0981(81)90177-5
- Butler, S.N., Bird, F.L., 2008. Temporal changes in burrow structure of the thalassinidean ghost shrimps *Trypaea australiensis* and *Biffarius arenosus*. *J. Nat. Hist.* 42, 2041–2062. doi:10.1080/00222930802254656

C

- Cadée, G.C., 2001. Sediment dynamics by bioturbating organisms, in: Reise, K. (Ed.), *Ecological Comparisons of Sedimentary Shores*, Ecological Studies. Springer, Berlin, Heidelberg. doi:10.1007/978-3-642-56557-1
- Cadée, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Netherlands J. Sea Res.* 10, 440–460. doi:10.1016/0077-7579(76)90020-X
- Calizza, E., Costantini, M.L., Carlino, P., Bentivoglio, F., Orlandi, L., Rossi, L., 2013. *Posidonia oceanica* habitat loss and changes in litter-associated biodiversity organization: A stable isotope-based preliminary study. *Estuar. Coast. Shelf Sci.* 135, 137–145. doi:10.1016/j.ecss.2013.07.019
- Campos, E., de Campos, A.R., Manriquez, I., 2009. Intertidal thalassinidean shrimps (Thalassinidea, Callianassidae and Upogebiidae) of the west coast of Baja California, Mexico: annotated checklist, key for identification, and symbionts. *Crustaceana* 82, 1249–1263. doi:10.1163/001121609X12481627024454
- Chennu, A., Volkenborn, N., de Beer, D., Wetthey, D.S., Woodin, S.A., Polerecky, L., 2015. Effects of bioadvection by *Arenicola marina* on microphytobenthos in permeable sediments. *PLoS One* 10, e0134236. doi:10.1371/journal.pone.0134236
- Clarke, K.R., Warwick, R.M., 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd ed. PRIMER-E: Plymouth, UK; 2001.
- Cochran, J.K., 1985. Particle mixing rates in sediments of the eastern equatorial Pacific: Evidence from ^{210}Pb , $^{239,240}\text{Pu}$ and ^{137}Cs distributions at MANOP sites. *Geochim. Cosmochim. Acta* 49, 1195–1210. doi:10.1016/0016-7037(85)90010-9
- Coelho, V.R., Cooper, R.A., deAlmeida Rodrigues, S., 2000. Burrow morphology and behavior of the mud shrimp *Upogebia omissa* (Decapoda: Thalassinidea: Upogebiidae). *Mar. Ecol. Prog. Ser.* 200, 229–240.
- Combes, C., 2001. *Parasitism: the ecology and evolution of intimate interactions*. University of Chicago Press, Chicago.
- Contessa, L., Bird, F.L., 2004. The impact of bait-pumping on populations of the ghost shrimp

Trypaea australiensis Dana (Decapoda: Callinassidae) and the sediment environment. *J. Exp. Mar. Bio. Ecol.* 304, 75–97. doi:10.1016/j.jembe.2003.11.021

Covich, A.P., Austen, M.C., Bärlocher, F., Chauvet, E., Cardinale, B.J., Biles, C.L., Inchausti, P., Dangles, O., Solan, M., Gessner, M.O., Stutzner, B., Moss, B., 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *Bioscience* 54, 767–775. doi:10.1641/0006-3568(2004)054[0767:TROBIT]2.0.CO;2

D

D'Andrea, A.F., DeWitt, T.H., 2009. Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-dependent effects. *Limnol. Oceanogr.* 54, 1911–1932. doi:10.4319/lo.2009.54.6.1911

Dale, N.G., 1974. Bacteria in intertidal sediments: Factors related to their distribution. *Limnol. Oceanogr.* 19, 509–518.

Darwin, C.R., 1881. The formation of vegetable mould, through the action of worms, with observations on their habits. London.

De Backer, A., Van Coillie, F., Montserrat, F., Provoost, P., Van Colen, C., Vincx, M., Degraer, S., 2011. Bioturbation effects of *Corophium volutator*: Importance of density and behavioural activity. *Estuar. Coast. Shelf Sci.* 91, 306–313. doi:10.1016/j.ecss.2010.10.031

De Montaudouin, X., Wegeberg, A.M., Jensen, K.T., Sauriau, P.G., 1998. Infection characteristics of *Himasthla elongata* cercariae in cockles as a function of water current. *Dis. Aquat. Organ.* 34, 63–70. doi:10.3354/dao034063

Delefosse, M., Kristensen, E., 2012. Burial of *Zostera marina* seeds in sediment inhabited by three polychaetes: Laboratory and field studies. *J. Sea Res.* 71, 41–49. doi:10.1016/j.seares.2012.04.006

Delefosse, M., Kristensen, E., Crunelle, D., Braad, P.E., Dam, J.H., Thisgaard, H., Thomassen, A., Høilund-Carlsen, P.F., 2015. Seeing the Unseen-Bioturbation in 4D: Tracing Bioirrigation in Marine Sediment Using Positron Emission Tomography and Computed Tomography. *PLoS One* 10, e0122201. doi:10.1371/journal.pone.0122201

Delgard, M.-L., 2013. Etude des effets et du rôle des herbiers à *Zostera noltii* sur la biogéochimie

des sédiments intertidaux. Ph.D. Thesis. (213 p) Université Bordeaux1.

- Delgard, M.-L., Deflandre, B., Deborde, J., Richard, M., Charbonnier, C., Anschutz, P., 2013. Changes in Nutrient Biogeochemistry in Response to the Regression of *Zostera noltii* Meadows in the Arcachon Bay (France). *Aquat. Geochemistry* 19, 241–259. doi:10.1007/s10498-013-9192-9
- Delgard, M.L., Deflandre, B., Bernard, G., Richard, M., Kochoni, E., Charbonnier, C., Cesbron, F., Metzger, E., Grémare, A., Anschutz, P., 2016. Benthic oxygen exchange over a heterogeneous *Zostera noltei* meadow in a temperate coastal ecosystem. *Mar. Ecol. Prog. Ser.* 543, 55–71. doi:10.3354/meps11570
- Dewitt, T.H., 2009. The Effects of Bioturbation and Bioirrigation on Seagrasses, in: Nelson, W.G. (Ed.), *Seagrasses and Protective Criteria: A Review and Assessment of Research Status*. United States Environmental Protection Agency, EPA/600/R-09/050.
- Do, V.T., 2012. Évolution et santé des herbiers à *Zostera noltii* dans le bassin d’Arcachon à travers la dynamique de la macrofaune benthique associée. <http://www.theses.fr/2012BOR14561>. Ph.D. Thesis. (181 p) Université Bordeaux 1.
- Dobbs, F.C., Guckert, J.B., 1988. *Callianassa trilobata* (Crustacea: Thalassinidea) influences abundance of meiofauna and biomass, composition, and physiologic state of microbial communities within its burrow. *Mar. Ecol. Prog. Ser.* 45, 69–79. doi:10.3354/meps045069
- Duarte, C.M.M., Middelburg, J.J.J., Caraco, N., 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1–8. doi:10.5194/bg-2-1-2005
- Duffy, J.E., 2006. Biodiversity and the functioning of seagrass ecosystems. *Mar. Ecol. Prog. Ser.* 311, 233–250. doi:10.3354/meps311233
- Dumbauld, B.R., Chapman, J.W., Torchin, M.E., Kuris, A.M., 2011. Is the collapse of Mud shrimp (*Upogebia pugettensis*) populations along the Pacific coast of North America caused by outbreaks of a previously unknown bopyrid isopod parasite (*Orthione griffenis*)? *Estuaries and Coasts* 34, 336–350. doi:10.1007/s12237-010-9316-z
- Dumbauld, B.R., Holden, D.L., Langness, O.P., 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest Estuaries? *Environ. Biol. Fishes* 83, 283–296. doi:10.1007/s10641-008-9333-y

- Dumbauld, B.R., Wyllie-Echeverria, S., 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquat. Bot.* 77, 27–42. doi:10.1016/S0304-3770(03)00077-9
- Dworschak, P., 2000. Global diversity in the Thalassinidea (Decapoda). *J. Crustac. Biol.* 20, 238–245.
- Dworschak, P.C., 2001. The Burrows of *Callianassa tyrrhena* (Petagna 1792) (Decapoda: Thalassinidea). *Mar. Ecol.* 22, 155–166. doi:10.1046/j.1439-0485.2001.00748.x
- Dworschak, P.C., 1988. The biology of *Upogebia pusilla* (PETAGNA) (Decapoda, Thalassinidea) III. Growth and Production. *Mar. Ecol.* 9, 51–77. doi:10.1111/j.1439-0485.1988.tb00198.x
- Dworschak, P.C., 1987a. Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea). *Investig. Pesq.* 51, 421–429.
- Dworschak, P.C., 1987b. The Biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) II. Environments and Zonation. *Mar. Ecol.* 8, 337–358. doi:10.1111/j.1439-0485.1987.tb00193.x
- Dworschak, P.C., 1983. The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea) I. The burrows. *Mar. Ecol.* 4, 19–43. doi:10.1111/j.1439-0485.1987.tb00193.x
- Dworschak, P.C., 1981. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda:Thalassinidea). *J. Exp. Mar. Bio. Ecol.* 52, 25–35. doi:10.1016/0022-0981(81)90168-4
- Dworschak, P.C., Koller, H., Abed-Navandi, D., 2006. Burrow structure, burrowing and feeding behaviour of *Corallianassa longiventris* and *Pestarella tyrrhena* (Crustacea, Thalassinidea, Callianassidae). *Mar. Biol.* 148, 1369–1382. doi:10.1007/s00227-005-0161-8

F

- Felder, D.L., 2001. Diversity and ecological significance of deep-burrowing macrocrustaceans in coastal tropical waters of the Americas (Decapoda: Thalassinidea). *Interciencia* 26, 440–449.
- Fernandes, S.O., Javanaud, C., Michotey, V.D., Guasco, S., Anschutz, P., Bonin, P., 2015. Coupling of bacterial nitrification with denitrification and anammox supports N removal in intertidal sediments (Arcachon Bay, France). *Estuar. Coast. Shelf Sci.*

doi:10.1016/j.ecss.2015.10.009

Flach, E., Tamaki, A., 2001. Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Ariake Sound in Japan, in: Reise, K. (Ed.), *Ecological Comparisons of Sedimentary Shores*. Springer Berlin Heidelberg, pp. 149–172. doi:10.1007/978-3-642-56557-1_8

Ford, A.T., 2008. Can you feminise a crustacean? *Aquat. Toxicol.* 88, 316–21. doi:10.1016/j.aquatox.2008.04.013

Forster, S., Graf, G., 1995. Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterranea* and “piston-pumping” by *Lanice conchilega*. *Mar. Biol.* 123, 335–346. doi:10.1007/BF00353625

François, F., Gerino, M., Stora, G., Durbec, J.P., Poggiale, J.C., 2002. Functional approach to sediment reworking by gallery-forming macrobenthic organisms: Modeling and application with the polychaete *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* 229, 127–136. doi:10.3354/meps229127

François, F., Poggiale, J.-C., Durbec, J.-P., Stora, G., 1997. A New Approach for the Modelling of Sediment Reworking Induced by a Macrobenthic Community. *Acta Biotheor.* 45, 295–319. doi:10.1023/A:1000636109604

Froelich, P.N., Klinkhammer, G.P., Bender, M.L., Luedtke, N.A., Heath, G.R., Cullen, D., Dauphin, P., Hammond, D., Hartman, B., Maynard, V., 1979. Early oxidation of organic matter in pelagic sediments of the eastern equatorial Atlantic: suboxic diagenesis. *Geochim. Cosmochim. Acta* 43, 1075–1090.

G

Gagnon, J.-M., Beaudin, L., Silverberg, N., Mauviel, A., 2013. Mesocosm and in situ observations of the burrowing shrimp *Calocaris templemani* (Decapoda: Thalassinidea) and its bioturbation activities in soft sediments of the Laurentian Trough. *Mar. Biol.* 160, 2687–2697. doi:10.1007/s00227-013-2262-0

Gallinari, M., Ragueneau, O., DeMaster, D.J., Hartnett, H., Rickert, D., Thomas, C., 2008. Influence of seasonal phytodetritus deposition on biogenic silica dissolution in marine

- sediments—Potential effects on preservation. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55, 2451–2464. doi:10.1016/j.dsr2.2008.06.005
- Ganthy, F., 2011. Rôle des herbiers de zostères (*Zostera noltii*) sur la dynamique sédimentaire du Bassin d'Arcachon. <http://www.theses.fr>. Ph.D. thesis. (284 p) Université Bordeaux 1.
- Ganthy, F., Soissons, L., Sauriau, P.G., Verney, R., Sottolichio, A., 2015. Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments. *Sedimentology* 62, 997–1023. doi:10.1111/sed.12170
- Gayanilo, F.C.J., Sparre, P., Pauly, D., 2005. FAO-ICLARM Stock Assessment Tools II (FiSAT II). Revised Version. FAO, Rome.
- Gerino, M., Aller, R.C., Lee, C., Cochran, J., Aller, J.Y., Green, M.A., Hirschberg, D., 1998. Comparison of Different Tracers and Methods Used to Quantify Bioturbation During a Spring Bloom: 234-Thorium, Luminophores and Chlorophyll a. *Estuar. Coast. Shelf Sci.* 46, 531–547.
- Gerino, M., Stora, G., Durbec, J.-P., 1994. Quantitative estimation of biodiffusive and bioadvective sediment mixing : In situ experimental approach. *Oceanol. Acta* 17, 547–554.
- Glud, R.N., 2008. Oxygen dynamics of marine sediments. *Mar. Biol. Res.* 4, 243–289. doi:10.1080/17451000801888726
- Glud, R.N., Gundersen, J.K., Røy, H., Jørgensen, B.B., 2003. Seasonal dynamics of benthic O₂ uptake in a semienclosed bay: Importance of diffusion and faunal activity. *Limnol. Oceanogr.* 48, 1265–1276. doi:10.4319/lo.2003.48.3.1265
- Grasshoff, K., Ehrhardt, M., Kremling, K., 1999. *Methods of Seawater Analysis*, Wiley-Vch. ed.
- Grémare, A., Duchêne, J.-C., Rosenberg, R., David, E., Desmalades, M., 2004. Feeding behaviour and functional response of *Abra ovata* and *A. nitida* compared by image analysis. *Mar. Ecol. Prog. Ser.* 267, 195–208.
- Griffen, B., 2009. Effects of a newly invasive parasite on the burrowing mud shrimp, a widespread ecosystem engineer. *Mar. Ecol. Prog. Ser.* 391, 73–83. doi:10.3354/meps08228
- Grigg, N.J., Webster, I.T., Ford, P.W., 2007. Non-destructive measurement of the time evolution of burrowing shrimp mound topography. *Mar. Ecol. Prog. Ser.* 329, 157–168.

doi:10.3354/meps329157

H

- Hanekom, N., Erasmus, T., 1988. Variations in size compositions of populations of *Upogebia africana* (Ortmann) (Decapoda, Crustacea) within the Swartkops estuary and possible influencing factors. South African J. Zool. 23, 259–265. doi:10.1080/02541858.1988.11448111
- Hanekom, N.M., Baird, D., 1987. Oxygen consumption of *Callinassa kraussi* Stabbing (Thalassinidea, Decapoda, Crustacea) in relation to various environmental conditions. South African J. Zool. 22, 183–189. doi:10.1080/02541858.1987.11448044
- Hargrad, B.T., 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnol. Oceanogr. 17, 583–596.
- Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S., Wilson, W.G., 2007. Ecosystem engineering in space and time. Ecol. Lett. 10, 153–164. doi:10.1111/j.1461-0248.2006.00997.x
- Hatcher, M.J., Dick, J.T.A., Dunn, A.M., 2012. Diverse effects of parasites in ecosystems: Linking interdependent processes. Front. Ecol. Environ. 10, 186–194. doi:10.1890/110016
- Heck, K., Hays, G., Orth, R., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136. doi:10.3354/meps253123
- Hemminga, M.A., Duarte, C.M., 2000. Seagrass ecology. Cambridge University Press.
- Hill, B., 1981. Respiratory adaptations of three species of *Upogebia* (Thalassinidea, Crustacea) with special reference to low tide periods. Biol. Bull. 160.
- Hollertz, K., Duchêne, J.-C., 2001. Burrowing behaviour and sediment reworking in the heart urchin *Brissopsis lyrifera* Forbes (Spatangoida). Mar. Biol. 139, 951–957. doi:10.1007/s002270100629
- Holmer, M., Andersen, F., Holmboe, N., Kristensen, E., Thongtham, N., 1999. Transformation and exchange processes in the Bangrong mangrove forest-seagrass bed system, Thailand. Seasonal and spatial variations in benthic metabolism and sulfur biogeochemistry. Aquat. Microb. 20,

203–212.

Hong, J.-S., Lee, C.-L., 2014. First record of the Thalassinid *Upogebia issaeffi* (Balss, 1913) (Crustacea: Decapoda: Upogebiidae) in Korean waters. *Ocean Sci. J.* 49, 73–82. doi:10.1007/s12601-014-0008-7

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., Iii, F.C., Ewel, J.J., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75, 3–35. doi:10.1890/04-0922

Howe, R.L., Rees, A.P., Widdicombe, S., 2004. The impact of two species of bioturbating shrimp (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *J. Mar. Biol. Assoc. United Kingdom* 84, 629–632. doi:10.1017/S002531540400966Xh

Huettel, M., Gust, G., 1992. Impact of bioturbation on interfacial solute exchange in permeable sediments. *Mar. Ecol. Prog. Ser.* 89, 253–267. doi:10.3354/meps089253

Hughes, T.E., 1940. The effects on the fat and starch metabolism of *Gebia* by the parasite *Gyge Branchialis*. *J. Exp. Biol.* 17, 331–336.

Hymel, S.N., Plante, C.J., 2000. Feeding and bacteriolytic responses of the deposit-feeder *Abarenicola pacifica* (Polychaeta: Arenicolidae) to changes in temperature and sediment food concentration. *Mar. Biol.* 136, 1019–1027. doi:10.1007/s002270000301

J

Jensen, H., McGlathery, K., Marino, R., Howarth, R., 1998. Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnol. Oceanogr.* 43, 799–810.

Jensen, K.T., Mouritsen, K.N., 1992. Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator* - the possible role of trematodes. *Helgoländer Meeresunter* 46, 329–339.

Jones, C., Lawton, J., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–

386.

Jordan, M.A., Welsh, D.T., Dunn, R.J.K., Teasdale, P.R., 2009. Influence of *Trypaea australiensis* population density on benthic metabolism and nitrogen dynamics in sandy estuarine sediment: A mesocosm simulation. *J. Sea Res.* 61, 144–152. doi:10.1016/j.seares.2008.11.003

Jordana, E., Duchêne, J.-C., Charles, F., Grémare, A., Amouroux, J.-M., 2000. Experimental study of suspension-feeding activity in the serpulid polychaete *Ditrupa arietina* (O.F. Müller). *J. Exp. Mar. Bio. Ecol.* 252, 57–74. doi:10.1016/S0022-0981(00)00231-8

K

Kaldy, J.E., Eldridge, P.M., Cifuentes, L. a., Jones, W.B., 2006. Utilization of DOC from seagrass rhizomes by sediment bacteria: ¹³C-tracer experiments and modeling. *Mar. Ecol. Prog. Ser.* 317, 41–55. doi:10.3354/meps317041

Kato, M., Itani, G., 1995. Commensalism of a Bivalve, *Peregrinamor ohshimai*, with a thalassinidean burrowing shrimp, *Upogebia major*. *J. Mar. Biol. Assoc. United Kingdom* 75, 941. doi:10.1017/S0025315400038261

Katrak, G., Bird, F.L., 2003. Comparative effects of the large bioturbators, *Trypaea australiensis* and *Heloecius cordiformis*, on intertidal sediments of Western Port, Victoria, Australia. *Mar. Freshw. Res.* 54, 701–708. doi:10.1071/MF03015

Kevrekidis, T., Gouvis, N., Koukouras, A., 1997. Population dynamics, reproduction and growth of *Upogebia pusilla* (Decapoda, Thalassinidea) in the evros delta (north aegean sea). *Crustaceana* 70, 799–812. doi:10.1163/156854097X00249

Kinne, O., 1970. Vol I, Environmental Factors, Part 1, Chapter 3: Temperature, in: *Marine Ecology, A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters*. Wiley-Interscience, London, pp. 407–514.

Kinoshita, K., 2002. Burrow structure of the mud shrimp *Upogebia major* (Decapoda: Thalassinidea: Upogebiidae). *J. Crustac. Biol.* 22, 474–480. doi:10.1651/0278-0372(2002)022[0474:BSOTMS]2.0.CO;2

Kinoshita, K., Itani, G., Uchino, T., 2010. Burrow morphology and associated animals of the mud shrimp *Upogebia yokoyai* (Crustacea: Thalassinidea: Upogebiidae). *J. Mar. Biol. Assoc. UK*

90, 947–952. doi:10.1017/S0025315410000214

Kinoshita, K., Wada, M., Kogure, K., Furota, T., 2008. Microbial activity and accumulation of organic matter in the burrow of the mud shrimp, *Upogebia major* (Crustacea: Thalassinidea). *Mar. Biol.* 153, 277–283. doi:10.1007/s00227-007-0802-1

Kinoshita, K., Wada, M., Kogure, K., Furota, T., 2003. Mud shrimp burrows as dynamic traps and processors of tidal-flat materials. *Mar. Ecol. Prog. Ser.* 247, 159–164. doi:10.3354/meps247159

Klute, A., Dirksen, C., 1986. Hydraulic Conductivity and Diffusivity: Laboratory Methods, in: Klute, A. (Ed.), *Methods of Soil Analysis: Part 1 — Physical and Mineralogical Methods*. American Society of Agronomy, pp. 687–700. doi:10.2136/sssabookser5.1.2ed.c28

Kneer, D., Asmus, H., Vonk, J.A., 2008. Seagrass as the main food source of *Neaxius acanthus* (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutierei* (Thalassinidea: Callianassidae). *Estuar. Coast. Shelf Sci.* 79, 620–630. doi:10.1016/j.ecss.2008.05.013

Koike, I., Mukai, H., 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. *Mar. Ecol. Prog. Ser.* 12, 185–190.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *J. Sea Res.* 59, 30–43. doi:10.1016/j.seares.2007.05.004

Kristensen, E., 2001. Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments Presented during the ACS Division of Geochemistry symposium ?Biogeochemical Consequences of Dynamic Interactions Between Benthic Fa. *Geochem. Trans.* 2, 92. doi:10.1039/b108114d

Kristensen, E., 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426, 1–24. doi:10.1023/A:1003980226194

Kristensen, E., Kostka, J., 2005. Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions, in: *Macro- and Microorganisms in Marine Sediments*. pp. 125–157. doi:10.1029/60CE08

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C., Banta, G., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Mar. Ecol. Prog. Ser.* 446, 285–302. doi:10.3354/meps09506

L

Lajtner, J., Lucić, A., Marušić, M., Erben, R., 2008. The effects of the trematode *Bucephalus polymorphus* on the reproductive cycle of the zebra mussel *Dreissena polymorpha* in the Drava River. *Acta Parasitol.* 53, 85–92. doi:10.2478/s11686-008-0011-1

Laverock, B., Gilbert, J.A., Tait, K., Osborn, A.M., Widdicombe, S., 2011. Bioturbation: impact on the marine nitrogen cycle. *Biochem. Soc. Trans.* 39, 315–20. doi:10.1042/BST0390315

Laverock, B., Smith, C.J., Tait, K., Osborn, a M., Widdicombe, S., Gilbert, J. a, 2010. Bioturbating shrimp alter the structure and diversity of bacterial communities in coastal marine sediments. *ISME J.* 4, 1531–44. doi:10.1038/ismej.2010.86

Lavesque, N., Pascal, L., Gouillieux, B., Sorbe, J.-C., Bachelet, G., Maire, O., 2016. *Heteromysis (Heteromysis) microps* (Crustacea, Mysidae), a commensal species for *Upogebia pusilla* (Crustacea, Upogebiidae) in Arcachon Bay (NE Atlantic Ocean). *Mar. Biodivers. Rec.* 9, 14. doi:10.1186/s41200-016-0001-1

Lee, K.-S., Park, S.R., Kim, Y.K., 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *J. Exp. Mar. Bio. Ecol.* 350, 144–175. doi:10.1016/j.jembe.2007.06.016

Leiva, F.P., Urbina, M.A., Cumillaf, J.P., Gebauer, P., Paschke, K., 2015. Physiological responses of the ghost shrimp *Neotrypaea uncinata* (Milne Edwards 1837) (Decapoda: Thalassinidea) to oxygen availability and recovery after severe environmental hypoxia. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 189, 30–7. doi:10.1016/j.cbpa.2015.07.008

Lindqvist, S., Gilbert, F., Eriksson, S.P., Hulth, S., 2013. Activities by *Hediste diversicolor* under different light regimes: Experimental quantification of particle reworking using time-resolved imaging. *J. Exp. Mar. Bio. Ecol.* 448, 240–249. doi:10.1016/j.jembe.2013.06.014

Liu, W., 2015. Two new species of the genus *Upogebia* leach, 1814 (Crustacea: Decapoda: Gebiidea: Upogebiidae) from the south China sea. *Raffles Bull. Zool.* 63, 418–425.

- Lohrer, A.A.M., Thrush, S.S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* 431, 1092–1095. doi:10.1038/nature03042
- Longbottom, M.R., 1970. The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. *J. Exp. Mar. Bio. Ecol.* 5, 138–157. doi:10.1016/0022-0981(70)90013-4
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91, 3–17. doi:10.1034/j.1600-0706.2000.910101.x
- Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J. P., Hector A., Hooper D. U., Huston m. A., Raffaelli D., Schmid B., Tilman D., Wardle D. A., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*. 294, 804–808. doi:10.1126/science.1064088
- Loucaides, S., Van Cappellen, P., Roubex, V., Moriceau, B., Ragueneau, O., 2011. Controls on the Recycling and Preservation of Biogenic Silica from Biomineralization to Burial. *Silicon* 4, 7–22. doi:10.1007/s12633-011-9092-9

M

- Maire, O., Barras, C., Gestin, T., Nardelli, M.-P., Romero-Ramirez, A., Duchêne, J.-C., Geslin, E., 2016. How does macrofaunal bioturbation influence the vertical distribution of living benthic foraminifera? *Mar. Ecol. Prog. Ser.* 561, 83–97. doi:10.3354/meps11929
- Maire, O., Duchêne, J.-C., Bigot, L., Grémare, A., 2007a. Linking feeding activity and sediment reworking in the deposit-feeding bivalve *Abra ovata* with image analysis, laser telemetry, and luminophore tracers. *Mar. Ecol. Prog. Ser.* 351, 139–150. doi:10.3354/meps07147
- Maire, O., Duchêne, J.-C., Grémare, A., Malyuga, V.S., Meysman, F.J.R., 2007b. A comparison of sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and wintertime, with a comparison between two models of sediment reworking. *J. Exp. Mar. Bio. Ecol.* 343, 21–36. doi:10.1016/j.jembe.2006.10.052
- Maire, O., Duchêne, J.-C., Rosenberg, R., Braga de Mendonça Jr., J., Grémare, A., 2006. Effects of food availability on sediment reworking in *Abra ovata* and *A. nitida*. *Mar. Ecol. Prog. Ser.*

319, 135–153.

Maire, O., Duchêne, J.C., Amouroux, J.M., Grémare, A., 2007c. Activity patterns in the terebellid polychaete *Eupolyornia nebulosa* assessed using a new image analysis system. *Mar. Biol.* 151, 737–749. doi:10.1007/s00227-006-0519-6

Maire, O., Lecroart, P., Meysman, F.J.R., Rosenberg, R., Duchêne, J.-C., Grémare, A., 2008. Quantification of sediment reworking rates in bioturbation research: a review. *Aquat. Biol.* 2, 219–238. doi:10.3354/ab00053

Maire, O., Merchant, J.N., Bulling, M., Teal, L.R., Grémare, A., Duchêne, J.-C., Solan, M., 2010. Indirect effects of non-lethal predation on bivalve activity and sediment reworking. *J. Exp. Mar. Bio. Ecol.* 395, 30–36. doi:10.1016/j.jembe.2010.08.004

Masse, C., 1708. Mémoires sur la carte du 6ième carré de la Générale de Médoc et partie de Guienne et de Saintonge. *Bull. Soc. Hist. Arch. d'Arcachon* 78, 39–45.

Mateo, M.A., Cebrian, J., Dunton, K., Mutchler, T., 2006. Carbon flux in seagrass ecosystems, in: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer Netherlands, pp. 159–192. doi:10.1007/978-1-4020-2983-7

Mayer, L.M., 1994a. Surface area control of organic carbon accumulation in continental shelf sediments. *Geochim. Cosmochim. Acta* 58, 1271–1284. doi:10.1016/0016-7037(94)90381-6

Mayer, L.M., 1994b. Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chem. Geol.* 114, 347–363. doi:10.1016/0009-2541(94)90063-9

McGrew, M., Hultgren, K.M., 2011. Bopyrid parasite infestation affects activity levels and morphology of the eusocial snapping shrimp *Synalpheus elizabethae*. *Mar. Ecol. Prog. Ser.* 431, 195–204. doi:10.3354/meps09123

Meißner, K., Bick, A., 1997. Population dynamics and ecoparasitological surveys of *Corophium volutator* in coastal waters in the Bay of Mecklenburg (southern Baltic Sea). *Dis. Aquat. Org.* 29, 169–179. doi:10.3354/dao029169

Mermillod-Blondin, F., François-Carcaillet, F., Rosenberg, R., 2005. Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. *J. Exp. Mar. Bio. Ecol.* 315, 187–209. doi:10.1016/j.jembe.2004.09.013

- Mermillod-Blondin, F., Rosenberg, R., 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquat. Sci.* 68, 434–442. doi:10.1007/s00027-006-0858-x
- Meysman, F.J.R., Boudreau, B.P., Middelburg, J.J., 2003. Relations between local, nonlocal, discrete and continuous models of bioturbation. *J. Mar. Res.* 61, 391–410. doi:10.1357/002224003322201241
- Meysman, F.J.R., Galaktionov, O.S., Cook, P.L.M., Janssen, F., Huettel, M., Middelburg, J.J., 2007. Quantifying biologically and physically induced flow and tracer dynamics in permeable sediments. *Biogeosciences* 4, 627–646. doi:10.5194/bg-4-627-2007
- Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol. Evol.* 21, 688–695. doi:10.1016/j.tree.2006.08.002
- Mikheev, V.N., Pasternak, A.F., Valtonen, E.T., Taskinen, J., 2014. Increased ventilation by fish leads to a higher risk of parasitism. *Parasit. Vectors* 7, 281. doi:10.1186/1756-3305-7-281
- Mischler, J., Johnson, P.T.J., Mckenzie, V.J., Townsend, A.R., 2016. Parasite infection alters nitrogen cycling at the ecosystem scale. *J. Anim. Ecol.* 85, 817–828. doi:10.1111/1365-2656.12505
- Moore, J., 2002. *Parasites and the behavior of animals*. Oxford University Press.
- Mouritsen, K.N., McKechnie, S., Meenken, E., Toynbee, J.L., Poulin, R., 2003. Spatial heterogeneity in parasite loads in the New Zealand cockle: the importance of host condition and density. *J. Mar. Biol. Assoc. UK* 83, 307–310. doi:10.1017/S0025315403007124h
- Mouritsen, K.N., Poulin, R., 2010. Parasitism as a determinant of community structure on intertidal flats. *Mar. Biol.* 157, 201–213. doi:10.1007/s00227-009-1310-2
- Mouritsen, K.N., Poulin, R., 2005. Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos* 108, 344–350. doi:10.1111/j.0030-1299.2005.13507.x
- Mouritsen, K.N., Poulin, R., 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124 Suppl, S101–S117. doi:10.1017/S0031182002001476

Moyo, R., Pillay, D., Baeza, J.A., 2017. Symbiont-mediated shifts in sandprawn behaviour: Implications for ecosystem functioning in marine soft-sediment ecosystems. *J. Exp. Mar. Bio. Ecol.* 486, 296–304. doi:10.1016/j.jembe.2016.10.022

N

Na, T., Gribsholt, B., Galaktionov, O.S., Lee, T., Meysman, F.J.R., 2008. Influence of advective bio-irrigation on carbon and nitrogen cycling in sandy sediments. *J. Mar. Res.* 66, 691–722. doi:10.1357/002224008787536826

Naeem, S., Loreau, M., Inchausti, P., 2000. Biodiversity and ecosystem functioning : the emergence of a synthetic ecological framework 3–17.

Nanri, T., Fukushige, M., Ubaldo, J.P., Kang, B.-J., Masunari, N., Takada, Y., Hatakeyama, M., Saigusa, M., 2010. Occurrence of abnormal sexual dimorphic structures in the gonochoristic crustacean, *Upogebia major* (Thalassinidea: Decapoda), inhabiting mud tidal flats in Japan. *J. Mar. Biol. Assoc. UK* 91, 1049–1057. doi:10.1017/S0025315410001712

Nates, S.F., Felder, D.L., 1998. Impacts of Burrowing Ghost Shrimp, Genus *Lepidophthalmus* Crustacea: Decapoda: Thalassinidea, on Penaeid Shrimp Culture. *J. World Aquac. Soc.* 29, 188–210. doi:10.1111/j.1749-7345.1998.tb00978.x

Nel, P., Branch, G., 2013. Assessment of the abundance and distribution of burrowing sandprawns and mudprawns (*Callichirus* and *Upogebia* species) in Langebaan Lagoon, South Africa. *African J. Mar. Sci.* 35, 195–208. doi:10.2989/1814232X.2013.795914

Nelson, S., Simmons, M., Knight, A., 1986. The energy burden of the bopyrid parasite *Argeia pauperata* (Crustacea, isopoda) on the grass shrimp *Crangon franciscorum* (Crustacea, crangonidae). *Comp. Biochem. Physiol. Part A Physiol.* 83, 121–124. doi:10.1016/0300-9629(86)90098-8

Ní Longphuirt, S., Ragueneau, O., Chauvaud, L., Martin, S., Jean, F., Thouzeau, G., Leynaert, A., 2009. Diurnal heterogeneity in silicic acid fluxes in shallow coastal sites: Causes and implications. *Estuar. Coast. Shelf Sci.* 82, 495–502. doi:10.1016/j.ecss.2009.02.014

Nickell, L.A., Atkinson, R., 1995. Functional morphology of burrows and trophic modes of three thalassinidean shrimp species, and a new approach to the classification of thalassinidean

burrow morphology. *Mar. Ecol. Prog. Ser.* 128, 181–197.

Nielsen, O.I., Gribsholt, B., Kristensen, E., Revsbech, N.P., 2004. Microscale distribution of oxygen and nitrate in sediment inhabited by *Nereis diversicolor*: Spatial patterns and estimated reaction rates. *Aquat. Microb. Ecol.* 34, 23–32. doi:10.3354/ame034023

Nizzoli, D., Bartoli, M., Cooper, M., Welsh, D.T., Underwood, G.J.C., Viaroli, P., 2007. Implications for oxygen, nutrient fluxes and denitrification rates during the early stage of sediment colonisation by the polychaete *Nereis* spp. in four estuaries. *Estuar. Coast. Shelf Sci.* 75, 125–134. doi:10.1016/j.ecss.2007.03.035

Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Mar. Ecol. Prog. Ser.* 332, 11–23. doi:10.3354/meps332011

O

Orth, R.J.R., Carruthers, T.T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. *Bioscience* 56, 987–996. doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Orvain, F., Le Hir, P., Sauriau, P.-G., Lefebvre, S., 2012. Modelling the effects of macrofauna on sediment transport and bed elevation: Application over a cross-shore mudflat profile and model validation. *Estuar. Coast. Shelf Sci.* 108, 64–75. doi:10.1016/j.ecss.2011.12.036

P

Papaspyrou, S., Gregersen, T., Cox, R., Thessalou-Legaki, M., Kristensen, E., 2005. Sediment properties and bacterial community in burrows of the ghost shrimp *Pestarella tyrrhena* (Decapoda: Thalassinidea). *Aquat. Microb. Ecol.* 38, 181–190. doi:10.3354/ame038181

Papaspyrou, S., Thessalou-Legaki, M., Kristensen, E., 2004. Impact of *Pestarella tyrrhena* on benthic metabolism in sediment microcosms enriched with seagrass and macroalgal detritus. *Mar. Ecol. Prog. Ser.* 281, 165–179. doi:10.3354/meps281165

Pascal, L., de Montaudouin, X., Grémare, A., Maire, O., 2016a. Dynamics of the *Upogebia pusilla*–

- Gyge branchialis* marine host–parasite system. Mar. Biol. 163, 195. doi:10.1007/s00227-016-2969-9
- Pascal, L., Maire, O., Volkenborn, N., Lecroart, P., Bichon, S., de Montaudouin, X., Grémare, A., Deflandre, B., 2016b. Influence of the mud shrimp *Upogebia pusilla* (Decapoda: Gebiidea) on solute and porewater exchanges in an intertidal seagrass (*Zostera noltei*) meadow of Arcachon Bay: An experimental assessment. J. Exp. Mar. Bio. Ecol. 477, 69–79. doi:10.1016/j.jembe.2016.01.008
- Paterson, B.D., Thorne, M.J., 1995. Measurements of oxygen uptake, heart and gill bailer rates of the callianassid burrowing shrimp *Trypaea australiensis* Dana and its responses to low oxygen tensions. J. Exp. Mar. Bio. Ecol. 194, 39–52. doi:10.1016/0022-0981(95)00082-8
- Penha-Lopes, G., Bartolini, F., Limbu, S., Cannicci, S., Kristensen, E., Paula, J., 2009. Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands? Mar. Pollut. Bull. 58, 1694–1703. doi:10.1016/j.marpolbul.2009.06.015
- Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411. doi:10.1046/j.1461-0248.2002.00339.x
- Peterson, C.H., 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43, 343–359. doi:10.1007/BF00396928
- Philippart, C., 1994. Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. Mar. Ecol. Prog. Ser. 111, 251–257. doi:10.3354/meps111251
- Phillips, P.J., 1971. Observations on the Biology of Mudshrimps of the Genus *Callianassa* (Anomura: Thalassinidea) in Mississippi Sound. Gulf Res. Reports 3. doi:10.18785/grr.0302.03
- Pillay, D., Branch, G.G.M., Griffiths, C.L.C., Williams, C., Prinsloo, A., 2010. Ecosystem change in a South African marine reserve (1960–2009): role of seagrass loss and anthropogenic disturbance. Mar. Ecol. Prog. Ser. 415, 35–48. doi:10.3354/meps08733
- Pillay, D., Branch, G.M., 2011. Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. Oceanogr. Mar. Biol. 49, 137–192.
- Pillay, D., Branch, G.M., Forbes, A.T., 2008. Habitat change in an estuarine embayment:

- anthropogenic influences and a regime shift in biotic interactions. *Mar. Ecol. Prog. Ser.* 370, 19–31. doi:10.3354/meps07631
- Pillay, D., Branch, G.M., Forbes, A.T., 2007a. Experimental evidence for the effects of the thalassinidean sandprawn *Callianassa kraussi* on macrobenthic communities. *Mar. Biol.* 152, 611–618. doi:10.1007/s00227-007-0715-z
- Pillay, D., Branch, G.M., Forbes, A.T., 2007b. The influence of bioturbation by the sandprawn *Callianassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. *J. Exp. Mar. Bio. Ecol.* 344, 1–9. doi:10.1016/j.jembe.2006.10.044
- Pillay, D., Williams, C., Whitfield, A., 2012. Indirect effects of bioturbation by the burrowing sandprawn *Callichirus kraussi* on a benthic foraging fish, *Liza richardsonii*. *Mar. Ecol. Prog. Ser.* 453, 151–158. doi:10.3354/meps09642
- Pinn, E.H., Atkinson, R.J.A., Rogerson, A., 2001. Sexual dimorphism and intersexuality in *Upogebia stellata* (Crustacea: Decapoda: Thalassinidea). *J. Mar. Biol. Assoc. UK* 81, 1061–1062. doi:10.1017/S0025315401005070
- Plus, M., Dalloyau, S., Trut, G., Auby, I., de Montaudouin, X., Emery, E., Claire, N., Viala, C., 2010. Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuar. Coast. Shelf Sci.* 87, 357–366. doi:10.1016/j.ecss.2010.01.016
- Pörtner, H.O., 2002. Climate variations and the physiological basis of temperature dependent biogeography: Systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol. - A Mol. Integr. Physiol.* 132, 739–761. doi:10.1016/S1095-6433(02)00045-4
- Posey, M.H., Dumbauld, B.R., Armstrong, D.A., 1991. Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *J. Exp. Mar. Bio. Ecol.* 148, 283–294. doi:10.1016/0022-0981(91)90088-E
- Poulin, R., 1994. Meta-analysis of parasite-induced behavioural changes. *Anim. Behav.* 48, 137–146. doi:10.1006/anbe.1994.1220

Q

- Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., Queir, A.M., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Colen, C. Van, Hoey, G. Van, Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecol. Evol.* 3, 3958–85. doi:10.1002/ece3.769
- Quintana, C.O., Hansen, T., Delefosse, M., Banta, G., Kristensen, E., 2011. Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. *J. Exp. Mar. Bio. Ecol.* 397, 179–187. doi:10.1016/j.jembe.2010.12.006

R

- Rao, A.M.F., Malkin, S.Y., Montserrat, F., Meysman, F.J.R., 2014. Alkalinity production in intertidal sands intensified by lugworm bioirrigation. *Estuar. Coast. Shelf Sci.* 148, 36–47. doi:10.1016/j.ecss.2014.06.006
- Reimers, C.E., Wakefield, W.W., 1989. Flocculation of siliceous detritus on the sea floor of a deep Pacific seamount. *Deep Sea Res. Part A, Oceanogr. Res. Pap.* 36, 1841–1861. doi:10.1016/0198-0149(89)90115-5
- Reise, K., 2002. Sediment mediated species interactions in coastal waters. *J. Sea Res.* 48, 127–141.
- Reisinger, L.S., Lodge, D.M., 2016. Parasites alter freshwater communities in mesocosms by modifying invasive crayfish behavior. *Ecology* 97, 1497–1506. doi:10.1890/15-1634.1
- Repetto, M., Griffen, B.D., 2011. Physiological consequences of parasite infection in the burrowing mud shrimp, *Upogebia pugettensis*, a widespread ecosystem engineer. *Mar. Freshw. Res.* 63, 60–67. doi:10.1071/MF11158
- Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J. Mar. Res.* 28, 150–178.
- Riisgård, H., Kamermans, P., 2001. Switching between deposit and suspension feeding in coastal zoobenthos, in: *Ecological Comparisons of Sedimentary Shores*. Springer Berlin Heidelberg, pp. 73–101. doi:10.1007/978-3-642-56557-1

- Riisgård, H.U., Banta, G.T., 1998. Irrigation and deposit feeding by the lugworm *Arenicola marina*, characteristics and secondary effects on the environment. A review of current knowledge. *Vie Milieu* 48, 243–257.
- Riisgård, H.U., Vedel, A., Boye, H., Larsen, P.S., 1992. Filter-net structure and pumping activity in the polychaete *Nereis diversicolor*: effects of temperature and pump-modelling. *Mar. Ecol. Prog. Ser.* 83, 79–89. doi:10.3354/meps083079
- Robles, R., Tudge, C., Dworschak, P.C., Poore, G., Felder, D.L., 2009. Molecular phylogeny of the Thalassinidea based on nuclear and mitochondrial genes, in: Martin, J.W., Crandall, K.A., Felder, D.L. (Eds.), *Decapod Crustacean Phylogenetics*. pp. 309–326.
- Romero-Ramirez, A., Grémare, A., Bernard, G., Pascal, L., Maire, O., Duchêne, J.-C., 2016. Development and validation of a video analysis software for marine benthic applications. *J. Mar. Syst.* 162, 4–17. doi:10.1016/j.jmarsys.2016.03.003
- Rosenberg, R., Grémare, A., Duchêne, J.-C., Davey, E., Frank, M., 2008. 3D visualization and quantification of marine benthic biogenic structures and particle transport utilizing computer-aided tomography. *Mar. Ecol. Prog. Ser.* 363, 171–182. doi:10.3354/meps07463
- Rowden, A.A., Jones, M.B., 1995. The burrow structure of the mud-shrimp *Callianassa subterranea* (Decapoda: Thalassinidea) from the North Sea. *J. Nat. Hist.* 29, 1155–1165. doi:10.1080/00222939500770491
- Rowden, A.A., Jones, M.B., 1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). *J. Exp. Mar. Bio. Ecol.* 173, 265–272. doi:10.1016/0022-0981(93)90057-U
- Rowden, A.A., Jones, M.B., Morris, A.W., 1998. The role of *Callianassa subterranea* (Montagu) (Thalassinidea) in sediment resuspension in the North Sea. *Cont. Shelf Res.* 18, 1365–1380. doi:10.1016/S0278-4343(98)00048-X
- Røy, H., Huettel, M., Jørgensen, B.B., 2005. The influence of topography on the functional exchange surface of soft sediments, assessed from sediment topography measured in situ. *Limnol. Oceanogr.* 50, 106–112. doi:10.4319/lo.2005.50.1.0106
- Røy, H., Hüttel, M., Jørgensen, B.B., 2002. The role of small-scale sediment topography for oxygen flux across the diffusive boundary layer. *Limnol. Oceanogr.* 47, 837–847.

doi:10.4319/lo.2002.47.3.0837

S

- Saglam, H., Bascinar, N.S., 2008. Feeding ecology of thornback ray (*Raja clavata* Linnaeus, 1758) on the Turkish coast of the south-eastern Black Sea. *Mar. Biol. Res.* 4, 451–457. doi:10.1080/17451000802233393
- Sasaki, A., Nakao, H., Yoshitake, S., Nakatsubo, T., 2014. Effects of the burrowing mud shrimp, *Upogebia yokoyai*, on carbon flow and microbial activity on a tidal flat. *Ecol. Res.* 29, 493–499. doi:10.1007/s11284-014-1149-y
- Sato, M., Uchida, H., Itani, G., Yamashita, H., 2001. Taxonomy and Life History of the Scale Worm *Hesperonoe hwanghaiensis* (Polychaeta: Polynoidae), newly Recorded in Japan, with Special Reference to Commensalism to a Burrowing Shrimp, *Upogebia major*. *Zoolog. Sci.* 18, 981–991. doi:10.2108/zsj.18.981
- Sato, T., Egusa, T., Fukushima, K., Oda, T., Ohte, N., Tokuchi, N., Watanabe, K., Kanaiwa, M., Murakami, I., Lafferty, K.D., 2012. Nematomorph parasites indirectly alter the food web and ecosystem function of streams through behavioural manipulation of their cricket hosts. *Ecol. Lett.* 15, 786–793. doi:10.1111/j.1461-0248.2012.01798.x
- Schulte-Oehlmann, U., Oehlmann, J., Fioroni, P., Bauer, B., 1997. Imposex and reproductive failure in *Hydrobia ulvae* (Gastropoda: Prosobranchia). *Mar. Biol.* 128, 257–266. doi:10.1007/s002270050090
- Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Judson Kenworthy, W., La Nafie, Y. a., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., Tussenbroek, B. Van, Vergara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. *Biol. Conserv.* 144, 1961–1971. doi:10.1016/j.biocon.2011.04.010
- Shull, D.H., Yasuda, M., 2001. Size-selective downward particle transport by cirratulid polychaetes. *J. Mar. Res.* 59, 453–473. doi:10.1357/002224001762842271
- Siebert, T., Branch, G., 2005a. Interactions between *Zostera capensis* and *Callianassa kraussi*: influences on community composition of eelgrass beds and sandflats. *African J. Mar. Sci.* 27,

357–373. doi:10.2989/18142320509504095

Siebert, T., Branch, G., 2005b. Interactions between *Zostera capensis*, *Callianassa kraussi* and *Upogebia africana*: deductions from field surveys in Langebaan lagoon, South Africa. *African J. Mar. Sci.* 27, 345–356. doi:10.2989/18142320509504094

Siebert, T., Branch, G.M., 2006. Ecosystem engineers: Interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi* and their indirect effects on the mudprawn *Upogebia africana*. *J. Exp. Mar. Bio. Ecol.* 338, 253–270. doi:10.1016/j.jembe.2006.06.024

Smith, A.E., Chapman, J.W., Dumbauld, B.R., 2008. Population Structure and Energetics of the Bopyrid Isopod Parasite *Orthione griffenis* in Mud Shrimp *Upogebia pugettensis*. *J. Crustac. Biol.* 28, 228–233. doi:10.1163/20021975-99990368

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004a. Extinction and ecosystem function in the marine benthos. *Science*. 306, 1177–1180. doi:10.1126/science.1103960

Solan, M., Wigham, B.D., Hudson, I.R., Kennedy, R., Coulon, C.H., Norling, K., Nilsson, H.C., Rosenberg, R., 2004b. In situ quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. *Mar. Ecol. Prog. Ser.* 271, 1–12. doi:10.3354/meps271001

Stachowicz, J.J., Bruno, J.F., Duffy, J.E., 2007. Understanding the Effects of Marine Biodiversity on Communities and Ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 38, 739–766. doi:10.1146/annurev.ecolsys.38.091206.095659

Stamhuis, E.J., Reede-Dekker, T., van Etten, Y., de Wiljes, J.J., Videler, J.J., 1996. Behaviour and time allocation of the burrowing shrimp *Callianassa subterranea* (Decapoda, Thalassinidea). *J. Exp. Mar. Bio. Ecol.* 204, 225–239.

Stamhuis, E.J., Schreurs, C.E., Videler, J.J., 1997. Burrow architecture and turbative activity of the thalassinid shrimp *Callianassa subterranea* from the central North Sea. *Mar. Ecol. Prog. Ser.* 151, 155–163.

Stamhuis, E.J., Videler, J.J., 1998. Optimal foraging in the thalassinidean shrimp *Callianassa subterranea* Improving food quality by grain size selection. *J. Exp. Mar. Bio. Ecol.* 228, 197–208.

- Stapleton, K.L., Long, M., Bird, F.L., 2001. Comparative feeding ecology of two spatially coexisting species of ghost shrimp, *Biffarius arenosus* and *Trypaea Australiensis* (Decapoda: Callianassidae). *Ophelia* 55, 141–150. doi:10.1080/00785236.2001.10409481
- Suchanek, T.H., 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *J. Mar. Res.* 41, 281–298.
- Suykerbuyk, W., Bouma, T.J., van der Heide, T., Faust, C., Govers, L.L., Giesen, W.B.J.T., de Jong, D.J., van Katwijk, M.M., 2012. Suppressing antagonistic bioengineering feedbacks doubles restoration success. *Ecol. Appl.* 22, 1224–1231. doi:10.1890/11-1625.1
- Swinbanks, D.D., Luternauer, J.L., 1987. Burrow distribution of thalassinidean shrimp on a Fraser Delta tidal flat, British Columbia. *J. Paleontol.* 61, 315–332.
- Swinbanks, D.D., Murray, J.W., 1981. Biosedimentological zonation of Boundary Bay tidal flats, Fraser River Delta, British Columbia. *Sedimentology* 28, 201–237. doi:10.1111/j.1365-3091.1981.tb01677.x

T

- Tamaki, A., 1994. Extinction of the trochid gastropod, *Umboonium (Suchium) moniliferum* (Lamarck), and associated species on an intertidal sandflat. *Res. Popul. Ecol. (Kyoto)*. 36, 225–236. doi:10.1007/BF02514939
- Thomas, F., Adamo, S., Moore, J., 2005. Parasitic manipulation: where are we and where should we go? *Behav. Processes* 68, 185–199. doi:10.1016/j.beproc.2004.06.010
- Thomas, F., Poulin, R., Meeüs, T. de, Guégan, J.-F., Renaud, F., 1999. Parasites and ecosystem engineering : what roles could they play ? *Oikos* 84, 167–171.
- Thomas, F., Renaud, F., Demee, T., Poulin, R., 1998. Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone? *Proc. R. Soc. B Biol. Sci.* 265, 1091–1096. doi:10.1098/rspb.1998.0403
- Thompson, R.K., Pritchard, A.W., 1969. Respiratory adaptations of two burrowing crustaceans, *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biol. Bull.* 136, 274–287.

- Truesdale, V.W., Smith, C.J., 1976. The automatic determination of silicate dissolved in natural fresh water by means of procedures involving the use of either α - or β -molybdosilicic acid. *Analyst* 101, 19. doi:10.1039/an9760100019
- Tucker, B.W., 1930. Memoirs: On the effects of an Epicaridan Parasite, *Gyge branchialis*, on *Upogebia littoralis*. *Q. J. Microsc. Sci.* s2-74, 1–118.
- Tunberg, B., 1986. Studies on the population ecology of *Upogebia deltaura* (Leach) (Crustacea, Thalassinidea). *Estuar. Coast. Shelf Sci.* 22, 753–765. doi:10.1016/0272-7714(86)90097-1
-

U

- Ubaldo, J.P., Nanri, T., Takada, Y., Saigusa, M., 2014. Prevalence and patterns of infection by the epicaridean parasite, *Gyge ovalis* and the emergence of intersex in the estuarine mud shrimp, *Upogebia major*. *J. Mar. Biol. Assoc. UK* 94, 557–566. doi:10.1017/S0025315413001392
- Ullman, W.J., Aller, R.C., 1989. Nutrient release rates from the sediments of Saginaw Bay, Lake Huron. *Hydrobiologia* 171, 127–140. doi:10.1007/BF00008173
-

V

- Valdemarsen, T., Wendelboe, K., Egelund, J.T., Kristensen, E., Flindt, M.R., 2011. Burial of seeds and seedlings by the lugworm *Arenicola marina* hampers eelgrass (*Zostera marina*) recovery. *J. Exp. Mar. Bio. Ecol.* 410, 45–52. doi:10.1016/j.jembe.2011.10.006
- van Wesenbeeck, B.K., van de Koppel, J., Herman, P.M.J., Bakker, J.P., Bouma, T.J., 2007. Biomechanical warfare in ecology; negative interactions between species by habitat modification. *Oikos* 116, 742–750. doi:10.1111/j.0030-1299.2007.15485.x
- Volkenborn, N., 2012. Bioturbation and effects on sediment biogeochemistry [WWW Document]. URL <http://cosee.umaine.edu/climb/cmvt/index.cfm#/?id=7810&timer=1367> (accessed 11.28.16).
- Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J., Reise, K., 2007a. Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuar. Coast. Shelf Sci.* 74, 331–343. doi:10.1016/j.ecss.2007.05.001
-

- Volkenborn, N., Polerecky, L., Hedtkamp, S.I.C., van Beusekom, J.E.E., de Beer, D., 2007b. Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. *Limnol. Oceanogr.* 52, 1898–1909. doi:10.4319/lo.2007.52.5.1898
- Volkenborn, N., Polerecky, L., Wetthey, D.S., DeWitt, T.H., Woodin, S.A., 2012. Hydraulic activities by ghost shrimp *Neotrypaea californiensis* induce oxic–anoxic oscillations in sediments. *Mar. Ecol. Prog. Ser.* 455, 141–156. doi:10.3354/meps09645
- Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and stabilizing bioengineers on tidal flats: cascading effects of experimental exclusion. *Helgol. Mar. Res.* 63, 27–35. doi:10.1007/s10152-008-0140-9
- Vonk, J.A., Kneer, D., Stapel, J., Asmus, H., 2008. Shrimp burrow in tropical seagrass meadows: An important sink for litter. *Estuar. Coast. Shelf Sci.* 79, 79–85. doi:10.1016/j.ecss.2008.03.003

W

- Waldbusser, G.G., Marinelli, R.L., 2006. Macrofaunal modification of porewater advection: role of species function, species interaction, and kinetics. *Mar. Ecol. Prog. Ser.* 311, 217–231. doi:10.3354/meps311217
- Walker, S.P., 1977. *Probopyrus pandalicola*: discontinuous ingestion of shrimp hemolymph. *Exp. Parasitol.* 41, 198–205. doi:10.1016/0014-4894(77)90145-X
- Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, a R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* 106, 12377–12381. doi:10.1073/pnas.0905620106
- Webb, A.P., Eyre, B.D., 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Mar. Ecol. Prog. Ser.* 268, 205–220.
- Welsh, D., Bartoli, M., Nizzoli, D., Castaldelli, G., Riou, S., Viaroli, P., 2000. Denitrification, nitrogen fixation, community primary productivity and inorganic-N and oxygen fluxes in an intertidal *Zostera noltii* meadow. *Mar. Ecol. Prog. Ser.* 208, 65–77. doi:10.3354/meps208065

- Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100. doi:10.1890/0012-9658(2003)084[1083:Arotii]2.0.Co;2
- Wethey, D.S., Woodin, S.A., 2005. Infaunal hydraulics generate porewater pressure signals. *Biol. Bull.* 209, 139–45.
- Wethey, D.S., Woodin, S.A., Volkenborn, N., Reise, K., 2008. Porewater advection by hydraulic activities of lugworms, *Arenicola marina*: A field, laboratory and modeling study. *J. Mar. Res.* 66, 255–273. doi:10.1357/002224008785837121
- Wheatcroft, R.A., 1991. Conservative tracer study of horizontal sediment mixing rates in a bathyal basin, California borderland. *J. Mar. Res.* 49, 565–588. doi:10.1357/002224091784995792
- Williams, J.D., An, J., 2009. The cryptogenic parasitic isopod *Orthione griffenis* Markham, 2004 from the eastern and western Pacific. *Integr. Comp. Biol.* 49, 114–126. doi:10.1093/icb/icp021
- Williams, J.D., Boyko, C.B., 2012. The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). *PLoS One* 7, e35350. doi:10.1371/journal.pone.0035350
- Wohlgemuth, D., Solan, M., Godbold, J.A., 2016. Specific arrangements of species dominance can be more influential than evenness in maintaining ecosystem process and function. *Sci. Rep.* 6, 39325. doi:10.1038/srep39325
- Wood, E.D., Armstrong, F.A.J., Richards, F.A., 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *J. Mar. Biol. Assoc. United Kingdom* 47, 23–31. doi:10.1017/S002531540003352X
- Woodin, S.A., Wethey, D.S., Volkenborn, N., 2010. Infaunal hydraulic ecosystem engineers: cast of characters and impacts. *Integr. Comp. Biol.* 50, 176–87. doi:10.1093/icb/icq031

Z

- Ziebis, W., Forster, S., Huettel, M., Jørgensen, B.B., 1996. Complex burrows of the mud shrimp *Callinassa truncata* and their geochemical impact in the sea bed. *Nature* 382, 619–622. doi:10.1038/382619a0

Données supplémentaires

Annexe I : Positive interaction between seagrass (*Zostera noltei*) and burrowing mud shrimp (*Upogebia pusilla*), a preliminary field study

Introduction

Recreational fishermen in Arcachon bay have long known that the highest abundances of their favorite bait, the mud shrimp *Upogebia pusilla* locally called “machotte”, are found in intertidal seagrass meadows. This preliminary work was aiming at testing the hypothesis that this endobenthic thalassinid crustacean species is indeed positively interacting with the dwarf grass *Zostera noltei* and, if so, to determine what are the main reasons of this association. The methodology used to test this hypothesis and the first results are presented below in the form of a short note.

Materials and methods

Study site

Located on the French Atlantic coast, Arcachon Bay (44°40'N, 1°10'W; Fig. 1) is a macro-tidal lagoon (tide range: 0.9 – 4.9 m) of 180 km² connected to the ocean by a narrow channel (2 - 3 km wide for about 12 km long). The inner part (156 km²) consist mostly in intertidal areas (115 km²), which are covered by large *Zostera noltei* meadows (70 km²) considered as the largest dwarf grass meadow in Europe (Auby and Labourg 1996; Plus et al. 2010). The bay receives freshwater inputs from the “canal des étangs” located in the North part and mostly from the Leyre River situated in the south-eastern part. Water temperature seasonally fluctuates between 6 and 25 °C and salinity between 27 and 36 (Auby et al. 2011).

Sampling procedure

Fifteen intertidal stations spread across Arcachon Bay were investigated in June 2014 (**Figure AI.1**). At each station, one small (3 cm inner diameter, 10 cm long) and nine large (9.4 cm inner diameter, 25 cm long) sediment cores were collected by hand, using transparent acrylic tubing (15 and 40 cm long, respectively) for further sediment characteristics analyses. A vertical photograph of the sediment surface was consistently taken within three 50 × 50 cm squares to

estimate the mean leaf coverage at low tide. A sample of seagrass (including roots and rhizomes) was also collected using a 25×25 cm hand corer and placed in a plastic bag to prevent material loss during transport.

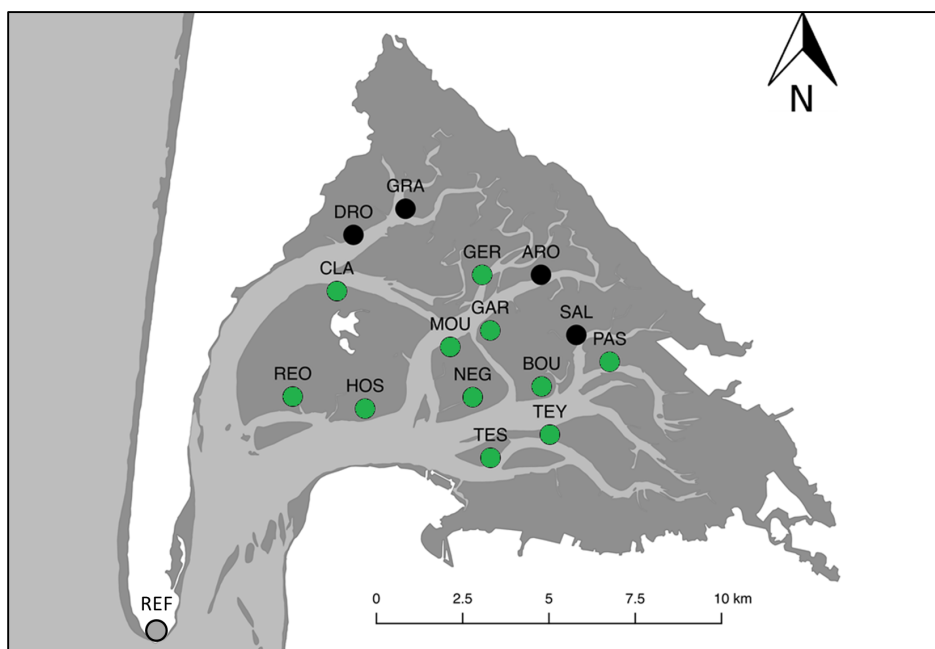


Figure AI.1 : Location of the sampling sites in Arcachon Bay (ARO: Arouillet; BOU : Bourrut; CLA : Le Cla; DRO: Drole; GAR : Garrèche; GER: Germanan; GRA: Graveyron; HOS : Les Hosses; MOU : Les Moussettes; NEG : La Nègue; PAS : Passant; REO : La Réousse; SAL: Salos; TES : Le Tes; TEY : Le Teychan) and the reference point (REF) from which the distance from the sea was measured. *Light grey*: ocean and subtidal area; *Dark grey*: intertidal area; *White*: land; *Green spots*: location with *U. pusilla*; *Black spots*: location without *U. pusilla*

The average density of *Upogebia pusilla* was determined by counting burrows within three 4×4 m squares randomly positioned over the mudflat. To identify interconnected galleries of a single burrow we used a bait piston pump, which was positioned on one opening and then gently operated to induce a water jet through all other burrow holes. Additionally, the maximal mud shrimp density was similarly measured within a 1×1 m square positioned within the highest burrow density area. At the same time, about 55 mud shrimp were collected using the bait piston pump and immediately isolated in individual plastic bags to avoid aggression and appendage loss. They were brought back to the laboratory, where the muscle of five of them was collected, pooled and then grounded into powder using a ball mill after being freeze-dried. The other mud shrimp were anesthetized by cold (15 min at -18 °C) before being preserved in 4 % formaldehyde.

Sediment characteristics and seagrass biomass

The median grain diameter (D_{50}) of the 20 first centimetres of the sediment column was assessed using a laser microgranulometer (MALVERN® Master sizer S).

The sediment porosity was assessed by slicing a large sediment core every 5 mm from the top to 2 cm depth, every 10 mm between 2 and 10 cm depth and every 50 mm between 10 and 20 cm depth. Each sediment slice was weighed and immediately frozen. The loss of water was measured after freeze-drying and corrected for sea salt content.

The sediment permeability was measured in small sediment cores by the “constant head method”, which consists in measuring the flow of water through the sediment matrix at a given hydraulic pressure (Klute and Dirksen 1986). The hydraulic conductivity (K in m s^{-1}) was calculated using equation (1):

$$K = (V \times L) / (h \times A \times t) \quad (1)$$

Where V is the volume of water collected (m^3) over a given time period T (s), L is the sediment core length (m), h is the height of the water column (pressure head, m), A is the surface area of the sediment-water interface (m^2) and t is the duration of water collecting.

The permeability (k in m^2) was then calculated using equation (2):

$$k = (K \times m) / (d \times g) \quad (2)$$

Where K is the hydraulic conductivity (m s^{-1}), m is the porewater viscosity ($\text{g m}^{-1} \text{s}^{-1}$), d is the water density (g m^{-3}) and g is the gravity ($= 9.81 \text{ m s}^{-2}$).

The Total Nitrogen (TN) and Organic Carbon content (OC) was measured on homogenized freeze-dried samples used for porosity calculation (see above), with an automatic CN analyser (ThermoFinnigan Flash EA2000 Series). For OC measurements, the sediment was previously acidified with 2M HCl (overnight at 50°C) to remove carbonates. The isotopic ratio of the surface sediment (0-0.5 cm depth) and the sediment column (15-20 cm depth) were analysed using an isotope ratio mass spectrometer (Isoprime, GV instrument) connected to the CN analyser. According to the recommendation of the IUPAC, isotopic data are expressed in the conventional delta notation (Coplen 2011):

$$\delta^{13}\text{C}_{\text{sample}} \text{ or } \delta^{15}\text{N}_{\text{sample}} = (R_{\text{sample}} \div R_{\text{standard}}) - 1 \quad (3)$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ and the references were Vienna Pee Dee Belemnite limestone (V-PDB) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. Analytical uncertainties were $< 0.2 \text{ ‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and $< 0.2 \text{ mol mol}^{-1}$ for C:N ratio.

Seagrass dry weights ($\pm 0.1 \text{ mg}$) were assessed after freeze-drying.

***Upogebia pusilla* analyses**

Mud shrimp Total length (TL) was measured from the tip of the rostrum to the tip of the telson and rounded down to the last millimetre. Sex was determined based on the presence or absence of gonopore and pleopod 1 (Pinn et al. 2001; Ubaldo et al. 2014; Pascal et al. 2016). Individual dry weights (DW, $\pm 0.1 \text{ mg}$) were assessed after 48 h at 60 °C .

Mud shrimp nitrogen and carbon contents were measured on mud shrimp muscle powders without acidification using the same protocol as for sediment (see above). Carbon and nitrogen stable isotope were used to determine the main food sources of *Upogebia pusilla* after fractionation-correction of 2 ‰ for $\delta^{13}\text{C}$ and 4 ‰ for $\delta^{15}\text{N}$ (Yokoyama et al. 2005).

Data analysis

Differences in mud shrimp density, individual TL and individual DW between stations were assessed using one-way ANOVAs. The main ecological factors responsible for the significant differences were then identified using stepwise regressions. Six environmental parameters were considered: the median grain size, the sediment porosity, the sediment C:N ratio, the seagrass biomass, the mean altitude of the station and the distance to the ocean. This last value was obtained by measuring the linear distance between a given station and a reference point (**Figure AI.1**) located at the entrance of the bay. Sediment total nitrogen and organic carbon contents were not taken into account because of their strong collinearity with C:N ratio (variance inflation factor > 10). The sediment permeability was also removed from the analyses because of a lack of variability between the 15 studied stations. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in mud shrimp between surficial sediment and sediment column were assessed using one-way ANOVAs. .

For all statistical analyses, *a posteriori* *t* tests corrected using the Holm-Sidak procedure (HS *t* test) was used to assess differences among factors, whenever necessary. Data normality was tested using Shapiro-Wilk test and variance homogeneity using Bartlett's test. Statistical analyses were performed on untransformed data.

Results

Upogebia pusilla densities

Among the 15 sampled stations, *Upogebia pusilla* occurred in 12 and was then consistently associated with *Zostera noltei* (**Table AI.1**). Among the three sites where *U. pusilla* was absent, one was vegetalized while the two others were not (*i.e.*, bare sediment) (**Table AI.1**). Mud shrimp density significantly varied between stations (**Table AI.2**). Stepwise multiple linear regression analyse showed that 56 % of this variation could be explained by the seagrass DW with a positive relationship between these two variables (**Table AI.3**). It is worth noting that the station “Germanan” is the only one characterized by a high seagrass DW but a low mud shrimp density.

Table AI.1 : Mean (\pm SD) values of *Upogebia pusilla* and environmental variables in each station. The variation coefficients associated with vertical variability are given in brackets

	Réousse	Cla	Drole	Hosses	Graveyron	Moussettes	Nègue	Tes	Germanan	Garrèche	Bourut	Teychan	Arouillet	Salos	Passant
<i>Upogebia pusilla</i>															
Mean density	6.8 \pm 0.7	5.7 \pm 0.2	0.0	2.9 \pm 0.4	0.0	2.5 \pm 0.5	4.9 \pm 0.6	2.6 \pm 1.1	0.4 \pm 0.1	1.6 \pm 0.1	2.4 \pm 0.0	4.1 \pm 1.7	0.0	0.0	0.2 \pm 0.1
Max density	39.0	34.0	0.0	17.0	0.0	14.0	23.0	22.0	3.0	9.0	15.0	19.0	0.0	0.0	1.0
Mean length (mm)	43.1 \pm 5.6	46.3 \pm 5.2	--	43.8 \pm 5.9	--	43.5 \pm 4.4	44.2 \pm 5.7	42.0 \pm 7.1	--	43.9 \pm 5.6	44.6 \pm 5.4	46.1 \pm 5.6	--	--	42.5 \pm 4.4
Mean DW (g)	0.4 \pm 0.2	0.4 \pm 0.1	--	0.4 \pm 0.1	--	0.4 \pm 0.1	0.5 \pm 0.2	0.3 \pm 0.2	--	0.4 \pm 0.1	0.4 \pm 0.1	0.4 \pm 0.1	--	--	0.3 \pm 0.1
N (% DW)	11.9	12.1	--	11.8	--	12.2	12.8	12.3	11.8	12.8	12.6	11.5	--	--	12.4
C (% DW)	43.6	43.0	--	43.4	--	41.8	44.2	43.0	42.1	45.8	43.0	44.2	--	--	44.2
C:N (Mol/Mol)	4.3	4.2	--	4.3	--	4.0	4.0	4.1	4.2	4.2	4.0	4.5	--	--	4.1
Habitat															
D50 (μ m)	109.4	85.2	28.2	173.5	24.7	130.4	133.7	131.5	23.0	154.5	163.1	191.9	76.7	92.4	31.3
TN (% DW)	0.1 (9.8)	0.1 (13.3)	0.1 (8.0)	0.0 (11.4)	0.1 (6.9)	0.1 (19.1)	0.1 (15.6)	0.1 (13.0)	0.3 (6.7)	0.1 (20.6)	0.1 (16.8)	0.1 (17.4)	0.1 (11.4)	0.3 (6.3)	0.1 (5.27)
OC (% DW)	0.9 (10.6)	0.9 (13.2)	1.3 (8.4)	0.2 (13.1)	1.4 (7.2)	0.4 (21.3)	0.5 (20.3)	0.7 (16.8)	2.7 (7.5)	0.8 (23.8)	0.7 (16.7)	0.5 (21.5)	1.1 (11.8)	2.6 (4.9)	0.6 (7.7)
C:N (Mol/Mol)	14.3 (3.0)	11.6 (3.5)	11.6 (3.6)	8.7 (6.4)	12.2 (2.6)	10.9 (4.8)	11.3 (7.9)	12.1 (5.8)	11.5 (1.5)	11.4 (3.4)	11.8 (2.4)	9.0 (4.2)	11.1 (2.9)	12.0 (3.0)	13.2 (3.9)
Porosity (Volume ratio)	0.6 (15.5)	0.6 (9.6)	0.7 (4.5)	0.4 (8.3)	0.7 (6.2)	0.5 (8.5)	0.5 (9.0)	0.5 (9.7)	0.8 (6.3)	0.5 (16.6)	0.5 (12.0)	0.5 (10.8)	0.6 (10.3)	0.8 (3.9)	0.5 (3.8)
Perméability (m ²)	1.55E-14	2.92E-14	1.94E-13	3.53E-12	3.26E-13	6.47E-14	8.51E-12	1.29E-13	4.45E-14	6.95E-14	6.94E-13	3.04E-14	1.17E-13	8.54E-14	8.73E-14
Seagrass DW (g m ⁻²)	35.6	34.3	0.0	23.0	0.0	18.7	32.7	15.5	40.6	13.2	20.6	30.2	7.5	0.0	5.1
Altitude (m)	-0.7	-0.9	1.2	-0.6	0.2	-1.0	-0.2	0.2	0.6	-0.6	-0.1	0.1	0.1	0.1	0.4
Distance to Ocean (m)	4546	7829	9439	5187	10262	8185	7788	7476	10328	9358	9667	9321	11524	11284	11745

Table AI.2 : ANOVA results of station effects on *Upogebia pusilla* mean density, individual total length (TL) and individual dry weight (DW).

Source	df	MS	F	P value
Density				
Station	10	13.880	36.095	< 0.001
Residual	22	0.385		
TL				
Station	9	118.413	3.753	< 0.001
Residual	650	32.554		
DW				
Station	9	0.152	7.392	< 0.001
Residual	650	0.0206		
$\delta^{13}\text{C}$				
Station	2	10.632	26.178	< 0.001
Residual	37	0.406		
$\delta^{15}\text{N}$				
Station	2	72.748	517.687	< 0.001
Residual	37	0.141		

Upogebia pusilla total length and dry weight

The average TL and individual DW of mud shrimp significantly differed between the 12 inhabited stations (**Table AI.2**). Stepwise multiple linear regression showed that 88 % of this spatial variation could be explained by the sediment C:N ratio, the seagrass DW and the distance to the ocean. The relationship between the mud shrimp total length and the C:N ratio was positive whilst it was negatively correlated with the seagrass DW and the distance to ocean (**Table AI.3**). Similarly, mud shrimp DW significantly differed between stations. 69 % of this spatial variation could be explained by seagrass DW with a positive relationship between these two variables (**Table AI.3**).

Table AI.3 : Stepwise multiple linear regression results of environmental variables involved in the prediction of *Upogebia pusilla* mean density, individual total length (TL) and individual dry weight (DW). The absence of coefficient indicates that variable is not included in the model. * indicates significant factor effect

Dependent variable	Density			TL			DW		
Analyse of variance									
R²		0.56			0.88			0.69	
F		17.719			15.044			17.856	
p value		< 0.001*			0.003*			0.003*	
Correlation of environmental variables									
	Coefficient	F	p value	Coefficient	F	p value	Coefficient	F	p value
Constant	0.0315	--	--	41.176	--	--	0.268	--	--
D50	--	2.213	0.159	--	1.285	0.300	--	0.0245	0.880
C/N	--	0.302	0.591	-0.331	7.957	0.030*	--	0.0636	0.807
Porosity	--	3.469	0.053	--	0.938	0.370	--	0.371	0.559
Seagrass	0.118	17.7199	< 0.001*	0.137	33.143	0.001*	0.00467	17.856	0.003*
Altitude	--	0.0176	0.896	--	0.0169	0.901	--	1.002	0.346
Distance to ocean	--	3.337	0.056	0.000415	14.030	0.010*	--	0.539	0.484

Isotopic analyses

Upogebia pusilla muscle showed relatively constant isotopic signatures within Arcachon Bay (**Figure AI.2**). $\delta^{13}\text{C}$ signature was slightly but significantly higher (HS *t* test, $t = 6.904$ and 5.542 , $p < 0.001$ in both cases relatively to sediment surface and sediment column, respectively) in *U. pusilla* than in both, sediment surface and sediment column (-17.7 ± 0.4 vs. -18.9 ± 0.6 and -18.5 ± 0.8 ‰ for *U. pusilla*, sediment surface and sediment column, respectively). $\delta^{15}\text{N}$ signature was significantly higher (HS *t* test, $t = 25.061$ and 30.501 , $p < 0.001$ in both cases relatively to sediment surface and sediment column, respectively) in *U. pusilla* than in both, sediment surface and sediment column (8.9 ± 0.4 vs. 5.2 ± 0.3 and 4.4 ± 0.4 ‰ for *U. pusilla*, sediment surface and sediment column, respectively). Both sediment surface and sediment column showed constant isotopic signatures over Arcachon Bay (**Fig. AI.2**). However, sediment surface and sediment column had different isotopic signature. Indeed, $\delta^{15}\text{N}$ composition was significantly higher in sediment surface than in sediment column (HS *t* test, $t = 5.662$, $p < 0.001$) whereas $\delta^{13}\text{C}$ composition was similar between sediment surface and sediment column (HS *t* test, $t = 1.418$, $p = 0.165$).

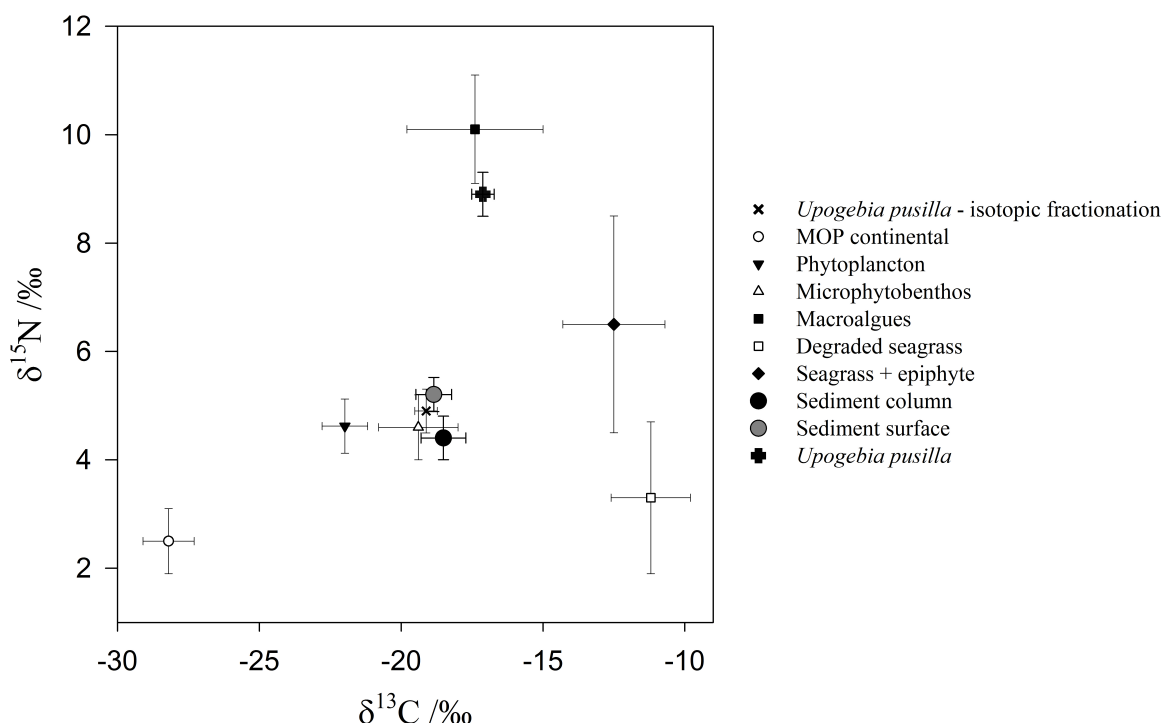


Figure AI.2 : Biplot showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of *Upogebia pusilla* specimens, *U. pusilla* specimens minus isotopic fractionation, sediment surface, sediment column. Data for phytoplankton, microphytobenthos, macroalgues, degraded seagrass, seagrass + epiphyte, and continental particulate organic matter in Arcachon Bay came from Dubois et al. 2012 and FELIBA project (V. DAVID & N. SAVOYE, unpublished data)

Discussion

One of the major concerns in ecology is to understand the mechanisms that structure natural communities and to determine why and how the mean density of a given species is likely to strongly vary between apparently closely related areas. In Arcachon Bay, the spatial distribution and abundance of *Upogebia pusilla* seems to be tightly dependent on the presence of *Zostera noltei* (field observations). More precisely, stepwise multiple linear regressions showed that the mud shrimp density is also significantly linked to the seagrass biomass (Table 3). This result may appear surprising at first since numerous previous studies investigating interactions between thalassinid crustaceans and seagrasses consistently report negative interactions (Brenchley 1981; Brenchley 1982; Suchanek 1983; Dumbauld and Wyllie-Echeverria 2003; Siebert and Branch 2005; Siebert and Branch 2006; Siebert and Branch 2007; Berkenbusch et al. 2007; Pillay and Branch 2011; Pillay et al. 2011). On one hand, through their intense bioturbation activity, thalassinidean species increase sediment erodability and resuspension thereby strongly reducing water clarity and photosynthetic capacities of seagrasses. On the other hand, seagrass roots and rhizomes enhance sediment stability, compactness and silt content which, altogether, limit the locomotion and burrow construction of large endobenthic species including burrowing crustaceans. However, Siebert & Branch (2005) observed a clear positive interaction between *Zostera capensis* and the mud shrimp *Upogebia africana*. They have hypothesized that this filter-feeding species may directly benefit (1) from the stabilisation of the sediment column by the seagrass for the construction of their burrow but also (2) indirectly from the exclusion of the deposit-feeder *Callianassa kraussi*, which may disrupt their burrows. In Arcachon Bay, any other mud shrimp species has been found neither in vegetated or bare intertidal sediment (Blanchet 2004; Blanchet et al. 2004). Therefore, it is very unlikely that the relatively high densities of *U. pusilla* observed in seagrass meadows may result from the exclusion of another mud shrimp. The most probable hypothesis is that seagrasses provide the sediment stability required for the construction of (semi-)permanent burrows, one of the main features of filter-feeding thalassinideans. Moreover, seagrass leaves attenuate the hydrodynamic intensity above the seafloor that traps suspended particles and enhances sedimentation rates of small organic particles (Ganthy et al. 2014). This positive relationship could also be partly explained by a trophic link in some species which directly or indirectly (*via* microbial gardening) feed on seagrass senescent material (Vonk et al. 2008). However, isotope measurements show that in

Arcachon bay seagrass is not the main food source of *U. pusilla* but rather phytoplankton, microphytobenthos and sedimented organic matter (**Figure AI.2**).

Conversely, *Z. noltei* may benefit from sediment oxygenation caused by burrow ventilation, which also avoid reduced toxic accumulation (e.g., sulphides) in porewaters (Suykerbuyk et al. 2012). The burying of seagrass seeds by sediment turnover may also reduce predation threat and facilitating their germination (Delefosse and Kristensen 2012). The station “Germanan” is the only one where a positive relationship between *U. pusilla* and *Z. noltei* is not obvious. Indeed, the mud shrimp density is low compared to other stations exhibiting well developed seagrass meadows. Two hypotheses may explain this particular singularity: (1) the seagrass biomass is there too high (the highest among the 15 sampled stations) so that, the shoot-root system binds the sediment and thus hinders the construction of deep burrows (Siebert and Branch 2006) and (2) the high altitude (the highest among the 12 stations with *U. pusilla*) lead to prolonged daily desiccation periods which thus drastically reduce filter-feeding opportunities (Cottet et al. 2007). Our results also revealed a positive relationship between seagrass biomass and *U. pusilla* TL and DW which could highlight that a stable sedimentary habitat may facilitate mud shrimp filter-feeding as reducing the proportion of time devoted to burrow maintenance (Siebert and Branch 2005).

In conclusion, this study provide circumstantial evidence for a positive effect of *Z. noltei* on *U. pusilla* as (1) they shared the same distribution, (2) mud shrimp is absent in bare mudflats, (3) mud shrimp (i) density (ii) TL and (iii) DW are positively linked to the seagrass biomass This positive relationship seems mainly due to the direct effect *Z. noltei* on the sediment stability.

References

- Auby I, Bost CA, Budzinski H, et al (2011) Régression des herbiers de zostères dans le Bassin d’Arcachon : état des lieux et recherche des causes Régression des herbiers de zostères dans le Bassin d’Arcachon : état des lieux et recherche des causes. IFREMER 155 <http://archimer.ifremer.fr/doc/00054/16507/>.
- Auby I, Labourg P-J (1996) Seasonal dynamics of *Zostera noltii* hornem. In the bay of arcachon (France). J Sea Res 35:269–277. doi: 10.1016/S1385-1101(96)90754-6
- Berkenbusch K, Rowden AA, Myers T (2007) Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. J Exp Mar Bio Ecol 341:70–84. doi: 10.1016/j.jembe.2006.10.026
- Blanchet, H., 2004. Structure et fonctionnement des peuplements benthiques du bassin d’Arcachon. Université Bordeaux I, 223p.
- Blanchet, H., de Montaudouin, X., Lucas, A., Chardy, P., 2004. Heterogeneity of macrozoobenthic assemblages within a *Zostera noltii* seagrass bed: diversity, abundance, biomass and structuring factors. Estuar. Coast. Shelf Sci. 61, 111–123. doi:10.1016/j.ecss.2004.04.008
- Brenchley GA (1982) Mechanisms of spatial competition in marine soft-bottom communities. J Exp Mar Bio Ecol 60:17–33. doi: 10.1016/0022-0981(81)90177-5
- Brenchley GA (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J Mar Res 39:767–790.
- Coplen TB (2011) Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. Rapid Commun Mass Spectrom 25:2538–2560. doi: 10.1002/rcm.5129
- Cottet M, de Montaudouin X, Blanchet H, Lebleu P (2007) *Spartina anglica* eradication experiment and in situ monitoring assess structuring strength of habitat complexity on marine macrofauna at high tidal level. Estuar Coast Shelf Sci 71:629–640. doi: 10.1016/j.ecss.2006.09.014
- Delefosse M, Kristensen E (2012) Burial of *Zostera marina* seeds in sediment inhabited by

-
- three polychaetes: Laboratory and field studies. *J Sea Res* 71:41–49. doi: 10.1016/j.seares.2012.04.006
- Dubois S, Savoye N, Grémare A, et al (2012) Origin and composition of sediment organic matter in a coastal semi-enclosed ecosystem: An elemental and isotopic study at the ecosystem space scale. *J Mar Syst* 94:64–73. doi: 10.1016/j.jmarsys.2011.10.009
- Dumbauld BR, Wyllie-Echeverria S (2003) The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquat Bot* 77:27–42. doi: 10.1016/S0304-3770(03)00077-9
- Ganthy F, Soissons L, Sauriau P-G, et al (2014) Effects of short flexible seagrass *Zostera noltei* on flow, erosion and deposition processes determined using flume experiments. *Sedimentology* n/a-n/a. doi: 10.1111/sed.12170
- Klute A, Dirksen C (1986) Hydraulic Conductivity and Diffusivity: Laboratory Methods. In: Klute A (ed) *Methods of Soil Analysis: Part 1 — Physical and Mineralogical Methods*. American Society of Agronomy, pp 687–700
- Kneer D, Asmus H, Vonk JA (2008) Seagrass as the main food source of *Neaxius acanthus* (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutierei* (Thalassinidea: Callianassidae). *Estuar Coast Shelf Sci* 79:620–630. doi: 10.1016/j.ecss.2008.05.013
- Pascal L, de Montaudouin X, Grémare A, Maire O (2016) Dynamics of the *Upogebia pusilla*–*Gyge branchialis* marine host–parasite system. *Mar Biol* 163:195. doi: 10.1007/s00227-016-2969-9
- Pillay D, Branch GM (2011) Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanogr Mar Biol* 49:137–192.
- Pillay D, Branch GM, Dawson J, Henry D (2011) Contrasting effects of ecosystem engineering by the cordgrass *Spartina maritima* and the sandprawn *Callianassa kraussi* in a marine-dominated lagoon. *Estuar Coast Shelf Sci* 91:169–176. doi: 10.1016/j.ecss.2010.10.010
- Pinn EH, Atkinson RJA, Rogerson A (2001) Sexual dimorphism and intersexuality in *Upogebia stellata* (Crustacea: Decapoda: Thalassinidea). *J Mar Biol Assoc UK* 81:1061–
-

1062. doi: 10.1017/S0025315401005070

Plus M, Dalloyau S, Trut G, et al (2010) Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuar Coast Shelf Sci* 87:357–366. doi: 10.1016/j.ecss.2010.01.016

Siebert T, Branch G (2005) Interactions between *Zostera capensis*, *Callianassa kraussi* and *Upogebia africana*: deductions from field surveys in Langebaan lagoon, South Africa. *African J Mar Sci* 27:345–356. doi: 10.2989/18142320509504094

Siebert T, Branch GM (2006) Ecosystem engineers: Interactions between eelgrass *Zostera capensis* and the sandprawn *Callianassa kraussi* and their indirect effects on the mudprawn *Upogebia africana*. *J Exp Mar Bio Ecol* 338:253–270. doi: 10.1016/j.jembe.2006.06.024

Siebert T, Branch GM (2007) Influences of biological interactions on community structure within seagrass beds and sandprawn-dominated sandflats. *J Exp Mar Bio Ecol* 340:11–24. doi: 10.1016/j.jembe.2006.08.007

Suchanek TH (1983) Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidea) bioturbation. *J Mar Res* 41:281–298.

Suykerbuyk W, Bouma TJ, van der Heide T, et al (2012) Suppressing antagonistic bioengineering feedbacks doubles restoration success. *Ecol Appl* 22:1224–1231. doi: 10.1890/11-1625.1

Ubaldo JP, Nanri T, Takada Y, Saigusa M (2014) Prevalence and patterns of infection by the epicaridean parasite, *Gyge ovalis* and the emergence of intersex in the estuarine mud shrimp, *Upogebia major*. *J Mar Biol Assoc UK* 94:557–566. doi: 10.1017/S0025315413001392

Vonk JA, Kneer D, Stapel J, Asmus H (2008) Shrimp burrow in tropical seagrass meadows: An important sink for litter. *Estuar Coast Shelf Sci* 79:79–85. doi: 10.1016/j.ecss.2008.03.003

Yokoyama H, Tamaki A, Harada K, et al (2005) Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. *Mar Ecol Prog Ser* 296:115–128. doi: 10.3354/meps296115

Contribution

Study conception: L. PASCAL, O. MAIRE, X. de MOUTAUDOUIN, A. GREMARE

Biometry measurements: numerous trainees, A. DAIRAIN, L. PASCAL

Sediment characteristics: L. PASCAL

Isotopic analyses: C. LIENART, N. SAVOYE, K. CHARLIER, L. PASCAL

Data analyses: L. PASCAL

Annexe II : Moulages de terrier *in-situ*

Méthode

Des moulages de terriers ont été effectués *in-situ* sur le site de “la Nègue” en Août 2014. De la résine polyester (Soromap) a été placée dans des sachets congélations (~500 mL). Le catalyseur (volume = 5 % du volume de résine) a été placé dans un pilulier le temps du transport. Une fois sur site, des ouvertures de terriers d'*Upogebia pusilla* ont été sélectionnées aléatoirement sur une zone d'environ 100 m². Avant de verser la résine, le catalyseur a été versé dans le sachet congélation et mélangé de manière homogène à la résine. Enfin, le mélange « Résine + Catalyseur » a été versé dans une des ouvertures du terrier à l'aide d'un entonnoir. Les ouvertures associées au terrier ont été repérées en observant l'eau s'échapper hors du terrier au fur et à mesure que de la résine y était introduite. De la résine a été versée jusqu'à ce que l'ensemble du terrier en soit rempli. Les moulages de terriers ont été récupérés, à la main, environ deux jours plus tard. Au laboratoire, la profondeur, l'étendu horizontale et le diamètre des terriers ont été mesurés. Enfin, le nombre d'ouverture et de chambre de retournement ont été comptées.



Figure AII.1 : Trois photographies de moulages de terrier présent sur papier millimétré (un carré = 1 cm)

Table AII.1 : Measurements of burrow horizontal spreading, depth, diameter and count of burrow openings and turning chambers assessed on resin cast of *Upogebia pusilla* burrow. Gray line (resin cast number 5) corresponds to a juvenile burrow; associated values are not taking into account in the computing of average (\pm SD) values.

Number	Horizontal spreading (cm)	Depth (cm)	Burrow openings	Turning chambers	Burrow diameter (cm)	Turning chamber diameter (cm)
1	85,9	28,3	3	5	1,6 \pm 0,1	2,5 \pm 0,2
2	55,9	20,9	2	3	1,5 \pm 0,1	2,4 \pm 0,2
3	18	48,6	2	5	1,7 \pm 0,4	2,6 \pm 0,4
4	19	36,6	2	4	1,6 \pm 0,1	2,2 \pm 0,5
5	9,6	12,5	2	7	0,6 \pm 0,0	1,4 \pm 0,3
6	54,8	30,4	3	8	1,7 \pm 0,1	2,9 \pm 0,5
7	33,2	40,5	3	4	1,6 \pm 0,1	2,6 \pm 0,4
8	31,6	29	4	5	1,4 \pm 0,2	2,3 \pm 0,5
9	21,2	34,3	2	4	1,5 \pm 0,1	2,9 \pm 0,2
10	37,1	35,1	2	3	1,3 \pm 0,1	2,9 \pm 0,2
11	34,2	22,5	2	5	1,4 \pm 0,0	2,5 \pm 0,5
Moyenne	39,1 \pm 21,1	32,6 \pm 8,3	2,5 \pm 0,7	4,6 \pm 1,4	1,5 \pm 0,1	2,6 \pm 0,2

Annexe III : Relations biométriques

Cette annexe correspond au « supplementary material » cité dans le chapitre 3 – Partie A : « Dynamics of the *Upogebia pusilla*-*Gyge branchialis* marine host-parasite system » (« **Appendix 3A.1** »). Ces données ont été publiées avec l'article scientifique correspondant dans la revue *Marine Biology* (2016, 163 : 195 ; doi : 10.1007/s00227-016-2969-9)

Table AIII.1 : Biometry relationships for *U. pusilla* according to sex categories. Different lines in sex category indicate significant between sex categories differences (ANCOVA, $p < 0.05$) in the considered biometric relationship. AFDW: Ash-free Dry Weight of total shrimp (g); CL: Cephalo-thoracic carapace Length (mm); DW: total shrimp Dry Weight (g); DW2pr: Dry Weight of 2 Productylus; MM: Male; FF: Female; FM: Feminized Male; FW: total Fresh Weight (g); Lpl: Length of pleopod (mm); Lpr: Length of productylus (mm); TL: Total Length (mm); Wpr: Width of productylus (mm)

Sex categories	Biometric relationship	N	r ²
MM	$\log DW = 3.067 \log TL - 5.467$	170	0.77
FF	$\log DW = 2.610 \log TL - 4.780$	394	0.67
FM	$\log DW = 2.947 \log TL - 5.369$	38	0.62
MM	$CL = 0.549 TL - 5.996$	41	0.70
FF	$CL = 0.431 TL - 1.772$	93	0.62
FM	No data		
MM	$Lpr = 0.172 TL - 0.095$	138	0.59
FF	$Lpr = 0.080 TL + 2.640$	277	0.37
FM	$Lpr = 0.102 TL + 0.095$	37	0.53
MM	$Wpr = 0.126 TL - 1.267$	138	0.63
FF & FM	$Wpr = 0.043 TL + 0.874$	310	0.45
MM	No pleopod		
FF & FM	$Lpl = 0.094 TL + 0.171$	362	0.54
MM	$\log DW_{2pr} = 3.619 \log TL - 7.126$	34	0.75
FF & FM	$\log DW_{2pr} = 2.358 \log TL - 5.313$	93	0.35
MM & FF	$AFDW = 0.758 DW - 0.011$	132	0.95
FM	No data		
MM	$FW = 4.796 DW + 0.402$	23	0.86
FF	$FW = 4.352 DW + 0.528$	57	0.72
FM	No data		

Annexe IV : Romero-Ramirez et al. 2016

Development and validation of a video analysis software for marine benthic applications

A. Romero-Ramirez, A. Grémare, Guillaume Bernard, Ludovic Pascal, Olivier Maire, J.C. Duchêne

University of Bordeaux - CNRS, EPOC, UMR 5805, F33120 Arcachon, France

Article publié dans la revue Journal of Marine System⁵

162:4-17,2016 ; doi : 10.1016/j.jmarsys.2016.03.003

⁵ Ce manuscrit correspond à la version acceptée de l'article et présente des différences mineures par rapport à la version éditée. Cette dernière est disponible sur le site de l'éditeur : <http://www.sciencedirect.com/science/article/pii/S0924796316300057>

Abstract

Our aim in the EU funded JERICO project was to develop a flexible and scalable imaging platform that could be used in the widest possible set of ecological situations. Depending on research objectives, both image acquisition and analysis procedures may indeed differ. Up to now the attempts for automating image analysis procedures have consisted of the development of pieces of software specifically designed for a given objective. This led to the conception of a new software: AVIExplore. Its general architecture and its three constitutive modules: AVIExplore – Mobile, AVIExplore – Fixed and AVIExplore – ScriptEdit are presented. AVIExplore provides a unique environment for video analysis. Its main features include: (1) image selection tools allowing for the division of videos in homogeneous sections, (2) automatic extraction of targeted information, (3) solutions for long-term time-series as well as large scale image acquisition, (4) real time acquisition and in some cases real time analysis, (5) a large range of customized image-analysis possibilities through a script editor. The flexibility of use of AVIExplore is illustrated and validated by three case studies: (1) Coral identification and mapping, (2) Identification and quantification of different types of behaviors in a mud shrimp, and (3) Quantification of filtering activity in a passive suspension-feeder. The accuracy of the software is measured comparing with visual assessment. It is: 90.2 %, 82.7%, and 98.3% for the three case studies, respectively. Some of the advantages and current limitations of the software as well as some of its foreseen advancements are then briefly discussed.

Software availability

Name: AVIExplore

First available: 2015

Language: Microsoft Visual C# and C++

Requirements:

- Hardware: Pentium PC or equivalent with at least 2GB of RAM

- Software: Microsoft Windows 7. Microsoft Framework v4.5. The AVI standard is used and the compression format selected is Microsoft MPEG4 Version 2

Software size: 77Mb

Availability: on request to authors

Free for research and educational purposes.

1. Introduction

Imaging technologies are currently used to address different questions related to marine benthic ecology (see Solan et al., 2003 for review) including: (1) the assessment of benthic biodiversity (Mallet and Pelletier, 2014; Spencer et al., 2005), (2) the study of faunal composition (Cuvelier et al., 2012; Duffy et al., 2014), (3) habitat mapping (Williams et al., 2012), (4) the characterization and quantification of behaviors and biological activities (Grémare et al., 2004; Jordana et al., 2000; Maire et al., 2007a; Matabos et al., 2011; Matabos et al., 2015), (5) the quantification of sediment reworking (Bernard et al., 2012; Maire et al., 2007b), and (6) ecological quality assessment (Rosenberg et al., 2009).

Imaging is a non-destructive technique that: (1) allows for the saving of initial raw information and thus for potential re-analysis, and (2) records both visible benthic organisms and other biological/ biogeochemical parameters resulting from biological activity such as the apparent Redox Potential Discontinuity on Sediment Profile Images (Romero-Ramirez et al., 2013). The reasons for choosing imaging technologies differ depending on the aim of each study. As an example, benthos and epibenthos sampling strategies at deep seabed present some difficulties (Jamieson et al. 2013): (1) the use of trawls and sleds does not allow for quantitative samplings, (2) the use of traps and suction samplers result in biased samplings resulting from differences in feeding regimes and motility, and (3) the use of grabs and box corers is complicated by the use of long wires and possible heterogeneities in sediment penetrability. Furthermore there are several designs for sampling epibenthos and their efficiencies are substrate-dependent (i.e. beam trawls for soft bottoms or suction samplers for hard bottoms). None of the sampling gears are recommended as a standard for a quantitative epibenthos assessment across all substrate types (Rees and Service, 1993). Moreover, some species from the epibenthos community are very mobile, making them difficult to capture when sampling. In this context, video and image analysis has proven to be an alternative and sometimes the only (i.e. hydrothermal vents, (Cuvelier et al., 2012)) *in situ* tool adequate to assess the epibenthos at all substrate types in a qualitative and/or quantitative manner.

In or ex situ imaging devices for benthic surveys can be deployed from different platforms (Smith and Rumohr, 2013), which can be divided into two main types: static platforms such as benthic landers (Roberts et al., 2005), and (2) mobile platforms such as Remote Operated Vehicles (ROV) or Autonomous Underwater Vehicles (AUV). Each type of platform provides image sequences with their own specificities that have to be taken into

account during processing. Both static and mobile platforms produce series of images often acquired under different light conditions (especially when deployed in shallow waters) because of: (1) changes in water turbidity, (2) changes in the intensity of natural light, and/or (3) the development of biofilms. In addition the series of images derived from mobile platforms need to be geo-referenced to produce sound habitat mapping.

Although the use of automated image acquisition systems is clearly currently spreading worldwide (Mallet and Pelletier, 2014), corresponding analyses are still most often achieved manually/visually (Cuvelier et al., 2012; Matabos et al., 2011; Sarrazin et al., 1997; Spencer et al., 2005; Vertino et al., 2010). Significant efforts have been made to automatically or semi-automatically process isolated images using either generic (Birchenough et al., 2012; de Moura Queirós et al., 2011) or specific software (Teixidó et al., 2011; Romero-Ramirez et al., 2013). With the arrival of newer video sensors, the tendency towards increasing video duration, image resolution and time frequency acquisition, makes corresponding image analysis very time-consuming (Edgington et al., 2006). Locating sequences of images containing important information would lighten this task (Lebart et al. 2003). Moreover, the complexity of the information contained in each image makes it highly operator-dependent (Cuvelier et al., 2012; Germano et al., 2011). There have been some attempts to generate automated image-analysis procedures (Aguzzi et al., 2011; Edgington et al., 2006; Kannappan and Tanner, 2013; Lebart et al., 2003; Mane and Pujari, 2014; Nowak et al., 2008; Romero-Ramirez et al., 2013; Teixidó et al., 2011). These have included both the automatic detection (Aguzzi et al., 2011; Edgington et al., 2006; Kannappan and Tanner, 2013) and in some cases even the identification of large epibenthic organisms on videos using either fixed (Aguzzi et al., 2011) or mobile cameras (Edgington et al., 2006). Given the large variety of possible applications of imaging in benthic ecology, a flexible software, which could provide users with an assistance for the widest possible set of all applications is however clearly still missing.

One of the aims of the JERICO project (<http://www.jerico-fp7.eu/>) was to develop the use of image analysis techniques to monitor a large set of biological components and processes recorded either at high frequency and/or over large scales using automated or semi-automated procedures. In this context, we report here on the AVIExplore software that provides a unique flexible environment for automated video analysis. AVIExplore proposes different interfaces to analyze videos originating from imaging devices set on mobile and/or fixed platforms. The principal features of AVIExplore are: (1) to provide image selection tools

allowing for the division of videos in homogeneous subsections, (2) to allow for the automatic extraction of targeted information, (3) to propose solutions for long-term time-series as well as large scale image acquisition, (4) to allow for real time acquisition and in some cases real time analysis, (5) to provide a large range of customized image-analysis possibilities through a script editor. This paper presents the principles and the structure of the AVIExplore software. Its capacities are also illustrated via the presentation of several case studies for which it has already been used. These include an: (1) automated search for coral colonies in a video recorded using a mobile imaging platform, (2) automated behavior identification of *Upogebia pusilla* within the sediment column of a thin aquarium based on a video recorded using a fixed device, and (3) automated assessment of temporal changes in the filtering activity of a passive suspension feeding benthic species based on a video of the sediment surface recorded with a fixed device.

2. AVIExplore software description

2.1. Generalities and common features

AVIExplore is a software that allows acquisition and analysis of standardised AVI videos. It presents a graphical user interface (**Figure AIV.1**) that allows access to three different modules:

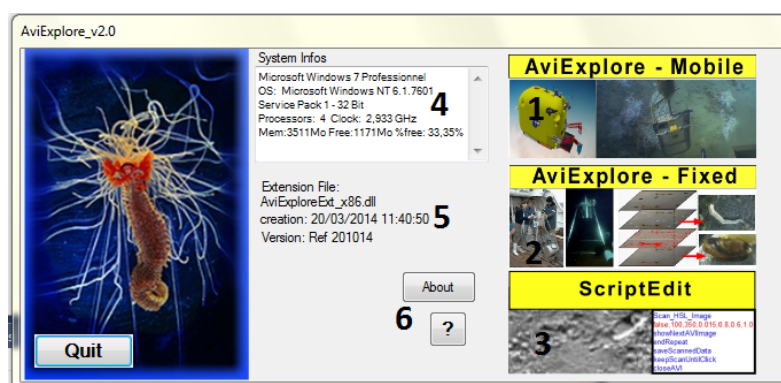


Figure AIV.1 : AVIExplore graphical user interface: (1) AVIExplore – Mobile module, (2) AVIExplore – Fixed module, (3) AVIExplore – ScriptEdit module, (4) summary of system characteristics, (5) extension files for future versions, and (6) software manual and information.

(1) AVIExplore - Mobile. This module allows the extraction of information from videos taken with moving sensors and cameras. It has two working modes: real time and recorded video.

(2) AVIExplore - Fixed. This module allows for the survey of activity on surfaces by using videos taken with a fixed camera. It has two working modes: real time and recorded video.

(3) ScriptEdit. This module can be seen as a tool that allows writing and testing scripts in view of their use in the other two AVIExplore modules. It is however a standalone module that can be used to compute data from videos or images.

The three modules of AVIExplore use a similar internal structure (**Figure AIV.2**). Images are extracted from video sources; each incoming image being called 'Origin Image'. The result of applying an operation (for example contrast enhancement) on an 'Origin Image' is saved as a 'Work Image'. If the user needs to apply a second operation, he can either save it as 'Secondary Work Image' or rewrite on the initial 'Work Image'. In order to speed up operations, it is possible to work with greyscale images, which are then saved as a 'Grey Image'. Operations can be bidirectional as a 'Work image' can become an 'Origin Image'. However, in this case, this transformation is not reversible as the return to the initial 'Origin image' is impossible. A mask is a tool used to select a subset of pixels in an image. These masks can be directly drawn by the user or computed using a script. Binary hexadecimal masks are used as internal structures to store intermediate information. They can be saved and loaded using an external file (*.msk). Other Regions Of Interests (ROIs) can also be drawn by the user and saved in a different external file (*.roi). ROIs can be converted in internal binary regions for computations.

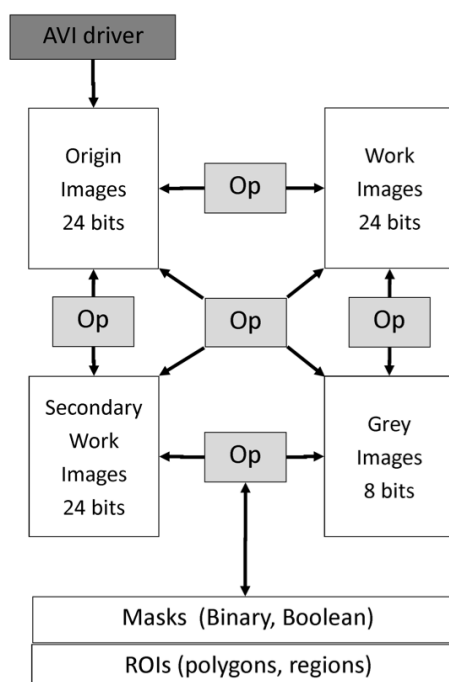


Figure AIV.2 : Internal structure of AVIExplore. Origin, work and secondary work images are 24 bit bitmaps for color images and video frames. Gray images are 8 bit images. Regions of interest (ROIs) and masks are structures saved in external files, which can be loaded on demand. Op: operation

External files are similar within the three modules. They gather different types of information (**Figure AIV.3**): (1) the AVI input file (main input), (2) script files to process images (processing), (3) ROI files to store working areas (service), (4) mask files to get fast mask loading (service), (5) data and companion files to store intermediate results (information), (6) time and position files which can be of interest for image tracking collected with mobile carriers (information), and (7) export information in text files.

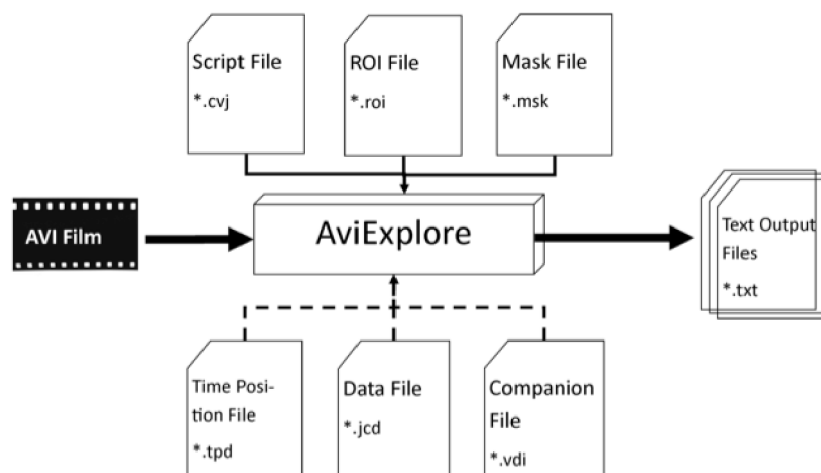


Figure AIV.3 : External files generated by AVIExplore. Continuous arrows refer to files that must be loaded by the user. Dashed arrows refer to files automatically loaded by the software.

The graphic user interfaces of each of the three modules share a similar structure with: (1) a displayed window, (2) a strip menu, and (3) a scrollbar for video timing. However, depending on the module, the functionalities present on the left side of the window may differ (**Figure AIV.4**).



Figure AIV.4 : AVIExplore – Mobile, AVIExplore – Fixed and AVIExplore – ScriptEdit module's general graphic user interface: (1) video display window, (2) strip menu, (3) video time scrollbar, and (4) area differing between modules.

AVIExplore can be used for different purposes namely: (1) image acquisition, (2) testing of image-analysis procedures and image analysis *per se* (**Figure AIV.5**). The user may

consider AVIExplore real time acquisition mode (which is present within both the AVIExplore - Fixed and the AVIExplore - Mobile modules) for acquiring a video to be analyzed with another module. During testing, different functions can be tried out in order to optimize and automatize the image-analysis procedure, which will then be applied to a whole acquisition sequence or a batch of acquisition sequences. The AVIExplore - ScriptEdit module indeed allows for saving and then loading back any of the so-tested scripts

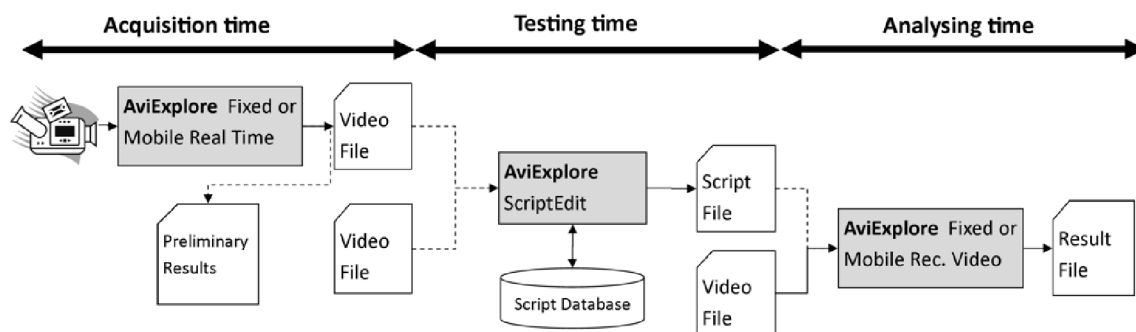


Figure AIV.5 : Interactions between different modules and modes of AVIExplore.

2.2. The AVIExplore Real Time acquisition mode

Real time acquisition can be achieved for both mobile and fixed platforms through AVIExplore - Mobile and AVIExplore - Fixed modules. The main advantages of monitoring real time acquisition using AVIExplore are: (1) an absolute control of image frequency acquisition, (2) the possibility for real time video treatments, which includes the possibility of applying different filters to incoming images as well as the use of masks and the selection of objects. The user may then choose to directly save results and no longer original images, which can prove valuable when using acquisition memory limited devices. There is however a clear limitation for real time analyses: the flow of incoming images cannot be interrupted. Processing time must therefore remain less than the time lag between consecutive images. As a consequence, computing loops online is not possible. This can be avoided by saving the original video and analyzing it afterwards.

2.3. The AVIExplore – Mobile module

AVIExplore - Mobile handles both the video to be analyzed and a geolocalization file, which is used to locate each image and associated identified objects in space. Sophisticated Remotely Operated Vehicles (ROVs) usually produce this file when acquiring images but

other mobile acquisition carriers do not. If the information concerning the location of the images is available through another way (e.g. a Log book), the user can generate a geolocalization file by himself. If not, the user can still proceed with image-analysis but in this case, identified objects will not be geographically located. The corresponding format for the geolocalization file is specified on **Table AIV.1**.

Table AIV.1 : Format of Geolocalization File: (1) Explanation, (2) Example

Number of images		1340			
Date and time [mm/dd/yyyy hh:mm:ss.ss]		10/14/2007 21:35:04.10			
Complementary information		Device info			
Date and time [mm/dd/yyyy hh:mm:ss.ss]	10/14/2007 21:35:04.10	39,5655667	18,4361983	548	
Latitude	10/14/2007 21:35:09.10	39,5655667	18,43618	548	
Longitude		...			
Depth					
(1)		(2)			

The first step when analyzing a video is to extract its images (**Figure AIV.6A**). When using AVIExplore, it is recommended to first proceed with a global scene analysis. This procedure extracts features (**Table AIV.2**) from the images and generates a companion file containing relevant metadata, which are used for a fast comparison between images. This process allows for the identification of common: (1) properties, and (2) objects between images. It can be used to define sections of the original video where the presence of the same specific object is suspected and which therefore can be processed using the same image analysis procedure (script). The values of the extracted features can be exported on a text file for post-treatment. Object detections can be done either on this module or on the Script Editor module. The section on AVIExplore - ScriptEdit module describes the type of extracted information that can be exported.

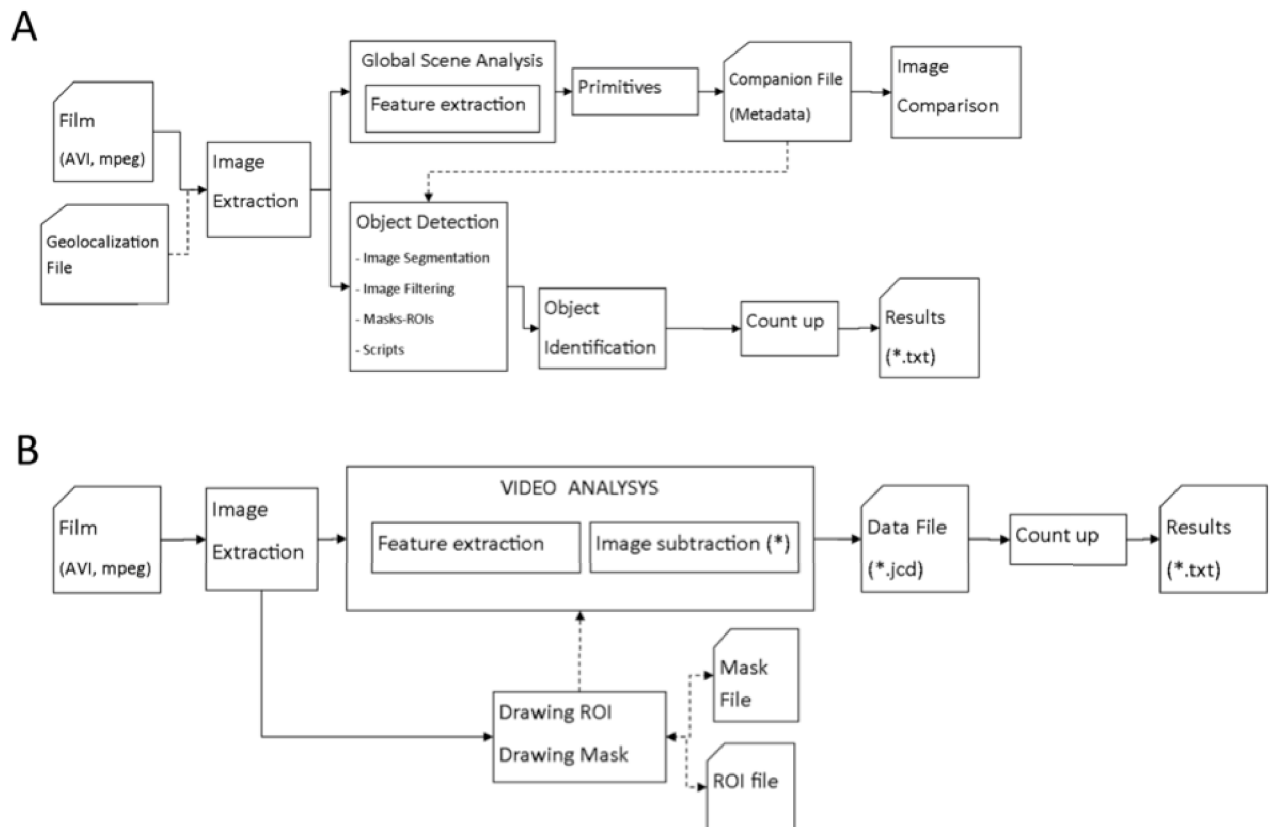


Figure AIV.6 : A: AVIExplore – Mobile: Typical flowchart of a video obtained with a mobile device, B: AVIExplore – Fixed: Typical flowchart of a video obtained with a fixed device.

Table AIV.2 : List of extracted features by the AVIExplore - Mobile module. In (1-6) i, j are the horizontal and vertical coordinates in the Greylevel Co-occurrence Matrix, P is the cell value.

List of Extracted Features	Description
Number of objects (SURF)	The number of objects found on an image when using “Speeded Up Robust Feature” for object detection
Object size (SURF)	The size of objects found on an image when using “Speeded Up Robust Feature” for object detection
Spatial moment	Weighted average of the intensities of the image pixels
Variance	Mean variance of the greyscale image
Hu1	First Hu moment for pattern recognition (Hu, 1962)
Hu2	Second Hu moment for pattern recognition (Hu, 1962)
Angular second moment (GLCM)	Also known as uniformity, it is the sum of squares of entries in the greylevel co-occurrence matrix (GLCM) (1): $\sum_{i,j=0}^{N-1} P_{i,j}^2$
Energy (GLCM)	Square root of the angular second moment
Entropy (GLCM)	Amount of information of the image needed for the image compression, it represents spatial disorder (2): $\sum_{i,j=0}^{N-1} -P_{i,j} \ln P_{i,j}$
Contrast (GLCM)	Measure of the intensity contrast between a pixel and its neighbor over the whole image. Sum of squares variance in the GLCM (3): $\sum_{i,j=0}^{N-1} P_{i,j} (i - j)^2$
Dissimilarity (GLCM)	Measure that defines the variation of grey level pairs (pixel and its neighbor) in an image (4): $\sum_{i,j=0}^{N-1} P_{i,j} i - j $
Inverse Difference Moment (GLCM)	Also called homogeneity. Measures of the closeness of the distribution of elements in the GLCM to the GLCM diagonal (5): $\frac{\sum_{i=0}^{N-1} \sum_{j=0}^{N-1} P_{i,j}}{1+(i-j)^2}$
Mean_i (GLCM)	The mean based on the reference pixels (μ_i)
Mean_j (GLCM)	The mean based on the neighbor pixels (μ_j)
Variance_i (GLCM)	Measures the dispersion around the mean, of values within the GLCM (σ_i, σ_j)
Variance_j (GLCM)	
Correlation (GLCM)	Measure of how correlated a pixel is to its neighbor over the whole image (6): $\sum_{i,j=0}^{N-1} P_{i,j} \left[\frac{(i-\mu_i)(j-\mu_j)}{\sqrt{\sigma_i^2 + \sigma_j^2}} \right]$
Hue	The Hue histogram
R	The red channel histogram
G	The green channel histogram
B	The blue channel histogram
Grey	The greylevel histogram

2.5. The AVIExplore - Fixed module

This module allows for surveying biological activity based on videos collected using a fixed carrier either *in* or *ex situ*. The analysis of a fixed video starts by extracting its images, which are then subtracted between each other (**Figure AIV.6B**). Three different types of subtraction are proposed: (1) ‘Previous’, (2) ‘Gap’, and (3) ‘Reference image’. When the ‘previous’ type is selected, the subtraction is carried out between all pairs of consecutive images. When the ‘Gap’ type, the subtraction is carried out between all pairs of images separated by a fixed number of images. When the ‘Reference image’ type is selected, the subtraction is always carried out between the current and a fixed reference image (which usually corresponds to the start of the recording and/or to a zero level of activity). Subtraction results can be expressed in three different modes: (1) absolute values, (2) positive values and (3) negative values. Both the type of subtraction and its combination with other parameters (**Table AIV.3**) must be adjusted by the user depending on image quality and desired analyses, although some default values are proposed. The user may choose to focus on some areas of the images by drawing a ROI or a mask. Image subtractions are then only achieved within the selected area and no longer in the whole image. At the end of the analysis a ‘Data File’ is created and loaded. The ‘Data File’ is a binary file that can be understood as a metadata companion file which allows the user to directly visualize the subtraction results. On this module, the user can choose to export those results obtaining two different text files. The first file includes for each image the position (barycenter) and size (number of pixels) of each isolated region where the subtraction result is bigger than the specified threshold. The second file provides the mean position (barycenter and standard deviation) and the total size (total number of pixels) of all the regions where the subtraction result is bigger than the specified threshold found on an image. The section describing the AviExplore - ScriptEdit module provides more examples of the extracted information that could be exported.

Table AIV.3 : List of parameters to select for analyzing when using the AVIExplore - Fixed module

Parameters to adjust	Description
Diff Mode	Type of subtractions
diffType	Expression of subtraction
Th	Threshold for subtraction difference
Min Sz	Minimum size of search objects
Max Sz	Maximum size of search objects
Use ROI	Use of a drawn region of interest
Use Mask	Use of a drawn Mask
Gap	Number of images between subtraction
	Reference image number

2.6. The AVIExplore – ScriptEdit module

The AVIExplore – ScriptEdit module allows writing and testing scripts, which can later be used in another AVIExplore module. However the AVIExplore – ScriptEdit module is also a standalone program that can proceed with the complete analysis of a video and produce a result file. Available functions and commands that can be used within this module can be divided into:

- (1) Video management and visualization functions.
- (2) Image processing operations. Some of these operations allows for: color filtering, image segmentation, edge detection, image and histogram equalization, morphological processing and noise removal.
- (3) Looping. Set of commands that allow applying one operation to a set of images.
- (4) Export and log. Functions that allow either to have a log or a result text file.
- (5) Masks and ROIs. Set of functions allowing the use of masks and ROIs within a script. Those masks and ROIs can either be the result of an image processing operation or designed by the user.

The detailed description of the high number of functions available is provided in the AVIExplore manual, which is embedded in the software and available online (http://www.epoc.u-bordeaux.fr/index.php?lang=fr&page=eq_ecobioc_aviexplore).

Depending on the scope of the analysis, dedicated searches must be carried out to identify/classify objects. The user can choose which information to export, some examples are: the number of objects on an image, the surface and the perimeter of each object, the width and the length of the minimum bounding rectangle of an object, the position of each object, the mean and standard deviation of all the positions and surfaces of all the objects on an image.

The ScriptEdit module proposes a functionality to help the user write scripts. This functionality provides the users with the parameters required by all specific functions. The current version of the software includes examples of object detection and identification routines (needed for the mobile module) to help the user building their own scripts and to provide insights on which kind of operations are relevant to obtain specific information. Scripts can be saved within a Microsoft access database and then become easily accessible for subsequent analyses. The AVIExplore – ScriptEdit module has a complementary utility for video edition, including: (1) cropping, (2) reducing duration, (3) reducing resolution, (4) changing frame frequency acquisition, (4) extracting images, and (5) building a video from extracted images.

3. Case studies

3.1. AVI-Explore – Mobile: Mapping of deep corals

3.1.1. General context

In the last decade live deep-water corals have been reported in the Ionian Sea at the Santa Maria de Luca (SML) Province (Taviani et al., 2005; Tursi et al., 2004). The most reported predominant species in this area are *Lophelia pertusa* and *Madrepora oculata*, both species present a multi-branch morphology that can provide ecological niches, refuges and substrates for a multitude of other species (Tursi et al., 2004). The SML Province contains living and dead isolated colonies of those deep-water corals as well as coral patches (Savini et al., 2005; Vertino et al., 2010). Different tools have been used to identify and characterize both macrofauna and habitats within the SML province (Mastrototaro et al., 2010; Tursi et al., 2004, Savini and Corselli, 2010, Taviani et al., 2005).

In this context, video imagery acquired with ROVs has been used to detect macrohabitat and determine main seafloor features that includes the percentage of recognizable dead and/or live coral colonies (Vertino et al., 2010). This last analysis was achieved but at a low spatial resolution and apparently by direct visual video observation

(Vertino et al., 2010). We report here on the use of the AVIExplore software to analyze another video collected in the same area. Our specific aims consisted in automatically: (1) detecting corals, and (2) differentiating between apparently dead and living coral patches.

3.1.2. Materials and methods

The analyzed video was recorded with a remotely operated vehicle (ROV) *Victor-6000* during the MEDECO cruise, which took place aboard the French R/V *Pourquoi Pas?* This ROV was equipped with a SONY DXC990 3 CCD camcorder (resolution of 720x576 pixels, frame rate of 25fps, duration 2 hours and 5 seconds). The study area covers 0.022 km². The video contained a total of 180,133 images. Because of the deployment of an automatic flash device, overexposed images were removed every 298 images. A total of 179,529 images were thus considered for the analysis. The video was processed using the AVIExplore – Mobile module. A region of Interest (ROI) was created to exclude imbedded text from the analysis (**Figure AIV.7**). Two different scripts were executed to assess the surface of: (1) apparently dead and living corals within each image (**Table AIV.4A**), and (2) only apparently living corals within each image (**Table AIV.4B**). The main feature used to determine living corals was its white-color (**Figure AIV.8**). A visual assessment was completed on a subsection (1330 images) to validate the so-obtained results. Images were then visually classified as: images with corals and images without corals. A comparison between the two assessment modes (visual and automatized via AVIExplore) was achieved. Total accuracy was computed as the number of images for which both classification modes were similar divided by the total number of compared images. An analysis of the types of errors and their frequency of occurrence was also carried out. False positive errors corresponded to the fact that AVIExplore classified an image as containing corals whereas the same image was visually classified as not containing corals. False negative errors corresponded to the fact that AVIExplore classified an image as not containing corals whereas the same image was visually classified as containing corals.

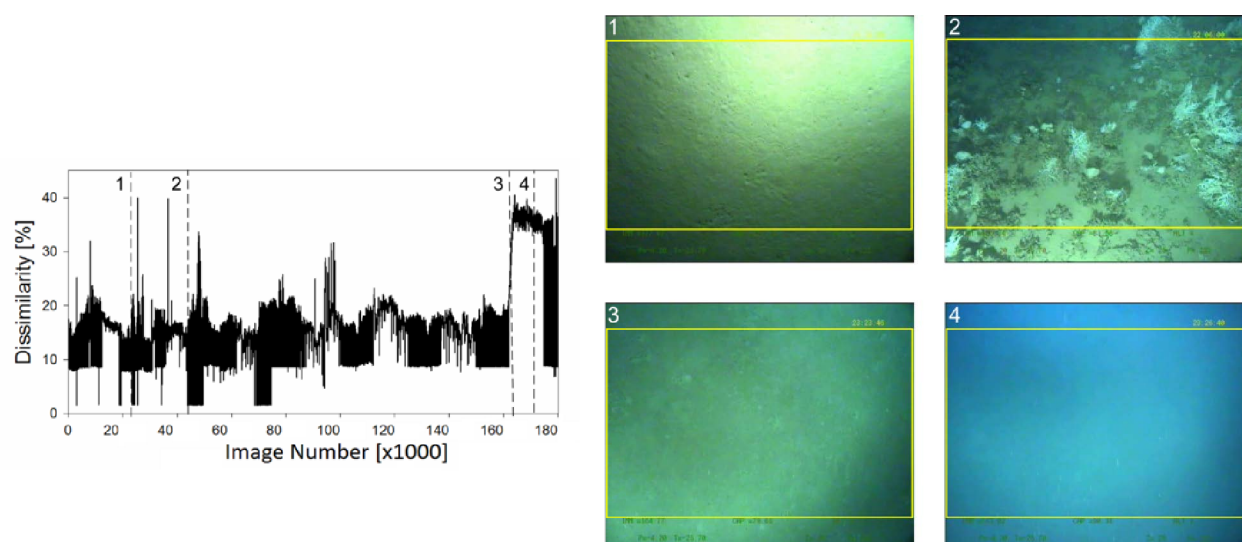


Figure AIV.7 : Coral mapping case study: dissimilarities of Grey-Level Co-occurrence Matrix for each image of the video. Numbered vertical dashed lines indicate different images which are shown on the right. 1 and 2: images of the water-sediment interface, 3: image of the water-sediment interface at high altitude and 4: image of the water column.

Table AIV.4 : Coral mapping case study: Details of the two scripts used to: detect, quantify the surface, visualize and save each analyzed image. For (A) apparently living and dead corals, and (B) apparently living corals.

Living and dead corals	Living corals
<pre> openLogFile true repeat 0,NbImg getRawHSLMask 80,200,true,110,350, 0.1,1.0,0.1,1.0 CopyOriginToBinBuf DilateMask binBuf eraseMaskBlobs 1,600,100000 fillBinBufHoles 140 reloadCurAVIImage ShowMask Origin,binBuf,0 CountPixelsInMask 1 WriteOneINTTextValue saveJpeg (DirectoryFolder\),100 showNextAVIImage 1 endRepeat closeLogFile </pre>	<pre> openLogFile true repeat 0,NbImg getRawHSLMask 50,200,true,110,350, 0.1,1.0,0.1,1.0 CopyOriginToBinBuf DilateMask binBuf eraseMaskBlobs 1,300,100000 fillBinBufHoles 140 reloadCurAVIImage BinarizeRGB 100,255,150,255,150,255, 1,1,1,0,0,true,Mask,Origin,true CountPixelsInMask 0 WriteOneINTTextValue saveJpeg (DirectoryFolder\),100 showNextAVIImage 1 endRepeat closeLogFile </pre>

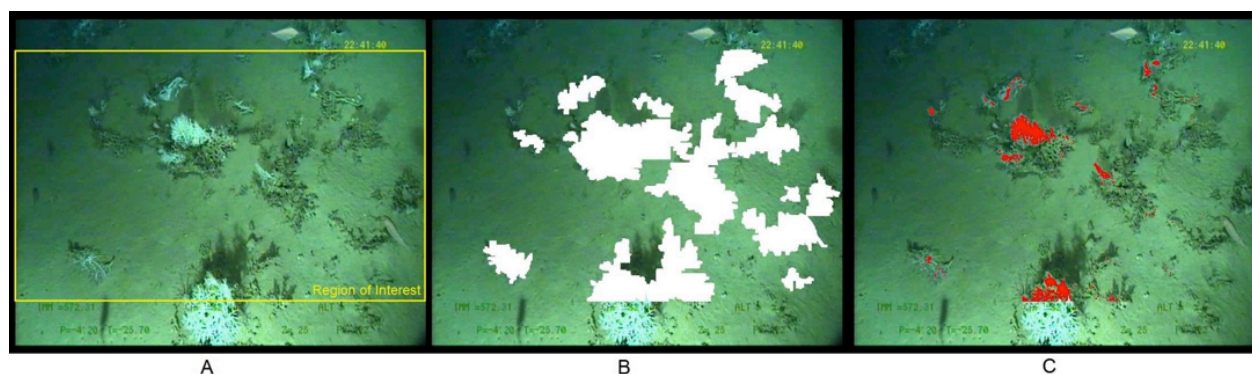


Figure AIV.8 : Coral mapping case study: results of the execution of the two scripts on a single image. (A) Original image showing the delimitation of ROI in yellow, (B) image with white overlay covering apparently dead and living corals, and (C) image with a red overlay covering only apparently living corals.

3.1.3. Results

The dissimilarity in the Grey-Level Co-occurrence Matrix (GLCM) computed from each image on the video was computed during the global scene analysis (**Table AIV.2**). This allowed us to identify (**Figure AIV.7**) a continuous sequence of images featuring high dissimilarity of their GLCM. The direct visualization of those images showed that they were recording the water column and no longer the water-sediment interface. They were thus discarded and only 161,000 images were considered for the identification of corals. An example of the results of the two executed scripts is shown in **Figure AIV.8**. These results were combined with the geolocalization file allowing for the mapping of apparently dead and apparently living coral colonies (**Figure AIV.9**). Agreement between images classified by the software and visually was achieved for 90.2% of the 1330 tested images. False positive and false negative error frequencies were 5.4 and 4.3%, respectively. Main sources of false positive errors were the presence of: (1) other megafauna, (2) fishes and (3) suspended sediment. Negative errors were mainly due to small corals and/or bad light conditions. Also, in some cases, corals were not so clearly visible but the human operator tended to infer their existence because the same corals could be seen on the previous image.

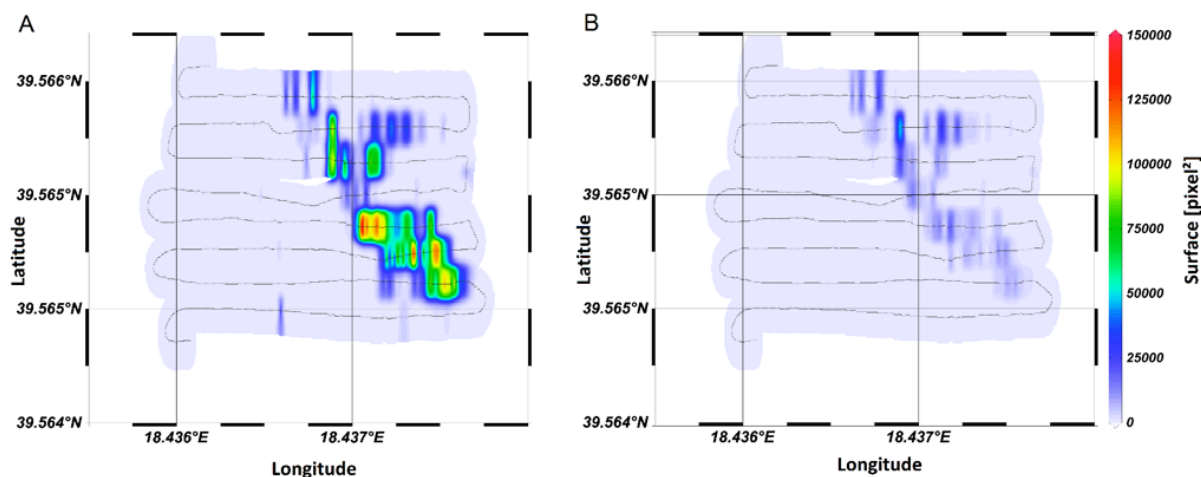


Figure AIV.9 : Coral mapping case study: Mapping of (A) apparently dead and living corals, and (B) apparently living corals

3.2. AVIExplore – Fixed: Identification and quantification of different types of behaviors in the mud shrimp *Upogebia pusilla*

3.2.1. General context

Burrowing crustaceans are among the most efficient bioturbators inhabiting marine soft sediments (Pillay and Branch, 2011). These organisms dig large galleries deep (up to 1m) in the sediment column and therefore rework large amount of particles. They also strongly increase the rate of exchanges between the sediment column and the overlying water through the ventilation of their burrows (Coelho et al., 2000; Webb and Eyre, 2004). High frequency time series of ventilation by burrowing invertebrates have been collected both *in situ* using pressure sensors (Volkenborn et al., 2012; Wethey and Woodin, 2005; Wethey et al., 2008) and *ex situ* using planar optodes (Volkenborn et al., 2007; Volkenborn et al., 2010; Volkenborn et al., 2012). Corresponding studies however remain largely descriptive since ventilation is highly dependent on animal behavior, which is very difficult to monitor in burrowing crustaceans because these organisms spend most of their time in their burrow. Up to now the description or the identification of different types of behaviors of burrowing crustaceans has only been achieved visually (Coelho et al., 2000; Dworschak, 1987; Stamhuis et al., 1996). The establishment of a quantitative relationship linking activity and sediment reworking, such as the one recently established by Maire et al., (2007d) for sediment reworking by the bivalve *Abra ovata*, is therefore still lacking for these bioturbators in spite of their potentially major role in the functioning of some coastal ecosystems. Here, we report on the use of AVIExplore to automatically assess and quantify different behaviors by the mud

shrimp *Upogebia pusilla*, which is common within the seagrass meadows of the Arcachon Bay (France). Our study is based on a video of a lateral view of a flat aquarium recorded in the laboratory.

3.2.2. Materials and methods

Our experiment was carried out in a large flat aquarium (40 × 25 × 2 cm) filled with 25 cm of natural sieved (0.5 mm mesh) sediment overlaid with 15 cm of aerated seawater. The sediment was left to settle for 48 h in the aquarium and the mud shrimp was introduced 1 week prior the beginning of the video recording the experiment to fully establish its burrow. The video (duration: 13h 20min, frequency of image acquisition: 0.1Hz, resolution: 2560 × 1920 pixels) was then recorded under infra-red light using a μ Eye camera (IDS®) controlled by a computer. The visual analysis of this movie allowed for the identification of several types of behaviors, namely: ‘Resting/ventilating’, ‘Burrowing’ and ‘Walking’. During ‘Resting/ventilating’, the mud shrimp remains at the same location within its burrow and its movements are restricted (e.g. to abdomen contractions and pleopod beating). During ‘Burrowing’, the mud shrimp moves within its burrow but only over a limited distance and it occasionally displaces sediment. During ‘Walking’, the mud shrimp moves within its burrow over large distances. During the present study, we used the AVIExplore – Fixed module to automatically analyze the video and to quantify these three behaviors. A ROI corresponding to the visible part of the burrow was first drawn (**Figure AIV.10A**). Each image was then subtracted from the preceding one and pixels featuring a positive differences higher than 30 (threshold value on an overall scale between 0 and 255 set after preliminary trials) were identified. For each pair of consecutive images, the AVIExplore – Fixed module generated: (1) the number of pixels within the ROI differing between the two images, and (2) the barycenter of those pixels. A signal treatment combining these two pieces of information was then defined to assess the behavior of the mud shrimp at each given time of the monitoring (**Figure AIV.11**). If the shape of the signal related to the number of pixels modified between two images is flat or consists either in a single peak or consecutive isolated peaks, then the attributed behavior for the corresponding images is ‘Resting/Ventilating’. If the signal has another shape, the range of positions of related pixels is used to differentiate between ‘Burrowing’ (small range) and ‘Walking’ (large range).

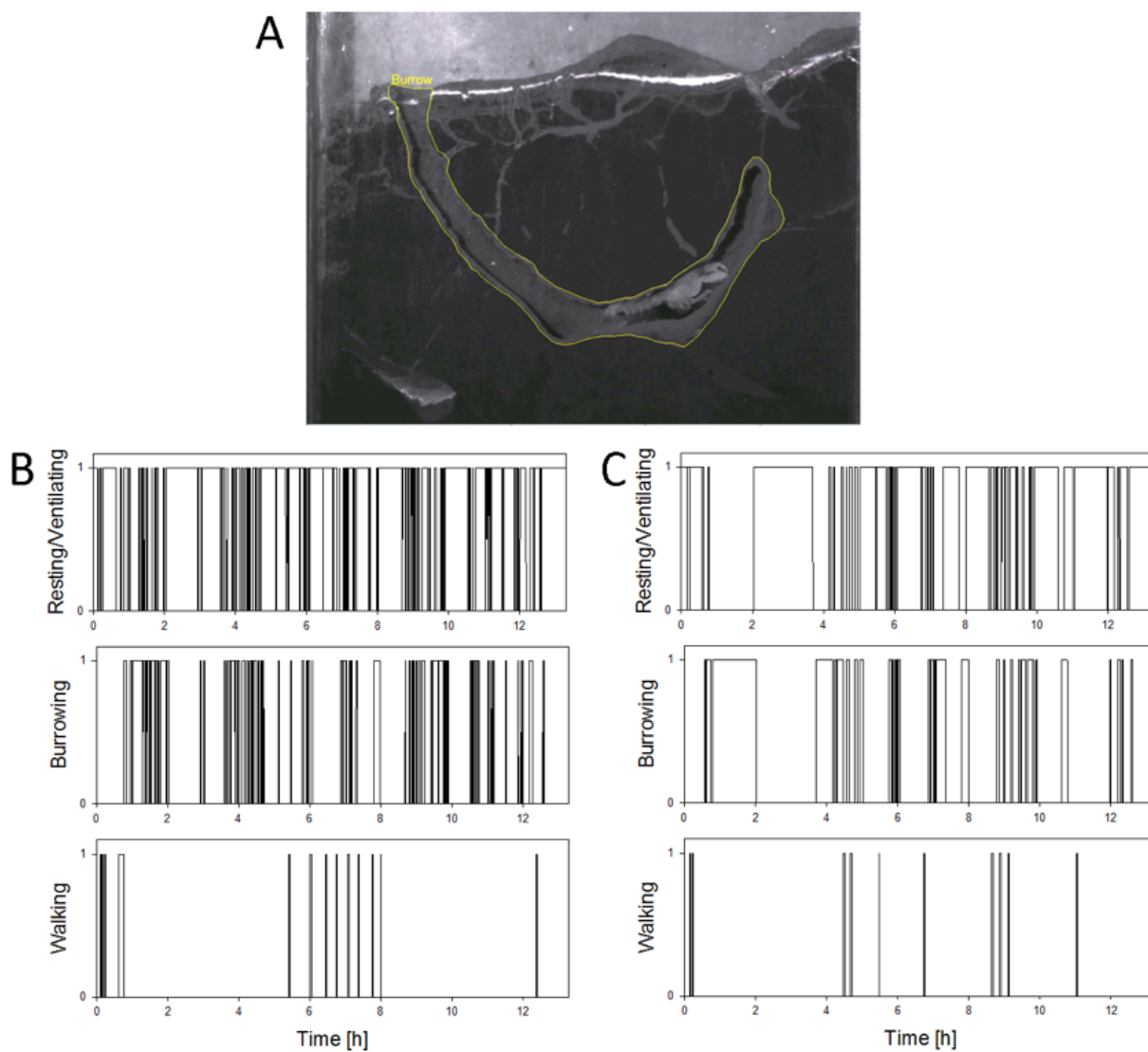


Figure AIV.10 : Mud shrimp case study: (A) Example of an image extracted from the video with an ROI corresponding to the delimitation of the visible part of the burrow, (B) Automatic and (C) Visual assessment of the temporal changes in the occurrence of the three monitored behaviors: ‘Resting/ventilating’, ‘Burrowing’ and ‘Walking’




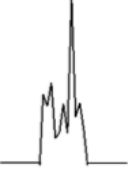
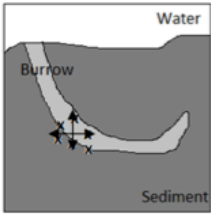
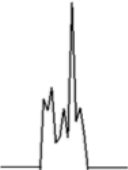
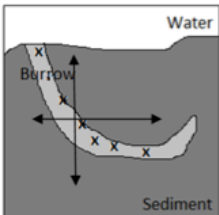
Extracted Information from film		Associated Behaviour
Shape of signal (Number of pixels modified between two consecutive images)	Range of position (Barycenter)	
	Zero	Resting or ventilation
	Zero	Resting or ventilation
	Small	Resting or ventilation
	Small 	Burrowing
	Large 	Walking

Figure AIV.11 : Mud shrimp case study: Combination of AVIExplore extracted features to assess the three different behaviors of *Upogebia pusilla*.

The results were compared with those originating from a visual analysis of the video. Accuracy was assessed as the proportion of images which were attributed the same behavior by the two procedures. An error analysis is carried out to understand the sense of miss classified behaviors.

3.2.2.1. Results

Temporal changes in the occurrence of the three types of behaviors are shown in **Figure AIV.10B**. The mud shrimp spent most of its time (i.e., 70.1%) ‘Resting/ventilating’, versus 26.1% ‘Burrowing’ and only 3.7% ‘Walking’. These figures can be compared with those originating from the visual observation of the video: 67.5% ‘Resting/ventilating’, 30.2% ‘Burrowing’, and 2.3% ‘Walking’. The total accuracy was 82.7% with higher discrepancies between the two methods corresponding to confusion between ‘Burrowing’ with either ‘Resting/ventilating’ (**Table AIV.5**). Except for ‘Resting/ventilating’, we observed that there was a lag of a few images between the end of each period of time corresponding to a given behavior as recorded visually and using AVIExplore. This discrepancy was attributed to differences in sensitivity between the sensor and the eye of the operator. When adjusting this lag for ‘Burrowing’ and ‘Walking’, there was only a slight improvement in the overall accuracy (83.7%). The existence of these lags therefore cannot be considered as the main source of discrepancies between automated and visual analyzes. Besides this general agreement, the analysis of the time series derived from automated and visual assessments clearly showed some difficulties in assessing positive ‘Walking’ and to a lesser extent positive ‘Burrowing’ behaviors.

Table AIV.5 : Mud shrimp case study: Frequency of occurrence of the different types of discrepancies between the visual and the automated analysis.

		Visual Analysis		
		Resting or ventilating	Burrowing	Walking
Automated Analysis	‘Resting/ventilating’		7.9 %	0.8%
	‘Burrowing’	4.1 %		1.2 %
	‘Walking’	2.0%	1.1 %	

3.3. AVIExplore – Fixed: Quantification of filtering activity in the passive suspension-feeding polychaete *Ditrupa arietina*

3.3.1. General context

The composition of littoral benthic macrofauna show major temporal changes in the Gulf of Lions apparently in relation with climatic oscillation such as the North Atlantic

Oscillation (Grémare et al., 1998a; Grémare et al., 1998b) and the Western Mediterranean oscillation (Bonifácio, 2015). Within the Littoral Fine Sands community (Labrune et al., 2008), the polychaete *Ditrupa arietina* is by far the species featuring the largest changes in abundances with densities between 0 and more than 11,000 individuals.m⁻² (Grémare et al., 1998b). This species may have an impact on carbon fluxes through: (1) the construction of its calcareous tusk-shaped tube (Medernach et al., 2000), and (2) nutrition. The corresponding impact depends on the intensity of filtering activity. Jordana et al. (2000) have therefore described and quantified the filtering activity of this species using a software specifically designed. During the present study, we use AVIExplore to analyze one of their videos and to show the ability of this new software to quantify the filtering activity of *D. arietina* in a completely automatized way.

3.3.2. Materials and methods

The experimental setup is described in (Jordana et al., 2000). Briefly, worms were collected by dredging and kept in the laboratory in tanks filled with a thin layer of well-sorted fine sand supplied with running ambient sea water. During the experiment per se, 15 worms were geometrically positioned upward, with tube openings, 1 cm above the sediment surface (**Figure AIV.12A**) in a 60.3 x 40.3 x 20 cm aquarium filled with a 10cm thick layer of well sorted fine sand and 30 l of filtered seawater. Polychaete worm filtering activity was monitored during 9 h using a CCD-ICS059 AI video sensor (VLSI Vision Ltd®) with an image frequency acquisition of 0.017 Hz. The video was analyzed using the AVIExplore – Fixed module. Fifteen ROIs were drawn close to the shadow of the extremity of each tube, where the openings of gills crowns were most visible (**Figure AIV.12B**). A fixed reference image with all gill crowns fully retracted was subtracted from each current images. ‘Dark’ pixels featuring negative differences lower than -30 (threshold fixed after preliminary trials) were identified and considered as indicative of gill crown deployment. They were summed for each ROI and the corresponding data were exported as text files. Filtering activity was defined as the ratio of the current number of ‘dark’ pixels divided by the maximum number of ‘dark’ pixels recorded at any given time within the corresponding ROI. Assuming, that maximal extension of the gill crown was achieved for all 15 worms during the observation period, this index allows for direct comparisons between worms irrespective of their size and position within the recorded field.

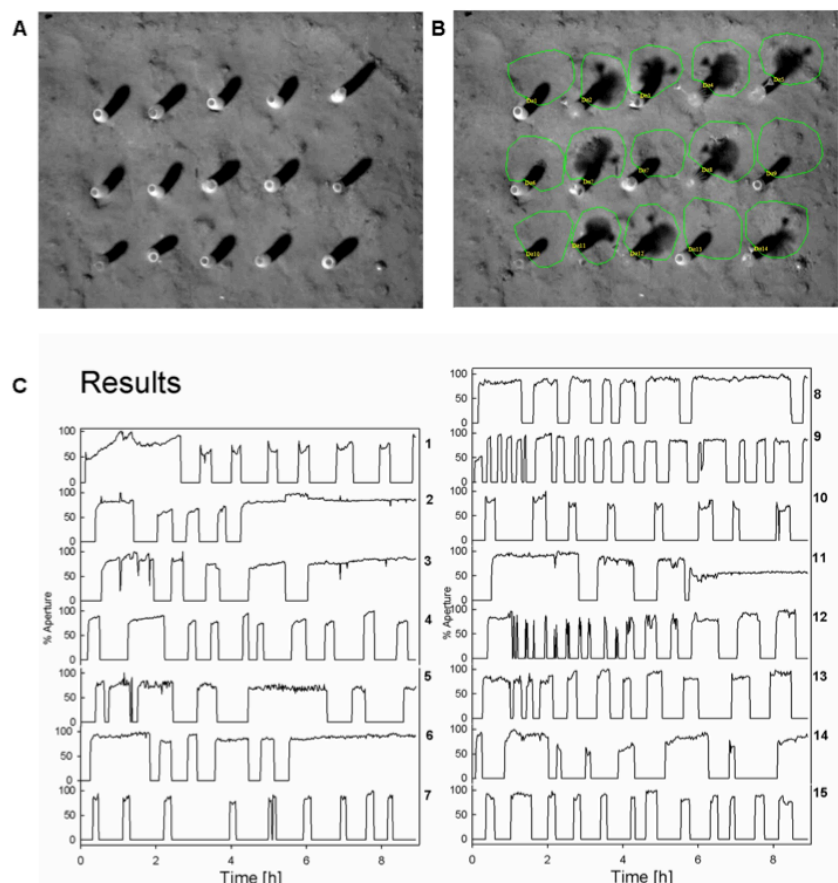


Figure AIV.12 : Passive suspension-feeder case study: (A) Reference image showing the disposition of the 15 studied worms with their retracted gill-crowns, (B) Localization of the 15 ROIs around the shadow of the top extremity of the tubes where extended gill-crowns (10 worms) can be observed, (C) Temporal changes in individual filtering activities.

Validation was achieved on one of the 15 specimens and accuracy was assessed as the proportion of images for which there was an agreement between visual and AviExplore assessment.

3.3.3. Results

Temporal changes in the filtering activity of each of the 15 studied worms are shown in **Figure AIV.12C**. The general pattern and the degree of cycle were clearly worm dependent. The level of synchronicity between individual worms was low since the number of simultaneously filtering worms varied between 2 and 13 and did not follow any clear pattern (**Figure AIV.13A**). The cumulated time devoted to filtration also varied strongly between individuals as indicated by the fact that, by the end of the 9 h monitoring period, the time spent filtering by each worm was between 1 h 33 min and 7 h 10 min. (**Figure**

AIV.13B). Overall, these results and conclusions are in full agreement with those of Jordana et al. (2000).

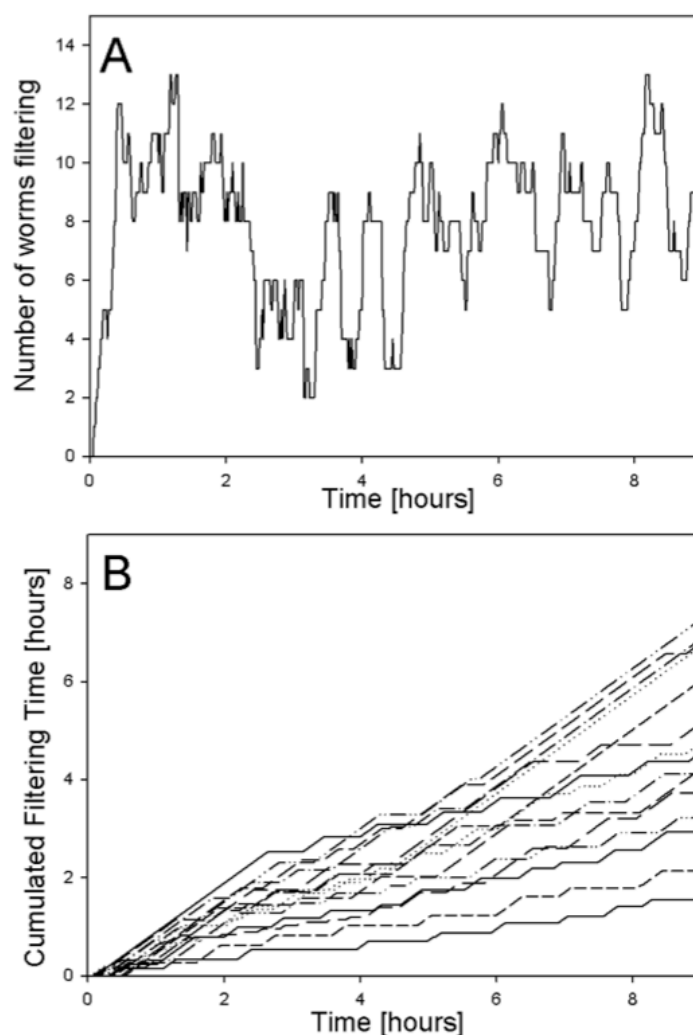


Figure AIV.13 Passive suspension-feeder case study: (A) Temporal changes in the number of worms filtering (B) Temporal changes in individual cumulated filtering activities.

Accuracy was 98.3%. A systematic error has been identified; the filtering activity of the analyzed specimen started one image before when visually assessed.

4. Discussion

The increase of the use of imaging in benthic ecology has resulted in a high diversity of image acquisition modes (including mobile and fixed platforms as well as ex and in situ deployments) and image characteristics (stability or variability in illumination and image quality). Image analysis, especially when applied to video clearly constitutes a bottleneck when using imaging for ecological studies. Another possible flaw of this technique is that it

may prove highly operator-dependent due to the complexity of the information: (1) contained, and (2) to be extracted from each image (Cuvelier et al., 2012). Software developments may clearly help overcoming these two drawbacks. At present such developments have been mostly customized to specific acquisition procedures and ecological applications. Along this line, and within JERICO, our own research group has recently produced the SPIArcBase software, which is specifically dedicated to the processing of sediment profile images (Romero-Ramirez et al., 2013). The aim of the development of the AVIExplore is much more ambitious. The goal is to provide a single platform flexible enough to automate the image analysis procedures requested by the largest possible sets of image acquisition platforms and ecological implications. In order to do so, we have followed a three-pronged approach: (1) building two modules specifically designed to process the video acquired with mobile and fixed image acquisition platforms and to tackle associated ecological questions, and (2) providing a module specifically designed to elaborate and test new specific image analysis procedures, which could prove necessary to tackle specific ecological questions, and (3) leaving the software open to new developments through the possibility of including new libraries depending on their compatibility with the AVIExplore. The three case studies carried out aimed at showing the real flexibility of the AVIExplore software. The following discussion will show some of the advantages of having used the AVIExplore software based on the experiments gained during these trials.

4.1. The AVIExplore – Mobile module

Edgington et al. (2006) emphasized the fact that the potential of ROVs and underwater observatories for collecting long-term observations is constrained by the time and effort to view and quantify the data. They thereby underlined the need for new software developments for processing videos obtained from mobile platforms. A first difficulty when processing those videos is that they often cover different habitats, which may correspond to very different images, which may therefore require different image analysis procedures. Applying all of those procedures to the whole video may rapidly become time consuming and could possibly lead to significant errors as well. AVIExplore therefore offers the possibility of defining sections of videos that are composed of similar images, and therefore can be processed using the same script. This is based on image comparison achieved on the Grey-Level Co-occurrence Matrix. Moreover, this procedure may prove useful even when a single habitat is monitored. This was the case during the coral mapping case study, where it facilitated the reduction of the number of analyzed images from 179,529 to 161,000 (i.e., by 10%) of the

images to analyze. The reason for that was that the video recorder was no longer recording the sediment water interface but the water column by the end of the video. We strongly believe that in the future, this procedure will also prove useful in defining section of videos characterized by dissimilarities due to various characteristics including: light conditions, image quality levels, angle of view, contrast, clarity, and presence of objects.

The AVIExplore – Mobile module also presents a high potential for assessment of benthic (mega)fauna. The visual assessment of benthic epibenthos is indeed often restricted to presence/absence data or to operator-dependent semi-quantitative data, which led Cuvelier et al. (2012) to plea for the development of automated image analysis procedures. A difficulty then consists in correcting the surfaces within the image to account both for the altitude and the inclination of the camera. During the ‘Coral mapping’ case study, the surface of corals was only quantified as pixel² because the information regarding both sensor altitude and inclination were lacking. Should such information be available during future uses, we would recommend to proceed to appropriate corrections (e.g., as briefly described in Robert and Juniper, 2012) on the raw surface data exported by AVIExplore. Along the same line, during the ‘Coral mapping’ study, we did not account for possible overlap between images. Here again, this could be handled through appropriate post-treatments (e.g. according to Morris et al., 2014) of AVIExplore exported raw surfaces.

4.2. The AVI – Explore – Fixed module

The AVIExplore – Fixed module gathers the experience gained by our research group through the developments of pieces of software specifically designed to process videos in view of assessing movements and activities of several benthic invertebrates and communities (Bernard et al., 2012; Duchêne et al., 2000; Duchêne and Queiroga, 2001; Duchêne and Rosenberg, 2001; Grémare et al., 2004; Hollertz and Duchêne, 2001; Maire et al., 2007a; Maire et al., 2007c). In its present form the AVIExplore – Fixed module mainly involves image subtraction procedures, which can first be achieved between the current image and a fixed reference image. This procedure is especially appropriate for the quantitative assessment of activity as was for example the case in the ‘Quantification of filtering activity in the passive suspension-feeding polychaete *Ditrupa arietina*’ case study. However, when used alone, it is clearly limited in the recognition of different kinds of behavior, which would require a time-series analysis of the so-recorded activity, such as achieved during the mud

shrimp case study or by Grémare et al. (2004) for categorizing inhalant siphon activity by the deposit-feeding clams *Abra ovata* and *A. nitida*.

The AVIExplore – Fixed module offers a much more straightforward possibility to assess movements and to categorize activities. It consist in achieving subtraction between each pair of consecutive (or separated by a constant lag) images. This procedure was used during the ‘Identification and quantification of different types of behaviors in the mud shrimp *Upogebia pusilla*’ case study. It generated a limited number of parameters including the distance of the barycenters of the pixels modified between two consecutive pairs of images, which proved efficient in attributing three different types of behavior to the mud shrimp *Upogebia pusilla*. However, we believe that the use of other features and/or machine learning algorithms may result on better classification results.

One clear limitation of the proposed method was that we were not able to clearly distinguish between ‘Resting’ and ‘ventilating’, which may result from a too low: (1) frequency acquisition (0.1 Hz) relative to the beating frequency of pleopods (0.5 Hz, LP personal observation), and (2) number of considered movement characteristics. Regarding this last point, a complexity of the number and characteristics of considered parameters (i.e., a holistic feature extraction approach) may certainly prove very useful as it has already been the case in several other imagery fields (Madhvanath and Govindaraju, 2001; Rodriguez et al., 2007; Turk and Pentland, 1991).

In its present forms the AVIExplore – Fixed module allows for the assessment of the trajectory of isolated objects/organisms through the plots of the position of consecutive barycenters of modified pixels identified by image subtraction. Such a capacity has proven useful in the assessment of swimming capacities in pelagic larvae of benthic organisms (Duchêne and Nozais, 1994; Nozais et al., 1997). Benthic ecologists are nevertheless more and more interested in the study of individual movements occurring within groups of objects/organisms. Bernard et al. (2012) for example developed a specific application to monitor the individual displacement of fluorescent sediment particles (luminophores). This requires the elaboration of a complex research algorithm (involving both the analysis of distances and directions of movements between consecutive pairs of images), which are currently not included in the AVIExplore – Fixed module. Depending on the interaction with future users, we may integrate such an approach within later version of AVIExplore.

4.3. The AVI – Explore – ScriptEdit module

The Avi-Explore–ScriptEdit module allows for the analysis, processing and visualization of videos and images. In its current version, it includes a large set of functions for analyzing individual images. As demonstrated during the present study, it already constitutes a powerful tool that can be used for different purposes, e.g.: detection and quantification of organisms (see the Deep corals case study) and the detection/quantification of different kinds of activities. Other applications can be already foreseen such as: (1) the analysis of swimming (fishes and benthic invertebrate larvae) patterns, and (2) the study of specific processes such as the dynamics of benthic settlement and early recruitment.

As it stands, the Avi-Explore – ScriptEdit module nevertheless does not allow for the quantitative assessment of some specific processes. As an example, recent imaging applications in benthic ecology have included the 2D analysis of sediment reworking, which requires the establishment of vertical profiles of luminophores concentrations. The first step of this procedure consists in defining the water-sediment interface, which can either be achieved manually or automatically (Romero-Ramirez et al., 2013). Its second step consists in flattening this interface (Maire et al., 2006), which consists in transferring its position to the first pixel row of each pixel column. At present, none of the corresponding procedures are included in the AVIExplore–ScriptEdit module. Here again, and depending on interactions with future users, we may integrate them within a later version of AVIExplore.

References

- Aguzzi, J., Costa, C., Robert, K., Matabos, M., F., A., Juniper, S.K., Manesatti, P., 2011. Automated Image Analysis for the Detection of Benthic Crustaceans and Bacterial Mat Coverage Using the VENUS Undersea Cabled Network. *Sensors* 11, 10534-10556.
- Bernard, G., Grémare, A., Maire, O., Lecroart, P., Meysman, F.J.R., Ciutat, A., Deflandre, B., Duchêne, J.C., 2012. Experimental assessment of particle mixing fingerprints in the deposit-feeding bivalve *Abra alba* (Wood). *Journal of Marine Research* 70, 689-718.
- Birchenough S.N.R., Parker R.E., McManus E., Barry J., 2012. Combining bioturbation and redox metrics: Potential tools for assessing seabed function. *Ecological Indicators* 12, 8-16.
- Bonifácio, P., 2015. Étude de l'état actuel et des variations temporelles de la composition de la macrofaune benthique des substrats meubles du golfe du Lion, Méditerranée occidentale, École doctorale sciences et environnements écologie évolutive, fonctionnelle et des communautés. University of Bordeaux.
- Coelho, V.R., Cooper, R.A., de Almeida Rodrigues, S., 2000. Burrow morphology and behavior of the mud shrimp *Upogebia omissa* (Decapoda: Thalassinidea: Upogebiidae). *Marine Ecology Progress Series* 200, 229-240.
- Cuvelier, D., de Busserolles, F., Lavaud, R., Floc'h, E., Fabri, M.-C., Sarradin, P.-M., Sarrazin, J., 2012. Biological data extraction from imagery "How far can we go?" A case study from the Mid-Atlantic Ridge. *Marine Environmental Research* 82, 15-27.
- de Moura Queirós, A., Hiddink, J., Johnson, G., Cabral, H., Kaiser, M., 2011. Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. *Biological Invasions* 13, 1059-1075.
- Diaz, R.J., Trefry, J.H., 2006. Comparison of sediment profile image data with profiles of oxygen and Eh from sediment cores. *Journal of Marine Systems* 62, 164-172.
- Duchêne, J.C., Jordana, E., Charles, F., Grémare, A., Amouroux, J.M., 2000. Experimental study of filtration activity in *Ditrupa arietina* (Annelida Polychaeta) using an automated image analysis system. *Oceanologica Acta* 23, 805-8017.
- Duchêne, J.C., Nozais, C., 1994. Light influence on larval emission and vertical swimming in the terebellid worm *Eupolymnia nebulosa*. *Mémoires du Muséum National d'Histoire Naturelle Zoologie* 162, 405-412.
- Duchêne, J.C., Queiroga, H., 2001. Use of an intelligent CCD camera for the study of endogenous vertical migration rhythms in first zoeae of the crab *Carcinus maenas*. *Marine Biology* 139, 901-909.
- Duchêne, J.C., Rosenberg, R., 2001. Marine benthic faunal activity patterns on a sediment surface assessed by video numerical tracking. *Marine Ecology Progress Series* 223, 113-119.

-
- Duffy, G.A., Lundsten, L., Kuhnz, L.A., Paull, C.K., 2014. A comparison of megafaunal communities in five submarine canyons off Southern California, USA. *Deep Sea Research Part II: Topical Studies in Oceanography* 104, 259-266.
- Dworschak, P.C., 1987. Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrhena* (Crustacea, Decapoda, Thalassinidea). *Investigación Pesquera* 51(1), 421-429.
- Edgington, D.R., Danelle, E., Cline, E., Davis, D., 2006. Detecting, Tracking and Classifying Animals in Underwater Video, *OCEANS IEEE*, Boston, 1-5.
- Germano, J.D., Rhoads, D.C., Valente, R.M., Carey, D.A., Solan, M., 2011. The use of sediment profile imaging (SPI) for environmental impact assessment and monitoring studies: Lessons learned from the past four decades. *Oceanography and Marine Biology: An annual Review* 49, 235-297.
- Grémare, A., Amouroux, J.M., Vétion, G., 1998a. Long-term comparison of macrobenthos within the soft bottoms of the Bay of Banyuls-sur-mer (northwestern Mediterranean Sea). *Journal of Sea Research* 40, 281-302.
- Grémare, A., Duchêne, J.C., Rosenberg, R., David, E., Desmalades, M., 2004. Feeding behaviour and functional response of *Abra ovata* and *A. nitida* compared by image analysis. *Marine Ecology Progress Series* 267, 195-208.
- Grémare, A., Sarda, R., Medernach, L., Jordana, E., Pinedo, S., Amouroux, J.M., Martin, D., Nozais, D., Charles, F., 1998b. On the Dramatic Increase of *Ditrupa arietina* O.F. Müller (Annelida: Polychaeta) Along Both the French and the Spanish Catalan Coasts. *Estuarine Coastal and Shelf Science* 47, 447-457.
- Hollertz, K., Duchêne, J.C., 2001. Burrowing behaviour and sediment reworking in the heart urchin *Brissopsis lyrifera* Forbes (Spatangoida). *Marine Biology* 139, 951-957.
- Hu, M.K., 1962. Visual pattern recognition by moments invariants. *IRE transaction of information theory*, 179-187.
- Jamieson, A.J., Boorman, B., Jones, D.O.B., 2013. Deep-Sea Benthic Sampling, in: *Methods for the Study of Marine Benthos*. Fourth Edition. Blackwell Science Ltd, Oxford, p. 285-347.
- Jordana, E., Charles, F., Grémare, A., Amouroux, J.M., Chretiennot-Dinet, M.J., 2001a. Food sources, ingestion and absorption in the suspension-feeding polychaete *Ditrupa arietina* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology* 266, 219-236.
- Jordana, E., Duchêne, J.-C., Charles, F., Grémare, A., Amouroux, J.-M., 2000. Experimental study of suspension-feeding activity in the serpulid polychaete *Ditrupa arietina* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology* 252, 57-74.
- Jordana, E., Grémare, A., Lantoine, F., Courties, C., Charles, F., Amouroux, J.M., G., V., 2001b. Seasonal changes in the grazing of coastal picoplankton by the suspension-feeding polychaete *Ditrupa arietina* (O.F. Müller). *Journal of Sea Research* 46, 246-259.

- Kannappan, P., Tanner, H.G., 2013. Automated detection of scallops in their natural environment, Control & Automation (MED), 2013 21st Mediterranean Conference on, pp. 1350-1355.
- Labrune, C., Grémare, A., Amouroux, J.-M., Sardá, R., Gil, J., Taboada, S., 2008. Structure and diversity of shallow soft-bottom benthic macrofauna In the Gulf of Lions (NW Mediterranean). Helgoland Marine Research 62, 201-214.
- Lebart, K., Smith, C., Trucco, E., Lane, M., 2003. Automatic indexing of underwater survey video: algorithm and benchmarking method, IEEE Journal of Oceanic Engineering 28(4), 673-686.
- Madhvanath, S., Govindaraju, V., 2001. The Role of Holistic Paradigms in Handwritten Word Recognition. IEEE Transaction on Pattern analysis and machine intelligence 23 (2), 149-164.
- Maire, O., Duchêne, J.C., Rosenberg, R., Braga de, M., J.B., Antoine, G., 2006. Effects of food availability on sediment reworking in *Abra ovata* and *A. nitida**. Marine Ecology Progress Series 319, 135-153.
- Maire, O., Amouroux, J.-M., Duchêne, J.-C., Grémare, A., 2007a. Relationship between filtration activity and food availability in the Mediterranean mussel *Mytilus galloprovincialis*. Marine Biology 152, 1293-1307.
- Maire, O., Duchêne, J.C., Grémare, A., Malyuga, V.S., Meysman, F.J.R., 2007b. A comparison of sediment reworking rates by the surface deposit-feeding bivalve *Abra ovata* during summertime and wintertime, with a comparison between two models of sediment reworking. Journal of Experimental Marine Biology and Ecology 343, 21-36.
- Maire, O., Duchêne, J.C., Amouroux, J.M., Grémare, A., 2007c. Activity patterns in the terebellid polychaete *Eupolyornia nebulosa* assessed using a new image analysis system. Marine Biology 151, 737-749.
- Maire, O., Duchêne, J.C., Bigot, L., Grémare, A., 2007d. Linking feeding activity and sediment reworking in the deposit-feeding bivalve *Abra ovata* with image analysis, laser telemetry, and luminophore tracers. Marine Ecology Progress Series 351, 139-150.
- Mallet, D., Pelletier, D., 2014. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952-2012). Fisheries Research 154, 44-62.
- Mane, K.T., Pujari, V.G., 2014. A Novel Approach for Species Detection from Oceanographic Video, Advanced Computing & Communication Technologies (ACCT), 2014 Fourth International Conference on, pp. 42-46.
- Mastrototaro, F., D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P., Gherardi, M., Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C., Boero, F., Taviani, M., Tursi, A., 2010. Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): An update. Deep Sea Research Part II: Topical Studies in Oceanography 57, 412-430.

-
- Matabos, M., Aguzzi, J., Robert, K., Costa, C., Menesatti, P., Company, J.B., Juniper, S.K., 2011. Multi-parametric study of behavioural modulation in demersal decapods at the VENUS cabled observatory in Saanich Inlet, British Columbia, Canada. *Journal of Experimental Marine Biology and Ecology* 401, 89-96.
- Matabos, M., Piechaud, N., De Montigny, F., Sarradin, P.-M., Sarrazin, J., 2015. The VENUS cabled observatory as a method to observe fish behaviour and species assemblages in a hypoxic fjord, Saanich Inlet (British Columbia, Canada). *Canadian Journal of Fisheries and Aquatic Sciences* 72, 24-36.
- Medernach, L., Jordana, E., Grémare, A., Nozais, C., Charles, F., Amouroux, J.M., 2000. Population dynamics, secondary production and calcification in a Mediterranean population of *Ditrupa arietina* (Annelida: Polychaeta). *Marine Ecology Progress Series* 199, 171-184.
- Morris, K.J., Bett, B.J., Durden, J.M., Huvenne, V.A.I., Milligan, R., Jones, D.O.B., McPhail, S.D., Robert, K., Bailey, D.M., Ruhl, H.A., 2014. A new method for ecological surveying of the abyss using autonomous underwater vehicle photography. *Limnology and Oceanography* 12, 795-809.
- Nowak, B.M., Whitney, T., Ackley, S.F., 2008. Analysis of ROV video imagery for krill identification and counting under Antarctic sea ice, *Autonomous Underwater Vehicles, 2008. AUV 2008. IEEE/OES*, pp. 1-9.
- Nozais, C., Duchêne, J.C., Bhaud, M., 1997. Control of position in the water column by the larvae of *Poecilochaetus serpens*, (Polychaeta): the importance of mucus secretion. *Journal of Experimental Marine Biology and Ecology* 210, 91-106.
- Pillay, D., Branch, G.M., 2011. Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. *Oceanography Marine Biology Annual Review* 49, 137-192.
- Rees, H.L., Service, M.A., 1993. Development of improved strategies for monitoring the epibenthos at sewage sludge disposal sites, in *Aquatic Environment Monitoring Report*. Directorate of fisheries Research, Lowestoft, pp. 55-65.
- Robert, K., Juniper, S.K., 2012. Surface-sediment bioturbation quantified with cameras on the NEPTUNE Canada cabled observatory. *Marine Ecology Progress Series* 453, 137-149.
- Roberts, J.M., Peppe, O.C., Dodds, L.A., Mercer, D.J., W.T., T., Gage, J.D., Meldrum, D.T., 2005. Monitoring environmental variability around cold-water coral reefs: the use of a benthic photolander and the potential of seafloor observatories, in: Freiwald, A., Roberts, J.M. (Eds.), *Cold-Water Corals and Ecosystems*. Springer Berlin Heidelberg, pp. 483-502.
- Rodriguez, R.V., Evans, N.W.D., Lewis, R.P., Fauve, B., Mason, J.S.D., 2007. An experimental study on the feasibility of footsteps as a biometric, *Signal Processing Conference, 2007 15th European*, pp. 748-752.

- Romero-Ramirez, A., Grémare, A., Desmalades, M., Duchêne, J.C., 2013. Semi-automatic analysis and interpretation of sediment profile images. *Environmental Modelling & Software* 47, 42-54.
- Rosenberg, R., Magnusson, M., Nilsson, H.C., 2009. Temporal and spatial changes in marine benthic habitats in relation to the EU Water Framework Directive: The use of sediment profile imagery. *Marine Pollution Bulletin* 58, 565-572.
- Sarrazin, J., Robigou, V., Juniper, S.K., Delaney, J.R., 1997. Biological and geological dynamics over four years on a high-temperature sulfide structure at the Juan de Fuca Ridge hydrothermal observatory. *Marine Ecology Progress Series* 153, 5-24.
- Savini, A., Bue, N.L., Malinverno, E., Corselli, C., Geronimo, I.D., Rosso, A., Tursi, A., 2005. Carbonate mounds on the apulian continental slope: morphology, distribution and their relation with dead and living deep water corals 23° GNGTS, Rome.
- Savini, A., Corselli, C., 2010. High-resolution bathymetry and acoustic geophysical data from Santa Maria di Leuca Cold Water Coral province (Northern Ionian Sea - Apulian continental slope). *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 326-344.
- Smith, C.J., Rumohr, H., 2013. Imaging Techniques, in: *Methods for the Study of Marine Benthos*. Fourth Edition. Blackwell Science Ltd, Oxford, p. 97.
- Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., Wenzhöfer, F., Kennedy, B., Henriques, C., Battle, E., Carey, D., Iocco, L., Valente, R., Watson, J., Rosenberg, R., 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *Journal of Experimental Marine Biology and Ecology*, 285-286, 313-338.
- Spencer, M.L., Stoner, A.W., Ryer, C.H., Munk, J.E., 2005. A towed camera sled for estimating abundance of juvenile flatfishes and habitat characteristics: Comparison with beam trawls and divers. *Estuarine, Coastal and Shelf Science* 64, 497-503.
- Stamhuis, E., Reede-Dekker, T., van Etten, Y., de Wiljes, J., Videler, J., 1996. Behaviour and time allocation of the burrowing shrimp *Callinassa subterranea* (Decapoda, Thalassinidea). *Journal of Experimental Marine Biology and Ecology* 204, 225-239.
- Taviani, M., Remia, A., Corselli, C., Freiwald, A., Malinverno, E., Mastrototaro, F., Savini, A., Tursi, A., 2005. First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). *Facies* 50, 409-417.
- Teixidó, N., Albajes-Eizagirre, A., Bolbo, D., Le Hir, E., Demestre, M., Garrabou, J., Guigues, L., Gili, J.M., Piera, J., Prelot, T., Soria-Frisch, A., 2011. Hierarchical segmentation-based software for cover classification analyses of seabed images (Seascape). *Marine Ecology Progress Series* 431, 45-53.
- Turk, M., Pentland, A., 1991. Eigenfaces for recognition. *Journal of Cognitive Neuroscience* 3, 72-86.

-
- Tursi, A., Mastrototaro, F., Matarrese, A., Maiorano, P., D'Onghia, G., 2004. Biodiversity of the white coral reefs in the Ionian Sea (Central Mediterranean). *Chemistry and Ecology* 20, 107-116.
- Vertino, A., Savini, A., Rosso, A., Di Geronimo, I., Mastrototaro, F., Sanfilippo, R., Gay, G., Etiope, G., 2010. Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 380-396.
- Volkenborn, N., Polerecky, L., Hedtkamp, S.I.C., Van Beusekom, J., Beer, D.d., 2007. Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. *Limnology and Oceanography* 52, 1898-1909.
- Volkenborn, N., Polerecky, L., Wethey, D.S., DeWitt, T.H., Woodin, S.A., 2012. Hydraulic activities by ghost shrimp *Neotrypaea californiensis* induce oxic-anoxic oscillations in sediments. *Marine Ecology Progress Series* 455, 141-156.
- Volkenborn, N., Polerecky, L., Wethey, D.S., Woodin, S.A., 2010. Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnology and Oceanography* 55, 1231-1247.
- Webb, A., Eyre, B., 2004. Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Marine Ecology Progress Series* 268, 205-220.
- Wethey, D.S., Woodin, S.A., 2005. Infaunal hydraulics generate porewater pressure signals. *Biological Bulletin* 209, 139-145.
- Wethey, D.S., Woodin, S.A., Volkenborn, N., Reise, K., 2008. Porewater advection by hydraulic activities of lugworms, *Arenicola marina*: A field, laboratory and modeling study. *Journal of Marine Research* 66, 255-273.
- Williams, S.B., Pizarro, O.R., Jakuba, M.V., Johnson, C.R., Barrett, N.S., Babcock, R.C., Kendrick, G.A., Steinberg, P.D., Heyward, A.J., Doherty, P.J., Mahon, I., Johnson-Roberson, M., Steinberg, D., Friedman, A., 2012. Monitoring of Benthic Reference Sites: Using an Autonomous Underwater Vehicle. *Robotics & Automation Magazine, IEEE* 19, 73-84.

Annexe V : Lavesque et al. 2016

***Heteromysis (Heteromysis) microps* (Crustacea, Mysidae), a commensal species for
Upogebia pusilla (Crustacea, Upogebiidae) in Arcachon Bay (NE Atlantic Ocean)**

NICOLAS LAVESQUE^{1,2*}, LUDOVIC PASCAL^{1,2}, BENOIT GOUILLIEUX^{1,2}, JEAN-
CLAUDE SORBE^{1,2}, GUY BACHELET^{1,2} AND OLIVIER MAIRE^{1,2}

¹ Univ. Bordeaux, EPOC, UMR 5805, Station Marine d’Arcachon, 2 Rue du Professeur
Jolyet, 33120 Arcachon, France

² CNRS, EPOC, UMR 5805, Station Marine d’Arcachon, 2 Rue du Professeur Jolyet, 33120
Arcachon, France

*Article publié dans la revue Marine Biodiversity Records*⁶

9(1):14,2016 ; doi: 10.1186/s41200-016-0001-1

⁶ Ce manuscrit correspond à la version acceptée de l’article et présente des différences mineures par rapport à la version éditée. Cette dernière est disponible sur le site de l’éditeur : <http://mbr.biomedcentral.com/articles/10.1186/s41200-016-0001-1>

ABSTRACT:

Background

The mysid *Heteromysis (Heteromysis) microps* is reported for the first time in the Bay of Biscay. During surveys carried out between March and September 2015 in Arcachon Bay, mysid specimens were fortuitously collected from *Upogebia pusilla* burrows.

Results

Details on morphology, colour pattern and behaviour of *H. microps* are provided.

Conclusions

Commensalism was frequently mentioned for *Heteromysis* species but never reported for *H. microps*. In this study, commensalism seems to be proved between the mysid and its host *U. pusilla*.

BACKGROUND

The thalassinidean mud shrimp *Upogebia pusilla* (Petagna, 1792) occurs in high densities in intertidal flats in the NE Atlantic and in shallow lagoons in the Mediterranean Sea. As its Y-shaped burrows penetrates deep into the sediment (up to 1 m), this shrimp is considered an important ecosystem engineer (Jones *et al.*, 1994; Pillay and Branch, 2011). Indeed, through its intense bioturbation activity, it greatly influences sedimentary biogeochemical processes and enhances fluxes across the sediment-water interface with knock-on effects on the whole benthic communities (Ziebis *et al.*, 1996; D'Andrea and DeWitt, 2009; Pascal *et al.* 2016). *Upogebia* also intensively ventilate their burrows through pleopod beating (Dworschak, 1981) for respiratory and trophic requirements (Sato *et al.*, 2001). Deep and well irrigated mud-shrimp burrows represent efficient refuges against predation for a variety of commensal species such as shrimps (e.g. *Betaeus longidactylus* Lockington, 1877) (Campos *et al.*, 2009), pea crabs (e.g. *Scleroplax granulata* Rathbun, 1894) (Campos, 2006), bivalves (e.g. *Peregrinamor ohshimai* Shôji, 1938) (Kato and Itani, 1995), polychaetes (e.g. *Hesperonoe hwanghaiensis* Uschakov & Wu, 1959) (Sato *et al.*, 2001), phoronids (e.g. *Phoronis pallida* Silén, 1952) (Santaga, 2004) and goby fishes (e.g. *Eutaeniichthys gilli* Jordan & Snyder, 1901) (Henmi and Itani, 2014). During a recent study aiming at quantifying the influence of *U. pusilla* on porewater exchanges and nutrient cycling (Pascal *et al.* 2016), specimens of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) were fortuitously collected in their burrows from tidal flats of Arcachon Bay, thus providing the opportunity for new observations on the morphology and behaviour of this rare species in European waters.

RESULTS

SYSTEMATICS

Family MYSIDAE Haworth, 1825

Subfamily Heteromysinae Norman, 1892

Genus *Heteromysis* S.I. Smith, 1873

Subgenus *Heteromysis* (*Heteromysis*) S.I. Smith, 1873

Heteromysis (*Heteromysis*) *microps* (G.O. Sars, 1877)

Type species: *Heteromysis* (*Heteromysis*) *formosa* Smith, 1873

Material examined

For the 68 specimens of *H. microps* collected, size and sex were determined. The sex-ratio of the population was 2:3 (male:female). Brooding females were absent from March samples and represented 44.4% and 60% of the total females in July and September, respectively. The size range of individual BL was measured in each demographic category: 5.59-9.27 mm (7.42 ± 1.10 mm; $\bar{x} \pm s$) in males, 5.27-8.73 mm (6.44 ± 0.84 mm) in females and 6.99-9.44 mm (8.07 ± 0.87 mm) in brooding females. Juveniles were never collected during our survey.

Generic diagnosis (according to Wittmann, 2000)

Heteromysinae with eyes normal. Appendix masculina representing a very small setose lobe or reduced to a setose ridge. Antennal scale usually short, setose all around, without or with a small apical article. Mouthparts normal; labrum not produced into a spiniform process. First thoracic endopod with a large endite on the basis, and smaller endites on ischium and merus (an additional small, conical endite may be present on the coxa, although rarely noted by previous authors). Third thoracic endopod subchela-like (gnathopod), with enlarged carpopropodus and strong dactylus. Carpopropodus of fourth to eighth thoracic endopods with 3-7 articles. Penis long and more or less cylindrical. Pleopods entire, reduced to small plates in both sexes; non-dimorphic (subgenus *Heteromysis*) or dimorphic (some other subgenera). Uropods normal, entire; exopod with setae all around; endopod without or in most species with stout setae along inner margin. Telson with stout setae on lateral margins; distinct apical cleft present, margins of cleft with a number of laminae.

Description

Based on two males (Arcachon Marine Station Collection), BL = 7.52 mm and 7.89 mm, Arcachon Bay, March 2015.

Antennal scale small, shorter than antennular peduncle. *Sternal processes* absent in females, present on second to eighth sternites in males: first anterior one with blunt bifid apex, subsequent ones with more or less acute bifid tip and the last posterior one very reduced and cone-shaped (**Figure AV.2A**). *Endopod of thoracopod 3* (gnathopod) very robust, longer than cephalothorax, non-dimorphic; merus large, bearing 12 cuspidate setae on ventral margin of inner face (from 11 to 16 for other specimens), 9 cuspidate setae on ventral margin of outer face (from 8 to 11 for other specimens), 1 sub-distal seta on dorsal margin (**Figure AV.2B**),

ventrodistal part with an inner roundish lobe and an outer acute lobe between which carpopropodus folds down; carpopropodus with one pair of cuspidate setae at ventrodistal angle between which dactylus bends down to form a powerful subchela; dactylus with 3 long, tip-curved setae along outer face (**Figure AV.2B**). *Pleopods* normal, non-dimorphic. *Telson* cleft, with 1 stout seta on basal third of lateral margin, followed by a naked portion and then 9 stout setae on distal half (7 to 10 stout setae on other specimens) (**Figure AV.2C**). *Uropod* endopod with 1 stout seta on proximal part of inner margin, near statocyst (**Figure AV.2D**).

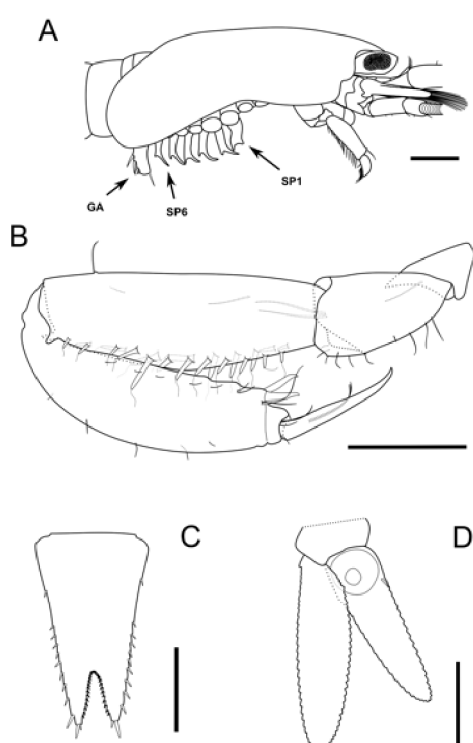


Figure AV.2 : Adult males of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) from Arcachon Bay (Arcachon Marine Station collection: A: male, BL = 7.89 mm; B-D: male, BL = 7.52 mm). (A) lateral view. SP1: first sternal process; SP6: sixth sternal process; GA: genital appendage; (B) right thoracopod 3 endopod, inner view; (C) telson, ventral view; (D) right uropod, ventral view. Scale bars: 0.5 mm.

Remarks (based on Sars (1877) and Tattersall and Tattersall (1951))

Sars (1877) described only adult females and Tattersall and Tattersall (1951) described only a single adult male. All the data on females given by the last authors were depicted from Sars (1877).

Telson:

Tattersall and Tattersall (1951) re-described *H. microps* with a telson armed with 12-14 stout setae on each side. The Arcachon specimens show no more than 11 stout setae (one near the base and 10 on the distal half) as first described by Sars (1877) in the original description of *H. microps*.

Thoracopod 3:

All the Arcachon specimens bear 3 long setae on their dactylus. Tattersall and Tattersall (1951) mentioned the presence of two subdistal pairs of small stout setae as well as a pair of distal finger-like projections along the ventral margin of the carpopropodus (proximal article). However, in Sars's original description of this species (1877; Fig. 20-9), the subdistal stout setae are clearly more developed and the 'distal finger-like projections' are in fact represented as a pair of articulated stout setae (shorter than the other ones). Our own observations on Arcachon specimens confirm Sars's original interpretation (a pair of distal stout setae, not finger-like projections), but without two pairs of stout setae along the carpopropodus inner margin (rarely with one short pair). Tattersall and Tattersall (1951) mentioned the presence of 10 sensitive stout pedestal setae (probably 12 of these setae in Sars's original description) and one distal setal tuft along the merus inner margin. Such a setal tuft was not observed in Arcachon specimens and 11-16 sensitive stout pedestal setae were counted on their merus inner margin. Furthermore, setal ornamentation shows some slight

differences between right and left thoracopod 3 endopods, when considering a single specimen.

Coloration

As the specimens were observed alive after capture, new data on their colour pattern can be provided. General appearance orange (**Figure AV.3A**). Cornea brown-golden, surrounded by pink-red coloration (**Figure AV.3B**). Eyes and antennae iridescent (**Figure AV.3B**). Cephalon rust-coloured (**Figure AV.3A**). Rust-coloured chromatophores scattered dorsally and laterally over carapace and between 6th abdominal segment and telson. Appendages and uropods not pigmented. Eggs brown. The body coloration disappeared within a few minutes after fixation (alcohol or formalin).

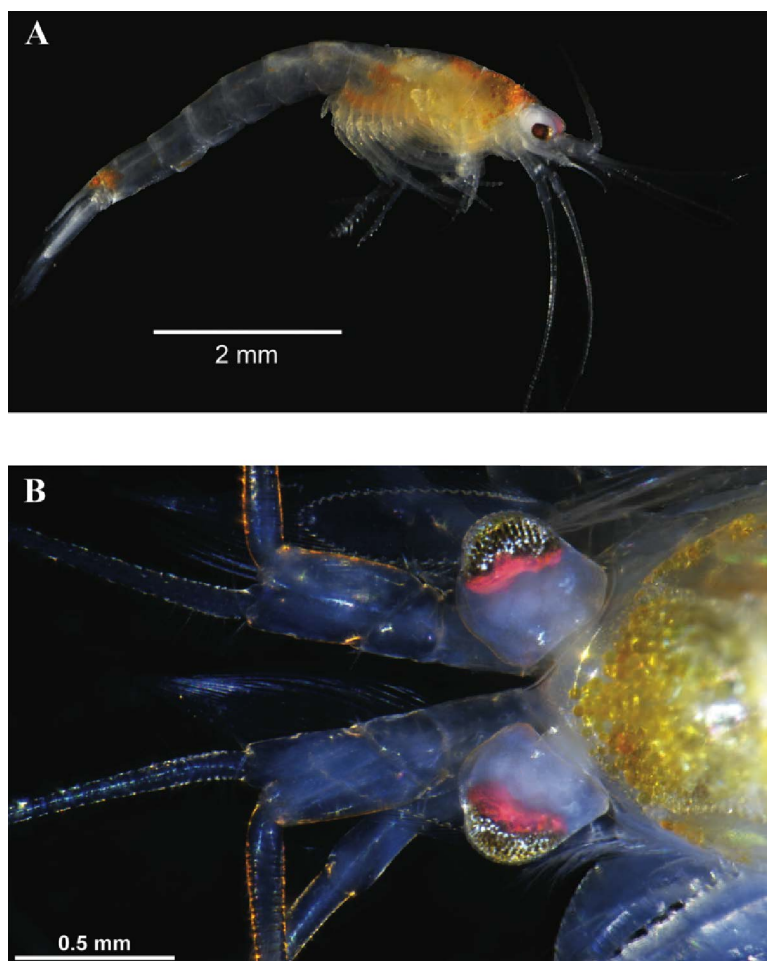


Figure AV.3 : Living male specimen of *Heteromysis (Heteromysis) microps* (G.O. Sars, 1877) from Arcachon Bay (BL = 7.52 mm) (Arcachon Marine Station collection, same specimen as in Fig. 2 B-D). (A) lateral view; (B) anterior part.

Geographical distribution and habitat

Relatively rare species, from Norwegian coast to Mediterranean Sea (Tattersall and Tattersall 1951; Tattersall, 1967; Dauvin and Vallet, 1997). In coastal areas, from 6 to 33 m depth, on mud to pebble bottoms (Zouhiri *et al.*, 1998), *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows (Wittmann, 2001) and, according to the present study, within burrows of *U. pusilla* in intertidal *Zostera noltei* meadows.

DISCUSSION

The genus *Heteromysis* is divided in 4 subgenera and is the most speciose of the Mysidae with 82 species currently considered valid (Mees, 2015). Only one species was previously mentioned from the southern Bay of Biscay: *Heteromysis (Heteromysis) norvegica* G.O. Sars, 1882, on bathyal bottoms (Frutos and Sorbe, 2014). Members of this genus are generally distributed in coastal warm-water regions and most of the species are restricted to small geographical areas (Fukuoka, 2005). This study reports on the first record of *H. microps* in the Bay of Biscay, and most importantly, its first record in association with another invertebrate species. Despite an important number of macrobenthic studies since the 1960s in Arcachon Bay (see Blanchet, 2004) and particularly in *Z. noltei* meadows (Blanchet *et al.*, 2004), *H. microps* was never found in that bay. Therefore, this mysid should not be considered as a new inhabitant of Arcachon Bay, and its absence in previous ecological studies can be explained by the lack of specific investigations on *Upogebia pusilla* burrows before 2015. *H. microps* is probably commensal with this burrowing shrimp. As it usually occurs on soft bottoms (Zouhiri *et al.*, 1998) and in seagrass meadows (Wittmann, 2001), the association found in this study could be a local phenomenon.

Coastal mysids, and particularly species belonging to the genus *Heteromysis*, are known to prefer complex habitats such as dense vegetation, shells and gravels or to live in association with different invertebrate species (Wittmann, 2008). Commensalism in the genus

Heteromysis was first demonstrated by Clarke (1955), describing an association between *Heteromysis actiniae* Clarke, 1955 and the sea-anemone *Bartholomea annulata* (Lesueur, 1817) in Bahamas Islands (Tattersall, 1967). *Heteromysis* species are known to have various hosts like sponges, corals, gorgonians, sea anemones, brittle stars and hermit crabs inhabiting empty shells (Wittmann, 2008; Wittmann *et al.*, 2014). In Arcachon Bay, *Upogebia* burrows provide peculiar microhabitats where mysids can live more safely against predation and environmental perturbations as well as against desiccation at low tide.

According to Dworschak (1987), *U. pusilla* is primarily a filter-feeding species, generating a water flow into its burrow by pleopods beating. Astall *et al.* (1997) demonstrated that the mean irrigation rate into the burrows of *Upogebia deltaura* (Leach, 1815) and *U. stellata* (Montagu, 1808) were 149.5 ml.h⁻¹ and 139.7 ml.h⁻¹, respectively. The suspended material associated with water flow is driven to the “basket” formed by the long setae beared by pereopods 1-2, then transferred to the mouthparts by maxilliped 3 (Dworschak, 2004). As *H. microps* is a suspension feeder (Mees, 2016), this species could take advantage of the particle flow generated by the *Upogebia* host within its burrow. This nutritional model has been previously reported by Vannini *et al.* (1994) for *Heteromysis (Gnathomysis) harpax* (Hilgendorf, 1878). This latter species is associated with hermit crabs belonging to the genus *Dardanus* Paul'son, 1875 and ingests suspended particles brought into the gill chamber by the host. According to Dworschak (1987), *U. pusilla* is also a deposit feeder via a ‘gardening’ behaviour. Indeed, this decapod can actively store detritus and plant fragments in the walls of its burrow, consuming them with their associated microflora. Mysids are also able to pick up detritus particles with their anterior thoracopods (Albertson, 2004). Unexpectedly, the huge thoracopod 3 of *H. microps* (a morphological peculiarity of this genus) does not appear to be related to a predator behaviour but could be used to consume the organic particles stored in *Upogebia* burrows. Furthermore, San Vicente and Monniot (2014) suggested that the enlarged

thoracopod endopods of Heteromysinae could be used as weapons. With the adoption of a symbiotic life in these taxa, it is suggested that these weaponries probably have played an important role in determining the behaviour and morphological evolution of such mysids (Vannini *et al.*, 1993).

CONCLUSIONS

In this study, commensalism seems to be proved between the mysid and its host. As the mysid associate remains external and was never found in another habitat in Arcachon Bay, the association between *H. microps* and *U. pusilla* may be classified as obligatory ectocommensalism (Nardon and Charles, 2002; San Vicente and Monniot, 2014). *H. microps* seems to take advantage of the filter feeding and the gardening behaviour of *U. pusilla*. Furthermore, *H. microps* is clearly protected from predators within *U. pusilla* burrows.

Further studies will be conducted to understand the behaviour of both species (laboratory experiments in thin aquariums, each colonized by one *U. pusilla* specimen). These mesocosm observations will allow answering different questions: (1) what is the behaviour of mysids during night time? Indeed, *Heteromysis* species become actively pelagic at night while they live sheltered during daytime (Tattersall, 1967; Wittmann, 2008); (2) are mysids able to breed within *Upogebia* burrows, thereby benefiting from some protection for their offspring?; (3) are mysids expelled from burrows during the breeding period of *U. pusilla*?

METHODS

Study area

Arcachon Bay is a 180-km² macrotidal coastal lagoon (maximum tidal range: 4.9 m) located on the south-western coast of France (**Figure AV.1**). This lagoon is connected with the Atlantic Ocean by a narrow channel and receives freshwater inputs in its south-eastern

part (Leyre River). It is characterized by large intertidal flats (115 km²), the lower parts of which are used for cupped oyster [*Crassostrea gigas* (Thunberg, 1793)] farming. Most of the intertidal area (46.2 km²) is covered by seagrass beds, *Zostera noltei* Hornemann, 1832 (Plus *et al.*, 2010). In the inner lagoon, tidal channels represent an area of 71 km², with 1.02 km² occupied by eelgrass beds, *Zostera marina* Linnaeus, 1753 (Plus *et al.*, 2010).

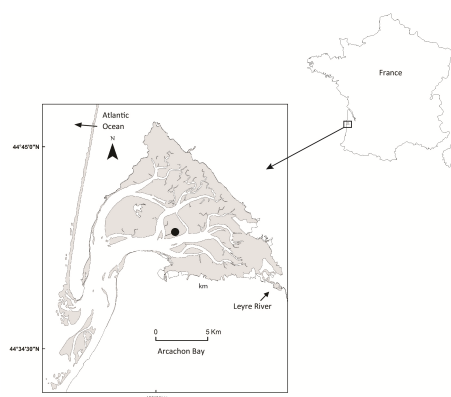


Figure AV.1 : Sampling site (“Le Navire Brûlé”) of *Heteromysis* (*Heteromysis*) *microps* (G.O. Sars, 1877) in Arcachon Bay (SW France).

Material examined

During surveys carried out between March and September 2015, 68 mysid specimens were fortuitously collected from *Upogebia pusilla* burrows (0-1 individual per burrow), using a bait piston pump and later on identified as *Heteromysis* (*Heteromysis*) *microps* according to the identification key published by Wittmann (2008) for Atlantico-Mediterranean species. Sampling was carried out at low tide within a homogeneous patch of *Z. noltei* at “Navire Brûlé” site (temperature from 7 to 21°C, salinity from 21.9 to 32.8) (**Figure AV.1**). All specimens were examined under a Nikon SMZ25 stereomicroscope and photographed with a Nikon DS-Ri 2 camera, after anaesthetizing them with magnesium chloride (MgCl₂). An image of one specimen was drawn with a Wacom Intuos 5 tablet, using Inkscape software (v.0.48). Body length BL was measured with the NIS-Elements Analysis software from the rostrum anterior margin to the telson apex.

REFERENCES

- Albertson J. Trophic interactions involving mysid shrimps (Mysidacea) in the near-bottom habitat in the Baltic Sea. *Aquat Ecol.* 2004;38:457-69. doi: 10.1023/B:AECO.0000035163.30037.38
- Astall CM, Taylor AC, Atkinson JA. Behavioural and physiological implications of a burrow-dwelling lifestyle for two species of upogebiid mud-shrimp (Crustacea: Thalassinidea). *Estuar Coast Mar Sci.* 1997;44:155-68. doi:10.1006/ecss.1996.0207
- Blanchet H. Structure et fonctionnement des peuplements benthiques du bassin d'Arcachon. Bordeaux: University of Bordeaux; 2004.
- Blanchet H, de Montaudouin X, Lucas A, Chardy P. Heterogeneity of macrozoobenthic assemblages within a *Zostera noltii* seagrass bed: diversity, abundance, biomass and structuring factors. *Estuar Coast Mar Sci.* 2004;61:111-23. doi:10.1016/j.ecss.2004.04.008
- Campos E. Systematics of the genus *Scleroplax* Rathbun, 1893 (Crustacea: Brachyura: Pinnotheridae). *Zootaxa.* 2006;1344:33-41. doi: <http://dx.doi.org/10.11646/%25x>
- Campos E, De Campos AR, Manriquez I. Intertidal thalassinidean shrimps (Thalassinidea, Callianassidae and Upogebiidae) of the west coast of Baja California, Mexico: Annotated checklist, key for identification, and symbionts. *Crustaceana.* 2009;82:1249-63. doi: 10.1163/001121609X12481627024454.
- Clarke WD. A new species of the genus *Heteromysis* (Crustacea, Mysidacea) from the Bahama Islands, commensal with a sea-anemone. *Am Mus Novit.* 1955;1716:1-13.
- D'Andrea AF, DeWitt TH. Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-

- dependent effects on organic matter remineralization and nutrient cycling. *Limnol Oceanogr.* 2009;54:1911-32. doi:10.4319/lo.2009.54.6.1911
- Dauvin JC, Vallet JC. Apports d'échantillonnages suprabenthiques à la faunistique de la Manche et à la biogéographie du plateau continental nord-ouest européen. Crustacés et Pycnogonides. *Cah Biol Mar.* 1997;38:251-66.
- Dworschak PC. The pumping rates of the burrowing shrimp *Upogebia pusilla* (Petagna) (Decapoda: Thalassinidea). *J Exp Mar Biol Ecol.* 1981;52:25-35.
- Dworschak PC. Feeding behavior of *Upogebia pusilla* and *Callinassa tyrrhena* (Crustacea, Decapoda, Thalassinidea). *Invest Pesq.* 1987;51:421-29.
- Dworschak PC. Biology of Mediterranean and Caribbean Thalassinidea (Decapoda). In: Tamaki A, editor. Proceedings of the Symposium "Ecology of large bioturbators in tidal flats and shallow sublittoral sediments – from individuals behavior to their role as ecosystem engineers". Nagasaki: Nagasaki University; 2004. p.15-22.
- Frutos I, Sorbe JC. Bathyal suprabenthic assemblages from the southern margin of the Capbreton Canyon ("Kostarrenkala" area), SE Bay of Biscay. *Deep Sea Res II.* 2014; 102:291-309. doi:10.1016/j.dsr2.2013.09.010.
- Fukuoka K. A new species of *Heteromysis* (Mysida, Mysidae) associated with sponges, from the Uraga Channel, Central Japan, with notes on distribution and habitats within the genus *Heteromysis*. *Crustaceana.* 2005;77:1353-73. doi: 10.1163/1568540043165976
- Henmi Y, Itani G. Burrow utilization in the goby *Eutaeniichthys gilli* associated with the mud shrimp *Upogebia yokoyai*. *Zool Sci.* 2014;31:523-28.
- Jones CG, Lawton JH, Shachak M. Organisms as ecosystem engineers. *Oikos.* 1994;69:373-86.

-
- Kato M, Itani G. Commensalism of a bivalve, *Peregrinamor ohshimai*, with a thalassinidean burrowing shrimp, *Upogebia major*. J Mar Biol Assoc UK. 1995;75:941-47. doi:10.1017/S0025315400038261
- Mees J. *Heteromysis*. In: Mees, J. and Meland K. (Eds) (2012 onwards) World List of Lophogastrida, Stygiomysida and Mysida. World Register of Marine Species. 2015. <http://marinespecies.org/aphia.php?p=taxdetails&id=119863>. Accessed 27 Jul 2015.
- Mees J. *Heteromysis (Heteromysis) microps*. In: Mees, J. and Meland K. (Eds) (2012 onwards) World List of Lophogastrida, Stygiomysida and Mysida. World Register of Marine Species. 2016. <http://marinespecies.org/aphia.php?p=taxdetails&id=120037>. Accessed 3 Jan 2016.
- Nardon P, Charles H. Morphological aspects of symbiosis. In: Seckbach J editor. Symbiosis: Mechanisms and Systems. Dordrecht: Kluwer Academic Publishers; 2002. p. 15-44.
- Pascal L, Maire O, Volkenborn N, Lecroart P, Bichon S, de Montaudouin X, Grémare A, Deflandre B. Influence of the mud shrimp *Upogebia pusilla* (Decapoda: Gebiidea) on solute and porewater exchanges in an intertidal seagrass (*Zostera noltei*) meadow of Arcachon Bay: An experimental assessment. J Exp Mar Biol Ecol. 2016;477: 69-79. doi:10.1016/j.jembe.2016.01.008.
- Pillay D, Branch GM. Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. Oceano Mar Biol. 2011;49:137-92.
- Plus M, Dalloyau S, Trut G, Auby I, de Montaudouin X, Emery E, Noel C, Viala C. Long-term evolution (1988-2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). Estuar Coast Shelf Sci. 2010;87:357-66. doi:10.1016/j.ecss.2010.01.016.

- San Vicente C, Monniot F. The ascidian-associated mysid *Corellamysis eltanina* gen.nov., sp.nov. (Mysida, Mysidae, Heteromysinae): a new symbiotic relationship from the Southern Ocean. *Zootaxa*. 2014;3780:323-46. doi: 10.11646/zootaxa.3780.2.6.
- Santaga A. Waterborne behavioral cue for the actinotroch larva of *Phoronis pallida* (Phoronida) produced by *Upogebia pugettensis* (Decapoda: Thalassinidea). *Biol Bull*. 2004;207:103-15.
- Sars GO. Nye bidrag til Kundskaben om Middelhavets Invertebratfauna: I. Middelhavets Mysider. *Arch Math Naturvid*. 1877;2:10-119, Tabs 1-36.
- Sato M, Uchida H, Itani G, Yamashita H. Taxonomy and life history of the scale worm *Hesperonoe hwanghaiensis* (Polychaeta: Polynoidae), newly recorded in Japan, with special reference to commensalism to a burrowing shrimp, *Upogebia major*. *Zool Sci*. 2001;18:981-91. doi: <http://dx.doi.org/10.2108/zsj.18.981>
- Tattersall OS. A survey of the genus *Heteromysis* (Crustacea: Mysidacea) with descriptions of five new species from tropical coastal waters of the Pacific and Indian Oceans, with a key for the identification of the known species of the genus. *Trans Zool Soc London*. 1967; 31:157-93.
- Tattersall WM, Tattersall OS. *The British Mysidacea*. London: The Ray Society; 1951.
- Vannini M, Ruwa RK, Innocenti G. Notes on the behavior of *Heteromysis harpax*, a commensal mysid living in hermit crab shells. *Ethol Ecol Evol*. 1994;3:137-42.
- Wittmann KJ. *Heteromysis arianii* sp. n., a new benthic mysid (Crustacea, Mysidacea) from coralloid habitats in the Gulf of Naples (Mediterranean Sea). *Ann. Nat.hist. Mus. Wien*. 2000;102:279-90.

- Wittmann KJ. Centennial changes in the near-shore mysid fauna of the Gulf of Naples (Mediterranean Sea), with description of *Heteromysis riedli* sp. n. (Crustacea, Mysidacea). *Mar Ecol.* 2001;22:85-109.
- Wittmann KJ. Two new species of Heteromysini (Mysida: Mysidae) from the island of Madeira (N.E. Atlantic), with notes on sea anemone and hermit crab commensalisms in the genus *Heteromysis* S.I. Smith, 1873. *Crustaceana.* 2008;81:351-74. doi:10.1163/156854008783564037
- Wittmann KJ, Ariani AP, Lagardère JP. Chapter 54. Orders Lophogastrida Boas, 1883, Stygiomysida Tchindonova, 1981, and Mysida Boas, 1883 (also known collectively as Mysidacea). In: Vaupel Klein JC, von Charmantier-Daures M, Schram FR, editors. *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea.* Revised and updated, as well as extended from the *Traité de Zoologie* [founded by P.-P. Grassé], Volume 4 Part B. Leiden: Brill; 2014. p. 189-396.
- Ziebis W, Forster S, Huettel M, Jørgensen BB. Complex burrows of the mud shrimp *Callinassa truncata* and their geochemical impact in the sea bed. *Nature.* 1996;382:619-22.
- Zouhiri S, Vallet C, Mouny P, Dauvin JC. Spatial distribution and biological rhythms of suprabenthic mysids from the English Channel. *J Mar Biol Assoc UK.* 1998;78: 1181-202.