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ÉCOLE DOCTORALE SCIENCES ET ENVIRONNEMENTS
ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES COMMUNAUTÉS

Par Paulo BONIFÁCIO

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

Sous la direction de : Antoine GRÉMARE
(co-directrice : Céline LABRUNE)

Soutenue le 26 février 2015

Membres du jury :

M. BACHELET, Guy, Directeur de Recherche CNRS, Université de Bordeaux	Président
M. DESROY, Nicolas, Chargé de Recherche, Ifremer Dinard	Rapporteur
M. SANTOS, Paulo, Professeur, Universidade Federal de Pernambuco	Rapporteur
M. GRALL, Jacques, Ingénieur de Recherche, Université de Bretagne Occidentale	Examinateur
M. SARDÁ, Rafael, Directeur de Recherche, Centre d'Etudis Avançats de Blanes	Examinateur
M. GRÉMARE, Antoine, Professeur, Université de Bordeaux	Directeur
Mme. LABRUNE, Céline, Ingénieur de Recherche CNRS, UPMC	Co-directrice
M. AMOUROUX, Jean-Michel, Chargé de Recherche CNRS Honoraire, UPMC	Invité

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

Résumé : Mes objectifs consistaient à : (1) fournir une description de l'état actuel des communautés de la macrofaune benthique du golfe du Lion et à étudier leur variations temporelles entre 1998 et 2010 à partir de 91 stations, (2) tester le contrôle de la macrofaune par les variables climatiques à partir du suivi de 4 stations pendant 10 ans en baie de Banyuls-sur-Mer, (3) évaluer l'impact des apports du Rhône sur la macrofaune à partir de 5 stations échantillonnées dans le panache de dilution à 4 périodes hydrologiques différentes, et (4) actualiser le statut de qualité écologique des habitats benthiques du golfe. Mes résultats ont montré la conservation des communautés entre 1998 et 2010, confirmé l'influence de la NAO et du Rhône sur la composition des communautés benthiques de l'ensemble du golfe. Ils ont aussi confirmé le contrôle des descripteurs de la macrofaune par les oscillations climatiques, en particulier par la WeMO qui semble influencer le plus la macrofaune surtout en hiver. Les stations les plus impactées par les variations de débit du Rhône se situent à proximité immédiate de son embouchure. Les communautés benthiques y sont négativement affectées en périodes de crues et positivement affectées en période d'étiage estival. J'ai enfin mis à jour les niveaux de sensibilité/tolérances des espèces méditerranéennes, confirmer l'existence de disparités importantes entre les résultats dérivés de l'utilisation d'indices biotiques différents et montrer que les indices testés indiquent tous une tendance générale à la stabilité.

Mots clés : Communautés benthique, Macrofaune, Diversité, Comparaison à long terme, Rhône, Oscillations climatiques, Indices biotiques, Méditerranée nord-occidentale.

Study of the present state and of recent temporal changes in the benthic macrofauna composition of Gulf of Lions soft-bottoms macrobenthic communities, NW Mediterranean

Abstract: My main aims consisted in: (1) assessing the present state and recent (1998_2010) changes in benthic macrofauna composition of the Gulf of Lions soft-bottom communities through the long term comparison of 91 stations; (2) testing the current paradigm regarding the control of those communities by climatic parameters through a 10-year monitoring of 4 stations located in the Bay of Banyuls-sur-Mer; (3) assessing the influence of Rhône River inputs on the composition of benthic macrofauna through the sampling, of 5 stations , under 4 hydrological regimes; and (4) updating the ecological quality status of Gulf of Lions benthic habitats. My results have shown the persistence of the same 3 communities between 1998 and 2010, the strong influence of both the NAO and the Rhône River on benthic macrofauna composition in the whole Gulf. They also showed a control of benthic macrofauna by climatic oscillations with the WeMO contributing most especially during wintertime. Moreover, the stations most impacted by Rhône River inputs were located close to its mouth. They are negatively affected during floods and positively affected during dry periods. Lastly, I have updated the sensitivity/tolerance levels of Mediterranean species and confirmed the existence of major discrepancies in the results derived from different biotic indices used, although all tested indices indicated an overall stability in the ecological quality status of benthic habitats between 1998 and 2010.

Environnements et Paléoenvironnements Océaniques et Continentaux
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YOU HAVE MADE YOUR WAY FROM WORM TO MAN,
AND MUCH WITHIN YOU IS STILL WORM.

THUS SPOKE ZARATHUSTRA (NIETZSCHE)

Aux illustres chercheurs Fauvel, Laubier, Ramos, Guille, Picard,
Pérès, Salen-Picard, Bellan et Amouroux pour leurs contributions
à l'étude de la macrofaune benthique méditerranéenne

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CHAPITRE I

INTRODUCTION GÉNÉRALE

1 LA MACROFAUNE BENTHIQUE : DÉFINITION, RÔLE FONCTIONNEL ET STRUCTURATION

La macrofaune benthique (**Figure 1**) des substrats meubles correspond aux organismes d'une taille supérieure à 1 mm vivant sur ou étroitement associés aux sédiments. Elle est composée majoritairement par les phyla Annelida (classe Polychaeta), Arthropoda (subphylum Crustacea), Mollusca et Echinodermata. D'autres espèces appartenant à des groupes souvent présents en faible abondance (tels que les phyla Chordata, Cnidaria, Echiura, Nemertea, Phoronida, Platyhelminthes et Sipuncula), peuvent également y contribuer. Ces animaux montrent le plus souvent un développement larvaire pélagique (Thorson, 1961).

Figure 1. Diversité des animaux qui compose la macrofaune benthique au large d'Argelès-sur-Mer (Céline LABRUNE).

La macrofaune benthique joue un rôle fondamental dans le fonctionnement des écosystèmes marins. Elle constitue la base des réseaux trophiques (Darnaude et al., 2004 ; Harmelin-Vivien et al., 2009) et participe au recyclage de la matière organique via les processus de nutrition et de bioturbation. Les consommateurs primaires de la macrofaune benthique sont adaptés à exploiter une source de nourriture très pauvre (car fortement diluée dans une matrice inorganique) ce qui se traduit entre autres par des taux d'ingestion et des efficacités d'absorption particulièrement élevés (Lopez et Levinton, 1987). Le passage au travers de leur tube digestif au cours du processus de nutrition : (1) affecte donc de grandes quantités de matière organique, et (2) transforme profondément cette matière. Le terme de bioturbation recouvre, quant à lui, 2 processus différents : (1) la bioirrigation, c'est-à-dire la pénétration en profondeur dans la colonne sédimentaire de l'eau oxygénée sus-jacente provoquée par les organismes vivant dans le sédiment pour assurer leur respiration ; et (2) le remaniement sédimentaire, c'est-à-dire les mouvements des particules sédimentaires induits par la macrofaune benthique. De manière générale, la bioturbation modifie la zonation verticale des conditions redox dans les premiers centimètres de la colonne sédimentaire. Elle contrôle ainsi la structuration des communautés bactériennes associées, principaux acteurs de la dégradation de la matière organique sédimentée. Ce faisant, la macrofaune benthique contrôle très largement de manière indirecte le futur (i.e., resuspension, enfouissement, intégration au réseau trophique et minéralisation) de la matière organique sédimentée (Rhoads, 1974 ; Rosenberg, 2001 ; Meysman et al., 2006).

1.1 Populations et communautés

L'ensemble des individus d'une même espèce et qui occupent un même écosystème est désigné sous le terme de population. La composante vivante d'un même écosystème est composée de plusieurs populations d'espèces différentes qui partagent le même biotope et qui forment la communauté, dont la composition est structurée par 2 types de facteurs :

(1) *les facteurs abiotiques qui correspondent aux paramètres physico-chimiques du milieu.* La profondeur et la granulométrie sont souvent considérées comme les principaux facteurs qui structurent les communautés benthiques dans les eaux côtières (Pérès et Picard, 1964 ; Pearson et al., 1985 ; Rosenberg et al., 1987 ; Snelgrove et Butman, 1994). De manière générale, la granulométrie est fonction de l'hydrodynamisme qui est généralement plus puissant dans les milieux peu profonds que dans les milieux profonds dans lesquels les particules fines tendent à se déposer. On observe par conséquent classiquement une granulométrie plus fine au large qu'à la côte, même si certaines exceptions existent comme cela peut être le cas pour les sédiments hétérogènes relictes du bord du plateau continental du golfe du Lion dont l'envasement est empêché par le courant Nord (Durrieu de Madron et al., 2000 ; Grémare et al., 2002 ; Ferré et al., 2005).

(2) *les facteurs biotiques qui correspondent aux interactions entre individus appartenant soit à une même espèce* (i.e., relations intraspécifiques), *soit à des espèces différentes* (i.e., relations interspécifiques). Un bon exemple de telles interactions est constitué par les réseaux trophiques avec l'existence : (1) de relations de type « prédateur-proie » dites « verticales », et (2) de relations de compétition dites « horizontales ». De telles interactions peuvent prendre des formes durables de type parasitisme, symbiose ou commensalisme. La macrofaune benthique, et plus spécifiquement l'interaction entre les déposivores et les suspensivores, a, quant à elle, servi d'illustration au concept d'amensalisme (Rhoads et Young, 1970, 1971 ; Levinton, 1972 ; Wildish, 1985) qui décrit la manière dont une espèce nuit à une autre sans elle-même en retirer d'avantage particulier.

2 RÉPONSE DE LA MACROFAUNE AUX PERTURBATIONS NATURELLES ET ANTHROPIQUES : CONCEPTION ET UTILISATION DES INDICES BIOTIQUES EN VUE DE CARACTÉRISATION DU NIVEAU DE QUALITÉ ÉCOLOGIQUE DES HABITATS

2.1 Le modèle de succession secondaire

La mobilité réduite de la macrofaune benthique ainsi que l'existence de stades sensibles pendant son cycle de vie la rend tributaire des conditions du milieu. La durée de vie (de quelques jours à plusieurs années) des espèces qui la constituent lui confère par ailleurs des propriétés d'intégration (et donc de « mémoire ») des changements environnementaux à ces mêmes échelles de temps. L'analyse de la composition des communautés de macrofaune benthique est par conséquent classiquement utilisée en tant qu'indicateur de l'existence de perturbations environnementales et plus largement de changements environnementaux et ceci quelles que soient leurs origines (Pearson et Rosenberg, 1978 ; Borja et al., 2000, 2003 ; Simboura et Zenetos, 2002 ; Rosenberg et al., 2004 ; Dauvin et Ruellet, 2007 ; Muxika et al., 2007).

Une des difficultés liées à l'utilisation de la macrofaune benthique en vue de la caractérisation du niveau de qualité écologique des habitats réside dans la multiplicité des perturbations possibles qui est elle-même susceptible d'engendrer des modifications différentes dans la composition des communautés benthiques. Plusieurs auteurs ont cherché à la lever en établissant des modèles à vocations génériques. Le plus célèbre d'entre eux est sans nul doute celui de Pearson et Rosenberg (1978) qui décrit la réponse des communautés benthiques à un enrichissement en matière organique. Sa possible généralisation repose sur le fait que toute perturbation serait susceptible d'engendrer, soit directement, soit indirectement (i.e., via une diminution de la biomasse de la macrofaune benthique), un tel enrichissement (e.g. Cardell et al., 1999). Ce modèle est présenté en **Figure 2**. L'axe horizontal correspond à un gradient croissant de perturbation qui peut être indifféremment temporel ou spatial. A l'initiation de la perturbation, on observe tout d'abord une légère augmentation de la richesse spécifique et de la biomasse de la macrofaune benthique. Si la perturbation s'accentue, les espèces les plus sensibles commencent à disparaître ce qui provoque une diminution de la biomasse alors que l'abondance reste constante car ces espèces sont le plus souvent de grande taille et présentes en faibles effectifs. Si la perturbation s'accentue encore, d'autres espèces légèrement moins sensibles disparaissent alors que les espèces tolérantes continuent d'être présentes. La communauté passe alors par le point dit « écotone » durant lequel coexistent des espèces présentant des niveaux moyens de sensibilité et de tolérance (d'où un nombre intermédiaire d'espèces) et durant lequel la biomasse est faible. Passé ce stade, la richesse spécifique continue de diminuer avec l'intensité de la perturbation alors que quelques espèces dites « opportunistes » tendent à pulluler ce qui contribue à faire fortement augmenter l'abondance et dans une moindre mesure (du fait de leur petite taille) la biomasse. Enfin, en cas de perturbation maximale, l'environnement devient anoxique et azoïque.

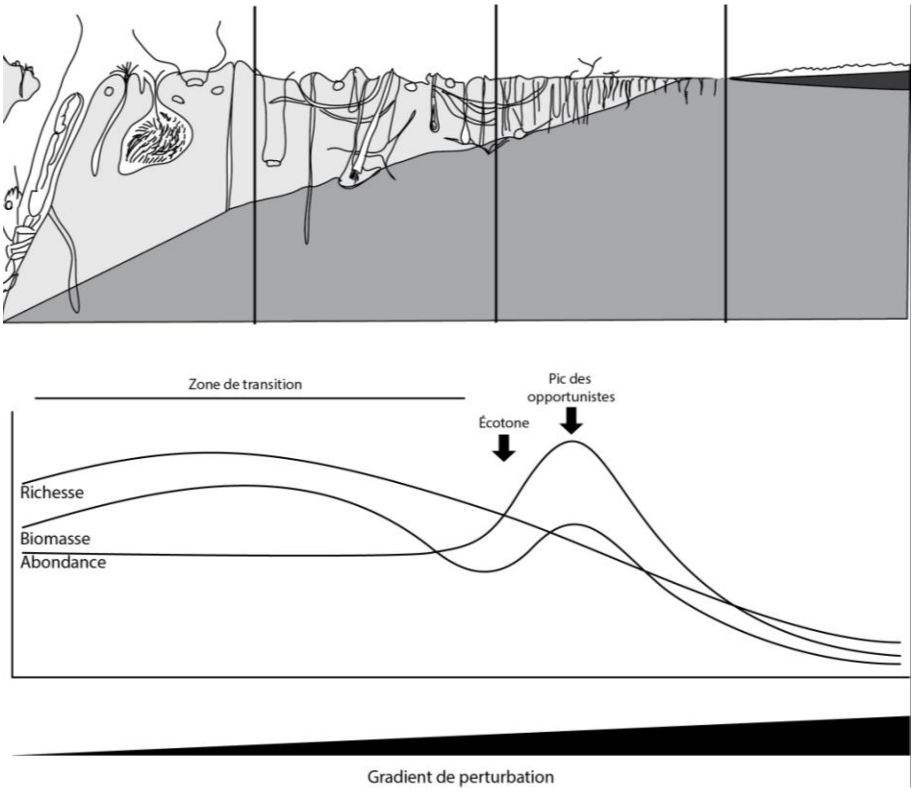

Figure 2. Modèle de réponse du macrobenthos à un enrichissement organique. Ce modèle décrit les stades de succession de la macrofaune en termes de richesse spécifique, biomasse et abondance le long d'un gradient (spatial ou temporel) de perturbation croissant de gauche à droite. Lu de la droite vers la gauche ce même modèle décrit la réponse de la macrofaune benthique à une diminution de l'intensité de la perturbation (modifié de Pearson et Rosenberg, 1978).

Ce modèle a constitué la base de plusieurs approches permettant d'interpréter les données relatives à la composition de la macrofaune benthique en termes de qualité écologique des habitats. La première, et la plus simple d'entre elles, développée dans l'article même de Pearson et Rosenberg (1978), consiste à identifier des espèces indicatrices, soit d'habitats perturbés (espèces dites « tolérantes »), soit d'habitats non perturbés (espèces dites « sensibles »). Ces espèces sont sélectionnées à partir de leur abondance et de leur fréquence d'occurrence dans des groupes de stations perturbées et non perturbées. En fonction de leur nature sensible ou tolérante, la présence d'espèces indicatrices donne une première évaluation qualitative de l'état écologique de l'habitat considéré. Plusieurs auteurs ont ainsi identifié des espèces caractéristiques de différentes conditions de perturbation (e.g. Pearson et Rosenberg, 1978 ; Bourcier, 1980 ; Glémarec et Hily, 1981 ; Bellan et Bourcier, 1984). La présence d'espèces indicatrices « sensibles » reflète une bonne qualité environnementale alors que la présence d'espèces indicatrices « tolérantes » (dont les espèces opportunistes) traduit au contraire une dégradation du milieu.

2.2 Les indices biotiques

La seconde approche consiste à construire des indices biotiques. La mise en œuvre de ces indices comprend fondamentalement 3 étapes (**Figure 3**). La première consiste à résumer l'information contenue dans le tableau espèces-abondances caractérisant la station étudiée sous la forme d'un nombre unique. Cet indice est ensuite transformé en un rapport de qualité écologique (Ecological Quality Ratio, EQR) par division avec la valeur du même indice biotique calculé pour une station de référence dont l'état écologique « high » (excellent) est avéré. Ce rapport de qualité écologique est ensuite converti en un statut de qualité écologique (Ecological Quality Status, EcoQ) à l'aide d'une échelle appropriée.

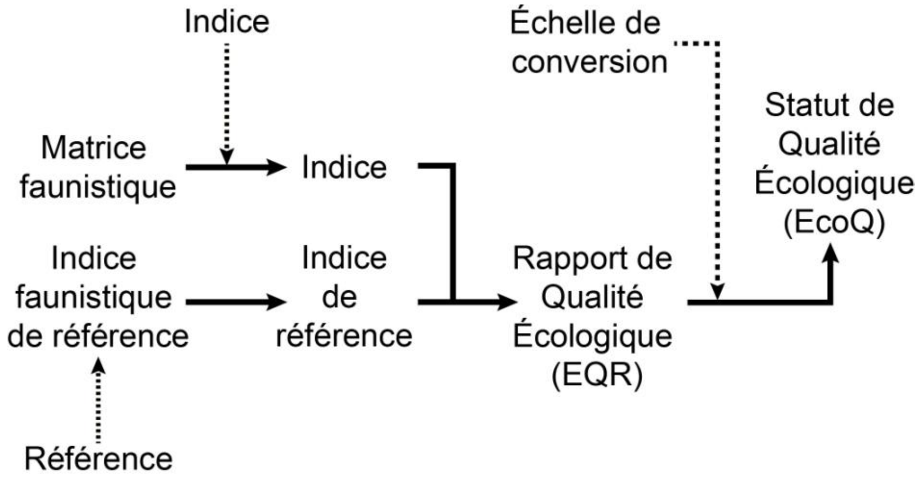

Figure 3. Principales étapes de calcul et de conversion d'un indice biotique en statut de qualité écologique.

Plusieurs indices biotiques ont été développés, en particulier récemment avec l'émergence des directives cadres européennes sur l'eau (Water Framework Directive, WFD, 2000/60/EC) et sur la Stratégie pour le Milieu Marin (Marine Strategy Framework Directive, MSFD, 2008/56/EC) : Borja et al. (2000, 2003), Simboura et Zenetos (2002), Rosenberg et al. (2004), Dauvin et Ruellet (2007) et Muxika et al. (2007). Au-delà de leur diversité, ces indices peuvent être regroupés en 2 grandes catégories : (1) les indices basés sur le concept de sensibilité/tolérance, et (2) les indices basés sur la déviation par rapport à un état de référence connu.

2.3 Le concept de sensibilité/tolérance

Les indices basés sur le concept de sensibilité/tolérance (e.g. I2EC, Grall et Glemarec (1997) ; AMBI, Borja et al. (2000, 2003) ; BENTIX, Simboura et Zenetos (2002) ; BQI, Rosenberg et al. (2004) ; BOPA, Dauvin et Ruellet (2007) ; M-AMBI, Muxika et al. (2007)) sont de loin les plus nombreux et les plus répandus. Ils constituent en fait une extension du concept d'espèces indicatrices qu'ils cherchent à utiliser sous une forme quantitative. La première étape consiste à attribuer à chaque espèce un niveau de sensibilité/tolérance qui peut être soit discret et déterminé à partir d'une analyse de la littérature (e.g. I2EC, AMBI, BENTIX et M-AMBI), soit continu et dérivé de la richesse spécifique des stations dans lesquelles l'espèce est présente (e.g. BQI). Ces valeurs servent ensuite de base au calcul d'un niveau de sensibilité/tolérance moyen pondéré par l'abondance des différentes espèces ; niveau qui peut ensuite lui-même être corrigé (e.g. BQI et M-AMBI) ou non (e.g. AMBI) par la diversité et/ou l'abondance de la macrofaune à la station considérée. Le calcul du rapport de qualité écologique peut ensuite être réalisé (e.g. BQI et M-AMBI) ou non (e.g. AMBI) et les niveaux de qualité écologique dérivés à partir d'une échelle de conversion : (1) unique et universelle (e.g. AMBI), (2) dérivée de la valeur maximale de l'indice observé pour chaque habitat donné (e.g. BQI), ou (3) dérivée de 2 références théoriques pour chaque habitat donné (e.g. M-AMBI). Plusieurs études récentes ont comparé l'utilisation de 2 de ces indices (i.e., l'AMBI et le BQI) sur les mêmes jeux de données (Marín-Guirao et al., 2005 ; Labrune et al., 2006 ; Fleischer et al., 2007 ; Grémare et al., 2009 ; Dimitriou et al., 2012 ; Labrune et al., 2012). La plupart d'entre elles ont conclu à l'existence de disparités majeures liées à l'attribution de niveaux de sensibilité/tolérance différents à des espèces dominantes (Labrune et al., 2006 ; Grémare et al., 2009).

Plus généralement, on peut légitimement s'interroger sur la pertinence d'attribuer un niveau de sensibilité/tolérance unique à une espèce susceptible de se trouver soumise à des perturbations de natures différentes. Rhoads et al. (1985) ont étudié l'impact des apports particulaires liquides et solides des grands fleuves sur la composition de la macrofaune benthique. Le modèle général qu'ils proposent (**Figure 4**) montre clairement que la variation spatiale de la composition de la macrofaune benthique dans les zones directement soumises à l'influence des fleuves résulte de 2 processus distincts. A proximité immédiate de l'embouchure la diminution de l'abondance de la macrofaune benthique est causée par de forts taux de sédimentation et par l'instabilité du sédiment qui en découle. Dans cette zone, on trouve par conséquent des organismes fouisseurs qui supportent bien l'arrivée constante de sédiments comme par exemple l'holothurie *Labidoplax digitata* et l'annélide polychète *Sternaspis scutata*. Plus au large, les variations spatiales de la composition de la macrofaune benthique reflètent celle du flux de matière organique particulaire descendant. Les apports de sels nutritifs continentaux ainsi que la diminution de la turbidité dans cette zone favorisent en effet la production primaire et donc la présence de suspensivores et d'espèces bioturbatrices qui creusent des terriers comme les crustacés du genre *Calianassa*.

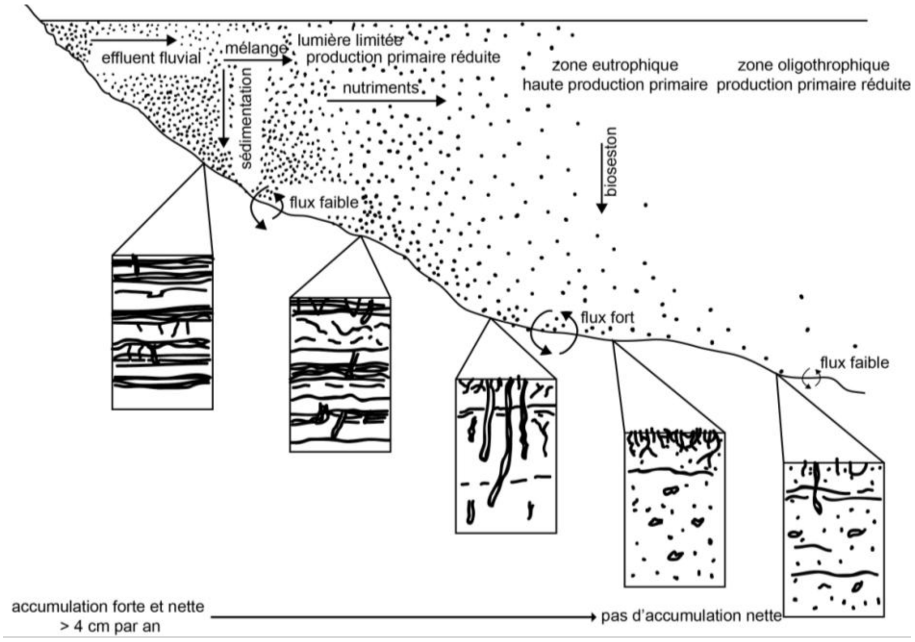

Figure 4. Modèle généralisé des processus intervenant sur la plateforme continentale en relation avec les débits liquides et solides d'un grand fleuve (tiré de Rhoads, 1985).

2.4 Le choix des stations de référence

La question de l'évaluation de la sensibilité/tolérance n'est pas la seule à poser problème. L'identification d'une référence en excellent état écologique se trouve de nos jours très fortement compliquée dans des environnements pratiquement tous anthropisés à un plus ou moins fort degré (Warwick et al., 2003). L'utilisation de références historiques n'est pas non plus forcément sans présenter de difficulté dans l'hypothèse où les communautés des habitats étudiés présentent également une dynamique temporelle « naturelle ».

Un bon exemple de cet état de fait est fourni par la série à long terme de la macrofaune benthique sur le site dit de « Pierre Noire » en baie de Morlaix suite à la marée noire de l'Amoco Cadiz intervenue au printemps 1978. Les travaux conduits par Ibanez et Dauvin (1988) puis Dauvin (1998) montrent en effet une absence de retour, respectivement 10 et 20 ans après la catastrophe, des communautés de la macrofaune de ce site à leur état *ante* marée noire (**Figure 5**) ; et ceci alors même que les concentrations en hydrocarbures de ce site avaient apparemment retrouvé un niveau acceptable dès l'hiver 1981 (Dauvin (1984) cité par Poggiale et Dauvin (2001)). L'hypothèse la plus probable pour expliquer cet état de fait est que la communauté biologique étudiée présente une dynamique « naturelle » à laquelle se sont superposés les effets de la marée noire. Une telle intrication des échelles temporelles associées à différentes causes de modifications de la composition de la macrofaune benthique est susceptible de rendre caduque l'utilisation de toute référence historique d'un bon état écologique si la composante « naturelle » de la variation temporelle de la macrofaune benthique induit des modifications de l'indice biotique considéré (Labrune et al., 2006).

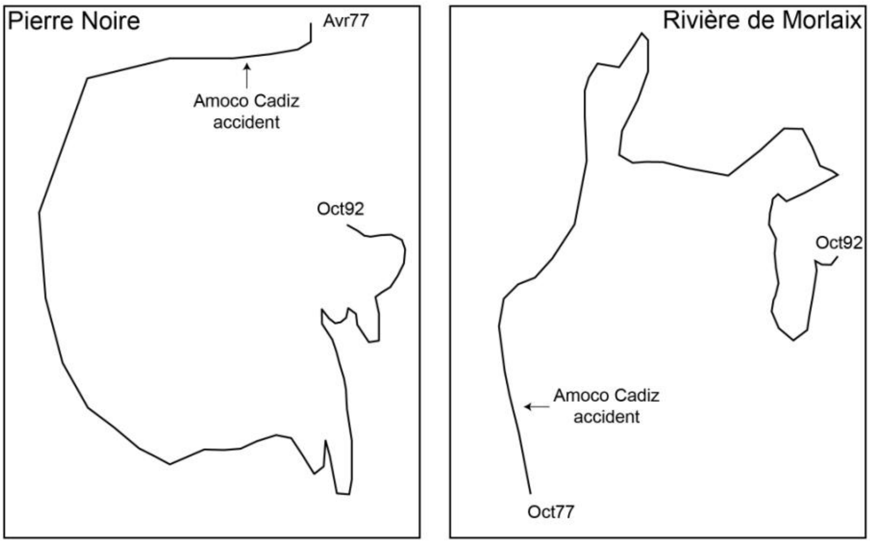

Figure 5. MDS basé sur l'abondance de la macrofaune benthique à différentes dates d'échantillonnage entre octobre 1977 et octobre 1992 à 2 sites de la baie de Morlaix affectés par la marée noire causée par l'Amoco Cadiz (tiré de Fromentin et al., 1997). Stress ≈ 0,05 pour les 2 analyses.

Les indices basés sur la déviation par rapport à un état de référence (e.g. B-IBI, Weisberg et al., 1997 ; MISS, Lavesque et al., 2009) constituent en eux-mêmes un rapport de qualité écologique. Leur mode de calcul consiste à comparer la valeur d'un jeu de paramètres à la distribution de fréquence de ce même paramètre dans un ensemble de stations présentant un excellent niveau de qualité écologique. Chaque paramètre fait ainsi l'objet d'un score de 1 ou de 0 suivant que sa valeur est compatible ou non avec celles observées dans le cas d'un excellent niveau écologique. La valeur de l'indice à la station considérée est ensuite obtenue par sommation de l'ensemble de ces scores. L'intérêt de ces indices réside dans le fait qu'il leur est possible de combiner un grand nombre de paramètres de natures différentes (i.e., physiques, chimiques et biologiques) ; et ceci même si la question des poids respectifs à leur accorder est le plus souvent éludée. Le principal frein à leur utilisation reste néanmoins la quasi-impossibilité de disposer d'un nombre de stations de référence en excellent état écologique suffisamment grand pour générer des distributions de référence fiables et précises des paramètres sélectionnés (voir plus haut la difficulté à disposer d'une seule station de référence valide).

3 LES VARIATIONS À LONG TERME DE LA COMPOSITION DE LA MACROFAUNE BENTHIQUE

Des variations temporelles de la composition de la macrofaune benthique ont été mises en évidence dans la plupart des environnements marins, depuis la zone côtière et le plateau continental (e.g. Pearson et al., 1985 ; Rosenberg et al., 1987 ; Kröncke, 1992 ; Josefson et al., 1993 ; Carpentier et al., 1997 ; Grémare et al., 1998a ; Afli et Glémarec, 2000 ; Dauvin, 2000 ; Wieking et Kröncke, 2001, 2003 ; Salen-Picard et Arlhac, 2002 ; Franke et Gutow, 2004 ; Reichert et Buchholz, 2006 ; Labrune et al., 2007b ; Hily et al., 2008 ; Schückel et al., 2010 ; Kröncke, 2011 ; Dauvin et Pezy, 2013) jusqu'à la mer profonde (Blake et Grassle, 1994 ; Blake et al., 2009 ; Cartes et al., 2015). Au-delà d'un aspect purement descriptif, ces travaux se sont également donnés pour objectifs : (1) d'identifier les facteurs régissant la variabilité de la macrofaune benthique à long terme, et (2) de prédire de futurs changements de composition (Kröncke et al., 1998 ; Dippner et Kröncke, 2003). De manière générale, les changements temporels peuvent être approchés selon 2 modalités principales :

(1) *les comparaisons à long terme d'un nombre limité de situations ponctuelles dans le temps* et/ou d'un nombre plus grand de situations mais séparées par des intervalles de temps longs et/ou irréguliers (e.g. Pearson et al., 1985 ; Reise et Schubert, 1987 ; Rosenberg et al., 1987 ; Kröncke, 1992 ; Josefson et al., 1993 ; Grémare et al., 1998a ; Afli et Glémarec, 2000 ; Dauvin, 2000 ; Massé, 2000 ; Wieking et Kröncke, 2001 ; Bradshaw et al., 2002 ; Franke et Gutow, 2004 ; Perus et Bonsdorff, 2004 ; Reichert et Buchholz, 2006 ; Reiss et al., 2006 ; Reiss et Kröncke,

2006 ; Callaway et al., 2007 ; Labrune et al., 2007b ; Van Hoey et al., 2007 ; Hily et al., 2008 ; Schückel et al., 2010 ; Kröncke, 2011 ; Köncke et al., 2011 ; Dauvin et Pezy, 2013) ; et

(2) *la réalisation de suivis à long terme dans lesquels plusieurs événements d'échantillonnages*, séparés par un intervalle de temps régulier, sont comparés (e.g. Beukema, 1985 ; Carpentier et al., 1997 ; Fromentin et al., 1997 ; Dauvin, 1998 ; Kröncke et al., 1998, 2001 ; Tunberg et Nelson, 1998 ; Beukema et al., 2000 ; Hagberd et Tunberg, 2000 ; Lloret et al., 2001 ; Salen-Picard et al., 2002 ; Salen-Picard et Arlhac, 2002 ; Warwick et al., 2002 ; Wieking et Kröncke, 2003 ; Neumann et al., 2008 ; Frid et al., 2009 ; Harmelin-Vivien et al., 2009 ; Kröncke et al., 2013 ; Rousi et al., 2013).

Les comparaisons à long terme sont clairement plus faciles à mettre en œuvre car leur réalisation ne nécessite que l’existence d’une étude de référence valide pour laquelle il s’agit de s’assurer de l’utilisation de protocoles d’échantillonnage et d’analyse strictement identiques ou à défaut compatibles. Elles constituent par conséquent un bon outil de diagnostic de l’existence de variations temporelles significatives. Leur aptitude à identifier les facteurs contrôlant ces changements s’avère par contre extrêmement limitée. Cette recherche de causalité s’appuie en effet toujours, dans un premier temps au moins, sur la mise en corrélation des changements faunistiques avec ceux des variables indépendantes supposées ; approche qui s’avère souvent peu efficace dans le cas des comparaisons à long terme du fait du petit nombre de situations comparées.

La réalisation de suivis à long terme nécessite au contraire un investissement beaucoup plus conséquent. De tels suivis sont par conséquent plus rares et souvent associés au suivi de perturbations potentielles (e.g. Ibanez et Dauvin, 1988 ; Fromentin et al., 1997 ; Dauvin, 1998) même si ils permettent une mise en corrélation beaucoup plus solide des variations des paramètres faunistiques et environnementaux et par là l’élaboration d’hypothèses plus robustes sur le déterminisme des variations des compositions des communautés de la macrofaune benthique.

3.1 Réponse aux changements climatiques

Tous les écosystèmes sont soumis aux forces climatiques et environnementales et il est supposé que leurs variations induisent une réponse des communautés (Möllmann et Diekmann, 2012). Selon Scheffer et al. (2001), cette réponse peut être : (1) graduelle ; (2) brutale quand des seuils critiques sont atteints ; ou (3) caractérisée par l’existence de plusieurs états stables dans une gamme de conditions environnementales, en fonction notamment de la trajectoire de ces conditions. De tels changements ont été mis en évidence en mer du Nord, à partir de l’analyse des variations temporelles du phytoplancton, du zooplancton, du benthos et des poissons. Ils ont ensuite été reliés aux anomalies de températures observées entre 1978/1982 (conditions froides) et à partir de 1988 (conditions chaudes) (Beukema, 1985 ; Reid et al., 1990 ; Kröncke et al., 1998 ; Clark et Frid, 2001 ; Edwards et al., 2001 ; Reid et al., 2001). La température étant un des facteurs contrôlés par la NAO (North Atlantic Oscillation ; Hurrell, 1995), celle-ci peut elle-même contrôler indirectement les variations temporelles de la composition de la faune, dont la macrofaune benthique (Kröncke et al., 1998 ; Dippner et Kröncke, 2003). Dans le sud de la mer du Nord, près de l'ile de Nordeney, Kröncke et al. (1998) ont ainsi montré qu’entre 1978 et 1995 à chaque printemps, l'abondance et le nombre d'espèces de la macrofaune benthique entre 12 et 20 m de profondeur étaient bien corrélés avec les valeurs hivernales de l'indice NAO. Dippner et Kröncke (2003) ont ensuite établi un modèle prédictif des variations de richesse spécifique, d’abondance et de biomasse de la macrofaune benthique à partir de la valeur hivernale de la NAO. L’hypothèse du contrôle des principales caractéristiques de la macrofaune benthique par la NAO via les températures hivernales est par ailleurs en accord avec les observations de Beukema et al. (1985), sur la dynamique de population de l’oursin *Echinocardium cordatum*, qui montrent une nette réduction de son abondance après des hivers rigoureux.

Conversi et al. (2010) en cherchant à déterminer les causes des changements soudains observés en 1987 dans les variations de l'abondance : (1) du zooplancton des mers Adriatique et Ligure, ainsi que (2) de la biomasse des anchois en mer Adriatique, ont montré que toutes les variables physiques (pression au niveau de la mer et température de l'eau de surface) et climatiques (NAO et Northern Hemisphere

Temperature indices) testées ont subi un grand changement (« regime shift ») entre 1986 et 1988. Leur interprétation est qu'un tel « shift » a pu causer les changements faunistiques observés. Cette hypothèse a ensuite été renforcée par les travaux de Garcia-Comas et al. (2011) sur la composition des communautés zooplanctoniques de la rade de Villefranche-sur-Mer.

Dans le Nord-Ouest de la Méditerranée les effets de la NAO rapportés jusqu'à maintenant sont principalement liés aux débarquements des pêches dans les deltas du Rhône et de l'Ebre (Lloret et al., 2001). Les débits liquides de ces 2 fleuves sont corrélés négativement avec l'indice NAO. Les débarquements de pêche, par exemple la pieuvre-blanche *Eledone cirrhosa*, sont négativement affectés par la réduction du débit liquide de ces 2 fleuves et donc, indirectement et négativement affectés par la phase positive de la NAO (Lloret et al., 2001). Dans le même esprit, Salen-Picard et al. (2002) et Labrune et al. (2007b) ont respectivement suggéré que la NAO pouvait indirectement contrôler les fluctuations des débarquements de *Solea solea* de la pêcherie du Rhône et des changements de composition des communautés de la macrofaune benthique de la baie de Banyuls-sur-Mer. Toujours dans le golfe du Lion, Martín et al. (2012) ont observé une corrélation significative entre les valeurs annuelles de l'indice régional WeMO (Western Mediterranean Oscillation ; Martin-Vide et Lopez-Bustins, 2006) et les débarquements de pêches de sardines et d'anchois sur la côte catalane. Ils ont suggéré que la phase positive de cet indice, qui est significativement corrélée avec une réduction de la température de l'eau de surface et avec l'augmentation du débit liquide du Rhône, favoriserait le recrutement de ces 2 espèces. Dans ce cas précis, la WeMO, s'est montrée plus apte que la NAO à expliquer les variations des captures par unité d'effort de pêche (Martín et al., 2012).

4 LE GOLFE DU LION : UN BON MODÈLE D'ÉTUDE DES VARIATIONS SPATIO-TEMPORELLES DE LA COMPOSITION DE LA MACROFAUNE BENTHIQUE

4.1 L'hydrographie

Le golfe du Lion s'étend sur 400 km de zone côtière entre le cap Creus (Espagne) et le cap Croisette (Marseille, France) (**Figure 6**). Il est alimenté par plusieurs fleuves côtiers dont le plus important est de très loin le Rhône qui a contribué entre 1977 et 2004 à 92,6 et 94,1% de ses apports continentaux liquides et solides, respectivement (**Table 1**).

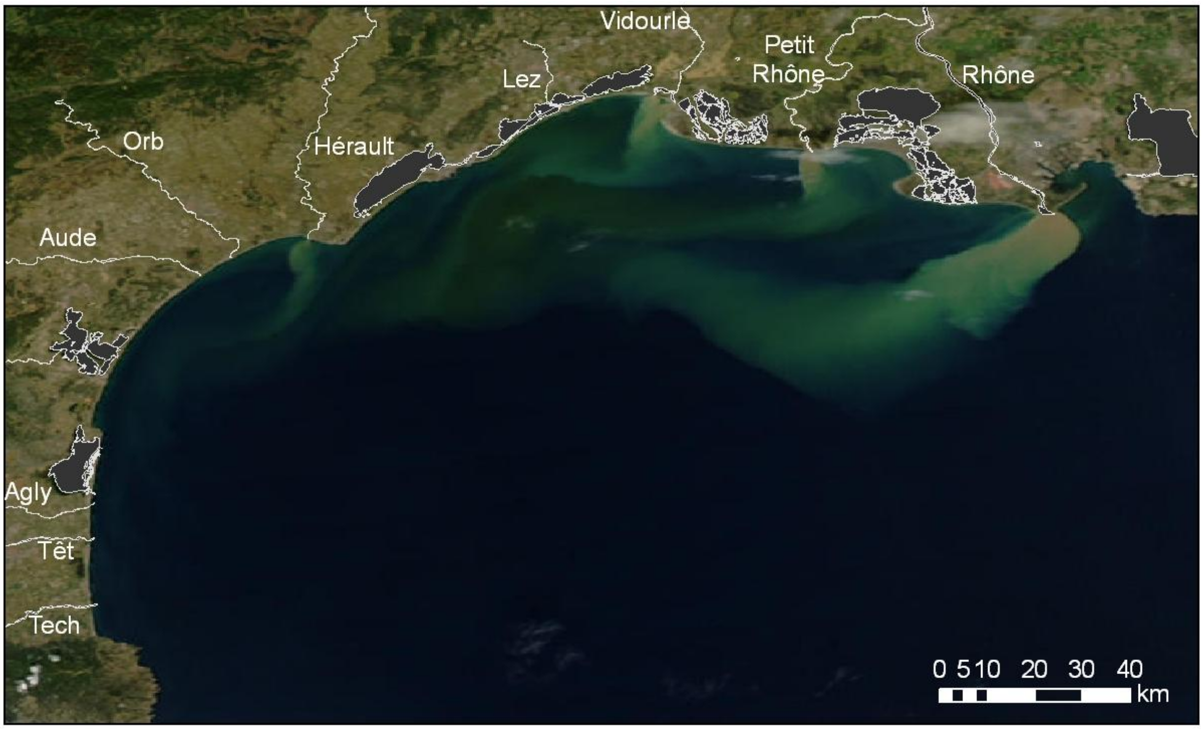

Figure 6. Carte du golfe du Lion montrant les panaches des principaux fleuves après un épisode de crue (tiré de http://visibleearth.nasa.gov/view.php?id=61703).

Table 1. Moyennes annuelles (entre 1977 et 2004) des débits liquide et solide des principaux fleuves alimentant le golfe du Lion. Les % des apports continentaux correspondants sont également fournis (données tirées de Bourrin et al., 2006).

Fleuve	Débit liquide (10^6 $m^3.an^{-1}$)		Débit solide (10^6 $t.an^{-1}$)	
	Moyenne annuelle	%	Moyenne annuelle	%
Tech	301,47	0,5	0,032	0,3
Têt	341,54	0,6	0,061	0,6
Agly	193,44	0,3	0,098	0,9
Aude	1197,61	2,0	0,194	1,8
Orb	841,64	1,4	0,11	1,0
Hérault	1281,58	2,1	0,088	0,8
Lez	68,65	0,1	0,003	0,0
Vidourle	215,44	0,4	0,051	0,5
Rhône	55812,43	92,6	10,147	94,1

4.2 Débit liquide et solide du Rhône

Le bassin hydrologique de ce fleuve est très hétérogène et couvre environ 97800 km^2 (Pont, 1997 ; Pont et al., 2002). Son débit liquide journalier est sujet à de fortes variations, faisant du Rhône un grand fleuve de type « méditerranéen ». Les débits minimums sont observés en été tandis que les débits maximums sont observés pendant les crues hivernales ou printanières (**Figure 7**). Un débit liquide >3000 $m^3.s^{-1}$ est considéré comme indicatif d'un événement de crue (Pont, 1997).

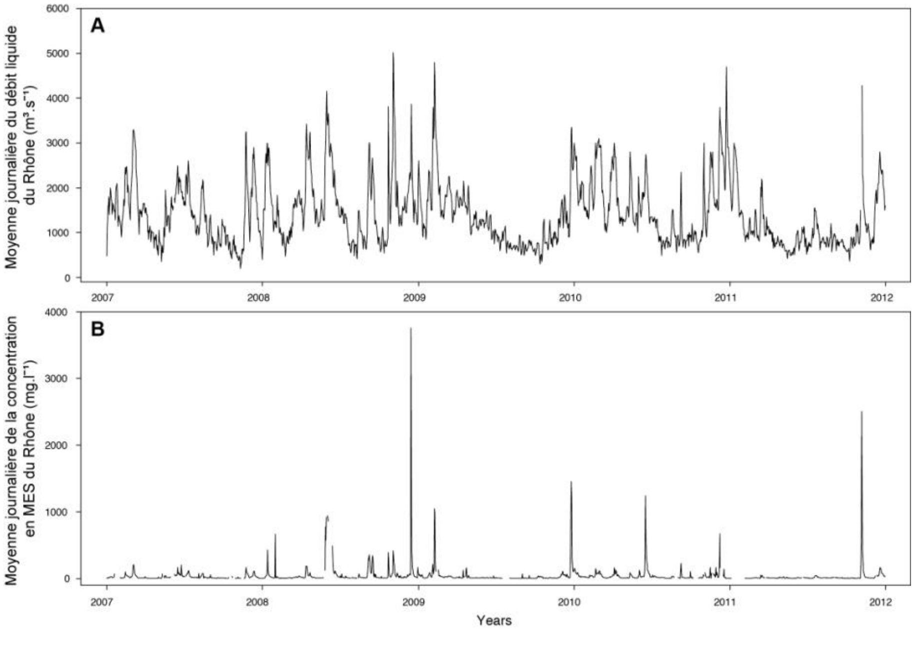

Figure 7. Évolution temporelle de la valeur moyenne journalière du débit liquide (A) et de la concentration en Matière particulaire en Suspension (MES) (B) dans le Rhône entre 2007 et 2012 (données fournies par le service d'observation MOOSE).

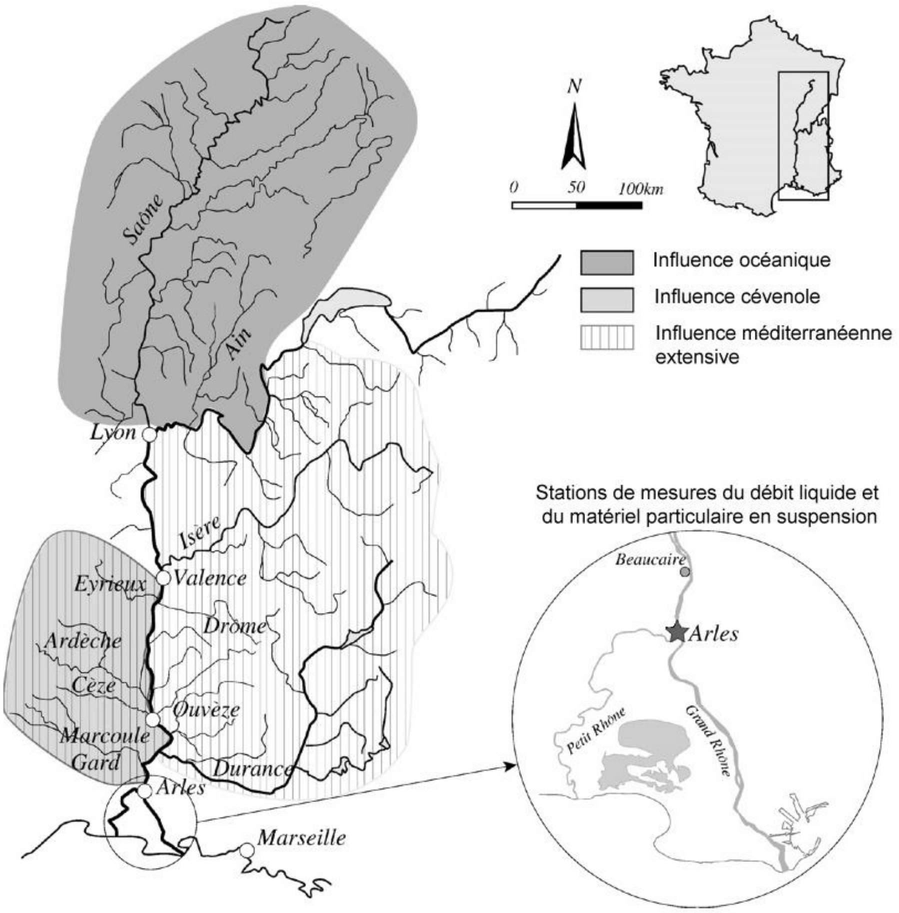

Figure 8. Bassin versant du Rhône montrant les zones affectées par les précipitations associées aux 3 types de crues (océaniques, cévenoles et méditerranéennes extensives). Les crues généralisées correspondent à une combinaison de ces 3 types (voir texte pour détails ; tiré de Antonelli et al., 2008)

Pont (1997) a identifié 4 types de crues du Rhône (**Figure 8**) : (1) les crues *océaniques* qui sont associées aux précipitations qui touchent la partie nord du bassin hydrologique et sont caractérisées par un débit du fleuve régulier et lent ainsi que par des concentrations réduites en MES (<500 mgDW.l^{-1}), (2) les crues *cévenoles* qui sont liées à d'intenses précipitations dans le Sud-Ouest du bassin et sont caractérisées par leur survenue soudaine et violente entraînant une augmentation rapide du débit, (3) les crues *méditerranéennes extensives* qui sont liées aux précipitations qui affectent la totalité du bassin versant sud et sont associées aux vagues pluvieuses automnales sur chacun des affluents, et (4) les crues *généralisées* qui correspondent aux différentes combinaisons entre ces 3 types de crues.

4.3 Les phénomènes climatiques

Le golfe du Lion présente un plateau continental important dont la largeur est maximale dans sa partie centrale (i.e., 80 km au niveau du cap d'Agde) et dont le relief est assez lisse et régulier avec des isobathes parallèles et régulièrement espacées. Le talus continental bordant ce plateau est entaillé de plusieurs canyons sous-marins qui jouent un rôle important dans les transferts de matière entre le plateau et la mer profonde. Du fait de l'orographie locale les vents soufflent fort pendant la plus grande partie de l'année (Millot, 1990). La tramontane est le vent de Nord-Ouest. Elle influe sur le bilan thermique de l’eau de mer et engendre parfois des épisodes de formation d’eaux profondes (cascading) en hiver (Durrieu de Madron et al., 2013). Du fait de la limitation du fetch, ce vent n’engendre par contre pas de houle de hauteur significative importante et donc pas d’évènement de resuspension significatif. Les vents de Sud-Est sont par contre le plus souvent associés à de fortes houles entrainant des événements de resuspension majeurs jusqu’à une profondeur d’environ 30 m (Ferré et al., 2005), ainsi qu’à des précipitations parfois violentes (épisodes dits « cévenoles »). De manière générale, ces régimes sont contrôlés par des phénomènes climatiques tels que l'Oscillation Nord Atlantique (NAO) et l'Oscillation Méditerranéenne Occidentale (WeMO) (**Figure 9**).

La NAO est un phénomène climatique qui correspond aux variations de différences de pressions au niveau de la mer dans la circulation atmosphérique de l’Océan Atlantique Nord (Hurell, 1995). L'indice associé est calculé à partir du mouvement saisonnier de l’anticyclone des Açores et de la dépression Islandaise qui contrôle la force et la direction des vents à travers l’Atlantique (**Figure 9**). Les phénomènes climatiques et météorologiques associés aux variations saisonnières de la NAO entre ces 2 zones varient de manière latitudinale (Hurell, 1995) : (1) la phase *positive* est liée à des étés frais, des hivers doux et humides dans le nord de l’Europe ainsi qu’à une activité plus intense de tempêtes que dans le nord de l’Europe, et (2) la phase *négative* est liée à des hivers froids et secs en Europe du nord et une activité plus intense de tempêtes dans le sud de l'Europe et dans la mer Méditerranée.

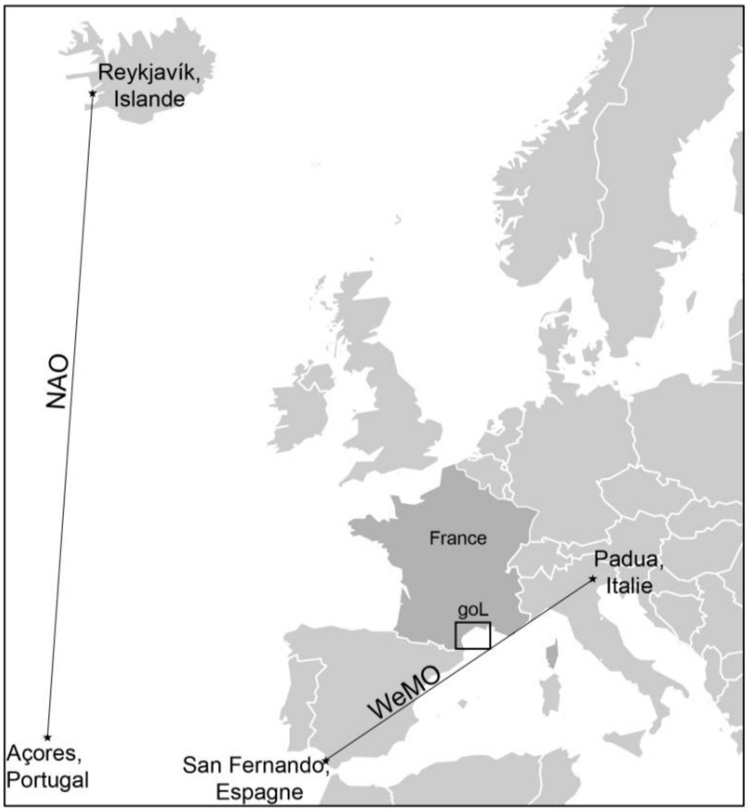

Figure 9. Schéma montrant les zones de référence pour le calcul des indices NAO (Hurell, 1995) et WeMO (Martin-Vide et Lopez-Bustins, 2006). goL : golfe du Lion.

La WeMO a été proposée par Martin-Vide et Lopez-Bustins (2006). Ce phénomène climatique régional correspond aux variations de la différence de pression atmosphérique mesurée au niveau de la mer à San Fernando (Espagne) et à Padua (Italie). La phase *positive* de l'indice correspond à des pressions plus élevées en Espagne qu'en Italie, entrainant une dominance des vents de Nord-Ouest qui n'induisent que peu de remise en suspension des sédiments (**Figure 10**). Au contraire, la phase *négative* de l'indice correspond à des pressions plus élevées à Padua qu'à San Fernando. Ces différences de pressions entrainent des vents d'Est qui provoquent des événements de resuspension majeurs dans le golfe du Lion.

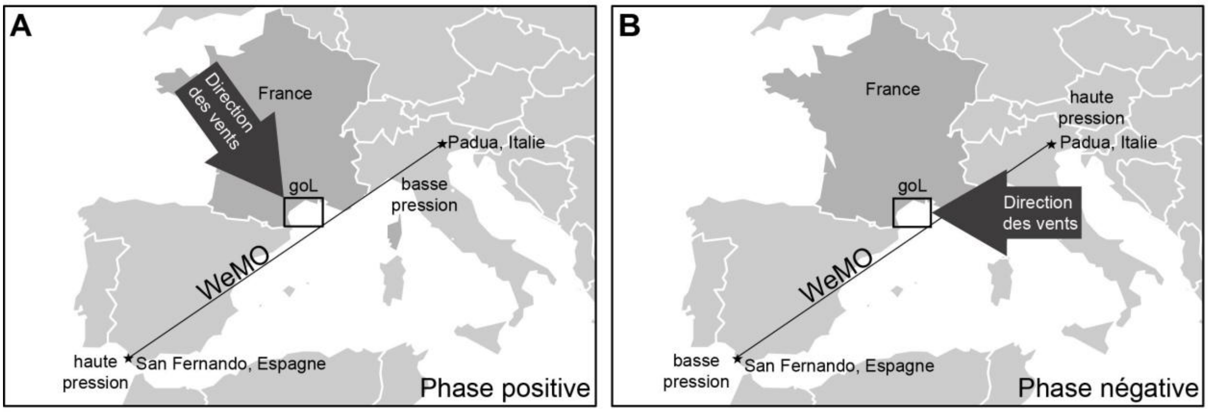

Figure 10. Direction des vents (flèches noires) associé aux phases positive (A) et négative (B) de la WeMO. goL : golfe du Lion.

4.4 La distribution spatiale des sédiments

Le courant dominant dans le golfe du Lion est le courant Nord, longtemps connu sous le nom de courant Liguro-Provençal (Millot, 1990), qui coule depuis le Nord-Est vers le Sud-Ouest et constitue une barrière aux échanges entre le plateau et la mer ouverte. La décharge solide du Rhône peut atteindre jusqu'à 5 400 10^3 tonnes à la suite des grands épisodes de crues (7 jours; Antonelli et al., 2008). Ces apports se déposent massivement à proximité immédiate de l'embouchure où Cathalot et al. (2010) ont ainsi pu observer un dépôt de vase d'environ 30 cm faisant suite à un épisode de crue du Rhône. De manière générale, le delta du Rhône est composé par 3 compartiments sédimentaires (Aloisi, 1986) : (1) le *front du delta* situé entre 5 et 30 m de profondeur, (2) le *prodelta* entre 30 et 60 m de profondeur, et (3) la *zone distale* entre 60 et 100 m de profondeur. Le prodelta du Rhône est caractérisé par un fort taux de sédimentation, alors qu'au large la sédimentation est réduite (Zuo et al., 1997 ; Radakovitch et al., 1999 ; Miralles et al., 2005).

Les sédiments du prodelta du Rhône et des autres fleuves côtiers sont ensuite périodiquement remis en suspension sous l'effet de la houle générée par les vents de Sud-Est. Pendant leur temps de séjour dans la colonne d'eau les particules sédimentaires remises en suspension sont entrainées vers le Sud-Est sous l'effet du courant Nord et de ses diverticules. Les cycles de sédimentation-resuspension-transport sédimentaire ainsi induits assurent le transport des sédiments fins jusqu'à l'extrémité Sud-Ouest du golfe où la largeur du plateau continental est faible et qui est entaillée par le canyon Lacaze-Duthiers qui constitue une voie de transfert privilégiée d'exportation de matière particulaire vers la mer profonde (Buscail et al., 1990).

Sur la carte de distribution sédimentaire des fonds marins du golfe du Lion (**Figure 11** ; Aloisi et al., 1973) on distingue classiquement à grande échelle : (1) *le cordon infralittoral* composé de sables fins bien calibrés avec des tâches d'envasement au niveau des prodeltas, (2) *les vases circalittorales* composées de proportions variables de sables et vases, et (3) *les sédiments hétérogènes* composés plutôt par des sédiments grossiers situés en bord de plateau et dont l'envasement est empêché par le fort hydrodynamisme généré par le courant Nord.

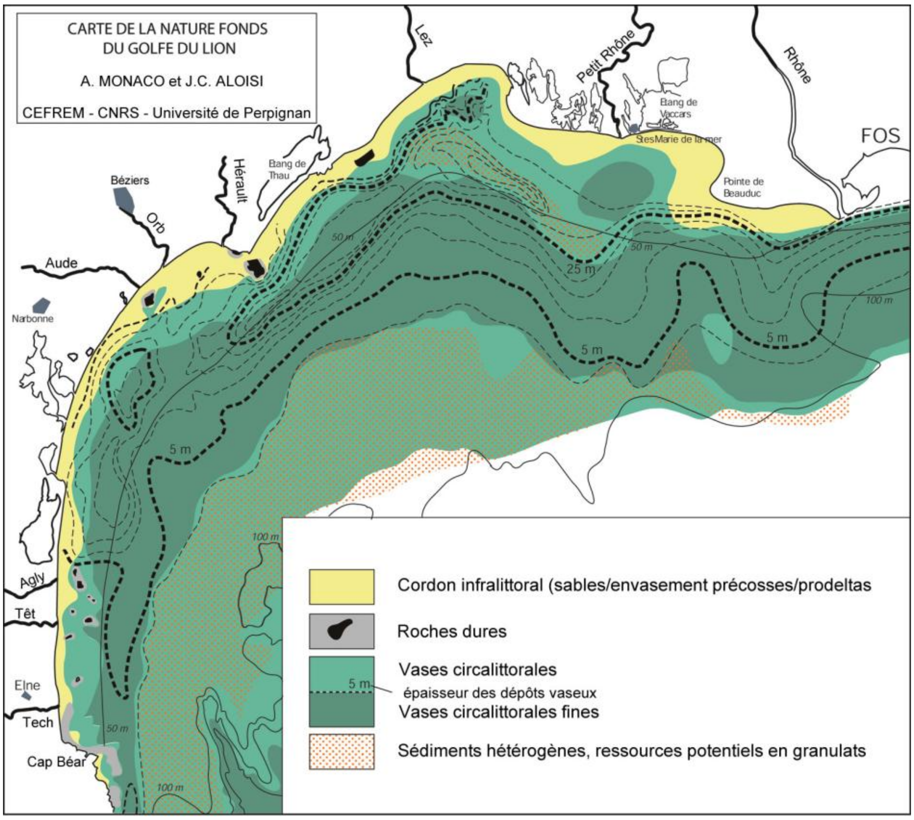

Figure 11. Carte sédimentologique du golfe du Lion (tiré de Aloisi, 1973).

4.5 Description des communautés benthiques du golfe du Lion

Historiquement, la macrofaune benthique du golfe du Lion a été étudiée d'une part sur la côte Provençale (région à l'extrême Nord-Est du golfe du Lion) par Picard (1965) et d'autre part sur la côte Catalane française (région à l'extrême Sud-Ouest du golfe du Lion) par Guille (1970). Ces 2 études ont conduit à des dénominations de communautés différentes dans la gamme de profondeur allant de 0 à 50 mètres de profondeur (**Table 2**):

(1) sables fins bien calibrés, vases détritiques et vases terrigènes côtières pour Picard (1965), et

(2) communauté à *Spisula subtruncata*, communauté à *Nephtys hombergii*, communauté à *Scoloplos armiger*, communauté à *Nucula sulcata* et communauté à *Venus ovata* pour Guille (1970).

La composition de la macrofaune benthique à l'échelle de la globalité du golfe du Lion n'a été pour la première fois décrite que presque 40 ans plus tard (Labrune et al., 2007a, 2008). Ces auteurs ont échantillonné 21 radiales à 10, 20, 30, 40 et 50 m entre la frontière espagnole et l'embouchure du Rhône. A partir de leurs propres résultats et de leur comparaison avec ceux des 2 études précédentes, ils ont proposé une nouvelle dénomination des communautés de la macrofaune benthique du golfe du Lion (i.e., sables fins littoraux, vases sableuses littorales et vases terrigènes côtières). Les sables fins infralittoraux sont localisés entre 10 et 20 m de profondeur et caractérisés par la présence de *Ditrupa arietina*, *Owenia fusiformis*, Tanaidacea et *Spisula subtruncata*. La communauté des vases sableuses littorales est localisée à environ 30 m de profondeur. Elle est caractérisée par la présence de *D. arietina*, *Lumbrineris latreilli*, *Turritella communis* et Tanaidacea. La communauté des vases terrigènes côtières est située entre 40 et 50 m de profondeur et caractérisée par la présence de *Sternaspis scutata*, *L. latreilli* et *Nephtys incisa*. Labrune et al. (2007a) ont également établi une équivalence avec les classifications antérieures (**Table 2**).

Table 2. Equivalence entre les classifications des communautés benthiques du golfe du Lion dans la zone 0-50 m telles que proposées par Picard (1965), Guille (1970) et Labrune et al. (2007a, 2008). (Tiré de Labrune et al., 2007a)

Guille (1970)	Picard (1965)	Labrune et al. (2007a)
Communauté *Spisula subtruncata* Communauté *Nephtys hombergii*	Sables fins bien calibrés	Sables fins infralittoraux (Littoral Fine Sands, LFS)
Entre les communautés à *Nephtys hombergii* et *Scoloplos armiger*	Vases détritiques	Vases sableuses littorales (Littoral Sandy Mud, FSM)
Communauté *Nucula sulcata*	Vases terrigènes	Vases terrigènes côtières (Terrigenous Coastal Mud, TCM)

Au-delà de son intérêt propre, le seul fait que cette unification soit possible suggère le maintien, sur une période de près de 40 ans, de la structuration de la macrofaune benthique du golfe du Lion dans la zone bathymétrique 0-50 m. Une telle stabilité constitue un élément important car il permet d'envisager sereinement l'étude des variations temporelles de la composition de chacune des communautés. Une des principales différences entre la composition des communautés identifiées par Picard (1965) et par Guille (1970), d'une part, puis par Labrune et al. (2007a, 2008), d'autre part, résidait en effet dans la très forte abondance en 1998 d'espèces comme *Ditrupa arietina* et *Lumbrineris latreilli* alors que ces mêmes espèces étaient absentes ou très peu présentes dans les années 1960.

4.6 Les variations temporelles de composition de la macrofaune benthique du golfe du Lion

Les variations temporelles de la composition de la macrofaune benthique dans le golfe du Lion n'ont été jusqu'ici spécifiquement abordées que par le biais de comparaisons à long terme, conduites soit directement sur une zone géographique restreinte (Grémare et al. 1998a ; Labrune et al., 2007b), soit indirectement à une échelle géographique plus large (Grémare et al., 1998b). Grémare et al. (1998a) ont comparé les compositions de la macrofaune benthique à 7 stations représentatives des 4 communautés identifiées par Guille (1970) en 1967/68 et en 1994 (**Figure 12**).

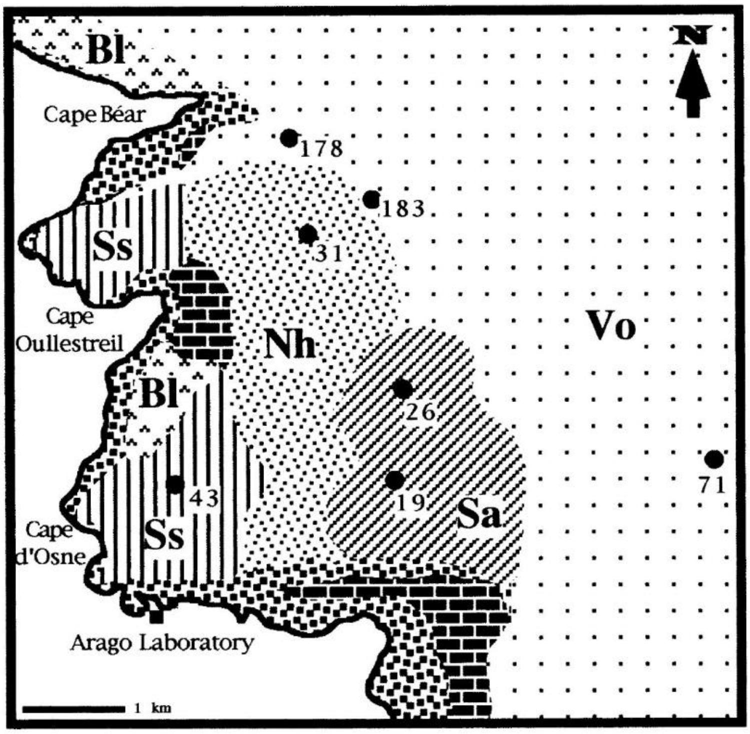

Figure 12. Distribution spatiale des communautés de la macrofaune benthique dans la baie de Banyuls-sur-Mer. La station 71 n'a pas été ré-échantillonnée en 2003. Communauté à *Spisula subtruncata* (Ss), communauté à *Nephtys hombergii* (Nh), communauté à *Scoloplos armiger* (Sa), communauté à *Venus ovata* (Vo) et communauté à *Branchiostoma lancelatum* (Bl). (Carte initialement tirée de Guille, 1970 et ensuite modifiée par Grémare et al., 1998a).

Ils ont conclu à l'existence de différences de composition significatives pour les 4 communautés mais plus particulièrement marquées pour les communautés à *Spisula subtruncata* et *Nephtys hombergii* avec notamment l'émergence de l'annélide polychète *Ditrupa arietina* qui était totalement absente en 1967/68 et très largement dominante en 1994. Devant l'amplitude de ce changement, Grémare et al. (1998b) ont cherché à déterminer sil était restreint à la seule baie de Banyuls-sur-Mer ou bien sil concernait au contraire une échelle géographique plus large. Ils ont pour cela réalisé une méta-analyse rassemblant les quelques signalisations historiques antérieures à 1970 et les différentes études conduites depuis la fin des années 1980 sur la portion de côte comprise entre Barcelone et Palavas-les-Flots. Ils ont ainsi mis en évidence l'existence de fortes abondances de *D. arietina* sur l'ensemble de la zone étudiée depuis la fin des années 1980, ce qui suggérait que les changements de composition de la macrofaune benthique initialement observés en baie de Banyuls-sur-Mer n'affectaient pas uniquement cette baie. Les premiers éléments relatifs à la dynamique temporelle de ces changements ont été fournis par Labrune et al. (2007b). Ces auteurs ont à nouveau échantillonné 6 stations (i.e., les 7 stations de la **Figure 12** à l'exception de la station 71) situées en baie de Banyuls-sur-Mer en 2003. Leurs résultats ont confirmé l'existence de changements temporels au sein des 4 communautés étudiés avec, en 2003, une tendance à un retour à une situation proche de celle de 1967/68 pour les communautés à *S. subtruncata* et *N. hombergii* (**Figure 13**). Ce point s'est avéré particulièrement important car il a suggéré, au moins pour les 2 communautés les moins profondes, l'idée d'une cyclicité dans les changements et donc de leur possible contrôle par des phénomènes eux-mêmes cycliques, par exemple susceptibles d'être liés à des oscillations climatiques de type NAO (Labrune et al., 2007b).

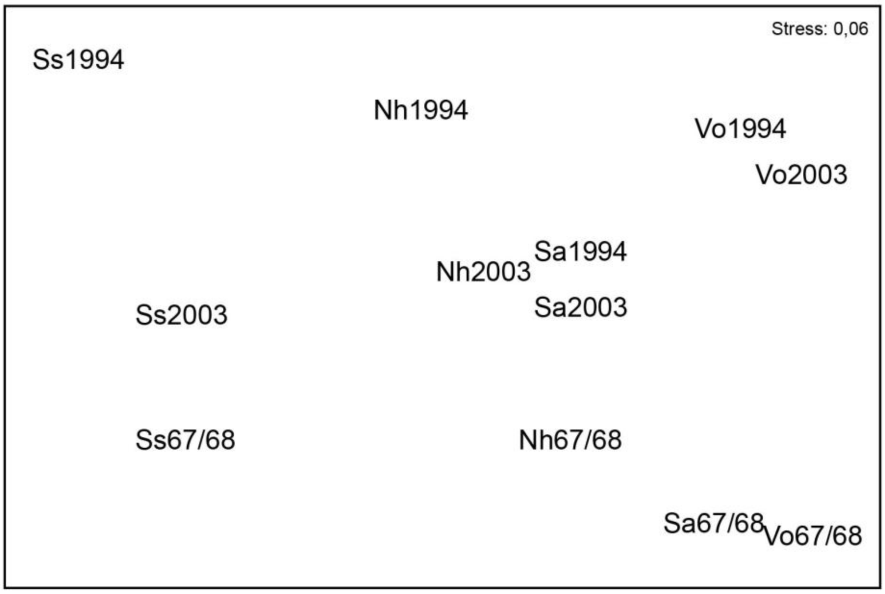

Figure 13. MDS basé sur l'abondance de la macrofaune benthique à 4 stations de la baie de Banyuls-sur-Mer échantillonnées par Guille (1970) en 1967/68, Grémare et al. (1998a) en 1994 et Labrune et al. (2007b) en 2003. Ss : communauté à *Spisula subtruncata*, Nh : communauté à *Nephtys hombergii*, Sa : communauté à *Scoloplos armiger*, Vo : communauté à *Venus ovata*. (Tiré de Labrune et al., 2007b).

Dans le cas particulier du golfe du Lion la recherche des causes des changements faunistiques s'est en effet trouvée fortement limitée par le fait que seulement 2 (Grémare et al. 1998a) puis 3 (Labrune et al. 2007b) situations pouvaient être comparées. Afin de contourner cette difficulté, cette recherche s'est : (1) concentrée sur les 2 communautés dans lesquelles l'annélide polychète *Ditrupa* *arietina* était dominante en 1994, (2) basée sur le fait que la dynamique de population de cette espèce était instable sur de petites échelles d'espace et de temps, et (3) basée sur certaines des caractéristiques de ses premiers stades benthiques. L'observation d'une légère décroissance, entre 1967/68 et 1994 du contenu en particules fines des sédiments des communautés à *Spisula subtruncata* et *Nephtys hombergi* ainsi que : (1) l'existence d'un tube muqueux non encore calcifié induisant une flottabilité positive chez les premiers stades benthiques de *D. arietina* et nécessitant un ancrage de son extrémité postérieure sur des grains de sédiment (**Figure 14A**, Medernach et al., 2000), et (2) la démonstration du caractère critique de ces stades dans le succès effectif de son recrutement (**Figure 14B**, Medernach et al., 2000), ont conduit Grémare et al. (1998a) à établir l'hypothèse que l'émergence de *D. arietina* (et donc par extension les autres changements faunistiques observés) était liée à un « nettoyage » des sédiments de leurs particules fines (susceptibles de défavoriser un ancrage efficace des premiers stades juvéniles) sous l'effet d'épisodes de remise en suspension apparemment plus nombreux en 1994 qu'en 1967/68 (Grémare et al., 1998a).

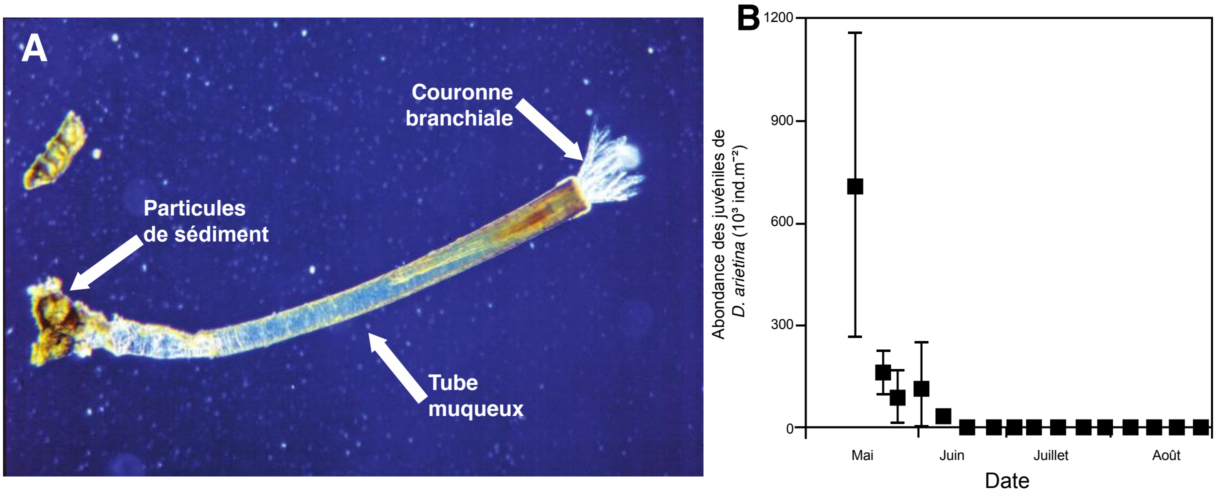

Figure 14. Morphologie (A) et variations temporelles de la densité des premiers stades benthiques de *Ditrupa arietina* entre le 14 mai et le 26 août 1997 à une station de la baie de Banyuls-sur-Mer (B). Les barres verticales correspondent aux écart-types. (Modifié d'après Medernach et al., 2000). (Photo : Jean Lecomte, CNRS).

Cette hypothèse a ensuite été partiellement contredite par Labrune et al. (2007b) qui, sur la base de 2 modes de reconstruction différents des épisodes de remise en suspension, ont montré qu'au contraire l'année 1994 correspondrait à une

NAO positive et à un nombre faible d'événements de remise en suspension pendant la période printanière durant laquelle intervient le recrutement de *Ditrupa arietina*. Tout comme ceux de Grémare et al. (1998a, b), les résultats de Labrune et al. (2007b) sont cohérents avec un contrôle de l'émergence de *D. arietina* par des modifications de la fréquence des événements de resuspension, elle-même dépendante de la phase de la NAO. Labrune et al. (2007b) ont donc suggèré que ce contrôle était direct alors que Grémare et al. (1998a) supposaient une action indirecte via une diminution de la fraction fine des sédiments sableux. Cette différence est d'importance car elle implique d'une part une corrélation négative entre le nombre d'événements de remise en suspension et l'abondance de *D. arietina* et, d'autre part, une corrélation positive entre les valeurs de l'indice NAO et l'abondance de *D. arietina*.

L'hypothèse de causalité (régissant les changements de composition de la macrofaune benthique récemment observés dans le golfe du Lion) formulée par Labrune et al. (2007b) est toujours celle qui fait aujourd'hui référence. Cette hypothèse demeure toutefois fragile du fait des bases mêmes de son élaboration (i.e., comparaison à long terme, extrapolation des mécanismes de contrôle à court terme de la dynamique de population de Ditrupa arietina*). Elle gagnerait maintenant clairement à être testée par le biais : (1) d'une comparaison à long terme conduite à l'échelle de l'ensemble du golfe du Lion, et (2) d'un suivi à long terme conduit sur une zone plus restreinte.*

Comme on l'a vu plus haut, le golfe du Lion recueille les eaux d'un fleuve majeur, le Rhône, qui est connu pour affecter son régime trophique général (moins oligotrophe que l'ensemble de la Méditerranée) et sa turbidité (plus élevée que l'ensemble de la Méditerranée). Les impacts de ce fleuve sur les variations de la composition de la macrofaune benthique n'ont été jusqu'ici que peu documentés. Tout au plus peut-on noter que lors de la description de ces communautés, Labrune et al. (2007a, 2008) ont signalé l'existence de 2 formes de la communauté des vases sableuses littorales en fonction de l'éloignement à l'embouchure du Rhône. Les effets du fleuve à proximité de son embouchure ont, par contre, été mieux étudiés (Salen-Picard et al., 2003 ; Hermand et al., 2008 ; Harmelin-Vivien et al., 2009 ; Labrune et al., 2012). Certaines études, conduites sur la totalité de la macrofaune benthique, se sont focalisées sur les distributions spatiales et ont montré l'existence de forts gradients longitudinaux (Hermand et al., 2008 ; Harmelin-Vivien et al., 2009 ; Labrune et al., 2012). Une autre étude (Salen-Picard et al., 2003) s'est au contraire focalisée sur la relation liant les variations de débit du Rhône et les changements temporels de composition de l'assemblage des annélides polychètes à une station à 70 m de profondeur. De manière générale, ces résultats ont montré l'impact des variations du débit liquide du fleuve sur 2 groupes d'espèces : (1) le premier composé essentiellement d'espèces opportunistes, répondant rapidement (i.e., dans un délai de 3 mois), et (2) le second composé essentiellement d'espèces stables, répondant avec un décalage temporel de 1 à 2 ans. Ces résultats sont intéressants car ils suggèrent l'existence de facteurs de contrôle particuliers de la composition des communautés de la macrofaune benthique à proximité du Rhône. On peut néanmoins s'interroger sur leur extrapolation du fait de : (1) la dualité des facteurs de contrôle constitutifs du modèle général proposé par Rhoads et Young (1970) et Rhoads (1985) pour les zones directement influencées par les grands fleuves (voir ci-dessus), et (2) l'existence de forts gradients spatiaux au large du Rhône et de leurs interactions avec les variations temporelles du débit de ce fleuve.

Dans ce contexte, il semble particulièrement intéressant : (1) de confirmer l'existence ou non d'un impact à grande échelle spatiale du fleuve Rhône sur la composition des communautés benthiques du golfe du Lion à partir d'outils de traitement de données plus appropriés (i.e., modélisation spatiale), et (2) d'étudier les effets des variations de débit sur la composition faunistique à proximité de son embouchure en échantillonnant un gradient spatial d'éloignement à la côte pour des phases d'apports liquides et solides contrastées.

4.7 Les conséquences des changements temporels de la composition de la macrofaune sur les indices biotiques

Un dernier point intéressant réside dans les conséquences des changements temporels de la composition de la macrofaune du golfe du Lion sur l'utilisation de ce compartiment en tant que base de la caractérisation écologique des habitats benthiques. Labrune et al. (2006) ont, les premiers, comparé l'utilisation de plusieurs indices biotiques pour réaliser une telle évaluation à l'échelle de l'ensemble du golfe du Lion (**Figure 15**). Ils ont notamment conclu à l'existence de contradictions majeures entre l'AMBI (Borja et al., 2000) et le BQI (Rosenberg et al., 2004) du fait de l'attribution de niveaux de sensibilité/tolérance différents à certaines espèces dominantes dont *Ditrupa arietina*.

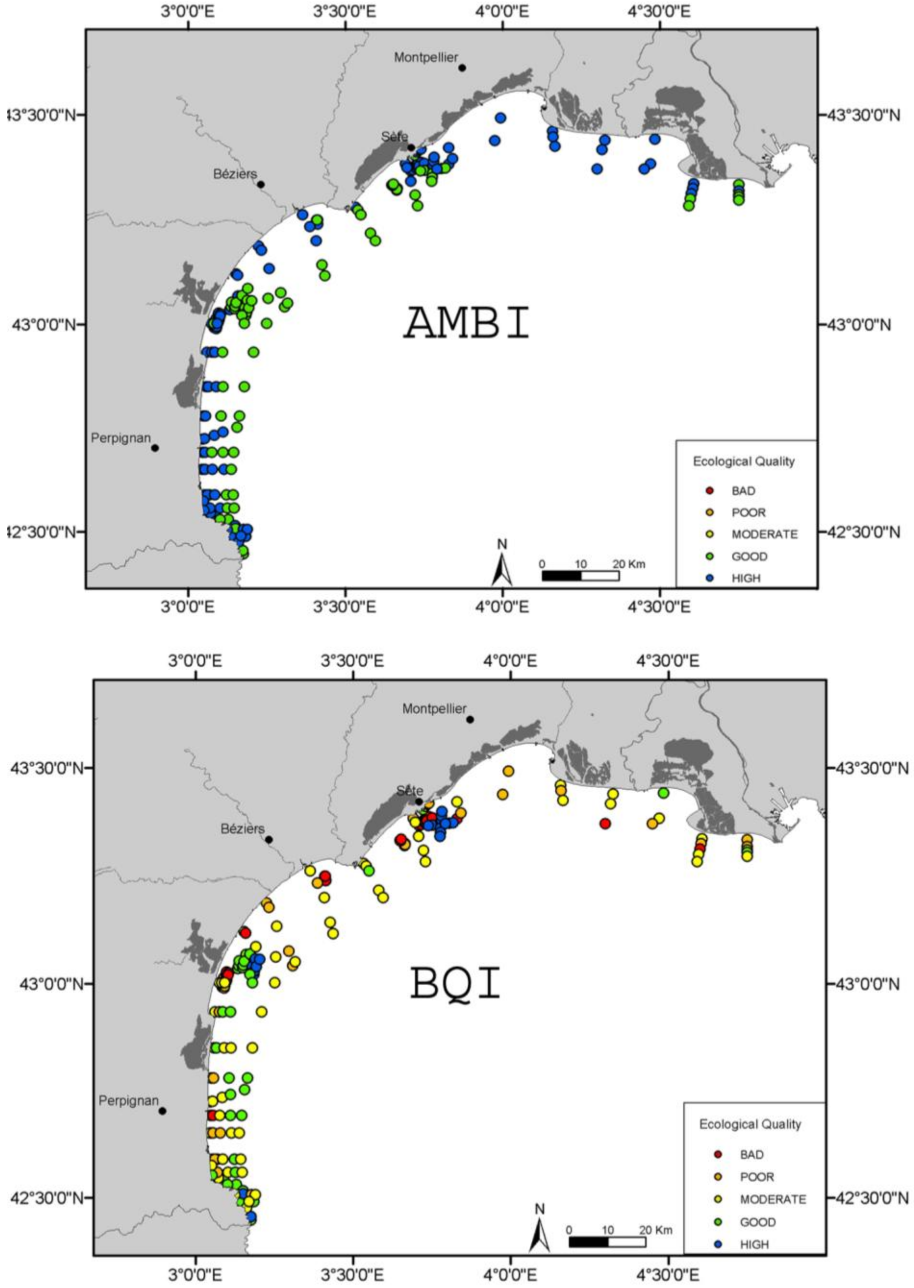

Figure 15. Cartes montrant les disparités des statuts de qualité écologique attribués par l'AMBI (A) et le BQI (B) aux habitats benthiques du golfe du Lion (tiré de Labrune et al., 2006)

Ce résultat posait clairement la question de l'identification du meilleur de ces 2 indices biotiques. Cette question a été abordée par Labrune et al. (2012) à partir de la comparaison avec une approche indépendante de caractérisation du statut écologique des habitats benthiques : l'imagerie sédimentaire. Cette approche consiste à prendre puis analyser des photographies *in situ* des premiers centimètres de la colonne sédimentaire (Rhoads et Young, 1970 ; Rhoads et Cande, 1971 ; Young et Rhoads, 1971 ; Rhoads et Germano, 1982 ; voir la revue de Germano, 2011). L'intensité des traces d'activité biologique ainsi que la profondeur moyenne de la couche oxygénée peuvent ensuite servir de base à la détermination d'un statut de qualité écologique. Une telle approche a déjà été appliquée avec succès dans le golfe du Lion par Grehan et al. (1992) puis par Rosenberg et al. (2003). Ces derniers auteurs ont d'ailleurs conclu à la bonne compatibilité des niveaux de similarité des stations caractérisées par le biais de l'imagerie sédimentaire et de l'analyse de la composition de la macrofaune benthique. Sur la base de l'échantillonnage de 16 stations situées sur un gradient côte-large au droit de l'embouchure du Rhône, Labrune et al. (2012) ont montré la meilleure corrélation du BQI avec les données issues de l'imagerie sédimentaire ainsi qu'avec le gradient de concentration en carbone organique sédimentaire et ainsi suggéré la supériorité de cet indice sur les autres indices testés (dont l'AMBI et le M-AMBI). Ils ont néanmoins souligné que la possibilité de généralisation de ce résultat à d'autres zones géographiques restait encore à démontrer.

A partir des comparaisons à long terme effectuées en baie de Banyuls-sur-Mer évoquées ci-dessus (Grémare et al., 1998a ; Labrune et al., 2007b), Labrune et al. (2006) ont également conclu à l'existence de variations temporelles majeures dans les valeurs de ces 2 indices en lien avec des variations de composition faunistique pourtant largement attribuées à des facteurs dits « naturels » (**Figure 16**). Ce résultat pose clairement la question de l'utilisation, implicite ou explicite, de références historiques ; et ceci en particulier dans le cas de l'AMBI qui se base sur une échelle unique pour convertir directement l'indice en statut de qualité écologique (Borja et al., 2004).

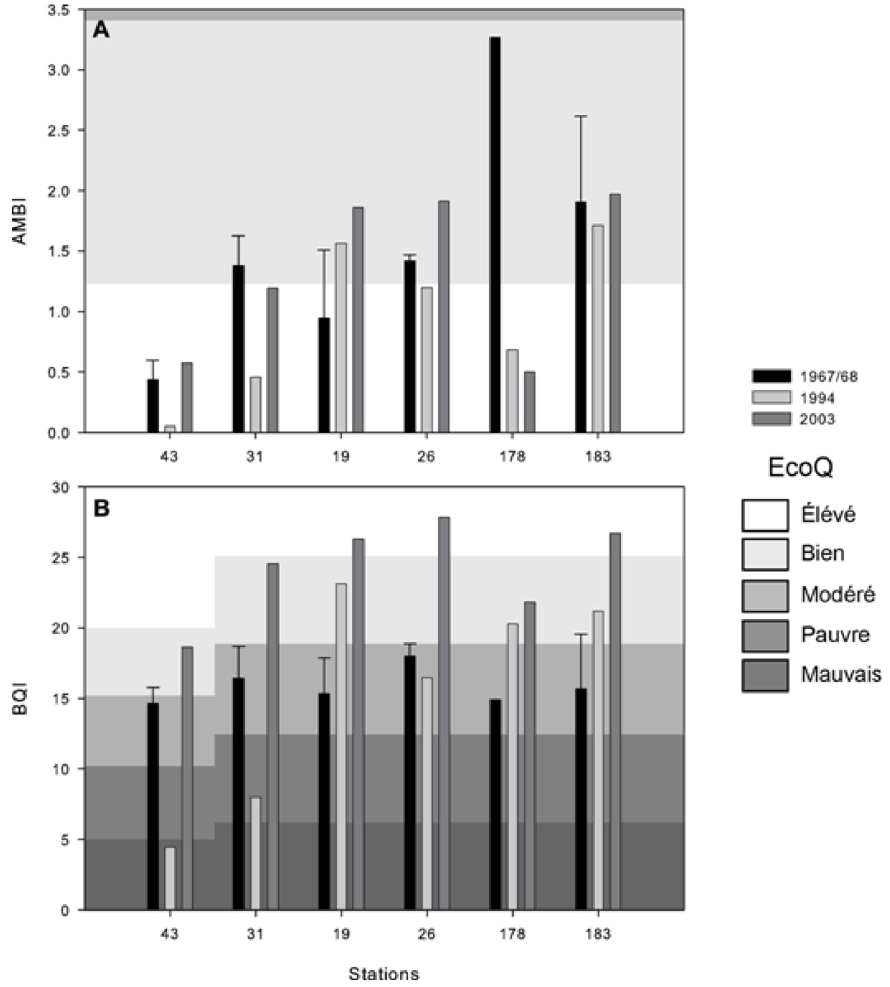

Figure 16. Variations temporelles des valeurs de l'AMBI et du BQI ainsi que des statuts de qualité écologique dérivés aux 6 stations de la baie de Banyuls-sur-Mer dont les compositions de la macrofaune benthique ont fait l'objet d'une comparaison à long terme entre 1967/68, 1994 et 2003. (Tiré de Labrune et al., 2006)

Dans ce contexte, il semble particulièrement intéressant : (1) d'actualiser les cartes de statut de qualité écologique actuellement disponibles pour le golfe du Lion puisque celles-ci reposent sur un échantillonnage conduit en 1998, (2) de confirmer ou non l'existence de variations temporelles significatives dans les valeurs des indices testés et les statuts de qualité écologique dérivés, (3) d'élargir la gamme des indices testés à ceux dernièrement développés (e.g. M-AMBI ; Muxika et al., 2007), et enfin (4) de poursuivre la comparaison des indices testés avec les informations dérivées de l'imagerie sédimentaire et ceci pour une zone géographique présentant des caractéristiques moins contrastées que le prodelta du Rhône.

5 PRINCIPAUX OBJECTIFS ET STRUCTURATION DE LA THÈSE

Les principaux objectifs de cette thèse consistent à : (1) fournir une description de l'état actuel et des variations temporelles de composition de la macrofaune benthique de substrats meubles du golfe du Lion, (2) tester l'hypothèse actuellement retenue pour expliquer ces changements, (3) mieux analyser l'impact du fleuve majeur qu'est le Rhône sur la structuration des communautés benthiques, et enfin (4) fournir une cartographie actualisée du statut de qualité écologique des habitats benthiques et analyser les effets des changements faunistiques intervenus récemment sur cette évaluation. L'analyse conduite ci-dessus de l'état actuel des connaissances relatives à cette zone géographique nous a conduit à distinguer 4 études à caractère complémentaire mais différant par les zones géographiques ainsi que les échelles spatiales et temporelles appréhendées. Dans le cadre de cette thèse, ces 4 études seront présentées sous la forme d'autant de manuscrits scientifiques, soit publiés (Bonifácio et al., 2014), soit pratiquement prêts à être soumis pour publication.

La première étude (**Chapitre II**) est intitulée « **Long-term (1998-2010) large-scale comparison of soft-bottom benthic macrofauna in the Gulf of Lions, NW Mediterranean Sea** ». Elle consiste en une revisite conduite en 2010 des stations échantillonnées en 1998 par Labrune et al. (2007a, 2008) lors de la description des communautés benthiques du golfe du Lion. Il s'agit plus spécifiquement de : (1) montrer pour la première fois directement l'existence de variations temporelles de composition de la macrofaune benthique à l'échelle de l'ensemble du golfe du Lion, (2) de mieux tester l'hypothèse d'un contrôle de certains de ces changements par la NAO à partir de 2 échantillonnages effectués dans des phases différentes, et (3) de mieux évaluer l'impact du fleuve Rhône sur la composition des communautés de la macrofaune benthique sur une grande échelle spatiale.

La seconde étude (**Chapitre III**) est intitulée « **Long-term study of the relation between macrobenthic communities and climate variability in the Bay of Banyuls-sur-Mer, NW Mediterranean Sea** ». Elle repose sur un suivi (périodicité annuelle, durée de 10 ans) des compositions de la macrofaune benthique à 4 stations représentatives des principales communautés benthiques de la baie de

Banyuls-sur-Mer. Son principal objectif consiste à tester plus avant le contrôle de la composition de ces communautés par des processus et des variables climatiques.

La troisième étude (**Chapitre IV**) est intitulée « **Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition off the Rhône River in relation with its hydrological regime** ». Son objectif principal consiste à évaluer les effets des variations des débits liquides et solides du Rhône sur : (1) les caractéristiques qualitatives et quantitatives des sédiments de surface, et (2) la composition des communautés de la macrofaune benthique, ainsi que (3) les interactions potentielles liant ces 2 compartiments. Son originalité réside dans la combinaison des aspects spatiaux et temporels (i.e., gradient côte-large de 5 stations échantillonnées sous 4 conditions de débit différentes) de son plan d'échantillonnage. Cette étude a déjà fait l'objet d'une publication dans la revue *Estuarine Coastal and Shelf Science* 151, 196–209.

La quatrième et dernière étude (**Chapitre V**) est intitulée « **Long-term (1998-2010) large-scale comparison of the ecological quality status of Gulf of Lions benthic habitats** ». Ses objectifs principaux consistent à évaluer : (1) le statut de qualité écologique du golfe du Lion en 2010 en se basant sur l'utilisation de 3 indices biotiques (AMBI, M-AMBI, BQI) et d'un indice de qualité du sédiment (BHQ) basé sur l'imagerie sédimentaire, et (2) l'évolution de ce statut entre 1998 et 2010.

Les principales conclusions et perspectives issues de ces différentes études sont enfin présentées dans une dernière partie (**Chapitre VI**).

CHAPITRE II

COMPARAISON À LONG TERME ET A GRANDE ÉCHELLE DE LA COMPOSITION DE LA MACROFAUNE BENTHIQUE DES SUBSTRATS MEUBLES DU GOLFE DU LION, MÉDITERRANÉE OCCIDENTALE

LONG-TERM (1998-2010) LARGE-SCALE COMPARISON OF SOFT-BOTTOM BENTHIC MACROFAUNA COMPOSITION IN THE GULF OF LIONS, NW MEDITERRANEAN SEA

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ABSTRACT

We achieved a long term (i.e., 1998-2010) large scale (i.e., whole Gulf of Lions) of benthic macrofauna composition in the Gulf of Lions based on the resampling of 91 stations located along 21 inshore-offshore transects. Results show that the 3 main benthic communities identified in 1998 were still present in 2010 although their compositions significantly changed. There was a significant interaction between spatial and temporal effects in controlling benthic macrofauna composition. Temporal changes in benthic macrofauna compositions were clearly most important at shallow stations (i.e., in the Littoral Fine Sand community) than at deep ones (i.e., Terrigenous Coastal Mud community). These results are in good agreement with the current paradigm according to which NAO is indirectly (i.e., through changes in the frequency of occurrence and the intensity of storms) controlling benthic macrofauna composition in the Gulf of Lions. This hypothesis is further supported by a meta-analysis of changes in the average and maximal yearly abundances of the polychaete *Ditrupa arietina*. At last, the spatial modelling of 1998 and 2010 benthic macrofauna compositions both suggested a significant effect of Rhône River inputs on the spatial distribution of benthic macrofauna in the Gulf of Lions.

Keywords: Zoobenthos, Temporal variations, Species diversity, Continental shelves, Coastal waters, Mediterranean Sea, France, Gulf of Lions, Beta diversity, Space-time interaction

1 INTRODUCTION

The distribution of benthic macrofauna is mainly structured by 2 types of factors: (1) abiotic factors such as climatic conditions, hydrodynamism, currents, physical and chemical nature of the sediment and most disturbances induced by anthropogenic actions (Pearson and Rosenberg, 1978; Posey et al., 1996; Tunberg and Nelson, 1998; Warwick et al., 2002; Akoumianaki and Nicolaidou, 2007; Guizien et al., 2010); and (2) biotic factors directly linked to the populations themselves (e.g., bioturbation) (Dauwe et al., 1998). Historically, a lot of attention has been given to the role of abiotic factors in the structuration of benthic communities (Pérès and Picard, 1964). It is currently admitted that environmental variables such as granulometry (which is closely linked to depth and hydrodynamism) play a major role in the distribution of benthic communities in coastal waters (Karakassis and Elefheriou, 1997; Labrune et al., 2007a; Gogina et al., 2010; Mutlu et al., 2010). Moreover, it has been shown that anywhere in the world, comparable communities can be find in comparable types of habitats (e.g., Gambi and Giagrande, 1986). These communities are composed by closely related (vicariant; Thorson, 1957) species. The composition of benthic macrofauna may, however, vary with time and even the identity of dominant species may change from one year to the other. Changes of this kind have been highlighted by several authors around the world such as in the southern North Sea (Kröncke et al., 1998, 2001), in western Sweden (Tunberg and Nelson, 1998; Hagberg and Tunberg, 2000) or in the Mediterranean Sea (Grémare et al. 1998a; Salen-Picard et al., 2002; Labrune et al., 2007b).

Benthic macrofauna communities in the Gulf of Lions were described by Picard (1965) on the Provençal coast (eastern part of the Gulf of Lions), and by Guille (1970) on the Catalan coast (south-western part of the Gulf of Lions). These studies were carried out independently and they resulted in slightly different typologies. Based on a large scale study of benthic macrofauna in the whole Gulf of Lions carried out during 1998, Labrune et al. (2007a) proposed a new typology consisting of 3 community types and established the correspondence between the 2 typologies previously proposed by Picard (1965) and Guille (1970). Up to now, temporal changes in benthic macrofauna composition in the Gulf of Lions have only been assessed through small spatial scales studies and only at the 2 extremities of the Gulf of Lions.

In the Bay of Banyuls-sur-Mer, SW Gulf of Lions, previous studies (Grémare et al., 1998a; Labrune et al., 2007b) have suggested a relationship between climatic variability and changes in benthic macrofauna composition. These studies identified long-term changes in several communities between 1967/68, 1994 and 2003. Such changes dealt with temporal fluctuations in: (1) total species richness, and (2) abundances of the polychaetes *Ditrupa arietina, Scoloplos armiger* and *Notomastus latericeus*. Moreover, by coupling the studies of changes in benthic macrofauna composition with autoecological studies of *D. arietina* (Medernach et al., 2000), they suggested that the North Atlantic Oscillation (NAO) could drive changes in benthic macrofauna composition (Grémare et al., 1998a; Labrune et al., 2007b). Positive phases of the NAO are associated with stormy conditions over northern Europe (Hurrell, 1995), whereas conversely, negative phases are associated with stormy conditions over southern Europe and the Mediterranean Sea. NAO was therefore suggested to be one of the factors indirectly structuring benthic macrofauna in the Gulf of Lions through the frequency of strong resuspension events, which may affect recruitment success (Grémare et al., 1998a; Labrune et al., 2007b). In NE Gulf of Lions, previous studies have also shown major changes in benthic macrofauna composition in relation with: (1) the construction and the functioning of the Fos harbour (Salen-Picard et al., 1997; Massé, 2000), and (2) water and particulate flows from the Rhône River (Massé, 2000; Salen-Picard et al, 2002; Salen-Picard et al, 2003; Harmelin-Vivien et al., 2009; Bonifácio et al., 2014), which is the most important river of NW Mediterranean (Durrieu de Madron et al., 2000; Bourrin et al., 2006).

Although, both NAO and Rhône River flows have been suggested to play an important role structuring the benthic macrofauna communities at small spatial scales (Salen-Picard et al., 2002), they are also likely to play a role over the whole Gulf of Lions (Grémare et al., 1998b). Based on a meta-analysis of benthic macrofauna data collected along the portion of coast between Barcelona and Palavas-les-Flôts before 1970 and during the 1990s, Grémare et al. (1998b) indeed showed that the increase of *Ditrupa arietina* occurred over this whole area. Moreover, based on the 1998 large scale sampling, Labrune et al. (2007a, 2008) concluded to the existence of 2 slightly different modalities of the Littoral Sandy Mud community depending on the geographical distance to the Rhône River Mouth, which suggests that the effect of this river on benthic macrofauna composition may be large-scale as well. Within this context, the present study aimed at: (1) assessing changes in benthic macrofauna composition in the Gulf of Lions between 1998 and 2010, (2) further investigate the current hypothesis regarding the effect of NAO on benthic macrofauna composition, and (3) directly testing the hypothesis of an effect of the Rhône River on benthic macrofauna composition over the whole Gulf of Lions.

2 MATERIALS AND METHODS

2.1 Study area

The Gulf of Lions (**Figure 1**) is located in the NW Mediterranean. It extends about 110 km from South to North and 140 km from West to East. Several rivers flow along its 400 km of coast (Bourrin et al., 2006) but the Rhône River has, by far, the most important effect on its functioning (Durrieu de Madron et al., 2000).

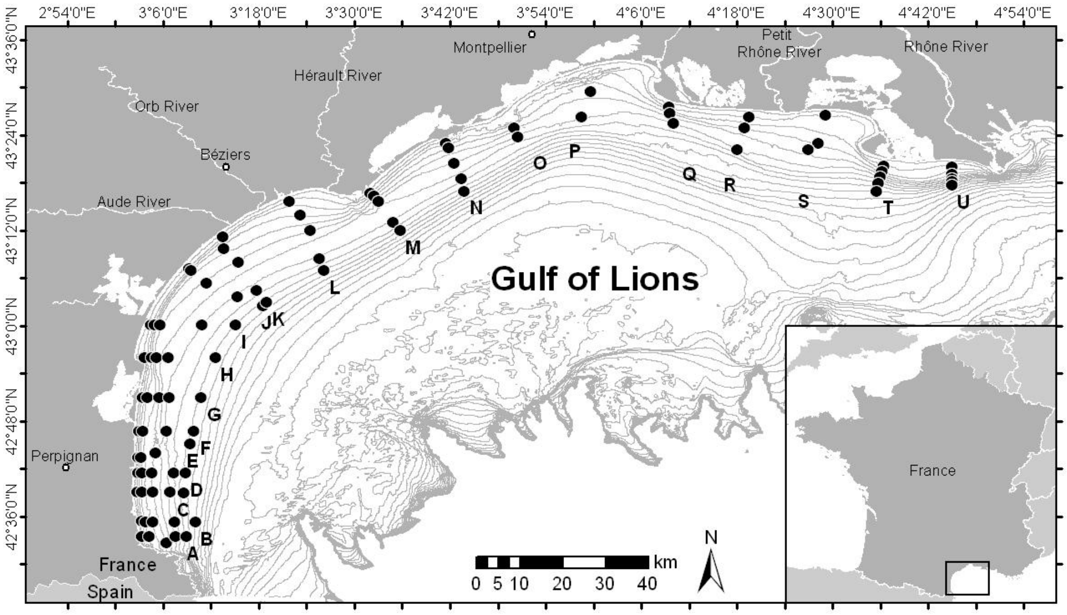


Figure 1. Locations of the 21 sampled transects all along the coast of the Gulf of Lions, NW Mediterranean Sea.

2.2 Rhône River flow

The hydrological basin of Rhône River covers around 98000 km^2 with a mean annual water flow about 1700 m^3.s^{-1} and a mean daily flow between 600 and 11000 m^3.s^{-1} (**Figure 2A**) depending on seasons and flood (Pont, 1997; Pont et al., 2002; Antonelli et al., 2008). This river is the main source of riverine particulate matter inputs to the Gulf of Lions accounting for 80% of total particulate inputs (Aloisi et al., 1977; Durrieu de Madron et al., 2000). The Rhône River water flow data used during the present study were kindly provided by Banque Hydro (http://www.hydro.eaufrance.fr/).

2.3 North Atlantic Oscillation (NAO)

The North Atlantic Oscillation (**Figure 2B**) is the major force governing climate variability (anomalies) in the atmospheric circulation causing changes in the surface westerlies across the North Atlantic onto Europe (Hurrell, 1995). These changes can be displayed through several indices of NAO calculated using different approaches. In the present study a widely known linear technique (PC-based) was used. It corresponds to the time series of the leading Empirical Orthogonal Function (EOF) of Surface Level Pressure anomalies over the Atlantic sector (20°-80°N, 90°W-40°E). This index is used to measure NAO throughout the year, tracking the seasonal movements of the Icelandic low and the Azores high pressure areas (Hurrell and Deser, 2010). NAO index data was provided by the Climate Analysis Section (NCAR; https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based). Eight-years moving averages were calculated based on annual NAO indices.

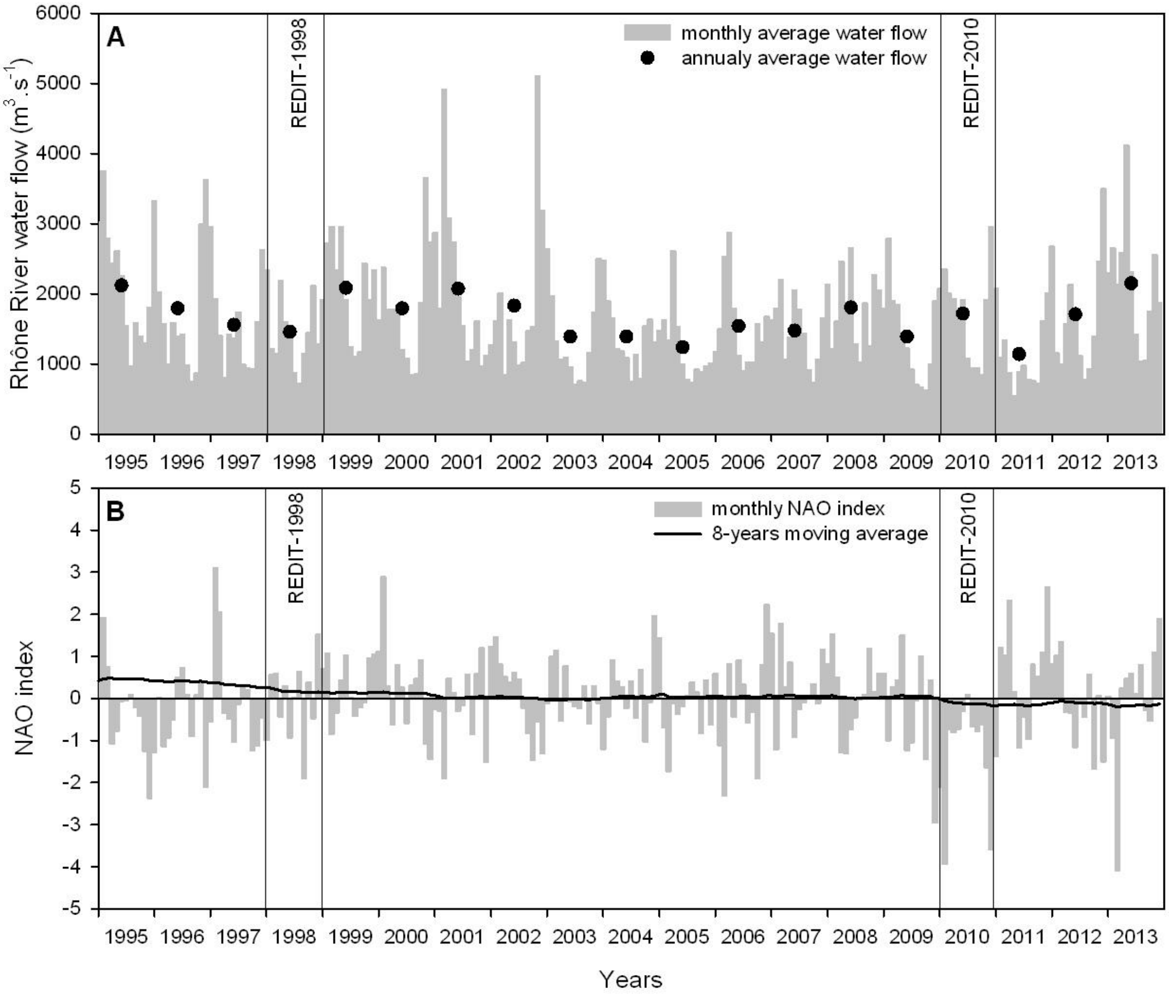


Figure 2. Temporal variability in monthly average of (A) the Rhône River water flow with its corresponding annual average flow and (2) the NAO index with its corresponding 8-years moving average. Vertical lines indicate the years of sampling and the corresponding cruises.

2.4 Sampling

Ninety-one stations were sampled for benthic macrofauna and surface sediment characteristics during August and September 2010 (REDIT-2010 cruise) on board of the R/V Thetys and Nereis II. These stations were located along 21 inshore/offshore transects (identified by letters, A to U) between the Spanish/French border and the mouth of the Rhône River (**Figure 1**). This scheme was designed to allow for a long term comparison with similar data collected during the REDIT-1998 cruise, which was carried out during September and October 1998 involving the sampling of 92 stations along the same transects (Labrune et al., 2007a, 2008). Most transects were sampled at 10, 20, 30, 40 and 50 m depth. Transects E, F, O and P were not sampled at 10, 20, 30 and 40 m depth, respectively. The station E at 40 m was sampled in 1998 but not in 2010. Consequently, 91 stations were sampled during both years so that their benthic macrofauna compositions could be directly compared. In the following, each station will be designated by the combination of a letter and a number, which correspond to the sampled transect and the sampling depth, respectively.

As sampling stations were located between 10 and 50 m depth, the corresponding macrobenthic communities are: (1) the Littoral Fine Sands (LFS; Labrune et al., 2007a, 2008) which is mainly composed of fine sand and corresponds to the *Spisula subtruncata* community and part of the *Nephtys hombergii* community described by Guille (1970) and to the Well Sorted Fine Sand community described by Picard (1965); (2) the Littoral Sandy Mud (LSM; Labrune et al., 2007a, 2008) which is mainly composed of sandy mud or muddy sand sediments and corresponds to part of the *N. hombergii* community and the *Scoloplos armiger* community described by Guille (1970) and to the Muddy Detritic community described by Picard (1965); and (3) the Terrigenous Coastal Mud (TCM; Labrune et al., 2007a, 2008) which is mainly composed by muddy or pure mud sediments and corresponds to the *Nucula sulcata* community described by Guille (1970) and to the Terrigenous Coastal Mud community described by Picard (1965).

2.5 Sediment characteristics

At each station, a 0.1 m^2 van Veen grab was taken for granulometry and CHN analyses. The upper half centimetre of the grab content was sampled, homogenized, conditioned and frozen on board. Samples used for sedimentary organics assessments were later freeze-dried. Back to the laboratory, sediment granulometry was assessed using a Malvern Mastersizer® 2000 laser microgranulometer and expressed as median grain diameter ($D_{0.5}$ in µm). The percentage of fines content (%<63 µm) was also calculated. Organic carbon (OC) concentrations were measured on homogenized samples using a CHN Perkin Elmer 2400 (in 1998) and a CHN Thermo Finnigan Flash EA1112 (in 2010) analyzer, after acidification with 1N HCl (overnight, at 50°C) to remove carbonates (Cauwet et al., 1990).

2.6 Benthic macrofauna

At each station, 3 other grabs were collected. Samples were sieved on board over a 1 mm mesh and fixed with 5% formalin buffered in seawater. Macrofauna was then sorted, identified to the lowest tractable taxonomic level (most often species) and counted. All procedures were strictly identical to those used by Labrune et al. (2007a, 2008).

2.7 Data analysis

Synonyms of scientific names of species were updated using the World Register of Marine Species (WoRMS, 2014). Species with possible doubtful identifications were pooled to homogenise species lists and taxonomic resolutions between cruises. Indicator species (Dufrêne and Legendre, 1997; De Cáceres and Legendre, 2009) were identified based on specificity (i.e., presence at only a single sampling depth) and fidelity (i.e., presence at a majority of stations of this sampling depth).

Univariate global descriptors of benthic macrofauna

Abundance, station species richness (αSR) and Pielou's evenness (J’) were used as global descriptors of α diversity. Pielou's evenness indicates how homogeneous the individual abundance of species within a station are.

Based on the total number of individuals and species recorded at each depth, we derived rarefaction and extrapolation curves after Colwell et al. (2012). Both curves were sample-based (with each station corresponding to a single sample unit) and thus derived from the Bernouilli product model (equations 17 and 18 in Colwell et al., 2012). Rarefaction and extrapolation curves, so called accumulation curves (Colwell et al., 2012) were nevertheless plotted using individuals as an index of sampling effort. The overall species richness at each sampled depth (γSR) was defined as the asymptotic value of the corresponding extrapolation component of the accumulation curve.

Paired *t*-tests with permutations were used to evaluate whether there were uniform changes across stations in tested parameters between 1998 and 2010. The null hypothesis in such a test was that the mean of the difference of the tested parameter between all paired samples was 0 (i.e., no uniform trend in temporal changes across stations). For each parameter, the probability distribution under the null hypothesis was evaluated by restricted permutations of paired observations.

Multivariate analyses

Multivariate analyses were conducted using the Hellinger distance metric, which adequately captures ecological gradients and does not attribute too much weight to rare species (Legendre and Gallagher, 2001). The Hellinger transformation replaces raw abundance scores by the square root of relative abundances. Computing Euclidean distances on this new matrix yields the Hellinger distance matrix, which can be used as an input for methods that preserve the Euclidean distance between objects (e.g., PCA, STI) to reach ecologically meaningful results.

In order to visualize spatiotemporal patterns we used unconstrained ordination (Principal Component Analysis, PCA) and non-hierarchic clustering techniques (K-means). K-means clustering was computed for all sites and both sampling periods. We conducted clustering from k=2 to k=5 groups, with 100 random starts for each value of k. We used tile plots to visualize how k-means clusters relate to depth and sampling year. In these plots squared area of each tile is proportional to the frequency in the three-way (k-means cluster, depth, year) contingency table, which allows row-wise and column-wise comparisons. We also tested whether multivariate homogeneity of group dispersions was achieved for groups obtained by crossing the depth and year factors (i.e., 10 groups) using the PERMDISP procedure (Anderson, 2001, 2006).

The current work being based on stations that were sampled both in 1998 and 2010, the first question of interest regarding β diversity was whether there existed persistent spatial patterns across the 2 sampling years, that is, whether or not space-time interaction could explain a significant part of the variance in benthic community composition. Finding a significant space-time interaction implies that benthic community compositions differed between sampling times and that corresponding changes differed between stations. Because our sampling design was without replication, it was necessary to under-fit a model to test for the significance of a space-time interaction. During the present study, we used the model 5 of Legendre et al. (2010).

As the space-time interaction was significant, we modelled spatial structures separately for each sampling year. This was achieved through spatial eigenfunction analysis and Redundancy Analysis (RDA) of the Hellinger transformed community matrices. We used both distance-based Moran's Eigenvector Maps (dbMEM; Dray et al., 2006) and Asymmetric Eigenvector Maps (AEM; Blanchet et al., 2008b) to model non-directional and directional spatial processes. The rationale for using directional spatial modelling is that the Rhône River exerts a NW-SW influence on the system (see above). For AEM construction, we set the origin of the connection graph East of the most Eastern sampling stations (i.e., towards the mouth of the Rhône River), and chose a rook connection patterns where only sites at the same depth were linked from East to West. For the non-directional spatial processes, we used the longest branch of the minimum spanning tree as a threshold for dbMEM construction. Moreover, if present, the linear spatial trend was removed prior to dbMEM analysis. Median grain diameter ($D_{0.5}$), fines content (%<63 µm), and organic carbon (OC) concentration were also used as a set explanatory parameters. Forward selection of explanatory parameters was conducted on each set of variables (i.e. AEM, dbMEM, environmental) separately (Blanchet et al., 2008a). Variance was then partitioned among sets of explanatory parameters - and an eventual linear trend – by way of partial RDA (Borcard et al, 2002).

Unless stated otherwise, all analyses were conducted using the R language (R Core Team, 2014) and the following packages: AEM (Blanchet et al., 2013), indicspecies (De Cáceres and Legendre, 2009), packfor (Dray et al., 2013), PCNM (Legendre et al., 2013), SoDA (Chambers, 2013), STI (Legendre et al. 2012), vegan (Oksanen et al., 2013) and vcd (Meyer et al. 2013). t.paired.perm.R (P. Legendre) is available at http://adn.biol.umontreal.ca/~numericalecology/Rcode/.

Meta-analysis of the relationship between the NAO index and the abundance of Ditrupa arietina

We compiled several scientific publications and grey literature (e.g., impact assessment studies) carried out in the Gulf of Lions between 1989 and 2013 and report both maximal and average (at stations where it was present) yearly abundances of the polychaeta *Ditrupa arietina* (**Table 1**). Corresponding time series were then compared with those of the NAO index and the 8-years moving average of this index (see also above).

Table 1. Main characteristics of the individual surveys included in the meta-analysis of temporal changes in yearly maximal and yearly average abundances of *Ditrupa arietina*. A: Grey literature, B: Scientific publications

A: Grey literature		
Location	**Year**	**Reference**
Sète	1993	IARE and BCEOM, 1993a
Montpellier	1993	IARE and IFREMER, 1993b
Narbonne and Gruissan	1995	Amouroux and Grémare, 1995
Sète	1999	Bornens et al., 2000a
Port-La-Nouvelle	2000	Bornens et al., 2000b
Argelès-sur-Mer	2001	Amouroux and Grémare, 2001a
Paulilles	2001	Amouroux and Grémare, 2001b
Sète	2001	CREOCEAN and ECOSIT, 2001
Off Têt River	2009	SESAME program
Banyuls-sur-Mer	2002, 2006	Amouroux and Grémare, 2003; Amouroux and Grémare, 2006
Gulf of Lions	2006, 2009, 2012	Pelaprat et al., 2007, 2010, 2013
Cerbère	2007, 2009	Thorin and Dolbeau, 2007; Thorin, 2009

B: Scientific publications		
Location	**Year**	**Reference**
Marèsme (Spain)	1989	Grémare et al., 1998b
Bay of Banyuls-sur-Mer	1994	Grémare et al., 1998a
Portbou (Spain)	1995	Grémare et al., 1998b
Palamos (Spain)	1995	Grémare et al., 1998b
Blanes (Spain)	1995	Grémare et al., 1998b
French sandy coast	1996	Grémare et al., 1998b
Banyuls-sur-Mer	1996	Grémare et al., 1998b
French rocky coast	1996	Grémare et al., 1998b
Bay of Banyuls-sur-Mer	1994-1998	Medernach et al., 2000
Gulf of Lions	1998	Labrune et al., 2007a
Bay of Banyuls-sur-Mer	2003	Labrune et al., 2007b
Bay of Banyuls-sur-Mer	2006	Guizien et al., 2010
Gulf of Lions	2010	Present study

3 RESULTS

3.1 Sediments characteristics

For most stations, temporal changes in $D_{0.5}$, fines content (%<63 µm) and OC contents were restricted (**Figure 3**). Paired *t*-tests with permutations showed significant ($p<0.05$) temporal changes at stations located at 40 m depth for $D_{0.5}$ and at 40 and 50 m depth for fines content. Corresponding changes consisted in an increase in $D_{0.5}$ and to a decrease in fines content between 1998 and 2010. Conversely, there was no significant change in OC contents.

3.2 General characteristics of benthic macrofauna

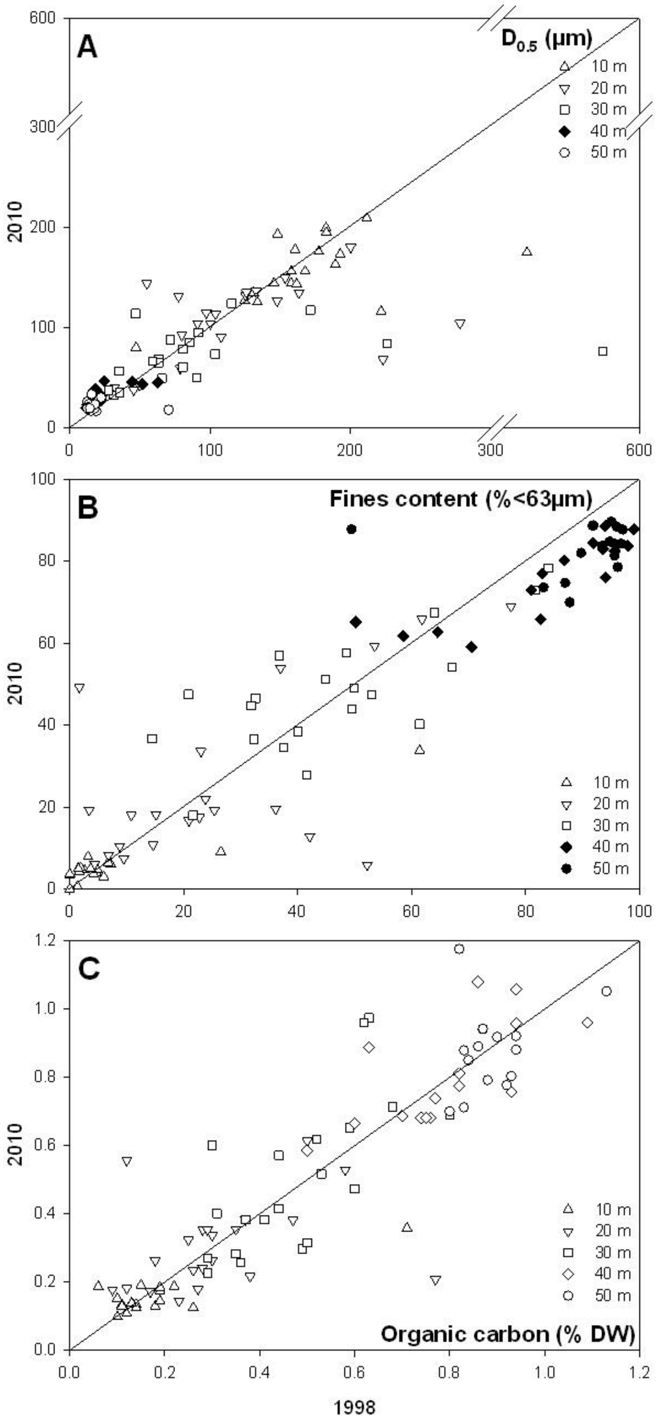
For an almost similar sampling effort, the total number of individuals collected was much higher in 1998 (i.e., 26806) than in 2010 (i.e., 16066). Conversely, the number of identified taxa was slightly lower in 1998 (380 and 408 taxa in 1998 and 2010, respectively).

During both sampling cruises benthic macrofauna was mainly composed of polychaetes (relative abundances of 62.8 and 41.2% in 1998 and 2010, respectively) followed by crustaceans (relative abundances of 14.3 and 24.2% in 1998 and 2010, respectively), molluscs (relative abundances of 18.6 and 19% in 1998 and 2010, respectively), sipunculans (relative abundances of 0.9 and 9.4% in 1998 and 2010, respectively) and miscellaneous groups, including echinoderms, echiurans, cnidarians, hemichordates, nemerteans, platyhelminthes and phoronideans (total relative abundances of 3.5 and 6.2% in 1998 and 2010, respectively). In 1998 *Ditrupa arietina* (Polychaeta) accounted for 27.5% of total abundance followed by *Owenia fusiformis* (Polychaeta) and *Turritella communis* (Mollusca) (9.8 and 6.4%, respectively). In 2010 *Aspidosiphon muelleri* (Sipuncula) and *Sternaspis scutata* (Polychaeta) were the most abundant taxa (7.5 and 6.0%, respectively) followed by *Galathowenia oculata* (Polychaeta, 4.3%).

In 1998, the most frequent taxa were: Tanaidacea, *Lumbrineris* spp., *Glycera* spp., *Ampelisca diadema* and *Notomastus latericeus*, which were present at 87.9, 86.8, 71.4, 57.1 and 54.9% of the sampled stations, respectively. In 2010 the most frequent taxa were: *Ampelisca sarsi*, *Glycera* spp., Ampharetidae, Tanaidacea, *Ampelisca typica*, which were present at 85.7, 84.6, 81.3, 80.2 and 73.6% of the sampled stations, respectively. Major species, such as *Ditrupa arietina*, *Owenia fusiformis*, *Turritella communis*, *Aspidosiphon muelleri*, *Sternaspis scutata* and *Galathowenia oculata,* were present, respectively, at 47.3, 42.9, 46.2, 26.4, 44 and 49.5% of the stations sampled in 1998 *versus* 26.4, 40.7, 37.4, 36.3, 46 and 73.6% of the stations sampled in 2010.

3.3 Univariate global descriptors of benthic macrofauna

Temporal changes in abundances were significant for the 10, 20 and 50 m deep stations (**Figure 4A**). Abundances decreased between 1998 and 2010 at shallow (i.e., 10 and 20 m) stations and conversely increased at deep (i.e., 50 m) stations. Temporal changes in species αSR were significant for the 20 and 50 m deep stations (**Figure 4B**). αSR decreased between 1998 and 2010 at 20 m deep stations and conversely increased at 50 m deep stations. Temporal changes in J’ were significant for the 10, 20 and 50 m deep stations (**Figure 4C**). J’ increased between 1998 and 2010 at shallow (i.e., 10 and 20 m) stations and conversely decreased at deep (i.e., 50 m) stations.

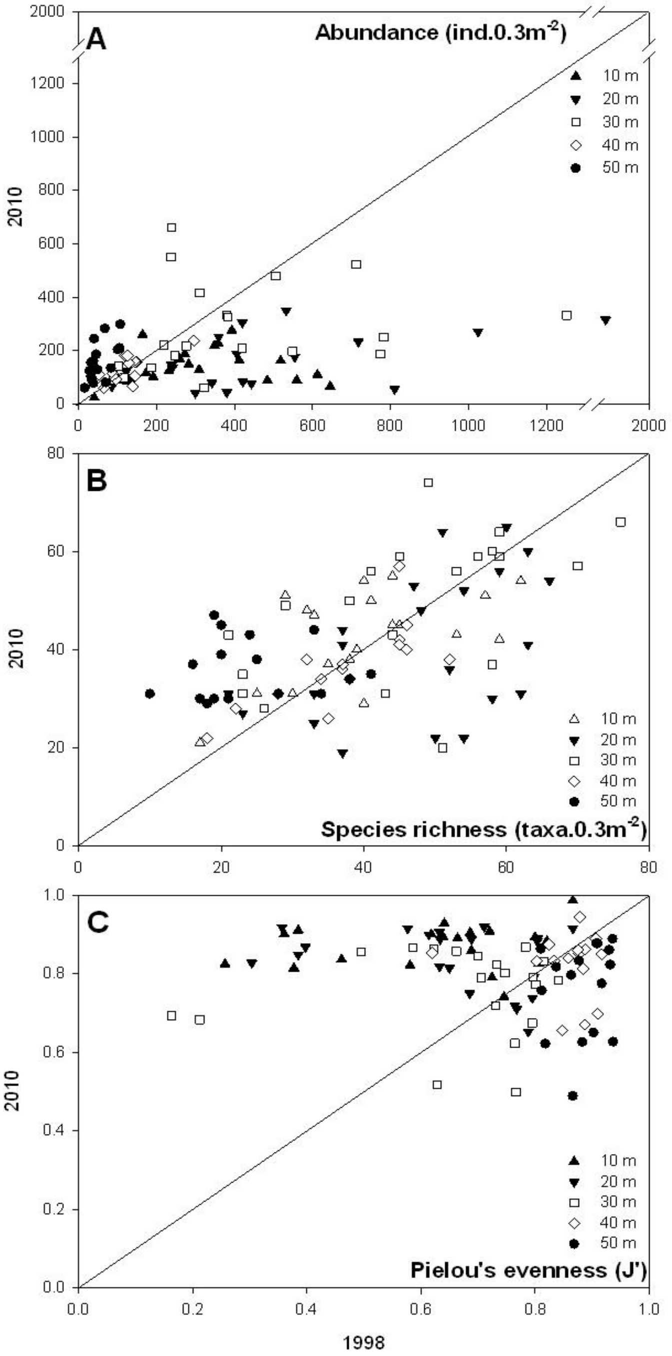


Depth (m)	$D_{0.5}$ (µm)	
	t-statistic	permutational *p*-value
10	-0.18	0.864
20	-0.87	0.415
30	-1.29	0.205
40	**2.53**	**0.027***
50	0.68	0.602

Depth (m)	Fines content (%<63µm)	
	t-statistic	permutational *p*-value
10	-0.27	0.964
20	-0.11	0.919
30	0.63	0.531
40	**-3.52**	**0.004***
50	**-2.21**	**0.048***

Depth (m)	Organic carbon (% DW)	
	t-statistic	permutational *p*-value
10	-0.94	0.423
20	-0.12	0.902
30	0.68	0.504
40	0.32	0.772
50	-0.28	0.820

Figure 3. Spatiotemporal changes in surface sediments characteristics by depth: (A) mean of $D_{0.5}$ (breaks in axes between 300 and 400 *µ*m), (B) mean of fines content (%<63 *µ*m) and (C) mean of organic carbon content. Results of corresponding paired *t*-test with permutations. *p*-values < 0.05 are in bold and indicated by "*" in tables and by full symbols in charts. The signal of the *t*-statistic indicates the direction of changes between 1998 and 2010. Diagonal line indicates *y*=*x*.



Depth (m)	Abundance (ind.0.3m^{-2})	
	t-statistic	permutational *p*-value
10	**-4.54**	**0.001***
20	**-3.77**	**0.001***
30	-1.85	0.083
40	0.77	0.438
50	**6.84**	**0.001***

Depth (m)	Species richness (taxa.0.3m^{-2})	
	t-statistic	permutational *p*-value
10	1.10	0.280
20	**-2.38**	**0.027***
30	0.85	0.407
40	-0.44	0.688
50	**4.65**	**0.002***

Depth (m)	Pielou's evenness (J')	
	t-statistic	permutational *p*-value
10	**6.12**	**0.001***
20	**4.20**	**0.002***
30	1.97	0.067
40	-1.07	0.328
50	**-3.99**	**0.001***

Figure 4. Spatiotemporal changes in the global descriptors of benthic macrofauna by depth: (A) abundance (breaks in axes between 1300 and 1900 ind.0.3 m^{-2}), (B) station species richness and (C) Pielou's evenness. Results of corresponding paired *t*-test with permutations. *p*-values < 0.05 are in bold and indicated by "*" in tables and by full symbols in charts. The signal of the *t*-statistic indicates the direction of changes between 1998 and 2010. Diagonal line indicates *y*=*x*.

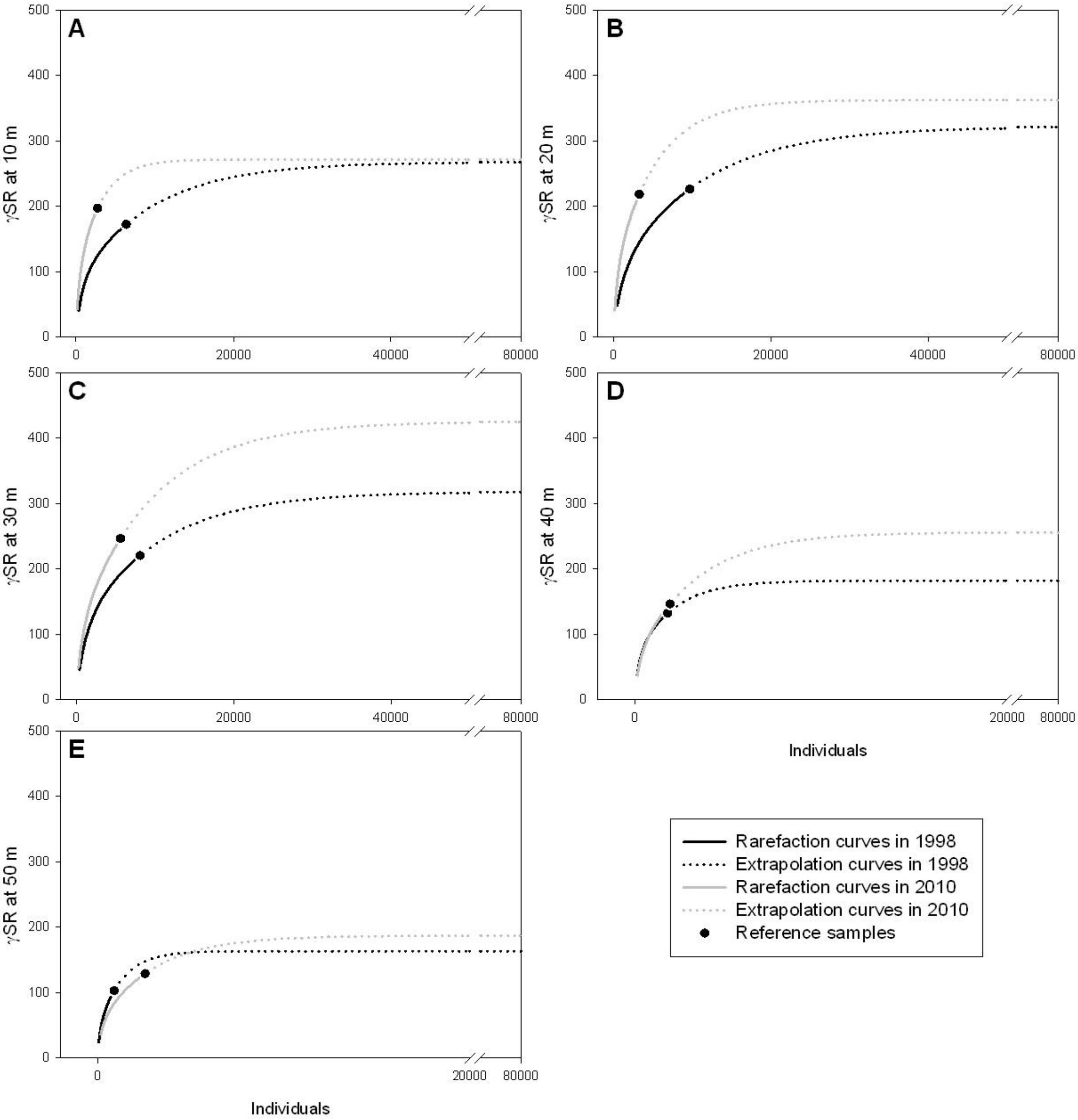


Figure 5. Sampled-based species accumulation curves (sensu Colwell et al., 2012) for each sampling depth and sampling years. Filled black circles correspond to reference samples (i.e., a pool of all samples collected at a given sampling depth during a given sampling year). The parts of the curves left to these points correspond to rarefaction curves, whereas the parts of the curves right to these points correspond to extrapolation curves. The asymptotes of the later are estimates of γSR (see text for details).

Temporal changes in the accumulation curves at each sampling depth are shown in **Figure 5**. Overall, differences between the 1998 and 2010 curves tended to decrease with sampling depth. For 10 m deep stations, there were important differences in the rarefaction component of the two curves, which likely reflected the above-mentioned difference in equitability (**Figure 5A**). Conversely, the extrapolation components of the 2 curves (i.e., 267 and 271 species in 1998 and 2010, respectively) showed almost similar asymptotic γSR values. The same pattern was true to a lesser extent at the 20 and 30 m deep stations, which resulted in slightly higher γSR in 2010 than in 1998 (i.e., 361 *versus* 321 species, and 424 *versus* 317 species for 20 and 30 m deep stations, respectively; **Figures 5B, C**). For the 40 m deep stations, there was no difference in the rarefaction components of the accumulation curve and conversely a slightly higher γSR in 2010 than in 1998 (255 *versus* 181 species, respectively; **Figure 5D**). Finally, the accumulation curves of the 50 m deep stations were almost similar in 1998 and 2010 (γSR of 187 and 163 species, respectively; **Figure 5E**).

3.4 Multivariate analyses: identification of community and community changes

The first axis of the PCA (**Figure 6A**) accounted for 18.9% of the total variance of benthic macrofauna composition. It mostly corresponded to a depth gradient with shallow stations on the left-hand side and deep stations on the right-hand side. The second axis explained 8.2% of the total variance of benthic macrofauna compositions. It was interpreted as a temporal axis segregating the 2010 (upper part) from the 1998 (lower part) sampling years. In spite of the low amount of variance explained these two axis thus account for both for spatial and temporal effects on benthic macrofauna composition. The fact that the projections of the same stations in 1998 and 2010 tended to be closer for deep than for shallow stations suggests a significant interaction between spatial and temporal effects (see also above). The PCA plot of species (**Figure 6B**) showed that *Ditrupa arietina*, *Owenia fusiformis* and *Spisula subtrucata* were most associated with shallow stations, whereas conversely, *Sternaspis scutata* was the species most associated with deep stations. *D.* arietina, *Turritella communis* and *Lumbrineris latreilli* were most associated with the 1998 cruise, whereas *Ampelisca sarsi*, *S. subtruncata* and *S. scutata* were most associated with the 2010 cruise.

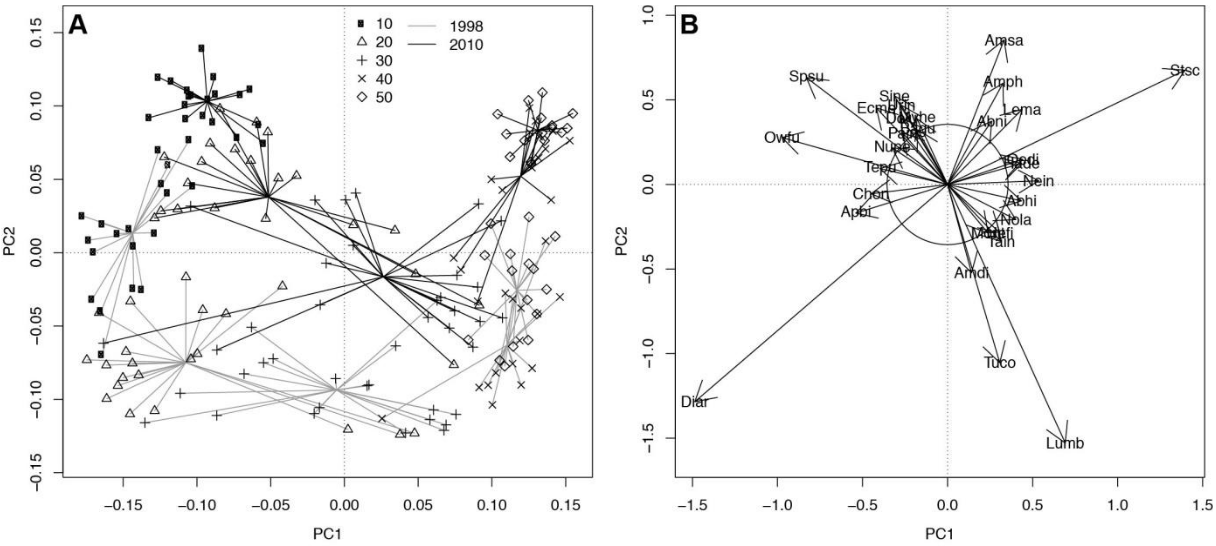


Figure 6. 2-dimensional plot of the PCA based on benthic macrofauna composition showing: (A) the projections of each combination of sampling stations and sampling years distribution of stations year-depth crossed (grey lines for 1998 and black lines for 2010) and (B) major species of each group of station: *Ampelisca sarsi* (Amsa), *Ampelisca diadema* (Amdi), Ampharetidae (Amph), *Aponuphis bilineata* (Apbi), *Ditrupa arietina* (Diar), *Echinocardium mediterraneum* (Ecme), *Leptocheirus mariae* (Lema), *Lumbrineris* spp. (Lumb), *Nephtys incisa* (Nein), *Owenia fusiformis* (Owfu), *Siphonoecetes neapolitanus* (Sine), *Spisula subtruncata* (Spsu), *Sternaspis scutata* (Stsc), *Turritella communis* (Tuco) and *Urothe intermedia* (Urin). The equilibrium concentration circle is also indicated.

The results of K-means grouping are shown in **Figure 7**. With k=3 groups, observations were rather clearly partitioned along a depth gradient, regardless of year, with deep (40-50 m) and shallow (10-20 m) stations clearly separated but both slightly overlapping with the cluster formed by intermediate (30 m deep) stations. For k=4 groups, the shallow stations were separated in 3 clusters in relation with sampling year, while other clusters remain unchanged. With k=5, deeper stations also formed two distinct clusters in relation with sampling year, conversely to 30 m deep stations, which remained grouped. Here again, these results are compatible with the existence of a significant interaction of spatial and temporal effects on benthic macrofauna composition (see also above).

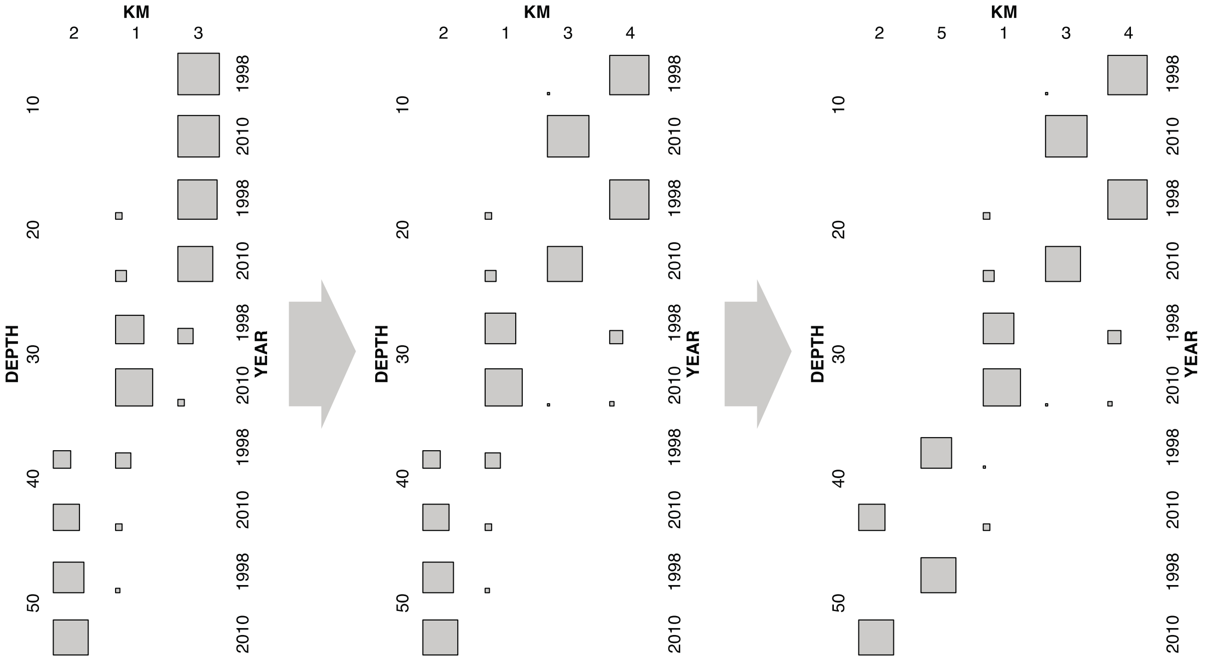


Figure 7. The benthic macrofauna grouping by the K-means in 3, 4 and 5 groups.

3.5 Changes in benthic macrofauna species composition

The indicator species best characterizing the cluster corresponding to the 10 and 20 m deep stations (i.e., the Littoral Fine Sands community of Labrune et al., 2007a, 2008) were: *Nephtys hombergii*, *Euspira* spp., *Nephtys cirrosa*, *Eumida sanguinea* and *Timarete filigera* in 1998*, versus*: *Fustiaria rubescens*, *Callista chione*, *Lucinella divaricata*, *Thracia phaseolina* and *Leucothoe pachycera* in 2010 (**Table 2**). The most abundant species associated with this community in 1998 were *Ditrupa arietina* (32.5%), *Owenia fusiformis* (16.4%), S*pisula subtruncata* (5.8%), *Turritella communis* (4.5%) and Tanaidacea (3.1%) *versus Galathowenia oculata* (6.7%), *S. subtruncata* (5.5), *Siphonoecetes neapolitanus* (5.1%), Tanaidacea (3.9%) and *Dosinia lupinus* (2.7%) in 2010 (**Table 3**).

In 1998, the indicators species best characterizing the cluster corresponding to the 30 m deep stations (i.e., the Littoral Sandy Mud community of Labrune et al., 2007a, 2008) were: *Abra prismatica*, Mysida, *Prionospio cirrifera*, *Eteone foliosa* and *Pseudomystides limbata versus Aspidosiphon muelleri*, *Aricidea* spp., *Syllis* spp. *Peresiella clymenoides* and Syllidae in 2010 (**Table 2**). The most abundant species associated with this community in 1998 were *Ditrupa arietina* (26.0%), *Turritella* *communis* (11.5%), *Lumbrineris* spp. (10.3%), Tanaidacea (6.1%) and *Leptocheirus mariae* (2.6%) *versus Aspidosiphon muelleri* (17.8%), *Lumbrineris* spp. (7.4%), *T. communis* (5.3%), *Nephtys kersivalensis* (4.2%) and *Galathowenia oculata* (4.1%) in 2010 (**Table 3**).

Table 2. Indicator species of macrobenthic communities between 1998 and 2010. ***: p< 0.001, ** : p<0.01, *: p<0.05.

1998			**2010**		
Littoral Fine Sands	**Statistic**	***p*-value**	**Littoral Fine Sands**	**Statistic**	***p*-value**
Nephtys hombergii	0.946	0.005 **	*Fustiaria rubescens*	0.648	0.005 **
Euspira spp	0.688	0.005 **	*Callista chione*	0.646	0.005 **
Nephtys cirrosa	0.657	0.005 **	*Lucinella divaricata*	0.645	0.005 **
Eumida sanguinea	0.555	0.005 **	*Thracia phaseolina*	0.574	0.005 **
Timarete filigera	0.524	0.005 **	*Leucothoe pachycera*	0.405	0.015 *
Mendicula ferruginosa	0.516	0.005 **	*Oxynoe olivacea*	0.387	0.01 **
Autonoe angularis	0.463	0.005 **	*Cylichna cylindracea*	0.323	0.01 **
Mysta picta	0.447	0.005 **	*Melinna cristata*	0.316	0.035 *
Spio filicornis	0.445	0.005 **			
Paradoneis fulgens	0.316	0.04 *			

Littoral Sandy Mud	**Statistic**	***p*-value**	**Littoral Sandy Mud**	**Statistic**	***p*-value**
Abra prismatica	0.549	0.005 **	*Aspidosiphon muelleri*	0.768	0.005 **
Mysida	0.504	0.005 **	*Aricidea* spp.	0.541	0.005 **
Prionospio cirrifera	0.493	0.005 **	*Syllis* spp.	0.53	0.005 **
Eteone foliosa	0.438	0.005 **	*Peresiella clymenoides*	0.41	0.005 **
Pseudomystides limbata	0.43	0.005 **	Syllidae	0.373	0.025 *
Medicorophium rotundirostre	0.399	0.01 **	*Atylus vedlomensis*	0.366	0.02 *
Anapagurus bicorniger	0.399	0.005 **	*Cereus* spp.	0.359	0.03 *
Urothoe elegans	0.387	0.015 *	*Spiophanes viriosus*	0.349	0.005 **
Mediomastus spp.	0.374	0.02 *	*Aonides* spp.	0.316	0.045 *
Ampelisca spinipes	0.347	0.04 *	*Nucula hanleyi*	0.316	0.05 *
Isopoda	0.346	0.04 *	*Malmgreniella* spp.	0.287	0.045 *
Cossura spp.	0.293	0.045 *			

Terrigenous Coastal Mud	**Statistic**	***p*-value**	**Terrigenous Coastal Mud**	**Statistic**	***p*-value**
Levinsenia gracilis	0.689	0.005 **	*Scolanthus* spp.	0.566	0.005 **
Harmothoe glabra	0.596	0.005 **	*Calocaris macandreae*	0.498	0.005 **
Marphysa bellii	0.567	0.005 **	*Maera grossimana*	0.479	0.005 **
Malmgrenia andreapolis	0.508	0.005 **	*Jaxea nocturna*	0.467	0.005 **
Prionospio multibranchiata	0.44	0.005 **	*Malmgreniella lilianae*	0.464	0.005 **
Ancistrosyllis groenlandica	0.381	0.005 **	*Athanas nitescens*	0.435	0.005 **
Eunereis longissima	0.363	0.01 **	*Virgularia mirabilis*	0.43	0.005 **
			Malmgreniella polypapillata	0.311	0.03 *

In 1998, the indicator species best characterizing the cluster corresponding to the 40 and 50 m stations (i.e., the Terrigenous Coastal Mud community of Labrune et al., 2007a, 2008) were: *Levinsenia gracilis*, *Harmothoe glabra*, *Marphysa belli*, *Malmgreniella andreapolis* and *Prionospio multibranchiata versus Scolanthus* spp., *Calocaris macandreae*, *Maera grossimana*, *Jaxea nocturna* and *Malmgreniella lilianae* in 2010 **(Table 2**). The most abundant species associated with this community in 1998 were *Lumbrineris* spp. (14.8%), *Sternaspis scutata* (8.7%), *Aspidosiphon muelleri* (4.5%), Tanaidacea (4.3%) and *Heteromastus filiformis* (4.1%) *versus Sternaspis scutata* (21.1%), *Leptocheirus mariae* (11.7%), *Ampelisca sarsi* (7.9%), Ampharetidae (4.3%) and Tanaidacea (4.2%) in 2010 (**Table 3**).

Table 3. Relative abundances (%) of the five most abundant species for each macrobenthic community (most abundant species within each community are in bold) between 1998 and 2010. LFS: Littoral Fine Sands, LSM: Littoral Sandy Mud and TCM: Terrigenous Coastal Mud.

	1998			2010		
Species	**LFS**	**LSM**	**TCM**	**LFS**	**LSM**	**TCM**
Ampelisca sarsi	0.2	0.1	0.0	1.9	2.4	**7.9**
Ampharetidae	0.0	0.6	0.2	1.4	2.2	**4.3**
Aspidosiphon muelleri	0.1	0.9	**4.5**	2.4	**17.8**	1.5
Ditrupa arietina	**32.5**	**26.0**	1.5	2.2	3.1	0.0
Dosinia lupinus	0.1	0.3	0.0	**2.7**	0.6	0.0
Heteromastus filiformis	0.0	0.1	**4.1**	0.1	1.2	0.3
Leptocheirus mariae	0.0	**2.6**	1.7	0.1	0.6	**11.7**
Lumbrineris spp.	1.8	**10.3**	**14.8**	1.8	**7.4**	2.8
Galathowenia oculata	0.6	1.0	0.6	**6.7**	**4.1**	1.4
Nephtys kersivalensis	0.0	0.0	1.1	2.6	**4.2**	0.3
Owenia fusiformis	**16.4**	0.1	0.0	1.9	1.0	0.0
Siphonoecetes neapolitanus	0.0	0.3	0.0	**5.1**	2.3	0.0
Spisula subtruncata	**5.8**	0.2	0.0	**5.5**	0.1	0.0
Sternaspis scutata	0.1	0.1	**8.7**	0.1	0.5	**21.1**
Tanaidacea	**3.1**	**6.1**	**4.3**	**3.9**	3.7	**4.2**
Turritella communis	**4.5**	**11.5**	2.7	1.4	**5.3**	0.4

3.6 Multivariate analyses: Interaction between spatial and temporal effects, spatial modelling

There was a significant interaction between spatial and temporal effects on benthic macrofauna composition (*F*=1.398, *p*=0.001). This interaction accounted for 20.3% of the total variance of overall (i.e., 1998 + 2010) benthic macrofauna composition.

Using (1) dbMEMs (together with a linear trend component), (2) AEM (Rhône River influence), and (3) environmental variables as sets of explanatory variables for each year separately, our models accounted for 44% (Adj-R^2, *F*=2.780, *p*=0.005) and 42% (Adj-R^2, *F*=2.710, *p*=0.005) of the variance of benthic macrofauna composition in 1998 and 2010, respectively (**Figure 8**). AEM explained 28 and 31% of variance in benthic macrofauna composition during 1998 and 2010, respectively, *versus* only 25 and 22% for dbMEMS. During both years, "pure" (i.e., non-associated with environmental factors and linear trend) contributions accounted for 17% of the variance of benthic macrofauna composition. During both years, the joint effect of AEM and dbMEM was limited (3 and 4%) and the spatial linear trend was negligible (3%). Finally, while environmental variables accounted for 25 and 22 % of total variance in 1998 and 2010, respectively, their "pure" (i.e., non-spatial) contributions to the variance of benthic macrofauna composition remained negligible (3% during both sampling years).

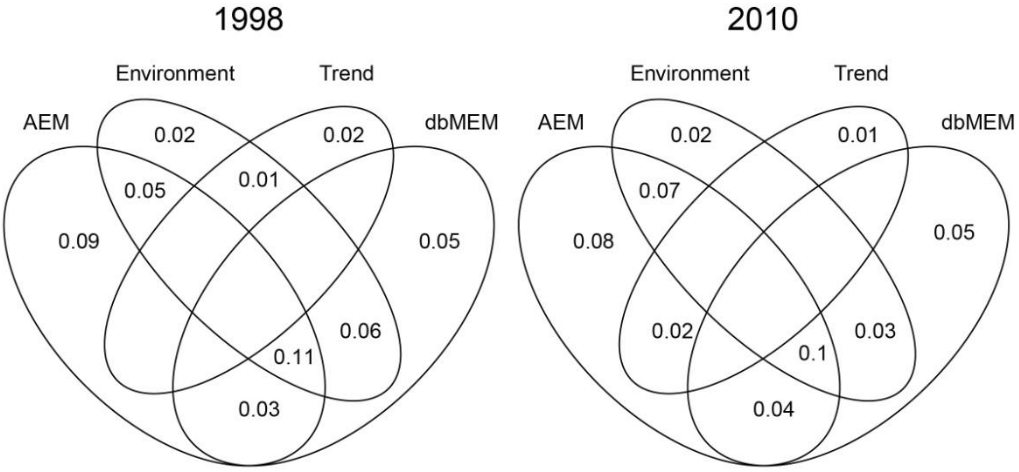


Figure 8. Partitioning of the variances of 1998 and 2010 benthic macrofauna compositions between explanatory variables.

4 DISCUSSION

4.1 Changes in sediments characteristics

The spatial distribution patterns of the sediment characteristics assessed during the present study were similar to those observed in 1998 (Labrune et al., 2008). The classical decreasing inshore/offshore gradient in sediment granulometry (Durrieu de Madron et al., 2000; Grémare et al., 2002; Mutlu et al., 2010; Martins et al., 2012) and the corresponding opposite gradient in organic carbon concentrations (Durrieu de Madron et al., 2000; Tesi et al., 2007; Martins et al., 2012) was conserved as well as the negative correlation between these 2 parameters (Martins et al., 2012). Despite, overall restricted changes in all 3 considered sediment characteristics, fines content at 40 and 50 m depth were significantly lower in 2010 than in 1998, whereas $D_{0.5}$ at 40 m depth was significantly higher. Previous changes in sediment granulometry in the shallow areas of the Gulf of Lions have been attributed to changes in the frequency of strong resuspension events (Grémare et al., 1998a). Resuspension events associated with strong waves and currents can have a direct impact down to 30 m depth (Ferré et al., 2005) but extreme ones can affect sediments down to 60 m depth as observed along the Ebro shelf (Puig et al., 2001; Palanques et al., 2002), and even deeper in the Blanes Canyon (Sanchez-Vidal et al., 2012). A higher frequency of strong resuspension events in 2010 than in 1998 is consistent with the strongly negative values of the NAO index and the negative 8-years moving average during this year, whereas conversely, monthly NAO index values observed in 1998 were alternatively positive and negative and did not reach extreme values (**Figure 2B**). However, the hypothesis of a control of sediment granulometry through strong resuspension events remains questionable, because it is not clear why such a mechanism would not have primarily resulted in changes of sediment granulometry of shallower stations as well. One possibility, which should be further tested through long-term observations, is that the number and intensity of resuspension events in 1998 were already sufficient to clear shallowest sediments of their fines.

4.2 Conservation of the same benthic communities between 1998 and 2010

Not surprisingly, since, based on the 1998 sampling, Labrune et al. (2007a, 2008) were able to homogenize the denomination of the Gulf of Lions communities identified much earlier by Guille (1970) and Picard (1965), our results show that the same 3 communities were basically present in 1998 and 2010. Our non-hierarchical clustering (K-means, with k=3) indeed resulted in a strictly spatial grouping of stations without any temporal (i.e., between years) interference. The bathymetric distributions of stations among these 3 clusters was thus coherent with the one of the 3 communities (i.e., Littoral Fine Sands (LFS) community, Littoral Sandy Muds (LSM) community and Terrigenous Coastal Muds (TCM) community) identified by Labrune et al. (2007a, 2008). This further reinforces the use of a single terminology for denominating the communities of the whole studied area as proposed by Labrune et al. (2007a, 2008). Moreover, the results of our K-means with k=4 and k=5 showed that between-years changes were affecting independently these 3 communities. This suggests that between-years changes were largely superimposed to the same structuration of benthic communities. In spite of changes in their composition (see also below), the same 3 communities were thus clearly present in 1998 and 2010 and it is then sound to describe changes in their benthic macrofauna composition and infer possible causes independently for each community.

Based on the occurrence of two sub-clusters of stations associated with the NE and SW parts of the LSM community, Labrune et al. (2007a, 2008) first highlighted a possible large-scale influence of the Rhône River on benthic macrofauna composition. However, they did not statistically test this hypothesis and did not extend it, neither to LFS community nor to TCM community, as well. During the present study, we used a model containing environmental variables together with both non directional (i.e., dbMEMs) and directional (i.e., AEM, which were coded to reflect station proximity with the Rhône River mouth at each depth) explanatory variables to account for changes in benthic macrofauna composition in 1998 and 2010, separately. In both cases, spatial effects were dominant, with AEM contributing more than dbMEMs, which supports the existence of a directional spatial effect, reflecting the distance to the Rhône River. It would now be interesting to further explore such an effect by: (1) repeating our statistical procedure using a more complex coding of spatial data (e.g., considering each community and no longer each depth for the basis of a rook coding), and (2) using the same statistical procedure independently on each community to assess possible different effects of the Rhône River.

4.3 Temporal changes in benthic macrofauna composition between 1998 and 2010

Interaction between spatial and temporal effects

Our results confirm, but at a much larger scale than Grémare et al. (1998a) and Labrune et al. (2007b), the occurrence of important temporal changes in the composition of benthic macrofauna community. They also show that they are differing in their intensity depending on depth/communities. Our results indeed showed the existence of a significant interaction between spatial and temporal effects on benthic macrofauna composition. Second, our non-hierarchical clustering with k=4 and k=5, showed that the between-years effect occurred first (i.e., at k=4) at 10 and 20 m deep stations (i.e., LFS community) and then at 40 and 50 m deep stations (i.e., TCM community). Results of our PCA also showed that the benthic macrofauna composition of the LSM community (i.e., 30 m deep stations) also changed between 1998 and 2010. The fact that these changes were not put in evidence using non-hierarchical clustering up to 5, probably reflects the higher within-year heterogeneity in their macrofauna composition, probably in relation with the Rhône River influence (see above) as already shown by Labrune et al. (2007a, 2008) for the 1998 sampling year. Otherwise, our results suggest that LFS stations showed stronger changes in their macrofauna composition between 1998 and 2010 than TCM ones, which is consistent with those of Labrune et al. (2007a) who observed stronger temporal changes in the benthic macrofauna composition of sandy than of muddy communities between 1994 and 2003.

Shallow (LFS and LSM) communities

Based on: (1) long term comparisons (i.e., 1967/68, 1994 and 2003) of benthic macrofauna composition achieved at a restricted number of stations in the Bay-of Banyuls-sur-Mer, and (2) autoecologial studies carried out on the polychaete *Ditrupa arietina* (Medernach et al., 2000), temporal changes in both LSF and LSM benthic macrofauna compositions are currently attributed to fluctuations in the frequency of storms in relation with the NAO (Labrune et al., 2007b) as already proposed in the North Sea (Kröncke et al., 1998, 2001; Tunberg and Nelson, 1998). By showing that the occurrence of changes in benthic macrofauna composition within the 3 main communities identified by Labrune et al. (2007a, 2008) during two sampling years characterized by contrasted values of the NAO index (1998 was at the end of a positive NAO period, whereas 2010 was at the beginning of a negative one), our results support that this hypothesis may also hold for the whole Gulf of Lions, which retrospectively supports the approach used by Grémare et al. (1998a) and then by Labrune et al. (2007b) to infer causal relationships regarding the changes in benthic macrofauna composition in the shallow bottom of the Gulf of Lions.

We further tested this hypothesis by using a meta-analysis combining several spatial surveys conducted over a long period of time, as achieved by Grémare et al. (1998b) to first establish that temporal changes in benthic macrofauna in the Gulf of Lions were large-scale. This approach allowed for assessing the relationship between changes in the NAO index and in the abundance of *Ditrupa arietina*. Our results indeed confirmed those of Grémare et al. (1998a, b) and Labrune et al. (2007b) in showing that this species is the most representative of temporal changes in benthic macrofauna composition within both the LFS and LCM communities. In the LFS community, we indeed observed a significant decrease in αSR associated with a significant reduction of total abundance and an increase in evenness between 1998 and 2010, which were primarily attributable to the important reduction in the abundance and, consequently, in the dominance of *D. arietina*. Conversely, there were no significant changes in αSR, abundance and Pielou's evenness in the LSM community between 1998 and 2010. This resulted from the combined effect of the decrease of *D. arietina* and of the increase of *Aspidosiphon muelleri*. In 1998, *A. muelleri* was mostly present at 40 and 50 m depth (i.e., in the TCM community), whereas in 2010 it was mostly found at 30 m (i.e., in the LSM community). Ferrero-Vincente et al. (2013) observed that *A. muelleri* does not show any significant preference for muddy or sandy sediments and tends to be present in similar abundances in both environments. However, these authors also showed that individuals of *A. muelleri* preferentially live in *D. arietina* tubes. The increase in the availability of these tubes resulting from the decline of *D. arietina* within the LSM community in 2010 may thus account for the corresponding increase of *A. muelleri*. Moreover, changes in availability of empty shelter shells, together with competition with sipunculans, can also influence the distribution of Tanaidacea (Ferrero-Vicente et al., 2013). In this sense, the most important changes in benthic macrofauna composition that occurred within the LSM community can also be considered as related to those regarding the abundance of *D. arietina*. The time series of average and maximal abundances of *D. arietina* and of the NAO index all show the same temporal pattern (**Figure 9**). Three distinct time periods can be distinguished based on the 8-years moving average of the NAO index: (1) 1989-2000, which is characterized by positive values, (2) 2000-2010, which is characterized by values close to 0, and (3) 2010-2013, which is characterized by negative values. The first of these periods is also characterized by high (both average and maximal) abundances of *D. arietina* conversely to the two other ones. Overall these results are consistent with the current paradigm of an indirect (i.e., through the frequency and the intensity of storms) control of NAO on the benthic macrofauna composition of both LFS and LSM communities in the Gulf of Lions (Labrune et al., 2007b).

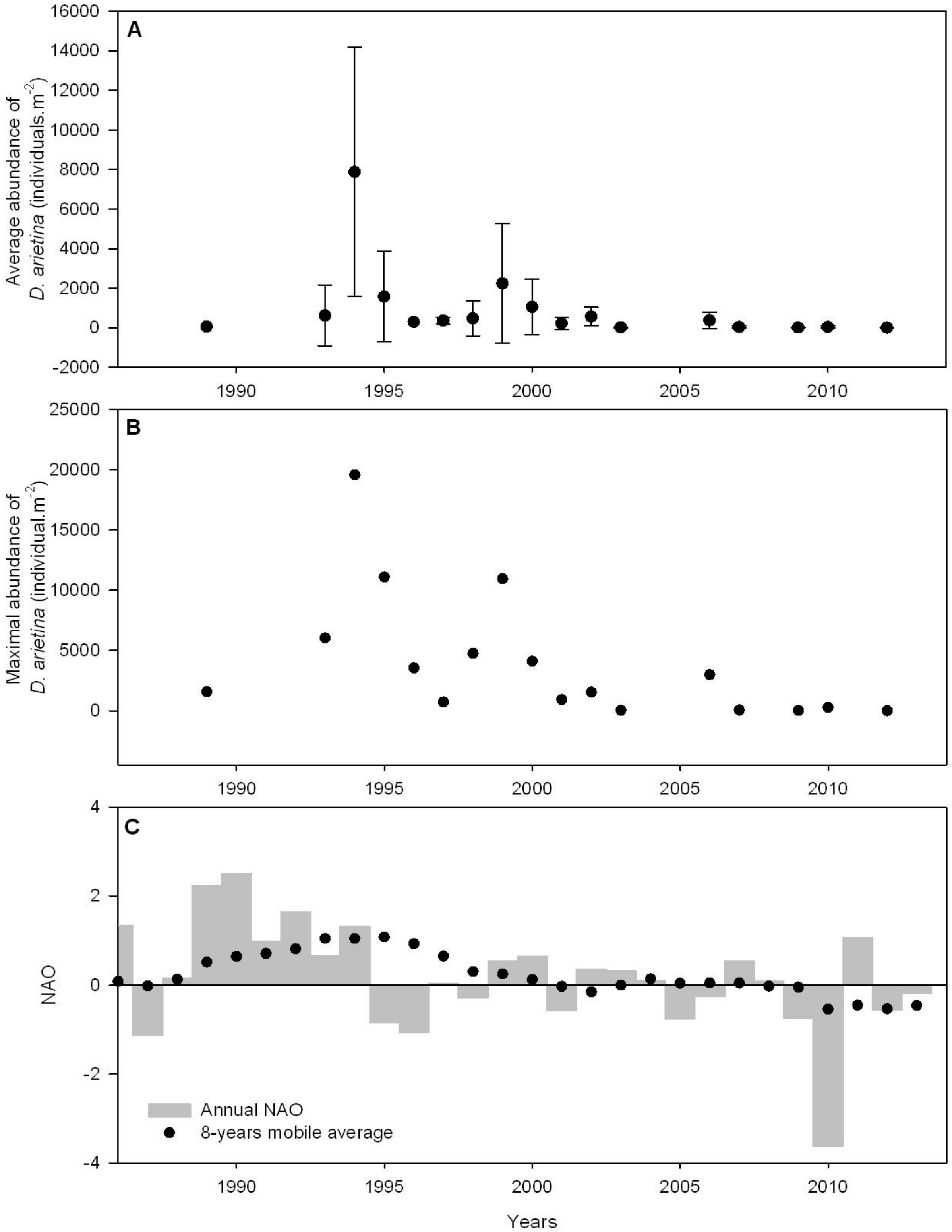


Figure 9. Average (A) and maximal (B) abundances of *Ditrupa arietina* observed between 1989 and 2012 along the Catalan French Coast in relation with changes in the yearly and 8-years moving averages of the NAO index (C).

Deep (TCM) community

All global univariate characteristics of benthic macrofauna composition changed significantly between 1998 and 2010 with higher values of abundance and species richness, and lower values of Pielou's evenness in 2010. High abundances and low evenness in 2010 were associated with the increase of *Sternaspis scutata*, which is a typical species of the TCM community (Picard, 1965; Salen-Picard et al., 2003; Labrune et al., 2007b; Bonifácio et al., 2014). Grémare et al. (1998a) already observed significant changes in the benthic macrofauna composition of this community in the Bay of Banyuls-sur-Mer between 1967/68 and 1994. They attributed it to a change in sediment granulometry. Our results are consistent with these observations and interpretation. They also suggest that the influence of major storms on sediment granulometry may occur down to 50 m, which is coherent with the fact that 2010 was associated with a negative value of the NAO index. Interestingly, and based on the sampling of the same stations as Grémare et al. (1998a), Labrune et al. (2007b) reported only minor changes in the benthic macrofauna composition of the TCM community between 1994 and 2003. Unfortunately, these authors did not provide any sediment granulometry data. Nevertheless, the analysis of the NAO time-series shows that this time period was associated with either positive or close to 0 values of the 8-years moving average of the NAO index, which suggests that strong resuspension events may have then only seldom occurred. The exact interactions between: NAO, storm frequency and intensity, and benthic macrofauna composition intensity should now be better assessed based on long-term monitoring.

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REFERENCES

Akoumianaki, I., Nicolaidou, A., 2007. Spatial variability and dynamics of macrobenthos in a Mediterranean delta front area: the role of physical processes. Journal of Sea Research 57, 47–64.

Amouroux, J.M., Grémare, A., 1995. Etude d'impact de la construction d'une station d'épuration sur l'émissaire de Narbonne-Plage Gruissan. 9 pp.

Amouroux, J.M., Grémare, A., 2001a. Etude des populations benthiques présentes au large d'Argelès sur mer: choix du site pour une opération de clapage. Conseil Général des P.O. pour le port de Port-Vendres. 10 pp.

Amouroux, J.M., Grémare, A., 2001b. Etude de la macrofaune marine benthique de la baie de Paulilles avant la réalisation des travaux de réhabilitation du site post-industriel de Paulilles Rapport pour le Conservatoire du Littoral. 13 pp.

Amouroux, J.M., Grémare, A., 2003. Etude d'impact de l'émissaire de la station d'épuration de Banyuls sur mer. 5 pp.

Amouroux, J.M., Grémare, A., 2006. Etude d'impact de l'émissaire de la station d'épuration de Banyuls sur mer. 5 pp.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253.

Blanchet, F.G., Legendre, P., Borcard, D., 2008a. Forward selection of explanatory variables. Ecology 89, 2623–2632.

Blanchet, F.G., Legendre, P., Borcard, D., 2008b. Modelling directional spatial processes in ecological data. Ecological Modelling 215, 325–336.

Blanchet, F.G., Legendre, P., Gauthier, O., 2013. AEM: Tools to construct Asymmetric eigenvector maps (AEM) spatial variables. R package version 0.5-1/r118. http://R-Forge.R-project.org/projects/sedar/

Bonifácio, P., Bourgeois, S., Labrune, C., Amouroux, J.M., Escoubeyrou, K., Buscail, R., Romero-Ramirez, A., Lantoine, F., Vétion, G., Bichon, S., Desmalades, M., Rivière, B., Deflandre, B., Grémare, A., 2014. Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition off the Rhône River in relation to its hydrological regime. Estuarine, Coastal and Shelf Science 151, 196–209.

Borcard, D., Legendre, P. Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Borcard, D., Legendre., P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153, 51–68.

Bornens. P., Riou, S., Grosdemange, D., Hontebeyrie, B., Musard, O., Bougio, Y., 2000a. Etude environnementale du site d'immersion des matériaux de dragage du port de Sète, IN VIVO, Service maritime et de Navigation du Languedoc Roussillon.

Bornens, P., Riou, S., Grosdemange, D., Hontebeyrie, B., Musard, O., Bougio, Y., 2000b. Etude environnementales du site d'immersion des matériaux de dragage du chenal maritime de Port-La-Nouvelle. Service Maritime et de Navigation du Languedoc-Roussillon. 79 pp.

Bourrin, F., Durrieu de Madron, X., Ludwig, W., 2006. Contribution to the study of coastal rivers and associated prodeltas to sediment supply in Gulf of Lions (NW Mediterranean Sea). Vie et Milieu/Life and Environnement 56: 307-314.

Chambers, J.M., 2013. SoDA: Functions and Examples for "Software for Data Analysis". R package version 1.0-6. http://CRAN.R-project.org/package=SoDA

Colwell, R. K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5, 3–21.

Colwell, R. K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

CREOCEAN, ECOSITE, 2001. Suivi écologique du rejet des effluents de la STEP de Sète – Etat du site un an après la mise en service de l'émissaire Année 1 – Rapport année 2001, Sivom de la Mer & des Etangs.

Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Marine Ecology Progress Series 173, 67–83.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statical inference. Ecology 90, 3566–3574.

Dray, S., Legendre, P., Peres-Neto, P. R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196, 483–493.

Dray., S., Legendre., P., Blanchet, F.G., 2013. packfor: Forward Selection with permutation (Canoco p.46). R package version 0.0-8/r109. http://R-Forge.R-project.org/projects/sedar/

Dufrene, M., Legendre., P., 1997. Species assemblages and indicators species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Durrieu de Madron, X., Abassi, A., Heussner, S., Monaco, A., Aloisi, J.C., Radakovitch, O., Giresse, P., Buscail, R., Kerherve, P., 2000. Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanologica Acta 23, 717–730.

Ferré, B., Guizien, K., Durrieu de Madron, X., Palanques, A., Guillén, J., Grémare, A., 2005. Fine-grained sediment dynamics during a strong storm event in the inner-shelf of the Gulf of Lion (NW Mediterranean). Continental Shelf Research 25, 2410–2427.

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, Á., Sánchez-Lizaso, J.L., 2013. Limiting factors on the distribution of shell/tube-dwelling sipunculans. Journal of Experimental Marine Biology and Ecology 446, 345–354.

Gambi, M.C., Giangrande, A., 1986. Distribution of soft-bottom polychaetes in two coastal areas of the Tyrrhenian Sea (Italy): Structural analysis. Estuarine, Coastal and Shelf Science 23, 847–862.

Gogina, M., Glockzin, M., Zettler, M.L., 2010. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 1. Causal analysis. Journal of Marine Systems 79, 112–123.

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., Sardá, R., Medernach, L., Jordana, E., Pinedo, S., Amouroux, J.M., Martin, D., Nozais, C., 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.

Grémare, A., Medernach, L., De Bovée, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). Marine Ecology Progress Series 234, 85–94.

Guille, A., 1970. Bionomie benthique du plateau continental de la côte catalane française. II – Les communautés de la macrofaune. Vie et Milieu 21, 149–280.

Guizien, K., Charles, F., Hurther, D., Michallet, H., 2010. Spatial redistribution of *Ditrupa arietina* (soft bottom Mediterranean epifauna) during a moderate swell event. Continental Shelf Research 30, 239–251.

Hagberg, J., Tunberg, B.G., 2000. Studies on the covariation between physical factors and the long-term variation of the marine soft bottom macrofauna in Western Sweden. Estuarine, Coastal and Shelf Science 50, 373–385.

Harmelin-Vivien, M.L., Bănaru, D., Dierking, J., Hermand, R., Letourneur, Y., Salen-Picard, C., 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). Animal Biodiversity and Conservation 32, 135-145.

Hurrell, J.W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269, 676–679.

Hurrell, J.W., Deser, C., 2010. North Atlantic climate variability: The role of the North Atlantic Oscillation. Journal of Marine Systems 79, 231–244.

IARE, BCEOM, 1993a. Détermination du point de rejet de l'émissaire de la ville de Sète. 41 pp.

IARE, IFREMER, 1993b. Evaluation des conséquences du rejet en mer de la station d'épuration de Montpellier. 60 pp.

Karakassis, I., Eleftheriou, A., 1997. The continental shelf of Crete: structure of macrobenthic communities. Marine Ecology Progress Series 160, 185–196.

Kröncke, I., Dippner, J.W., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communites off Nordeney (East Frisia, Germany) in relation to climate variability. Marine Ecology Progress Series 167, 25–36.

Kröncke, I., Zeiss, B., Rensing, C., 2001. Long-term variability in macrofauna species composition off the Island of Nordeney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Senckenbergiana Maritima 31, 65–82.

La Porta, B., Tomassetti, P., Lomiri, S., Marzialetti, S., Vani, D., Penna, M., Lanera, P., Nicoletti, L., 2011. Ecology and spatial distribution of selected polychaete species from the Italian continental shelf. Italian Journal of Zoology 78, 290–303.

Labrune, C., Grémare, A., Amouroux, J.-M., Sardá, R., Gil, J., Taboada, S., 2007a. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuarine, Coastal and Shelf Science 71, 133–147.

Labrune, C., Grémare, A., Guizien, K., Amouroux, J.M., 2007b. Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): A reappraisal. Journal of Sea Research 58, 125–143.

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.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., De Cáceres, M., Borcard, D. 2010. Community surveys through space and time: testing the space-time interaction in the absence of replication. Ecology 91, 262–272

Legendre, P., Borcard, D., De Caceres, M., 2012. STI: Space-time ANOVA models without replications.. R package version 1.0.2.

Legendre, P., Borcard, D., Blanchet, F.G., Dray, S., 2013. PCNM: MEM spatial eigenfunction and principal coordinate analyses. R package version 2.1-2/r109. http://R-Forge.R-project.org/projects/sedar/

Martins, R., Azevedo, M.RL., Mamede, R., Sousa, B., Freitas, R., Rocha, F., Quintino, V., Rodrigues, A.M., 2012. Sedimentary and geochemical characterization and provenance of the Portuguese continental shelf soft-bottom sediments. Journal of Marine Systems 91, 41–52.

Massé, H.L., 2000. Long-term changes in sand-bottom macrofauna along the coast of Provence (northwest Mediterranean Sea). Oceanologica Acta 23, 229–242.

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.

Meyer, D., Zeileis, A., Hornik, K.,. 2013. vcd: Visualizing Categorical Data. R package version 1.3-1.

MSFD, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union L164, 19–40.

Mutlu, E., Çinar, M.E., Ergev, M.B., 2010. Distribution of soft-bottom polychaetes of the Levantine coast of Turkey, eastern Mediterranean Sea. Journal of Marine Systems 79, 23–35.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre,P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Palanques, A., Puig, P., Guillén, J., Jiménez, J., Gracia, V., Sánchez-Arcilla, A., Madsen, O., 2002. Near-bottom suspended sediment fluxes on the microtidal low-energy Ebro continental shelf (NW Mediterranean). Continental Shelf Research 22, 285–303.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic sucession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16, 229–311.

Pelaprat, C., Agreil, M., Chery, A., Pete, D., Michele, L., Lejeune, P., 2007. Mise en œuvre du contrôle de surveillance au titre de la directive cadre eau pour l'indicateur benthos de substrat meuble dans le district corse (Eaux côtières) – Contrat STARESO/IFREMER

Pelaprat, C., Donnay, A., Chery, A., Missa, A., Lejeune, P. 2010. Mise en œuvre du contrôle de surveillance et opérationnel au titre de la directive cadre eau pour l'indicateur benthos de substrat meuble dans le district corse (Eaux côtières) - Contrat STARESO/IFREMER.

Pelaprat, C., Labrune, C., Amouroux, J.M., Donnay, A., Frejefond, C., Chery, A., Lejeune, P., 2013. Mise en oeuvre du contrôle de surveillance au titre de la directive cadre eau pour l'indicateur benthos de substrat meuble (Eaux côtières) 2012 - Contrat STARESO/IFREMER N/Ref 13/30530017.

Picard, J., 1965. Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise. Recueil des Travaux de la Station Marine d'Endoume 52, 1–160.

Posey, M., Lindberg, W., Alphin, T., Vose, F., 1996. Influence of storm disturbance on an offshore benthic community. Bulletin of Marine Science 59, 523–529.

Puig, P., Palanques, A., Guillén, J., 2001. Near-bottom suspended sediment variability caused by storms and near-inertial internal waves on the Ebro mid continental shelf (NW Mediterranean). Marine Geology 178, 81–93.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Salen-Picard, C., Bellan, G., Bellan-Santini, D., Arlhac, D., Marquet, R., 1997. Changements à long terme dans une communauté benthique d'un golfe méditerranéen (golfe de Fos). Oceanologica Acta 20, 299–310.

Salen-Picard, C., Darnaude, A., Arlhac, D., Harmelin-Vivien, M., 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. Oecologia 133, 380–388.

Salen-Picard, C., Arlhac, D., Alliot, E., 2003. Responses of a Mediterranean soft bottom community to short-term (1993–1996) hydrological changes in the Rhone river. Marine environmental research 55, 409–427.

Sanchez-Vidal, A., Canals, M., Calafat, A.M., Lastras, G., Pedrosa-Pamies, R., Menendez, M., Medina, R., Company, J.B., Hereu, B., Romero, J., Alcoverro, T., 2012. Impacts on the deep-sea ecosystem by a severe coastal storm. PloS one 7, e30395.

Thorin, S., Dolbeau, X., 2007. Suivi à long terme des communautés benthiques des substrats meubles dans la Réserve Naturelle Marine de Cerbère-Banyuls – champagne 2007. Conseil Général des Pyrénées Orientales, 52 pp.

Thorin, S., 2009. Suivi à long terme des communautés benthiques des substrats meubles dans la Réserve Naturelle Marine de Cerbère-Banyuls - champagne 2009. Conseil Général des Pyrénées Orientales, 64 pp.

Thorson, G., 1957. Bottom communities (sublittoral or shallow shelf). Geological Society of America Memoirs 67, 461–534.

Tunberg, B.G., Nelson, W.G., 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Marine Ecology Progress Series 170, 85–94.

Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J., Tapp, J.F., 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Marine Ecology Progress Series 234, 1–13.

WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Union, L327, 1–73.

WoRMS Editorial Board, 2014. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2014-04-10.

CHAPITRE III

ETUDE À LONG TERME DE LA RELATION LIANT LES COMMUNAUTÉS BENTHIQUES ET LA VARIABILITÉ CLIMATIQUE EN BAIE DE BANYULS-SUR-MER, MÉDITERRANÉE OCCIDENTALE

LONG-TERM STUDY OF THE RELATION BETWEEN MACROBENTHIC COMMUNITIES AND CLIMATE VARIABILITY IN THE BAY OF BANYULS-SUR-MER, NW MEDITERRANEAN SEA

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ABSTRACT

The relationship between the climatic variability and the benthic macrofauna composition was assessed at 4 stations located in the Bay of Banyuls-sur-Mer (NW Mediterranean Sea). These stations were sampled each autumn/winter between 2004 and 2013 and analysed for sediment granulometry and benthic macrofauna composition both in terms of abundances and biomasses. Corresponding temporal changes were correlated with two climatic indices and a set of environmental parameters integrated over 3 different time periods (i.e., whole year, springtime and wintertime). Our results confirm the occurrence of major temporal changes in the composition of macrobenthic communities within the Gulf of Lions. They also show that: (1) WeMO is a better climatic index than NAO for describing changes in benthic macrofauna composition, (2) winter is a better integration period than spring and the whole year for describing those changes, and (3) Rhône River water flow is likely involved in the control of benthic macrofauna composition in the whole Gulf of Lions.

Keywords: Benthic macrofauna composition, Zoobenthos, Temporal changes, Climatic variability, Mediterranean Sea, Gulf of Lions, Western Mediterranean Oscillation, North Atlantic Oscillation

1 INTRODUCTION

As the impact of human activities on marine ecosystems is increasing, ecological assessment is becoming a central topic for the management of European seas (WFD, 2000/60/EC; MSFD, 2008/56/EC; Vačkář et al., 2012; De Backer et al., 2014). In order to assess to which extent human activities impact natural systems, it is essential to distinguish anthropogenic impacts from natural (e.g. climatic) variability. The North Atlantic Oscillation (NAO) is the major source of interannual variability in the atmospheric circulation in the North Atlantic (Hurell, 1995). NAO indices provide a good summary of general weather patterns influencing marine ecosystems and affecting the abundance, biomass, growth and survival rates of marine organisms (Drinkwater et al., 2003). The NAO largely controls local changes in a large set of meteorological parameters such as water temperature, salinity, winds and storms. Several authors have highlighted the consequences of changes in these parameters and thus of NAO on: (1) zooplankton communities in the Western Mediterranean (Fernández de Puelles et al., 2004) and in the North-Atlantic and the North Sea (Fromentin and Planque, 1996), (2) fisheries in the NW Mediterranean Sea (Lloret et al., 2001) and (3) benthic macrofauna composition in the North Sea (Tunberg and Nelson, 1998; Kröncke et al., 1998, 2001; Hagberg and Tunberg, 2000; Rees et al., 2006). Between 1978 and 1995, Kröncke et al. (1998) sampled seasonally 5 stations located between 12 and 20 m depth off the Island of Nordeney. They showed that the abundance and species richness of benthic macrofauna sampled between April and July was correlated significantly with the NAO index. They suggested that the mediator between NAO and benthic macrofauna was the sea surface temperature in late winter and early spring. This hypothesis was supported by further observations such as the decrease of *Echinocardium cordatum* populations after severe winters (Beukema, 1985).

Lloret et al. (2001) were the first to correlate climatic oscillations with biological parameters in NW Mediterranean. These authors studied the relationship between fish and invertebrate landings, the water flows of the Rhône and Ebre Rivers and the NAO index. They reported: (1) a negative correlation between the water flow of these two rivers and the NAO, and (2) a positive correlation between the landings of 13 species of fishes and invertebrates and water flows. They suggested a link between recruitment and local environmental conditions such as river discharge, wind and global environmental conditions (NAO). Recent papers on NW Mediterranean have focussed on the Western Mediterranean Oscillation index (WeMO index) rather than the classical NAO index as a proxy of local climatic variability (Martin-Vide and Lopez-Bustins, 2006; Martín et al., 2012). These two indices do not correlate when computed on an annual basis or in wintertime (Martin-Vide and Lopez-Bustins, 2006; Martín et al., 2012). The WeMO has shown to be more relevant than the NAO to account for monthly precipitation anomalies (Martin-Vide and Lopez-Bustins, 2006; Martin-Vide et al., 2008). Martín et al. (2012) showed that positive WeMO index values correlated significantly with low Sea Surface Temperature (SST) and high river run-offs, which have a significant positive effect on sardine and anchovy landings per unit effort. Conversely, and based on a 45 year time series, Keller et al. (2014) did not show any influence on the landings of *Sepia officinalis* in the Western Mediterranean, neither by the NAO nor by the WeMO index but only by SST.

Most of benthic macrofauna data available in the Gulf of Lions (e.g. Salen-Picard, 1981; Grémare et al., 1998a, 1998c; Massé, 2000; Labrune et al., 2007a, b, 2008) have been collected over too short time periods to soundly assess their correlation with climatic oscillations other than by achieving long term comparisons (Grémare et al., 1998a; Labrune et al., 2007b). In 1967/68, Guille (1970) first described the benthic macrofauna communities of the soft bottoms of the Catalan French coast. Grémare et al. (1998a) then showed the occurrence of major changes in both sediment granulometry and macrofauna composition between 1967/68 and 1994. These authors suggested that these changes were due to the decrease in fine particles probably caused by an increase in the frequency of the easterly storms. By using a different procedure in assessing resuspension event, Labrune et al. (2007b) suggested that positive NAO index periods were related to low frequency of strong resuspension events and high abundances and biomass of benthic fauna. Their underlying hypothesis was that the low frequency of resuspension events, especially during springtime, contributes to favour a good recruitment of benthic macrofauna. Therefore, they suggested that the positive periods of NAO index would affect indirectly and positively the abundance and biomass of benthic macrofauna as observed for the polychaete *Ditrupa arietina*, one of the most abundant species in sandy stations during 1994 and 2003 to a lower extent.

In this context, the main objective of this study was to assess changes in benthic macrofauna composition and sediment granulometry based on a 2004 to 2013 time series collected in the Bay of Banyuls-sur-Mer, and in relation with changes in both the NAO and WeMO indices and in the main meteorological parameters affecting the NW Mediterranean Sea. In order to do so, the present study focusses on benthic macrofauna composition at 4 stations representative of the main benthic communities described by Guille (1970).

2 MATERIALS AND METHODS

2.1 Study area and sampled stations

The Bay of Banyuls-sur-Mer is located within the Gulf of Lions in the NW Mediterranean Sea (**Figure 1**). Four stations, located in the 4 main benthic communities (Guille, 1970; Labrune et al., 2007b) within this bay, were sampled once a year between 2004 and 2013 (**Table 1**): station 43 is located within the *Spisula subtruncata* community (Ss) and its sediment consists in well-sorted fine sand; station 31 is located in the *Nephtys hombergii* community (Nh) and its sediment consists in muddy sand; station 26 is located in the *Scoloplos armiger* community (Sa) and its sediment consists in sandy mud; and station 183 is located in the *Venus ovata* community (Vo) and its sediment consists in mud. All 4 stations were sampled both for benthic macrofauna and sediment granulometry during the end of autumn/beginning of winter on board of RV *Nereis* II.

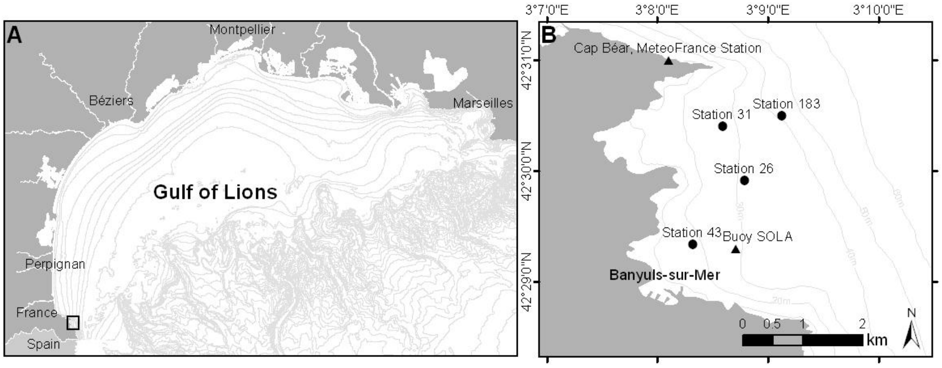

Figure 1. Delimitation of the study area in the Gulf of Lions (A) and location of the 4 sampled stations within the Bay of Banyuls-sur-Mer (B).

Table 1. Location (WGS84, degrees and decimal minutes) and depth of the 4 sampled stations.

Station	Community	Latitude (N)	Longitude (E)	Depth (m)
43	*Spisula subtruncata*	42°29.33’	03°08.32’	15
31	*Nephtys hombergii*	42°30.40’	03°08.59’	26
26	*Scoloplos armiger*	42°29.92’	03°08.79’	31
183	*Venus ovata*	42°30.50’	03°09.11’	43

Granulometry

At each station, a 0.1 m^2 van Veen grab was taken for sediment granulometry. Sediment granulometry analyses were performed on fresh sediment using a Malvern Mastersizer® 2000 laser microgranulometer and expressed as median grain diameter ($D_{0.5}$) and in volume percentages of size grain fractions (<30 µm, 30-63 µm, 63-250 µm, 250-500 µm, 500-2000 µm). Sediment granulometry data are lacking for station 183 during 2005 and 2006.

Benthic macrofauna

At each station, 5 other grabs were collected, immediately sieved on a 1 mm mesh and fixed with 5% formalin buffered in seawater. At the laboratory, macrofauna was sorted, identified to the lowest tractable taxonomic level (most often species) and counted. Biomasses were assessed on each combination of phyla and feeding types by measuring the weight-loss after combustion (450°C, 5h) of dried samples.

2.2 Climatic indices

North Atlantic Oscillation (NAO)

The North Atlantic Oscillation is responsible for changes in the trajectories of surface westerlies across the North Atlantic onto Europe (Hurrell, 1995). Such changes can be described through several indices. During the present study we used the index developed by Hurrell and Deser (2010). Positive values are typically associated with stronger-than-average westerlies and storms over Northern Europe and milder weather with less-than-average storms over Western Europe and the Mediterranean Sea. Corresponding data were provided by the Climate Analysis Section (NCAR, Boulder, USA, https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based).

Western Mediterranean Oscillation (WeMO)

The WeMO is a low-frequency variability pattern of atmospheric circulation that was first described by Martin-Vide and Lopez-Bustins (2006). Its index (WeMO index) corresponds to the difference of standardised surface atmospheric pressures in San Fernando (Spain) and Padua (Italy) (**Figure 2**). The North of the Italy is subjected to relative high barometric variability owing the influence of the central European anticyclone and the Ligurian low pressure area, while South Western Spain is frequently subjected to the influence of the Azores anticyclone. The transect linking these two zones matches with the NW Mediterranean Sea. During the positive phase, the anticyclone over the Azores encloses the South-West of Spain and the low pressures in the Ligurian Gulf result in winds blowing from the NW. During the negative phase, the central European anticyclone located north of Italy and a low-pressure centre, in the Iberian SW, result in winds blowing from the East. In the Bay of Banyuls-sur-Mer, the negative phase is therefore associated with easterlies, which lead to frequent resuspension events. The WeMO index data used during the present study originate from http://www.ub.edu/gc/English/wemo.htm.

Both for NAO and WeMO indices, the winter value for year *n* corresponds to an average from December year *n*-1 to February year *n*. Annual and spring values corresponded to the average of monthly values from January to December and from March to May, respectively.

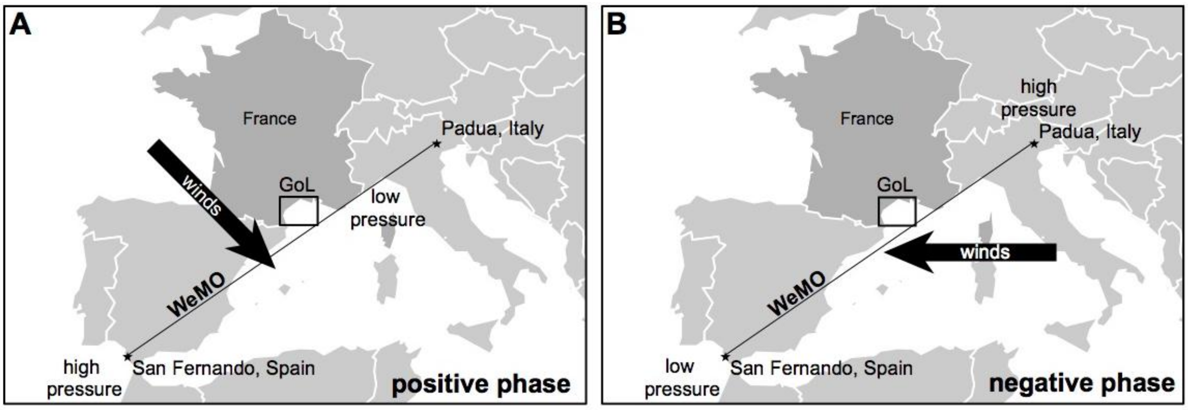

Figure 2. Patterns of WeMO influence over the North-Western Mediterranean Sea during its positive (A) and negative (B) phases (modified from http://www.ub.edu/gc/English/wemo.htm). GoL: Gulf of Lions.

2.3 Environmental parameters

The water flow of the Rhône River was provided by Banque Hydro (http://www.hydro.eaufrance.fr). Air temperature, precipitation, wind speed and Sea-Level Pressure (SLP) were measured daily at Cap Bear station by Meteo France. During the present study, we used the monthly averaged data available at https://donneespubliques.meteofrance.fr. Suspended Particulate Matter concentrations (SPM) were measured weekly 5 m above the bottom of the SOLA (Service d'Observation du Laboratoire Arago, Bay of Banyuls-sur-Mer, 27 m depth) station within the framework of the Service d'Observation en Milieu Littoral (http://somlit.epoc.u-bordeaux1.fr/fr). We used the criteria 2 (C2) proposed by Labrune et al. (2007b) as a proxy for intense resuspension events. Briefly put, such an event was assumed to take place during each day featuring both a wind direction between 90° and 170° and a decrease in SLP higher than 5 hPa between: (1) the day before and the day of measurement or (2) the day of measurement and the day after. For all parameters, seasonal values were computed as described above for NAO and WeMO indices.

2.4 Data analysis

Granulometry

Hierarchical clustering (Euclidean distance, group average linking) was performed on the percentages of size grain fractions (<30 µm, 30-63 µm, 63-250 µm, 250-500 µm, 500-2000 µm). ANOSIM tests were used to assess the significance of internal structures within each sub-cluster (Clarke, 1993).

Benthic macrofauna

Replicated samples were pooled. Synonyms of scientific names of species were updated using the World Register of Marine Species (WoRMS, 2014). Species with possible doubtful identifications were pooled to homogenise species lists and taxonomic resolutions between cruises. Species richness (SR, in taxa.0.5m^{-2}), total abundance (in ind.0.5m^{-2}) and biomass (in mgAFDW.0.5m^{-2}) were used as global descriptors of benthic macrofauna composition. Abundance-based compositions were compared through nMDS and hierarchical clustering (square-root transformed data, Bray-Curtis similarity, group average linking). ANOSIM tests were used to assess the significance of internal structures within each sub-cluster (Clarke, 1993). SIMilarity PERcentages analyses (Clarke et al. 2008) were performed to identify the species contributing most to between sub-clusters dissimilarity.

Relationships linking climatic variability, environmental parameters and benthic macrofauna

Linear correlations were first used to assess the relationships between (annual, Spring and Winter) NAO and WeMO indices, and: (1) main environmental parameters (see above), (2) $D_{0.5}$ and percentage of fines, (3) global descriptors of benthic macrofauna (SR, abundance and biomass), and (4) the abundances of the 5 species contributing most to temporal dissimilarities in benthic macrofauna composition within the 3 main clusters resulting from the hierarchical analysis. The significance of the correlations between the similarity matrices based on NAO and WeMO indices, and the similarity matrices based on: (1) main environmental parameters, (2) sediment granulometry fractions and (3) the abundances of benthic macrofauna were assessed through Mantel tests. A *BEST* procedure (Clarke and Ainsworth, 1993) was performed to identify the subset of variables that best described temporal changes in benthic macrofauna composition at each station. The global set of tested variables included: WeMO index, NAO index, suspended particulate matter (SPM), precipitation, air temperature, wind speed, Sea Level Pressure (SLP), Rhône River water flow, criteria 2 (C2) and sediment granulometry. Some of these parameters were excluded to avoid co-correlation. This procedure was carried out for the whole year, springtime and wintertime. All statistical procedures except linear correlations (done with R language; R Core Team, 2014) were completed using the PRIMER 6® software package.

3 RESULTS

3.1 Temporal changes in climatic indices and environmental parameters

Strong temporal changes in annual, spring and winter values of the NAO index were recorded between 2004 and 2013 (**Figure 3A**). The annual NAO index was between -0.76 (2005) and 1.07 (2011) except in 2010, when it was extremely low (-3.62). In spring the NAO index presented an alternation of phases with a period close to two years. In winter the values of the NAO index were close (although slightly more positive) to the ones of the annual NAO index. Strong temporal changes in annual, spring and winter values of the WeMO index were observed between 2004 and 2013 as well (**Figure 3B**). The annual WeMO index was negative and tended to be constant around -0.09 except in 2011 (-0.92). In spring the WeMO index presented values close to the annual ones except in 2011. In winter, the WeMO index showed a decreasing trend between 2004 and 2008 and an increasing one between 2010 and 2012-2013.

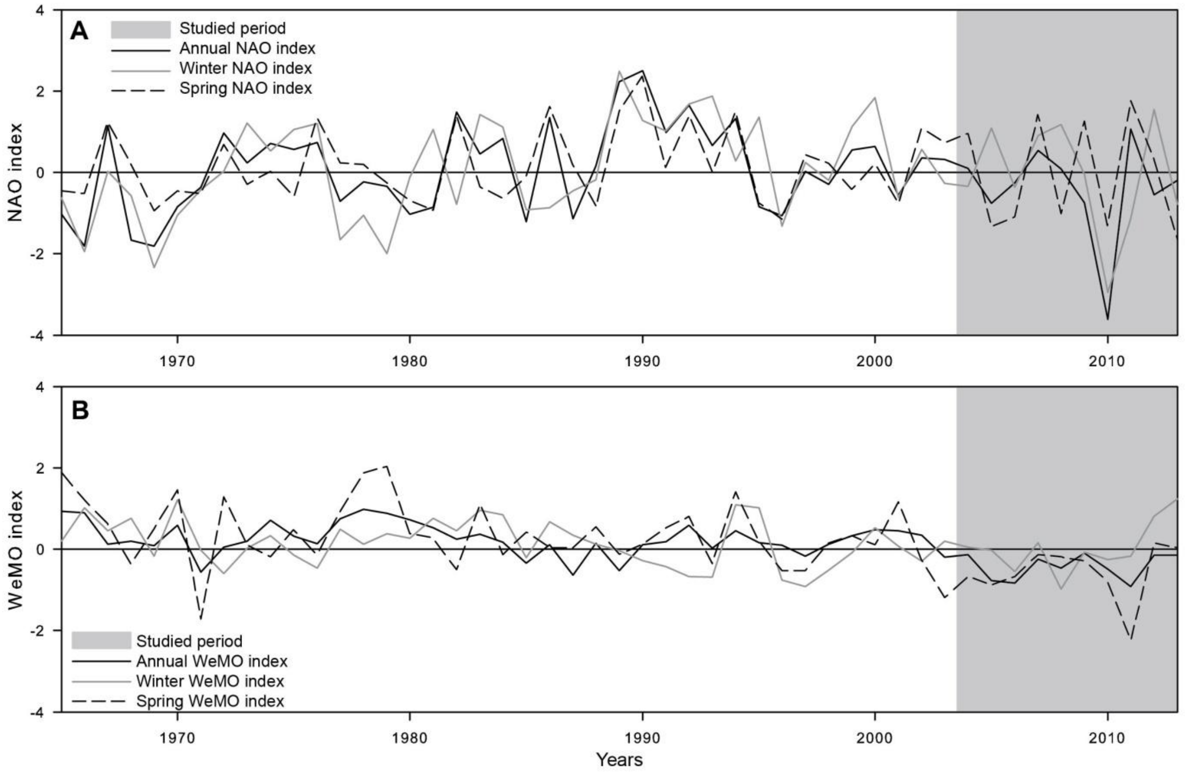

Figure 3. Temporal changes in annual (black line), spring (dash line) and winter (grey line) values of the NAO (A) and WeMO indices (B). The period under study is highlighted.

Temporal changes in the main assessed environmental parameters are not shown but their correlation with the values of both the NAO and the WeMO indices over: (1) an annual period, (2) spring time and (3) wintertime are shown in **Table 2**. Both NAO and WeMO indices tended to correlate better with environmental parameters during wintertime than during springtime and during the whole year. The winter values of the NAO index correlated significantly with precipitation, Rhône River flow, SLP and C2; *versus* precipitation, wind speed, Rhône River Water flow and SPM for the winter values of the WeMO index.

Table 2. Correlation coefficients of the linear regression models linking climatic variables and environmental parameters. *** p<0.001, ** p<0.01, * p<0.05.

	NAO index			WeMO index			
Environmental variables	**Annual**	**Spring**	**Winter**	**Annual**	**Spring**	**Winter**	**N**
Air temperature	0.39 **	0.34 *	0.27	-0.42 **	-0.29 *	0.03	53
SLP	0.61 ***	0.51 ***	0.89 ***	-0.11	-0.07	-0.18	54
Wind speed	-0.08	0.03	0.17	-0.02	0.25	0.38 **	54
Precipitation	-0.10	-0.13	-0.29 *	-0.04	-0.13	-0.35 *	54
Rhône River water flow	-0.37 ***	-0.40 ***	-0.37 ***	0.42 ***	0.51 ***	0.40 ***	94
SPM	0.07	0.19	-0.37	-0.12	-0.28	0.65 *	10
Criteria 2	-0.20	0.08	-0.34 *	0.21	0.00	-0.02	48

3.2 Temporal changes in sediment granulometry

Temporal changes in $D_{0.5}$ were limited at stations 43 and 26, high at station 31, and intermediate at station 183 (**Table 3, Figure 4A**). Sediment at station 43 was composed of well-sorted fine sands with $D_{0.5}$ between 188 (2004) and 223 µm (2011). Sediment at station 31 was composed of muddy sands with $D_{0.5}$ between 102 (2013) and 193 µm (2009). Sediment at station 26 was composed of sandy mud with $D_{0.5}$ between 64 (2012) and 86 µm (2009). Sediment at station 183 was composed of mud with $D_{0.5}$ between 59 µm (2004) and 120 µm (2013). Temporal changes in the percentage of fines were low at station 43, high at station 31 and intermediate at station 26 and 183 (**Table 3, Figure 4B**). At station 43, fines were absent between 2008 and 2012. Otherwise, their proportion was between 0.5 (2006) and 2.2% (2005, 2007). At station 31, the proportion of fines was between 14.1 (2009) and 30.8% (2013). At station 26, a clear decreasing trend in the proportion of fines was observed between 2005 (49.0%) and 2009 (34.8%). This was followed by an increasing trend up to 40.1% in 2012. At station 183, the proportion of fines was between 39.0 (2013) and 55.3% (2012). There was no significant correlation between NAO and WeMO indices and either $D_{0.5}$ or the proportion of fines at any station (data not shown, $p>0.05$ in all cases).

The hierarchical clustering based on sediment granulometry (**Figure 5**) showed the occurrence of significant temporal changes within each community associated to the 4 main clusters (at an 21% dissimilarity level). Cluster I corresponded to station 43 and could be subdivided in 2 sub-clusters: (Ia) years 2004-2007, 2008, 2009, 2010, 2012 and 2013; and (Ib) years 2008, 2009 and 2011. Cluster II corresponded to station 31 and could be subdivided in 2 sub-clusters: (IIa) years 2004, 2005 and 2010-2012, and (IIb) years 2006-2008 and 2013. Cluster III corresponded to station 26 and could be subdivided in 2 sub-clusters: (IIIa) years 2004-2007 and 2012, and (IIb) years 2008 and 2010, 2012 and 2013. Cluster IV corresponded to station 183 and could be subdivided in 2 sub-clusters: (IVa) years 2004, 2007, 2010, 2012 and 2013, and (IVb) years 2008, 2009 and 2011. Three samples did not group with any cluster: stations 31 and 26 in 2009, and station 183 in 2013. ANOSIM test showed significant changes between sub-clusters within each 4 main cluster ($R>0.759$, $p<0.02$). The only significant correlation between climatic indices and sediment granulometry was observed at station 43 during springtime for WeMO (Mantel test, $\rho=0.44$, $p<0.05$).

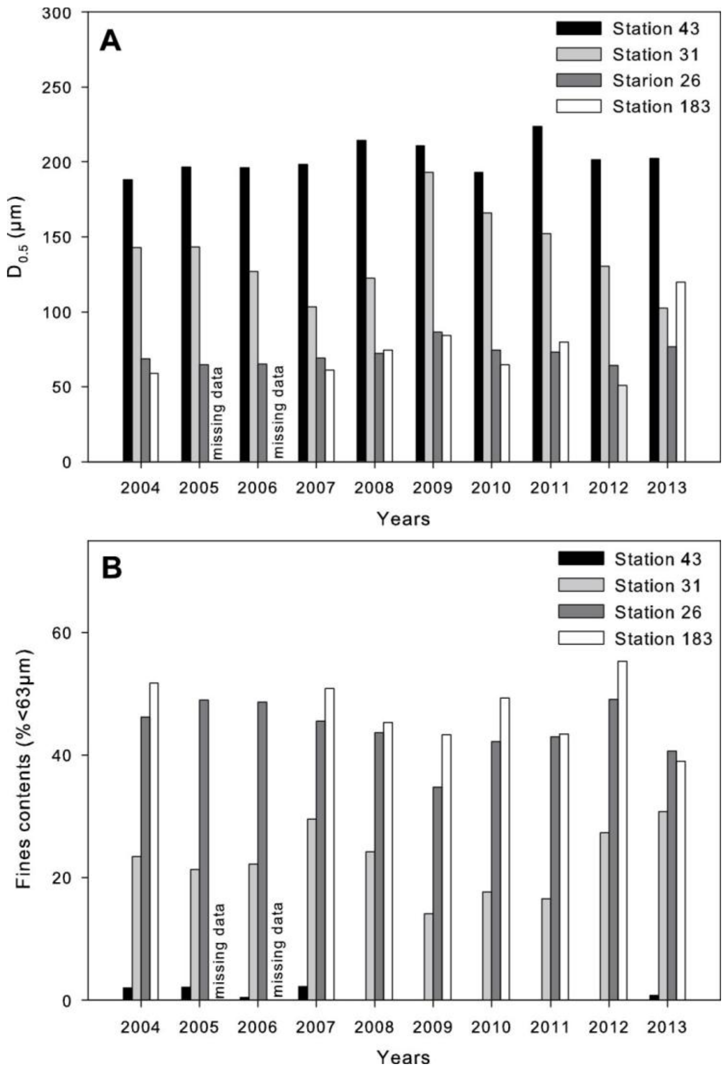

Figure 4. Temporal changes in average $D_{0.5}$ (μm) (A) and fine contents (%<63μm) (B).

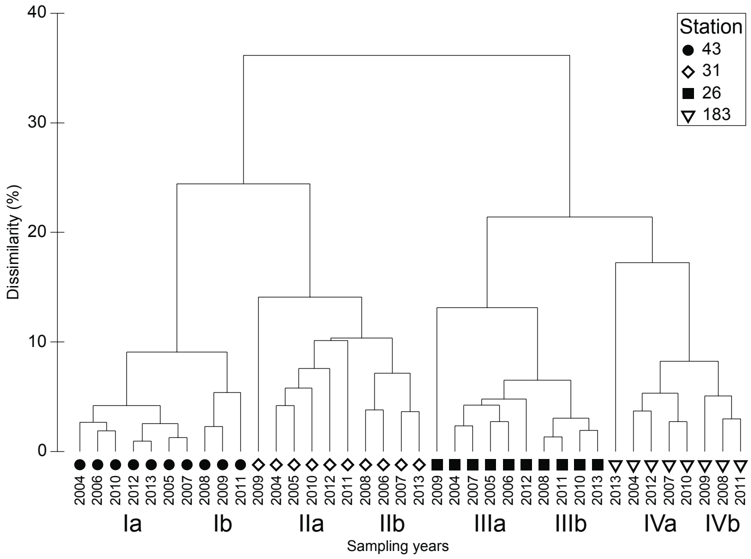

Figure 5. Hierarchical clustering (Euclidean distance and average group method) of normalized size grain fractions (<30 *µ*m, 30-63 *µ*m, 63-250 *µ*m, 250-500 *µ*m, 500-2000 *µ*m).

Table 3. Global descriptors of sediment granulometry ($D_{0.5}$ in *µ*m and proportion of fines) and benthic macrofauna composition (Species richness in taxa.0.5m^{-2}, abundance in ind.m^{-2} and biomass in mgAFDW.0.5m^{-2}

Station	Descriptor	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
43	$D_{0.5}$	188.2	196.5	196.0	198.4	214.4	210.9	193.0	223.6	201.6	202.4
	%<63µm	2.1	2.2	0.5	2.2	0.0	0.0	0.0	0.0	0.0	0.8
	Species richness	38	26	25	58	29	16	32	45	49	43
	Abundance	208	613	113	251	73	41	70	97	141	355
	Biomass	0.42	0.97	0.12	0.49	0.58	0.04	0.04	0.38	0.14	0.54
31	$D_{0.5}$	142.8	143.5	126.8	103.2	122.6	193.0	166.0	152.3	130.6	102.7
	%<63µm	23.4	21.4	22.2	29.5	24.2	14.1	17.7	16.5	27.3	30.8
	Species richness	56	54	30	52	34	46	41	45	64	105
	Abundance	437	222	153	378	132	516	401	529	500	796
	Biomass	0.47	0.37	0.16	0.28	0.18	0.52	0.39	0.44	0.54	2.09
26	$D_{0.5}$	68.6	64.5	64.9	69.3	72.1	86.6	74.4	73.3	64.3	76.7
	%<63µm	46.2	49.0	48.6	45.5	43.7	34.8	42.2	43.0	49.1	40.6
	Species richness	63	66	55	72	48	48	93	71	108	98
	Abundance	512	443	363	396	171	235	509	658	998	837
	Biomass	1.12	3.44	2.14	0.79	0.29	0.36	1.21	0.91	1.03	3.10
183	$D_{0.5}$	59.0	NA	NA	61.1	74.5	84.1	64.6	79.7	51.0	120.0
	%<63µm	51.7	NA	NA	50.8	45.3	43.3	49.3	43.4	55.3	39.0
	Species richness	83	62	53	72	55	54	101	90	110	83
	Abundance	455	425	186	387	275	208	602	576	723	446
	Biomass	1.82	2.70	1.24	5.57	1.79	2.90	2.63	3.98	4.64	2.27

3.3 Temporal changes in benthic macrofauna

Overall, 15431 specimens belonging to 448 taxa were identified during the present study. A main pattern was observed for temporal changes in macrobenthos species richness (SR) and abundance (**Table 3, Figure 6**). It consisted in: (1) a decreasing trend from 2004 to 2008/2009 with a higher value in 2007 at all stations, and (2) an increasing trend from 2010 to 2013 occasionally associated with lower values in 2011 and 2013 at deeper stations (SR at station 26; and both SR and abundance at station 183). Conversely, changes in biomass did not show any clear temporal pattern.

The nMDS (**Figure 7A**) showed that temporal changes in benthic macrofauna composition were most important at station 43. The hierarchical clustering (**Figure 7B**) showed the existence of 3 main clusters at a 32% similarity level: (I) all sampling years of station 43; (II) all sampling years of station 31, except 2013; and (III) all sampling years of stations 26 and 183 and the 2013 sampling of station 31. Cluster I and II could be subdivided in 2 sub-clusters each: (Ia) years 2004, 2005, 2007 and 2013; (Ib) years 2006, 2008 and 2010-2012; (IIa) years 2005, 2006 and 2008; and (IIb) years 2004, 2007 and 2009-2012. Cluster III could be subdivided in 3 sub-clusters: (IIIa) 2005-2009 of stations 26 and 183; (IIIb) years 2010-2013 of stations 26 and 183 plus the year 2013 of station 31; and (IIIc) year 2004 of stations 26 and 183. ANOSIM test showed the occurrence of significant differences between sub-clusters within each main cluster ($R>0.745$, $p<0.018$ in all cases).

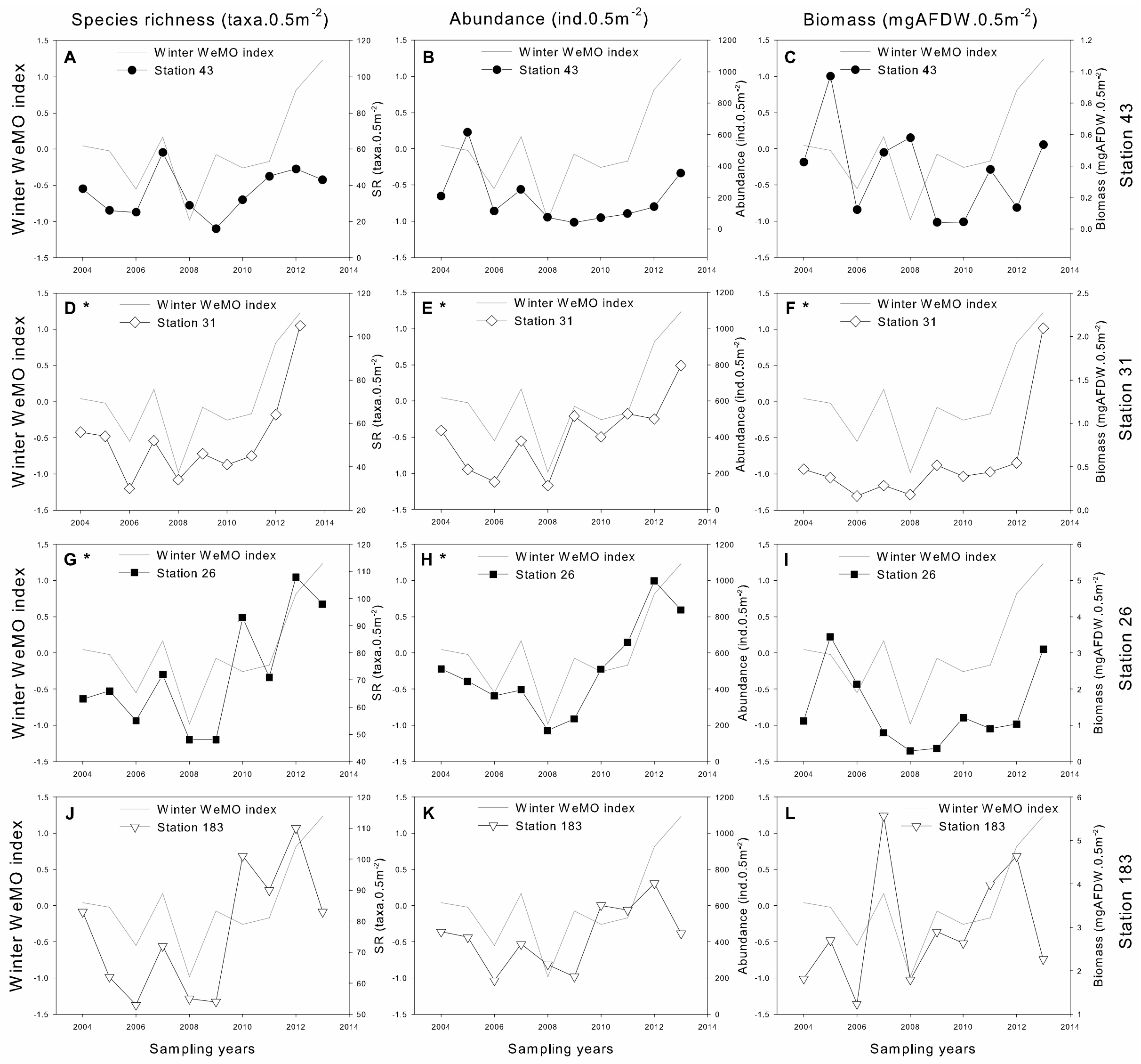

Figure 6. Temporal changes in the winter WeMO index and benthic macrofauna species richness (SR), abundance and biomass for each station. Station 43 (A, B, C), station 31 (D, E, F), station 26 (G, H, I) and station 183 (J, K, L). *: significant (p<0.05) correlation.

The species most responsible for dissimilarity between clusters Ia and Ib were *Ditrupa arietina* (55.6%), *Siphonoecetes neapolitanus* (2.8%) and *Apseudopsis latreillii* (2.4%) (**Table 4**). The species most responsible for dissimilarity between clusters IIa and IIb were *Aspidosiphon muelleri* (28.2%), *D. arietina* (23.9%) and *Owenia fusiformis* (3.7%). The species most responsible for dissimilarity between clusters IIIa and IIIb were *A. muelleri* (15.6%), *Turritella communis* (7.7%) and *Galathowenia oculata* (7.2%). The species most responsible for dissimilarity between clusters IIIa and IIIc were *T. communis* (13.7%), *A. latreillii* (8.2%) and *Lumbrineris* *latreilli* (5.0%). The species most responsible for dissimilarity between clusters IIIb and IIIc were *A. muelleri* (14.2%), *T. communis* (7.2%) and *G. oculata* (6.0%).

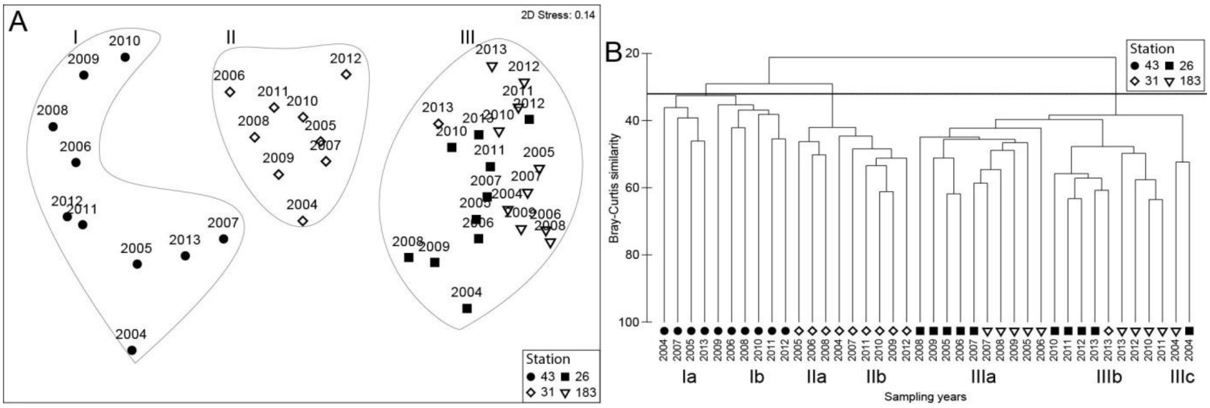

Figure 7. Non-metric Multidimensional Scaling (nMDS) (A) and hierarchical clustering (square-root transformed data, Bray-Curtis similarity and average group method) (B) of macrofauna species abundance data.

Table 4. Abundances, contribution and cumulative contributions to dissimilarities in benthic macrofauna composition of the 5 species most responsible for dissimilarity between the sub-clusters identified in Figure 7B.

Sub-clusters	Species	Av. Abund.	Av. Abund.	Contrib. %	Cumul. %
Ia & Ib		Ia	Ib		
	Ditrupa arietina	243.8	21.8	55.6	55.6
	Siphonoecetes neapolitanus	6.5	8.3	2.9	58.5
	Apseudopsis latreillii	7.3	0.3	2.4	60.9
	Urothoe grimaldii	5.8	1.3	2.1	62.9
	Urothoe intermedia	8.0	6.8	1.7	64.6
IIa & IIb		IIa	IIb		
	Aspidosiphon muelleri	43.0	160.2	28.2	28.2
	Ditrupa arietina	15.3	117.0	23.9	52.1
	Owenia fusiformis	8.0	19.8	3.7	55.8
	Anapagurus breviaculeatus	17.0	7.5	3.2	59.1
	Turritella communis	1.0	11.8	2.9	61.9
IIIa & IIIb		IIIa	IIIb		
	Aspidosiphon muelleri	29.2	119.6	15.6	15.6
	Turritella communis	10.0	62.7	7.7	23.4
	Galathowenia oculata	4.2	53.1	7.2	30.5
	Nephtys kersivalensis	27.5	50.6	6.0	36.5
	Apseudopsis latreillii	35.9	15.4	5.4	41.9
IIIa & IIIc		IIIa	IIIc		
	Turritella communis	10.0	80.5	13.7	13.7
	Apseudopsis latreillii	35.9	43.5	8.2	21.9
	Lumbrineris latreilli	29.2	18.5	5.0	26.9
	Aspidosiphon muelleri	29.2	11.5	4.5	31.4
	Nephtys kersivalensis	27.5	27.0	4.0	35.4

IIIb & IIIc		IIIb	IIIc		
	Aspidosiphon muelleri	119.5	11.5	14.1	14.1
	Turritella communis	62.7	80.5	7.2	21.4
	Galathowenia oculata	53.1	3.0	6.0	27.4
	Apseudopsis latreillii	15.4	43.5	4.9	32.3
	Nephtys kersivalensis	50.6	27.0	4.6	36.9

3.4 Relationship between climatic indices, environmental parameters, sediment granulometry and benthic macrofauna

Neither the annual nor the winter values of the NAO index correlated significantly with any global descriptor of benthic macrofauna at any station (**Table 5**). Conversely, the spring values of the NAO index correlated significantly with benthic macrofauna biomass at station 26. Neither the annual nor the spring values of the WeMO index correlated significantly with any global descriptor of benthic macrofauna at any station (**Table 5**). Conversely, the winter values of the WeMO correlated significantly with benthic macrofauna SR and abundance at stations 31 and 26 and with benthic macrofauna biomass at station 31 (**Table 5**). Moreover, the general pattern of temporal changes in SR and abundances observed at all stations matched well with the consecutive decreasing and increasing trends recorded for the winter values of WeMO (see above). The peaks in SR and abundances observed at all 4 stations in 2007 seemed linked to high winter WeMO values, whereas the low SR and abundances recorded in 2008 tended to be associated with strongly negative values of the WeMO index (**Table 3, Figure 6**). The only significant correlations between similarity matrices based on climatic indices and (1) benthic macrofauna species abundances and (2) biomass groups were observed at station 31 for WeMO values during wintertime (Mantel tests, $\rho=0.47$ and $\rho=0.61$, respectively, $p<0.01$ in both cases).

There was no significant correlation between NAO index values and the abundances of species contributing most to dissimilarities between sub-clusters at all 4 sampled stations. The only significant ($p<0.05$ in all cases) correlations between WEMO values and the abundances of these species were recorded for wintertime WeMO and with: (1) *Turritella communis* (station 31 and 26), (2) *Aspidosiphon muelleri* (station 26 and 183) (**Figure 8**).

Table 5. Correlation coefficients of the linear regression models linking climatic variables and global descriptors of benthic macrofauna. *** p<0.001, ** p<0.01, * p<0.05.

Station	Benthic macrofauna	NAO index			WeMO index		
		Annual	Spring	Winter	Annual	Spring	Winter
43	Species richness	0.37	0.35	0.14	0.21	0.06	0.51
	Abundance	0.10	-0.35	0.31	-0.11	0.06	0.38
	Biomass	0.37	-0.24	0.43	-0.23	-0.07	0.04
31	Species richness	0.11	-0.18	0.02	0.50	0.37	0.92 ***
	Abundance	0.05	0.22	-0.31	0.51	0.08	0.82 **
	Biomass	0.04	-0.30	-0.19	0.40	0.29	0.79 **
26	Species richness	-0.32	-0.19	-0.19	0.26	0.21	0.76 *
	Abundance	0.02	-0.01	-0.06	0.19	0.05	0.82 **
	Biomass	-0.10	-0.63 *	-0.04	-0.28	0.00	0.41
183	Species richness	-0.28	0.12	-0.32	0.21	-0.08	0.54
	Abundance	-0.22	0.10	-0.17	0.07	-0.16	0.49
	Biomass	0.22	0.59	0.28	0.19	0.03	0.37

Neither $D_{0.5}$ nor the proportion of fines correlated with any global descriptor of benthic macrofauna at stations 31, 26 and 183. The only significant correlations were reported between the proportion of fines and both benthic macrofauna abundance and biomass at station 43 (r=0.73 and r=0.64, respectively, p<0.05 in both cases). The only significant correlation between sediment granulometric composition and benthic macrofauna composition was observed at station 183 for biomass (Mantel test, ρ=0.64, p<0.05).

When computed on an annual basis, no set of variables could account for temporal changes in benthic macrofauna abundance and biomass at any station (**Figure 9**). This was also the case for benthic macrofauna abundance with springtime climatic indices, environmental and granulometrical parameters except for macrofauna biomass at station 26, which correlated with the combination of air temperature, precipitation, wind speed and SPM. When computed during winter, subsets of climatic indices, environmental and granulometrical parameters correlated significantly with changes in benthic macrofauna abundance at stations 31, 26 and 183 and with biomass at station 31 (**Figure 9**). The corresponding sets of contributing variables included: (1) WeMO index, precipitation, and Rhône River water flow (abundance, station 31), (2) WeMO index, precipitation, and C2 (abundance station 26), (3) precipitation and Rhône River water flow (abundance, station 183), and (4) WeMO index, precipitation, wind speed, Rhône River water flow and SPM (biomass, station 31).

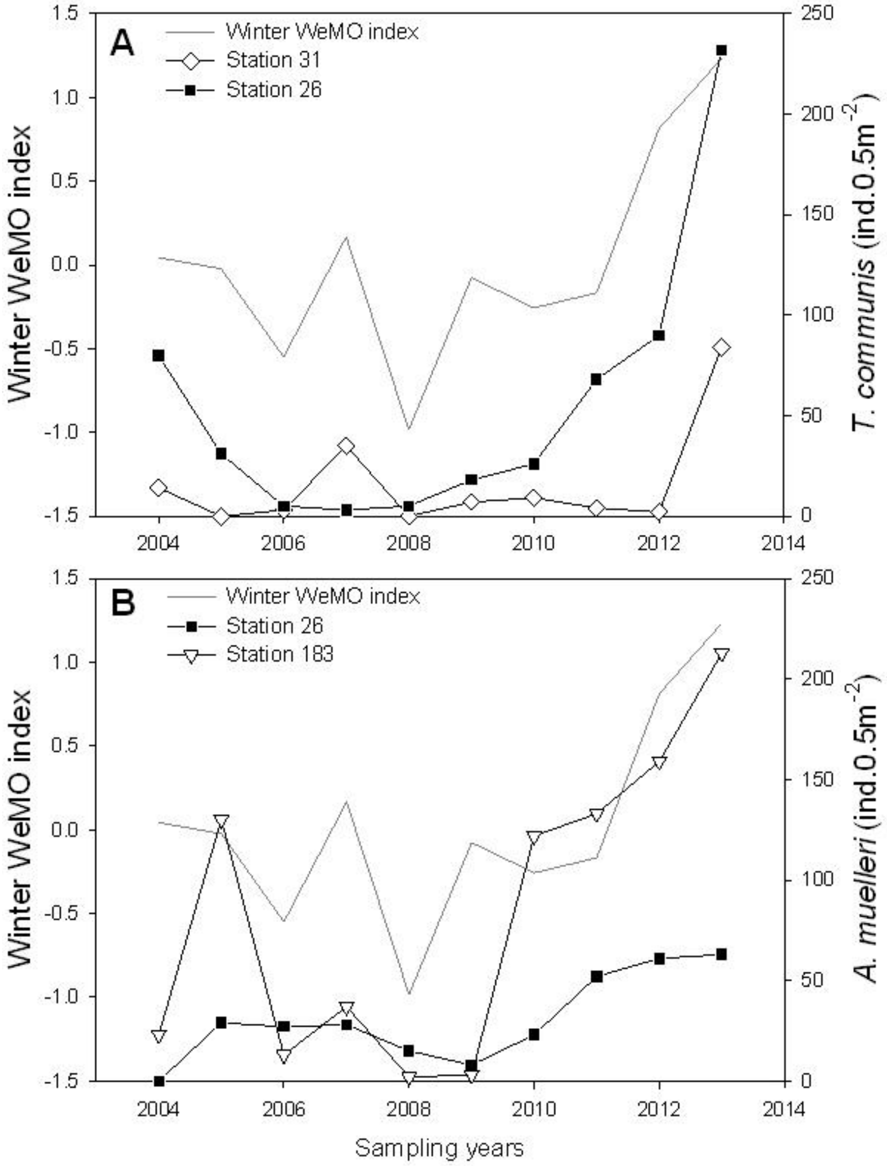

Figure 8. Temporal changes in winter WeMO index and the abundance of *Turritella communis* (A) and *Aspidosiphon muelleri* (B).

Abundance	**Annual**				**Spring**				**Winter**			
Station	**43**	**31**	**26**	**183**	**43**	**31**	**26**	**183**	**43**	**31**	**26**	**183**
NAO index					x	x			x	x	x	x
WeMO index		■								■	■	
Air temperature												
SLP							x	x				
Wind speed					x	x	■					
Precipitation								■	■	■	■	■
Rhône River water flow		■	■			■	x	x		■		■
SPM		■			■		■	■				
C2						■					■	
$D_{0.5}$				■			■					
Fines contents (%<63µm)	■	x	x	x	■	x	x	x	■	x	x	x
ρ	0.39	0.37	-0.04	0.20	0.48	0.35	0.43	0.34	0.54	0.68 **	0.66 *	0.56 *

Biomass	**Annual**				**Spring**				**Winter**			
Station	**43**	**31**	**26**	**183**	**43**	**31**	**26**	**183**	**43**	**31**	**26**	**183**
NAO index	■				x	x		■			x	x
WeMO index			■							■		
Air temperature	■						■					
SLP						■	x	x	x	x	■	
Wind speed					x	x	■		■	■		
Precipitation							■			■		■
Rhône River water flow		■				■	x	x		■	■	
SPM	■		■		■	■	■	■		■		
C2					■				■			
$D_{0.5}$				■								
Fines contents (%<63µm)		x	x	x		x	x	x	■	x	x	x
ρ	0.50	0.50	0.23	0.27	0.27	0.38	0.60 *	0.28	0.30	0.74 **	0.33	0.32

Figure 9. Results from the *Best* procedure used to link benthic macrofauna abundance and biomass composition with climatic indices (computed over different time scales), environmental and granulometric parameters. ***: p<0.001, **: p<0.01, *: p<0.05. x: parameter not included due to co-correlation. Black cells correspond to the parameters retained in the final model. Cells with an X correspond to the parameters, which were not included in the model due to co-correlation.

4 Discussion

Based on: (1) the initial observation of the boom of populations of the serpulid polychaete *Ditrupa arietina* in the Bay of Banyuls-sur-Mer, (2) long term comparisons of benthic fauna composition in the same bay and later at the scale of the whole Gulf of Lions, and (3) data compilation regarding the dynamics of the indicator species *D. arietina* along the Spanish and French Catalan Coast, Grémare et al. (1998a, c) and then Labrune et al. (2007b) showed the occurrence of major temporal changes in the composition of benthic macrofauna composition in the Gulf of Lions. Based on a detailed study of the population dynamics of *D. arietina* and the morphological characteristics of its early benthic stages (i.e., positive buoyancy before tube calcification, Medernach et al., 2000), Labrune et al. (2007b) proposed that the abundance of this species and thus the composition of shallow communities could be regulated by the occurrence of resuspension events occurring during its recruitment period (e.g. springtime). Bonifácio et al. (**Chapter II**) further tested this hypothesis by carrying a long term comparison of benthic macrofauna composition in the whole Gulf of Lions between 1998 and 2010 (two years characterized by an annual NAO index of -0.29 and -3.62, respectively). They also compiled annual NAO and *D. arietina* abundance data at the scale of the whole Gulf of Lions between 1965 and 2013. Overall, their results reinforced the hypothesis put forward by Labrune et al. (2007b) and the postulated role of NAO in controlling benthic macrofauna composition in the Gulf of Lions.

However, all these studies were either based on long term comparison data (Grémare et al., 1998a; Labrune et al., 2007b) or on indicator species (Grémare et al. 1998c; Medernach et al., 2000), which clearly complicates ecological interpretations and reduces the strength of derived conclusions (Pearson et al., 1985; Rosenberg et al., 1987; Grémare et al., 1998a) as compared to studies based on long time series and/or the analysis of whole community composition (Kröncke et al., 1998, 2001). Within this context, the present work consisted in the acquisition and analysis of long time series collected within the Bay of Banyuls-sur-Mer at 4 stations, which may be considered as representative of the main benthic communities described by Guille (1970).

4.1 Temporal changes in benthic macrofauna composition and potential indicator species

Our results first confirm the occurrence of major temporal (i.e., interannual) changes in the composition of benthic macrofauna at the 4 studied stations. They also tend to support the fact that recent changes were highest at station 43. In this sense they support previous observations by Labrune et al. (2007b). Conversely they do not support the fact that these changes tend to be higher at station 31 than at stations 26 and 183 (Labrune et al., 2007b; **Figure 14 in Chapter I**). Furthermore, the acquisition of our 10 years time series allowed for the identification of the species most responsible for interannual differences in benthic macrofauna composition at each station. Although its maximal abundances at station 43 during the present time series (1110 ind.m^{-2} in 2005) was about 3 times lower than in 1994 (Labrune et al., 2007b), *Ditrupa arietina* was identified as such at both sandy stations, which confirmed its interest as an indicator of temporal changes in benthic macrofauna composition occurring within sandy communities (Grémare et al., 1998c; Labrune et al., 2007b). Another potential indicator species at station 31, which was to a lesser extent already identified by Labrune et al. (2007b, Table 2) is the sipunculid *Aspidosiphon muelleri*. Our data also lead to the identification of *A. muelleri* and *Turritella communis* as potential indicator species at stations 26 and 183. Here again, this is in partial agreement with the results of Labrune et al. (2007b) who identified *T. communis* and *A. muelleri* as two of the species contributing most to dissimilarities in the 1967/68/1994/2003 benthic macrofauna composition of stations 26 and 183, respectively. Ferrero-Vincente et al. (2013) showed that shelter availability can be a limiting factor of the distribution of this sipunculid. These animals are observed inhabiting empty tubes of *D. arietina* and gastropod shells (Ferrerro-Vincente et al., 2014). During the present study, *A. muelleri* was found both in *D. arietina* tubes and *T. communis* shells. It contributed to more than 10% of total abundance at stations 31 and 183 . The smallest individuals were observed at station 31 (Bonifácio, personal observation) probably because of the presence of tubes of *D. arietina* favoured juveniles (Ferrerro-Vincente et al., 2014), whereas larger individuals found at station 183 tended to inhabit the shells of *T. communis*. It is therefore likely that the information provided by these three species would prove largely redundant since *A. muelleri* tend to occupy the empty tubes of *D. arietina* and *T. communis* (Ferrero-Vicente et al., 2013, 2014).

4.2 NAO and WeMO indices, integration periods

Two of the major results from the present study were the lack of: (1) apparent cyclicality in the composition of benthic macrofauna (a period of 8-9 years would be expected in the case of a tight control by the NAO), and (2) correlation between annual NAO and either the global characteristics or the composition of benthic macrofauna at all 4 sampled stations. These results are both in clear disagreement with the postulated role of NAO in controlling changes in benthic macrofauna composition in the coastal zone of the Gulf of Lions (Labrune et al., 2007b; Bonifácio et al., **Chapter II**).

Regarding the first point, WeMO and NAO indices can both be seen as proxies for changes in environmental parameters (Ottersen et al., 2001; Drinkwater et al., 2009). However, NAO is explicitly referring to the North Atlantic whereas WeMO has been specifically designed for Western Mediterranean (Martin-Vide and Lopez-Bustin, 2006). It is therefore not surprising that these authors showed a better correlation of the WeMO index than of the NAO index with precipitations on the eastern coastline of the Iberian Peninsula. Along the same line, Martín et al. (2012) also showed a much better correlation between the WeMO than the NAO with the water flow of the Rhône River. Our results are fully consistent with these data since we also observed better correlations: (1) between the WeMO than the NAO and the water flow of the Rhône River (as computed for the “considered integration periods”), and (2) between the winter WeMO than the winter NAO and precipitation. Furthermore, SPM only correlated with winter WeMO, which tends to support the use of WeMO rather than NAO as a climatic index in the NW Mediterranean.

Regarding the most appropriate integration period, it has first been suggested that NAO has a stronger control on the climate of the Northern Hemisphere during wintertime. During this season the magnitude and spatial coherence of atmospheric circulation variability as well as the influence of circulation changes and large-scale precipitation is stronger (Osborn et al., 1999; Osborn, 2006). Our own results suggest that such a reinforcement of climatic forcing influences the WeMO in the same way as indicated by the fact that the number of environmental parameters, which correlate significantly with WeMO was highest during wintertime. There are also good ecological rationales to believe that seasonal integration periods are more appropriate than annual ones to correlate climatic indices and/or environmental parameters with biological data. The negative effects of severe winter temperature on benthic macrofauna communities has been for example underlined in: the zone off the Island of Nordeney (Kröncke et al., 1998, 2001), in the German Bight (Neumann et al., 2008) and in the Wadden Sea (Beukema et al., 2000). During the present study, we found much better correlation between wintertime than annual and springtime WeMO and global benthic macrofauna descriptors at stations 31 (all 3 descriptors) and stations 26 (SR and abundance). We also found significant positive correlations between wintertime WeMO and the abundances of *Turritella communis* at stations 31 and 26 and *Aspidosiphon muelleri* at stations 26 and 183 (two species which accounted most for temporal changes in benthic macrofauna composition within cluster III, **Figure 7**). Moreover, it was not possible to define any subset of climatic indices, environmental and granulometrical data integrated over a full year or over springtime significantly accounting for temporal changes in benthic macrofauna abundance at any station, whereas such subsets could be identified at stations 31, 26 and 183 when climatic indices, environmental and granulometrical parameters were integrated over wintertime. Overall, this supports the idea that wintertime may constitute a key period in controlling benthic macrofauna composition in the Gulf of Lions as well. It should nevertheless be pointed out that our sampling took place during this season as well, which may partly account for this result although the integration period of both climatic indices and environmental parameters corresponded to the winter before sampling.

4.3 Key environmental parameters involved

In the North Sea, the key environmental parameter controlling benthic macrofauna composition is wintertime temperature. Some of our results suggest that this is not the case in NW Mediterranean. First, two of the potential indicator species identified during the present study (i.e., *Ditrupa arietina* and *Turritella communis*) are both suspension-feeders. *T. communis* can remain buried in mud filtering for long period unless disturbed (Yonge, 1946). This author reported that it is very sensitive to SPM and that it stops its inhalant current as soon as fines enter in its mantle cavity. Thus, the negative phase of wintertime WeMO index, related with a high frequency of resuspension events, may have a strong impact on the population dynamics of this particular species. The environmental parameters identified as potentially contributing to control temporal changes in benthic macrofauna composition (based on abundances at stations 31, 26 and 183 and biomasses at station 31) were: winter WeMO, winter precipitation, winter Rhône River water flow, winter C2, winter SPM and winter wind speed. Interestingly, most of these parameters are linked with hydrosedimentary processes. SPM, C2 and wind speed are all directly or indirectly related to sediment resuspension within the Bay of Banyuls-sur-Mer (Grémare et al., 1998b, 2003; Ferré et al., 2005; Labrune et al., 2007b), whereas the Rhône River is the main source of continental particles for the Gulf of Lions (Durrieu de Madron et al., 2000). The impact of the Rhône River on benthic macrofauna composition has already been described in the immediate vicinity of the Rhône River mouth (Salen-Picard et al., 2002, 2003; Darnaude et al., 2004; Bonifácio et al., 2014). Interestingly, Labrune et al. (2007a) also pinpointed that the composition of the Littoral Sandy Mud community slightly differed in the NE and SW part of the Gulf of Lions and attributed this to the proximity of the Rhône River. Since then, and based on the re sampling of the same stations in 2010, Bonifácio et al. (**Chapter II**) showed that the explicit modelling of the proximity of the Rhône River significantly increased the proportion of the variance of the composition of benthic macrofauna at the 5 sampled depths (i.e., 10, 20, 30, 40 and 50 m). Our own data support these results and suggest that temporal changes in Rhône River water flow may influence benthic macrofauna composition over the whole Gulf of Lions.

5 CONCLUSIONS

Overall, our results confirm the occurrence of major temporal changes in the composition of macrobenthic communities within the Gulf of Lions. They also support the use of several indicator species (i.e., *Ditrupa arietina*, *Turritella communis* and to a lesser extent *Aspidosiphon muelleri*) as proxies for those changes. Our results are also in partial agreement with the current paradigm according to which changes in benthic macrofauna composition were determined by climatic drivers through environmental (hydro sedimentary) processes. Nevertheless, and because it is the first one involving the acquisition of long term time series, our study allowed to refine this paradigm by showing that: (1) WeMO is a better climatic index than NAO for describing changes in the global descriptors of benthic macrofauna at Banyuls-sur-Mer, (2) Winter is a better integration period than spring and the whole year for describing those changes, and (3) Rhône River water flow is probably involved in the control of benthic macrofauna composition in the whole Gulf of Lions.

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REFERENCES

Beukema, J.J., 1985. Growth and dynamics in populations of *Echinocardium cordatum* living in the North Sea off the Dutch North coast. Netherlands Journal of Sea Research 19, 129–134.

Beukema, J.J., Essink, K., Dekker, R., 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. Journal of Animal Ecology 69, 31–44.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 171–143.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Darnaude, A.M., Salen-Picard, C., Polunin, N.V., Harmelin-Vivien, M.L., 2004. Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). Oecologia 138, 325–332.

De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J., Hostens, K., 2014. Similar diversity-disturbance responses to different physical impacts: three cases of small-scale biodiversity increase in the Belgian part of the North Sea. Marine pollution bulletin 84, 251–262.

Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., Ottersen, G., Pershing, A. J., Walker, H., 2003. The Response of Marine Ecosystems to Climate Variability Associated with the North Atlantic Oscillation, in The North Atlantic Oscillation: Climatic Significance and Environmental Impact (eds J. W. Hurrell, Y. Kushnir, G. Ottersen and M. Visbeck), American Geophysical Union, Washington, D. C, 279 pp.

Durrieu de Madron, X., Abassi, A., Heussner, S., Monaco, A., Aloisi, J.C., Radakovitch, O., Giresse, P., Buscail, R., Kerherve, P., 2000. Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanologica Acta 23, 717–730.

Fernandez de Puelles, M., Valencia, J., Vicente, L., 2004. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). ICES Journal of Marine Science 61, 492–500.

Ferré, B., Guizien, K., Durrieu de Madron, X., Palanques, A., Guillén, J., Grémare, A., 2005. Fine-grained sediment dynamics during a strong storm event in the inner-shelf of the Gulf of Lion (NW Mediterranean). Continental Shelf Research 25, 2410–2427.

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, Á., Sánchez-Lizaso, J.L., 2013. Limiting factors on the distribution of shell/tube-dwelling sipunculans. Journal of Experimental Marine Biology and Ecology 446, 345–354.

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, A., Sánchez-Lizaso, J.L., 2014. Observations on the ecology and reproductive biology of the sipunculan worm *Aspidosiphon muelleri* in temperate waters. Journal of the Marine Biological Association of the United Kingdom 94, 1629–1638.

Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134, 111–118.

Grémare, A., Amouroux, J.-M., Cauwet, G., Charles, F., Courties, C., De Bovée, F., Dinet, A., Devenon, J.L., De Madron, X.D., Ferre, B., Fraunie, P., Joux, F., Lantoine, F., Lebaron, P., Naudin, J.-J., Palanques, A., Pujo-Pay, M., Zudaire, L., 2003. The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. Oceanologica Acta 26, 407–419.

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., Amouroux, J.M., Charles, F., Medernach, L., Jordana, E., Nozais, C., Vêtions, G., Colomines, J.C., 1998b. Temporal changes in the biochemical composition of particulate organic matter sedimentation in the Bay of Banyuls-sur-Mer. Oceanologica Acta 21, 783–792.

Grémare, A., Sardá, R., Medernach, L., Jordana, E., Pinedo, S., Amouroux, J.M., Martin, D., Nozais, C., Charles, F., 1998c. 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.

Guille, A., 1970. Bionomie benthique du plateau continental de la côte catalane française. II - Les communautés de la macrofaune. Vie et Milieu 21, 149–280.

Hagberg, J., Tunberg, B.G., 2000. Studies on the Covariation between Physical Factors and the Long-Term Variation of the Marine Soft Bottom Macrofauna in Western Sweden. Estuarine, Coastal and Shelf Science 50, 373–385.

Hurrell, J.W., 1995. Decadal trends in the north atlantic oscillation: regional temperatures and precipitation. Science 269, 676–679.

Hurrell, J.W., Deser, C., 2010. North Atlantic climate variability: The role of the North Atlantic Oscillation. Journal of Marine Systems 79, 231–244.

Keller, S., Valls, M., Hidalgo, M., Quetglas, A., 2014. Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean. Estuarine, Coastal and Shelf Science 145, 31–40.

Kröncke, I., Dippner, J.W., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communites off Nordeney (East Frisia, Germany) in relation to climate variability. Marine Ecology Progress Series 167, 25–36.

Kröncke, I., Zeiss, B., Rensing, C., 2001. Long-term variability in macrofauna species composition off the Island of Nordeney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Senckenbergiana Maritima 31, 65–82.

Labrune, C., Grémare, A., Amouroux, J.-M., Sardá, R., Gil, J., Taboada, S., 2007a. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuarine, Coastal and Shelf Science 71, 133–147.

Labrune, C., Grémare, A., Guizien, K., Amouroux, J.M., 2007b. Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): A reappraisal. Journal of Sea Research 58, 125–143.

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.

Lloret, J., Lleonart, J., Sole, I., Fromentin, J.M., 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fisheries Oceanography 10, 33–50.

Martin-Vide, J., Lopez-Bustins, J.-A., 2006. The Western Mediterranean Oscillation and rainfall in the Iberian Peninsula. International Journal of Climatology 26, 1455–1475.

Martin-Vide, J., Sanchez-Lorenzo, A., Lopez-Bustins, J.-A., Cordobilla, M.J., Garcia-Manuel, A., Raso, J.M., 2008. Torrential rainfall in northeast of the Iberian Peninsula synoptic patterns and WeMO influence. Advances in Sciences and Research 2, 99–105.

Martín, P., Sabatés, A., Lloret, J., Martin-Vide, J., 2011. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. Climatic Change 110, 925–939.

Massé, H.L., 2000. Long-term changes in sand-bottom macrofauna along the coast of Provence (northwest Mediterranean Sea). Oceanologica Acta 23, 229–242.

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.

MSFD, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union L164: 19–40.

Neumann, H., Ehrich, S., Kröncke, I., 2008. Effects of cold winters and climate on the temporal variability of an epibenthic community in the German Bight. Climate Research 37, 241–251.

Pearson, T.H., Josefson, A.B., Rosenberg, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic?. Journal of Experimental Marine Biology and Ecology 92, 157–206.

Osborn, T.J., 2006. Recent variations in the winter North Atlantic Oscillation. Weather 61, 353–355.

Osborn, T.J., Conway, D., Hulme, M., Gregory, J.M., Jones, P., 1999. Air flow influences on local climate: observed and simulated mean relatioships for the United Kingdom. Climate Research 13, 173–191.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P., Stenseth, N., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128, 1–14.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rees, H.L., Pendle, M.A., Limpenny, C.E., Mason, C.E., Boyd, S.E., Birchenough, S., Vivian, C.M.G., 2006. Benthic responses to organic enrichment and climatic events in the western North Sea. Journal of the Marine Biological Association of the United Kingdom 86, 1–18.

Rosenberg, R., Gray., J.S., Josefson, A.B., Pearson, T.H., 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched?. Journal of Experimental Marine Biology and Ecology 105, 219–251.

Salen-Picard, C., 1981. Évolution d'un peuplement de Vase Terrigène Côtière soumis à des rejets de dragages dans le golfe de Fos. Tethys 10, 83–88.

Salen-Picard, C., Arlhac, D., Alliot, E., 2003. Responses of a Mediterranean soft bottom community to short-term (1993–1996) hydrological changes in the Rhone river. Marine environmental research 55, 409–427.

Salen-Picard, C., Darnaude, A., Arlhac, D., Harmelin-Vivien, M., 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. Oecologia 133, 380–388.

Tunberg, B.G., Nelson, W.G., 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Marine Ecology Progress Series 170, 85–94.

Vačkář, D., ten Brink, B., Loh, J., Baillie, J.E.M., Reyers, B., 2012. Review of multispecies indices for monitoring human impacts on biodiversity. Ecological Indicators 17, 58–67.

WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Union L327, 1–73.

WoRMS Editorial Board, 2014. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2014-04-10.

Yonge, C.M., 1946. On the habits of *Turritella communis* Risso. Journal of the Marine Biological Association of the UK 26, 377–380.

CHAPITRE IV

CHANGEMENTS SPATIO-TEMPORELS DES CARACTÉRISTIQUES DU SÉDIMENT DE SURFACE ET DE LA COMPOSITION DE LA MACROFAUNE BENTHIQUE AU LARGE DU RHÔNE, EN RELATION AVEC SON RÉGIME HYDROLOGIQUE

SPATIOTEMPORAL CHANGES IN SURFACE SEDIMENT CHARACTERISTICS AND BENTHIC MACROFAUNA COMPOSITION OFF THE RHÔNE RIVER IN RELATION WITH ITS HYDROLOGICAL REGIME

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Abstract

The consequences of changes in the water flow of the Rhône River on surface sediment characteristics and benthic macrofauna composition were assessed within 3 distinct areas: (1) the delta front, (2) the prodelta, and (3) the distal zone. Five stations were sampled during or closely after: (1) an oceanic flood (April 2007), (2) a generalized flood (May 2008), (3) a Cevenol flood (December 2008), and (4) a dry period (July 2011). Measurements of sediment characteristics included granulometry ($D_{0.5}$), bulk descriptors of sedimentary organics (OC, TN and THAA), descriptors of labile components of sedimentary organics (chloropigments, EHAA), and both descriptors of origin (Chl-*b*/Chl-*a*, C/N) and lability (Chl-*a*/(Chl-*a*+Phaeo-*a*), EHAA/THAA) of sedimentary organics. Sediment Profile Images were collected during April 2007, May 2008 and July 2011. Temporal changes in both sedimentary organics and benthic macrofauna were more important in the delta front and the prodelta than in the distal zone. Bulk characteristics of sedimentary organics presented decreasing inshore/offshore gradients during both April 2007 and July 2011 but not during May and December 2008. There were significant temporal changes in EHAA/THAA at all stations. Changes in benthic macrofauna composition differed between: (1) the delta front and the prodelta, and (2) the distal zone. In the former area, the dry period was associated with the establishment of a mature community characterized by high abundances and species richness. The best description of spatiotemporal changes in benthic macrofauna composition by surface sediment characteristics was obtained using $D_{0.5}$, Chl-*b*/Chl-*a*, Chl-*a*/(Chl-*a*+Phaeo-*a*) and EHAA, which supports the role of the quality of sedimentary organics in controlling benthic macrofauna composition.

Keywords: Mediterranean Sea, Rhône River, Floods, Temporal variations, Particulate organic matter, Zoobenthos

1 INTRODUCTION

River-dominated Ocean Margins (RiOMar) are land-ocean margin systems that are impacted by major rivers water, nutrient and particle discharges (McKee et al., 2004). As such they include large marine areas. RiOMar provide essential ecosystem services, such as habitat for many plant and animal species, nutrient recycling and fisheries (Levin et al., 2001) and are sensitive to a large diversity of natural and anthropogenic disturbances. On continental margins, in front of each river as well as lagoon mouths appears a preferential area of sediment accumulation under the wave storm base (Aloïsi and Monaco, 1975). These deposition areas, commonly named prodeltas, are the subaqueous extension of aerial deltas in the inner-shelf around 30 m water depth (Bourrin et al., 2006). River prodeltas (i.e., the underwater parts of river deltas) are hydrodynamic environments experimenting high nutrient and terrestrial organic matter inputs, which enhance primary production (Cruzado and Velasquez, 1990; Lochet and Leveau, 1990). Their benthic compartiments are affected by several co-occurring sedimentary (e.g. sedimentation/resuspension) and biogeochemical (e.g. bioturbation/mineralization) processes (Aller, 1998; Lansard et al., 2009; Pastor et al., 2011a, b). Together with shelf sediments, deltaic sediments are the most important area for organic carbon burial (Hedges and Keil, 1995) and for the decomposition of both terrestrial and marine particulate organic matter (POM) (Aller, 1998).

Deltaic sedimented POM is usually composed of: (1) continental (e.g. vascular land plants debris and soil-derived POM exported by rivers), and (2) marine material (e.g. marine autochthonous primary production and advective inputs) (Hedges et al., 1988; Goni et al., 1998; Leithold and Hope, 1999; Gordon and Goni, 2003). The balance between both sources clearly shifts from the dominance of continental to marine inputs along inshore/offshore gradients (Vonk et al., 2010). River floods affect temporal changes in this balance. They are important in controlling both the quantity and the quality of continental POM exported to the sea. These 2 parameters vary seasonally depending on water flows (Pont, 1997) and are also affected by drainage basin compositions. Dry seasons are usually associated with strong contributions of marine production, conversely to wet seasons, which are typically associated with strong contributions of soil-derived POM and plant debris carried by strong flows (Yu et al., 2002). Although many studies have been devoted to the assessment of the relationships between spatiotemporal changes in deltaic sedimentary organics and hydrological regimes (Leithold and Hope, 1999; Bianchi et al., 2002; Yu et al., 2002), no real consensus has been reached yet regarding: (1) the quality (i.e., lability) of continental inputs (Leeuw and Largeau, 1993; Wakeham and Canuel, 2006; Mayer et al., 2008; Vonk et al., 2010), and (2) the effects of different types of floods on spatiotemporal changes in sedimentary organics within RiOMar.

The long-term impact of riverine inputs (e.g. sediments, organic matter) in controlling benthic macrofauna composition is well recognized as well. This paradigm was initially established based on the studies of major rivers such as the Amazon (Aller and Aller, 1986; Aller and Stupakoff, 1996) and the Changjiang (Rhoads et al., 1985; Aller and Aller, 1986). It has then been verified for smaller rivers (Occhipinti-Ambrogi et al., 2005; Wheatcroft, 2006; Akoumianaki and Nicolaidou, 2007; Harmelin-Vivien et al., 2009; Akoumianaki et al., 2013). According to the conceptual model proposed by Rhoads et al. (1985) spatial changes in benthic macrofauna composition off (major) rivers result from 2 opposite effects, namely: (1) a reduction of benthic macrofauna at the immediate vicinity of the river mouth due to the inputs of large quantities of sediments resulting in high sedimentation rates and instability, and (2) an increase of benthic macrofauna further offshore resulting from moderate organic enrichment. Conversely, there is no consensus about the occurrence of short-term effects of river inputs on benthic macrofauna, which were reported by Occhipinti-Ambrogi et al. (2005) and by Akoumianaki et al. (2013) but not by Wheatcroft (2006). Part of this discrepancy may result from differences between studies in the relative locations of monitored stations relative to inshore/offshore gradients. There is therefore a clear need for new studies combining appropriate spatial and temporal sampling to better describe the effects of changes in riverine inputs on benthic macrofauna composition.

The Rhône River (**Figure 1**) is the major source of freshwater and terrigenous particles to the Gulf of Lions (Aloisi et al., 1977). Its drainage Basin shows a strong geological heterogeneity and is subjected to highly fluctuating climatic conditions (Pont, 1997; Pont et al., 2002). Mean annual water and particle flows are 1700 $m^3.s^{-1}$ and 7400 10^3 $t.y^{-1}$ (Pont et al., 2002). Temporal changes in water (up to 11000 $m^3.s^{-1}$)

and particle flows (up to 22700 10^3 $t.y^{-1}$ in years with strong floods) are very high, which is a characteristic of Mediterranean Rivers (Pont et al., 2002; Antonelli et al., 2008). Rhône River floods may be classified (Pont, 1997) as: (1) oceanic when resulting from precipitations in the Northern Basin and characterized by water flows rising slowly and regularly, (2) Cevenol when resulting from intense precipitations in the South-Western Basin and characterized by sudden and violent increase in water flows, (3) extensive Mediterranean when resulting from precipitations affecting the whole Southern Basin and mostly often associated with autumnal western perturbations, and (4) generalized when corresponding to a combination of the 3 first types. These events strongly differ in terms of both the quantity (Pont, 1997) and the origin (Eyrolle et al., 2012) of the particles transferred to the sea. The Rhône River prodelta is characterized by high sedimentation rates (0.40-0.65 $cm.y^{-1}$ as assessed through ^{210}Pb measurements), which then decrease offshore (0.20 $cm.y^{-1}$) (Zuo et al., 1997; Radakovitch et al., 1999; Miralles et al., 2005). It constitutes a transitional depositional area for terrigenous particles, associated organic matter and contaminants (Roussiez et al., 2005), which are later transferred to the deep sea through a succession of resuspension events mostly caused by storms (Ulses et al., 2008). Overall, strong temporal changes in its hydrological regime together with the heterogeneity of its drainage basin and classical spatial gradients within the deltaic area make the Rhône River an excellent model for the assessment of the effect of a major Mediterranean river on sedimentary organics and benthic macrofauna characteristics.

Spatiotemporal changes in surface sediment characteristics off the Rhône River have already been assessed in several studies (Alliot et al., 2003; Tesi et al., 2007; Lansard et al., 2009; Cathalot et al., 2010; Bourgeois et al., 2011; Pastor et al., 2011b; Cathalot et al., 2013). Part of these studies (Lansard et al., 2009; Cathalot et al., 2010) have mostly dealt with the assessment of sediment organic matter remineralization and thus have only considered a limited set of bulk biochemical descriptors. Others have included a wider set of biochemical parameters but have been restricted to an assessment of spatial changes (Alliot et al., 2003; Bourgeois et al., 2011; Pastor et al., 2011a, b; Cathalot et al., 2013). To our knowledge, the study by Tesi et al. (2007) is the only one, which combined the study of 2 contrasted situations in terms of Rhône River flows with the sampling of a large number of stations and the assessment of a reasonably large set of sedimentary organics biochemical characteristics. However, it still did not include classical organic matter quality descriptors such as EHAA/THAA and Chl-*a*/(Chl-*a*+Phaeo-*a*).

Several studies have assessed spatiotemporal changes in benthic macrofauna composition off the Rhône River as well (Salen-Picard et al., 2003; Hermand et al., 2008; Harmelin-Vivien et al., 2009; Labrune et al., 2012). A few of them have dealt with: (1) the whole benthic macrofauna but were restricted to a single sampling date (Hermand et al., 2008; Harmelin-Vivien et al., 2009; Labrune et al., 2012). They have shown the occurrence of strong longitudinal gradients in benthic macrofauna composition, which limits their use to ca 10 stations sampled only once in assessing the impact of Rhône River water flow (Hermand et al., 2008; Harmelin-Vivien et al., 2009). Another study was conversely restricted to the assessment of polychaete fauna at a single 70 m deep station but focussed on the assessment of the relationship linking Rhône River water flows and fauna compositions based on repeated seasonal sampling (Salen-Picard et al., 2003). It has suggested the dependency of benthic macrofauna composition on temporal changes in the Rhône River water flow with the distinction between 2 groups of species: one responding rapidly (i.e., around 3 months) and mostly composed of opportunistic species adapted to organically rich environments, and a second one responding with a 1-2 year time lag and mostly composed of (more) stable species. The question of the extrapolation of these results to other areas off the Rhône River mouth however still remains fully open due to the occurrence of strong spatial gradients and of their possible interactions with temporal changes in Rhône River water flow.

In this context, the aim of this work was to further assess the effect of changes in Rhône River water flows on both: (1) the quantitative and qualitative characteristics of surface sediment, (2) benthic macrofauna composition, and (3) the possible control of the latter by the former.

2 MATERIALS AND METHODS

2.1 Study area

The Rhône River hydrological basin covers an area of 97800 km² (**Figure 1**) with a mean daily flow between 602 and 11000 $m^3.s^{-1}$ (Pont et al., 2002; Antonelli et al., 2008). Low flows are usually recorded during summer whereas high flows occur during winter and spring (Pont, 1997). The mean daily concentration of suspended particulate matter (SPM) is 180 $mgDW.l^{-1}$. It can decrease to 26 $mgDW.l^{-1}$ during dry periods (Pont et al., 2002). The Rhône River accounts for about 80% of total particulate matter riverine inputs to the Gulf of Lions (Aloisi et al., 1977; Durrieu de Madron et al., 2000). There are 3 distinct sedimentary units in front of its mouth (Aloisi, 1986): (1) the delta front between 5 and 30 m depth, (2) the prodelta between 30 and 60 m depth, and (3) the distal zone between 60 and 100 m.

2.2 Rhône River flows

Rhône River water flow ($m^3.s^{-1}$) and SPM ($mgDW.l^{-1}$) were measured in Arles, (47.5 km upstream of the river mouth, data provided by MOOSE: Mediterranean Ocean Observing System on Environment - http://www.moose-network.fr).

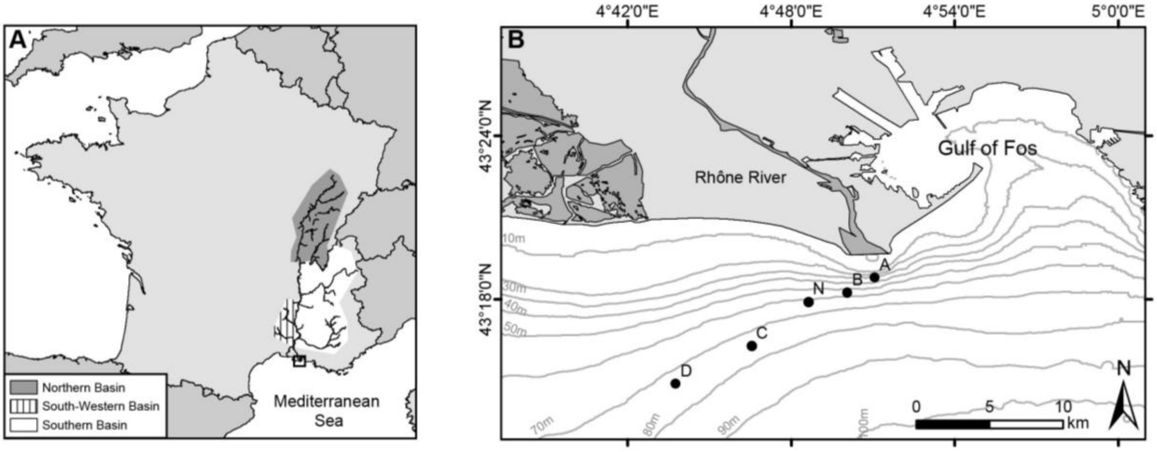

Figure 1. Delimitations of the different Rhône River basins (A) (from Antonelli et al., 2008) and locations of the 5 sampled stations within the Rhône River mouth area (B) (Gulf of Lions, North-Western Mediterranean Sea).

2.3 Sampling

The 5 sampled stations were located between 2 and 13 km off the Rhône River mouth along a gradient corresponding to the preferential direction of the river plume (**Figure 1, Table 1**). Station A was in the delta front; station B in the prodelta and stations N, C and D in the distal zone. Sampling took place in April 2007, May and December 2008 and July 2011 for: (1) sediment characteristics and (2) benthic macrofauna. Sediment Profile Images (SPIs) were also collected in April 2007, May 2008 and July 2011.

Table 1. Latitude, longitude (WGS84, degrees and decimal minutes), depth and distance from the Rhône River mouth of the 5 sampled stations.

Station	Latitude (N)	Longitude (W)	Depth (m)	Distance from the Rhône River mouth (km)
A	43°18.690’	04°51.042’	24	1.9
B	43°18.013’	04°50.068’	54	3.0
N	43°17.626’	04°47.896’	67	5.5
C	43°16.343’	04°46.565’	76	8.6
D	43°14.917’	04°43.613’	74	13.0

2.4 Sediment characteristics

Sediment cores (9.5 cm internal diameter) were collected using an Oktopus® GmbH MUC 8/100 multicorer in April 2007, May 2008 and December 2008; and an Oktopus® GmbH MC 6 multicorer in July 2011. There were 3 cores per sampled station. The upper half centimetre of each core was sliced and homogenized. Each sample was then split in two subsamples (one for granulometry and pigment and one for biochemistry) and frozen at -20°C. The subsamples used for organic carbon, total nitrogen and amino acids were later freeze-dried.

Granulometry

Sediment granulometry was assessed using a Malvern Mastersizer® 2000 laser microgranulometer and expressed as median grain diameter ($D_{0.5}$). There was no replicate at stations N, C and D in December 2008 and all stations in July 2011.

Organic carbon and total nitrogen

Organic carbon and total nitrogen concentrations (OC and TN, respectively) were measured on homogenized, precisely weighed samples with an automatic CN-analyzer LECO 2000, after acidification with 2M HCl (overnight, at 50 °C) in order to remove carbonates prior to the analyses of organic carbon (Cauwet et al., 1990). Precision for OC and TN measurements are about 2%. C/N ratios were expressed as atomic ratios. There was no replicate for OC in May and December 2008 and for TN in May and December 2008 and July 2011.

Chloropigments

Triplicated (100 to 500 mgFW) samples were extracted overnight (5°C in darkness) in 5 ml of 90% acetone (final concentration). Fluorescence measurements were then performed using a Perkin Elmer® LS55 spectrofluorometer according to Neveux and Lantoine (1993). This allowed for the quantification of chlorophyll-*a* (Chl-*a*), chlorophyll-*b* (Chl-*b*) and phaeophytin-a (Phaeo-*a*).

Amino acids

Total hydrolysable amino acids (THAA) and enzymatically hydrolysable amino acids (EHAA) were analysed on triplicates. THAA were extracted by acid hydrolysis. EHAA were extracted following the biomimetic approach proposed by Mayer et al. (1995). THAA and EHAA were analysed as isoindole derivatives following reaction with an orthophtaldialdehyde solution (Lindroth and Mopper, 1979). During July 2011, THAA and EHAA were quantified by fluorescence measurements (excitation wavelength of 340 nm and emission wavelength of 453 nm) using a Perkin Elmer® LS55 fluorescence spectrometer. During April 2007, May 2008 and December 2008, fluorescent derivatives were separated by reverse-phase high-performance liquid chromatography (Gynkotek-Dionex system) on a C18 HPLC column using non-linear gradient of methanol-acetate buffer, and detected by fluorescence at 450 nm using an excitation wavelength of 335 nm.

2.5 Benthic macrofauna

At each station, 5 samples of 0.1 m^2 were collected using a van Veen grab, sieved on a 1 mm mesh and fixed (5% buffered formalin). Macrofauna were then sorted, identified to the lowest tractable taxonomic group and counted.

2.6 Sediment Profile Images

SPIs were collected using two similar Ocean Imaging® systems. Ten deployments were carried out at each station, except in May 2008 (4 deployments at station A and 9 at station N due to bad weather conditions). SPIs were analyzed using the SpiArcBase software (Romero-Ramirez et al., 2013).

2.7 Data analysis

Sediment characteristics

Non-Metric Multidimensional Scaling (nMDS) and hierarchical clustering (Euclidean distance, group average linking) were performed on normalized sediment characteristics ($D_{0.5}$, OC, TN, THAA, EHAA, Chl-*a*, Chl-*b*, Chl-*b*/Chl-*a*, Phaeo-*a*, C/N, EHAA/THAA and Chl-*a*/(Chl-*a*+Phaeo-*a*)). The significance of differences among the groups derived from hierarchical clustering was tested using SIMilarity PROFile (SIMPROF) procedure (Clarke et al., 2008).

Benthic macrofauna

Total abundance, species richness (SR) and Pielou’s evenness (J’) were used as bulk descriptors of benthic macrofauna compositions. SR is the number of species present in a sample whereas J’ indicates how homogeneous is the individual abundance of each species within a sample. J’ is between 0 and 1. This last value indicates that all species are represented by the same number of individuals.

Replicated samples were pooled and abundance-based compositions were also compared through nMDS and hierarchical clustering (square-root transformed data, Bray-Curtis similarity, group average linking). SIMPROF tests (were used together with ANOSIM for the cluster composed by stations N, C and D) to assess the significance of internal structures in identified clusters (Clarke et al., 2008). SIMilarity PERcentages analyses (Clarke, 1993) were performed to identify the species contributing most to between-clusters dissimilarity.

Relationships linking sediment characteristics and benthic macrofauna compositions

A BIO-ENV procedure (Clarke and Ainsworth, 1993) was performed to identify the subset of sediment characteristics, which best described spatiotemporal changes in benthic macrofauna composition. The set of tested sediment characteristics included $D_{0.5}$, Chl-*a*, Chl-*b*/Chl-*a*, Phaeo-*a*, Chl-*a*/(Chl-*a*+Phaeo-*a*), EHAA, THAA, EHAA/THAA, OC and C/N. The correlations of each retained environmental variable with benthic macrofauna compositions were assessed using Mantel tests.

All procedures were completed using the PRIMER 6® software package.

3 RESULTS

3.1 Rhône River flows

Strong temporal changes in daily water and particle flows were observed between 2007 and 2011 (**Figure 2**). The May 2008 cruise took place during a flood. The April 2007 and December 2008 cruises took place 42 and 26 days after a flood. Conversely, the July 2011 cruise took place after an extended (i.e., 191 day long) period of low water flows.

3.2 Sediment characteristics

Overall, sediments grains tended to be coarser and more variable in size among dates at station A (between 6.7 in May and 69.2 µm in December 2008; **Table 2, Figure 3A**). $D_{0.5}$ at station B was between 12.9 in July and 23.9 µm in May 2008. Surface sediments tended to be finer and less variable at stations N, C and D.

Temporal changes in OC, TN and THAA were the lowest at stations N, C and D. They were the highest at station A for OC (**Figure 3B**) and TN, and at station B for THAA (**Table 2**). All 3 descriptors showed decreasing values offshore during April 2007 and July 2011. Conversely, May and December 2008 were characterized by low values of OC, TN and THAA at station A and maximal ones at station B. This pattern was especially marked for THAA.

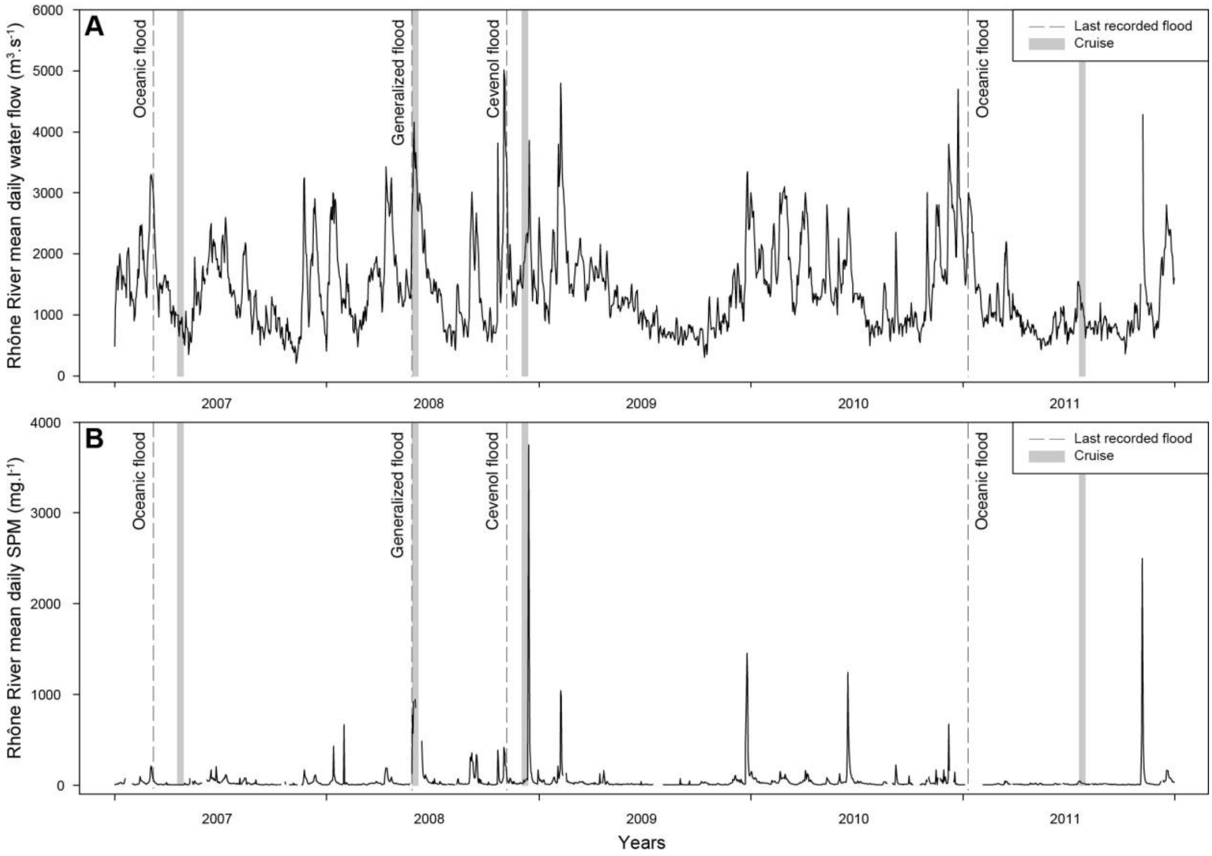

Figure 2. Temporal changes in Rhône River mean daily water flow (A) and suspended particulate matter (SPM) (B) between 2007 and 2011. Vertical dashed lines indicate the last floods (> 3000 m^3.s^{-1}) recorded before the 4 sampling cruises (vertical grey lines). The first 3 floods were characterized by Zebracki et al. (2015) and the last one based on SPM.

Overall, EHAA showed the same pattern for the 3 bulk descriptors of sedimentary organics with: (1) high temporal changes at station A, (2) decreasing inshore/offshore gradients during April 2007 and July 2011, and (3) low concentrations at station A and the highest concentrations at station B during May and December 2008 (**Table 2, Figure 3C**). Temporal changes in EHAA at station B were however low. Temporal changes in Chl-*a* (**Figure 3D**) and Chl-*b* were high at station A, intermediate at station B and low at stations N, C and D (**Table 2**). Decreasing inshore/offshore gradients were marked during April 2007 and July 2011. Concentrations at stations A and B were much higher during April 2007 than July 2011. Chl-*a* and Chl-*b* concentrations were maximal at station B during May and December 2008. This pattern was especially marked for Chl-*b* during December 2008.

Temporal changes in C/N were highest at station A (**Table 2**). It was especially high at station A in December 2008 and tended to be highest at this particular date than during the 3 other cruises at all other 4 stations. Temporal changes in Chl-*b*/Chl-*a* were the highest at station A, intermediate at station B, and low at stations N, C and D (**Table 2**). During April 2007, May 2008 and December 2008, there were clear inshore/offshore gradients with the highest values at stations A and B during December 2008. During July 2011, the highest Chl-*b*/Chl-*a* was recorded at station B.

Temporal changes in EHAA/THAA were slightly higher at station A than at the 4 other stations (**Table 2, Figure 3E**). EHAA/THAA always tended to be similar at all stations with the exception of station A during July 2011. EHAA/THAA also tended to be higher during July 2011 at all stations. Temporal changes in Chl-*a*/(Chl-*a*+Phaeo-*a*) were higher at station A than at the 4 other stations (**Table 2, Figure 3F**). There were always strong decreasing inshore/offshore gradients.

Table 2. Mean values of surface sediment and benthic macrofauna characteristics. Sta: Stations, $D_{0.5}$: median grain size, OC: organic carbon, TN: total nitrogen, C/N: ratio between organic carbon and total nitrogen, Chl-*a*: chlorophyll-*a*, Chl-*b*: chlorophyll-*b*, Chl-*b*/Chl-*a*: ratio between chlorophyll-*b* and chlorophyll-*a*, Phaeo-*a*: phaeophytin-*a*, Chl-*a*/(Chl-*a*+Phaeo-*a*): ratio between chlorophyll-*a* and the sum of chlorophyll-*a* and phaeophytin-*a*, EHAA: enzymatically hydrolysable amino acid, THAA: total hydrolysable amino acid, EHAA/THAA: ratio between enzymatically and total hydrolysable amino acids, SR: species richness and J': Pielou's evenness. ± standard deviation (*n*=3).

Cruise	Sta.	Sampling date	$D_{0.5}$ (0-0.5 cm) (μm)	OC (%DW)	TN (%DW)	C/N (atomic ratio)	Chl-*a* (μg.g^{-1}DW)	Chl-*b* (μg.g^{-1}DW)	Chl-*b*/Chl-*a* (%)	Phaeo-*a* (μg.g^{-1}DW)	Chl-*a*/(Chl-*a*+Phaeo-*a*) (%)	EHAA (mg.g^{-1}DW)	THAA (mg.g^{-1}DW)	EHAA/THAA (%)	Abundance (ind.m^{-2})	SR (taxa.0.5m^{-2})	J'
April 2007	**A**	4/20/2007	37.40±3.05	1.83±0.18	0.17±0.004	12.90±1.42	9.78±0.82	1.38±0.06	14.20±0.82	20.51±1.49	32.26±0.52	1.17±0.19	3.77±0.30	28.21±1.07	144	20	0.88
	B	4/20/2007	14.83±0.55	1.53±0.08	0.15±0.003	12.10±0.45	4.99±0.49	0.51±0.06	10.17±0.24	21.76±1.24	18.62±0.88	0.86±0.05	3.14±0.03	27.49±1.76	642	39	0.69
	N	4/24/2007	14.01±2.42	1.19±0.21	0.10±0.002	13.46±2.11	2.57±0.60	0.18±0.13	6.29±4.33	14.31±0.18	15.13±2.95	0.68±0.02	2.82±0.35	24.52±2.67	358	26	0.68
	C	4/23/2007	11.38±1.12	1.20±0.05	0.11±0.003	12.78±0.63	1.64±0.12	0.06±0.05	3.79±3.63	12.19±1.19	11.90±0.48	0.69±0.03	2.38±0.07	28.91±1.99	436	34	0.55
	D	4/23/2007	10.45±0.22	1.02±0.03	0.11±0.001	11.23±0.38	1.56±0.29	0.00	0.00	13.76±2.83	10.21±0.43	0.72±0.04	2.54±0.09	28.17±1.85	294	34	0.68
May 2008	**A**	5/29/2008	6.74±0.63	1.13	0.09	14.81	3.07±0.43	0.29±0.07	9.47±2.84	4.58±0.57	40.16±0.77	0.43±0.04	2.18±0.13	19.68±0.80	178	15	0.73
	B	5/28/2008	23.87±6.67	1.75	0.17	12.3	3.80±0.63	0.31±0.09	8.02±1.65	17.70±1.11	17.60±1.52	0.93±0.12	5.62±0.63	16.57±1.47	310	28	0.82
	N	5/30/2008	10.65±1.90	1.00	0.10	12.03	1.62±0.59	0.07±0.06	3.48±3.41	12.31±6.59	14.14±8.60	0.49±0.05	2.57±0.20	19.05±2.38	238	28	0.91
	C	5/30/2008	14.51±1.39	1.16	0.10	13.01	1.48±0.62	0.05±0.06	2.83±2.64	8.37±0.21	14.82±5.36	0.52±0.01	2.69±0.11	19.48±1.03	258	36	0.87
	D	06/08/2008	11.37±1.27	1.00	0.10	12.03	0.09±0.13	0.00	0.00	5.47±2.24	1.30±1.84	0.51±0.14	2.33±0.50	21.73±1.36	202	24	0.80
December 2008	**A**	12/04/2008	69.18±19.22	1.22	0.05	28.15	2.14±1.06	0.56±0.31	25.71±5.52	6.49±3.43	24.83±1.86	0.41±0.20	2.57±1.37	16.27±0.70	260	21	0.75
	B	12/03/2008	21.58±3.85	1.96	0.13	18.09	5.01±0.80	1.05±0.12	21.05±0.99	17.45±0.98	22.20±1.87	0.83±0.04	5.48±0.59	15.25±1.07	344	32	0.83
	N	12/08/2008	13.58	1.36	0.10	16.28	1.47±0.21	0.05±0.02	3.53±0.74	13.17±1.04	10.03±1.41	0.61±0.06	3.06±0.11	19.87±2.65	622	37	0.64
	C	12/04/2008	17.11	1.49	0.10	18.01	0.98±0.20	0.00	0.00	13.28±0.72	6.85±1.00	0.55±0.05	3.05±0.27	18.07±0.95	246	25	0.78
	D	12/08/2008	15.57	1.16	0.08	16.08	0.18±0.03	0.00	0.00	10.77±1.31	1.66±0.28	0.45±0.06	2.53±0.13	18.01±2.54	210	28	0.78
July 2011	**A**	7/26/2011	26.08	1.80±0.14	0.15	14.03	5.94±0.91	0.59±0.21	9.86±7.14	7.14±0.07	45.22±3.92	1.13±0.02	2.96±0.21	38.44±2.25	1522	57	0.61
	B	7/21/2011	12.92	1.54±0.14	0.14	12.98	1.04±0.54	0.17±0.11	15.85±6.52	6.52±1.90	13.24±2.62	0.81±0.07	2.71±0.20	30.04±2.12	1700	45	0.57
	N	7/30/2011	11.07	1.25±0.05	0.11	12.91	0.80±0.29	0.06±0.02	6.93±4.13	4.13±0.52	15.89±3.21	0.66±0.05	2.02±0.12	32.58±0.97	426	41	0.85
	C	7/25/2011	10.32	1.21±0.10	0.09	15.7	0.39±0.17	0.00	0.00	3.25±0.21	10.72±4.90	0.65±0.00	2.03±0.06	32.14±1.12	442	41	0.69
	D	7/28/2011	9.88	1.08±0.03	0.08	15.36	0.43±0.02	0.00	0.00	3.78±0.10	10.27±0.67	0.62±0.07	1.88±0.09	32.62±2.18	284	39	0.83

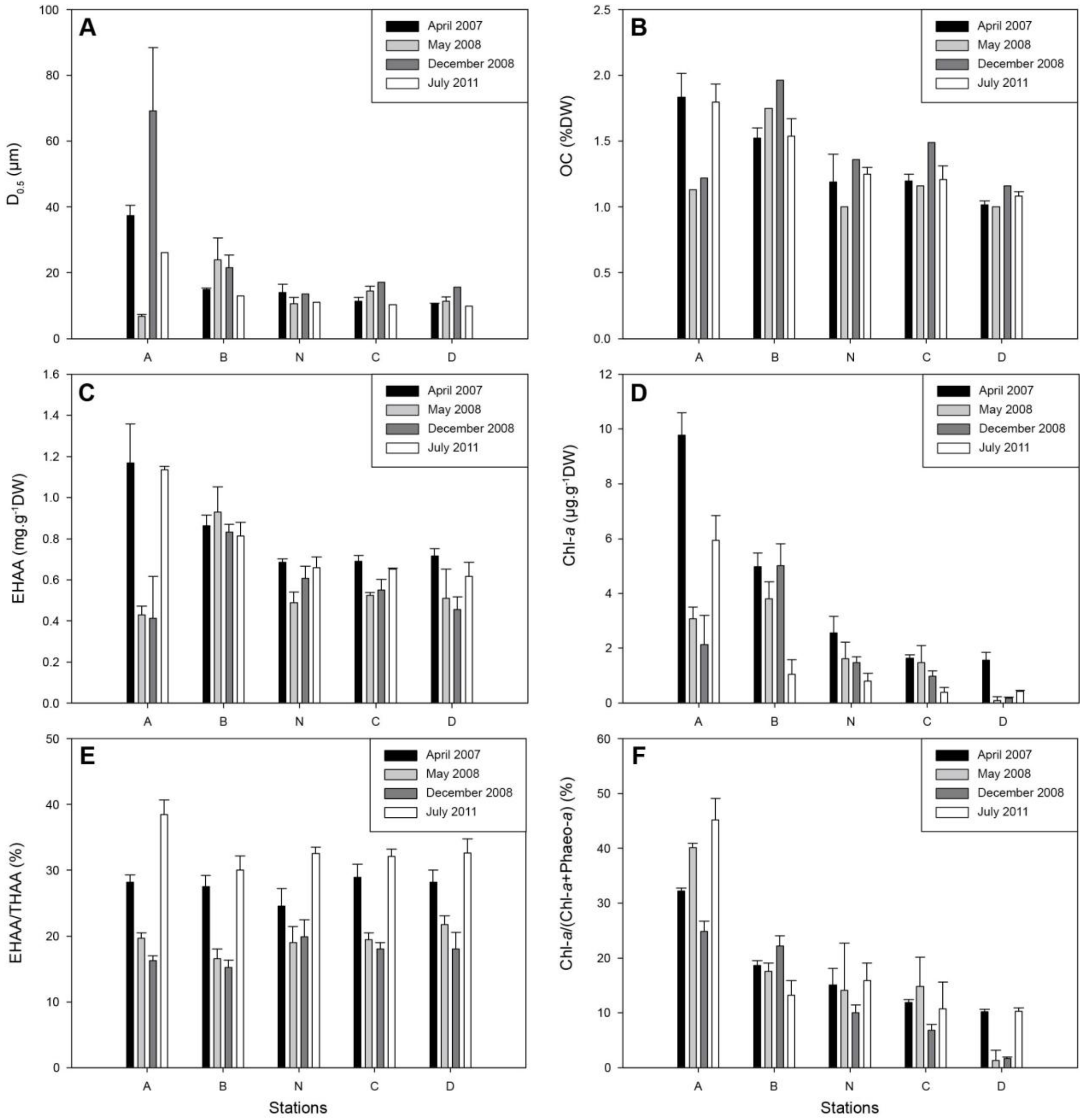

Figure 3. Spatiotemporal changes in surface sediment characteristics: $D_{0.5}$: median grain size (A), OC: organic carbon (B), EHAA: enzymatically hydrolysable amino acids (C), Chl-*a*: chlorophyll-*a* (D), EHAA/THAA: ratio between enzymatically and total hydrolysable amino acids (E) and Chl-*a*/(Chl-*a*+Phaeo-*a*): ratio between chlorophyll-*a* and the sum of chlorophyll-*a* and phaeophytin-*a* (F). Vertical bars are standard deviations.

The nMDS (**Figure 4A**) confirmed that the temporal variability of surface sediment characteristics was higher at station A, intermediate at station B and lower at stations N, C and D. Station A during May 2008, and station B during July 2011, showed the characteristics of sedimentary organics the closest to those of stations N, C and D. The hierarchical clustering (**Figure 4B**) confirmed this pattern with the identification of 4 significantly differing clusters: (I) station A in April 2007 and July 2011, and station B in April 2007, May and December 2008, (II) stations N, C and D in April 2007 and May 2008, (III) stations N and C in December 2008, and (IV) stations C and D in July 2011. Station A in May and December 2008, station D in December 2008 and stations B and N in July 2011 were not included in these main clusters.

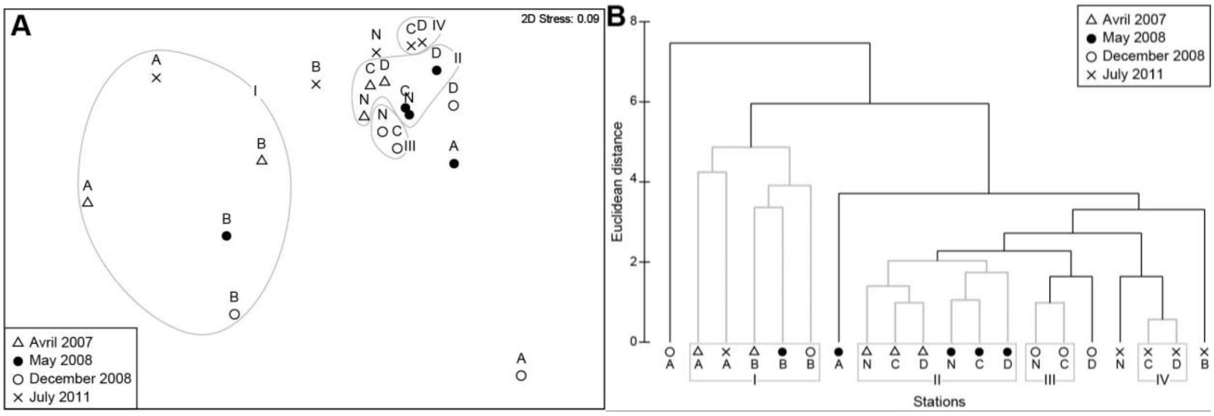

Figure 4. Non-metric Multidimensional Scaling (nMDS) (A) and hierarchical clustering (Euclidean distance and average group method) (B) of normalized surface sediment characteristics. Grey lines indicate groups of samples (combinations of stations and dates), which do not show significant differences in their characteristics (SIMPROF test, p>0.05). Letters refer to stations and symbols to dates.

3.3 Benthic macrofauna

4558 specimens belonging to 142 taxa were identified. Benthic macrofauna was mainly composed of polychaetes (80% of total overall abundance) followed by crustaceans and molluscs (7% each) and minor groups, including echinoderms, sipunculans, echiurans, cnidarians, hemichordates, nemerteans, platyhelminthes and phoronideans (for a total of 6%). *Sternaspis scutata* (Polychaeta) accounted for 36% of total abundance, whereas all other species accounted for less than 5% each. *S. scutata* (Polychaeta) was the top rank species at all stations except station A in April 2007 (*Thyasira flexuosa,* Mollusca), May 2008 (*Heteromastus filiformis*, Polychaeta) and December 2008 (*Polycirrus* sp.*,* Polychaeta); station B during December 2008 (*Lumbrineris latreilli,* Polychaeta); and station N in May 2008 (*Poecilochaetus serpens,* Polychaeta). Four taxa (*S. scutata*, *H. filiformis*, *Nephtys kersivalensis* (all

Polychaeta) and nemerteans) were always present at station A *versus* 13, 12, 11 and 13 taxa at stations B, N, C and D, respectively.

Temporal changes in abundances were higher at stations A and B, intermediate at station N lower at stations C and D (**Table 2, Figure 5A**). Abundances at station A were between 144 and 1522 ind.m^{-2} during April 2007 and July 2011. Abundances at station B were between 310 and 1700 ind.m^{-2} during May 2008 and July 2011. Temporal patterns were similar at these 2 stations except for higher abundances at station B during April 2007. Abundances at station N were between 238 and 622 ind.m^{-2} during May 2008 and December 2008. They were intermediate during April 2007 (358 ind.m^{-2}) and July 2011 (426 ind.m^{-2}). Abundances at station C and D were higher during April 2007 (436 and 294 ind.m^{-2}, respectively) and July 2011 (442 and 284 ind.m^{-2}, respectively)) and lower during May (258 and 202 ind.m^{-2} for stations C and D) and December 2008 (246 and 210 ind.m^{-2} for stations C and D).

Temporal changes in SR were the highest at station A (**Table 2, Figure 5B**). Both the lowest (15 taxa.0.5m^{-2} during May 2008) and the highest SR (57 taxa.0.5m^{-2} in July 2011) were recorded at this station. High SR were as well recorded at station B during April 2007 (39 taxa.0.5m^{-2}), station N during December 2008 (37 taxa.0.5m^{-2}) and station C during May 2008 (36 taxa.0.5m^{-2}). The only clear inshore/offshore gradient was recorded during July 2011 with SR ranging from 57 to 39 taxa.0.5m^{-2} at stations A and D, respectively.

J’ were between 0.55 (station C in April 2007) and 0.91 (station N in May 2008). It did not show any clear temporal or spatial patterns (**Table 2, Figure 5C**). At stations A and B, the lowest values were recorded during July 2011, when both total abundances and SR were the highest.

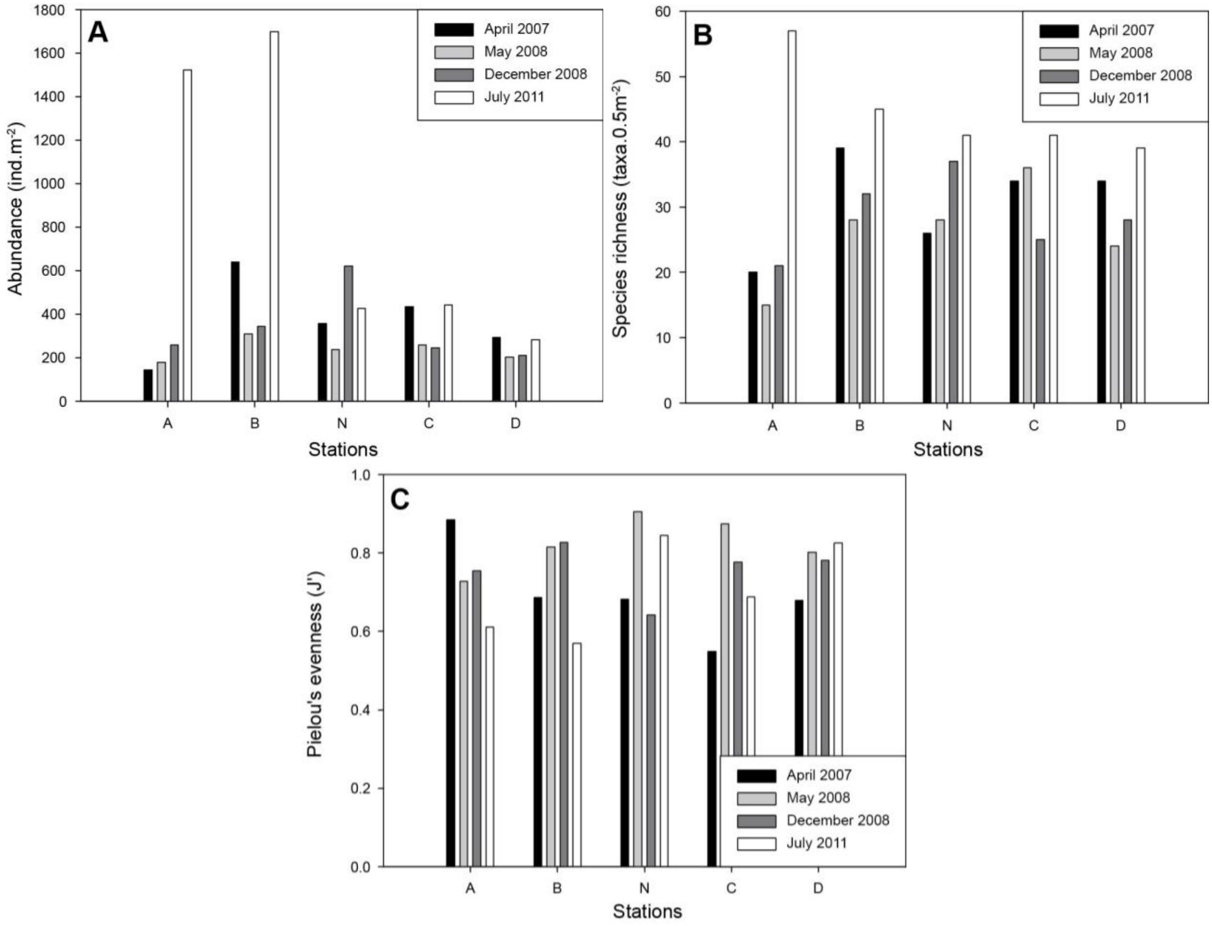

Figure 5. Spatiotemporal changes in benthic macrofauna main characteristics: abundance (A), species richness (B) and Pielou's evenness (C).

The nMDS (**Figure 6A**) showed that temporal changes in macrofauna composition were highest at station A, intermediate at station B and lowest at stations N, C and D. The hierarchical clustering (**Figure 6B**) confirmed this pattern with the identification of 4 clusters: (I) station A in April 2007, May and December 2008, (II) stations A and B in July 2011, (III) station B in April 2007, May and December 2008, and (IV) stations N, C and D during all cruises. There was no internal structure within this last cluster (SIMPROF tests, $p>0.05$). Conversely, the ANOSIM test ($\rho = 0.87$, $p=0.001$) showed significant temporal changes at stations N, C and D.

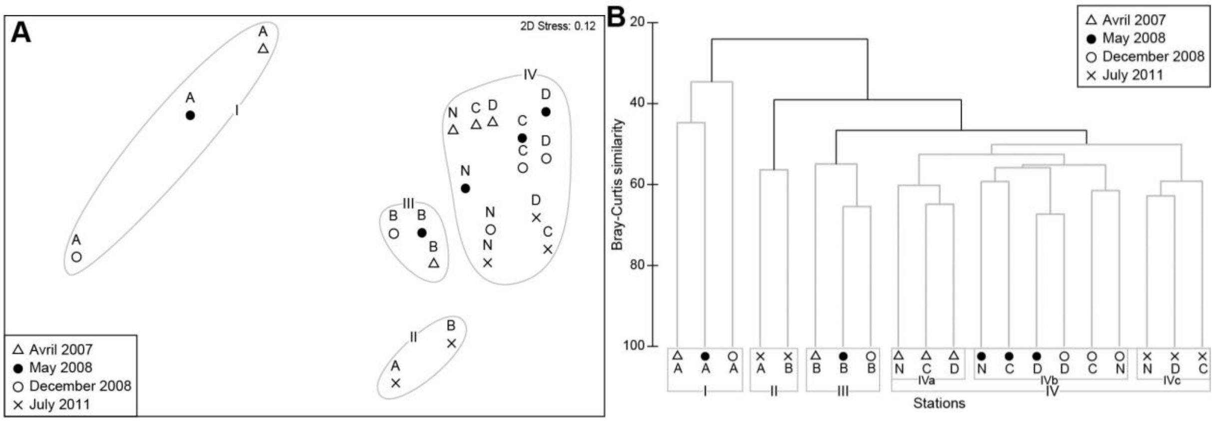

Figure 6. Non-metric Multidimensional Scaling (nMDS) (A) and hierarchical clustering (Bray-Curtis similarity and average group method) (B) of macrofauna abundance data (square-root transformed). Grey lines indicate groups of samples (combinations of stations and dates), which do not show significant difference in their macrofauna composition (SIMPROF test, p>0.05). Letters refer to stations and symbols to cruises.

Average dissimilarity between groups I and II was 76.6% with *Sternaspis scutata* (12.3%, Polychaeta), *Laonice cirrata* (5.2%, Polychaeta), *Lumbrineris latreilli* (4.6%, Polychaeta) and *Thyasira flexuosa* (4.2%, Mollusca) contributing most. Average dissimilarity between groups I and III was 70.7% with *Labidoplax digitata* (5.2%, Echinodermata), *S. scutata* (5.2%, Polychaeta), *L. latreilli* (5.1%, Polychaeta), *Nephtys hystricis* (4.62%, Polychaeta) and *Goniada maculata* (4.3%, Polychaeta) contributing most. Average dissimilarity between groups II and III was 54.3% with *S. scutata* (11.1%, Polychaeta), *L. cirrata* (6.5%, Polychaeta) and *T. flexuosa* (5.0%, Mollusca) contributing most. Average dissimilarity between subgroups IVa and IVb was 47.5% with *S. scutata* (7.7%, Polychaeta), *Athanas nitescens* (3.9%, Crustacea), *Harpinia dellavallei* (3.3%, Crustacea), *Chaetozone* spp. (3.1%, Polychaeta) and *Abra nitida* (3.0%, Mollusca) contributing most. Average dissimilarity between subgroups IVa and IVc was 50.9% with *S. scutata* (4.5%, Polychaeta), *Ampharete grubei* (4.3%, Polychaeta), *L. cirrata* (3.4%, Polychaeta) and *L. latreilli* (3.0%, Polychaeta) contributing most. Average dissimilarity between subgroups IVb and IVc was 49.4% with *A. grubei* (5.0%, Polychaeta), *L. cirrata* (4.4%, Polychaeta) and *S. scutata* (3.8%, Polychaeta) contributing most.

3.4 SPIs

Temporal changes in SPIs characteristics (**Figure 7**) were the strongest at station A with: (1) a very thin apparent Redox Potential Discontinuity (aRPD) layer and almost no biogenic structures in April 2007, (2) a thick flood layer with a few large biogenic structures in May 2008, and (3) an average thickness of the aRPD of 38 mm with numerous biogenic structures including tubes in July 2011. The flood layer observed in May 2008 was thickest at station A and then tended to decrease offshore (data not shown). The aRPD at stations B, N, C and D tended to be thicker in May 2008 than in April 2007 and in July 2011.

3.5 Relationship between sediment characteristics and benthic macrofauna compositions

The best correlation (ρ=0.795, p=0.01) between the similarity matrices of benthic macrofauna composition and sediment characteristics was found using $D_{0.5}$, Chl-*b*/Chl-*a*, Chl-*a*/(Chl-*a*+Phaeo-*a*) and EHAA. Each of these variables correlated positively with benthic macrofauna composition (Mantel tests, p=0.001 in all cases).

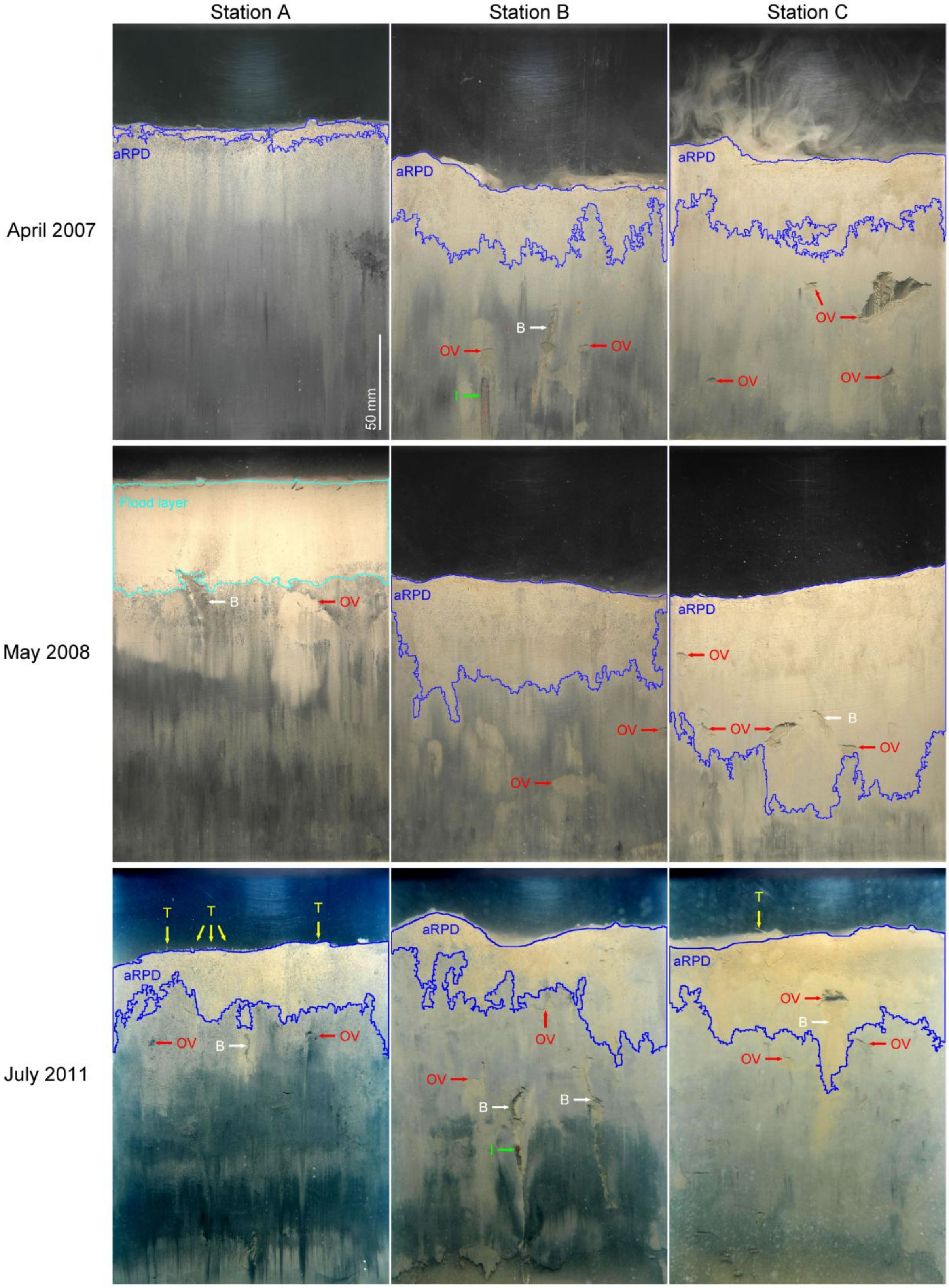

Figure 7. Examples of sediment profile images collected at 3 stations along the main inshore/offshore gradient (stations A, B and C) during 3 different cruises (April 2007, May 2008 and July 2011). The aRPD (apparent Redox Potential Discontinuity) is drawn in blue and the flood layer in light blue. Biogenic structures are also highlighted: OV: oxic voids (red), T: tubes (yellow), B: burrow (white), I: infauna (green).

4 DISCUSSION

4.1 Sampling in relation with the hydrological regime of the Rhône River

The distinction between the 4 types of floods of the Rhône River is often based on SPM, with oceanic floods associated with the lowest concentrations (i.e., <500 mgDW.l^{-1}) (Pont, 1997). It can also rely on the activities of ^{238}U, ^{232}Th, ^{137}Cs and $^{(239+240)}$Pu (Eyrolle et al., 2012). This last approach has been used to classify Rhône River floods between 2000 and 2012 (Zebracki et al., 2015). The March 2007, May 2008 and November 2008 floods were respectively classified as: oceanic, generalized and Cevenol. Sampling was thus associated with 3 different types of floods. Floods can also be of different intensities (Pont (1997); **Figure 2A**). In the last 20 years, several studies have reported water flows and suspended particulate discharges for different time periods: 1992-1995, 2003 and 2006-2008 (Pont, 2002; Antonelli et al., 2008; Eyrolle et al., 2012). Maximal water flow was reported by Antonelli et al (2008) in December 2003 with an extreme flow of 11000 m^{3}.s^{-1} for a total particulate discharge of 5400 10^{3}t.flood^{-1}. Maximal suspended particulate discharge was of 12624 10^{3}t.flood^{-1} in the 1992-1995 time period. The May 2008 flood, with a water flow of 4156 m^{3}.s^{-1} and a particulate discharge of 4670 10^{3} t.flood^{-1} (Eyrolle et al., 2012), can thus be considered as reasonably strong regarding particle flows. Conversely, the March 2007 and the November 2008 floods (3269 m^{3}.s^{-1} and 4806 m^{3}.s^{-1}, respectively) can be considered as of low and intermediate intensity based on water flows. Another source of heterogeneity is the time lag between the last floods and samplings. These were 42 and 26 days in April 2007 and December 2008, whereas the May 2008 cruise took place during the flood. The July 2011 cruise took place after an extended (i.e., 191 day long) period of low water flows. Sampling thus proved representative of a large variety of hydrological regimes and therefore allows for the assessment of the responses of both surface sediment characteristics and benthic macrofauna composition, provided that the temporal dynamics of such responses are properly taken into account.

4.2 Sedimentary organics

Quantitative changes

Previous studies have shown the occurrence of decreasing inshore/offshore gradient in sediment grain size (Cathalot et al., 2010; Bourgeois et al., 2011; Pastor et al., 2011b) and sedimentary organics concentrations (Alliot et al., 2003; Hermand et al., 2008; Lansard et al., 2009; Cathalot et al., 2010; Bourgeois et al., 2011). The resulting positive correlation between sediment grain size and sedimentary organics concentrations contradicts the general negative correlation linking these 2 parameters (Mayer, 1994). This mostly results from the fact that the Rhône River constitutes the major source of organic inputs in the studied area (Pastor et al., 2011b). During the present study, decreasing inshore/offshore gradients in both sediment grain size and sedimentary organic contents were observed during April 2007 and July 2011. Spatial distributions differed during May and December 2008 with: (1) much finer and much coarser sediments in the delta front, respectively; and (2) higher sedimentary organics concentrations in the prodelta than in the delta front at both dates. Differences in sediment grain size in the delta front can be related with: (1) the type of the last flood, and (2) the time lag between this flood and sampling. The occurrence of finer sediment in May 2008 probably results from the fact that the May 2008 generalized flood mostly affected the Durance River, which required the opening of the Serre-Ponçon dam. This resulted in the liberation of large amounts of fine particles, which later sedimented in the delta front as indicated by the flood layer observed on 29th May 2008 (**Figure 7**). Such a pattern was not observed at station B, which was sampled on 28th May 2008 (i.e., just at the beginning of the flood). However, Cathalot et al. (2010) later observed a 30 cm thick flood layer with low OC on 6th June 2008 near this station. Moreover, based on the analysis of ^{7}Be and ^{210}Pb$_{xs}$ activities on SPM collected in Arles, Eyrolle et al. (2012) suggested that SPM during the May 2008 flood mostly originated from the reworking of old degraded soils initially trapped in the Serre-Ponçon dam, which is known to trap organically poor fine clay particles originating from intense erosion acting on a soil lacking vegetation (Pont et al., 2002). Overall, the occurrence of finer surface sediment grain size in the delta front than in the prodelta during May 2008 largely results from the fact that station B was sampled before being affected by the deposition of the flood layer.

Accordingly, the occurrence of lower sedimentary organic contents in the delta front probably results from the fact that the OC of the sediment constitutive of the flood layer was low (Cathalot et al., 2010).

The occurrence of sandy sediments in the delta front in December 2008 probably results from 2 distinct processes. First, the November 2008 flood classified as Cevenol. Such events are sudden and result in high water and particle flows. Antonelli et al. (2008) found a positive correlation between SPM grain size in Arles and particle flow. Since, sandy particles settle quicker than fine particles, this may account for the occurrence of higher concentrations of sand following the flood. Another possible cause of the discrepancies in sediment grain size within the delta front between May and December 2008 is linked to the fact that station A was sampled during the flood in May and 26 days after the flood in December. Prodeltaic systems of the Gulf of Lions are areas of transitory deposits for continental inputs, which are later resuspended and transferred offshore (Buscail et al., 1995; Durrieu de Madron et al., 2000; Ulses et al., 2008). For instance, 2 kilometres off the Rhône River mouth, Marion et al. (2010) observed the erosion of a 5 cm deposits within 20 days after the November 2006 flood. Resuspension preferentially affects fines and mostly occurs during autumn and winter (Ulses et al., 2008). It may thus have contributed to clear surface sediments at station A of their finest components between their deposition (i.e., during the November 2008 flood) and December 2008 sampling. The occurrence of higher sedimentary organic concentrations in the prodelta during December 2008 may result from the granulometry effect (Mayer, 1994).

Qualitative changes

C/N and Chl-*b*/Chl-*a* ratios classically show decreasing inshore/offshore gradients off the Rhône River mouth (Lansard et al., 2009; Cathalot et al., 2010; Bourgeois et al., 2011). For both descriptors, results from the present study show no strong temporal changes except in December 2008 in the delta front and to a lesser extent in the prodelta where high Chl-*b*/Chl-*a* supported the contribution of continental plant detritus to sedimentary organics (Jeffrey, 1976; Meyers, 1994;

Hedges et al., 1997; Tesi et al., 2007; Cathalot et al., 2013). This may be related to the November 2008 Cevenol flood since these events mostly originate from the Cevennes area, which is densely forested. Besides changes in continental inputs, higher Chl-*b*/Chl-*a* close to the Rhône River mouth may also result from subsequent physical sorting (Tesi et al., 2007), which tends to export fine particles with lower contents of vascular plant detritus offshore (Goni et al., 1998; Leithold and Hope, 1999). This pattern is supported by spatiotemporal changes in C/N. The C/N of soil organic matter is typically between 7 and 15 (Baldock et al., 1992). Values recorded during April 2007, May 2008 and July 2011 were in the upper range (11-15) with no clear inshore/offshore gradient. Values recorded in December 2008 were higher with a clear decreasing inshore/offshore gradient, which is coherent with a higher contribution of continental vascular plant material (C/N>20; Baldock et al. (1992)) to sedimentary organics, and/or a reduction of this contribution due to dilution or preferential degradation during the transport offshore (Baldock et al., 1992). The first of these 2 hypotheses is probably the most valid because C/N ratios did not decrease offshore during the 3 other cruises and EHAA/THAA never decreased offshore.

Spatiotemporal changes in Chl-*a*/(Chl-*a*+Phaeo-*a*) and EHAA/THAA ratios clearly differed. Chl-*a*/(Chl-*a*+Phaeo-*a*) ratios always decreased offshore with, except to some extent in the delta front, no marked temporal change. Conversely, EHAA/THAA ratios showed no offshore gradient during either cruise but did show temporal changes with high values in July 2011, intermediate values in April 2007 and low values in May and December 2008. In the delta front Chl-*a*/(Chl-*a*+Phaeo-*a*) ratios correlated negatively with Chl-*b*/Chl-*a* ratios, which is coherent with the lower lability classically attributed to continental than to marine plant material (Wakeham et al., 1997). The decreasing trend and the lack of temporal changes at higher depth result from the fact that: (1) Rhône River inputs are the major source of plant material to the sediment/water interface of all stations, and (2) irrespective of slight differences in the original freshness of bulk plant materials, its most labile components are quickly degraded during their transfer offshore. EHAA/THAA ratios are indicative of a different, much larger and overall less labile component of sedimentary organics (Wakeham et al., 1997). The lack of offshore gradient probably results from the fact that the degradation taking place during the offshore transfer affects a minor fraction of the nitrogenous fraction of sedimentary organics. Conversely, the occurrence of significant temporal changes in EHAA/THAA may reflect differences in the lability of the nitrogenous component of sedimentary organics depending on seasons or hydrologic conditions of the Rhône River. Results from the present study suggest that such changes are mainly related with changes in the intensity of continental inputs with higher values during April 2007 (intermediate particle flow, oceanic flood) and July 2011 (low particle flow, dry period) and lower ones during May and December 2008 (high particle flows, generalized and Cevenol floods).

4.3 Benthic macrofauna

Although still significant in the distal zone (according to the results of the ANOSIM test at least), temporal changes in macrofauna composition were clearly much more marked in the delta front and to a lesser extent in the prodelta, which is similar to what was observed for surface sediment characteristics.

In the Rhône River delta front, sedimentation rates can reach up to 0.65 cm.y^{-1} (Zuo et al., 1997; Miralles et al., 2005) which, according to the model proposed by Rhoads et al. (1985), can account for minimal SR and abundance of benthic macrofauna in the delta front during April 2007, May and December 2008. The fact that benthic macrofauna SR (April 2007, May and December 2008) and abundances (April 2007) tended to be higher in the prodelta, which is located further offshore supports this model. Conversely, benthic macrofauna abundances in the delta front and the prodelta were close in May and December 2008 (i.e., following the generalized and Cevenol floods, respectively), which may be indicative of the extension of the negatively affected area during major floods and therefore also tends to support the Rhoads et al. (1985) model.

The nMDS and the analysis of benthic macrofauna characteristics at stations A and B show that July 2011 clearly differed from the 3 other sampling dates with: (1) much higher abundances and SR, and (2) higher abundances of *Sternaspis scutata* (Polychaeta)*, Laonice cirrata* (Polychaeta), *Lumbrineris latreilli* (Polychaeta, station A only) and *Thyasira flexuosa* (Mollusca). The extended period of reduced water flows before July 2011 clearly enhanced the establishment of a more mature benthic macrofauna community in the delta front and the prodelta. This community included both tube-dwelling and deep-burrowing macrofauna as indicated by sediment profile imagery in the prodelta (**Figure 7**). More generally, July 2011 corresponded to the inshore enlargement of the spatial distributions of several species including *Abra nitida* (Mollusca), *Abyssoninoe hibernica* (Polychaeta), *Alpheus glaber* (Crustacea), *Ampharete grubei* (Polychaeta), *Apseudes* spp. (Crustacea), *Chaetozone* spp. (Polychaeta), *Goniada maculata* (Polychaeta), *L. cirrata* (Polychaeta), *Malmgrenia lilianae* (Polychaeta), *T. flexuosa* (Mollusca) and *Thysanocardia procera* (Sipunculida), which were found up to the delta front. Such a positive effect of low flow on benthic macrofauna abundance and SR has already been reported for several major rivers (Aller and Stupakoff, 1996; Occhipinti-Ambrogi et al., 2005). This supports previous observations (on an annual basis and without any time lag in the response of benthic polychaete fauna to changes in Rhône River flow) by Harmelin-Vivien et al. (2009) and is also in good agreement with the Rhoads et al. (1985) model.

SPI data suggest an almost immediate impact of the May 2008 flood in the delta front with the onset of the deposition of a flood layer only 1 day after the beginning of the flood event (**Figure 7**). Together with subsequent observations by Cathalot et al. (2010) (see above) they suggest an almost immediate effect of the hydrological regime of the Rhône River on the composition of benthic macrofauna within its delta front and prodelta. Moreover, the analysis of temporal changes in benthic macrofauna compositions in the delta front and the prodelta shows that May 2008 (during a generalized flood) was intermediate between December 2008 (26 days after a Cevenol flood) and April 2007 (42 days after an oceanic flood). This underlines the importance of the type of floods relative to the time lag between last flood and sampling in affecting benthic macrofauna composition within the delta front.

Spatiotemporal changes in benthic macrofauna composition were much more reduced in the distal zone. Salen-Picard et al. (2003) reported a high interannual variability at a 70 m deep station which was attributed to interannual changes in the hydrological regime of the Rhône River. The results of the ANOSIM test support the existence of such variability, even though the overall weakness of differences in benthic macrofauna composition associated with 4 contrasted hydrological conditions clearly complicates the assessment of a causal relationship between water flows and benthic fauna compositions. The analysis of between-cruises similarities in benthic macrofauna compositions at stations in the distal zone shows that July 2011 was closest to December 2008 and farthest from April 2007, which differs from what was observed in the delta front and prodelta (see above). The balance between the 2 opposite effects constitutive of the Rhoads et al. (1985) model thus clearly differs in the delta front and in the distal zone. In the former, negative effects are most pronounced due to high sedimentation (Zuo et al., 1997; Miralles et al., 2005) and direct inputs of POM are occasionally so high that they negatively affect benthic macrofauna (Pearson and Rosenberg, 1978; Labrune et al., 2012). Conversely, disturbances resulting from sedimentation and direct POM inputs are much smaller in the distal zone, which tend to switch the overall balance of the effects of floods towards positive values. Such discrepancies between the delta front and the prodelta, and the distal zone probably account for differences in the nature and the intensity of the response of benthic macrofauna composition to changes in the hydrological regime of the Rhône River. They are as well likely to account for differences in the time lag associated with these responses since the negative effect of sedimentation is almost immediate (Wheatcroft, 2006), whereas, for some feeding types at least, the response to changes in POM availability is much longer (Salen-Picard et al., 2003).

4.4 Relationship between sediment characteristics and benthic macrofauna

Sediments characteristics, in general, and organic matter availability, in particular, are known to largely control both the spatial and temporal patterns of benthic macrofauna composition (Pearson and Rosenberg, 1978; Grémare et al., 2002; Labrune et al., 2012). The other way around, benthic macrofauna may also alter both the physical and biogeochemical properties of marine sediments through nutrition and/or bioturbation (Meysman et al., 2006; Bernard et al., 2012). Both of these interactions may contribute to the correlation between sediment characteristics and benthic macrofauna composition. Based on the sampling of 16 stations during April 2007, Labrune et al. (2012) reported that spatial changes in benthic macrofauna composition off the Rhône River mouth correlated with the OC contents of surface sediments. Pastor et al. (2011b) reported a similar correlation between OC and benthic oxygen consumption, with no significant effect of the quality/lability of sedimentary organics, which they attributed to the strong dominance of the organic matter source constituted by the inputs from the Rhône River. Results from the present study show that spatiotemporal changes in benthic macrofauna composition are best described when combining 4 factors including $D_{0.5}$, EHAA, Chl-*a*/(Chl-*a*+Phaeo-*a*) and Chl-*b*/Chl-*a*. Besides sediment granulometry ($D_{0.5}$), these include a quantitative descriptor of a labile component of sedimentary organics (EHAA) and a qualitative descriptor of sedimentary organics (Chl-*a*/(Chl-*a*+Phaeo-*a*)). Results from the present study thus support the better correlation found between meiofauna abundance and quantitative descriptors of labile (i.e., EHAA and lipids) rather than bulk (i.e., OC, TN and THAA) components of sedimentary organics already found in the open Gulf of Lions (Grémare et al., 2002). Moreover, they suggest that temporal changes in the quality of sedimentary organics in relation with changes in the hydrological regime of the Rhône River contribute to control temporal changes in the composition of benthic macrofauna.

There are however several lines of evidences suggesting that these parameters are not the only ones accounting for differences between the compositions of benthic macrofauna during July 2011 and the 3 other dates. First, OC and EHAA contents in the delta front and the prodelta were almost equivalent during April 2007 and July 2011, whereas the characteristics and the compositions of benthic macrofauna conversely strongly differed between these 2 dates. Second, the co-variation between abundance, SR and J’ did not match the classical Pearson and Rosenberg (1978) model since low evenness were associated with high abundances but also with high SR during July 2011. It is therefore likely that spatiotemporal changes in benthic macrofauna composition were also affected by other factors than the Rhône River water flow and resulting organic inputs. High abundances of small individuals of the dominant polychaete *Sternaspis scutata* (Polychaeta) during July 2011 may for instance result from a recent recruitment. This hypothesis is consistent with the reported preferential recruitment of this species during summertime in the Chinhae Bay (Lim and Hong, 1996). However, Hermand et al. (2008) reported the preferential recruitment of *S. scutata* (Polychaeta) during wintertime (i.e., December and January) off the Rhône River, which suggest that high abundances of *S. scutata* (Polychaeta) in the delta front and the prodelta in July 2011 are indeed associated with low water fluxes and do not result from an interaction with its lifecycle. This is further supported by the fact that low water flow periods are known to enhance the colonization of more inshore zones of the Amazon continental shelf by juveniles of benthic macrofauna (Aller and Stupakoff, 1996).

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REFERENCES

Akoumianaki, I., Nicolaidou, A., 2007. Spatial variability and dynamics of macrobenthos in a Mediterranean delta front area: the role of physical processes. Journal of Sea Research 57, 47–64.

Akoumianaki, I., Papaspyrou, S., Kormas, K.A., Nicolaidou, A., 2013. Environmental variation and macrofauna response in a coastal area influenced by land runoff. Estuarine, Coastal and Shelf Science 132, 34–44.

Aller, J.Y., Aller, R.C., 1986. General characteristics of benthic faunas on the Amazon inner continental shelf with comparison to the shelf off the Changjiang River, East China Sea. Continental Shelf Research 6, 291–310.

Aller, J.Y., Stupakoff, I., 1996. The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. Continental Shelf Research 16, 717–751.

Aller, R.C., 1998. Mobile deltaic and continental shelf muds as suboxic, fluidized bed reactors. Marine Chemistry 61, 143–155.

Alliot, E., Younes, W.A.N., Romano, J.C., Rebouillon, P., Massé, H., 2003. Biogeochemical impact of a dilution plume (Rhone River) on coastal sediments. Estuarine, Coastal and Shelf Science 57, 357–367.

Aloisi, J.C., 1986. Sur un modèle de sédimentation deltaïque: contribution à la connaissance des marges passives. Ph.D. Thesis, Université de Perpignan.

Aloïsi, J.C., Monaco, A., 1975. La sédimentation infralittorale. Les prodeltas nord-méditerranéens. Comptes Rendus de l'Académie des Sciences de Paris 280, 2833–2836.

Aloisi, J.C., Auffret, G.A., Auffret, J.P., Barusseau, J.P., Hommeril, P., Larsonneur, C., Monaco, A., 1977. Essai de modélisation de la sédimentation actuelle sur les plateaux continentaux français. Bulletin de la Société Géologique Française 7, 182–195.

Antonelli, C., Eyrolle, F., Rolland, B., Provansal, M., Sabatier, F., 2008. Suspended sediment and ^{137}Cs fluxes during the exceptional December 2003 flood in the Rhone River, southeast France. Geomorphology 95, 350–360.

Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M., Wilson, M.A., 1992. Aspects of the chemical structure of soil organic materials as revealed by solid–state ^{13}C NMR spectroscopy. Biogeochemistry 16, 1–42.

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.

Bianchi, T.S., Mitra, S., McKee, B.A., 2002. Sources of terrestrially-derived organic carbon in lower Mississippi River and Louisiana shelf sediments: implications for differential sedimentation and transport at the coastal margin. Marine Chemistry 77, 211–223.

Bourgeois, S., Pruski, A.M., Sun, M.Y., Buscail, R., Lantoine, F., Kerhervé, P., Vétion, G., Rivière, B., Charles, F., 2011. Distribution and lability of land-derived organic matter in the surface sediments of the Rhône prodelta and the adjacent shelf (Mediterranean Sea, France): a multi proxy study. Biogeosciences 8, 3107–3125.

Bourrin, F., Durrieu de Madron, X., Ludwig, W., 2006. Contribution to the study of coastal rivers and associated prodeltas to sediment supply in Gulf of Lions (NW Mediterranean Sea). Vie et Milieu 56, 307–314.

Buscail, R., Pocklington, R., Germain, C., 1995. Seasonal variability of the organic matter in a sedimentary coastal environment: sources, degradation and accumulation (continental shelf of the Gulf of Lions – Northwestern Mediterranean Sea). Continental Shelf Research 15, 843–869.

Cathalot, C., Rabouille, C., Pastor, L., Deflandre, B., Viollier, E., Buscail, R., Grémare, A., Treignier, C., Pruski, A.M., 2010. Temporal variability of carbon recycling in coastal sediments influenced by rivers: assessing the impact of flood inputs in the Rhône River prodelta. Biogeosciences 7, 1187–1205.

Cathalot, C., Rabouille, C., Tisnérat-Laborde, N., Toussaint, F., Kerhervé, P., Buscail, R., Loftis, K., Sun, M.Y., Tronczynski, J., Azoury, S., Lansard, B., Treignier, C., Pastor, L., Tesi, T., 2013. The fate of river organic carbon in coastal areas: a study in the Rhône River delta using multiple isotopic ($\delta^{13}C$, $\Delta^{14}C$) and organic tracers. Geochimica et Cosmochimica Acta 118, 33–55.

Cauwet, G., Gadel, F., Sierra, M.M.D., Donard, O., Ewald, M., 1990. Contribution of the Rhone River to Organic-Carbon Inputs to the Northwestern Mediterranean-Sea. Continental Shelf Research 10, 1025–1037.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366, 56–69.

Cruzado, A., Velásquez, Z., 1990. Nutrients and phytoplankton in the Gulf of Lions, northwestern mediterranean. Continental Shelf Research 10: 931–942.

Durrieu de Madron, X., Abassi, A., Heussner, S., Monaco, A., Aloisi, J.C., Radakovitch, O., Giresse, P., Buscail, R., Kerhervé, P., 2000. Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanologica Acta 23, 717–730.

Eyrolle, F., Radakovitch, O., Raimbault, P., Charmasson, S., Antonelli, C., Ferrand, E., Aubert, D., Raccasi, G., Jacquet, S., Gurriaran, R., 2012. Consequences of hydrological events on the delivery of suspended sediment and associated radionuclides from the Rhône River to the Mediterranean Sea. Journal of Soils and Sediments 12, 1479–1495.

Goni, M.A., Ruttenberg, K.C., Eglinton, T.I., 1998. A reassessment of the sources and importance of land-derived organic matter in surface sediments from the Gulf of Mexico. Geochimica et Cosmochimica Acta 62, 3055–3075.

Gordon, E.S., Goni, M.A., 2003. Sources and distribution of terrigenous organic matter delivered by the Atchafalaya River to sediments in the northern Gulf of Mexico. Geochimica et Cosmochimica Acta 67, 2359–2375.

Grémare, A., Medernach, L., De Bovee, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). Marine Ecology Progress Series 234, 85–94.

Harmelin–Vivien, M.L., Bănaru, D., Dierking, J., Hermand, R., Letourneur, Y., Salen-Picard, C., 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). Animal Biodiversity and Conservation 32, 135–145.

Hedges, J.I., Clark, W.A., Cowie, G.L., 1988. Organic matter sources to the water column and surficial sediments of a marine bay. Limnology and Oceanography 33, 1116–1136.

Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Marine Chemistry 49, 81–115.

Hedges, J.I., Keil, R.G., Benner, R., 1997. What happens to terrestrial organic matter in the ocean? Organic Geochemistry 27, 195–212.

Hermand, R., Salen-Picard, C., Alliot, E., Degiovanni, C., 2008. Macrofaunal density, biomass and composition of estuarine sediments and their relationship to the river plume of the Rhone River (NW Mediterranean). Estuarine, Coastal and Shelf Science 79, 367–376.

Jeffrey, S.W., 1976. A report of green algal pigments in the central North Pacific Ocean. Marine Biology 37, 33–37.

Labrune, C., Romero-Ramirez, A., Amouroux, J.M., Duchêne, J.C., Desmalades, M., Escoubeyrou, K., Buscail, R., Grémare, A., 2012. Comparison of ecological quality indices based on benthic macrofauna and sediment profile images: a case study along an organic enrichment gradient off the Rhône River. Ecological Indicators 12, 133–142.

Lansard, B., Rabouille, C., Denis, L., Grenz, C., 2009. Benthic remineralization at the land–ocean interface: a case study of the Rhône River (NW Mediterranean Sea). Estuarine, Coastal and Shelf Science 81, 544–554.

Leeuw, J.W., Largeau, C., 1993. A review of macromolecular organic compounds that comprise living organisms and their role in kerogen, coal, and petroleum formation, in Organic Geochemistry (Eds. M.H. Engel and S.A. Macko). Springer US, pp. 23–72.

Leithold, E.L., Hope, R.S., 1999. Deposition and modification of a flood layer on the northern California shelf: lessons from and about the fate of terrestrial particulate organic carbon. Marine Geology 154, 183–195.

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4, 430–451.

Lim, H.S., Hong, J.S., 1996. Distribution and growth pattern of *Sternaspis scutata* (Polychaeta: Sternaspidae) in Chinhae Bay, Korea. Journal of the Korean Fisheries Society 29, 537–545.

Lindroth, P., Mopper, K., 1979. High performance liquid chromatographic determination of subpicomole amounts of amino acids by precolumn fluorescence derivatization with o-phthaldialdehyde. Analytical Chemistry 51, 1667–1674.

Lochet, F., Leveau, M., 1990. Transfers between a eutrophic ecosystem, the river Rhône, and an oligotrophic ecosystem, the north-western Mediterranean Sea. Hydrobiologia 207, 95–103.

Marion, C., Dufois, F., Arnaud, M., Vella, C., 2010. In situ record of sedimentary processes near the Rhône River mouth during winter events (Gulf of Lions, Mediterranean Sea). Continental Shelf Research 30, 1095–1107.

Mayer, L. 1994. Surface area control of organic carbon accumulation in continental shelf sediments. Geochimica et Cosmochimica Acta 58, 1271–1284.

Mayer, L.M., Schick, L.L., Allison, M.A., 2008. Input of nutritionally rich organic matter from the Mississippi River to the Louisiana coastal zone. Estuaries and Coasts 31, 1052–1062.

Mayer, L.M., Schick, L.L., Sawyer, T., Plante, C.J., Jumars, P.A., Self, R.L., 1995. Bioavailable amino acids in sediments: a biomimetic, kinetics-based approach. Limnology and Oceanography 40, 511–520.

McKee, B.A., Aller, R.C., Allison, M.A., Bianchi, T.S., Kineke, G.C., 2004. Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: benthic boundary layer and seabed processes. Continental Shelf Research 24, 899–926.

Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chemical Geology 114, 289–302.

Meysman, J.F.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look ar Darwin’s las idea. Trends in Ecology & Evolution 12, 688–695.

Miralles, J., Radakovitch, O., Aloisi, J.C., 2005. ^{210}Pb sedimentation rates from the Northwestern Mediterranean margin. Marine Geology 216, 155–167.

Neveux, J., Lantoine, F., 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least-square approximation technique. Deep Sea Research Part I: Oceanographic Research Papers 40, 1747–1765.

Occhipinti-Ambrogi, A., Savini, D., Forni, G., 2005. Macrobenthos community structural changes off Cesenatico coast (Emilia Romagna, Northern Adriatic), a six-year monitoring programme. Science of The Total Environment 353, 317–328.

Pastor, L., Cathalot, C., Deflandre, B., Viollier, E., Soetaert, K., Meysman, F.J.R., Ulses, C., Metzger, E., Rabouille, C., 2011a. Modeling biogeochemical processes in sediments from the Rhône River prodelta area (NW Mediterranean Sea). Biogeosciences 8, 1351–1366.

Pastor, L., Deflandre, B., Viollier, E., Cathalot, C., Metzger, E., Rabouille, C., Escoubeyrou, K., Lloret, E., Pruski, A.M., Vétion, G., Desmalades, M., Buscail, R., Grémare, A., 2011b. Influence of the organic matter composition on benthic oxygen demand in the Rhône River prodelta (NW Mediterranean Sea). Continental Shelf Research 31, 1008–1019.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic sucession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16, 229–311.

Pont, D., 1997. Les débits solides du Rhône à proximité de son embouchure: données récentes (1994–1995). Revue de Géographie de Lyon 72, 23–33.

Pont, D., Simonnet, J.P., Walter, A.V., 2002. Medium-term changes in suspended sediment delivery to the ocean: consequences of catchment heterogeneity and river management (Rhône River, France). Estuarine, Coastal and Shelf Science 54, 1–18.

Radakovitch, O., Charmasson, S., Arnaud, M., Bouisset, P., 1999. ^{210}Pb and caesium accumulation in the Rhône delta sediments. Estuarine, Coastal and Shelf Science 48, 77–92.

Rhoads, D.C., Boesch, D.F., Zhican, T., Fengshan, X., Liqiang, H., Nilsen, K.J., 1985. Macrobenthos and sedimentary facies on the Changjiang delta platform and adjacent continental shelf, East China Sea. Continental Shelf Research 4, 189–213.

Romero-Ramirez, A., Grémare, A., Desmalades, M., Duchêne, J.C., 2013. Semi-automatic analysis and interpretation of sediment profile images. Environmental Modelling and Software 47, 42–54.

Roussiez, V., Ludwig, W., Probst, J.L., Monaco, A., 2005. Background levels of heavy metals in surficial sediments of the Gulf of Lions (NW Mediterranean): an approach based on ^{133}Cs normalization and lead isotope measurements. Environmental Pollution 138, 167–177.

Salen-Picard, C., Arlhac, D., Alliot, E., 2003. Responses of a Mediterranean soft bottom community to short-term (1993–1996) hydrological changes in the Rhone River. Marine Environmental Research 55, 409–427.

Tesi, T., Miserocchi, S., Goni, M.A., Langone, L., 2007. Source, transport and fate of terrestrial organic carbon on the western Mediterranean Sea, Gulf of Lions, France. Marine Chemistry 105, 101–117.

Ulses, C., Estournel, C., Durrieu de Madron, X., Palanques, A., 2008. Suspended sediment transport in the Gulf of Lions (NW Mediterranean): impact of extreme storms and floods. Continental Shelf Research 28, 2048–2070.

Vonk, J.E., Sánchez-García, L., Semiletov, I., Dudarev, O., Eglinton, T., Andersson, A., Gustafsson, Ö., 2010. Molecular and radiocarbon constraints on sources and degradation of terrestrial organic carbon along the Kolyma paleoriver transect, East Siberian Sea. Biogeosciences 7, 3153–3166.

Wakeham, S.G., Lee, C., Hedges, J.I., Hernes, P.J., Peterson, M.J., 1997. Molecular indicators of diagenetic status in marine organic matter. Geochimica et Cosmochimica Acta 61, 5363–5369.

Wakeham, S.G., Canuel, E.A., 2006. Degradation and preservation of organic matter in marine sediments, in Marine organic matter: biomarkers, isotopes and DNA, The Handbook of Environmental Chemistry (Ed. J.K. Volkman). Springer-Verlag, Berlin/Heidelberg, pp. 295–321.

Wheatcroft, R.A., 2006. Time-series measurements of macrobenthos abundance and sediment bioturbation intensity on a flood-dominated shelf. Progress in Oceanography 71, 88–122.

Yu, Z., Zhang, Q., Kraus, T., Dahlgren, R.A., Anastasio, C., Zasoski, R.J., 2002. Contribution of amino compounds to dissolved organic nitrogen in forest soils. Biogeochemistry 61, 173–198.

Zebracki, M., Eyrolle-Boyer, F., Evrard, O., Claval, D., Mourier, B., Gairoard, S., Cagnat, X., Antonelli, C., 2015. Tracing the origin of suspended sediment in a large Mediterranean river by combining continuous river monitoring and measurement of artificial and natural radionuclides. Science of the Total Environment 502, 122–132.

Zuo, Z., Eisma, D., Gieles, R., Beks, J., 1997. Accumulation rates and sediment deposition in the northwestern Mediterranean. Deep Sea Research Part II 44, 597–609.

CHAPITRE V

COMPARAISON À LONG TERME ET À GRANDE ÉCHELLE DU STATUT DE LA QUALITÉ ÉCOLOGIQUE DES HABITATS BENTHIQUES DU GOLFE DU LION : MISE EN ŒUVRE DE PLUSIEURS INDICES BIOTIQUES ET DE L'IMAGERIE SÉDIMENTAIRE

LONG-TERM (1998-2010) LARGE-SCALE COMPARISON OF THE ECOLOGICAL QUALITY STATUS OF GULF OF LIONS BENTHIC HABITATS USING SEVERAL BENTHIC INDICES AND SEDIMENT PROFILE IMAGERY

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ABSTRACT

Several questions associated with the use of sensitivity/tolerance based biotic indices to infer the Ecological Quality status of benthic habitats in the Gulf of Lions are addressed during the present study, namely: (1) the effect of the size of the reference data base used when computing $ES50_{0.05}$ (i.e., the species sensitivity/tolerance measure used by BQI) and its consequences on the computation of this index, (2) correlations between the values and differences in the Ecological Quality status attributed by 3 biotic indices (i.e., AMBI, M-AMBI and BQI) and their comparisons with those derived from an independent assessment (i.e., Sediment Profile Imagery), and (3) a long-term (1998 and 2010) large-scale comparison of them. Our results showed: (1) a significant effect of the size of the reference data base on derived $ES50_{0.05}$ and associated BQI values and Ecological Quality Status, (2) a lack of correlation between the values of BQI on one side and AMBI and M-AMBI on the other side and a better agreement of AMBI and M-AMBI than BQI with BHQ (Sediment Profile Imagery derived index), and (3) a general agreement between the 3 tested indices in describing the lack of global trend for the Ecological Quality Status of the Gulf of Lions despite the occurrence of major changes in benthic macrofauna composition between 1998 and 2010. They are discussed in relation with future use and comparisons between biotic indices within the context of the Marine Strategy Framework Directive.

Keywords: Biotic indices, Sediment Profile Imaging, $ES50_{0.05}$, Water Directive, AMBI, M-AMBI, BQI, BHQ, NW Mediterranean

1 INTRODUCTION

The assessment of the Ecological Quality Status (EcoQ) of European marine waters is of increasing interest due to recent policy requirements associated with the Water Framework Directive (WFD; 200/60/EC) and the Marine Strategy Framework Directive (MSFD; 2008/56/EC). In this context, the analysis of benthic macrofauna composition is sound because of some of its characteristics including: reduced motility, existence of sensitive stages and temporal integration capacities. The exact modalities of the use of benthic macrofauna in view of assessing the EcoQ of marine habitats are however clearly still the subject of debates (Grémare et al., 2009).

First, there is still no consensus regarding the biotic index that should be preferentially used. Biotic indices can be either based on the concept of: (1) sensitivity/tolerance (Borja et al., 2000, 2003; Simboura and Zenetos, 2002; Rosenberg et al., 2004; Dauvin and Ruellet, 2007; Muxika et al., 2007) or (2) deviation from a set of reference stations with a good EcoQ (Lavesque et al., 2009). The most widely used (either alone or in combination with other parameters) biotic indices within the WFD are the AZTI Marine Biotic Index (AMBI; Borja et al., 2000), the Multivariate-AMBI (M-AMBI; Muxika et al., 2007) and the Benthic Quality Index (BQI; Rosenberg et al., 2004). They all belong to the first category, and are all based on the Pearson and Rosenberg (1978) paradigm, which describes the response of macrobenthic communities to organic enrichment. These indices, however, differ in the way of assessing species sensitivity/tolerance levels and in the inclusion or not of biodiversity descriptors (e.g. species richness and H' in BQI and M-AMBI) in their computation. Several studies have compared the use of BQI and AMBI on the same benthic macrofauna data sets (Marín-Guirao et al., 2005; Labrune et al., 2006; Fleischer et al., 2007; Grémare et al., 2009; Dimitriou et al., 2012; Labrune et al., 2012). Most of them have concluded to major discrepancies largely due to differences in the sensitivity/tolerance levels attributed to dominant species (Labrune et al., 2006; Grémare et al., 2009).

The assessment of species sensitivity/tolerance levels in AMBI is based on a synthesis of the literature knowledge, which results in a regularly updated list of species to 5 ecological groups (EG; http://ambi.azti.es). Conversely, in BQI, species sensitivity/tolerance levels ($ES50_{0.05}$) are derived from species richness (estimated through ES50) of the stations at which the considered species tend to be present. Assessing $ES50_{0.05}$ thus requires large data sets, which complicates the spread of the use of BQI (Grémare et al., 2009). Based on the MacroBen pan-European database, Grémare et al. (2009) have established 4 lists of $ES50_{0.05}$ for 4 distinct geographic areas including the Mediterranean Sea (www.marbef.org/documents/data/theme1/es50_005.xls) to facilitate the computation of BQI. The magnitude of changes in $ES50_{0.05}$ due to changes in the size of the data set they are computed from is still largely unknown although this parameter may contribute to discrepancies between AMBI and BQI in the assessment of species sensitivity/tolerance levels. The present study therefore firstly aimed at: (1) comparing the $ES50_{0.05}$ provided by Grémare et al. (2009) for the Mediterranean Sea with those derived from a larger data set including the Mediterranean component of the MacroBen database and the results of new studies carried out since then, and (2) assessing the consequences of the use of this new list on BQI computation.

In the case of major discrepancies in EcoQ assessments between biotic indices, an important question becomes: which index is providing the most satisfactory assessment? This question is difficult to tackle otherwise than qualitatively in the absence of independent quantitative information regarding the level of disturbance experienced by the stations to be characterized. In practice, this piece of information is most often lacking. One alternative possibility consists in comparing the outputs derived from the use of biotic indices with those of an independent method of EcoQ assessment (Labrune et al., 2012). The use of Sediment Profile Images (SPIs; Rhoads and Young, 1970; Rhoads and Cande, 1971; Young and Rhoads, 1971; Rhoads and Germano, 1982; see Germano et al., 2011 for review) is especially valuable in this particular context. This technique indeed allows deriving EcoQ from the information (i.e., the presence of biological structures and the vertical zonation of oxidized and reduced sediments) from *in situ* collected images of 2D vertical sections of muddy sediments (Nilsson and Rosenberg, 1997). The semi-automatic processing of SPIs has been recently facilitated by the development of dedicated software (SPIArcBase; Romero-Ramirez et al., 2013). A comparison between the values of the 3 above mentioned biotic indices and the Benthic Habitat Quality index (BHQ; Nilsson and Rosenberg, 1997) as a basis of

SPI-based EcoQ assessment has already been achieved by Labrune et al. (2012) for a set of 16 stations located along a gradient of organic enrichment off the Mouth of the Rhône River. These authors concluded that BQI correlated better with BHQ than AMBI and M-AMBI. There is however no reason to believe that this result necessarily holds for other geographic areas. The second aim of the present study was therefore to assess the relationships between the values and the derived EcoQ of BHQ, AMBI, M-AMBI and BQI based on a set of stations sampled in 2010 (Bonifácio et al., **Chapter II**) and located in the open Gulf of Lions where the natural disturbance gradient is much less marked than off the Rhône River.

The first step of the transformation of a biotic index in an EcoQ is the computation of an Ecological Quality Ratio (EQR), which basically consists in dividing the value of the biotic index at the station which is to be characterized by the value of the same index at a reference station which is known to be in a High EcoQ (e.g., Rosenberg et al., 2004; Kennedy et al. 2011). It is nowadays extremely difficult to identify truly pristine areas, which could be used as references (Warwick et al., 2003). Historical data are thus often used as such (Pearson et al., 1985; Rosenberg et al., 1987; Grémare et al., 1998), which can prove hazardous when the studied communities exhibit long term natural changes, which may result in natural changes in the values of biotic indices and thus in natural changes in derived EcoQ. This is apparently the case in the Gulf of Lions, where Grémare et al. (1998) and then Labrune et al. (2007b) have shown the occurrence of major changes in benthic macrofauna composition between 1967/1968, 1998 and 2003, which are likely related with periodic meteorological oscillations (see also Bonifácio et al., **Chapter III**) and result in drastic changes in the values of some biotic indices despite the apparent lack of major anthropogenic disturbances (Labrune et al., 2006). These authors provided the first large scale assessment of the EcoQ of benthic habitats in the Gulf of Lions based on the sampling of benthic macrofauna carried out in 1998 from the French-Spanish boarder to the Rhône River Mouth. The third aim of the present study therefore consisted in carrying out a long-term and large scale (1998-2010) comparison of the assessment of the EcoQ of the Gulf of Lions benthic habitats based on the re-sampling of the same set of stations and using the very same sampling gear and strategy as Labrune et al. (2007a, 2008).

2 MATERIALS AND METHODS

2.1 ES50$_{0.05}$

The values of ES50$_{0.05}$ established by Grémare et al. (2009) based on the MacroBen database were compared with those derived from an updated database including new data from the Gulf of Lions using a simple linear regression model. The same model was used to assess the relationships between the BQI computed for 3 subsets (based on the proportions of species with an attributed ES50$_{0.05,}$ see below) of sampling events of the updated database using the Grémare et al. (2009) and the updated ES50$_{0.05}$ lists. The slopes and intercepts of the corresponding models were compared using covariance analysis (ANCOVA).

2.2 Biotic indices

Benthic macrofauna composition and sediment granulometry in 2010

Macrobentic fauna was sampled during a cruise carried out on board of the RV *Thetys* II in August 2010. Sampled stations, sampling gear and sample replication scheme were strictly identical to those used by Labrune et al. (2007a, 2008) during their 1998 sampling. Sampled stations were located along 21 inshore-offshore transects (A-U) between the Spanish border and the Mouth of the Rhône River (**Figure 1**). Almost all transects were sampled at 10, 20, 30, 40 and 50 m depths. Overall, 101 stations were sampled. Benthic macrofauna was collected using a 0.1m² van Veen grab (3 replicates per site). Samples were sieved on a 1 mm mesh and fixed with 5% buffered formalin in seawater on board. Back at the laboratory, benthic macrofauna was manually sorted, identified to the lowest tractable taxa (i.e., most often species) and counted. Unidentified taxa were only taken into account when they could not be mistaken for other identified taxa. This procedure allowed for a direct comparison (i.e., between 1998 and 2010) at 91 stations (**Figure 1**). Taxa lists were homogenized between sampling years to avoid discrepancies in taxonomic resolution between the two studies (Labrune et al., 2008). Synonyms of scientific names of species were updated using the World Marine Register of Marine Species

(WoRMS, 2014). Species with possible doubtful identifications were pooled to homogenize species lists and taxonomic resolutions between 1998 and 2010. Univariate PERMANOVAs (Anderson, 2001; McArdle and Anderson, 2001) were used to assess changes in global descriptors (i.e., SR and abundance) of benthic macrofauna with depth. An additional grab was collected at each station. The upper half centimetre of its sediment content was sampled, homogenized and frozen (-20°C) on board. Back at the laboratory, sediment granulometry was assessed using a Malvern Mastersizer® 2000 laser microgranulometer. Here again, a univariate PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001) was used to assess the effect of depth on sediment $D_{0.5}$.

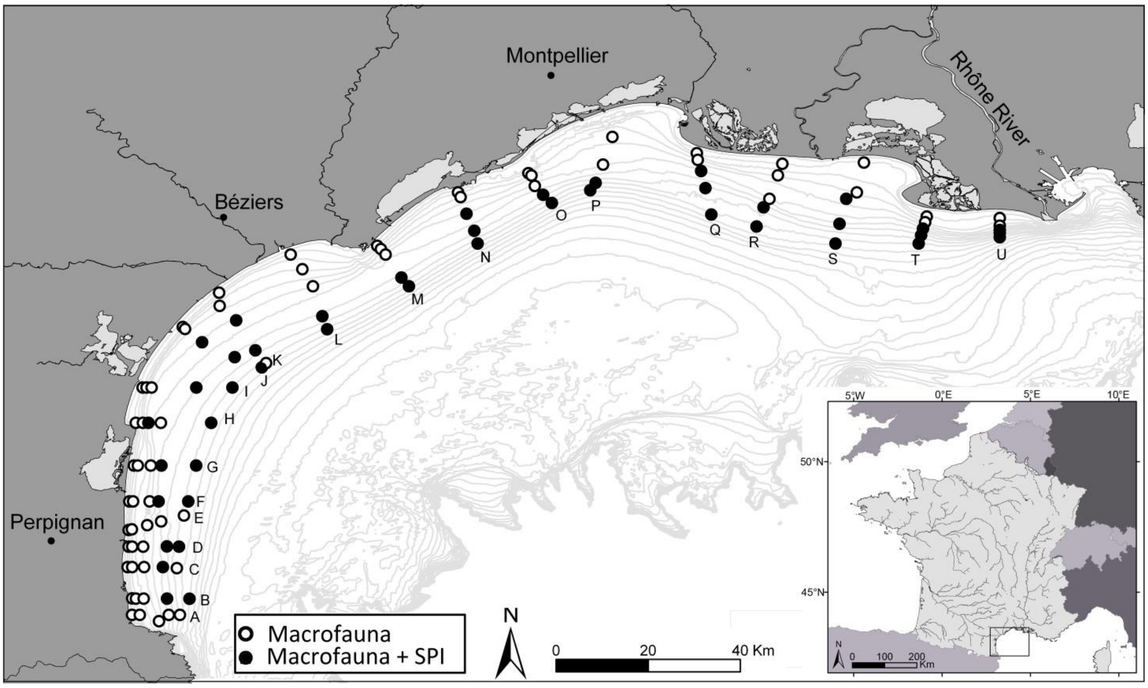

Figure 1: Map of the studied area showing the localizations of the 21 transects (A-U) and of the 101 stations sampled during the present study.

Computation of biotic indices

Macrofauna data were used to compute 3 biotic indices, namely: AMBI (Borja et al., 2000), M-AMBI (Muxika et al., 2007) and BQI (Rosenberg et al., 2004).

As stated above, AMBI uses a single expert based classification of macrobenthic species in 5 EG corresponding to different sensitivity/tolerance levels.

AMBI varies between 0 and 7. It does not compute any EQR and uses a single conversion scale into EcoQ. During the present study, AMBI was computed using the AMBI software (http://ambi.azti.es) and the October 2013 species EG classification. AMBI values were converted in EcoQ using the threshold values proposed by Borja et al. (2004) (**Table 1**).

M-AMBI is based on a multivariate approach that integrates species richness (SR), the Shannon diversity index (H’) and AMBI (Muxika et al., 2007). Besides the stations to be analyzed, M-AMBI also considers two hypothetical reference stations corresponding respectively to a high and a bad EcoQ. M-AMBI ranges between 0 and 1 and basically corresponds to the orthogonal projection, in a reduced space, of each station along the straight line linking the bad and high hypothetical reference stations. M-AMBI therefore constitutes an EQR, which can later be converted in an EcoQ using a single conversion scale. During the present study, M-AMBI was computed using the AMBI software (http://ambi.azti.es) and the October 2013 EG classification list. M-AMBI values were converted in EcoQ using the threshold values proposed by Muxika et al. (2007) (**Table 1**).

Table 1. Scales used to convert AMBI, M-AMBI, BQI and BHQ values into EcoQ.

Index	BAD	POOR	MODERATE	GOOD	HIGH	Reference
AMBI	(5.5-7.0)	(4.3-5.5)	(3.3-4.3)	(1.2-3.3)	(1.2-0)	Borja et al., 2004
M-AMBI	(0-0.2)	(0.2-0.39)	(0.4-0.53)	(0.6-0.77)	(0.77-1.0)	Muxika et al., 2007
BQI	(0-0.2)	(0.2-0.4)	(0.4-0.6)	(0.6-0.8)	(0.8-1.0)	Rosenberg et al., 2004
BHQ	(0-2)	(2-4)	(4-7)	(7-11)	(11-15)	Rosenberg et al., 2009

BQI (Rosenberg et al., 2004) derives species sensitivity/tolerance levels (i.e., $ES50_{0.05}$) from the distribution of species richness (estimated through ES50) at the stations at which the considered species is present. Assessing $ES50_{0.05}$ thus requires either large data sets or a reference list of $ES50_{0.05}$ for the considered geographic area. BQI varies along a positive open scale. It is converted in EQR by scaling relative to the maximal BQI measured within the considered community (Rosenberg et al., 2004). EQR is then converted in EcoQ based on the division of the 0-1 range in 5 equal classes (Rosenberg et al., 2004; **Table 1**). During the present study, the attribution of a station to a community was based on the direct mode analyses carried out by Labrune et al. (2007a, 2008) and Bonifácio et al. (**Chapter II**) for the 1998 and 2010 samplings, respectively. Overall, the distributions of stations between communities were largely similar for these two sampling dates (Bonifácio et al., **Chapter II**).

Comparison with Sediment Profile Images

Sediment Profile Images (SPIs) were collected in August (21 stations) and November 2010 (22 stations) using an Ocean Imaging Systems® fitted with a Nikon D70 digital simple-lens reflex camera. Since the penetration of this device in sandy sediments is limited (Germano et al., 2011), SPIs were only collected at muddy stations (i.e., mostly at 30, 40 and 50 m depth). At least 8 but most often 10 SPIs were collected at each station. Overall 417 SPIs were collected and then analyzed using the SpiArcBase software (Romero-Ramirez et al., 2013, http://spiarcbase.epoc.u-bordeaux1.fr/). The apparent Redox Potential Discontinuity (aRPD) was automatically computed using a single training dataset composed of 32 SPIs. Biogenic structures (oxic voids, burrows, infauna, tubes and feeding structures) were semi-automatically located, identified and characterized (size and position relative to the water-sediment interface). The Benthic Habitat Quality index (BHQ) was computed from each image according to (Nilsson and Rosenberg, 1997). BHQ considers 3 main components, namely: (1) biogenic structures at the sediment-water interface, (2) biogenic structures within the sediment column and (3) the average depth of the aRPD. BHQ ranges from 0 (bad EcoQ) to 15 (good EcoQ). For each station, average (i.e., between SPIs) BHQ were computed and converted in EcoQ using the threshold values proposed by Rosenberg et al. (2009) (**Table 1**). Simple linear regression models were used to assess the relationships between the values of the 3 above-mentioned biotic indices and BHQ for 2010 sampling events. Univariate PERMANOVAs (Anderson, 2001; McArdle and Anderson, 2001) were used to assess the significance of changes in SPIs characteristics and in BHQ with depth.

Comparisons of biotic indices and derived EcoQ between 1998 and 2010

Simple linear regression models were used to assess the relationships between the values of the three biotic indices in 1998 and 2010. For both years BQI computations were based on the updated $ES50_{0.05}$ list (see above).

3 RESULTS

3.1 Updating of the $ES50_{0.05}$ list

Our updated data base included 1242 stations and 1616 sampling events (1450 with an abundance >50 ind.$0.3m^{-2}$) *versus* 426 stations and 436 sampling events (396 with an abundance >50 ind.$0.3m^{-2}$) in the MacroBen database (**Table 2**). The 474 $ES50_{0.05}$ values computed from our updated data base are available at: http://resomar.cnrs.fr/squelettes/documents/ES50_005Mediterranean2014.txt. These values are between 1.26 (*Capitella capitata*) and 27.17 (*Tuberapseudes echinatus*). $ES50_{0.05}$ values computed by Grémare et al. (2009) and during the present study correlated positively (**Figure 2**). Differences between the two estimates of $ES50_{0.05}$ were between -2 and 2 for almost 70% of the species. The comparison with the y=x line suggests that inconsistencies between the two estimates mostly corresponded to higher $ES50_{0.05}$ values when computed by Grémare et al. (2009) than during the present study (ANCOVA, $p<0.0001$). The largest difference of this kind occurred for *Drilonereis filum* with $ES50_{0.05}$ of 20.27 and 5.45 when computed by Grémare et al. (2009) and during the present study, respectively. Conversely, *Harmothoe antilopes* was quite the unique species which featured a much higher $ES50_{0.05}$ when computed during the present study (i.e., 18.00) than based on Grémare et al. (2009) (i.e., 3.24).

BQI values were computed for only 1604 sampling events (since the benthic macrofauna of 12 of such events were only composed of species with no attributed $ES50_{0.05}$) using the $ES50_{0.05}$ list of Grémare et al. (2009) and the one derived from our updated database. Both values correlated positively ($Y=1.743 + 0,710X$, $r^2=0.887$, $p<0.0001$). The corresponding linear regression model nevertheless significantly differed from the y=x line (ANCOVA, $p<0.0001$), which may result from changes in $ES50_{0.05}$ values and/or in the proportion of individuals with an $ES50_{0.05}$. The updating of the $ES50_{0.05}$ list indeed resulted in an overall significant (Wilcoxon signed rank test, $p<0.001$) increase of 26.9% in the average proportions of individuals with an $ES50_{0.05}$ for the 1604 sampling events of the updated database. In order to unravel these two effects, we divided our data set into 3 subgroups differing in the proportions of individuals with an $ES50_{0.05}$: (1) more than 70% of individuals with an $ES50_{0.05}$ for both ways of computation, (2) more than 70% of individuals with an $ES50_{0.05}$ derived from the present study, (3) less than 70% of individuals with an $ES50_{0.05}$ for both ways of computation. For all 3 groups there were significant ($p<0.001$) correlations between BQI computed using both lists (**Figures 3A, B and C**, respectively). Moreover, there was no significant difference among groups in both the slopes (ANCOVA, p=0.246) and the intercepts (ANCOVA, p=0.534) of corresponding linear regression models even though the lack of fit of those models tended to decrease as the proportion of individuals with an $ES50_{0.05}$ increases. For all 3 subsets, corresponding linear regression models significantly differed from the y=x line (ANCOVA, $p<0.0001$ in all cases).

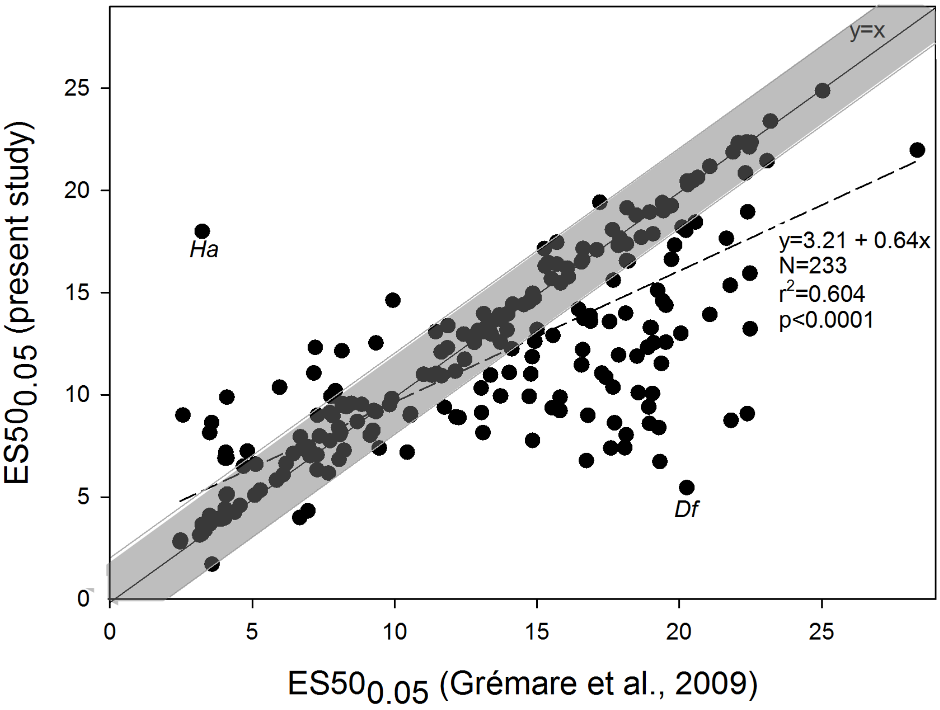

Figure 2. Relationship between the values of $ES50_{0.05}$. from Grémare et al. (2009) and those updated during the present study. The shaded area indicates a <2 absolute difference between the two estimates. Df: *Drilonereis filum*, Ha: *Harmothoe antilopes*. See text for details.

Table 2. Number of stations, and combinations of stations and sampling dates, used for the assessment of ES50$_{0.05}$ by Grémare et al. (2009) and during the present study.

	Location	Nb Stations	Nb of sampling events	Nb of sapling events with abundance > 50 ind.0.3m^{-2}	Temporal range	Reference
MACROBEN DATABASE	**Mediterranean**					
	Gulf of Lions	92			1998	(Vanden Berghe et al., 2009) http://www.marbef.org/modules.php?name=People&module=dataset&dasid=631#ref
	Northern Mediterranean Spanish Coast	2			1992-1997	
	Cretan shelf	255			1986-1997	
	Aegean Sea	29			1937-2000	
	Ionian Sea	19			1990-1992	
	Adriatic Sea	29			1934-2002	
	TOTAL:	426	436	396		
SUPPLEMANTARY DATA	**French Mediterranean (RESOMAR)**					
	Gulf of Lions	443			1967-2011	http://resomar.cnrs.fr/accueil/index.php
	Provencal Coast	98			1961-2009	
	TOTAL:	541	1123	1005		
	Northern Mediterranean Spanish Coast	57	57	49	1999	(Serrano-Samaniego, L.G., 2012)
OVERALL UPDATED DATA BASE	**Mediterranean Sea**	1242	1616	1450	1937-2011	

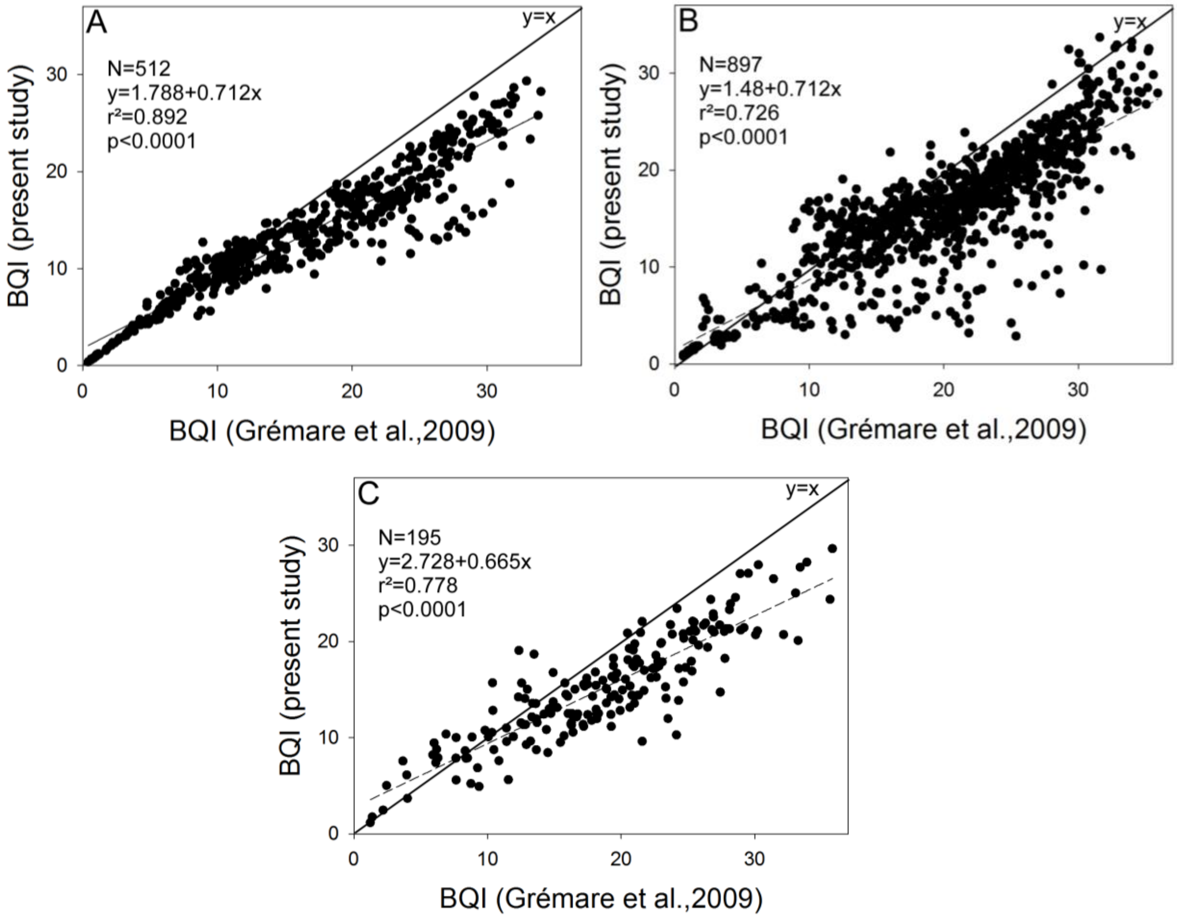

Figure 3. Relationships between BQI computed based on the $ES50_{0.05}$ of Grémare et al. (2009) and those updated during the present study 2010. (A) stations with more than 70% of individuals with an $ES50_{0.05}$ for both ways of computation, (B) stations with more than 70% of individuals with an $ES50_{0.05}$ derived from the present study, (C) stations with less than 70% of individuals with an $ES50_{0.05}$ for both ways of computation.

3.2 2010: Comparison between biotic indices and BHQ

Benthic macrofauna and SPIs

The characteristics of the benthic macrofauna collected in 2010 are fully described in Bonifácio et al. (**Chapter II**). Briefly put, 17191 individuals were collected and 474 taxa identified. The main characteristics of benthic macrofauna at the 5 sampled depths are listed in **Table 3** together with the average ($D_{0.5}$) and the range of median sediment grain size. Average $D_{0.5}$ significantly decreased with depth from ca 157.1 µm at 10 m depth to 21.8 µm at 50 m depth (PERMANOVA, p=0.001). Mean abundances, mean local species richness and overall species richness also changed significantly with depth (PERMANOVA, p=0.001 and p=0.006, for abundance and local species richness, respectively) and were all maximal at 30 m depth.

Different types of biogenic structures were observed in SPIs, namely tubes, oxic voids, burrows and infauna (**Figure 4**). The mean number of biogenic structures observed per image changed significantly with depth (**Table 3**, PERMANOVA, p=0.001). It tended to increase with depth from 6.7 at 30 m depth to 7.5 at 50 m depth. The same pattern was observed for mean aRPD (i.e., from 47.9 mm at 30 m depth to 69.0 mm at 50 m depth, PERMANOVA, p=0.001). A similar trend was observed for BHQ (i.e., from 7.8 at 30 m depth to 8.5 at 50 m depth) but it was not significant (PERMANOVA, p=0.140).

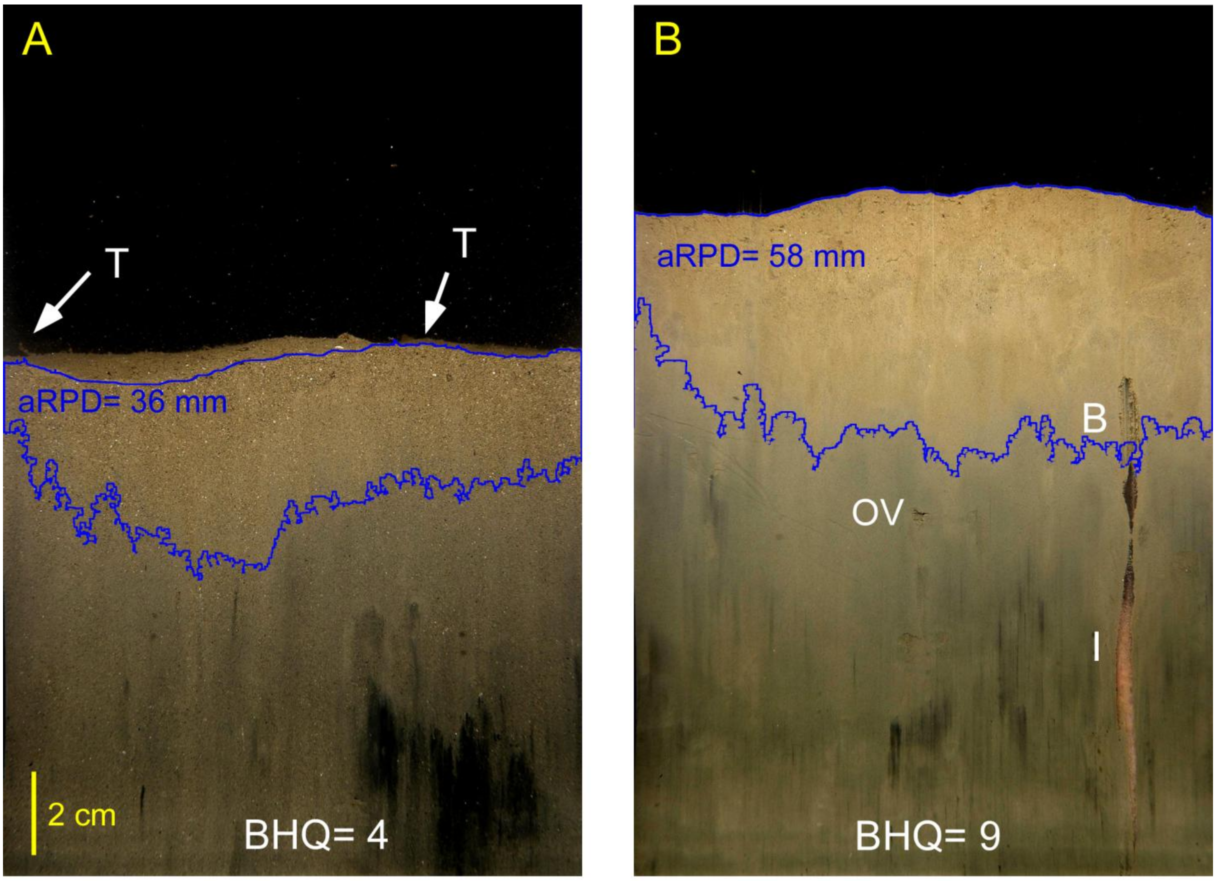

Figure 4. Examples of sediment profile images collected during 2010 at stations H30 (A) and S50 (B), which correspond to contrasted situations in terms of BHQ values. B: Burrow, I: Infauna, T: Tube, OV: Oxic Void. Blue lines correspond to the sediment-water interface and the apparent Redox Potential Discontinuity (aRPD).

Comparison between biotic indices and BHQ

The maps of the EcoQ status derived from the 3 biotic indices and from BHQ are shown in **Figure 5**. All stations were classified as either “Good” or “High” by AMBI and M-AMBI. Both indices tended to classify shallow stations as “High” and deeper stations as “Good”.

Sampled stations were classified from “Poor” to “High” by BQI. As opposed to AMBI and M-AMBI, BQI classified deepest stations (50 m) as “High” except U50 and S50. BHQ classified almost all stations as “Good” except for stations U30 and P40, which were classified as “Moderate”. There was a perfect agreement between the 4 tested indices for 22 of the 43 stations sampled for SPIs. Such an agreement between the 3 biotic indices was observed at 28 sites of the 101 stations sampled for benthic macrofauna.

Table 3. Depth-related changes in the main characteristics of benthic macrofauna global descriptors and sediment profile images.

Benthic macrofauna									Sediment Profile Images						
Depth (m)	**Nb of stations**	**Grain size (µm)**		**Abundance (ind. 0.3m^{-2})**		**Overall species richness**	**Local species richness (taxa 0.3m^{-2})**		**Nb of stations**	**aRPD (mm)**		**Nb of biogenic structures (image^{-1})**		**BHQ**	
		Mean	Range	Mean	Range		Mean	Range		Mean	Range	Mean	Range	Mean	Range
10	19	157.1	79.8 - 208.9	144.6	24 - 276	233	43.2	21 - 56	-	-	-	-	-	-	-
20	21	106.6	37.7 - 180.0	156.0	42 - 350	242	41.8	19 - 68	-	-	-	-	-	-	-
30	20	72.8	32.2 - 124.1	280.8	61 - 661	281	50.6	20 - 79	8	47.9	33.5 - 61.3	6.7	3.1 - 9.3	7.8	5.8 - 9.2
40	20	31.1	19.3 - 46.9	128.7	27 - 256	176	38.7	20 - 59	18	65.0	42.5 - 80.6	7.2	4.1 - 14.6	8.5	6.7 - 10.0
50	21	21.8	16.6 - 33.3	141.7	61 - 299	163	36.3	23 - 49	17	69.0	47.3 - 89.3	7.5	3.9 - 17.4	8.5	7.3 - 10.9

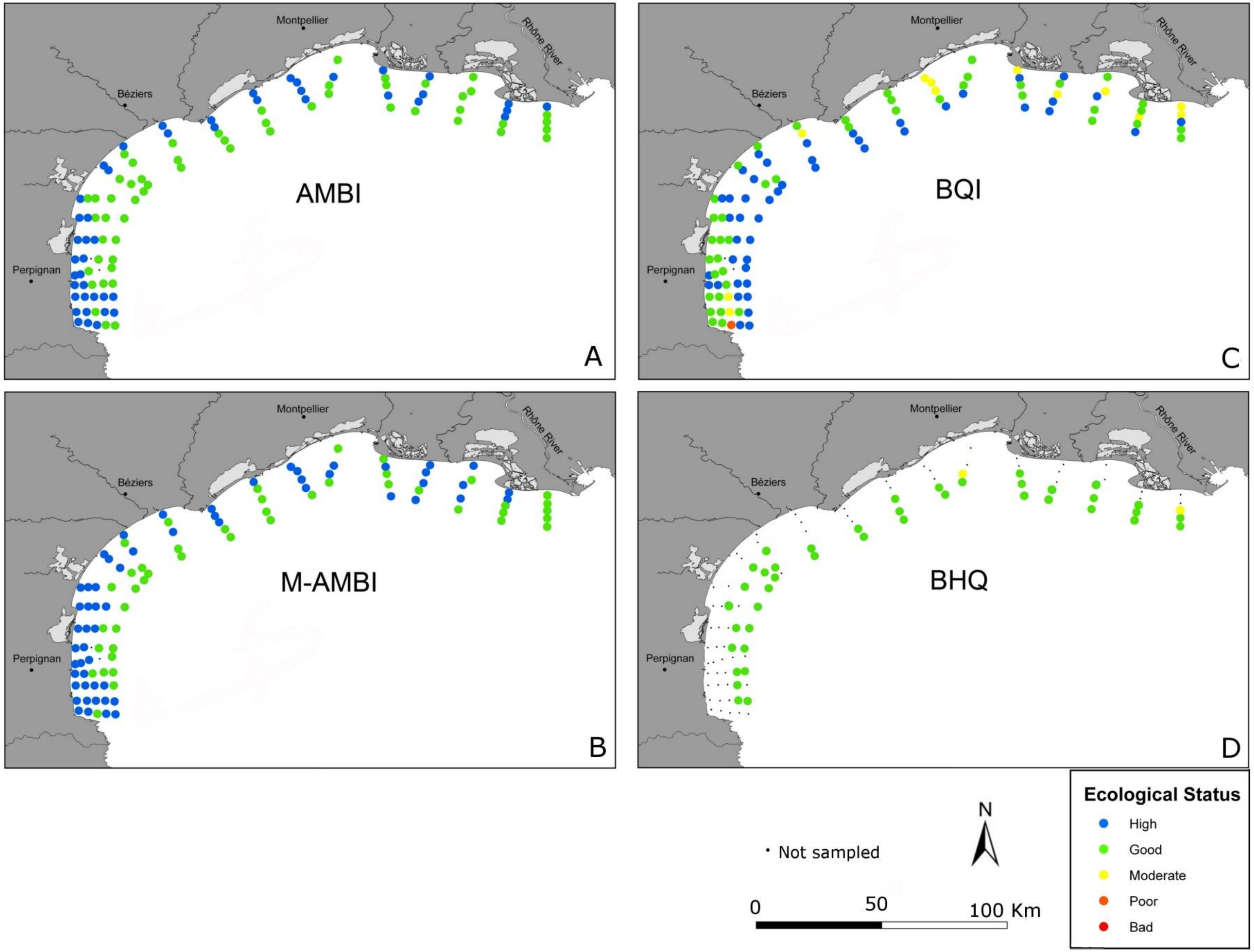

Figure 5. Maps showing the EcoQ of the stations sampled during 2010 as derived from: (A) AMBI, (B) M-AMBI, (C) BQI and (D) BHQ

The relationships between biotic indices and corresponding derived EcoQ status are shown in **Figure 6**. AMBI and M-AMBI correlated negatively (n=101, $r^2=0.47$, $p<0.0001$). Derived EcoQ were similar for 71 of 101 stations. Discrepancies between EcoQ were most numerous for 30 m depth stations. AMBI and BQI correlated positively although weakly (n=101, $r^2=0.28$, $p<0.0001$). Derived EcoQ were similar for only 22 of 101 stations. M-AMBI and BQI did not correlate significantly (n=101, $r^2=0.001$, p=0.75) and derived EcoQ were similar for 32 of 101 stations. Agreements between EcoQ were most numerous at 30 m depth stations.

The relationships between biotic indices derived from macrofauna and SPIs are shown in **Figure 7**. BHQ did not correlate significantly with AMBI (p=0.873), M-AMBI (p=0.537) and BQI (p=0.601). EcoQ derived from BHQ and from AMBI, M-AMBI and BQI were similar for 33, 30 and 12 sites of the 43 sampled sites, respectively. Discrepancies between EcoQ derived from BHQ and M-AMBI were most numerous at 30 m depth stations (**Figure 7E**).

3.3 1998-2010: Comparison of biotic indices and derived EcoQ

1998 and 2010 AMBI values correlated positively (**Figure 8A**; n=91, $r^2=0.44$, $p<0.0001$). Derived EcoQ were similar at 70 stations. There were 14 stations which improved their EcoQ by 1 level and conversely 7 stations with and EcoQ degraded by 1 level between 1998 and 2010 (**Figure 8D**). 1998 and 2010 M-AMBI values also correlated positively but only weakly (**Figure 8B**; n=91, $r^2=0.094$, p=0.003). Derived EcoQ were similar at 56 stations. There were 20 stations, which improved their EcoQ by 1 level and conversely 15 stations with an EcoQ degraded by 1 level between 1998 and 2010 (**Figure 8E**). 1998 and 2010 BQI values (both obtained by using the new $ES50_{0.05}$ list) did not correlate significantly (**Figure 8C**; n=91, $r^2=0.009$, p=0.38). Derived EcoQ were similar at 44 stations. There were 20 and 7 stations, which improved their EcoQ by 1 and 3 levels, respectively. Conversely, there were 16, 3 and 1 stations, with an ECOQ degraded by 1, 2 and 3 levels, respectively (**Figure 8F**).

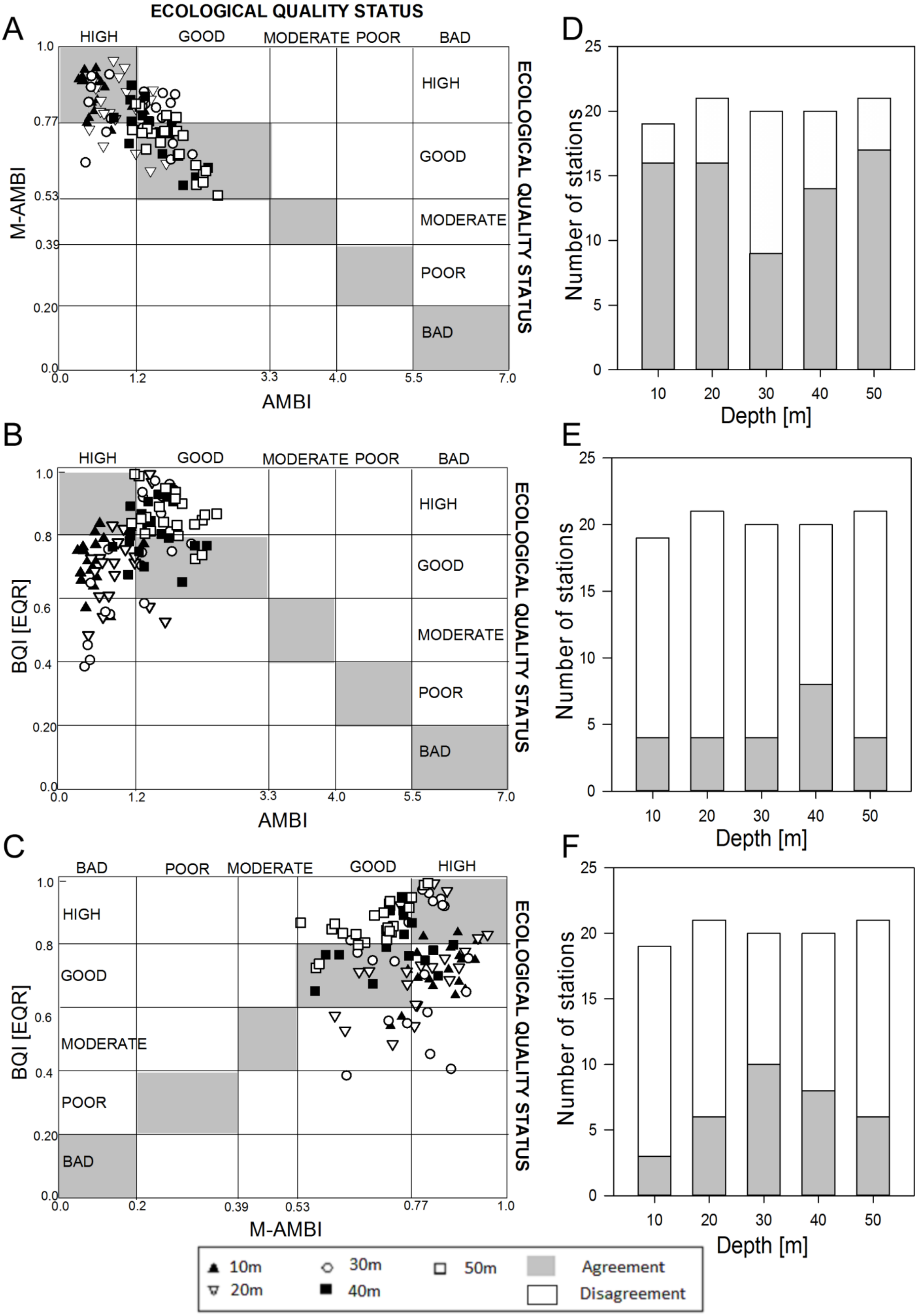

Figure 6. Comparisons of the values of biotic indices during 2010 and of the derived EcoQ: (A) AMBI *versus* M-AMBI, (B) AMBI *versus* BQI, (C) M-AMBI *versus* BQI. The corresponding proportions of agreements/disagreements in EcoQ are shown for each sampled depth in (D), (E) and (F), respectively.

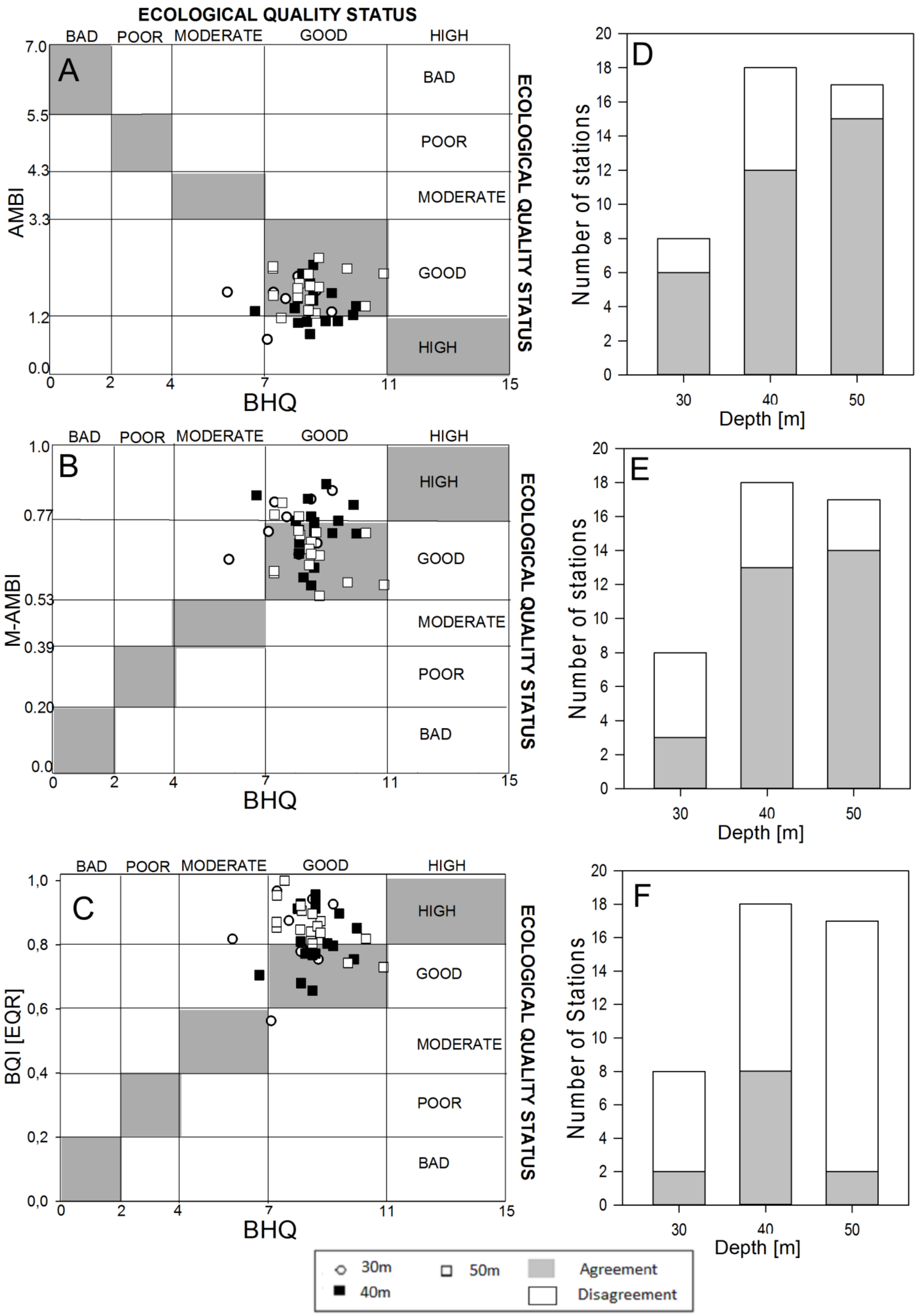

Figure 7. Comparisons of the values of the biotic indices during 2010 and their derived EcoQ with those derived from sediment profile imagery: (A) BHQ *versus* AMBI, (B) BHQ *versus* M-AMBI, (C) BHQ *versus* BQI. The corresponding proportions of agreements/disagreements in EcoQ are shown for each sampled depth in (D), (E) and (F), respectively.

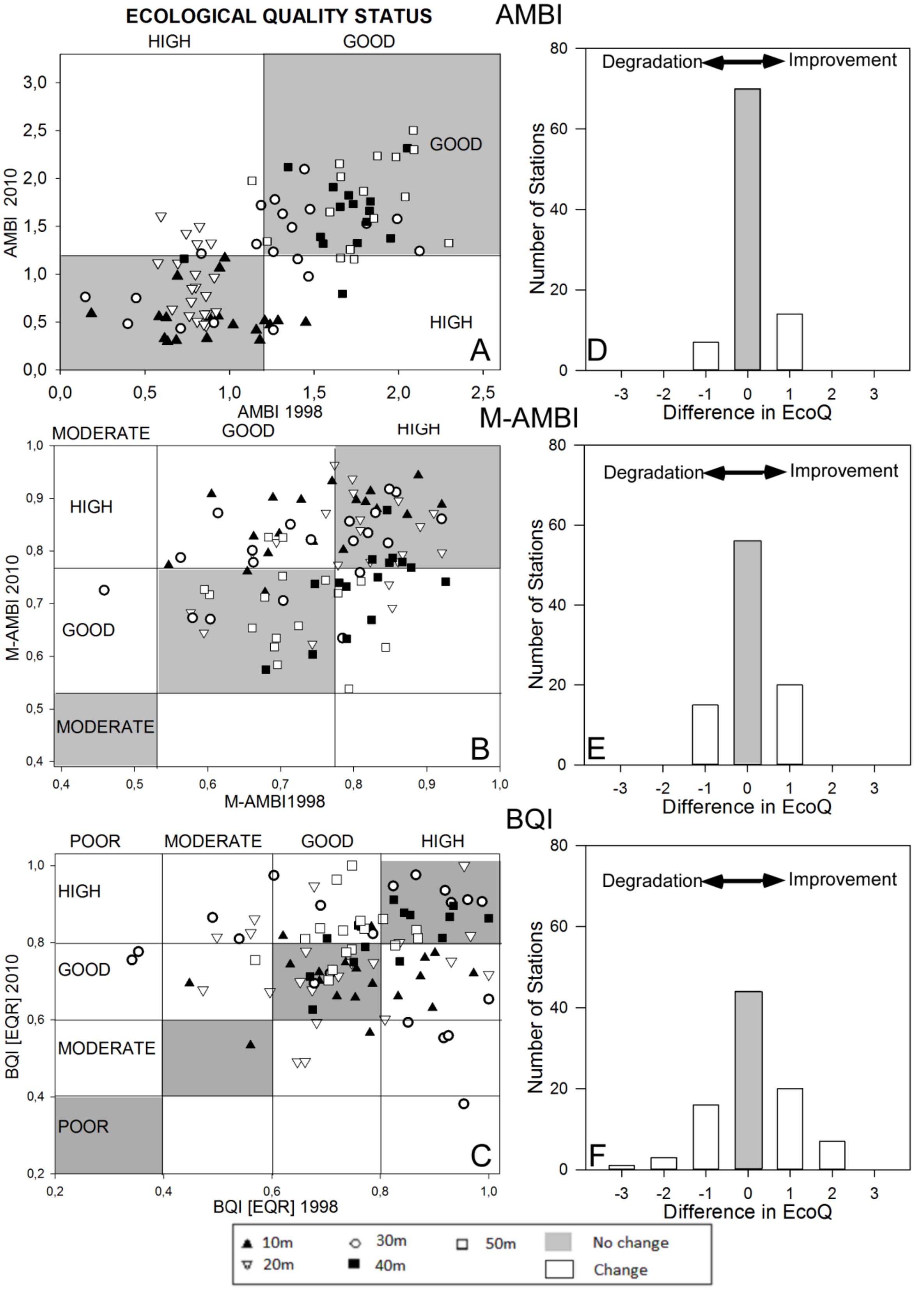

Figure 8. Comparisons of EcoQ between 1998 and 2010 based on: (A) AMBI, (B) M-AMBI and (C) BQI. The frequency distributions of the direction and magnitude of corresponding changes are shown in (D), (E) and (F), respectively.

4 DISCUSSION

4.1 Assessments of $ES50_{0.05}$ based on data sets differing in size

The assessment of species sensitivity/tolerance levels clearly constitutes a key step for the computation of BQI. In order to be sound this assessment must be based on a large array of stations/observations covering the whole range of possible EcoQ, and most importantly containing a significant amount of stations/observations with a bad EcoQ. There are also clear recommendations regarding: (1) minimal abundances (i.e., usually 50) for the stations/observations to be included in the computation, and (2) the minimal number of stations/observations (i.e., usually 20 but Puente and Diaz, 2008) at which a species must be present in order to be attributed an $ES50_{0.05}$ (Rosenberg et al., 2004; Leonardsson et al., 2009). Because of these two constraints and because it is based on the analysis of the frequency distributions of individuals over the ES50 of stations/observations, the computation of BQI typically requires a large data set. This difficulty in the spread of the use of BQI can be overcome by establishing a reference list of $ES50_{0.05}$. However, one of the reasons put forward for using BQI rather than AMBI is that the sensitivity/tolerance level of a given species may vary between geographical areas (Rosenberg et al., 2004). The establishment of a single and universal list of $ES50_{0.05}$ such as the one of AMBI EG is therefore clearly precluded, which led to the elaboration of regional lists (Grémare et al., 2009). Both for theoretical and practical reasons, the current use of BQI is therefore associated with the use of different lists of $ES50_{0.05}$, which are based on data sets largely differing in the number of samples involved (**Table 4**). The use of larger data sets may induce: (1) the possibility of computing $ES50_{0.05}$ values for a larger number of species, and (2) changes in $ES50_{0.05}$ values. Regarding this second point, our results clearly show that: (1) $ES50_{0.05}$, and (2) BQI values within a given regional area are affected by the size of the reference data set. This clearly raises the question of the use of BQI when $ES50_{0.05}$ are derived from rather small data sets. Furthermore, and although the threshold values of the final attribution of an EcoQ differ in each application (because they are based on the maximal BQI value recorded within each community), this may also alter EcoQ assessment depending on: (1) the general linearity of the regression model linking the two assessments of BQI values, and (2) the lack of fit of such a model. Regarding the first of these two points, our results clearly show that a simple linear regression model seems appropriate to describe the relationships linking the BQI values derived from the $ES50_{0.05}$ by proposed by Grémare et al. (2009) and derived from the present study. Regarding the second one, our results clearly show that the lack of fit of this model declines with the proportion of the individuals with an attributed $ES50_{0.05}$. In this sense, they support previous recommendations regarding minimal proportion of individuals which should be attributed a sensitivity/tolerance level.

Table 4. Literature review of the size of the data sets used to assess $ES50_{0.05}$. NP: Not Precised

Regional area	Number of sampling events used to calculate the $ES50_{0.05}$ or reference study	Reference
North Sea	1114	Rosenberg et al. (2004)
North Sea	Rosenberg et al. (2004)	Reiss and Kroncke (2005)
NW Mediterranean Sea	260	Labrune et al. (2006)
Baltic Sea	625	Zettler et al. (2007)
English Channel	604	Dauvin et al. (2007)
English Channel	NP	Ruellet and Dauvin (2007)
NE Atlantic Ocean	174	Puente and Diaz (2008)
English Channel	Dauvin et al. (2007)	Dauvin et al. (2008)
Baltic Sea	912	Fleischer and Zettler (2009)
NE Pacific Ocean	NP	Ranasinghe et al. (2009)
Mediterranean Sea	426	Grémare et al. (2009)
Norwegian and Barents Seas	204	Grémare et al. (2009)
North Sea	11664	Grémare et al. (2009)
NE Atlantic Ocean	115	Grémare et al. (2009)
Mediterranean Sea	NP	Grimes et al. (2010)
Eastern Mediterranean Sea	144	Borja et al. (2011)
Atlantic Ocean	637	Borja et al. (2011)
NE Atlantic Ocean	552	Borja et al. (2011)
North Sea	2245	Borja et al. (2011)
SW Pacific Ocean	4426	Keeley et al. (2012)
Eastern Mediterranean Sea	1010	Dimitriou et al. (2012)
NW Mediterranean Sea	Grémare et al. (2009)	Labrune et al. (2012)
North Sea	NP	Van Hoey et al. (2013)
Mediterranean Sea	Dimitriou et al. (2012)	Karakassis et al. (2013)
SW Pacific Ocean	NP	Keeley et al. (2014)
NW Mediterranean Sea	1616	Present study

4.2 EcoQ status of the Gulf of Lions: comparison between (biotic) indices

During the present study, the correlation between the values of, and the EcoQ attributed by, AMBI and M-AMBI were high, which is not surprising given the fact that AMBI is part of the computation of M-AMBI (Muxika et al., 2007). Our data nevertheless support previous results by Labrune et al. (2006) in showing some discrepancies between AMBI and BQI even though these discrepancies appeared lower, especially for shallow stations due to the decline between 1998 and 2010 of some dominant species (e.g., *Aspidosiphon muelleri*, *Ditrupa arietina*) which are attributed different sensitivity/tolerant levels by the two indices. Labrune et al. (2012) used both organic carbon concentrations and SPIs as independent proxies for the disturbance levels experienced by benthic habitats off the Rhône River to compare EcoQ assessments derived from AMBI, M-AMBI and BQI. During the present study, we also used SPIs to compare the assessments of EcoQ derived from the same 3 biotic indices. Our results show a lack of correlation between BHQ values and those of these 3 indices. They also show a much better match between derived EcoQ for BHQ and AMBI and M-AMBI than for BHQ and BQI. In this sense, they differ from the findings by Labrune et al. (2012) who reported a much better correlation between BHQ and BQI values than between AMBI and M-AMBI values. Obviously, a major difference between the two studies is the range of disturbance experienced by the sampled stations. BHQ values during the present study were between 5.8 and 10.9 *versus* 1.4 and 8.7 for Labrune et al. (2012). Moreover, almost all of the stations sampled during the present study were classified as “Good” by BHQ. This clearly contributed to increase the “noise” when assessing the relationships between BHQ and biotic indices values. Further studies assessing these relationships in more contrasted ecological situations are thus clearly needed.

4.3 EcoQ status of the Gulf of Lions: changes between 1998 and 2010

Besides the absolute values of biotic indices and their derived EcoQ, it is also interesting to assess whether the overall EcoQ of a given ecological system is stable, improving or decreasing. The so-called concept of “trajectory” is explicitly considered within the MSFD. The long-term comparison recently achieved between 1998 and

2010 showed significant changes in benthic macrofauna composition in the Gulf of Lions (Bonifácio et al., **Chapter II**). It was thus interesting to assess the consequences of such changes on the assessments of EcoQ. During the present study, this was achieved independently using the 3 tested biotic indices. Such a comparison could be achieved directly for AMBI because this index is using a single EG reference list and because its conversion scale is fixed and independent of the considered data set. Based on: (1) the similarity of the general maps drawn by Labrune et al. (2006; **Figure 16 in Chapter I**) and during the present study, (2) the fact that the AMBI-derived EcoQ of 77% of the sampled stations remained unchanged between these two dates and (3) the lack of global trend in changes in AMBI-derived EcoQ between these two dates; our results suggest a lack of trend, either negative or positive in temporal changes in the overall EcoQ of benthic habitats in the Gulf of Lions. Although Labrune et al. (2006) did not use M-AMBI, we were able to compute this index and derived EcoQ both in 1998 and 2010. Results were similar to those obtained for AMBI with still a majority (i.e., 62%) of stations with an M-AMBI derived EcoQ, which remained unchanged between 1998 and 2010 and a lack of any global trend for such changes. The situation was slightly different for BQI. The comparison between the general maps drawn by Labrune et al. (2006; **Figure 16 in Chapter I**) and during the present study indeed shows major differences and would suggest an overall improvement of the EcoQ of benthic habitats in the Gulf of Lions. However, it should be pointed out that: (1) Labrune et al. (2006) have derived their $ES50_{0.05}$ from a rather small data set (**Table 4**), (2) $ES50_{0.05}$ values and BQI values are clearly depending on the size of the data set used to derive $ES50_{0.05}$, and (3) potential consequences on EcoQ assessment are more difficult to assess because depending on the shape of the general relationship linking different estimates of BQI and on benthic macrofauna composition at each considered station. In order to unravel this effect, we have used the same updated list for comparing the EcoQ computed using BQI based on the 1998 (Labrune et al., 2006) and the 2010 (present study) samplings. Corresponding results confirmed those obtained for AMBI and M-AMBI with: (1) the occurrence of a (although slightly lower: 48%) majority of stations with a BQI-derived EcoQ unchanged between 1998 and 2010, and (2) the lack of global trend for these changes. From a methodological standpoint, our study therefore clearly shows that the use of different $ES50_{0.05}$ lists not only affects BQI values but also derived EcoQ. Another major result is that despite the occurrence of: (1) major changes in benthic macrofauna composition, and (2) inconsistencies (i.e., mostly between AMBI and M-AMBI on one side and BQI on the other side) in EcoQ assessments, all 3 indices provide a rather similar conclusion regarding the (lack of) temporal trend in the EcoQ of Gulf of Lions benthic habitats between 1998 and 2010.

Labrune et al. (2006) and then Grémare et al. (2009) pinpointed the importance of dominant species in the computation of biotic indices and suggested that these species could account for discrepancies when they are attributed different sensitivity levels by different indices. In 1998, this was the case for the polychaete *Ditrupa arietina* at 10-30 m depth. This species is attributed a rather low $ES50_{0.05}$ (i.e., 3.22) in our updated list. It was much less abundant in 2010 (Bonifácio et al., **Chapter II**) and therefore largely accounted for some of the temporal changes in EcoQ at shallow stations. Guizien et al. (2010) showed that *D. arietina* is highly sensitive to hydrodynamic conditions and frequently spatially redistributed. Consequently, they recommended discarding it from the computation of biotic indices. The analysis of changes in benthic macrofauna composition between 1998 and 2010 shows that the decline of *D. arietina* is general. In addition, its withdrawal would result in a drastic decline of the proportion of individuals with an attributed $ES50_{0.05}$ with important consequences on the computation of BQI. We therefore recommend to keep this particular species in the computation of biotic indices and to continue to assess the environmental factors controlling its population dynamics.

5 CONCLUSION AND FUTURE WORK

The present study primarily consisted in a long-term (1998-2010) and large-scale comparison of the EcoQ of shallow benthic habitats in the Gulf of Lions. To assess this main objective, it was necessary to consider 2 methodological questions: (1) which biotic index (i.e., between AMBI, M-AMBI and BQI) should preferentially be used? and (2) does the size of the reference data base affect the computation of BQI species sensitivity tolerance levels ($ES50_{0.05}$)? Our results first showed a significant effect of the size of the reference data base on derived $ES50_{0.05}$ and associated BQI values. A review of published BQI data suggests that this point should clearly be better considered and constrained during future use of this index. Our results also confirmed the overall lack of agreement between the values and derived EcoQ of BQI on one side and AMBI and M-AMBI on the other side. As opposed to Labrune et al. (2012) they suggest a better agreement of AMBI and M-AMBI than BQI with BHQ values and derived EcoQ. Further studies in ecologically contrasted areas are thus needed to compare the outputs of biotic indices and SPI. Finally, our results show a general agreement between the 3 tested indices in describing the lack of global trend for the Ecological Quality status of the Gulf of Lions despite: (1) the occurrence of major changes in benthic macrofauna composition between 1998 and 2010, and (2) the above mentioned discrepancies between the 3 tested biotic indices.

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REFERENCES

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58, 626–639.

Borja, A., Franco, J., Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Marine Pollution Bulletin 40, 1100–1114.

Borja, A., Muxika, I., Franco, J., 2003. The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Marine Pollution Bulletin 46, 835–845.

Borja, A., 2004. The biotic indices and the Water Framework Directive: the required consensus in the new benthic monitoring tools. Marine Pollution Bulletin 48, 405–408.

Borja, A., Barbone, E., Basset, A., Borgersen, G., Brkljacic, M., Elliott, M., Garmendia, J.M., Marques, J.C., Mazik, K., Muxika, I., Neto, J.M., Norling, K., Rodríguez, J.G., Rosati, I., Rygg, B., Teixeira, H., Trayanova, A., 2011. Response of single benthic metrics and multi-metric methods to anthropogenic pressure gradients, in five distinct European coastal and transitional ecosystems. Marine Pollution Bulletin 62, 499–513.

Dauvin, J.C., Ruellet, T., 2007. Polychaeta/Amphipod ratio revisited. Marine Pollution Bulletin 55, 80–90.

Dauvin, J.C., Ruellet, T., Desroy, N., Janson, A.L., 2007. The ecological quality status of the Bay of Seine and the Seine estuary: Use of biotic indices. Marine Pollution Bulletin 55, 241–257.

Dauvin, J.C., Fisson, C., Garnier, J., Lafite, R., Ruellet, T., Billen, G., Deloffre, J., Verney, R., 2008. A report card and quality indicators for the Seine estuary: from scientific approach to operational tool. Marine Pollution Bulletin 57, 187–201.

Dimitriou, P.D., Apostolaki, E.T., Papageorgiou, N., Reizopoulou, S., Simboura, N., Arvanitidis, C., Karakassis, I., 2012. Meta-analysis of a large data set with Water Framework Directive indicators and calibration of a Benthic Quality Index at the family level. Ecological Indicators 20, 101–107.

Fleischer, D., Grémare, A., Labrune, C., Rumohr, H., Vanden Berghe, E., Zettler, M.L., 2007. Performance comparison of two biotic indices measuring the ecological status of water bodies in the Southern Baltic and Gulf of Lions. Marine Pollution Bulletin 54, 1598–1606.

Fleischer, D., Zettler, M.L., 2009. An adjustment of benthic ecological quality assessment to effects of salinity. Marine Pollution Bulletin 58, 351–357.

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., 1998. 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., Labrune, C., Vanden Berghe, E., Amouroux, J.M., Bachelet, G., Zettler, M.L., Vanaverbeke, J., Fleischer, D., Bigot, L., Maire, O., Deflandre, B., Craeymeersch, J., Degraer, S., Dounas, C., Duineveld, G., Heip, C., Herrmann, M., Hummel, H., Karakassis, I., Kedra, M., Kendall, M., Kingston, P., Laudien, J., Occhipinti-Ambrogi, A., Rachor, E., Sardá, R., Speybroeck, J., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Wlodarska-Kowalczuk, M., Zenetos, A., 2009. Comparison of the performances of two biotic indices based on the MacroBen database. Marine Ecology Progress Series 382, 297–311.

Grimes, S., Ruellet, T., Dauvin, J.C., Boutiba, Z., 2010. Ecological Quality Status of the soft-bottom communities on the Algerian coast: General patterns and diagnosis. Marine Pollution Bulletin 60, 1969–1977.

Guizien, K., Charles, F., Hurther, D., Michallet, H., 2010. Spatial redistribution of *Ditrupa arietina* (soft bottom Mediterranean epifauna) during a moderate swell event. Continental Shelf Research 30, 239–251.

Karakassis, I., Dimitriou, P.D., Papageorgiou, N., Apostolaki, E.T., Lampadariou, N., Black, K.D., 2013. Methodological considerations on the coastal and transitional benthic indicators proposed for the Water Framework Directive. Ecological Indicators 29, 26–33.

Keeley, N.B., Forrest, B.M., Crawford, C., Macleod, C.K., 2012. Exploiting salmon farm benthic enrichment gradients to evaluate the regional performance of biotic indices and environmental indicators. Ecological Indicators 23, 453–466.

Keeley, N.B., Macleod, C.K., Hopkins, G.A., Forrest, B.M., 2014. Spatial and temporal dynamics in macrobenthos during recovery from salmon farm induced organic enrichment: When is recovery complete?. Marine Pollution Bulletin 80, 250–262.

Kennedy, R., Arthur, W., Keegan, B.F., 2011. Long-term trends in benthic habitat quality as determined by Multivariate AMBI and Infaunal Quality Index in relation to natural variability: A case study in Kinsale Harbour, south coast of Ireland. Marine Pollution Bulletin 62, 7, 1427–1436,

Labrune, C., Amouroux, J.M., Sarda, R., Dutrieux, E., Thorin, S.B., Rosenberg, R., Grémare, A., 2006. Characterization of the ecological quality of the coastal Gulf of Lions (NW Mediterranean). A comparative approach based on three biotic indices. Marine Pollution Bulletin 52, 34–47.

Labrune, C., Grémare, A., Amouroux, J.-M., Sardá, R., Gil, J., Taboada, S., 2007a. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuarine, Coastal and Shelf Science 71, 133–147.

Labrune, C., Grémare, A., Guizien, K., Amouroux, J.M., 2007b. Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): A reappraisal. Journal of Sea Research 58, 125–143.

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.

Labrune, C., Romero-Ramirez, A., Amouroux, J.M., Duchêne, J.C., Desmalades, M., Escoubeyrou, K., Buscail, R., Grémare, A., 2012. Comparison of ecological quality indices based on benthic macrofauna and sediment profile images: A case study along an organic enrichment gradient off the Rhône River. Ecological Indicators 12, 133–142.

Lavesque, N., Blanchet, H., de Montaudouin, X., 2009. Development of a multimetric approach to assess perturbation of benthic macrofauna in *Zostera noltii* beds, Journal of Experimental Marine Biology and Ecology 368, 101–112.

Leonardsson, K., Blomqvist, M., Rosenberg, R., 2009. Theoretical and practical aspects on benthic quality assessment according to the EU-Water Framework Directive – Examples from Swedish waters. Marine Pollution Bulletin 58, 1286–1296, Marín-Guirao, L., Cesar, A., Marin, A., Lloret, J., Vita, R., 2005. Establishing the ecological quality status of soft-bottom mining-impacted coastal water bodies in the scope of the Water Framework Directive. Marine Pollution Bulletin 50, 374–387.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

MSFD, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union L164, 19–40.

Muxika, I., Borja, A., Bald, J., 2007. Using historical data, expert judgement and multivariate analysis in assessing reference conditions and benthic ecological status, according to the European Water Framework Directive. Marine Pollution Bulletin 55, 16–29.

Nilsson, H.C., Rosenberg, R., 1997. Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images. Journal of Marine Systems 11, 249–264.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic sucession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16, 229–311.

Pearson, T.H., Josefson, A.B., Rosenberg, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic? Journal of Experimental Marine Biology and Ecology 92, 157–206.

Puente, A., Diaz, R.J., 2008. Is it possible to assess the ecological status of highly stressed natural estuarine environments using macroinvertebrates indices?. Marine Pollution Bulletin 56, 1880–1889.

Ranasinghe, J.A., Weisberg, S.B., Smith, R.W., Montagne, D.E., Thompson, B., Oakden, J.M., Huff, D.D., Cadien, D.B., Velarde, R.G., Ritter, K.J., 2009. Calibration and evaluation of five indicators of benthic community condition in two California bay and estuary habitats. Marine Pollution Bulletin 59, 5–13.

Reiss, H., Kröncke, I., 2005. Seasonal variability of benthic indices: An approach to test the applicability of different indices for ecosystem quality assessment. Marine Pollution Bulletin 50, 1490–1499.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28, 150–178.

Rhoads, D.C., Cande, S., 1971. Sediment profile camera for *in situ* study of organism sediment relations. Limnology and Oceanography 16, 110–114.

Rhoads, D.C., Germano, J.D., 1982. Characterization of organism-sediment relations using sediment profile imaging: An efficient method of remote ecological monitoring of the seafloor (Remots TM System). Marine Ecology Progress Series 8, 115–128.

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., Gray, J.S., Josefson, A.B., Pearson, T.H., 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched?. Journal of Experimental Marine Biology and Ecology 105, 219–251.

Rosenberg, R., Blomqvist, M., Nilsson, H.C., Cederwall, H., Dimming, A., 2004. Marine quality assessment by use of benthic species-abundance distributions: a proposed new protocol within the European Union Water Framework Directive. Marine Pollution Bulletin 49, 728–739.

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.

Ruellet, T., Dauvin, J.C., 2007. Benthic indicators: Analysis of the threshold values of ecological quality classifications for transitional waters. Marine Pollution Bulletin 54, 1707–1714.

Serrano-Samaniego, L.G., 2012. Distribution of soft-bottom polychaetes assemblages at different scales in shallow waters of the nothern Mediterranean Spanish coast. Ph. D Thesis. Universitat de Barcelona: Spain.

Simboura, N., Zenetos, A., 2002. Benthic indicators to use in Ecological Quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. Mediterranean Marine Science 3, 77–111.

Van Hoey, G., Permuy, D.C., Vandendriessche, S., Vincx, M., Hostens, K., 2013. An ecological quality status assessment procedure for soft-sediment benthic habitats: Weighing alternative approaches. Ecological Indicators 25, 266–278.

Vanden Berghe, E., Claus, S., Appeltans, W., Faulwetter. S., Arvanitidis, C., Somerfield, P., Aleffi, I., Amouroux, J.M., Anisimova, N., Bachelet, G., Cochrane, S., Costello, M., Craeymeersch, J., Dahle, S., Degraer, S., Denisenko, S., Dounas, C., Duineveld, G., Emblow, C., Escaravage, V., Fabri, M., Fleischer, D., Grémare, A., Herrmann, M., Hummel, H., Karakassis, I., Kedra, M., Kendall, M., Kingston, P., Kotwicki, L., Labrune, C., Laudien, J., Nevrova, E., Occhipinti-Ambrogi, A., Olsgard, F., Palerud, R., Petrov, A., Rachor, E., Revkov, N., Rumohr, H., Sarda, R., Sistermans, W., Speybroeck, J., Janas, U., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Wlodarska-Kowalczuk, M., Zenetos, A., Zettler, M., Heip, C., 2009. MacroBen integrated database on benthic invertebrates of European continental shelves: a tool for large-scale analysis across Europe. Marine Ecology Progress Series 382, 225–238.

Warwick, R.M., Emblow, C., Féral, J.P., Hummel, H., Avesaath, P.V., Heip., C., 2003. European Marine Biodiversity Research Sites. Netherlands Institute of Ecology - Centre for Estuarine and Marine Ecology, Yerseke, The Netherlands, 2003.

WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Union L327, 1–73.

Young, D. K., Rhoads, D. C., 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Marine Biology 11, 242–254

WoRMS, 2014. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2014-04-10.

Zettler, M.L., Schiedek, D., Bobertz, B., 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. Marine Pollution Bulletin 55, 258–270.

CHAPITRE VI

CONCLUSIONS GÉNÉRALES ET PERSPECTIVES

1 CONCLUSIONS

Les principaux objectifs de mon travail de thèse consistaient à : (1) fournir une description actuelle de la composition des communautés de la macrofaune benthique des substrats meubles du golfe du Lion et étudier leurs variations temporelles, (2) tester l'hypothèse suivant laquelle des phénomènes climatiques pourraient expliquer ces changements, (3) analyser l'impact du Rhône sur la structuration des communautés et (4) évaluer et fournir une cartographie actualisée du statut de qualité écologique des habitats benthiques du golfe du Lion et comparer les résultats obtenus avec l'évaluation effectuée en 1998 par Labrune et al. (2006).

1.1 Description des communautés et comparaison à long terme à l'échelle du golfe du Lion

Le premier résultat issu de la comparaison à long terme des 91 stations échantillonnées sur l'ensemble du golfe du Lion est la conservation des communautés benthiques identifiées par Labrune et al. (2007a). Bien que des changements de composition aient été mis en évidence au sein de chacune de ces communautés entre 1998 et 2010, ces dernières ont conservé leurs principales caractéristiques et leur intégrité, renforçant ainsi l'utilisation de la terminologie proposée par Labrune et al. (2007a) pour les désigner : Sables fins infralittoraux, Vases sableuses littorales et Vases terrigènes côtières.

Ces auteurs ont rapporté l'existence de 2 sous groupes dans la communauté des Vases sableuses littorales: (1) les stations localisées entre l'embouchure du Rhône et le cap d'Agde (à l'exception de celles situées dans la langue sableuse au large de Montpellier) ; et (2) les stations localisées entre le cap d'Agde et la frontière espagnole, moins influencées par le Rhône. Ces 2 sous-groupes ont été également retrouvés en 2010. Afin de consolider ce résultat, l'influence du Rhône sur la composition de la macrofaune benthique a été évaluée à l'aide d'un modèle incluant deux dimensions spatiales : une non-directionnelle et une directionnelle reflétant l'éloignement au Rhône à chaque profondeur (**Chapitre II**). Les résultats ont montré que la partie de la variance expliquée par la composante spatiale directionnelle était toujours (i.e., en 1998 et en 2010) supérieure à celle expliquée par la composante non-directionnelle. Le fait que l'effet de la composante spatiale directionnelle sur la composition des communautés benthiques ait été pratiquement similaire en 1998 et en 2010 est cohérent avec les valeurs voisines que le débit du Rhône présentait lors de ces deux années (**Figure 2A du Chapitre II**).

Les distributions spatiales de la granulométrie et du contenu organique des sédiments du golfe du Lion suivent la distribution classique caractérisée par une réduction de la taille du grain, ainsi que par l'augmentation de la proportion de particules fines et du contenu organique depuis la côte vers le large. Pour ce qui concerne la variation temporelle des caractéristiques du sédiment, seule la communauté des Vases terrigènes côtières (i.e., les stations localisées à 40 et 50 m) ont présenté une granulométrie significativement plus grossière en 2010 qu'en 1998. Grémare et al. (1998a) ont attribué les changements de la granulométrie des sédiments peu profonds aux épisodes de resuspension causés par les tempêtes. Dans le golfe du Lion, ces événements sont associés aux grandes houles qui peuvent exercer un impact direct jusqu'à 30 m de profondeur, voire plus profondément en cas d'événement extrême. En 2010 la NAO, ainsi que sa moyenne mobile de 8 ans, étaient fortement négatives. Nos données semblent donc effectivement suggérer une augmentation de la fréquence des événements de resuspension dans le golfe du Lion en 2010.

Les principales différences dans la composition faunistique des communautés benthiques entre 1998 et 2010 aux stations situées à 30 m de profondeur résident surtout dans: (1) les faibles abondances de la polychète *Ditrupa arietina* en 2010 par rapport à 1998 et (2) au contraire, les fortes abondances du sipunculidé *Aspidosiphon muelleri* en 1998 par rapport à 2010. Ces différences marquées en termes d'abondances et de dominances ont entrainé des valeurs d'équitabilité plus élevées en 2010 qu'en 1998. De plus, les stations à 20 m ont présenté une richesse spécifique plus importante en 1998 qu'en 2010 alors que la tendance était inversée aux stations à 50 m.

1.2 Le rôle des phénomènes climatiques dans l'explication des changements de composition de la macrofaune

Comparaison à long terme à l'échelle du golfe du Lion (1998 et 2010)

A partir de : (1) la comparaison à long terme de la macrofaune benthique à 4 stations de la baie de Banyuls-sur-Mer (Labrune et al., 2007b), et (2) du suivi écologique de la dynamique de population de *Ditrupa arietina* (Grémare et al., 1998), il a été suggéré que les variations temporelles des communautés peu profondes (i.e., les Sables fins infralittoraux et les Vases sableuses littorales) étaient liées aux variations de la fréquence des tempêtes sous le contrôle de la NAO. La fréquence plus élevée des événements de resuspension dans le golfe du Lion pendant les années où l'indice NAO est négatif causerait ainsi un impact négatif sur le recrutement de *D. arietina* (Labrune et al., 2007b). Les résultats obtenus dans le cadre de cette comparaison à long terme sont globalement cohérents avec cette hypothèse puisque 1998 correspond à la fin d'une phase positive de l'indice NAO tandis que 2010 correspond à la fin d'une phase « neutre » et au début d'une phase négative (avec une valeur de l'indice très négative cette année-là). Ces résultats sont également en accord avec des travaux précédemment conduits en mer du Nord qui ont mis en évidence un contrôle des communautés de la macrofaune benthique par la NAO, ainsi qu'en Méditerranée Nord-Occidentale qui ont montré une réduction du débarquement de pêche pendant les années où l'indice NAO est positif. Ces résultats sont également cohérents avec les évolutions des abondances de *D. arietina* rassemblées dans la présente étude pour le golfe du Lion pendant la période 1989-2012 (**Figure 9 du Chapitre II**). En effet, les abondances enregistrées entre 1990 et 2001 (i.e., pendant la phase positive de la NAO) sont globalement plus élevées que celles mesurées après 2001.

Les variations de composition de la macrofaune benthique dans la communauté des Vases terrigènes côtières semblent, quant à elles, liées aux variations de granulométrie des sédiments de surface. L'augmentation de cette granulométrie en 2010 pourrait résulter d'une augmentation de la fréquence, et peut-être de l'intensité des tempêtes. Là encore, ceci serait en accord avec l'hypothèse de Grémare et al. (1998a), telle que modifiée par Labrune et al. (2007b) à propos de la relation entre la NAO, la fréquence des épisodes de resuspension et la granulométrie des sédiments.

Suivi temporel des communautés de la baie de Banyuls-sur-Mer (2004 à 2013)

Afin de vérifier l'hypothèse de l'influence de la NAO sur la composition de la macrofaune benthique du golfe du Lion proposée par Labrune et al. (2007b) et confortée dans le **Chapitre II** de cette thèse, un suivi annuel de la composition de la macrofaune benthique à 4 stations de la baie de Banyuls-sur-Mer a été réalisé entre 2004 et 2013. Ce suivi a permis de mettre en relation la variabilité temporelle de la macrofaune benthique au sein des 4 principales communautés benthiques de cette baie avec : (1) des indices climatiques globaux tels que la NAO (North Atlantic Oscillation), la WeMO (Western Mediterranean Oscillation), (2) d'autres facteurs climatiques tels que la température de l'air, la pression atmosphérique au niveau de la surface, la vitesse des vents, les précipitations ainsi qu'avec un proxy des événements de resuspension proposé par Labrune et al. (2007b) et appelé critère 2 (C2), et (3) des facteurs environnementaux tels que le débit liquide du Rhône et la concentration en matière en suspension en baie de Banyuls-sur-Mer.

Les corrélations entre les différentes formes saisonnières de la NAO et de la WeMO avec les paramètres descriptifs globaux de la macrofaune benthique (richesse spécifique, abondance et biomasse) à chaque station ont mis en évidence que seule la valeur hivernale de l'indice WeMO était corrélée avec certains paramètres globaux de la macrofaune. Ainsi, cette corrélation était significative avec la richesse spécifique, l'abondance et la biomasse à la station 31 (communauté à *Nephtys hombergii*, actuelles Vases sableuses littorales) et avec la richesse spécifique et l'abondance à la station 26 (communauté à *Scoloplos armiger*, actuelles Vases sableuses littorales). Aux autres stations où ces corrélations n'étaient pas significatives, on notait par ailleurs néanmoins des tendances similaires.

Les analyses multivariées effectuées afin d'identifier les paramètres contrôlant la composition de la macrofaune benthique à chaque station n'ont pas permis de détecter un ensemble de variables unique susceptible d'expliquer les variations des abondances spécifiques ou des biomasses par groupe fonctionnel à toutes les stations. De manière générale, ce sont les variables hivernales qui expliquaient de la manière la plus satisfaisante les variations de composition de la macrofaune benthique. Ainsi, les paramètres dont les valeurs hivernales étaient significativement corrélés aux variations d'abondances spécifiques sont les suivants : (1) l'indice WeMO, les précipitations, et le débit du Rhône à la station 31 ; (2) l'indice WeMO, les précipitations, et le proxy C2 à la station 26 et (3) les précipitations et le débit du Rhône à la station 183. A la station 31 seulement, il a été possible d'identifier un jeu de paramètres dont les valeurs hivernales étaient significativement corrélées avec les biomasses. Ces paramètres sont les suivants: l'indice WeMO, les précipitations, la direction du vent, le débit du Rhône et la concentration de la matière en suspension.

Ces résultats suggèrent que la WeMO joue un rôle plus important que la NAO dans le contrôle de la composition des communautés benthiques de la baie de Banyuls-sur-Mer. Il est néanmoins important de souligner que le rôle important de la WeMO hivernale peut en partie être lié au fait que la macrofaune benthique a été échantillonnée pendant l'hiver. La phase positive de la WeMO est associée à des vents de Nord, une réduction des précipitations et de la température de l'air, ainsi qu'à une augmentation de la concentration en matières en suspension en baie de Banyuls-sur-Mer, et à une augmentation du débit liquide du Rhône. Ces conditions semblent favoriser le recrutement et la survie des espèces de la macrofaune benthique. Ainsi, et contrairement à des observations précédemment réalisées en mer du Nord, la température ne semble pas avoir d'effet négatif sur la macrofaune du golfe du Lion. De plus, l'influence du Rhône sur la composition de la macrofaune benthique est clairement suggérée, ce qui appuie certaines des conclusions établies à partir de l'étude présentée au **Chapitre II**.

La corrélation entre la WeMO et l'abondance de certaines espèces dominantes (notamment *Ditrupa arietina* dont les variations d'abondance ont été à l'origine de l'hypothèse d'un contrôle de la composition des communautés de la macrofaune benthique par des oscillations climatiques) a également été testée. Les abondances d'*Aspidosiphon muelleri* et *Turritella communis* étaient significativement corrélées avec les valeurs hivernales de l'indice WeMO, alors que les abondances de *D. arietina* ne l'étaient pas. Ces 3 espèces sont par ailleurs liées par le fait que *A. muelleri* occupe les coquilles vides de *D. arietina* et de *T. communis* (Murina et al., 1999 ; Ferrero-Vincente et al., 2013, 2014). Mes résultats suggèrent donc que *A.*

muelleri et *T. communis* pourraient également constituer de bons indicateurs des changements de composition de la macrofaune benthique dans le golfe du Lion.

Les deux études (**Chapitres II et III**) montrent clairement les limitations des conclusions qu'il est possible de tirer d'une comparaison à long terme comparé à celles susceptibles d'être dégagées d'un suivi à long terme. D'une part, la comparaison entre 1998 et 2010 nous suggère que les différences significatives dans la composition de la macrofaune benthique sont probablement liées à la NAO et au débit du Rhône. Alors que le suivi de dix ans nous confirme cette influence du Rhône mais nous suggère par contre que ces mêmes variations de composition sont plus liées à la WeMO qu'à la NAO.

1.3 L'impact du Rhône sur la structuration des communautés

Ce travail a permis de mettre en évidence l'influence des apports du Rhône sur les communautés benthiques à l'échelle de l'ensemble du golfe du Lion (**Chapitres II et III**). Certains travaux antérieurs ont néanmoins suggéré des modalités d'actions différentes d'impact des grands fleuves sur la composition de la macrofaune benthique en fonction de la distance à l'embouchure. Compte tenu du faible nombre de paramètres caractéristiques du sédiment mesurés lors des études précédentes, il s'était par ailleurs révélé impossible d'établir un lien entre le débit du Rhône, les caractéristiques du sédiment de surface et la composition de la macrofaune benthique.

Les variations de cette composition ont par conséquent été étudiées à partir de l'échantillonnage de 5 stations situées le long d'un gradient côte-large situé au large de l'embouchure du Rhône dans l'axe préférentiel de son panache. Cet échantillonnage a été réalisé sous 4 régimes hydrologiques différents : (1) en avril 2007, 42 jours après une crue océanique; (2) en mai 2008, pendant une crue généralisée; (3) en décembre 2008, 26 jours après une crue d'origine cévenole et (4) en juillet 2011, en période estivale et après un étiage prolongé. Ces 3 crues ont présenté des intensités différentes. La crue de mai 2008 a été la plus forte en termes de débit solide tandis que celle de novembre 2008 a été la plus forte en termes de débit liquide.

Les changements importants observés dans les caractéristiques du sédiment le long du gradient côte-large ont mis en évidence le rôle important de ces apports dans la concentration des composants organiques et inorganiques. Nous avons ainsi pu observer que les crues d'origine cévenole et généralisées étaient responsables de l'apport de grands volumes d'eau et de sédiment lié à un matériel particulaire plus réfractaire que celui véhiculé pendant la période estivale ou bien même pendant la crue océanique. Ces deux dernières situations étaient plutôt caractérisées par un flux d'eau régulier qui transportait de faibles quantités de sédiment auquel était associé du matériel plus labile**.** Les marqueurs d'origine (C/N et Chl-*b*/Chl-*a*) ont également mis en évidence un apport : (1) de sédiments déjà appauvris pendant la crue de mai 2008 et (2) de matériel d'origine continentale en décembre 2008. Une interprétation probable est que le délestage du barrage de Serre-Ponçon en mai 2008 a libéré une quantité importante de particules dont le contenu organique avait déjà été fortement dégradé (Eyrolle et al., 2012). L'apport de débris végétaux (eux-aussi réfractaires) avait par ailleurs déjà été observé dans l'embouchure du Rhône en décembre 2008 avec une origine attribuée au bassin versant du parc des Cévennes.

Les marqueurs de labilité de la matière organique particulaire sédimentée présentaient également des distributions spatio-temporelles différentes : (1) le ratio Chl-*a*/(chl-*a*+Phaeo-*a*) diminuait ainsi vers le large, tandis que (2) le rapport EHAA/THAA montrait des valeurs homogènes le long de ce même gradient mais différait par contre clairement d'une campagne à l'autre. Les pigments constituant une fraction extrêmement labile de la matière organique sédimentaire, une interprétation possible dans le fait que cette composante serait dégradée avec la même intensité lors du transit des particules depuis la côte vers le large et ceci quelles que soient les circonstances hydrologiques. Ceci ne serait par contre pas le cas pour la fraction moins labile constituée par les EHAA ce qui expliquerait l'absence de gradient côte-large et les différences entre campagnes observées pour ce dernier paramètre.

Mes résultats montrent enfin que la composition de la macrofaune benthique répond de manière différente selon l'origine des crues. Nous avons ainsi pu observer en juillet 2011 que l'abondance et la richesse étaient plus élevées à proximité immédiate de l’embouchure que dans la partie distale du delta. Cette situation était complétement inversée pendant ou peu après les périodes de crues. Ils sont en accord avec le modèle général représentant les processus intervenant sur la partie de la plateforme continentale affectée par les grands fleuves selon lequel : (1) la macrofaune benthique à proximité immédiate de l'embouchure est négativement affectée par les forts taux de sédimentation et l’instabilité physique associée, et (2) plus au large, cette même macrofaune est au contraire positivement affectée par l’augmentation, plus légère, du flux de matière organique particulaire descendant.

Dans le premier cas, les taux de sédimentation élevés associés aux événements de crue favorisent les espèces fouisseuses de subsurface qui pourront profiter du matériel organique enterré pour plus longtemps que les espèces de surface. Inversement, le flux réduit pendant la période estivale associé à un matériel plus labile favorise une plus grande abondance et diversité à travers le recrutement de certaines espèces (i.e., *Sternaspis scutata*) et la présence d‘espèces tubicoles à la surface du sédiment.

Dans la partie la plus distale du delta, la composition de la macrofaune benthique varie peu le long du gradient. Ceci pourrait indiquer qu’elle dépendrait plus de la variation interannuelle des variables environnementales que directement de celles du débit du Rhône comme proposé par Salen-Picard et al. (2003).

1.4 Evaluation des statuts de qualité écologique actualisés du golfe du Lion et comparaison avec les résultats obtenus en 1998

A partir des données de macrofaune benthique de la comparaison des stations étudiées entre 1998 et 2010 (**Chapitre II**), il a été possible d’actualiser la carte de la qualité écologique des habitats benthiques du golfe du Lion à partir de l’utilisation de trois indices biotiques.

Les 91 stations échantillonnées en 2010, ainsi qu’un certains nombre d’autres études, ont été utilisées pour établir une nouvelle liste d’$ES50_{0.05}$ (i.e., des valeurs de sensibilité/tolérance des espèces utilisées par l’indice BQI) pour la Méditerranée.

Cette nouvelle liste était basée sur 1616 événements d'échantillonnage alors que celle utilisée par Labrune et al. (2012) l'était sur seulement 260. Ainsi, l'un des principaux résultats issus de mon travail réside dans la mise en évidence de l'effet de la taille du jeu de données de référence utilisé pour dériver les valeurs d'$ES50_{0.05}$ sur : (1) les valeurs d'$ES50_{0.05}$ elles-mêmes, ainsi que (2) sur les valeurs de BQI associées.

De manière générale, les résultats obtenus à l'aide de l'AMBI et du M-AMBI se sont avérés étroitement corrélés, ce qui traduit simplement le fait que le M-AMBI est directement dérivé de l'AMBI. Au contraire, les valeurs du BQI n'étaient corrélées ni avec les valeurs de l'AMBI ni avec celles du M-AMBI. Comme déjà indiqué par Labrune et al. (2006, 2012), ceci est probablement lié au fait que ces deux catégories d'indices attribuent des niveaux de sensibilité/tolérance très différents, voire contradictoires, à certaines espèces susceptibles d'être dominantes. Ceci est par exemple le cas de *Ditrupa arietina* qui est identifiée comme une espèce tolérante dans le calcul du BQI du fait de sa dominance importante à un grand nombre de stations, notamment en 1998, alors qu'elle est placée dans le groupe écologique 1 (espèces sensibles) pour le calcul de l'AMBI.

A l'instar de Labrune et al. (2012), nous avons comparé les résultats obtenus pour chacun de ces 3 indices biotiques avec ceux dérivés d'une approche indépendante : l'imagerie sédimentaire. A l'inverse de ceux enregistrés dans le delta du Rhône par ces auteurs, et malgré l'absence de corrélation significative observée (qui peut s'expliquer par l'absence de gradient écologique fort), nos résultats suggèrent une meilleure adéquation du BHQ (i.e., indice issu de l'imagerie sédimentaire) avec le M-AMBI et l'AMBI qu'avec le BQI.

Malgré les changements observés dans la composition de la macrofaune et dans les caractéristiques du sédiment démontrés dans le **Chapitre II**, les statuts de l'état écologique des habitats benthiques enregistrés en 1998 et 2010 se sont avérés similaires pour la majorité des stations et ceci quel que soit l'indice biotique utilisé. Ce résultat est intéressant dans l'optique, non plus de l'attribution d'une valeur absolue d'un statut de qualité écologique, mais dans celle, suggérée par la DCSMM, de la description d'une trajectoire de ce même statut.

2 PERSPECTIVES

Les résultats de mon travail montrent que les changements de la composition de la macrofaune benthique du golfe du Lion présentent à la fois des composantes spatiales et temporelles. Ses conclusions ouvrent un large éventail de perspectives de recherche qui sont naturellement rattachées aux trois grands axes de mon travail que sont : (1) les variations temporelles de la composition de la macrofaune benthique du golfe du Lion, (2) l'impact du Rhône sur ces mêmes compositions, et (3) l'évaluation du statut écologique des habitats à partir de l'utilisation d'indices biotiques.

2.1 Les variations temporelles de la composition de la macrofaune benthique

Nous avons en tout premier lieu confirmé l'existence de changements temporels dans la composition des communautés de la macrofaune benthique du Golfe du Lion ; et pour la première fois directement montré que ces changements affectaient l'ensemble de ce golfe. Ce constat conforte *a posteriori* l'adoption de la baie de Banyuls-sur-Mer comme zone atelier, représentative des changements intervenus dans l'ensemble du golfe afin d'affiner l'étude de la causalité de ces changements. La nature de certains changements faunistiques observés conforte quant à elle l'utilisation d'espèces indicatrices des changements intervenus dans certaines communautés. Ceci est notamment le cas de l'annélide *Ditrupa arietina*, même si mes travaux ont également permis d'identifier d'autres espèces indicatrices potentielles comme *Turritella communis* et *Aspidosiphon muelleri*. Mes résultats ont également montré tout l'intérêt des suivis à long terme par rapport aux comparaisons du même nom pour mieux inférer les causes des changements de composition de la macrofaune avec notamment la mise en évidence de la supériorité de la WeMO par rapport à la NAO dans ce domaine particulier. Une certaine frustration demeure néanmoins à la fin de ce travail quant à la non-ambiguïté et la validité effective des paramètres explicatifs identifiés. Elle réside en partie dans les limites temporelles du suivi réalisé en baie de Banyuls-sur-Mer ainsi qu'en la faiblesse du nombre de variables environnementales mesurées.

Dans ce contexte, il pourrait s'avérer particulièrement intéressant : (1) de prolonger le suivi actuellement en cours en baie de Banyuls-sur-Mer afin que sa longueur atteigne au moins le double de la période des processus climatiques potentiellement impliqués (i.e., 8 ans pour la NAO), (2) d'augmenter et de diversifier le nombre de paramètres accessoires mesurés (e.g. mesures associées à la matière organique sédimentaire et/ou à la présence de certains contaminants ainsi qu'à l'intensité d'autres perturbations potentielles), (3) dintroduire une dimension saisonnière au plan d'échantillonnage puisque ce niveau d'intégration temporelle semble important pour les variables explicatives, et enfin (4) de réalise des études comparatives des compositions faunistiques avant et après tempête à l'échelle de la communauté et dans une optique de bilan quantitatif (à la différence de l'étude réalisée par Guizien et al. (2010) qui ne concernait que la seule Ditrupa arietina*).*

2.2 Les effets du Rhône sur la composition de la macrofaune benthique

Un autre aspect important de ce travail concerne les effets du Rhône sur la composition des communautés benthiques à petite et à grande échelle spatiale. A petite échelle spatiale, mes résultats ont montré un bon accord avec le modèle général proposé par Rhoads (1985). A grande échelle spatiale, ils ont confirmé, via l'utilisation de modèles incluant des dimensions spatiales directionnelles et non-directionnelles, les observations de Labrune et al. (2007b, 2008) relatives à l'existence de 2 sous-communautés de Vases sableuses littorales en fonction principalement de l'éloignement à l'embouchure du Rhône.

Des progrès très significatifs peuvent néanmoins encore être accomplis à ces 2 niveaux. Une des difficultés rencontrées lors de l'étude conduite à petite échelle spatiale a résidé dans le positionnement, non régulier, de l'échantillonnage vis-à-vis du dernier épisode de crue. En l'espèce, aucune information de type « haute fréquence » ne nous est encore disponible concernant les cinétiques d'impact et de cicatrisation associées à ce type d'événements. Il pourrait par conséquent s'avérer intéressant de rééditer le type d'études conduites sur le Rhône lors du présent travail mais en concentrant l'échantillonnage sur la période précédant et suivant immédiatement un épisode de crue particulier. Les difficultés associées, qu'il *convient de ne pas sous-estimer, concernent : (1) la disponibilité effective des moyens à la mer, et (2) l'impossibilité de contrôler a priori une séquence d'événements météorologiques. Pour ce qui concerne l'analyse des effets du Rhône à grande échelle spatiale, des travaux plus immédiatement réalisables concernent la méthode de codage de la composante spatiale directionnelle avec : (1) une analyse utilisant le codage actuel qui pourrait être réalisée profondeur par profondeur de manière à déceler des différences éventuelles en fonction de ce facteur, et (2) une analyse réalisée communauté par communauté qui pourrait impliquer un codage plus complexe que celui utilisé lors de la présente étude.*

2.3 L'évaluation de la qualité écologique des habitats benthiques à partir de l'utilisation d'indices biotiques

A la différence des deux points précédents, les conclusions et perspectives relatives à l'utilisation de la macrofaune benthique en tant que base du calcul d'indices biotiques ne sont pas strictement rattachées au golfe du Lion. Si ce travail a confirmé l'existence de disparités importantes entre indices biotiques, il n'a pas par contre permis de les lever. La comparaison des 3 indices biotiques testés avec les données issues de l'imagerie sédimentaire a ainsi conduit à des résultats opposés à ceux obtenus par Labrune et al. (2012) dans le seul prodelta du Rhône. Un autre résultat, extrêmement intéressant, mais qui mériterait encore d'être renforcé, réside dans le fait qu'au-delà des incohérences mentionnées ci-dessus, les 3 indices testés montrent tous la même (absence d') évolution du statut écologique des habitats benthiques du Golfe du Lion entre 1998 et 2010. Ce résultat est prometteur, et d'une certaine manière rassurant, dans l'optique de la mise en œuvre des programmes de surveillance de la DCSMM. Il demande néanmoins lui aussi à être confirmé.

Dans ce contexte, des études sont clairement nécessaires pour : (1) poursuivre les comparaisons entre indices biotiques et avec les informations dérivées de l'imagerie sédimentaire. Il apparaît souhaitable, au moins dans un premier temps, que ces travaux se focalisent sur quelques zones géographiques présentant des gradients écologiques marqués possiblement associés à des perturbations potentielles de différentes natures, (2) entamer un réel travail sur le niveau de *sensibilité/tolérance, en tout premier lieu pour les espèces dominantes pour lesquels ce niveau diffère grandement entre indices biotiques, (3) réaliser de nouvelles comparaisons à long terme et/ou initier des suivis du statut écologique de certains habitats à partir de l'utilisation de plusieurs indices biotiques afin de confirmer l'homogénéité de l'information dérivée de ces indices sur la dynamique temporelle des statuts de qualité écologique. Il apparaitrait souhaitable que ces travaux se focalisent d'abord sur des zones susceptibles de présenter des modifications de statut même si une première étape, immédiatement réalisable, consisterait à réaliser cette action sur les données du suivi réalisé en baie de Banyuls-sur-Mer.*

BIBLIOGRAPHIE

RÉFÉRENCES BIBLIOGRAPHIQUES GÉNÉRALES

Afli, A., Glémarec, M., 2000. Fluctuation à long terme des peuplements macrobenthiques dans le golfe du Morbihan (Bretagne, France). Cahiers de Biologie Marine 41, 67–89.

Akoumianaki, I., Nicolaidou, A., 2007. Spatial variability and dynamics of macrobenthos in a Mediterranean delta front area: the role of physical processes. Journal of Sea Research 57, 47–64.

Akoumianaki, I., Papaspyrou, S., Kormas, K.A., Nicolaidou, A., 2013. Environmental variation and macrofauna response in a coastal area influenced by land runoff. Estuarine, Coastal and Shelf Science 132, 34–44.

Aller, J.Y., Aller, R.C., 1986. General characteristics of benthic faunas on the Amazon inner continental shelf with comparison to the shelf off the Changjiang River, East China Sea. Continental Shelf Research 6, 291–310.

Aller, J.Y., Stupakoff, I., 1996. The distribution and seasonal characteristics of benthic communities on the Amazon shelf as indicators of physical processes. Continental Shelf Research 16, 717–751.

Aller, R.C., 1998. Mobile deltaic and continental shelf muds as suboxic, fluidized bed reactors. Marine Chemistry 61, 143–155.

Alliot, E., Younes, W.A.N., Romano, J.C., Rebouillon, P., Massé, H., 2003. Biogeochemical impact of a dilution plume (Rhône River) on coastal sediments. Estuarine, Coastal and Shelf Science 57, 357–367.

Aloisi, J.C., 1986. Sur un modèle de sédimentation deltaïque: contribution à la connaissance des marges passives. PhD Thesis, Université de Perpignan, Perpignan.

Aloisi, J.C., Got, H., Monaco, A., 1973. Carte géologique du précontinent languedocien au 1/250000ième. Netherlands: Enschede: International Institute for Aerial Survey and Earth Sciences.

Aloisi, J.C., Monaco, A., 1975. La sédimentation infralittorale. Les prodeltas nord-méditerranéens. Comptes Rendus de l'Académie des Sciences de Paris 280, 2833–2836.

Aloisi, J.C., Auffret, G.A., Auffret, J.P., Barusseau, J.P., Hommeril, P., Larsonneur, C., Monaco, A., 1977. Essai de modélisation de la sédimentation actuelle sur les plateaux continentaux français. Bulletin de la Société Géologique Française 7, 182–195.

Amouroux, J.M., Grémare, A., 1995. Etude d'impact de la construction d’une station d’épuration sur l’émissaire de Narbonne-Plage Gruissan. 9 pp.

Amouroux, J.M., Grémare, A., 2001a. Etude des populations benthiques présentes au large d'Argelès sur mer: choix du site pour une opération de clapage. Conseil Général des P.O. pour le port de Port-Vendres. 10 pp.

Amouroux, J.M., Grémare, A., 2001b. Etude de la macrofaune marine benthique de la baie de Paulilles avant la réalisation des travaux de réhabilitation du site post-industriel de Paulilles Rapport pour le Conservatoire du Littoral. 13 pp.

Amouroux, J.M., Grémare, A., 2003. Etude d’impact de l’émissaire de la station d’épuration de Banyuls sur mer. 5 pp.

Amouroux, J.M., Grémare, A., 2006. Etude d'impact de l'émissaire de la station d'épuration de Banyuls sur mer. 5 pp.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58, 626–639.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253.

Antonelli, C., Eyrolle, F., Rolland, B., Provansal, M., Sabatier, F., 2008. Suspended sediment and ^{137}Cs fluxes during the exceptional December 2003 flood in the Rhone River, southeast France. Geomorphology 95, 350–360.

Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M., Wilson, M.A., 1992. Aspects of the chemical structure of soil organic materials as revealed by solid-state ^{13}C NMR spectroscopy. Biogeochemistry 16, 1–42.

Bellan, G., Bourcier, M., 1984. Bilan écologique du detournement permanent d'un petit fleuve côtier dans l'émissaire d'eaux usées d'une grande ville. Marine Environmental Research 12, 83–111.

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.

Beukema, J.J., 1985. Growth and dynamics in populations of *Echinocardium cordatum* living in the North Sea off the Dutch North coast. Netherlands Journal of Sea Research 19, 129–134.

Beukema, J.J., Essink, K., Dekker, R., 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. Journal of Animal Ecology 69, 31–44.

Bianchi, T.S., Mitra, S., McKee, B.A., 2002. Sources of terrestrially-derived organic carbon in lower Mississippi River and Louisiana shelf sediments: implications for differential sedimentation and transport at the coastal margin. Marine Chemistry 77, 211–223.

Blake, J.A., Grassle, J.F., 1994. Benthic community structure on the U.S. South Atlantic slope off the Carolinas: spatial heterogeneity in a current-dominated system. Deep Sea Research Part II: Tropical Studies in Oceanography 41, 835–874.

Blake, J.A., Maciolek, N.J., Ota, A.Y., Williams, I.P., 2009. Long-term benthic infaunal monitoring at a deep-ocean dredged material disposal site off Northern California. Deep Sea Research II 56, 1775–1803.

Blanchet, F.G., Legendre, P., Borcard., D., 2008. Forward selection of explanatory variables. Ecology 89, 2623–2632.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Modelling directional spatial processes in ecological data. Ecological Modelling 215, 325–336.

Blanchet, F.G., Legendre, P., Gauthier, O., 2013. AEM: Tools to construct Asymmetric eigenvector maps (AEM) spatial variables. R package version 0.5–1/r118. http://R–Forge.R–project.org/projects/sedar/

Bonifácio, P., Bourgeois, S., Labrune, C., Amouroux, J.M., Escoubeyrou, K., Buscail, R., Romero-Ramirez, A., Lantoine, F., Vétion, G., Bichon, S., Desmalades, M., Rivière, B., Deflandre, B., Grémare, A., 2014. Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition off the Rhône River in relation to its hydrological regime. Estuarine, Coastal and Shelf Science 151, 196–209.

Borcard, D., Legendre, P. Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153, 51–68.

Borja, A., Franco, J., Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Marine Pollution Bulletin 40, 1100–1114.

Borja, A., Muxika, I., Franco, J., 2003. The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Marine Pollution Bulletin 46, 835–845.

Borja, A., Franco, J., Muxika, I., 2004. The biotic indices and the Water Framework Directive: the required consensus in the new benthic monitoring tools. Marine Pollution Bulletin 48, 405–408.

Borja, A., Barbone, E., Basset, A., Borgersen, G., Brkljacic, M., Elliott, M., Garmendia, J.M., Marques, J.C., Mazik, K., Muxika, I., Neto, J.M., Norling, K., Rodríguez, J.G., Rosati, I., Rygg, B., Teixeira, H., Trayanova, A., 2011. Response of single benthic metrics and multi-metric methods to anthropogenic pressure gradients, in five distinct European coastal and transitional ecosystems. Marine Pollution Bulletin 62, 499–513.

Bornens. P., Riou, S., Grosdemange, D., Hontebeyrie, B., Musard, O., Bougio, Y., 2000a. Etude environnementale du site d'immersion des matériaux de dragage du port de Sète, IN VIVO, Service maritime et de Navigation du Languedoc Roussillon.

Bornens, P., Riou, S., Grosdemange, D., Hontebeyrie, B., Musard, O., Bougio, Y., 2000b. Etude environnementales du site d’immersion des matériaux de dragage du chenal maritime de Port-La-Nouvelle. Service Maritime et de Navigation du Languedoc-Roussillon. 79 pp.

Bourcier, M., 1980. Evolution récente des peuplements macrobenthiques entre La Ciotat et les Iles Embiez (Côtes de Provence). Téthys 9, 197–206.

Bourgeois, S., Pruski, A.M., Sun, M.Y., Buscail, R., Lantoine, F., Kerhervé, P., Vétion, G., Rivière, B., Charles, F., 2011. Distribution and lability of land-derived organic matter in the surface sediments of the Rhône prodelta and the adjacent shelf (Mediterranean Sea, France): a multi proxy study. Biogeosciences 8, 3107–3125.

Bourrin, F., Durrieu de Madron, X., Ludwig W., 2006. Contribution to the study of coastal rivers and associated prodeltas to sediment supply in Gulf of Lions (NW Mediterranean Sea). Vie et Milieu 56: 307–314.

Bradshaw, C., Veale, L.O., Brand, A.R., 2002. The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities: a re-analysis of an historical dataset. Journal of Sea Research 47, 161–184.

Buscail, R., Pocklington, R. Daumas, R., Guidi, L., 1990. Fluxes and budget of organic matter in the benthic boundary layer over the northwestern Mediterranean margin. Continental Shelf Research 10, 1089-1122.

Buscail, R., Pocklington, R., Germain, C., 1995. Seasonal variability of the organic matter in a sedimentary coastal environment: sources, degradation and accumulation (continental shelf of the Gulf of Lions – Northwestern Mediterranean Sea). Continental Shelf Research 15, 843–869.

Callaway, R., Engelhard, G. H., Dann, J., Cotter, J., Rumohr, H., 2007. One century of North Sea epibenthos and fishing: comparison between 1902-1912, 1982-1985 and 2000 Marine Ecology Progress Series 346, 27–43.

Cardell, M.J., Sardá, R., Romero, J., 1999. Spatial changes in sublittoral soft-bottom polychaete assemblages due to river inputs and sewage discharges. Acta Oecologia 20, 343–351.

Carpentier, P., Dewarumez, J.M., Leprêtre, A., 1997. Long-term variability of the *Abra alba* community in the southern bight of North Sea. Oceanologica Acta 20, 283–290.

Cartes, J.E., Maynou, F., Fanelli, E., López-Pérez, C., Papiol, V., 2015. Changes in deep-sea fish and crustacean communities at 1000–2200 m in the Western Mediterranean after 25 years: relation to hydro-climatic conditions. Journal of Marine Systems 143, 138–153.

Cathalot, C., Rabouille, C., Pastor, L., Deflandre, B., Viollier, E., Buscail, R., Grémare, A., Treignier, C., Pruski, A.M., 2010. Temporal variability of carbon recycling in coastal sediments influenced by rivers: assessing the impact of flood inputs in the Rhône River prodelta. Biogeosciences 7, 1187–1205.

Cathalot, C., Rabouille, C., Tisnérat-Laborde, N., Toussaint, F., Kerhervé, P., Buscail, R., Loftis, K., Sun, M.Y., Tronczynski, J., Azoury, S., Lansard, B., Treignier, C., Pastor, L., Tesi, T., 2013. The fate of river organic carbon in coastal areas: a study in the Rhône River delta using multiple isotopic ($\delta^{13}C$, $\Delta^{14}C$) and organic tracers. Geochimica et Cosmochimica Acta 118, 33–55.

Cauwet, G., Gadel, F., Sierra, M.M.D., Donard, O., Ewald, M., 1990. Contribution of the Rhône River to organic-carbon inputs to the Northwestern Mediterranean Sea. Continental Shelf Research 10, 1025–1037.

Chambers, J.M., 2013. SoDA: Functions and Examples for "Software for Data Analysis". R package version 1.0–6. http://CRAN.R–project.org/package=SoDA

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 171–143.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92, 205–219.

Clark, R.A., Frid, C.L.J., 2001. Long-term changes in the North Sea ecosystem Environmental Reviews 9, 131–187.

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366, 56–69.

Colwell, R. K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5, 3–21.

Colwell, R. K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Conversi, A., Umani., S.F., Peluso, T., Molinero, J.C., Santojanni, A., Edwards, M., 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European Basins. PLoS ONE 5, e10633.

CREOCEAN, ECOSITE, 2001. Suivi écologique du rejet des effluents de la STEP de Sète – Etat du site un an après la mise en service de l'émissaire Année 1 – Rapport année 2001, Sivom de la Mer & des Etangs.

Cruzado, A., Velásquez, Z., 1990. Nutrients and phytoplankton in the Gulf of Lions, northwestern Mediterranean. Continental Shelf Research 10: 931–942.

Darnaude, A.M., Salen-Picard, C., Polunin, N.V., Harmelin-Vivien, M.L., 2004. Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). Oecologia 138, 325–332.

Dauvin, J.C., 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbation par les hydrocarbures de l'Amoco Cadiz. Thèse de doctorat d'Etat, Université de Paris.

Dauvin, J.C., 1998. The fine sand *Abra alba* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Marine Pollution Bulletin 36, 669–676.

Dauvin, J.C., 2000. The muddy fine sand *Abra alba – Melinna palmata* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spil. Marine Pollution Bulletin 40, 528–536.

Dauvin, J.C., Ruellet, T., 2007. Polychaeta/Amphipod ratio revisited. Marine Pollution Bulletin 55, 80–90.

Dauvin, J.C., Ruellet, T., Desroy, N., Janson, A.L., 2007. The ecological quality status of the Bay of Seine and the Seine estuary: Use of biotic indices. Marine Pollution Bulletin 55, 241–257.

Dauvin, J.C., Fisson, C., Garnier, J., Lafite, R., Ruellet, T., Billen, G., Deloffre, J., Verney, R., 2008. A report card and quality indicators for the Seine estuary: from scientific approach to operational tool. Marine Pollution Bulletin 57, 187–201.

Dauvin, J.C., Pezy, J.P., 2013. Long-term changes of the Seine estuary suprabenthos (1996–2012). Journal of Experimental Marine Biology and Ecology 448, 93–103.

Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. Marine Ecology Progress Series 173, 67–83.

De Backer, A., Van Hoey, G., Coates, D., Vanaverbeke, J., Hostens, K., 2014. Similar diversity-disturbance responses to different physical impacts: three cases of small-scale biodiversity increase in the Belgian part of the North Sea. Marine pollution bulletin 84, 251–262.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statical inference. Ecology 90, 3566–3574.

Dippner, J.W., Kröncke, I., 2003. Forecast of climate induced change in marine ecosystems. Climate Research 25, 179–182.

Dimitriou, P.D., Apostolaki, E.T., Papageorgiou, N., Reizopoulou, S., Simboura, N., Arvanitidis, C., Karakassis, I., 2012. Meta-analysis of a large data set with Water Framework Directive indicators and calibration of a Benthic Quality Index at the family level. Ecological Indicators 20, 101–107.

Dray, S., Legendre, P., Peres-Neto, P. R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196, 483–493.

Dray., S., Legendre., P., Blanchet, F.G., 2013. packfor: Forward Selection with permutation (Canoco p. 46). R package version 0.0–8/r109. http://R–Forge.R–project.org/projects/sedar/

Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., Ottersen, G., Pershing, A. J., Walker, H., 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation, in The North Atlantic Oscillation: climatic significance and environmental impact (Eds. J.W. Hurrell, Y. Kushnir, G. Ottersen and M. Visbeck). American Geophysical Union, Washington, D.C., 279 pp.

Dufrene, M., Legendre., P., 1997. Species assemblages and indicators species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Durrieu de Madron, X., Abassi, A., Heussner, S., Monaco, A., Aloisi, J.C., Radakovitch, O., Giresse, P., Buscail, R., Kerherve, P., 2000. Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanologica Acta 23, 717–730.

Durrieu de Madron, X., Houpert, L., Puig, P., Sanchez-Vidal, A., Testor, P., Bosse, A., Estournel, C., Somot, S., Bourrin, F., Bouin, M.N., Beauverger, M., Beguery, L., Calafat, A., Canals, M., Cassou, C., Coppola, L., Dausse, D., D'Ortenzio, F., Font, J., Heussner, S., Kunesch, S., Lefevre, D., Le Goff, H., Martín, J., Mortier, L., Palanques, A., Raimbault, P., 2013. Interaction of dense shelf water cascading and open-sea convection in the northwestern Mediterranean during winter 2012. Geophysical Research Letters 40, 1379–1385.

Edwards, M., Reid, P.C., Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the north-east Atlantic. ICES Journal of Marine Science 58, 39–49.

Eyrolle, F., Radakovitch, O., Raimbault, P., Charmasson, S., Antonelli, C., Ferrand, E., Aubert, D., Raccasi, G., Jacquet, S., Gurriaran, R., 2012. Consequences of hydrological events on the delivery of suspended sediment and associated radionuclides from the Rhône River to the Mediterranean Sea. Journal of Soils and Sediments 12, 1479–1495.

Fernandez de Puelles, M., Valencia, J., Vicente, L., 2004. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). ICES Journal of Marine Science 61, 492–500.

Ferré, B., Guizien, K., Durrieu de Madron, X., Palanques, A., Guillén, J., Grémare, A., 2005. Fine-grained sediment dynamics during a strong storm event in the inner-shelf of the Gulf of Lion (NW Mediterranean). Continental Shelf Research 25, 2410–2427.

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, Á., Sánchez-Lizaso, J.L., 2013. Limiting factors on the distribution of shell/tube-dwelling sipunculans. Journal of Experimental Marine Biology and Ecology 446, 345–354.

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, A., Sánchez-Lizaso, J.L., 2014. Observations on the ecology and reproductive biology of the sipunculan worm *Aspidosiphon muelleri* in temperate waters. Journal of the Marine Biological Association of the United Kingdom 94, 1629–1638.

Fleischer, D., Grémare, A., Labrune, C., Rumohr, H., Berghe, E.V., Zettler, M.L., 2007. Performance comparison of two biotic indices measuring the ecological status of water bodies in the Southern Baltic and Gulf of Lions. Marine Pollution Bulletin 54, 1598–1606.

Fleischer, D., Zettler, M.L., 2009. An adjustment of benthic ecological quality assessment to effects of salinity. Marine Pollution Bulletin 58, 351–357.

Franke, H.D., Gutow, L., 2004. Long-term in the macrozoobenthos around the rocky island of Helgoland (German Bight, Nort Sea). Helgoland Marine Research 58, 303–310.

Frid, C.L.J., Garwood, P.R., Robinson, L.A., 2009. Observing change in a North Sea benthic system: a 33 year time series. Journal of Marine Systems 77, 227–236.

Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134, 111–118.

Fromentin, J.M., Ibanez, F., Dauvin, J.C., Dewarumez, J.M., Elkaim, B., 1997. Long-term changes of four macrobenthis assemblages from 1978 to 1992. Journal of the Marine Biological Association of the UK 77, 287–310.

Gambi, M.C., Giangrande, A., 1986. Distribution of soft-bottom polychaetes in two coastal areas of the Tyrrhenian Sea (Italy): structural analysis. Estuarine, Coastal and Shelf Science 23, 847–862.

García-Comas, C., Stemmann, L., Ibanez, F., Berline, L., Mazzocchi, M.G., Gasparini, S., Picheral, M., Gorsky, G., 2011. Zooplankton long-term changes in the NW Mediterranean Sea: decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? Journal of Marine Systems 87, 216–226.

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.

Glémarec, M., Hily, C., 1981. Perturbations apportées à la macrofaune benthique de la baie de Concarneau par les effluents urbains et portuaires. Acta Oecologia 2, 139–150.

Gogina, M., Glockzin, M., Zettler, M.L., 2010. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 1. Causal analysis. Journal of Marine Systems 79, 112–123.

Goni, M.A., Ruttenberg, K.C., Eglinton, T.I., 1998. A reassessment of the sources and importance of land-derived organic matter in surface sediments from the Gulf of Mexico. Geochimica et Cosmochimica Acta 62, 3055–3075.

Gordon, E.S., Goni, M.A., 2003. Sources and distribution of terrigenous organic matter delivered by the Atchafalaya River to sediments in the northern Gulf of Mexico. Geochimica et Cosmochimica Acta 67, 2359–2375.

Grall, J., Glémarec, M., 1997. Using Biotic Indices to Estimate Macrobenthic Community Perturbations in the Bay of Brest. Estuarine Coastal and Shelf Science 44, 43–53.

Grehan, A.J., Keegan, B.F., Bhaud, M., Guille, A., 1992. Sediment profile imaging of soft substrates in the western Mediterranean: the extent and importance of faunal reworking. Comptes Rendus de l'Academie des Sciences Paris Serie III 315, 309–315.

Grémare, A., Amouroux, J.M., Vétion, G., 1998. 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., Amouroux, J.M., Charles, F., Medernach, L., Jordana, E., Nozais, C., Vétion, G., Colomines, J.C., 1998. Temporal changes in the biochemical composition of particulate organic matter sedimentation in the Bay of Banyuls-sur-Mer. Oceanologica Acta 21, 783–792.

Grémare, A., Sardá, R., Medernach, L., Jordana, E., Pinedo, S., Amouroux, J.M., Martin, D., Nozais, C., Charles, F., 1998. 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.

Grémare, A., Medernach, L., De Bovée, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). Marine Ecology Progress Series 234, 85–94.

Grémare, A., Amouroux, J.M., Cauwet, G., Charles, F., Courties, C., De Bovée, F., Dinet, A., Devenon, J.L., De Madron, X.D., Ferré, B., Fraunie, P., Joux, F., Lantoine, F., Lebaron, P., Naudin, J.J., Palanques, A., Pujo-Pay, M., Zudaire, L., 2003. The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. Oceanologica Acta 26, 407–419.

Grémare, A., Labrune, C., Vanden Berghe, E., Amouroux, J.M., Bachelet, G., Zettler, M.L., Vanaverbeke, J., Fleischer, D., Bigot, L., Maire, O., Deflandre, B., Craeymeersch, J., Degraer, S., Dounas, C., Duineveld, G., Heip, C., Herrmann, M., Hummel, H., Karakassis, I., Kędra, M., Kendall, M., Kingston, P., Laudien, J., Occhipinti-Ambrogi, A., Rachor, E., Sardá, R., Speybroeck, J., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Włodarska-Kowalczuk, M., Zenetos, A., 2009. Comparison of the performances of two biotic indices based on the MacroBen database. Marine Ecology Progress Series 382, 297–311.

Grimes, S., Ruellet, T., Dauvin, J.C., Boutiba, Z., 2010. Ecological Quality Status of the soft-bottom communities on the algerian coast: general patterns and diagnosis. Marine Pollution Bulletin 60, 1969–1977.

Guille, A., 1970. Bionomie benthiques du plateau continental de la côte catalane française. II – Les communautés de la macrofauna. Vie et Milieu 21, 149–280.

Guizien, K., Charles, F., Hurther, D., Michallet, H., 2010. Spatial redistribution of *Ditrupa arietina* (soft bottom Mediterranean epifauna) during a moderate swell event. Continental Shelf Research 30, 239–251.

Hagberg, J., Tunberg, B.G., 2000. Studies on the covariation between physical factors and the long-term variation of the marine soft bottom macrofauna in Western Sweden. Estuarine, Coastal and Shelf Science 50, 373–385.

Harmelin-Vivien, M.L., Bănaru, D., Dierking, J., Hermand, R., Letourneur, Y., Salen-Picard, C., 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). Animal Biodiversity and Conservation 32, 135–145.

Hedges, J.I., Clark, W.A., Cowie, G.L., 1988. Organic matter sources to the water column and surficial sediments of a marine bay. Limnology and Oceanography 33, 1116–1136.

Hedges, J.I., Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment and speculative synthesis. Marine Chemistry 49, 81–115.

Hedges, J.I., Keil, R.G., Benner, R., 1997. What happens to terrestrial organic matter in the ocean? Organic Geochemistry 27, 195–212.

Hermand, R., Salen-Picard, C., Alliot, E., Degiovanni, C., 2008. Macrofaunal density, biomass and composition of estuarine sediments and their relationship to the river plume of the Rhône River (NW Mediterranean). Estuarine, Coastal and Shelf Science 79, 367–376.

Hily, C., Le Loc'h, F., Grall, J., Glémarec, M., 2008. Soft bottom macrobenthic communities of North Biscay revisited: long-term evolution under fisheries-climate forcing. Estuarine, Coastal and Shelf Science 78, 413–425.

Hurrell, J.W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269, 676–679.

Hurrell, J.W., Deser, C., 2010. North Atlantic climate variability: the role of the North Atlantic Oscillation. Journal of Marine Systems 79, 231–244.

IARE, BCEOM, 1993a. Détermination du point de rejet de l'émissaire de la ville de Sète. 41 pp.

IARE, IFREMER, 1993b. Evaluation des conséquences du rejet en mer de la station d'épuration de Montpellier. 60 pp.

Ibanez, F., Dauvin, J.C., 1988. Long-term changes in a muddy fine sand *Abra alba* – *Melinna palmata* community from the Western English Channel. Marine Ecology Progress Series 49, 65–81.

Jeffrey, S.W., 1976. A report of green algal pigments in the central North Pacific Ocean. Marine Biology 37, 33–37.

Josefson, A.B., Jensen, J.N., Ærtebjerg, G., 1993. The benthos community structure anomaly in the late 1970s and early 1980s – a result of a major food pulse? Journal of Experimental Marine Biology and Ecology 172, 31–45.

Karakassis, I., Eleftheriou, A., 1997. The continental shelf of Crete: structure of macrobenthic communities. Marine Ecology Progress Series 160, 185–196.

Karakassis, I., Dimitriou, P.D., Papageorgiou, N., Apostolaki, E.T., Lampadariou, N., Black, K.D., 2013. Methodological considerations on the coastal and transitional benthic indicators proposed for the Water Framework Directive. Ecological Indicators 29, 26–33.

Keeley, N.B., Forrest, B.M., Crawford, C., Macleod, C.K., 2012. Exploiting salmon farm benthic enrichment gradients to evaluate the regional performance of biotic indices and environmental indicators. Ecological Indicators 23, 453–466.

Keeley, N.B., Macleod, C.K., Hopkins, G.A., Forrest, B.M., 2014. Spatial and temporal dynamics in macrobenthos during recovery from salmon farm induced organic enrichment: When is recovery complete? Marine Pollution Bulletin 80, 250–262.

Keller, S., Valls, M., Hidalgo, M., Quetglas, A., 2014. Influence of environmental parameters on the life-history and population dynamics of cuttlefish *Sepia officinalis* in the western Mediterranean. Estuarine, Coastal and Shelf Science 145, 31–40.

Kennedy, R., Arthur, W., Keegan, B.F., 2011. Long-term trends in benthic habitat quality as determined by Multivariate AMBI and Infaunal Quality Index in relation to natural variability: a case study in Kinsale Harbour, south coast of Ireland. Marine Pollution Bulletin 62, 7, 1427–1436.

Krönke, I., 1992. Macrofauna standing stock of the Dogger Banck. A comparison: III. 1950–54 versus 1985–87. A final summary. Helgoländer Wiss Meeresunters 46, 137–169.

Kröncke, I., Dippner, J.W., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communites off Nordeney (East Frisia, Germany) in relation to climate variability. Marine Ecology Progress Series 167, 25–36.

Kröncke, I., Zeiss, B., Rensing, C., 2001. Long-term variability in macrofauna species composition off the Island of Nordeney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Senckenbergiana Maritima 31, 65–82.

Kröncke, I., 2011. Changes in Dogger Bank macrofauna communities in the 20th century caused by fishing and climate. Estuarine, Coastal and Shelf Science 94, 234–245.

Kröncke, I., Reiss, H., Eggleton, J.D., Aldridge, J., Bergman, M.J.N., Cochrane, S., Craeymeersch, J.A., Degraer, S., Desroy, N., Dewarumez, J.M., Duineveld, G.C.A., Essink, K., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Nehring, S., Newell, R., Oug, E., Pohlmann, T., Rachor, E., Robertson, M., Rumohr, H., Schratzberger, M., Smith, R., Berghe, E.V., van Dalfsen, J., van Hoey, G., Vincx, M., Willems, W., Rees, H.L., 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuarine, Coastal and Shelf Science 94, 1–15.

Kröncke, I., Reiss, H., Dippner, J.W., 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. Estuarine, Coastal and Shelf Science 119, 79–90.

La Porta, B., Tomassetti, P., Lomiri, S., Marzialetti, S., Vani, D., Penna, M., Lanera, P., Nicoletti, L., 2011. Ecology and spatial distribution of selected polychaete species from the Italian continental shelf. Italian Journal of Zoology 78, 290–303.

Labrune, C., Amouroux, J.M., Sardá, R., Dutrieux, E., Thorin, S.B., Rosenberg, R., Grémare, A., 2006. Characterization of the ecological quality of the coastal Gulf of Lions (NW Mediterranean). A comparative approach based on three biotic indices. Marine Pollution Bulletin 52, 34–47.

Labrune, C., Grémare, A., Amouroux, J.M., Sardá, R., Gil, J., Taboada, S., 2007. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuarine, Coastal and Shelf Science 71, 133–147.

Labrune, C., Grémare, A., Guizien, K., Amouroux, J.M., 2007. Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): a reappraisal. Journal of Sea Research 58, 125–143.

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.

Labrune, C., Romero-Ramirez, A., Amouroux, J.M., Duchêne, J.C., Desmalades, M., Escoubeyrou, K., Buscail, R., Grémare, A., 2012. Comparison of ecological quality indices based on benthic macrofauna and sediment profile images: a case study along an organic enrichment gradient off the Rhône River. Ecological Indicators 12, 133–142.

Lansard, B., Rabouille, C., Denis, L., Grenz, C., 2009. Benthic remineralization at the land-ocean interface: a case study of the Rhône River (NW Mediterranean Sea). Estuarine, Coastal and Shelf Science 81, 544–554.

Lavesque, N., Blanchet, H., de Montaudouin, X., 2009. Development of a multimetric approach to assess perturbation of benthic macrofauna in *Zostera noltii* beds. Journal of Experimental Marine Biology and Ecology 368, 101–112.

Leeuw, J.W., Largeau, C., 1993. A review of macromolecular organic compounds that comprise living organisms and their role in kerogen, coal, and petroleum formation, in Organic Geochemistry (Eds. M.H. Engel and S.A. Macko). Springer US, pp. 23–72.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., De Cáceres, M., Borcard., D. 2010. Community surveys through space and time: testing the space-time interaction in the absence of replication. Ecology 91, 262–272

Legendre, P., Borcard, D., De Cáceres, M., 2012. STI: Space-time ANOVA models without replications. R package version 1.0.2.

Legendre, P., Borcard, D., Blanchet, F.G., Dray, S., 2013. PCNM: MEM spatial eigenfunction and principal coordinate analyses. R package version 2.1–2/r109. http://R–Forge.R–project.org/projects/sedar/

Leithold, E.L., Hope, R.S., 1999. Deposition and modification of a flood layer on the northern California shelf: lessons from and about the fate of terrestrial particulate organic carbon. Marine Geology 154, 183–195.

Leonardsson, K., Blomqvist, M., Rosenberg, R., 2009. Theoretical and practical aspects on benthic quality assessment according to the EU-Water Framework Directive – Examples from Swedish waters. Marine Pollution Bulletin 58, 1286–1296,

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4, 430–451.

Levinton, J., 1972. Stability and throphic structure in deposit-feeding and suspension-feeding communities. The American Naturalist 106, 472–485.

Lim, H.S., Hong, J.S., 1996. Distribution and growth pattern of *Sternaspis scutata* (Polychaeta: Sternaspidae) in Chinhae Bay, Korea. Journal of the Korean Fisheries Society 29, 537–545.

Lindroth, P., Mopper, K., 1979. High performance liquid chromatographic determination of subpicomole amounts of amino acids by precolumn fluorescence derivatization with o–phthaldialdehyde. Analytical Chemistry 51, 1667–1674.

Lloret, J., Lleonart, J., Sole, I., Fromentin, J.M., 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fisheries Oceanography 10, 33–50.

Lochet, F., Leveau, M., 1990. Transfers between a eutrophic ecosystem, the River Rhône, and an oligotrophic ecosystem, the north-western Mediterranean Sea. Hydrobiologia 207, 95–103.

Lopez, G.R., Levinton, J.S., 1987. Ecology of deposit-feeding animals in marine sediments. The Quaterly Review of Biology 62, 235–260.

Lopez-Bustins, J.A., 2007. The Western Mediterranean Oscillation and rainfall in the Catalan Countries. PhD Thesis, University of Barcelona, Barcelona.

Marín-Guirao, L., Cesar, A., Marin, A., Lloret, J., Vita, R., 2005. Establishing the ecological quality status of soft-bottom mining-impacted coastal water bodies in the scope of the Water Framework Directive. Marine Pollution Bulletin 50, 374–387.

Marion, C., Dufois, F., Arnaud, M., Vella, C., 2010. *In situ* record of sedimentary processes near the Rhône River mouth during winter events (Gulf of Lions, Mediterranean Sea). Continental Shelf Research 30, 1095–1107.

Martín, P., Sabatés, A., Lloret, J., Martin-Vide, J., 2011. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. Climatic Change 110, 925–939.

Martins, R., Azevedo, M.RL., Mamede, R., Sousa, B., Freitas, R., Rocha, F., Quintino, V., Rodrigues, A.M., 2012. Sedimentary and geochemical characterization and provenance of the Portuguese continental shelf soft-bottom sediments. Journal of Marine Systems 91, 41–52.

Martin-Vide, J., Lopez-Bustins, J.A., 2006. The Western Mediterranean Oscillation and rainfall in the Iberian Peninsula. International Journal of Climatology 26, 1455–1475.

Martin-Vide, J., Sanchez-Lorenzo, A., Lopez-Bustins, J.A., Cordobilla, M.J., Garcia-Manuel, A., Raso, J.M., 2008. Torrential rainfall in northeast of the Iberian Peninsula synoptic patterns and WeMO influence. Advances in Sciences and Research 2, 99–105.

Massé, H.L., 2000. Long-term changes in sand-bottom macrofauna along the coast of Provence (northwest Mediterranean Sea). Oceanologica Acta 23, 229–242.

Mayer, L. 1994. Surface area control of organic carbon accumulation in continental shelf sediments. Geochimica et Cosmochimica Acta 58, 1271–1284.

Mayer, L.M., Schick, L.L., Sawyer, T., Plante, C.J., Jumars, P.A., Self, R.L., 1995. Bioavailable amino acids in sediments: a biomimetic, kinetics–based approach. Limnology and Oceanography 40, 511–520.

Mayer, L.M., Schick, L.L., Allison, M.A., 2008. Input of nutritionally rich organic matter from the Mississippi River to the Louisiana coastal zone. Estuaries and Coasts 31, 1052–1062.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

McKee, B.A., Aller, R.C., Allison, M.A., Bianchi, T.S., Kineke, G.C., 2004. Transport and transformation of dissolved and particulate materials on continental margins influenced by major rivers: benthic boundary layer and seabed processes. Continental Shelf Research 24, 899–926.

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.

Meyer, D., Zeileis, A., Hornik, K., 2013. vcd: Visualizing Categorical Data. R package version 1.3–1.

Meyers, P.A., 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. Chemical Geology 114, 289–302.

Meysman, J.F.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look ar Darwin's las idea. Trends in Ecology & Evolution 12, 688–695.

Millot, C., 1990. The Gulf of Lions hydrodynamics. Continental Shelf Research 10, 9–11.

Miralles, J., Radakovitch, O., Aloisi, J.C., 2005. ^{210}Pb sedimentation rates from the Northwestern Mediterranean margin. Marine Geology 216, 155–167.

Möllmann, C., Diekmann, R., 2012. Chapter 4 – Marine ecosystem regime shifts induced by climate and overfishing: a review for the Northern Hemisphere, in Advances in Ecological Research (Eds. G. Woodward, U. Jacob and E.J. O'Gorman). Academic Press 47, pp. 303–347.

MSFD, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for Community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union L164, 19–40.

Murina, G.V.V., Pancucci-Papadopoulou M.A., Zenetos, A., 1999. The phylym Sipuncula in the eastern Mediterranean: composition, ecology, zoogeography. Journal of the Marine Biological Association of the UK 79, 821–830.

Mutlu, E., Çinar, M.E., Ergev, M.B., 2010. Distribution of soft-bottom polychaetes of the Levantine coast of Turkey, eastern Mediterranean Sea. Journal of Marine Systems 79, 23–35.

Muxika, I., Borja, A., Bald, J., 2007. Using historical data, expert judgement and multivariate analysis in assessing reference conditions and benthic ecological status, according to the European Water Framework Directive. Marine Pollution Bulletin 55, 16–29.

Neumann, H., Ehrich, S., Kröncke, I., 2008. Effects of cold winters and climate on the temporal variability of an epibenthic community in the German Bight. Climate Research 37, 241–251.

Neveux, J., Lantoine, F., 1993. Spectrofluorometric assay of chlorophylls and phaeopigments using the least-square approximation technique. Deep Sea Research Part I: Oceanographic Research Papers 40, 1747–1765.

Nilsson, H.C., Rosenberg, R., 1997. Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images. Journal of Marine Systems 11, 249–264.

Occhipinti-Ambrogi, A., Savini, D., Forni, G., 2005. Macrobenthos community structural changes off Cesenatico coast (Emilia Romagna, Northern Adriatic), a six-year monitoring programme. Science of The Total Environment 353, 317–328.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. vegan: Community Ecology Package. R package version 2.0–10. http://CRAN.R–project.org/package=vegan

Osborn, T.J., Conway, D., Hulme, M., Gregory, J.M., Jones, P., 1999. Air flow influences on local climate: observed and simulated mean relatioships for the United Kingdom. Climate Research 13, 173–191.

Osborn, T.J., 2006. Recent variations in the winter North Atlantic Oscillation. Weather 61, 353–355.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P., Stenseth, N., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128, 1–14.

Palanques, A., Puig, P., Guillén, J., Jiménez, J., Gracia, V., Sánchez-Arcilla, A., Madsen, O., 2002. Near-bottom suspended sediment fluxes on the microtidal low-energy Ebro continental shelf (NW Mediterranean). Continental Shelf Research 22, 285–303.

Pastor, L., Cathalot, C., Deflandre, B., Viollier, E., Soetaert, K., Meysman, F.J.R., Ulses, C., Metzger, E., Rabouille, C., 2011. Modeling biogeochemical processes in sediments from the Rhône River prodelta area (NW Mediterranean Sea). Biogeosciences 8, 1351–1366.

Pastor, L., Deflandre, B., Viollier, E., Cathalot, C., Metzger, E., Rabouille, C., Escoubeyrou, K., Lloret, E., Pruski, A.M., Vétion, G., Desmalades, M., Buscail, R., Grémare, A., 2011. Influence of the organic matter composition on benthic oxygen demand in the Rhône River prodelta (NW Mediterranean Sea). Continental Shelf Research 31, 1008–1019.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic sucession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology: An Annual Review 16, 229–311.

Pearson, T.H., Josefson, A.B., Rosenberg, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegatt becoming eutrophic? Journal of Experimental Marine Biology and Ecology 92, 157–206.

Pelaprat, C., Agreil, M., Chery, A., Pete, D., Michele, L., Lejeune, P., 2007. Mise en œuvre du contrôle de surveillance au titre de la directive cadre eau pour l’indicateur benthos de substrat meuble dans le district corse (Eaux côtières) – Contrat STARESO/IFREMER

Pelaprat, C., Donnay, A., Chery, A., Missa, A., Lejeune, P. 2010. Mise en œuvre du contrôle de surveillance et opérationnel au titre de la directive cadre eau pour l’indicateur benthos de substrat meuble dans le district corse (Eaux côtières) - Contrat STARESO/IFREMER.

Pelaprat, C., Labrune, C., Amouroux, J.M., Donnay, A., Frejefond, C., Chery, A., Lejeune, P., 2013. Mise en oeuvre du contrôle de surveillance au titre de la directive cadre eau pour l’indicateur benthos de substrat meuble (Eaux côtières) 2012 - Contrat STARESO/IFREMER N/Ref 13/30530017.

Pérès, J.M., Picard, J., 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. Recueil des Travaux de la Station Marine d'Endoume 31, 5–137.

Perus, J., Bonsdorff, E., 2004. Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. Journal of Sea Research 52, 45–56.

Picard, J., 1965. Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise. Recueil des Travaux de la Station Marine d'Endoume 52, 1–160.

Poggiale, J.C., Dauvin, J.C., 2001. Long term dynamics of three benthic *Ampelisca* (Crustacea-Amphipoda) populations from the Bay of Morlaix (western English Channel) related to their disappearance after the Amoco Cadiz oil spill. Marine Ecology Progress Series 214, 201–209.

Pont, D., 1997. Les débits solides du Rhône à proximité de son embouchure: données récentes (1994–1995). Revue de Géographie de Lyon 72, 23–33.

Pont, D., Simonnet, J.P., Walter, A.V., 2002. Medium-term changes in suspended sediment delivery to the ocean: consequences of catchment heterogeneity and river management (Rhône River, France). Estuarine, Coastal and Shelf Science 54, 1–18.

Posey, M., Lindberg, W., Alphin, T., Vose, F., 1996. Influence of storm disturbance on an offshore benthic community. Bulletin of Marine Science 59, 523–529.

Puente, A., Diaz, R.J., 2008. Is it possible to assess the ecological status of highly stressed natural estuarine environments using macroinvertebrates indices? Marine Pollution Bulletin 56, 1880–1889.

Puig, P., Palanques, A., Guillén, J., 2001. Near-bottom suspended sediment variability caused by storms and near-inertial internal waves on the Ebro mid continental shelf (NW Mediterranean). Marine Geology 178, 81–93.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R–project.org/.

Radakovitch, O., Charmasson, S., Arnaud, M., Bouisset, P., 1999. ^{210}Pb and caesium accumulation in the Rhône delta sediments. Estuarine, Coastal and Shelf Science 48, 77–92.

Ranasinghe, J.A., Weisberg, S.B., Smith, R.W., Montagne, D.E., Thompson, B., Oakden, J.M., Huff, D.D., Cadien, D.B., Velarde, R.G., Ritter, K.J., 2009. Calibration and evaluation of five indicators of benthic community condition in two California bay and estuary habitats. Marine Pollution Bulletin 59, 5–13.

Rees, H.L., Pendle, M.A., Limpenny, C.E., Mason, C.E., Boyd, S.E., Birchenough, S., Vivian, C.M.G., 2006. Benthic responses to organic enrichment and climatic events in the western North Sea. Journal of the Marine Biological Association of the United Kingdom 86, 1–18.

Reichert, K., Buchholz, F., 2006. Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. Helgoland Marine Research 60, 213–223.

Reid, P.C., Lancelot, C., Gieskes, W.W.C., Hagmeier, E., Weichart, G., 1990. Phytoplankton of the North Sea and its dynamics: a review. Netherlands Journal of Sea Research 26, 285–331.

Reid, P.C., Borges, M.F., Svendsen, E., 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fisheries Research 50, 163–171.

Reise, K., Schubert, A., 1987. Macrobenthic turnover in the subtidal Wadden Sea: the Norderaue revisited after 60 years. Helgoländer Meeresuntersuchungen 41, 69–82.

Reiss, H., Kröncke, I., 2005. Seasonal variability of benthic indices: an approach to test the applicability of different indices for ecosystem quality assessment. Marine Pollution Bulletin 50, 1490–1499.

Reiss, H., Kröncke, I., 2006. Temporal patterns of infaunal communities in the North Sea: internanual vs. intraannual variability. Senckenbergiana Maritima 36, 11–18.

Reiss, H., Meybohm, K., Kröncke, I., 2006. Cold winter effects on benthic macrofauna communities in near- and offshore regions of the North Sea. Helgoland Marine Research 60, 224-238.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28, 150–178.

Rhoads, D.C., Cande, S., 1971. Sediment profile camera for *in situ* study of organism sediment relations. Limnology and Oceanography 16, 110–114.

Rhoads, D.C., Young, D.K., 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). Marine Biology 11, 255–261.

Rhoads, D.C., 1974. Organism-sediment relations on the muddy seafloor. Oceanography and Marine Biology: An Annual Review 12, 263–300.

Rhoads, D.C., Germano, J.D., 1982. Characterization of organism-sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remots TM System). Marine Ecology Progress Series 8, 115–128.

Rhoads, D.C., Boesch, D.F., Zhican, T., Fengshan, X., Liqiang, H., Nilsen, K.J., 1985. Macrobenthos and sedimentary facies on the Changjiang delta platform and adjacent continental shelf, East China Sea. Continental Shelf Research 4, 189–213.

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., Gray., J.S., Josefson, A.B., Pearson, T.H., 1987. Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? Journal of Experimental Marine Biology and Ecology 105, 219–251.

Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Scientia Marina 65, 107–119.

Rosenberg, R., Grémare, A., Amouroux, J.M., Nilsson, H.C., 2003. Benthic habitats in the northwest Mediterranean characterised by sedimentary organics, benthic macrofauna and sediment profile images. Estuarine, Coastal and Shelf Science 57, 297-311.

Rosenberg, R., Blomqvist, M., Nilsson, H.C., Cederwall, H., Dimming, A., 2004. Marine quality assessment by use of benthic species-abundance distributions: a proposed new protocol within the European Union Water Framework Directive. Marine Pollution Bulletin 49, 728–739.

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.

Rousi, H., Laine, A.O., Peltonen, H., Kangas, P., Andersin, A.B., Rissanen, J., Sandberg-Kilpi, E., Bonsdorff, E., 2013. Long-term changes in coastal zoobenthos in the northern Baltic Sea: the role of abiotic environmental factors. ICES Journal of Marine Science 70, 440–451.

Roussiez, V., Ludwig, W., Probst, J.L., Monaco, A., 2005. Background levels of heavy metals in surficial sediments of the Gulf of Lions (NW Mediterranean): an approach based on ^{133}Cs normalization and lead isotope measurements. Environmental Pollution 138, 167–177.

Ruellet, T., Dauvin, J.C., 2007. Benthic indicators: analysis of the threshold values of ecological quality classifications for transitional waters. Marine Pollution Bulletin 54, 1707–1714.

Salen-Picard, C., 1981. Évolution d'un peuplement de Vasse Terrigène Côtière soumis à des rejets de dragages dans le golfe de Fos. Tethys 10, 83–88.

Salen-Picard, C., Bellan, G., Bellan-Santini, D., Arlhac, D., Marquet, R., 1997. Changements à long terme dans une communauté benthique d'un golfe méditerranéen (golfe de Fos). Oceanologica Acta 20, 299–310.

Salen-Picard, C., Arlhac, D., 2002. Long-term changes in a Mediterranean benthic community: relationships between the polychaete assemblages and hydrological variations of the Rhône River. Estuaries 25, 1121–1130.

Salen-Picard, C., Darnaude, A., Arlhac, D., Harmelin-Vivien, M., 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. Oecologia 133, 380–388.

Salen-Picard, C., Arlhac, D., Alliot, E., 2003. Responses of a Mediterranean soft bottom community to short-term (1993–1996) hydrological changes in the Rhone river. Marine environmental research 55, 409–427.

Sanchez-Vidal, A., Canals, M., Calafat, A.M., Lastras, G., Pedrosa-Pamies, R., Menendez, M., Medina, R., Company, J.B., Hereu, B., Romero, J., Alcoverro, T., 2012. Impacts on the deep-sea ecosystem by a severe coastal storm. PloS one 7, e30395.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Schückel, U., Ehrich, S., Kröncke, I., 2010. Temporal variability of three different macrofauna communities in the northern North Sea. Estuarine, Coastal and Shelf Science 89, 1–11.

Serrano-Samaniego, L.G., 2012. Distribution of soft-bottom polychaetes assemblages at different scales in shallow waters of the nothern Mediterranean Spanish coast. PhD Thesis, Universitat de Barcelona, Barcelona.

Simboura, N., Zenetos, A., 2002. Benthic indicators to use in Ecological Quality classification of Mediterranean soft bottom marine ecosystems, including a new Biotic Index. Mediterranean Marine Science 3, 77–111.

Snelgrove, P.V.R., Butman, C.A., 1994. Animal-sediment relationships revisited: cause versus effect. Oceanography and Marine Biology: An Annual Review 32, 111–177.

Tesi, T., Miserocchi, S., Goni, M.A., Langone, L., 2007. Source, transport and fate of terrestrial organic carbon on the western Mediterranean Sea, Gulf of Lions, France. Marine Chemistry 105, 101–117.

Thorin, S., Dolbeau, X., 2007. Suivi à long terme des communautés benthiques des substrats meubles dans la Réserve Naturelle Marine de Cerbère-Banyuls – champagne 2007. Conseil Général des Pyrénées Orientales, 52 pp.

Thorin, S., 2009. Suivi à long terme des communautés benthiques des substrats meubles dans la Réserve Naturelle Marine de Cerbère-Banyuls - champagne 2009. Conseil Général des Pyrénées Orientales, 64 pp.

Thorson, G., 1957. Bottom communities (sublittoral or shallow shelf). Geological Society of America Memoirs 67, 461–534.

Thorson, G., 1961. Length of pelagic life in marine invertebrates as related to larval transport by ocean currents, in Oceanography Publication 67 (Ed. M. Sears). American Association for the Advancement of Science, Washington, D.C. pp. 455–474.

Tunberg, B.G., Nelson, W.G., 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? Marine Ecology Progress Series 170, 85–94.

Ulses, C., Estournel, C., Durrieu de Madron, X., Palanques, A., 2008. Suspended sediment transport in the Gulf of Lions (NW Mediterranean): impact of extreme storms and floods. Continental Shelf Research 28, 2048–2070.

Vačkář, D., ten Brink, B., Loh, J., Baillie, J.E.M., Reyers, B., 2012. Review of multispecies indices for monitoring human impacts on biodiversity. Ecological Indicators 17, 58–67.

Van Hoey, G., Vincx, M., Degraer, S., 2007. Temporal variability in the *Abra alba* community determined by global and local events. Journal of Sea Research 58, 144–155.

Van Hoey, G., Permuy, D.C., Vandendriessche, S., Vincx, M., Hostens, K., 2013. An ecological quality status assessment procedure for soft-sediment benthic habitats: weighing alternative approaches. Ecological Indicators 25, 266–278.

Vanden Berghe, E., Claus, S., Appeltans, W., Faulwette, R.S., Arvanitidis, C., Somerfield, P., Aleffi, I., Amouroux, J.M., Anisimova, N., Bachelet, G., Cochrane, S., Costello, M., Craeymeersch, J., Dahle, S., Degraer, S., Denisenko, S., Dounas, C., Duineveld, G., Emblow, C., Escaravage, V., Fabri, M., Fleischer, D., Grémare, A., Herrmann, M., Hummel, H., Karakassis, I., Kedra, M., Kendall, M., Kingston, P., Kotwicki, L., Labrune, C., Laudien, J., Nevrova, E., Occhipinti-Ambrogi, A., Olsgard, F., Palerud, R., Petrov, A., Rachor, E., Revkov, N., Rumohr, H., Sardá, R., Sistermans, W., Speybroeck, J., Janas, U., Van Hoey, G., Vincx, M., Whomersley, P., Willems, W., Wlodarska-Kowalczuk, M., Zenetos, A., Zettler, M., Heip, C., 2009. MacroBen integrated database on benthic invertebrates of European continental shelves: a tool for large-scale analysis across Europe. Marine Ecology Progress Series 382, 225–238.

Vonk, J.E., Sánchez-García, L., Semiletov, I., Dudarev, O., Eglinton, T., Andersson, A., Gustafsson, Ö., 2010. Molecular and radiocarbon constraints on sources and degradation of terrestrial organic carbon along the Kolyma paleoriver transect, East Siberian Sea. Biogeosciences 7, 3153–3166.

Wakeham, S.G., Lee, C., Hedges, J.I., Hernes, P.J., Peterson, M.J., 1997. Molecular indicators of diagenetic status in marine organic matter. Geochimica et Cosmochimica Acta 61, 5363–5369.

Wakeham, S.G., Canuel, E.A., 2006. Degradation and preservation of organic matter in marine sediments, in Marine organic matter: biomarkers, isotopes and DNA, The Handbook of Environmental Chemistry (Ed. J.K. Volkman). Springer-Verlag, Berlin/Heidelberg, pp. 295–321.

Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J., Tapp, J.F., 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Marine Ecology Progress Series 234, 1–13.

Warwick, R.M., Emblow, C., Féral, J.P., Hummel, H., Avesaath, P.V., Heip., C., 2003. European marine biodiversity research sites. Netherlands Institute of Ecology – Centre for Estuarine and Marine Ecology, Yerseke, The Netherlands.

Weisberg, S.B., Ranasinghe, J.A., Dauer, D.M., Schaffner, L.C., Diaz, R.J., Frithsen, J.B., 1997. An estuarine Benthic Index of Biotic Integrity (B-IBI) for Cheasapeake Bay. Estuaries 20, 149–158.

WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Union L327, 1–73.

Wheatcroft, R.A., 2006. Time-series measurements of macrobenthos abundance and sediment bioturbation intensity on a flood-dominated shelf. Progress in Oceanography 71, 88–122.

Wieking, G., Kröncke, I., 2001. Decadal changes in microfauna communities on the Dogger Bank caused by large-scale climate variability. Senckenbergiana Maritima 31, 125–141.

Wieking, G., Kröncke, I., 2003. Macrofauna communities of the Dogger Bank (central North Sea) in the late 1990s: spatial distribution, species composition and trophic structure. Helgoland Marine Research 57, 34–46.

Wildish, D.J., 1985. Geographical distribution of macrofauna on sublittoral sediments of continental shelves: a modified thophic ratio concept, in Proceedings of the 19th European Marine Biology Symposium (Ed. P.E. Gibbs). Plymouth, Devon, UK, pp. 335-346.

WoRMS, 2014. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2014–04–10.

Yonge, C.M., 1946. On the habits of *Turritella communis* Risso. Journal of the Marine Biological Association of the UK 26, 377–380.

Young, D.K., Rhoads, D.C., 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Marine Biology 11, 242–254

Yu, Z., Zhang, Q., Kraus, T., Dahlgren, R.A., Anastasio, C., Zasoski, R.J., 2002. Contribution of amino compounds to dissolved organic nitrogen in forest soils. Biogeochemistry 61, 173–198.

Zebracki, M., Eyrolle-Boyer, F., Evrard, O., Claval, D., Mourier, B., Gairoard, S., Cagnat, X., Antonelli, C., 2015. Tracing the origin of suspended sediment in a large Mediterranean river by combining continuous river monitoring and measurement of artificial and natural radionuclides. Science of the Total Environment 502, 122–132.

Zettler, M.L., Schiedek, D., Bobertz, B., 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. Marine Pollution Bulletin 55, 258–270.

Zuo, Z., Eisma, D., Gieles, R., Beks, J., 1997. Accumulation rates and sediment deposition in the northwestern Mediterranean. Deep Sea Research Part II 44, 597–609.

ANNEXES

POSTERS ET ARTICLES

Posters

- **Bonifácio, P.,** Solveig, S., Labrune, C., Amouroux, J.-M., Escoubeyrou, K., Buscail, R., Romero-Ramirez, A., Lantoine, F., Vétion, G., Bichon, S., Desmalades, M., Rivière, B., Deflandre, B., Grémare, A. 2014. Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition of the Rhône River in relation with its hydrological regime. Journée d'Échanges Scientifiques – EPOC, 2014, Gujan Mestras.
- **Bonifácio, P**., Lavesque, N., Bachelet, G., Barnich, R., Parapar, J., Grémare, A. 2014. New records of deep-sea Polychaeta (Annelida) from the Capbreton Canyon (Bay of Biscay, NE Atlantic). XIV International Symposium on Oceanography of the Bay of Biscay, 2014, Bordeaux.

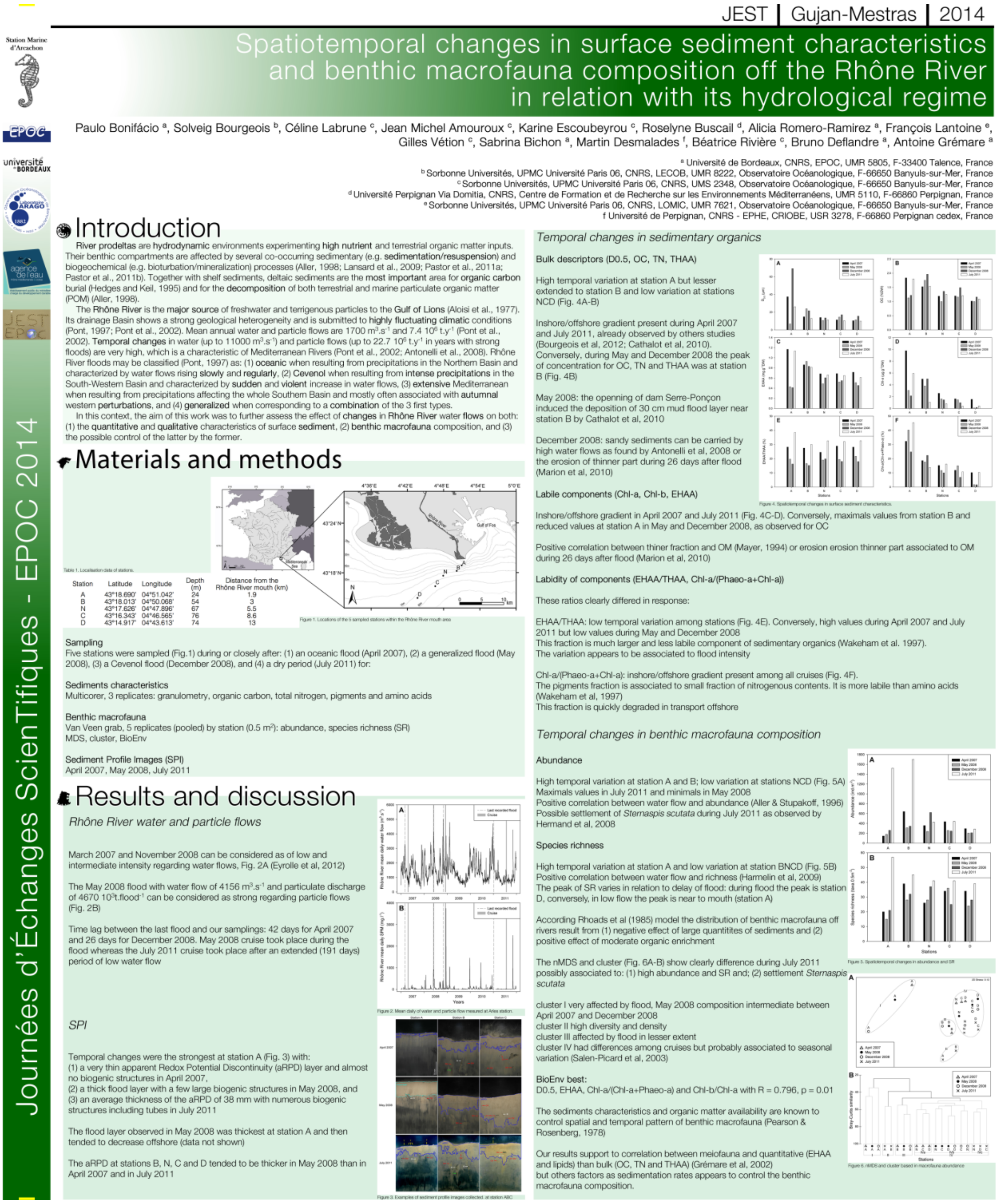
Articles acceptés

- **Bonifácio, P.,** Lavesque; N., Bachelet, G., Barnich, R., Parapar, J. *Anobothrus amourouxi* sp. nov., a new species of Ampharetidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic Ocean). Journal of the Marine Biological Association of the UK.

Articles publiés

- Jourde, J., Sampaio, L., Barnich, R., **Bonifácio, P.**, Labrune, C., Quintino, V., Sauriau, P-G. 2014. Malmgrenia sp. nov., a new Malmgrenia species (Polychaeta: Polynoidae) from western Mediterranean and North-East Atlantic with a key to the North-East Atlantic and Mediterranean Malmgrenia species. Journal of the Marine Biological Association of the UK 1–6.
- Lavesque, N., Gouillieux, B., de Montaudoin, X., Bachelet, G., **Bonifácio, P.**, Simonet, E. 2014. Premier signalement de l'espèce introduite *Grandidierella japonica* Stephensen, 1938 (Crustacea: Amphipoda : Aoridae) dans le bassin d'Arcachon. An aod - les cahiers naturalistes de l'Observatoire marin 3, 11-19.
- Lavesque, N., **Bonifácio, P.**, Meißner, K., Blanchet, H., Gouillieux, B., Dubois, S., Bachelet, G., 2014. New records of *Spio symphyta* and *Spio martinensis* ("Polychaeta": Canalipalpata: Spionidae) from Arcachon Bay (France), NE Atlantic. Marine Biodiversity.
- Khedhri, I., Lavesque, N., **Bonifácio, P.**, Djabou, H., Afli, A., 2014. First record of Naineris setosa (Verrill, 1900) (Annelida: Polychaeta: Orbiniidae) in the Western Mediterranean Sea. BioInvasions Records 3, 83–88
- Lavesque, N., Sorbe, J.-C., Bachelet, G., Gouillieux, B., de Montaudouin, X., **Bonifácio, P.**, Blanchet, H., Dubois, S., 2013. Recent discovery of *Paranthura japonica* Richardson, 1909 (Crustacea: Isopoda: Paranthuridae) in European marine waters (Arcachon Bay, Bay of Biscay). BioInvasions Records 2, 215–219.

Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition of the Rhône River in relation with its hydrological regime



Journées d'Échanges ScienTifiques - EPOC 2014

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Spatiotemporal changes in surface sediment characteristics and benthic macrofauna composition off the Rhône River in relation with its hydrological regime

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Introduction

River prodeltas are **hydrodynamic** environments experimenting **high nutrient** and terrestrial organic matter inputs. Their benthic compartments are affected by several co-occurring sedimentary (e.g. **sedimentation/resuspension**) and biogeochemical (e.g. bioturbation/mineralization) processes (Aller, 1998; Lansard et al., 2009; Pastor et al., 2011a; Pastor et al., 2011b). Together with shelf sediments, deltaic sediments are the **most important** area for **organic carbon** burial (Hedges and Keil, 1995) and for the **decomposition** of both terrestrial and marine particulate organic matter (POM) (Aller, 1998).

The **Rhône River** is the **major source** of freshwater and terrigenous particles to the **Gulf of Lions** (Aloisi et al., 1977). Its drainage Basin shows a strong geological heterogeneity and is submitted to **highly fluctuating climatic** conditions (Pont, 1997; Pont et al., 2002). Mean annual water and particle flows are 1700 $m^3.s^{-1}$ and 7.4 10^6 $t.y^{-1}$ (Pont et al., 2002). **Temporal changes** in water (up to 11000 $m^3.s^{-1}$) and particle flows (up to 22.7 10^6 $t.y^{-1}$ in years with strong floods) are very high, which is a characteristic of Mediterranean Rivers (Pont et al., 2002; Antonelli et al., 2008). Rhône River floods may be classified (Pont, 1997) as: (1) **oceanic** when resulting from precipitations in the Northern Basin and characterized by water flows rising **slowly** and **regularly**, (2) **Cevenol** when resulting from **intense precipitations** in the South-Western Basin and characterized by **sudden** and **violent** increase in water flows, (3) **extensive** Mediterranean when resulting from precipitations affecting the whole Southern Basin and mostly often associated with **autumnal** western **perturbations**, and (4) **generalized** when corresponding to a **combination** of the 3 first types.

In this context, the aim of this work was to further assess the effect of **changes** in **Rhône River** water **flows** on both: (1) the **quantitative** and **qualitative** characteristics of surface **sediment**, (2) **benthic macrofauna** composition, and (3) the possible control of the latter by the former.

Materials and methods

Table 1. Localisation data of stations.

Station	Latitude	Longitude	Depth (m)	Distance from the Rhône River mouth (km)
A	43°18.690'	04°51.042'	24	1.9
B	43°18.013'	04°50.068'	54	3
N	43°17.626'	04°47.896'	67	5.5
C	43°16.343'	04°46.565'	76	8.6
D	43°14.917'	04°43.613'	74	13

Figure 1. Locations of the 5 sampled stations within the Rhône River mouth area

Sampling
Five stations were sampled (Fig.1) during or closely after: (1) an oceanic flood (April 2007), (2) a generalized flood (May 2008), (3) a Cevenol flood (December 2008), and (4) a dry period (July 2011) for:

Sediments characteristics
Multicorer, 3 replicates: granulometry, organic carbon, total nitrogen, pigments and amino acids

Benthic macrofauna
Van Veen grab, 5 replicates (pooled) by station (0.5 m^2): abundance, species richness (SR)
MDS, cluster, BioEnv

Sediment Profile Images (SPI)
April 2007, May 2008, July 2011

Results and discussion

Rhône River water and particle flows

March 2007 and November 2008 can be considered as of low and intermediate intensity regarding water flows, Fig. 2A (Eyrolle et al, 2012)

The May 2008 flood with water flow of 4156 $m^3.s^{-1}$ and particulate discharge of 4670 $10^3t.flood^{-1}$ can be considered as strong regarding particle flows (Fig. 2B)

Time lag between the last flood and our samplings: 42 days for April 2007 and 26 days for December 2008. May 2008 cruise took place during the flood whereas the July 2011 cruise took place after an extended (191 days) period of low water flow

Figure 2. Mean daily of water and particle flow measured at Arles station.

SPI

Temporal changes were the strongest at station A (Fig. 3) with:
(1) a very thin apparent Redox Potential Discontinuity (aRPD) layer and almost no biogenic structures in April 2007,
(2) a thick flood layer with a few large biogenic structures in May 2008, and
(3) an average thickness of the aRPD of 38 mm with numerous biogenic structures including tubes in July 2011

The flood layer observed in May 2008 was thickest at station A and then tended to decrease offshore (data not shown)

The aRPD at stations B, N, C and D tended to be thicker in May 2008 than in April 2007 and in July 2011

Figure 3. Examples of sediment profile images collected. at station ABC

Temporal changes in sedimentary organics

Bulk descriptors (D0.5, OC, TN, THAA)

High temporal variation at station A but lesser extended to station B and low variation at stations NCD (Fig. 4A-B)

Inshore/offshore gradient present during April 2007 and July 2011, already observed by others studies (Bourgeois et al, 2012; Cathalot et al, 2010). Conversely, during May and December 2008 the peak of concentration for OC, TN and THAA was at station B (Fig. 4B)

May 2008: the openning of dam Serre-Ponçon induced the deposition of 30 cm mud flood layer near station B by Cathalot et al, 2010

December 2008: sandy sediments can be carried by high water flows as found by Antonelli et al, 2008 or the erosion of thinner part during 26 days after flood (Marion et al, 2010)

Figure 4. Spatiotemporal changes in surface sediment characteristics.

Labile components (Chl-a, Chl-b, EHAA)

Inshore/offshore gradient in April 2007 and July 2011 (Fig. 4C-D). Conversely, maximals values from station B and reduced values at station A in May and December 2008, as observed for OC

Positive correlation between thiner fraction and OM (Mayer, 1994) or erosion erosion thinner part associated to OM during 26 days after flood (Marion et al, 2010)

Labidity of components (EHAA/THAA, Chl-a/(Phaeo-a+Chl-a))

These ratios clearly differed in response:

EHAA/THAA: low temporal variation among stations (Fig. 4E). Conversely, high values during April 2007 and July 2011 but low values during May and December 2008
This fraction is much larger and less labile component of sedimentary organics (Wakeham et al. 1997).
The variation appears to be associated to flood intensity

Chl-a/(Phaeo-a+Chl-a): inshore/offshore gradient present among all cruises (Fig. 4F).
The pigments fraction is associated to small fraction of nitrogenous contents. It is more labile than amino acids (Wakeham et al, 1997)
This fraction is quickly degraded in transport offshore

Temporal changes in benthic macrofauna composition

Abundance

High temporal variation at station A and B; low variation at stations NCD (Fig. 5A)
Maximals values in July 2011 and minimals in May 2008
Positive correlation between water flow and abundance (Aller & Stupakoff, 1996)
Possible settlement of *Sternaspis scutata* during July 2011 as observed by Hermand et al, 2008

Species richness

High temporal variation at station A and low variation at station BNCD (Fig. 5B)
Positive correlation between water flow and richness (Harmelin et al, 2009)
The peak of SR varies in relation to delay of flood: during flood the peak is station D, conversely, in low flow the peak is near to mouth (station A)

According Rhoads et al (1985) model the distribution of benthic macrofauna off rivers result from (1) negative effect of large quantitites of sediments and (2) positive effect of moderate organic enrichment

Figure 5. Spatiotemporal changes in abundance and SR

The nMDS and cluster (Fig. 6A-B) show clearly difference during July 2011 possibly associated to: (1) high abundance and SR and; (2) settlement *Sternaspis scutata*

cluster I very affected by flood, May 2008 composition intermediate between April 2007 and December 2008
cluster II high diversity and density
cluster III affected by flood in lesser extent
cluster IV had differences among cruises but probably associated to seasonal variation (Salen-Picard et al, 2003)

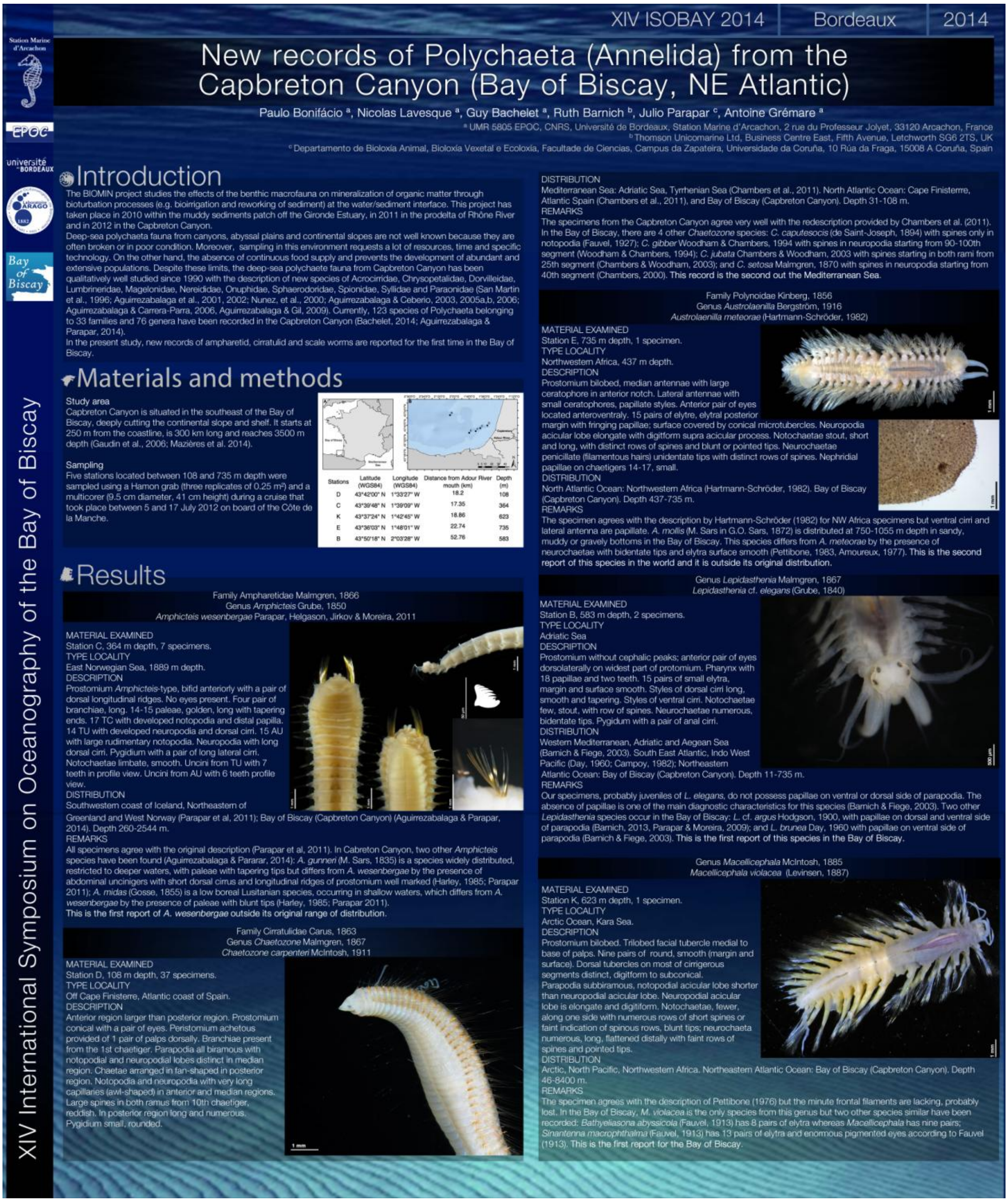
BioEnv best:
D0.5, EHAA, Chl-a/(Chl-a+Phaeo-a) and Chl-b/Chl-a with R = 0.796, p = 0.01

The sediments characteristics and organic matter availability are known to control spatial and temporal pattern of benthic macrofauna (Pearson & Rosenberg, 1978)

Our results support to correlation between meiofauna and quantitative (EHAA and lipids) than bulk (OC, TN and THAA) (Grémare et al, 2002)
but others factors as sedimentation rates appears to control the benthic macrofauna composition.

Figure 6. nMDS and cluster based in macrofauna abundance

New records of deep-sea Polychaeta (Annelida) from the Capbreton Canyon (Bay of Biscay, NE Atlantic)



New records of Polychaeta (Annelida) from the Capbreton Canyon (Bay of Biscay, NE Atlantic)

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Introduction

The BIOMIN project studies the effects of the benthic macrofauna on mineralization of organic matter through bioturbation processes (e.g. bioirrigation and reworking of sediment) at the water/sediment interface. This project has taken place in 2010 within the muddy sediments patch off the Gironde Estuary, in 2011 in the prodelta of Rhône River and in 2012 in the Capbreton Canyon.

Deep-sea polychaeta fauna from canyons, abyssal plains and continental slopes are not well known because they are often broken or in poor condition. Moreover, sampling in this environment requests a lot of resources, time and specific technology. On the other hand, the absence of continuous food supply and prevents the development of abundant and extensive populations. Despite these limits, the deep-sea polychaete fauna from Capbreton Canyon has been qualitatively well studied since 1990 with the description of new species of Acrocirridae, Chrysopetalidae, Dorvilleidae, Lumbrineridae, Magelonidae, Nereididae, Onuphidae, Sphaerodoridae, Spionidae, Syllidae and Paraonidae (San Martin et al., 1996; Aguirrezabalaga et al., 2001, 2002; Nunez, et al., 2000; Aguirrezabalaga & Ceberio, 2003, 2005a,b, 2006; Aguirrezabalaga & Carrera-Parra, 2006, Aguirrezabalaga & Gil, 2009). Currently, 123 species of Polychaeta belonging to 33 families and 76 genera have been recorded in the Capbreton Canyon (Bachelet, 2014; Aguirrezabalaga & Parapar, 2014).

In the present study, new records of ampharetid, cirratulid and scale worms are reported for the first time in the Bay of Biscay.

Materials and methods

Study area

Capbreton Canyon is situated in the southeast of the Bay of Biscay, deeply cutting the continental slope and shelf. It starts at 250 m from the coastline, is 300 km long and reaches 3500 m depth (Gaudin et al., 2006; Mazières et al. 2014).

Sampling

Five stations located between 108 and 735 m depth were sampled using a Hamon grab (three replicates of 0.25 m²) and a multicorer (9.5 cm diameter, 41 cm height) during a cruise that took place between 5 and 17 July 2012 on board of the Côte de la Manche.

Stations	Latitude (WGS84)	Longitude (WGS84)	Distance from Adour River mouth (km)	Depth (m)
D	43°42'00" N	1°33'27" W	18.2	108
C	43°39'48" N	1°39'09" W	17.35	364
K	43°37'24" N	1°42'45" W	18.86	623
E	43°36'03" N	1°48'01" W	22.74	735
B	43°50'18" N	2°03'28" W	52.76	583

Results

Family Ampharetidae Malmgren, 1866
Genus *Amphicteis* Grube, 1850
Amphicteis wesenbergae Parapar, Helgason, Jirkov & Moreira, 2011

MATERIAL EXAMINED
Station C, 364 m depth, 7 specimens.
TYPE LOCALITY
East Norwegian Sea, 1889 m depth.
DESCRIPTION
Prostomium *Amphicteis*-type, bifid anteriorly with a pair of dorsal longitudinal ridges. No eyes present. Four pair of branchiae, long. 14-15 paleae, golden, long with tapering ends. 17 TC with developed notopodia and distal papilla. 14 TU with developed neuropodia and dorsal cirri. 15 AU with large rudimentary notopodia. Neuropodia with long dorsal cirri. Pygidium with a pair of long lateral cirri. Notochaetae limbate, smooth. Uncini from TU with 7 teeth in profile view. Uncini from AU with 6 teeth profile view.
DISTRIBUTION
Southwestern coast of Iceland, Northeastern of Greenland and West Norway (Parapar et al, 2011); Bay of Biscay (Capbreton Canyon) (Aguirrezabalaga & Parapar, 2014). Depth 260-2544 m.
REMARKS
All specimens agree with the original description (Parapar et al, 2011). In Cabreton Canyon, two other *Amphicteis* species have been found (Aguirrezabalaga & Pararar, 2014): *A. gunneri* (M. Sars, 1835) is a species widely distributed, restricted to deeper waters, with paleae with tapering tips but differs from *A. wesenbergae* by the presence of abdominal uncinigers with short dorsal cirrus and longitudinal ridges of prostomium well marked (Harley, 1985; Parapar 2011); *A. midas* (Gosse, 1855) is a low boreal Lusitanian species, occurring in shallow waters, which differs from *A. wesenbergae* by the presence of paleae with blunt tips (Harley, 1985; Parapar 2011).
This is the first report of *A. wesenbergae* outside its original range of distribution.

Family Cirratulidae Carus, 1863
Genus *Chaetozone* Malmgren, 1867
Chaetozone carpenteri McIntosh, 1911

MATERIAL EXAMINED
Station D, 108 m depth, 37 specimens.
TYPE LOCALITY
Off Cape Finisterre, Atlantic coast of Spain.
DESCRIPTION
Anterior region larger than posterior region. Prostomium conical with a pair of eyes. Peristomium achetous provided of 1 pair of palps dorsally. Branchiae present from the 1st chaetiger. Parapodia all biramous with notopodial and neuropodial lobes distinct in median region. Chaetae arranged in fan-shaped in posterior region. Notopodia and neuropodia with very long capillaries (awl-shaped) in anterior and median regions. Large spines in both ramus from 10th chaetiger, reddish. In posterior region long and numerous. Pygidium small, rounded.
DISTRIBUTION
Mediterranean Sea: Adriatic Sea, Tyrrhenian Sea (Chambers et al., 2011). North Atlantic Ocean: Cape Finisterrre, Atlantic Spain (Chambers et al., 2011), and Bay of Biscay (Capbreton Canyon). Depth 31-108 m.
REMARKS
The specimens from the Capbreton Canyon agree very well with the redescription provided by Chambers et al. (2011). In the Bay of Biscay, there are 4 other *Chaetozone* species: *C. caputesocis* (de Saint-Joseph, 1894) with spines only in notopodia (Fauvel, 1927); *C. gibber* Woodham & Chambers, 1994 with spines in neuropodia starting from 90-100th segment (Woodham & Chambers, 1994); *C. jubata* Chambers & Woodham, 2003 with spines starting in both rami from 25th segment (Chambers & Woodham, 2003); and *C. setosa* Malmgren, 1870 with spines in neuropodia starting from 40th segment (Chambers, 2000). **This record is the second out the Mediterranean Sea.**

Family Polynoidae Kinberg, 1856
Genus *Austrolaenilla* Bergström, 1916
Austrolaenilla meteorae (Hartmann-Schröder, 1982)

MATERIAL EXAMINED
Station E, 735 m depth, 1 specimen.
TYPE LOCALITY
Northwestern Africa, 437 m depth.
DESCRIPTION
Prostomium bilobed, median antennae with large ceratophore in anterior notch. Lateral antennae with small ceratophores, papillate styles. Anterior pair of eyes located anteroventraly. 15 pairs of elytre, elytral posterior margin with fringing papillae; surface covered by conical microtubercles. Neuropodia acicular lobe elongate with digitform supra acicular process. Notochaetae stout, short and long, with distinct rows of spines and blunt or pointed tips. Neurochaetae penicillate (filamentous hairs) unidentate tips with distinct rows of spines. Nephridial papillae on chaetigers 14-17, small.
DISTRIBUTION
North Atlantic Ocean: Northwestern Africa (Hartmann-Schröder, 1982). Bay of Biscay (Capbreton Canyon). Depth 437-735 m.
REMARKS
The specimen agrees with the description by Hartmann-Schröder (1982) for NW Africa specimens but ventral cirri and lateral antenna are papillate. *A. mollis* (M. Sars in G.O. Sars, 1872) is distributed at 750-1055 m depth in sandy, muddy or gravely bottoms in the Bay of Biscay. This species differs from *A. meteorae* by the presence of neurochaetae with bidentate tips and elytra surface smooth (Pettibone, 1983, Amoureux, 1977). **This is the second report of this species in the world and it is outside its original distribution.**

Genus *Lepidasthenia* Malmgren, 1867
Lepidasthenia cf. *elegans* (Grube, 1840)

MATERIAL EXAMINED
Station B, 583 m depth, 2 specimens.
TYPE LOCALITY
Adriatic Sea
DESCRIPTION
Prostomium without cephalic peaks; anterior pair of eyes dorsolaterally on widest part of protomium. Pharynx with 18 papillae and two teeth. 15 pairs of small elytra, margin and surface smooth. Styles of dorsal cirri long, smooth and tapering. Styles of ventral cirri. Notochaetae few, stout, with row of spines. Neurochaetae numerous, bidentate tips. Pygidum with a pair of anal cirri.
DISTRIBUTION
Western Mediterranean, Adriatic and Aegean Sea (Barnich & Fiege, 2003). South East Atlantic, Indo West Pacific (Day, 1960; Campoy, 1982); Northeastern Atlantic Ocean: Bay of Biscay (Capbreton Canyon). Depth 11-735 m.
REMARKS
Our specimens, probably juveniles of *L. elegans*, do not possess papillae on ventral or dorsal side of parapodia. The absence of papillae is one of the main diagnostic characteristics for this species (Barnich & Fiege, 2003). Two other *Lepidasthenia* species occur in the Bay of Biscay: *L.* cf. *argus* Hodgson, 1900, with papillae on dorsal and ventral side of parapodia (Barnich, 2013, Parapar & Moreira, 2009); and *L. brunea* Day, 1960 with papillae on ventral side of parapodia (Barnich & Fiege, 2003). **This is the first report of this species in the Bay of Biscay.**

Genus *Macellicephala* McIntosh, 1885
Macellicephala violacea (Levinsen, 1887)

MATERIAL EXAMINED
Station K, 623 m depth, 1 specimen.
TYPE LOCALITY
Arctic Ocean, Kara Sea.
DESCRIPTION
Prostomium bilobed. Trilobed facial tubercle medial to base of palps. Nine pairs of round, smooth (margin and surface). Dorsal tubercles on most of cirrigerous segments distinct, digitform to subconical.
Parapodia subbiramous, notopodial acicular lobe shorter than neuropodial acicular lobe. Neuropodial acicular lobe is elongate and digitiform. Notochaetae, fewer, along one side with numerous rows of short spines or faint indication of spinous rows, blunt tips; neurochaeta numerous, long, flattened distally with faint rows of spines and pointed tips.
DISTRIBUTION
Arctic, North Pacific, Northwestern Africa. Northeastern Atlantic Ocean: Bay of Biscay (Capbreton Canyon). Depth 46-8400 m.
REMARKS
The specimen agrees with the description of Pettibone (1976) but the minute frontal filaments are lacking, probably lost. In the Bay of Biscay, *M. violacea* is the only species from this genus but two other species similar have been recorded: *Bathyeliasona abyssicola* (Fauvel, 1913) has 8 pairs of elytra whereas *Macellicephala* has nine pairs; *Sinantenna macrophthalma* (Fauvel, 1913) has 13 pairs of elytra and enormous pigmented eyes according to Fauvel (1913). **This is the first report for the Bay of Biscay.**

ANOBOTHRUS AMOUROUXI SP. NOV., A NEW SPECIES OF AMPHARETIDAE (POLYCHAETA) FROM THE CAPBRETON CANYON (BAY OF BISCAY, NE ATLANTIC OCEAN)

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A new species of Ampharetidae, *Anobothrus amourouxi* sp. nov., has been identified from bathyal depths of the Capbreton Canyon, Bay of Biscay (NE Atlantic Ocean). This new species is characterized by inner branchiae with transversal ciliated ridges, notochaetae from modified eighth thoracic unciniger with hirsute tips, uncini from thoracic unciniger with 6–7 teeth in lateral view arranged in two vertical rows in frontal view, fused segments II+III with paleae from SII and reduced notopodia without chaetae from SIII. An identification key for all hitherto described species of the genus *Anobothrus* is provided.

Keywords: Polychaeta, Ampharetidae, *Anobothrus*, taxonomy, new species, Bay of Biscay, Capbreton Canyon

1 INTRODUCTION

Members of the Family Ampharetidae (Annelida: Polychaeta) are widely distributed from intertidal to abyssal depths and are common in deep-sea environments like plains, hot vents or cold seeps (Böggemann, 2009; Reuscher *et al.*, 2009; Aguirrezabalaga & Parapar, 2014). According to Jirkov (2011), this family includes more than 200 valid species distributed in two subfamilies: Ampharetinae Malmgren, 1866 and Melinnae Chamberlin, 1919. The taxonomy of ampharetids is complex and recently the number of genera was proposed to be strongly reduced from 90 to 24 (Jirkov, 2011). The genus *Anobothrus* is one of the most speciose with 18 species currently considered valid, 10 of them described between 2008 and 2014 (Jirkov, 2008; Schüller, 2008; Reuscher *et al.*, 2009; Imajima *et al.*, 2013; Schüller & Jirkov, 2013).

The first studies concerning the deep-sea macrofauna of the Bay of Biscay started in the 19th century and several expeditions were conducted in the 1970s (Laubier, 1985). Since the 1990s, several new species of Polychaeta have been described in the Capbreton Canyon following new oceanographic cruises from 1987 to 1990 (San Martín *et al.*, 1996; Nuñez *et al.*, 2000; Aguirrezabalaga *et al.*, 2001, 2002; Aguirrezabalaga & Ceberio, 2003, 2005a, 2005b, 2006; Aguirrezabalaga & Carrera-Parra, 2006; Aguirrezabalaga & Gil, 2009; Aguirrezabalaga & Parapar, 2014). The Capbreton Canyon is situated in the southeast of the Bay of Biscay, beginning at 250 m from the coastline, in front of Hossegor city. It extends through 300 km before ending on the abyssal plain at 3500 m depth (Gaudin *et al.*, 2006; Mazières *et al.*, 2014). Currently disconnected from the Adour River, the canyon continues to be affected by its plume during 20% of the year (Petus *et al.*, 2014). The Capbreton Canyon separates the northern Aquitanian shelf from the narrower southern Cantabrian platform (Pascual *et al.*, 2004).

The main purpose of the BIOMIN project was to study the *in situ* impact of the biological diversity on the mineralization of the organic matter at the water-sediment interface. This study took place close to three river mouths: Rhône River (Gulf of Lions, Mediterranean Sea), Gironde Estuary and Adour River (Bay of Biscay, Atlantic Ocean). During this project a new species of *Anobothrus* was discovered in the

Capbreton Canyon. The present paper provides the description of this species as well as a key for world-wide hitherto described species of this genus.

2 MATERIALS AND METHODS

The third cruise of the BIOMIN project (BIOMIN-3) took place on board of the RV *Côtes de la Manche* in July 2012 in the Capbreton Canyon. Macrofauna was sampled at 5 stations situated between 108 to 735 m depth and between 18 and 52 km off the Adour River (**Figure 1**). At each station, samples were collected using a Hamon grab (3 replicates of 0.25 m²) and an Oktopus® GmbH MC 6 multicorer (9 replicates of 0.007 m²).

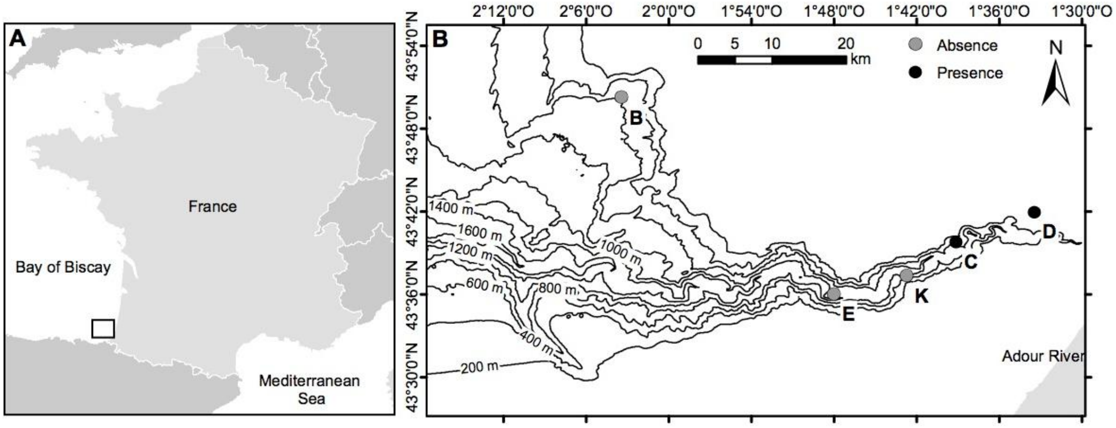

Figure 1. BIOMIN-3 cruise sampling stations in the Capbreton Canyon showing those with presence (black circles) and absence (grey circles) of Anobothrus amourouxi sp. nov.

Samples were sieved through a 1 mm mesh and the remaining fraction was immediately fixed in 5% buffered formalin. Back to the laboratory, organisms were sorted, identified to the lowest taxonomic level (in most cases to the species level) and counted.

Specimens of the new *Anobothrus* species were examined under a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Fi 2 camera. Some specimens were figured with a Wacom Intuos 5 tablet and Adobe Illustrator software. Length and width were measured with the NIS Elements Analysis software. Specimen used for examination with Scanning Electron Microscopy (SEM) was prepared by critical point drying, covered with gold and examined and photographed at the Servicios de Apoio á Investigación-SAI (Universidade da Coruña-UDC, Spain).

Type specimens were deposited in the Muséum National d'Histoire Naturelle (MNHN) (Paris, France) and Museo Nacional de Ciencias Naturales (MNCN) (Madrid, Spain). Additional non-type specimens were deposited in the Arcachon Marine Station.

Abbreviations used in the text: S = segment; TS = thoracic segment; TC = thoracic chaetiger; TU = thoracic unciniger; AU = abdominal unciniger.

3 RESULTS

SYSTEMATICS

Family AMPHARETIDAE Malmgren, 1866
Subfamily AMPHARETINAE Malmgren, 1866
Genus *Anobothrus* Levinsen, 1884

Type species: *Ampharete gracilis* Malmgren, 1866

Synonyms: *Anobothrella* Hartman, 1967: 155–156; *Melythasides* Desbruyères, 1978: 232–235; *Sosanides* Hartmann-Schröder, 1965: 243–246.

GENERIC DIAGNOSIS (EMENDED)

Prostomium trilobed, *Ampharete*-type, without glandular ridges. Buccal tentacles papillated or smooth. SII and SIII fused. Three to four pairs of branchiae (smooth or with transversal ciliated ridges or papillated), 3 pairs forming transversal row with or without gap arising from fused SII+III to SIV and the fourth pair, if present, situated behind this row, arising from SV. Notochaetae in fused SII+III originating from SII or SIII, or both. If present, notochaetae originating from SII varying in size from regular size to strongly enlarged (paleae). If present, notochaetae originating from SIII varying from reduced to regular size. If present, a pair of nephridrial papillae is situated in SIV behind innermost pair of branchiae or behind some anterior notopodia. Sixteen to seventeen TS. Thirteen to fifteen TC starting at SIII-IV. Eleven or twelve TU starting at SVI. Notopodial cirri absent. Circular whitish band in TU1, TU2 or TU3. Fourth-, fifth- or sixth-to-last thoracic unciniger with one or combined modifications: elevated notopodia and/or modified notochaeta and/or dorsal ridge. First two AU of thoracic type. Number of AU generally constant for each species. Abdominal rudimentary notopodia absent.

REMARKS

This emended generic diagnosis combines the emended diagnosis proposed by Schüller & Jirkov (2013) and Imajima *et al.* (2013) which in turn combine previous proposals by Jirkov (2008) and Reuscher *et al*. (2009). Here we add the presence of transversal ciliated ridges on branchiae as an additional morphological character in the genus which should be taken into account in species descriptions.

Anobothrus amourouxi sp. nov.

(**Figures 2–4**)

TYPE MATERIAL

Holotype: MNHN-1561, incomplete specimen (broken at 9th AU), one branchial filament lacking and two filaments deciduous, 2.57 mm long and 1.02 mm wide, station C1-INCUB (multicorer) (43°39'48"N, 01°39'09"W), 364 m depth, 7 July 2012.

Paratypes: MNHN-1562, complete specimen, all branchiae missing, 12.5 mm long and 1.5 mm wide, station C4-MFC (multicorer) (43°39'48"N, 01°39'09"W), 364 m depth, 16 July 2012; MNHN-1563, four specimens (two complete), 10.3–13.9 mm long and 1.1–1.3 mm wide, all without branchiae, two specimens with oocytes in body cavity, station D (1 specimen collected with Hamon grab, 3 specimens with multicorer) (43°42'00"N, 01°33'27"W), 108 m depth, 7 and 12 July 2012; MNCN-16.01/16069, complete specimen , three branchial filaments lacking, 6.63 mm long and 0.63 mm wide, station C1-INCUB (multicorer) (43°39'48"N, 01°39'09"W), 364 m depth, 7 July 2012; MNCN-16.01/16070, 2 branchiae in a STUB for SEM of the paratype MNCN-16.01/16069; MNCN-16.01/16071, complete specimen in SEM stub (broken at 2nd AU), all branchiae missing, 8.6 mm long and 1.0 mm wide, station C1-BIOIR (multicorer) (43°39'48"N, 01°39'09"W), 364 m depth, 7 July 2012.

ADDITIONAL MATERIAL

Six specimens (one complete, 12.5 mm long and 1.5 mm wide), all without branchiae, one specimen with ventral groove, station C (1 specimen collected with Hamon grab, 5 specimens with multicorer) (43°39'48"N, 01°39'09"W), 364 m depth, 7, 12 and 16 July 2012.

DIAGNOSIS

Inner branchiae with transversal ciliated ridges, other ones smooth. Only modified TU8 provided notochaetae with hirsute tips. Uncini from TU1 with 6–7 teeth in lateral view arranged in two vertical rows in frontal view. Uncini from AU3 with 4–5 teeth in lateral view arranged in three vertical rows in frontal view. SII+III fused with paleae from SII but with reduced notopodia without chaetae from SIII. 15 TC, 12 TU and 12 AU.

DESCRIPTION (BASED ON HOLOTYPE AND PARATYPES)

Prostomium trilobed and anteriorly rounded, *Ampharete*-type, without eye-spots. Buccal tentacles apparently smooth (**Figure 3B**).

Four pairs of long, gradually tapering, cirriform branchiae (**Figures 2A, D**). No gap between groups of branchiae. First three pairs of branchiophores arranged in a transversal line (inner, middle and outer pairs), forming a high fold, originating from fused SII+III. Fourth pair situated behind between inner and middle pairs, originating from SV (**Figure 2D**). Diameter of all branchiophores approximately equal. Middle and outer pairs of branchiae with branchiostyles longer and thicker than inner and posterior pairs (**Figure 2C**). Outer pair longer than remaining ones (**Figure 2B**). Middle, outer and fourth pairs of branchiae with smooth branchiostyles. Branchiostyles of inner pair of branchiae with tufts of cilia arranged in rows forming transversal ciliated ridges (visible in stereomicroscope) along the whole ventral side of the branchiostyle (**Figures 4C, D**). All branchiostyles presenting minuscule ciliated buttons (visible only under SEM) along their entire surface (**Figures 4E, F**). Right branchiostyle of inner pair thicker and longer than the left one. Fourth (posterior) pair of branchiae with thinnest and shortest branchiostyle.

One pair of nephridial papillae, not separated by gap, situated behind the base of innermost pair of branchiae (**Figure 2D**). Additional pairs of nephridial papillae present behind notopodia of TU1 and TU2 (visible under SEM, **Figure 3D**).

Fused SII+III with 12–16 gradually tapering paleae, longer and larger than the best-developed notochaetae (**Figures 2A, D; 3A**) from SII. The longest paleae surpassing the prostomium in lateral view. Fused SII+III (**Figures 2A; 3A**) with reduced notopodia, rounded in shape, hardly visible under the stereomicroscope, located behind the paleae, without chaetae, presenting a row of pores (**Figure 3C**) from SIII. From SIV (TC2) notopodia well developed with rounded to elongate lobes and well developed notochaetae. Seventeen TS and 15 TC. Twelve TU. TU3 with an anterior whitish band (**Figure 2A**). Fifth-to-last TU (TC11, TU8) with slightly elevated notopodia connected by a pronounced dorsal ridge (**Figures 2A; 3E, F**), sometimes as high as notopodial lobe (*Anobothrus*-type).

Abdomen with 12 AU. Neuropodia of first two abdominal uncinigers (AU1–2) of thoracic type (tori instead of pinnules; **Figure 2A**). Neuropodial lobe forming pinnules from AU3 to posterior end. Rudimentary notopodia and neuropodial cirri absent.

Notochaetae bilimbate. First two thoracic chaetigers (SIV–V; TC1–2) with 3-4 short notochaetae; subsequent chaetigers with 5 long and 4 short notochaetae. Notochaeta longer than notopodial lobe in TU. Notochaetae from modified TU8 with hirsute tips (**Figures 2F; 4A**). TU1 with 38–48 uncini, pectinate, with 6–7 teeth in lateral view, arranged in two vertical rows in frontal view (**Figures 2G; 4B**). AU3 with 25–35 uncini, situated in marginal position of neuropodial pinnule, pectinate, with 4–5 teeth in lateral view (**Figure 2H**), arranged in three vertical rows in frontal view.

Pygidium with terminal anus, without lateral papillae but with 3–5 dorsal minute folds (**Figure 2E**).

REMARKS

Anobothrus amourouxi sp. nov. is similar to *A. antarctica* Monro, 1939, *A. glandularis* (Hartmann-Schröder, 1965), *A. mironovi* Jirkov, 2008, *A. paleaodiscus* Schüller & Jirkov, 2013 and *A. patersoni* Jirkov, 2008 because they share the following characters: presence of paleae in fused SII+III from SII, four pairs of branchiae, circular band at TU3, 12 TU, modified fifth-to-last TU (TU8) and 12 AU. These species can be separated into two groups based on the presence or absence of notochaetae with hirsute tips at TU8: Group 1: *A. paleaodiscus*, *A. patersoni* and *A. mironovi* with smooth tips, and Group 2: *A. amourouxi* sp. nov., *A. antarctica* and *A. glandularis* with notochaetae with hirsute tips (but only in TU8). However, *A. amourouxi* sp. nov. and *A. antarctica* differ from *A. glandularis* for having both 15 TC and ciliated or papillated branchiae instead of 14 TC and smooth branchiae. Moreover, *A. antarctica* differs from *A. amourouxi* sp. nov. by presenting all branchiostyles papillated, from sparse to densely papillated (shaggy), while *A. amourouxi* sp. nov. presents only the inner pair provided with transversal ciliated ridges. Furthermore, *A. antarctica* has uncini from TU1 with 4–5 teeth, a large pair of nephridial papillae, and fused SII+III provided with notochaetae from SIII, while *A. amourouxi* sp. nov. has uncini from TU1 with 6–7 teeth, two groups of nephridial papillae, fused SII+III with reduced notopodia and without notochaetae from SIII. Indeed, in *A. amourouxi* sp. nov. the reduced notopodia from SIII at fused SII-III presents a row of pores instead of chaetae, a character also observed by Aguirrezabalaga & Parapar (2014: their figure 7E). These pores might be related to chaetae formation.

Although Imajima *et al.* (2013) suggested that the presence of transversal ciliated ridges on branchiae were related to the size of specimens, this could not be verified in *A. amourouxi* sp. nov. because the two biggest specimens (mature) lost their branchiae. However, no variation linked to age was observed for the other characters described here.

The *Anobothrus* species reported in the Northeast Atlantic waters are *A. gracilis* (Malmgren, 1866) and *A. patersoni* Jirkov, 2008. *A. gracilis* is a species described from Swedish coasts and has a wide distribution in the Arctic Ocean, North Atlantic Ocean (Iceland to Swedish West coast), and Northwest Pacific Ocean (Jirkov, 2008, 2011; Parapar *et al.*, 2014). *A. patersoni* is an exclusively abyssal species (3260-8292 m depth) described from North Pacific (Japan) but recorded also in the North Atlantic (Jirkov, 2008). In the Capbreton Canyon, Rallo *et al.* (1993) found a single specimen of *A. gracilis* between 358–410 m, and two incomplete specimens of *Anobothrus* aff. *gracilis* were also reported by Aguirrezabalaga & Parapar (2014), between 624–652 m depth. These records should be taken with caution as incomplete specimens may induce wrong identifications. These specimens might belong to *A. amourouxi* sp. nov. because *A. gracilis* share with the new species the possession of 15 TC, fused SII+III with reduced TC without notochaetae from SIII, 12 TU and circular band in TU3.

ETYMOLOGY

This species is dedicated to Dr. Jean-Michel Amouroux (Laboratoire Arago, Observatoire Océanologique de Banyuls-sur-Mer, France) for his friendship and many contributions to French benthic research.

DISTRIBUTION

Specimens of the new species were collected in the Capbreton Canyon muddy bottoms, between 108 and 364 m depth. In the same area Rallo *et al.* (1993) and Aguirrezabalaga & Parapar (2014) reported *Anobothrus gracilis* at 358–410 m depth and *Anobothrus* aff. *gracilis* at 624–652 m depth, respectively.

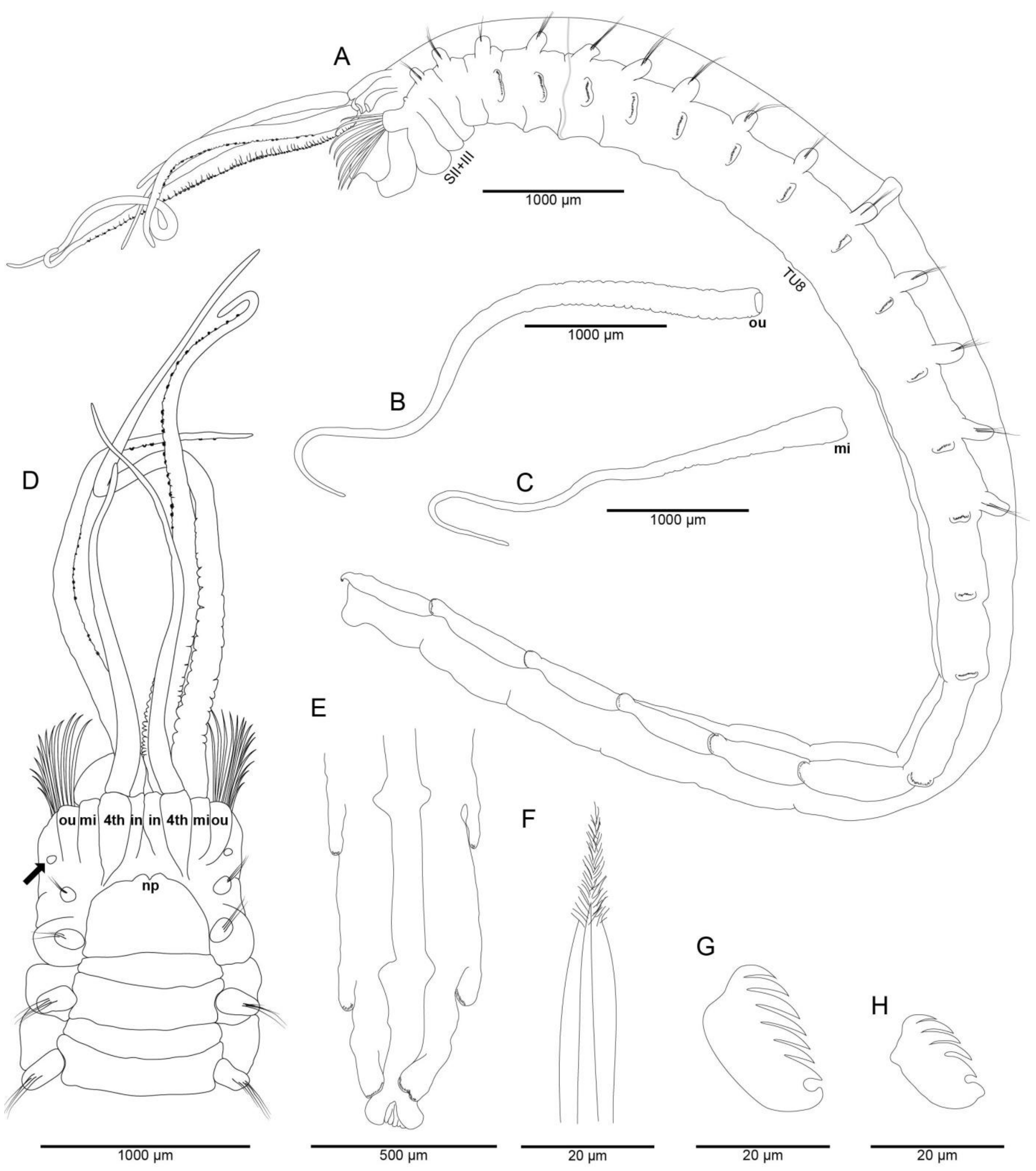

Figure 2. ***Anobothrus amourouxi*** **sp. nov., holotype (MNHN-1561): (A) lateral view, specimen incomplete, showing fused SII+III; (B) deciduous branchia from outer (ou) pair; (C) deciduous branchia from middle (mi) pair; (D) anterior region, dorsal view, indicating reduced notopodia at fused segments II+III (arrow), nephridial papillae (np) and pairs of branchiae: (in) inner, (mi) middle, (ou) outer and (4th) fourth pair. Paratype (MNHN-1562): (E) pygidium, ventral view; (F) hirsute tips of notochaeta from modified eighth thoracic chaetiger (TU8). Paratype (MNHN-1563): (G) uncinus from first thoracic uncinigers (TU1), lateral view; (H) uncinus from third abdominal unciniger (AU3), lateral view.**

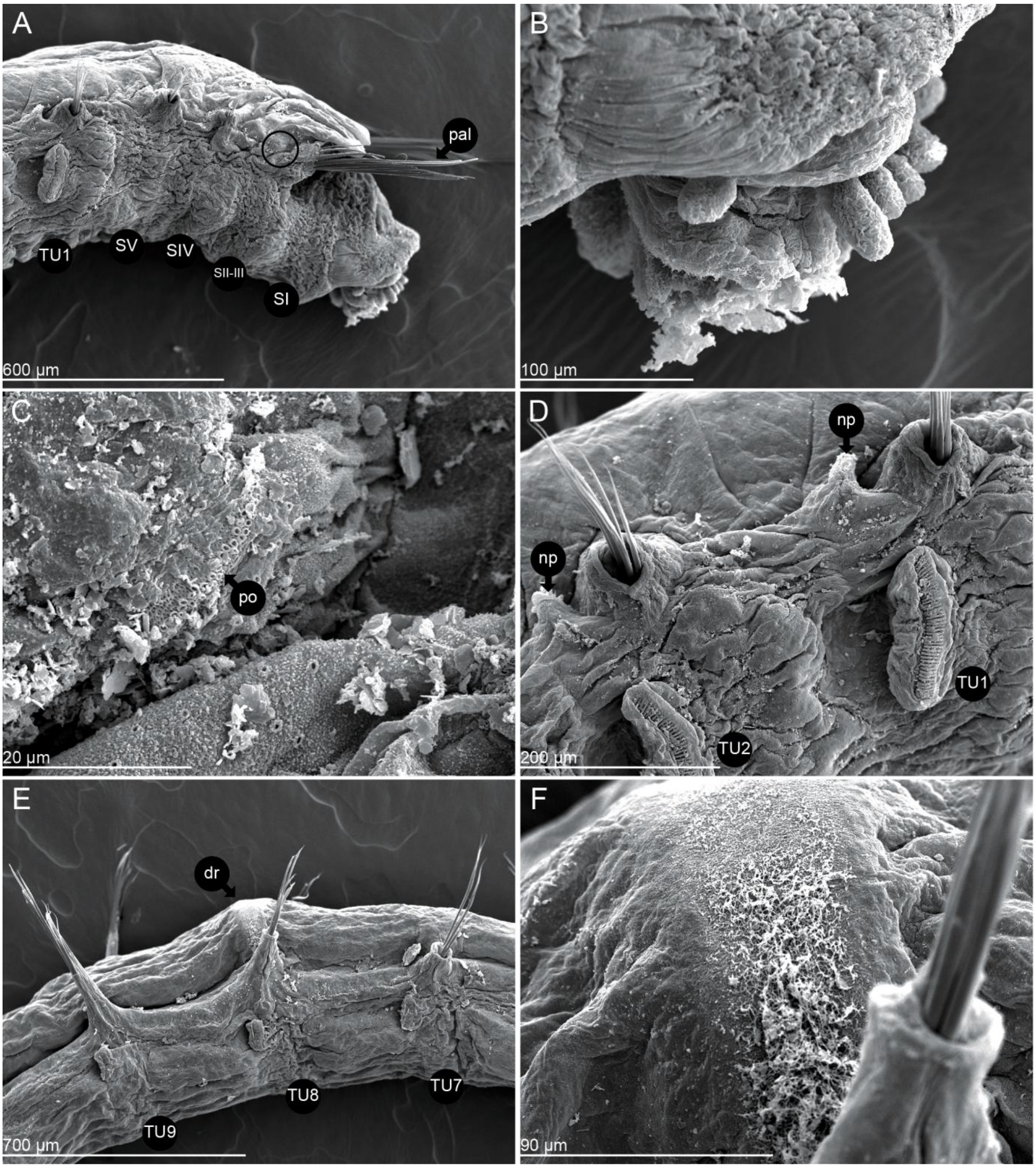

Figure 3. ***Anobothrus amourouxi*** **sp. nov., paratype (MNCN-16.01/16071): (A) anterior end, right lateral view, showing first five thoracic segments (SI–SV), and first thoracic unciniger (TU1); reduced notopodia (encircled) at fused segments II+III behind the paleae (pal); (B) detail of prostomium and buccal tentacles, lateral view; (C) notopodia of fused segments II+III showing a row of pores (po); (D) TU1 and TU2 showing position of nephridial pores (np); (E) TU8 showing a transversal dorsal ridge (dr); (F) detail of dorsal ridge at TU8.**

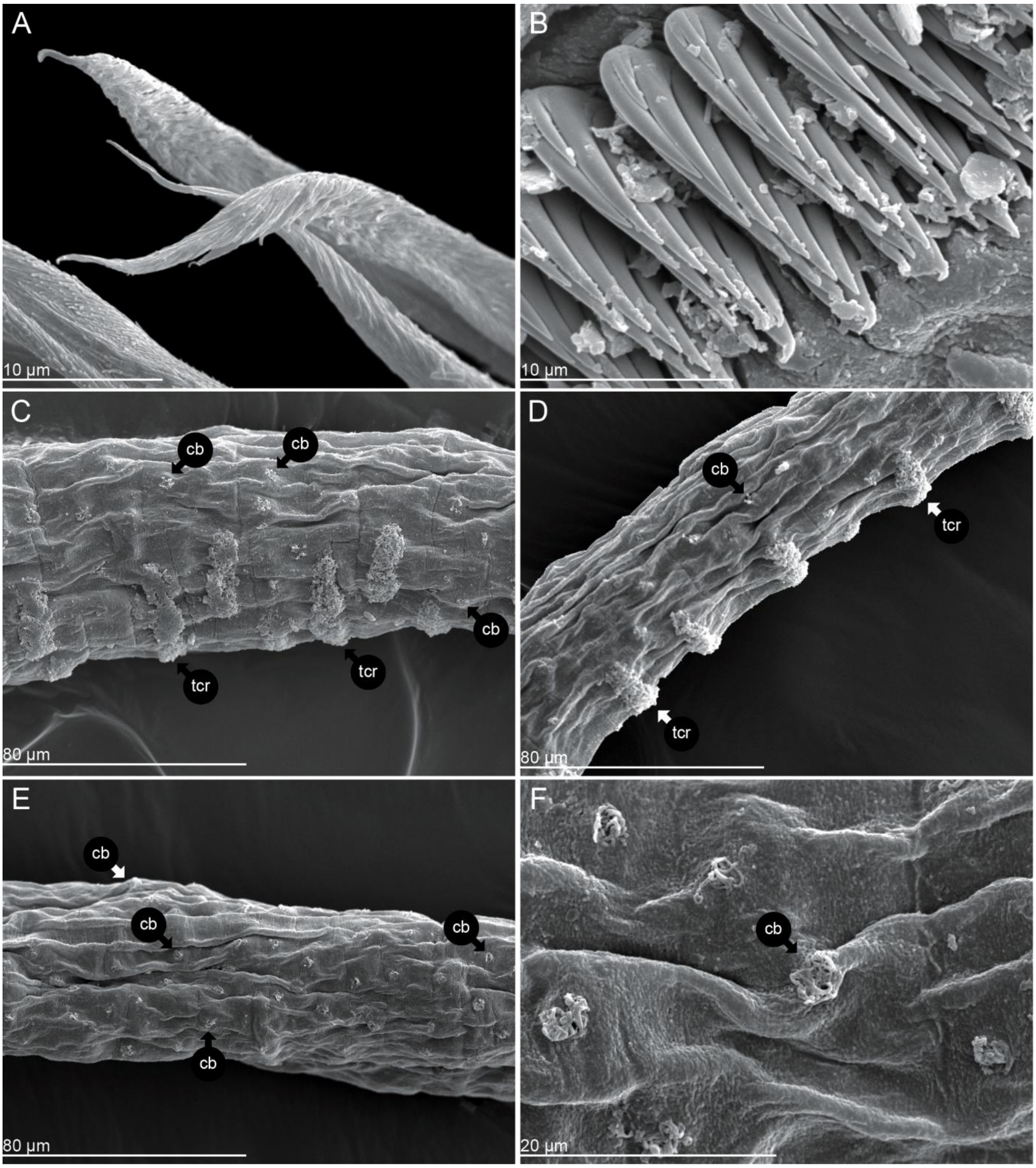

Figure 4. ***Anobothrus amourouxi*** **sp. nov., paratype (MNCN-16.01/16071): (A) hirsute tips of T8 modified notochaetae; (B) thoracic uncini, upper-frontal view. Paratype (MNCN-16.01/16070): (C-D) basal and median zones of inner ciliated branchia showing the transversal ciliated ridges (tcr) and ciliated buttons (cb); (E-F) median and distal zones of smooth branchiae showing the ciliated buttons (cb).**

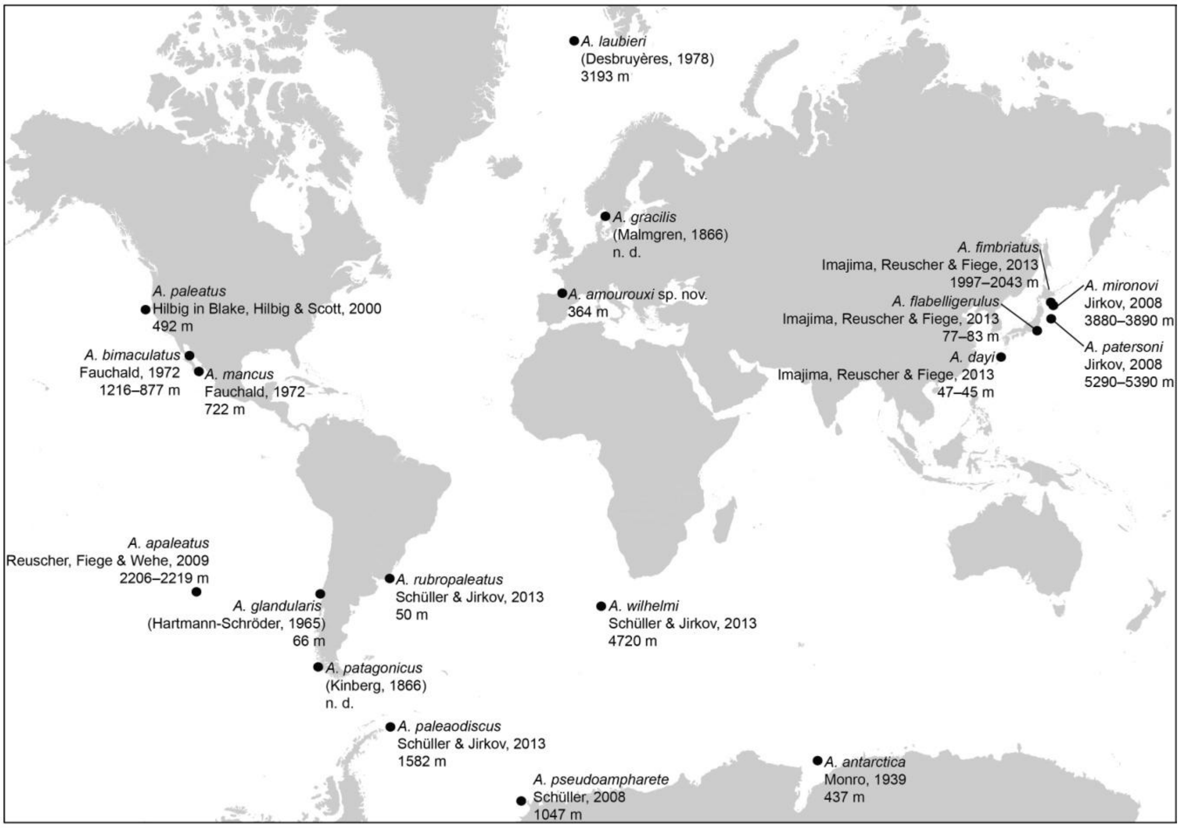

Fig. 5. World map showing location and depth of type locality of each currently considered valid species of *Anobothrus*.

KEY FOR IDENTIFICATION OF THE SPECIES OF THE GENUS *ANOBOTHRUS* IN THE WORLD

The following key accounts for the 18 species currently considered valid (Read, 2014) plus the new species here proposed. Described species are well distributed in the world ocean, but mainly concentrated in the southern hemisphere, NE Atlantic, Pacific coasts of North America and Japan. Nevertheless gaps still persist in the NW Atlantic, Indo-Malay Philippines archipelago and the coasts of Africa and Australia (**Figure 5**).

Five species were previously included in the genus *Anobothrus* but are currently considered invalid or excluded from this genus and thus excluded from the following key. *Anobothrus nasuta* (Ehlers, 1887), originally described in the genus *Amphicteis,* is supposed to belong to another genus (Jirkov, 2008; Schüller & Jirkov, 2013). *Anobothrus occidentalis* Hartman, 1969 and *Anobothrus trilobatus* Hartman, 1969 were re-examined by Hilbig (2000) and are presently considered as belonging to the genera *Sosanne* and *Eclysippe*, respectively. Finally, *Anobothrus nataliae* Jirkov, 2008 and *Anobothrus wakatakamaruae* Imajima, 2009 are considered junior synonyms of *Anobothrus paleatus* (Imajima *et al.*, 2013).

1. No paleae..2
- Paleae present 3

2. Modified notopodia with hirsute tips notochaetae...............................*A. fimbriatus*
- All notopodia without hirsute tips notochaetae ....*A. apaleatus*

3. 3 pairs of branchiae..4
- 4 pairs of branchiae..6

4. Modified notopodia on TU8 5
- Modified notopodia on TU9 .... *A. flabelligerulus*

5. Notochaetae present on fused segments II- III, prostomium *Ampharete*-type, branchiae forming transversal line ....*A. laubieri*
- Notochaetae absent on fused segments II-III, prostomium conical, wide gap between groups of branchiae ....*A. dayi*

6. Modified notopodia on TU6 .... *A. bimaculatus*

\- Modified notopodia on TU7 ....*A. mancus*

\- Modified notopodia on TU8 7

\- Modified notopodia on TU9 ....*A. paleatus*

7. Circular band on TU1 .... *A. patagonicus*

\- Circular band on TU2 (modified notochaetae without hirsute tips) 8

\- Circular band on TU3 9

8. Paleae colourless, fine, with base slimmer than (or equal to) most developed notochaetae, outer pairs of branchiae distinctly narrower than inner, 12–13 AU .. ………………………………………………………………………………..*A. wilhelmi*

\- Paleae reddish, stout, with base stouter than most developed notochaetae, branchiae with almost the same diameter, 13 AU .... *A. rubropaleatus*

9. Modified notopodia without notochaetae with hirsute tips 10

\- Only the modified notopodia with notochaetae with hirsute tips 11

\- All notopodia with notochaetae with hirsute tips.................................... *A. gracilis*

10. 3 teeth on uncini from TU1 (lateral view), paleae abruptly tapering to delicate tip ………………………………………………………………….*A. pseudoampharete*

- 8–9 teeth on uncini from TU1 (lateral view), diameter of all branchiophores more or less equal, less than 10 paleae, very conspicuous stout and long paleae .... …………………………………………………………………………*A. paleaodiscus*

- 5 teeth on uncini from TU1 (lateral view), fourth pair of branchiophores two times slimmer and shorter than others reduced and their branchiostyles many times shorter than others, paleae longer than best-developed notochaeta, gradually tapering..*A. patersoni*

- 5 teeth on uncini from TU1 (lateral view), inner and middle pairs of branchiophores shorter and slimmer than others ....*A. mironovi*

11. 6 teeth on uncini from TU1 (lateral view), surface of branchiostyle smooth, thoracic arrangement (fused SII-III with paleae from SII and without notochaetae from SIII)...*A. glandularis*

- 4–5 teeth on uncini from TU1 (lateral view), surface of all branchiostyles papillated, thoracic arrangement (fused SII-III with paleae from SII and notochaetae from SIII)..*A. antarctica*

- 6–7 teeth on uncini from TU1 (lateral view), surface of inner pair of branchiostyle with transversal ciliated ridges, thoracic arrangement (fused SII-III with paleae from SII and with reduced notopodia without notochaetae from SIII) .... *A. amourouxi* sp. nov.

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REFERENCES

Aguirrezabalaga F. and Carrera-Parra L. (2006) Lumbrineridae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of two new species. *Scientia Marina* 70(S3), 17–25.

Aguirrezabalaga F. and Ceberio A. (2003) Dorvilleidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of *Pettiboneia sanmartini* sp. nov. *Cahiers de Biologie Marine* 44, 41–48.

Aguirrezabalaga F. and Ceberio A. (2005a) *Sphaerodoropsis amoureuxi* and *S. stellifer*, two new species of Sphaerodoridae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic). *Cahiers de Biologie Marine* 46, 9–20.

Aguirrezabalaga F. and Ceberio A. (2005b) Spionidae (Annelida: Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with descriptions of a new genus and three new species. *Marine Biology Research* 1, 267–280.

Aguirrezabalaga F. and Ceberio A. (2006) *Flabelligena gascognensis* sp. nov. (Polychaeta: Acrocirridae), a new species from the Capbreton Canyon (Bay of Biscay, NE Atlantic). *Scientia Marina* 70(S1), 141–147.

Aguirrezabalaga F., Ceberio A. and Fiege D. (2001) *Octomagelona bizkaiensis* (Polychaeta: Magelonidae) a new genus and species from the Capbreton Canyon (Bay of Biscay, north-east Atlantic). *Journal of the Marine Biological Association of the United Kingdom* 81, 221–224.

Aguirrezabalaga F., Ceberio A. and Paxton H. (2002) Onuphidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of *Paradiopatra capbretonensis* sp. nov. *Steenstrupia* 27, 19–28.

Aguirrezabalaga F. and Gil J. (2009) Paraonidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of eight new species. *Scientia Marina* 73, 631–666.

Aguirrezabalaga F. and Parapar J. (2014) Deep-sea Ampharetidae (Polychaeta) from Capbreton Canyon (north-east Atlantic) with the description of a new species. *Journal of the Marine Biological Association of the United Kingdom* 94, 947–967.

Böggemann M. (2009) Polychaetes (Annelida) of the abyssal SE Atlantic. *Organisms, Diversity and Evolution* 9, 251–428.

Desbruyères D. (1978) *Melythasides laubieri* gen. sp. nov. Ampharetidae (Annélides Polychètes sédentaires) abyssal de la mer de Norvège. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 3^{e}sér., 353(514), 231–238.

Ehlers E. (1887) Florida-Anneliden (XXXI. Report on the Annelids). Reports on the results of dredging, under the Direction of L.F. Pourtalès, during the years 1868–1870, and of Alexander Agassiz, in the Gulf of Mexico (1877–78), and in the Caribbean Sea (1878–79), in the U.S. coast survey steamer "Blake". *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 15, 1–335.

Fauchald K. (1972) Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology* 7, 1–575.

Gaudin M., Mulder T., Cirac P., Berné S. and Imbert P. (2006) Past and present sedimentary activity in the Capbreton Canyon, southern Bay of Biscay. *Geo-Marine Letters* 26, 331–345.

Hartman O. (1967) Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology* 2, 1–387.

Hartman O. (1969) *Atlas of the sedentariate polychaetous annelids from California*. Allan Hancock Foundation, University of Southern California, Los Angeles.

Hartmann-Schröder G. (1965) Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 62, 1–384.

Hilbig B. (2000) Chapter 8. Family Ampharetidae Malmgren, 1867. In Blake J., Hilbig B. and Scott P. (eds) *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Vol. 7. Santa Barbara, CA: Santa Barbara Museum of Natural History, pp. 169–230.

Imajima M. (2009) Deep-sea benthic polychaetes off Pacific coast of the northern Honshu, Japan. In Fujita T. (ed) *Deep-sea fauna and pollutants off Pacific coast of northern Japan*. *National Museum of Nature and Science Monographs* 39, 39–192.

Imajima M., Reuscher M.G. and Fiege D. (2013) Ampharetidae (Annelida: Polychaeta) from Japan. Part II: Genera with elevated and modified notopodia. *Zootaxa* 3647, 137–166.

Jirkov I.A. (2008) Revision of Ampharetidae (Polychaeta) with modified thoracic notopodia. *Invertebrate Zoology* 5, 111–132.

Jirkov I.A. (2011) Discussion of taxonomic characters and classification of Ampharetidae (Polychaeta). *Italian Journal of Zoology* 78, Suppl 1, 78–94.

Kinberg J.G.H. (1866) Annulata nova. *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar* 23, 97–103.

Laubier L. (1985) Le programme BIOGAS. In Laubier L. and Monniot C. (eds) *Peuplements profonds du Golfe de Gascogne.* Paris: IFREMER, pp. 13–23.

Levinsen G.M.R. (1884) Systematisk-geografisk Oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. 2. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 1883, 92–350.

Malmgren A.J. (1866) Nordiska Hafs-Annulater. *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar* 22, 355–410.

Mazières A., Gillet H., Castelle B., Mulder T., Guyot C., Garlan T. and Mallet C. (2014) High-resolution morphobathymetric analysis and evolution of Capbreton submarine canyon head (Southeast Bay of Biscay—French Atlantic Coast) over the last decade using descriptive and numerical modeling. *Marine Geology* 351, 1–12.

Monro C.C.A. (1939) Polychaeta. *Antarctic Research Expedition Reports* 4(4), 87–156.

Nuñez J., Aguirrezabalaga F. and Ceberio A. (2000) Species of Nereididae from the Capbreton Canyon (Bay of Biscay, northeast Atlantic). *Bulletin of Marine Science* 67, 25–37.

Parapar J., Helgason G.V., Jirkov I. and Moreira J. (2014) Diversity and taxonomy of Ampharetidae (Annelida, Polychaeta) from Icelandic waters. *Polish Polar Research*, 35(2):311–340.

Pascual A., Cearreta A., Rodríguez-Lázaro J. and Uriarte, A. (2004) Chapter 3 Geology and Palaeoceanography. In Borja A. and Collins M. (eds) *Oceanography and marine environment of the Basque Country.* Amsterdam: Elsevier, pp. 53–73.

Petus C., Marieu V., Novoa S., Chust G., Bruneau N. and Froidefond J.M. (2014) Monitoring spatio-temporal variability of the Adour River turbid plume (Bay of Biscay, France) with MODIS 250-m imagery. *Continental Shelf Research* 74, 35–49.

Rallo A., García-Arberas L. and Isasi I. (1993) Fauna macrobéntica de los fondos del cañón de Capbretón: análisis faunístico de poliquetos, crustáceos y cnidarios y caracterización de puntos de muestro según estos descriptores. *Cahiers de Biologie Marine* 35, 69–90.

Read G. (2014) *Anobothrus* Levinsen, 1884. In Read G. and Fauchald K. (eds) *World Polychaeta database*. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=129158 on 2014-09-16.

Reuscher M., Fiege D. and Wehe T. (2009) Four new species of Ampharetidae (Annelida: Polychaeta) from Pacific hot vents and cold seeps, with a key and synoptic table of characters for all genera. *Zootaxa* 2191, 1–40.

San Martín G., Ceberio A. and Aguirrezabalaga F. (1996) *Exogone* species (Polychaeta: Syllidae: Exogoninae) from the Capbreton Canyon (Bay of Biscay, NE Atlantic). *Cahiers de Biologie Marine* 37, 249–258.

Schüller M. (2008) New polychaete species collected during the expeditions ANDEEP I, II, and III to the deep Atlantic sector of the Southern Ocean in the austral summers 2002 and 2005 – Ampharetidae, Opheliidae, and Scalibregmatidae. *Zootaxa* 1705, 51–68.

Schüller M. and Jirkov I.A. (2013) New Ampharetidae (Polychaeta) from the deep Southern Ocean and shallow Patagonian waters. *Zootaxa* 3692, 204–23.

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Malmgrenia louiseae sp. nov., a new scale worm species (Polychaeta: Polynoidae) from southern Europe with a key to European *Malmgrenia* species

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Malmgrenia louiseae *sp. nov. is described from both the western Mediterranean in the Gulf of Lions, and the north-east Atlantic from off Portugal and the Bay of Biscay. The species was found in muddy sediments in shallow water and is possibly associated with echiurids or synaptid holothurians.* Malmgrenia louiseae *sp. nov. can be clearly distinguished from all other known* Malmgrenia *species by the presence of an infra-acicular process in addition to the supra-acicular process on the acicular lobe of the neuropodia, the lack of microtubercules on the elytra, two kinds of notochaetae (stout with blunt tip and slender with fine pointed tip), and exclusively unidentate neurochaetae. An identification key to the north-east Atlantic and Mediterranean* Malmgrenia *species is provided.*

Keywords: Polychaeta, Polynoidae, taxonomy, *Malmgrenia*, Mediterranean, north-east Atlantic, associations

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INTRODUCTION

Five programmes monitoring benthic communities, independently carried out in the Gulf of Lions, Mediterranean, in Portuguese waters and in the Pertuis Charentais part of the Bay of Biscay led to the collection of several specimens of an unknown polynoid species. The review of these specimens during the 4th RESOMAR Benthos Taxonomic Workshop held in June 2013 in La Rochelle revealed that they belong to a hitherto unknown *Malmgrenia* species.

So far 10 species of *Malmgrenia* McIntosh, 1874 have been reported from the Mediterranean and the north-east Atlantic to which the new species *M. louiseae* sp. nov., described herein, has to be added (Table 1). They were either attributed to the genus *Malmgrenia* McIntosh, 1874 or *Malmgreniella* Hartman, 1967 by their respective original author and there has been some controversy in the literature regarding the correct generic name to be used (Barnich & Fiege, 2001; Muir & Chambers, 2008). Following ICZN Opinion (2009), which ruled that the usage of the generic name *Malmgrenia* McIntosh, 1874 is to be conserved, at least the north-east Atlantic and Mediterranean species should now be attributed to this genus.

Most of these species are known to live in association with echinoderms and other invertebrates such as tubicolous or terricolous species (Barel & Kramers, 1977; Pettibone, 1993). The potential associates are reported and a key to all *Malmgrenia* species found in the area is given.

MATERIALS AND METHODS

The specimens were collected from subtidal grab samples (Van Veen or Smith-McIntyre) in the following surveys or inventories of benthic macrofauna communities: CARTHAM in the Mediterranean (ASCONIT Consultants *et al.*, 2012), Guia marine outfall monitoring programme, ACOSHELF and MeshAtlantic in Portuguese waters, OBIONE in Bay of Biscay (Table 2; Figure 1).

The samples were washed with seawater onboard on a 1 mm mesh size and fixed in a 4% formalin-seawater solution. They were sorted in the laboratory and the specimens preserved in a 70% ethanol solution. All observations and measurements were carried out on fixed specimens. The animals were very fragile and most of the elytra were lost and bodies

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Table 1. *Malmgrenia* species known to occur in the Mediterranean and north-east Atlantic (cf. Pettibone, 1993; Barnich & Fiege, 2001, 2003).

Species	Mediterranean	North-east Atlantic
M. andreapolis McIntosh, 1874	X	X
M. arenicolae (de Saint Joseph, 1888)		X
M. castanea McIntosh, 1876	X	X
M. darbouxi (Pettibone, 1993)	X	X
M. lilianae (Pettibone, 1993)	X	X
M. ljungmani (Malmgren, 1867)	X	X
***M. louiseae* sp. nov.**	X	X
M. lunulata (Delle Chiaje, 1830)	X	X
M. marphysae McIntosh, 1876		X
M. mcintoshi Tebble & Chambers, 1982		X
M. polypapillata (Barnich & Fiege, 2001)	X	

fragmented during the washing steps. Also, body fragmentation and elytra losses occurred when live specimens were added to fresh water or alcohol.

The preserved specimens were studied and photographed using a stereomicroscope Leica M205C coupled to a digital camera Leica IC80HD and the Leica Application Software. Details of elytra and parapodia needed the use of a compound microscope (Leica DMIRB, coupled with a digital camera Olympus DP70 and the DP Controller software). The photographs of the holotype were used as the basis for drawings of the animal with the free vector graphics editor Inkscape.

Length (L) was measured from the anterior margin of the prostomium to the posterior border of the last segment (pharynx not included, if everted) and width (W) was taken at the widest segment, including parapodia but excluding chaetae.

The type material is deposited in the collections of the Muséum National d'Histoire Naturelle de Paris, France (MNHN), the Museu Nacional de História Natural e da Ciência de Lisboa, Portugal (MNHNC-UL) and the Senckenberg Museum Frankfurt, Germany (SMF).

SYSTEMATICS

Family POLYNOIDAE Kinberg, 1856

Genus *Malmgrenia* McIntosh, 1874

Type species *Malmgrenia andreapolis* McIntosh, 1874

Diagnosis (emended to include new species described herein)

Body flattened dorsoventrally, short, up to 46 segments, more or less covered by elytra or short tail uncovered (large specimens). Elytra 15 pairs on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32. Prostomium bilobed, without distinct cephalic peaks, with three antennae; lateral antennae with ceratophores inserted terminoventrally; two pairs of eyes, anterior pair usually dorsolaterally in front of widest part of prostomium, posterior pair dorsally near hind margin of prostomium. Parapodia biramous, noto- and neuropodia with elongate acicular lobe; tips of noto- and neuroacicula penetrating epidermis; neuropodia with or without supra-acicular or sub-acicular process. Notochaetae with rows of spines and blunt or pointed tips; neurochaetae more numerous, with rows of spines only distally and one or two kinds of tips: bidentate with secondary tooth subdistally and/or unidentate with pointed or knob-like tip.

Malmgrenia louiseae sp. nov. (Figure 2)

TYPE MATERIAL

Holotype: 1 complete specimen (cs) (MNHN POLY TYPE 1559), L 13.7 mm W 4.3 mm for 33 segments (fragmented); Gulf of Lions, Côte Catalane, CARTHAM B50, 24 August 2010, 3°09′57″E 42°35′19.6″N; 56 m, coastal mud, leg. C. Labrune and J-M. Amouroux.

Paratypes: 1 cs (MNHN POLY TYPE 1560), L 10.5 mm W 3.7 mm for 32 segments (fragmented); Bay of Biscay, Pertuis Charentais, OBIONE, Antioche, 22 August 2011, 1°18′30″W 46°05′03″N, 35 m, coastal muddy sand, leg. J. Jourde and P-G. Sauriau.

Table 2. Localities, geographic coordinates (WGS 84), sediment, depth, number of specimens collected and sampling dates of *Malmgrenia louiseae* sp. nov.

Localities	Coordinates	Sediment	Depth	N	Month/Year
Cascais-Guia	38°39′33.66″N 09°28′34.32″W	Mud	76 m	1	10/02
Cascais-Guia	38°39′37.86″N 09°24′58.50″W	Mud	34 m	1	10/02
Cascais-Guia	38°39′37.86″N 09°24′58.50″W	Mud	34 m	7	01/06, 10/08, 09/09
Cascais-Guia	38°39′31.62″N 09°26′06.36″W	Mud	48 m	1	10/07, 10/08
Cascais-Guia	38°39′33.66″N 09°28′34.32″W	Mud	76 m	1	10/08
Costa da Caparica	38°31′29.81″N 09°22′01.26″W	Mud	110 m	1	04/08
Figueira da Foz	40°02′18.23″N 09°10′28.50″W	Mud	100 m	1	06/10
Gulf of Lions, Côte Catalane	42°35′19.60″N 03°09′57.00″E	Sandy mud	56 m	2	08/10
Bay of Biscay, Pertuis Charentais	46°05′03.00″N 01°18′30.00″W	Sandy-mud	38 m	15	08-09-10/11, 01-02-03/12

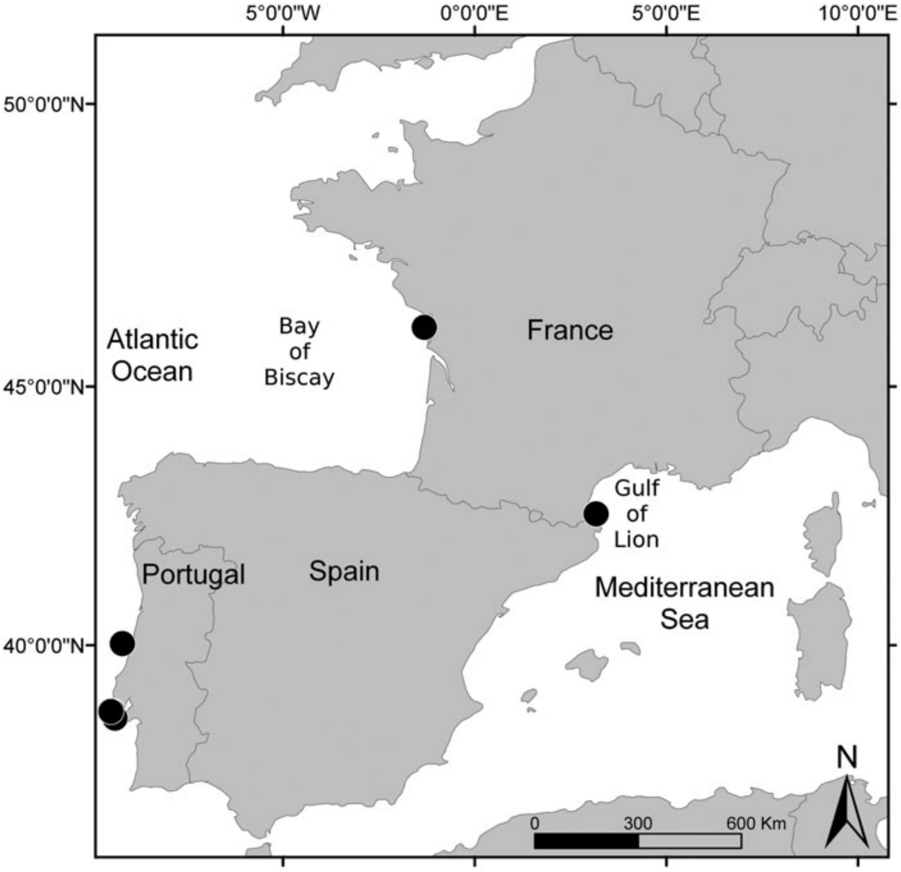

Fig. 1. Sampling locations of *Malmgrenia louiseae* sp. nov. between 2002 and 2012.

1 cs (SMF 23918), L 12.5 mm W 3.8 mm for 34 segments (fragmented); Bay of Biscay, Pertuis Charentais, OBIONE, Antioche, 28 March 2012, 1°18′30″W 46°05′03″N, 35 m, coastal muddy sand, leg. J. Jourde and P-G. Sauriau.

1 cs (MB29-000340), L 22 mm W 5 mm for 36 segments (fragmented); off Portugal, Cascais-Guia G29(2), October 2008, 9°24′58.50″W 38°39′37.86″N, 34 m, mud, leg. L. Sampaio and V. Quintino.

2 anterior fragments (MB29-000340), L 5.5 mm W 4.5 for 12 segments and L 3 mm W 2.5 mm for 11 segments; off Portugal, Cascais-Guia G29(2), October 2008, 9°24′58.50″W 38° 39′37.86″N, 34 m, mud, leg. L. Sampaio and V. Quintino.

DIAGNOSIS

Elytral surface smooth, microtubercules totally absent, outer lateral elytral margin with few small scattered papillae, posterior margin with fewer short papillae; neuropodia with an infra-acicular process in addition to the supra-acicular process; two types of notochaetae: upper ones stout with blunt tips and lower ones slender with very pointed tips; neurochaetae all unidentate, upper tapering to long, pointed tips.

DESCRIPTION (BASED ON HOLOTYPE)

Prostomium bilobed, without cephalic peaks; median antenna with ceratophore in anterior notch, style papillate, tapering to filiform tip; lateral antennae with ceratophores inserted terminoventrally and with papillate, tapering styles; palps smooth, long, tapering; anterior pair of eyes dorsolaterally in front of widest part of prostomium, posterior pair dorsally near hind margin (Figure 2A). Tentaculophores inserted laterally to prostomium, without chaetae, with a pair of papillate dorsal and ventral tentacular cirri, tapering to filiform tip. Second segment with first pair of elytra, biramous parapodia, ventral buccal cirri obviously longer than the following ventral cirri, papillate. 15 pairs of elytra for 33 chaetigers; elytra delicate, surface smooth; outer lateral and posterior elytral margin with few short papillae; surface near the outer lateral margin with very few scattered surface papillae of variable length (some as long as the largest marginal papillae); faint pigmentation in form of isolated spot near place of attachment of elytrophore and on the inner lateral part (Figure 2B–C). Styles of dorsal cirri papillate, tapering to filiform tip, extending beyond tips of neurochaetae; styles of ventral cirri with few papillae, tapering, shorter than neuropodia (Figure 2D). Parapodia biramous, both rami with single aciculum penetrating epidermis; notopodia with short, inconspicuous rounded preacicular lobe and longer, pointed acicular lobe; neuropodia with subconical prechaetal acicular lobe with longer, digitiform supra-acicular process and shorter, but conspicuous sub-acicular process, postchaetal lobe rounded (Figure 2D). Notochaetae with distinct rows of spines and of two kinds: upper ones stout with blunt tip and lower ones slender, tapering to very fine tip (Figure 2E1–E2); neurochaetae with rows of spines only in distal part; upper tapering to long, pointed, unidentate tip, lower ones with short bent enlarged distal part ending in blunt tip, middle ones of intermediate shape with blunt distal part (Figure 2E3–E5).

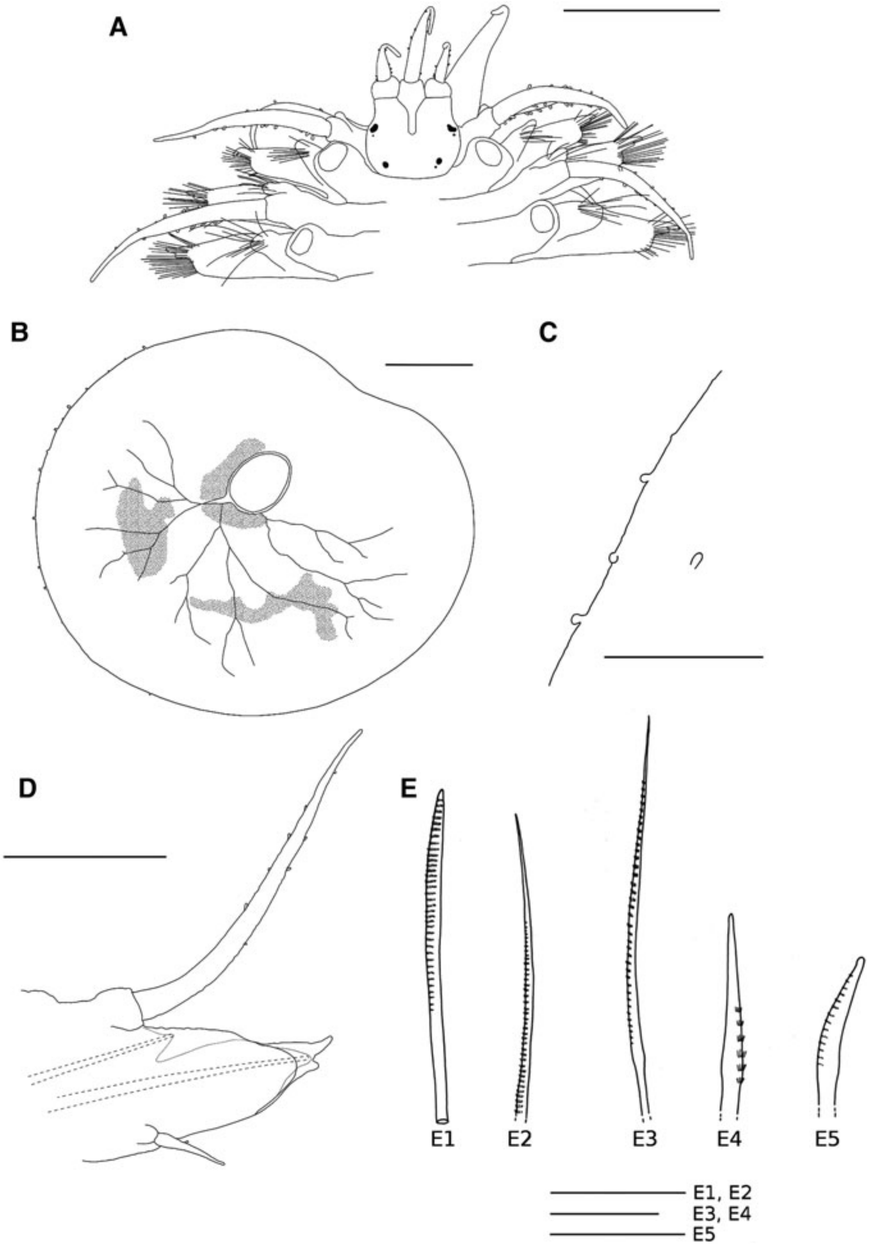

Fig. 2. *Malmgrenia louiseae* sp. nov., holotype (MNHN POLY TYPE 1559): (A) anterior end, dorsal view; (B) left middle elytron (9th); (C) detail of lateral margin of same; (D) right cirrigerous parapodium of chaetiger 12, posterior view; (E) chaetae, E1: upper notochaetae, E2: lower notochaetae, E3: upper neurochaetae, E4: middle neurochaetae, E5: lower neurochaetae. Scale bars: A, 1 mm; B, D, 500 μm; E1, E2, C, 100 μm; E3, E4, E5, 50 μm.

HABITAT

The species is currently known from muddy substrates, between 34 to 110 m depth (Table 2). Several potential hosts were found in the stations where the new species was collected. Thus, most of the Portuguese specimens were caught with the echiurid *Thalassema thalassemum* (Pallas, 1766) and one with the synaptid holothurian *Leptosynapta inhaerens* (O. F. Müller, 1776). However, specimens of *Malmgrenia louiseae* sp. nov. were never observed in immediate contact with the echiurid or the holothurian. In the Bay of Biscay, all the specimens were collected with *Leptosynapta* cf. *bergensis* (Östergren, 1905) and one specimen was observed in contact with the holothurian. The Mediterranean specimens were collected with the synaptid *Oestergrenia digitata* (Montagu, 1815).

DISTRIBUTION

Currently known from type locality in the Western Mediterranean (Gulf of Lions) and North-east Atlantic: Portuguese coasts (Cascais-Guia, Costa da Caparica and Figueira da Foz) and Bay of Biscay (Pertuis Charentais).

ETYMOLOGY

The species is named in honour of Louise Jourde, first author's daughter, born a few months before the beginning of this work.

REMARKS

Malmgrenia louiseae sp. nov. is unique due to its neuropodial sub-acicular process present in addition to the supra-acicular process which is known from several other *Malmgrenia* and many other polynoid species. It might be confused with

Malmgrenia lilianae (Pettibone, 1993), a species originally described from the south-west Atlantic (Pettibone, 1993), then reported for the Mediterranean (Barnich & Fiege, 2001, 2003) and now also recorded from the north-east Atlantic off Portugal (unpublished) and in the Bay of Biscay (unpublished). In both species elytra are devoid of microtubercles, with marginal papillae, and neurochaetae are exclusively unidentate. However, in *M. lilianae* there is only one kind of notochaetae (stout with pointed tip) and the sub-acicular process is absent. The identification key given below highlights further differences to other species in Europe.

KEY TO NORTH-EAST ATLANTIC AND MEDITERRANEAN *MALMGRENIA* SPECIES

1. Elytral margin with many long papillae 2
— Elytral margin with few scattered papillae or margin smooth 3
2. Elytral surface covered more or less completely by microtubercles; neurochaetae all unidentate, tapering to long, pointed tips, supra-acicular process digitiform *M. polypapillata*
— Elytral surface with patch of microtubercles in anterior part; neurochaetae bi- and unidentate; supra-acicular process absent *M. mcintoshi*
3. Elytral surface without microtubercles 4
— Elytral surface with microtubercles 5
4. Neuropodial acicular lobe with digitiform to conical supra-acicular process; short and long notochaetae stout with pointed tip; neurochaetae unidentate *M. lilianae*
— Neuropodial acicular lobe distally bilobed with digitiform to conical supra-acicular process and shorter sub-acicular process; short notochaetae with blunt tip, long notochaetae with slender, pointed tip; neurochaetae unidentate *M. louiseae* sp. nov.
5. Elytral surface covered more or less completely by microtubercles, neurochaetae usually all *bidentate* *M. ljungmani*
— Elytral surface with patch of microtubercles in anterior part; neurochaetae bi- and unidentate 6
6. Neuropodia without supra-acicular process *M. marphysae*
— Neuropodia with supra-acicular process 7
7. Short notochaetae stout, with blunt tip; long notochaetae slender, with pointed tip; upper and middle neurochaetae bidentate, lower unidentate *M. darbouxi*
— All notochaetae stout with blunt or pointed tip 8
8. Antennae and cirri smooth (short and thick) *M. castanea*
— Antennae and cirri papillate 9
9. Supra-acicular process small, digitiform *M. lunulata*
— Supra-acicular process wide bulbous or subconical 10
10. Neurochaetae usually all bidentate, unidentate neurochaetae (if present) with pointed tip *M. arenicolae*
— Upper and lower neurochaetae usually unidentate with knob-like tip, middle neurochaetae bidentate *M. andreapolis*

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REFERENCES

ASCONIT Consultants, UPVD, ADENA, OCEANIDE and LECOB (2012) Diagnostique scientifique des habitats marins du PNM Golfe du Lion. *Programme CARTHAM. Agence des Aires Marines Protégées.* Publ. Fr., 410 pp.

Barel C.D.N. and Kramers P.G.N. (1977) A survey of the echinoderm associates of the North-east Atlantic area. *Zoologische Verhandelingen* 156, 1–159.

Barnich R. and Fiege D. (2001) The Mediterranean species of Malmgreniella Hartman, 1967 (Polychaeta: Polynoidae: Polynoinae), including the description of a new species. *Journal of Natural History* 35, 1119–1142.

Barnich R. and Fiege D. (2003) The Aphroditoidea (Annelida: Polychaeta) of the Mediterranean Sea. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 559, 1–167.

ICZN Opinion (2009) Opinion 2233 (Case 3417) Malmgrenia McIntosh, 1874 (Annelida, Polychaeta, Polynoidae): usage conserved. *Bulletin of Zoological Nomenclature* 66, 1–3.

Muir A.I. and Chambers S.J. (2008) Case 3417 Malmgrenia McIntosh, 1874 (Annelida, Polychaeta, Polynoidae): proposed conservation of usage by designation of *Malmgrenia andreapolis* McIntosh, 1874 as the type species. *Bulletin of Zoological Nomenclature* 65, 12–16.

and

Pettibone M.H. (1993) Scaled Polychaetes (Polynoidae) associated with Ophiuroids and other invertebrates and review of species referred to

Malmgrenia McIntosh and replaced by *Malmgreniella* Hartman, with description of new taxa. *Smithsonian Contributions to Zoology* 138, 1–92.

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Premier signalement de l'espèce introduite *Grandidierella japonica* Stephensen, 1938 (Crustacea : Amphipoda : Aoridae) dans le bassin d'Arcachon

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Résumé

L'amphipode *Grandidierella japonica* Stephensen, 1938 est signalé pour la première fois dans le bassin d'Arcachon. Les spécimens ont été récoltés en 2012 et en 2013 au niveau de deux sites intertidaux de la lagune. Cette espèce, native de la mer du Japon, a pu être introduite accidentellement dans le bassin d'Arcachon lors de transferts d'huîtres.

Mots-clés : *Grandidierella japonica* ; amphipode ; espèce exotique ; bassin d'Arcachon ; transfert d'huîtres

First record of the non-native species *Grandidierella japonica* Stephensen, 1938 (Crustacea: Amphipoda: Aoridae) in Arcachon Bay

Abstract

The amphipod *Grandidierella japonica* Stephensen, 1938 is reported for the first time in Arcachon Bay. The specimens were collected in 2012 and in 2013 in two intertidal sites in the lagoon. This species, native to the Sea of Japan, may have been accidentally introduced in Arcachon Bay with oyster transfers.

Keywords: *Grandidierella japonica*; amphipod; exotic species; Arcachon Bay; oyster transfers

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Introduction

Les amphipodes de la famille des Aoridae sont actuellement représentés, dans les eaux marines européennes, par 33 espèces réparties en 9 genres (Horton & De Broyer, 2014). Parmi celles-ci, 10 espèces (en tenant compte de celles reclassées depuis lors dans les familles des Corophiidae et Unciolidae) ont été recensées dans les eaux littorales du golfe de Gascogne, au sud du parallèle 46°N, par Bachelet *et al.* (2003). A cette liste, est venue s'ajouter récemment *Grandidierella japonica* Stephensen, 1938, espèce non-indigène récoltée à différentes reprises entre 2010 et 2012 sur la côte est de l'île d'Oléron par Jourde *et al.* (2013). Espèce native du Pacifique nord-ouest (Chine, Japon, Corée) (Noël, 2011), *G. japonica* a été signalée pour la première fois en dehors de son aire de répartition en 1966 dans la baie de San Francisco (Chapman & Dorman, 1975). Elle est désormais présente sur toute la côte ouest des États-Unis (Greenstein & Tiefenthaler, 1997), au Mexique (Okolodkov *et al.,* 2007), à Hawaii (Coles *et al.,* 1999) et en Australie (Myers, 1981). En Europe, cette espèce a tout d'abord été signalée dans les îles Britanniques, à Southampton en juillet 1997 (Smith *et al.,* 1999), puis dans l'estuaire de l'Orwell en 2004 et 2005 (Ashelby, 2006), et enfin en baie de Marennes-Oléron en novembre 2010 (Jourde *et al.,* 2013). Dans le présent travail, la découverte récente de *G. japonica* est rapportée dans une localisation plus méridionale, le bassin d'Arcachon.

Matériel et méthodes

Le bassin d'Arcachon est une lagune macrotidale semi-fermée de 180 km^2, située sur la côte sud-ouest de la France. La lagune communique avec l'océan Atlantique par un étroit chenal et reçoit des apports en eau douce par différents tributaires dont la Leyre située au sud-est de la baie (figure 1). Le bassin d'Arcachon est caractérisé par une vaste zone intertidale (115 km^2) dont la partie basse est utilisée pour l'ostréiculture. Une grande partie de cette zone intertidale (46 km^2) est colonisée par un herbier à *Zostera (Zosterella) noltei* Hornemann, 1832 (Plus *et al.,* 2010).

Les échantillons ont été collectés aux niveaux de quatre stations en août 2012 et trois stations en octobre 2013 (figure 1 ; tableau 1). La faune a été prélevée à marée basse à l'aide d'un carottier ou d'une benne Ekman (15×15×15 cm^3). Le sédiment a été tamisé sur une maille de 1 mm ; le refus de tamis a été fixé dans une solution de formol à 4 % et ensuite transféré dans de l'éthanol à 70 %. Les spécimens ont été observés avec une loupe binoculaire Nikon SMZ 1500 et un microscope Nikon Eclipse E400. Ils ont été photographiés avec une caméra Nikon DS-Fi2, mesurés avec le logiciel NIS-Elements Analysis et un individu a été dessiné avec une tablette graphique Wacom Intuos 5 et le logiciel Inkscape.

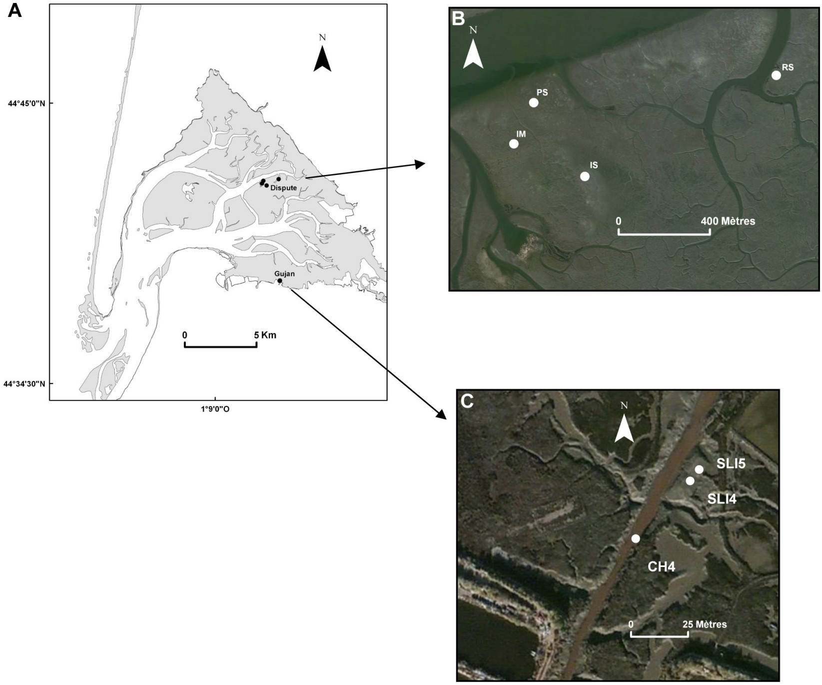

Figure 1 : Stations de collecte de l'amphipode *Grandidierella japonica* A. dans le bassin d'Arcachon, B. au niveau du site de la Dispute et C. de Gujan-Mestras.

Tableau 1 : Présence de *Grandidierella japonica* dans le bassin d'Arcachon. N = nombre d'individus collectés.

Site	Station	N	Date	Habitat	Niveau tidal
Dispute	IM	3	Août 2012	Vase	+1 m
Dispute	IS	16	Août 2012	Sables moyens	+1 m
Dispute	PS	9	Août 2012	*Zostera noltei*	+0,5 m
Dispute	RS	35	Août 2012	*Zostera noltei*	+1 m
Gujan	CH4	2	Octobre 2013	Sables vaseux	-0,5 m
Gujan	SLI4	2	Octobre 2013	Vase	+2,5 m
Gujan	SLI5	1	Octobre 2013	Vase	+2,5 m

Résultats

Un total de 68 individus de *Grandidierella japonica* (figure 2) a été collecté dans différents habitats du bassin d'Arcachon : 44 individus dans un herbier à *Zostera noltei* (stations PS, RS), 6 dans des vasières intertidales (stations IM, SLI4, SLI5), 16 dans des sables moyens intertidaux (station IS), et 2 dans un chenal sablo-vaseux d'une vingtaine de centimètres de profondeur (station CH4) (figure 1 ; tableau 1).

Figure 2 : *Grandidierella japonica* : vue latérale d'une femelle du bassin d'Arcachon (site de la Dispute, août 2012).

Ces individus sont difficilement différentiables des autres espèces d'Aoridae classiquement retrouvés dans les écosystèmes littoraux de la façade Atlantique française. Le genre *Grandidierella* Coutière, 1904 se caractérise par la présence de l'uropode 3 uniramé (figure 3), par la longueur de la rame de l'uropode 3 qui est plus de deux fois plus longue que le pédoncule (figure 3), par le troisième article de l'antenne 1 de taille inférieure à la moitié de la longueur de l'article 1 (figure 2) et enfin par le gnathopode 1 du mâle qui est du type carpochelé (carpe allongé pour former la pince avec le dactyle) (figure 4). Au sein du genre *Grandidierella*, seules cinq espèces présentent des rides, qui pourraient être des organes de stridulation (Stephensen, 1938), sur la marge antérieure du carpe du gnathopode 1 du mâle (figure 4B) : *G. japonica*, *G. perlata* Schellenberg, 1938, *G. taihuensis* Morino & Dai, 1990, *G. vietnamica* Dang, 1968 et *G. chaohuensis* Hou & Li, 2002 (Ariyama, 1996 ; Hou & Li, 2002 ; Jourde *et al.,* 2013). Parmi ces espèces, seule *G. japonica* possède trois dents sur le carpe du gnathopode 1 du mâle (figure 4A) (Chapman & Dorman, 1975 ; Jourde *et al.,* 2013). L'identification de *G. japonica* est d'autant plus complexe que les individus sont fragiles et perdent souvent leurs antennes et gnathopodes lors de la phase de tamisage.

Figure 3 : *Grandidierella japonica* : vue latérale de l'urosome. La flèche noire montre l'uropode 3 uniramé (site de la Dispute, août 2012).

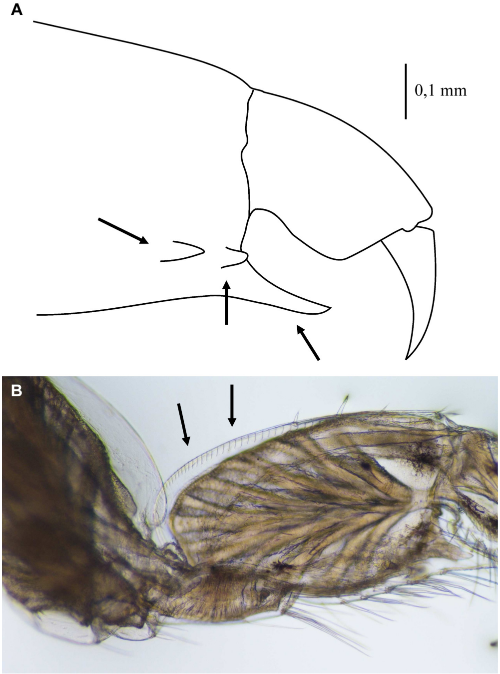

Figure 4 : *Grandidierella japonica*, gnathopode 1, mâle : A. dessin schématique indiquant les trois dents caractéristiques, B. détail des rides transversales sur la marge antérieure du carpe de gnathopode du mâle (site de la Dispute, août 2012).

Discussion

Contrairement à ce qui a pu être observé dans les îles Britanniques (Smith *et al.,* 1999 ; Ashelby, 2006) ou à Hawaii (Coles *et al.,* 1999), l'apparition de *Grandidierella japonica* dans le bassin d'Arcachon ne paraît pas être reliée aux activités de transports maritimes (eaux de ballast ou fouling). En effet, les conditions hydrodynamiques et les faibles profondeurs à l'entrée de la lagune empêchent les navires de commerce de rentrer dans le bassin d'Arcachon. De plus, cette espèce benthique n'a pas de phase de dispersion larvaire planctonique (Ashelby, 2006) et peut donc difficilement coloniser de nouveaux environnements par migration. C'est d'autant plus vrai que les ports de commerce les plus proches, à savoir ceux de Bayonne et Bordeaux, sont situés respectivement à 150 et 200 km de l'entrée du bassin d'Arcachon. Même si l'activité de plaisance arcachonnaise reste relativement locale, une arrivée par fouling sur des coques de voiliers n'est toutefois pas complètement à exclure.

L'hypothèse la plus probable semble être un transfert via l'ostréiculture, comme cela a pu être avancé récemment pour le bassin de Marennes-Oléron (Jourde *et al.,* 2013) ou précédemment pour la Californie (Chapman & Dorman, 1975) ou le Mexique (Okolodkov *et al.,* 2007). En effet, le bassin d'Arcachon est l'un des principaux centres ostréicoles en France, avec une production de 7 000 à 8 000 tonnes par an d'huîtres creuses *Crassostrea gigas* (Thunberg, 1793) (Scourzic *et al.,* 2011). L'huître creuse portugaise *Crassostrea angulata* (Lamarck, 1819), qui était cultivée dans le bassin d'Arcachon depuis la fin du XIX^{e} siècle, a été victime dans les années 1970 d'un virus qui a décimé les stocks (Goulletquer *et al.,* 2002). Afin de soutenir la filière ostréicole, des stocks de *C. gigas* en provenance du Japon ont été massivement introduits dans le bassin d'Arcachon entre 1971 et 1975 (Grizel & Héral, 1991). Le transfert d'huîtres est un vecteur d'introduction d'espèces exotiques très bien documenté (Gruet *et al.,* 1976 ; Verlaque *et al.,* 2007) et est à l'origine de l'arrivée de plusieurs espèces d'origine asiatique dans le bassin d'Arcachon (Bachelet *et al.,* 2004 ; Bachelet *et al.,* 2009 ; Lavesque *et al.,* 2013). Il est cependant difficile de savoir si ces espèces sont arrivées directement depuis le Japon dans les années 1970 ou si elles sont arrivées dans la lagune lors de transferts secondaires entre bassins ostréicoles. Ce dernier phénomène est très peu connu mais de grandes quantités d'huîtres sont transférées entre bassins ostréicoles en France et en Europe (Espagne, Irlande). Il est donc impossible de savoir depuis quand *G. japonica* est présente dans le bassin d'Arcachon sans connaître l'origine exacte de son introduction. C'est d'autant plus difficile qu'elle a peut-être été mal identifiée ou confondue avec des espèces proches pendant plusieurs années.

Cette confusion est liée au manque d'informations concernant cette espèce, *G. japonica* n'étant pas référencée dans les principales clés de détermination européennes. Par exemple, en utilisant la clé de Lincoln (1979), les individus femelles ne peuvent être identifiés qu'au niveau de la famille des Aoridae, alors que les mâles appartiendraient au genre *Microdeutopus* (Ashelby, 2006). Dans le cadre d'une étude d'impact, le site de Dispute (figure 1B) a été échantillonné régulièrement depuis 2002 (Lavesque *et al.,* 2009 ; Do *et al.,* 2012), mais *G. japonica* n'y a jamais été collecté alors qu'il y avait de fortes densités de *Microdeutopus gryllotalpa* Costa, 1853 et d'Aoridae non identifiés dans ces échantillons. Il s'agissait peut-être déjà de l'espèce *G. japonica*, ou d'un complexe d'Aoridés, mais malheureusement les spécimens ont été calcinés afin de déterminer des valeurs de biomasses. Il est donc impossible de savoir avec précision depuis quand *G. japonica* est présent dans le bassin d'Arcachon.

Contrairement à de nombreux amphipodes, l'écologie de cette espèce est relativement bien connue. Elle est principalement associée à des substrats vaseux ou sablo-vaseux intertidaux en zones saumâtres (estuaires, baies) (Chapman & Dorman, 1975). *G. japonica* construit des tubes en forme de « U » dans lesquels il est possible de trouver un mâle et une femelle. Les mâles peuvent également être observés dans des flaques à marée basse. L'espèce peut aussi être présente dans les récifs d'huîtres sauvages (Californie) ou dans les herbiers à zostères (Japon) (Nagata, 1960 ; Chapman & Dorman, 1975). Enfin, cet amphipode est connu pour être sensible aux pollutions métalliques et est utilisé pour tester la toxicité des sédiments (Nipper *et al.,* 1989). Il serait par contre favorisé par des milieux riches en matière organique (d'où sa présence dans la vase) et a déjà été trouvé à proximité de rejets d'eaux usées (Smith *et al.,* 1999). Cette espèce présente souvent de fortes abondances (Nagata, 1960 ; Chapman & Dorman, 1975) avec jusqu'à 5800 ind.m^2 près de Southampton en janvier 1998 (Smith *et al.,* 1999). Dans le bassin d'Arcachon, la plupart des individus ont été prélevés dans des habitats vaseux avec un maximum d'individus dans les herbiers à zostères naines (1 300 ind.m^2). Cette espèce a également été collectée dans des milieux sableux intertidaux ou de très faible profondeur (tableau 1). Les deux sites de prélèvements sont situés au niveau de zones ostréicoles. Le site de la Dispute (figure 1B) correspond à une ancienne « souille » où ont été enterrées plus de 100 000 m^3 de coquilles d'huîtres japonaises après des opérations de nettoyage d'anciens parcs. Ces stations sont également situées à proximité d'un chenal dont les rives sont recouvertes d'huîtres sauvages. Le site de Gujan (figure 1C) est situé au niveau d'un chenal qui alimente les bassins d'affinage d'huîtres. Ces indications renforcent donc l'hypothèse d'une introduction de *G. japonica* via des transferts d'huîtres, soit directement depuis le Japon, soit depuis un autre centre ostréicole européen.

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Références

Ariyama, H., 1996. Four species of the genus *Grandidierella* (Crustacea: Amphipoda: Aoridae) from Osaka Bay and the northern part of the Kii Channel, central Japan. *Publications of the Seto Marine Biological Laboratory,* **37,** pp. 167–191.

Ashelby, C., 2006. Records of the introduced amphipod *Grandidierella japonica* Stephensen 1938 (Crustacea: Amphipoda: Gammaridea: Aoridae) from the Orwell estuary, Suffolk. *Transactions of the Suffolk Natural History,* **42,** pp. 48–54.

Bachelet, G., Dauvin, J.-C. & Sorbe, J.-C., 2003. An updated checklist of marine and brackish water Amphipoda (Crustacea: Peracarida) of the southern Bay of Biscay (NE Atlantic). *Cahiers de Biologie Marine,* **44,** pp. 121–151.

Bachelet, G., Simon-Bouhet, B., Desclaux, C., Garcia-Meunier, P., Mairesse, G., de Montaudouin, X., Raigné, H., Randriambao, K., Sauriau, P. G. & Viard, F., 2004. Invasion of the eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on resident fauna. *Marine Ecology Progress Series,* **276,** pp. 147–159.

Bachelet, G., Blanchet, H., Cottet, M., Dang, C., de Montaudouin, X., de Moura Queirós, A., Gouillieux, B. & Lavesque, N., 2009. A round-the-world tour almost completed: first records of the invasive mussel *Musculista senhousia* in the north-east Atlantic (southern Bay of Biscay). *Marine Biodiversity Records,* **2,** pp. e119.

Chapman, J. W. & Dorman, J. A., 1975. Diagnosis, systematics, and notes on *Grandidierella japonica* (Amphipoda: Gammaridea) and its introduction to the Pacific coast of the United States. *Bulletin of the Southern California Academy of Sciences,* **74,** pp. 104–108.

Coles, S. L., DeFelice, R. C., Eldredge, L. G. & Carlton, J. T., 1999. Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. *Marine Biology,* **135,** pp. 147–158.

Do, V. T., de Montaudouin, X., Blanchet, H. & Lavesque, N., 2012. Seagrass burial by dredged sediments: Benthic community alteration, secondary production loss, biotic index reaction and recovery possibility. *Marine Pollution Bulletin,* **64,** pp. 2340–2350.

Goulletquer, P., Bachelet, G., Sauriau, P. G. & Noël, P., 2002. Open Atlantic coast of Europe - A century of introduced species into French waters. In *Invasive aquatic species of Europe: Distribution, impacts and management.* (Eds. Leppäkoski, E., Gollasch, S. & Olenin, S.) Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 276–290.

Greenstein, D. J. & Tiefenthaler, L. L., 1997. Reproduction and population dynamics of a population of *Grandidierella japonica* (Stephensen) (Crustacea: Amphipoda) in upper Newport Bay, California. *Bulletin of the Southern California Academy of Sciences,* **96,** pp. 34–42.

Grizel, H. & Héral, M., 1991. Introduction into France of the Japanese oyster (*Crassostrea gigas*). *Journal du Conseil International pour l'Exploration de la Mer,* **47,** pp. 399–403.

Gruet, Y., Héral, M. & Robert, J.-M., 1976. Premières observations sur l'introduction de la faune associée au naissain d'huîtres japonaises *Crassostrea gigas* (Thunberg), importé sur la côte atlantique française. *Cahiers de Biologie Marine,* **17,** pp. 173–184.

Horton, T. & De Broyer, C., 2014. Aoridae Stebbing, 1899. In: Horton, T., Lowry, J. & De Broyer, C. (2013 onwards) World Amphipoda Database. Accessed through: Costello, M. J., Bouchet, P., Boxshall, G., Arvantidis, C. & Appeltans, W. European Register of Marine Species. [cited 27/01/2014]. <`http://www.vliz.be/vmdcdata/narms/narms.php?p=taxdetails&id=101368`>.

Hou, Z. E. & Li, S. Q., 2002. A new species of the genus *Grandidierella* from Lake Chaohu, China (Crustacea: Amphipoda: Aoridae). *Acta Zootaxonomica Sinica,* **27,** pp. 225–234.

Jourde, J., Sauriau, P.-G., Guenneteau, S. & Caillot, E., 2013. First record of *Grandidierella japonica* Stephensen, 1938 (Amphipoda: Aoridae) from mainland Europe. *BioInvasions Records,* **2 (1),** pp. 51–55.

Lavesque, N., Blanchet, H. & de Montaudouin, X., 2009. Development of a multimetric approach to assess perturbation of benthic macrofauna in *Zostera noltii* beds. *Journal of Experimental Marine Biology and Ecology,* **368,** pp. 101–112.

Lavesque, N., Sorbe, J. C., Bachelet, G., Gouillieux, B., de Montaudouin, X., Bonifacio, P., Blanchet, H. & Dubois, S., 2013. Recent discovery of *Paranthura japonica* Richardson, 1909 (Crustacea: Isopoda: Paranthuridae) in European marine waters (Arcachon Bay, Bay of Biscay). *BioInvasions Records,* **2 (3),** pp. 215–219.

Lincoln, R. J., 1979. British Marine Amphipoda: Gammaridea. (Ed. British Museum (Natural History)) British Museum (Natural History), London. 658 p.

Myers, A. A., 1981. Taxonomic studies on the genus *Grandidierella* Coutière (Crustacea, Amphipoda). III. Fijian, Australian and Saudi Arabian species. *Bulletin du Muséum National d'Histoire Naturelle,* **3,** pp. 213–226.

Nagata, K., 1960. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. *Publications of the Seto Marine Biological Laboratory,* **8,** pp. 163–182.

Nipper, M. G., Greenstein, D. J. & Bay, S. M., 1989. Short- and long-term sediment toxicity test methods with the amphipod *Grandidierella japonica*. *Environmental Toxicology and Chemistry,* **8,** pp. 1191–1200.

Noël, P., 2011. Checklist of cryptogenic and alien Crustacea of the European Atlantic coast. In *In the wrong place — Alien marine crustaceans: distribution, biology and impacts.* (Eds. Galil, B. S., Clark, P. F. & Carlton, J. T.) Springer, Dordrecht, pp. 345–375.

Okolodkov, Y. B., Bastida-Zavala, R., Ibáñez, A. L., Chapman, J. W., Suárez-Morales, E., Pedroche, F. & Gutiérrez-Mendieta, F. J., 2007. Especies acuáticas no indígenas en México. *Ciencia y Mar,* **32,** pp. 29-67.

Plus, M., Dalloyau, S., Trut, G., Auby, I., de Montaudouin, X., Emery, E., Noël, C. & Viala, C., 2010. Long-term evolution (1988-2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuarine, Coastal and Shelf Science,* **87,** pp. 357–366.

Scourzic, T., Loyen, M., Fabre, E., Tessier, A., Dalias, N., Trut, G., Maurer, D. & Simonnet, B., 2011. Évaluation du stock d'huîtres sauvages et en élevage dans le Bassin d'Arcachon. Contrat Agence des Aires Marines Protégées & OCEANIDE. 70 p.

Smith, P., Perret, J., Garwood, P. & Moore, G., 1999. Two additions to the UK marine fauna: *Desdemona ornata* Banse, 1957 (Polychaeta, Sabellidae) and *Grandidierella japonica* Stephensen, 1938 (Amphipoda, Gammaridea). *Newsletter of the Porcupine Marine Natural History Society,* **2,** pp. 8–11.

Stephensen, K., 1938. *Grandidierella japonica* n. sp., a new amphipod with stridulating (?) organs from brackish water in Japan. *Annotationes Zoologicae Japonenses,* **17,** pp. 179–184.

Verlaque, M., Boudouresque, C. F. & Mineur, F., 2007. Oyster transfers as a vector for marine species introductions: a realistic approach based on the macrophytes. In *Impact of mariculture on coastal systems* (Ed. Briand, F.) *CIESM Workshop Monographs,* **32,** CIESM, Monaco, pp. 39–47.

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SENCKENBERG

ORIGINAL PAPER

New records of *Spio symphyta* and *Spio martinensis* ('Polychaeta': Canalipalpata: Spionidae) from Arcachon Bay (France), NE Atlantic

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Abstract This paper presents new records of *Spio symphyta* Meißner et al., 2011 and *Spio martinensis* Mesnil, 1896 ('Polychaeta': Canalipalpata: Spionidae) from Arcachon Bay (southern Bay of Biscay). For both species the new records represent an extension of their known distributional range. The two species have probably been present in Arcachon Bay for several years but were confused with other species of the genus *Spio*. *Spio symphyta* was identified at five locations in Arcachon Bay in 2009 and 2013 and *S. martinensis* at three stations in 2012 and 2013. A detailed and illustrated description of specimens from Arcachon Bay is provided. Important characters of *Spio* spp. occurring in the area are compared.

Keywords Arcachon Bay · NE Atlantic · New record · *Spio symphyta* · *Spio martinensis* · Spionidae

Introduction

The spionid polychaetes ('Polychaeta': Canalipalpata: Spionidae) are one of the most common groups in marine and estuarine environments all over the world. The Spionidae comprise more than 500 nominal species grouped into about 35 genera (Radashevsky 2012). The genus *Spio* currently contains 30 species (Bick and Meißner 2011) and is well represented in European waters. For instance, 11 species are reported from shallow waters around Britain and Ireland (Radashevsky 2012) and six species occur in the German EEZ of the North and Baltic Seas (Bick et al. 2010). Until now, only four *Spio* species have been recorded in France: *Spio decoratus* Bobretzky, 1870, *S. filicornis* (Müller, 1776), *S. martinensis* Mesnil, 1896, and *S. multioculata* (Rioja, 1918) (Bachelet, unpub. data; RESOMAR database (French marine stations and observatories network) http://resomar.cnrs.fr/bases/index.php). In France, *S. decoratus* is present from the North Sea to the Mediterranean Sea, *S. martinensis* from the North Sea to the Atlantic coast, and *S. multioculata* in the English Channel and Mediterranean Sea. The distribution of *S. filicornis* has to be reconsidered after the identity of the species has been fixed with the designation of a neotype in 2011 (Meißner et al. 2011).

In the present study, we report the first records of *S. symphyta* Meißner, Bick & Bastrop, 2011, and *S. martinensis* in Arcachon Bay (southern Bay of Biscay). In this location, only the occurrence of *S. filicornis* (Boisseau 1962; Cazaux 1973; Auby 1991) and *S. decoratus* (Bachelet and Dauvin 1993; Bachelet et al. 1996; Blanchet et al. 2005) has been reported since the beginning of the benthic surveys in the 1960s. For *S. symphyta*, the new record is the first outside the North Sea, the type locality of the species (Meißner et al. 2011). The occurrence of *S. filicornis* in the study area is discussed. Important characters of *Spio* spp. occurring in the area are compared.

Material and methods

Arcachon Bay is a 180-km^2 macrotidal (maximum tidal range: 4.9 m) coastal lagoon located on the southwestern coast of France (Fig. 1). This lagoon communicates with the Atlantic Ocean by a narrow channel and receives freshwater inputs in

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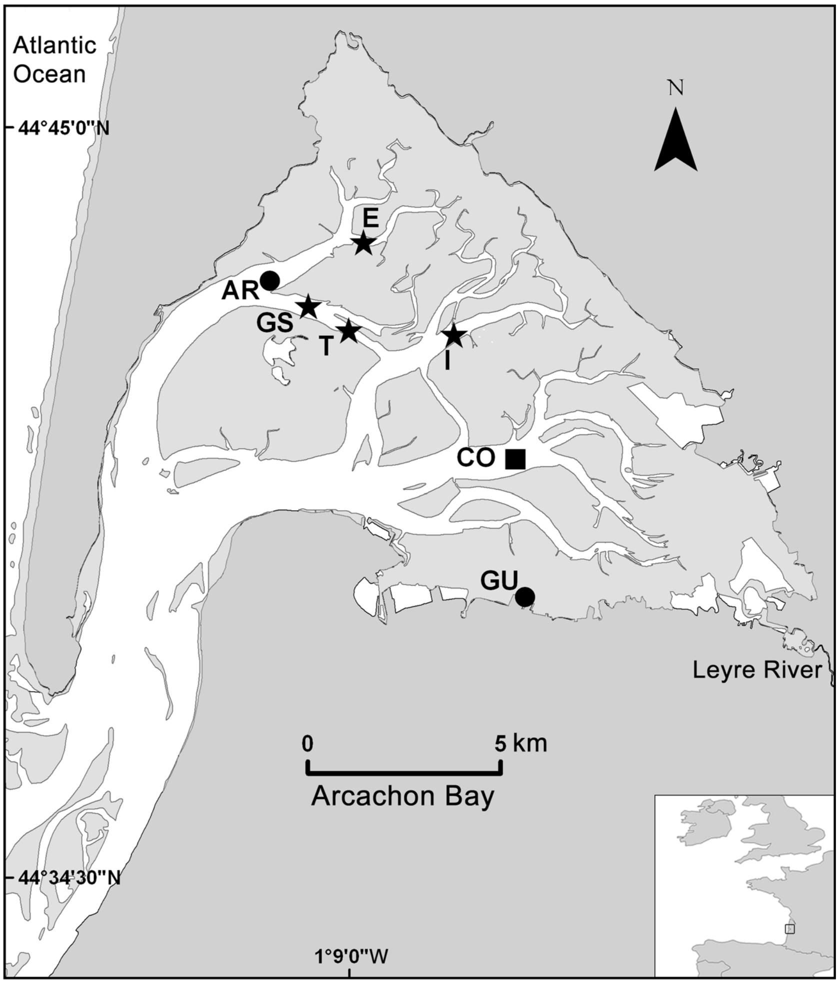
Fig. 1 Sampling stations of *Spio symphyta* (stars), *S. martinensis* (dots), and both species (square) in Arcachon Bay (Bay of Biscay)



its southeastern part (Leyre River). It is characterized by large intertidal flats (115 km^2), the lower parts of which are used for Pacific oyster [*Crassostrea gigas* (Thunberg, 1793)] farming. Most of the intertidal areas (46.2 km^2) are covered by the seagrass, *Zostera noltei* Hornemann, 1832 (Plus et al. 2010). In the inner lagoon, tidal channels represent 71 km^2, with 1.02 km^2 occupied by the eelgrass *Zostera (Zostera) marina* Linnaeus, 1753 (Plus et al. 2010).

Samples were collected from different stations in Arcachon Bay from 2009 to 2013 (Fig. 1, Table 1). Macrofauna was collected using a Van Veen grab or an Ekman grab. Sediment was sieved through a 1-mm mesh; the remaining fraction was fixed in 4 % formalin and later transferred into 70 % ethanol for morphological studies. Methyl green staining was applied for observation of some specimens with light microscopy.

Specimens were examined under a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Fi 2 camera. Some specimens were figured with a Wacom Intuos 5 tablet and the Inkscape software. Length and width were measured with the NIS-Elements Analysis software. For SEM studies, specimens were dehydrated in a graded ethanol series, critical point dried, sputter coated with gold, and examined with an FEI Quanta 200 scanning electron microscope.

Specimens from Arcachon Bay examined in the scope of this study were deposited in the Zoological Collections of Rostock University and in the collection of Arcachon Marine Station (Table 1).

Results

A total of 19 specimens of *Spio symphyta* was collected at five different stations in Arcachon Bay in 2009 and 2013, and 10 specimens of *S. martinensis* at three stations in 2012 and 2013 (Table 1). The morphology of all specimens was studied in detail and the results are presented in the following descriptions. Important characters of *Spio* spp. occurring along French coasts are collated in Table 2.

Systematic account

Spio symphyta Meißner, Bick & Bastrop, 2011
(Figs. 2 and 3)

Table 1 Records of *Spio symphyta* and *S. martinensis* in Arcachon Bay and information on their deposition.

Species	Stations	N	Date	Habitat	Tidal level	Latitude	Longitude	Material deposition
S. symphyta	E	1	Sep 2009	Muddy sands	−3.8 m	44°43'35 N	01°09'24 W	Arcachon Marine Station
S. symphyta	I	3	Sep 2009	Slipper limpet bed	−4.3 m	44°42'23 N	01°07'26 W	ZSRO-P 2255
S. symphyta	GS	9	Sep 2009	*Zostera* meadow	−3.9 m	44°42'41 N	01°10'24 W	Arcachon Marine Station
S. symphyta	T	1	Sep 2009	Mud	+1.5 m	44°42'23 N	01°09'31 W	Arcachon Marine Station
S. symphyta	CO	5	Apr 2013	Muddy sands	−6.0 m	44°40'40 N	01°06'13 W	Arcachon Marine Station
S. martinensis	CO	2	Jul 2012	Muddy sands	−6.0 m	44°40'40 N	01°06'13 W	Arcachon Marine Station
S. martinensis	CO	4	Apr 2013	Muddy sands	−6.0 m	44°40'40 N	01°06'13 W	ZSRO-P 2378
S. martinensis	AR	3	Apr 2013	Muddy sands	−5.0 m	44°43'04 N	01°11'08 W	Arcachon Marine Station
S. martinensis	GU	1	Oct 2013	Muddy sands	−0.5 m	44°38'46 N	01°05'51 W	ZSRO-P 2377

N=number of individuals collected

Table 2 Taxonomic characteristics of *Spio* species present along the French coasts.

	Spio symphyta (Meißner, Bick & Bastrop, 2011)	*Spio decoratus* Bobretzky, 1870	*Spio filicornis** (Müller, 1776)	*Spio martinensis* Mesnil, 1896	*Spio multioculata* (Rioja, 1918)
Prostomium	Rounded, shovel-like	Bluntly rounded	Slightly incised	Narrow, rounded	T-shaped
1st branchiae (*vs* following chaetigers)	Shorter	As long	Shorter	Shorter	As long?
Neuropodial hooks					
-chaetiger of first appearance	11 (10)	11	11	13-14	28-32
-number of hooks	5-12	9-11	5-9	5-8	6-8
-hook shape	Tridentate (uppermost tooth hardly visible)	Tridentate (uppermost tooth distinct)	Bidentate	Tridentate (uppermost tooth distinct)	Bidentate
Additional features	Peristomium and prostomium fused				Two groups of eyes

*occurrence questionable

Spio symphyta Meißner, Bick & Bastrop 2011: 19-23, figs. 11, 12
Spio filicornis (O.F. Müller, 1776): Böggemann 1997: 120, fig. 95
Spio cf. *filicornis* (North Sea) Bick et al. 2010: 166-168, figs. 3, 9d, 10
?*Spio* sp. nov. Sikorski 2001: 282, one figure.

Material examined Northeast Atlantic Ocean: France: Arcachon Bay; 19 specimens (Table 1)

Description (based on specimens from Arcachon Bay) All specimens incomplete, anterior fragments, longest specimen with 37 chaetigers, about 7.9 mm in length and 0.52 mm wide. Other specimens examined with 12 to 30 chaetigers, 2.0 to 6.1 mm in length and 0.31 to 0.65 mm in width. One palp present in one specimen (anterior fragment with 22 chaetigers, 4.9 mm long and 0.65 mm wide), reaching back to chaetigers 9–10.

Anterior part of the prostomium rounded, without median incision, anterolateral part slightly expanded giving it a shovel-like appearance (Fig. 2a, 3a); posterior part of prostomium slightly elevated (Fig. 3c); 2 pairs of black eyes arranged in trapezoid, anterior pair crescent-shaped or oval, widely spaced, posterior pair round, closely spaced (Figs. 2a, 3a); posterior part of prostomium fused with peristomium (Figs. 2a, 3a).

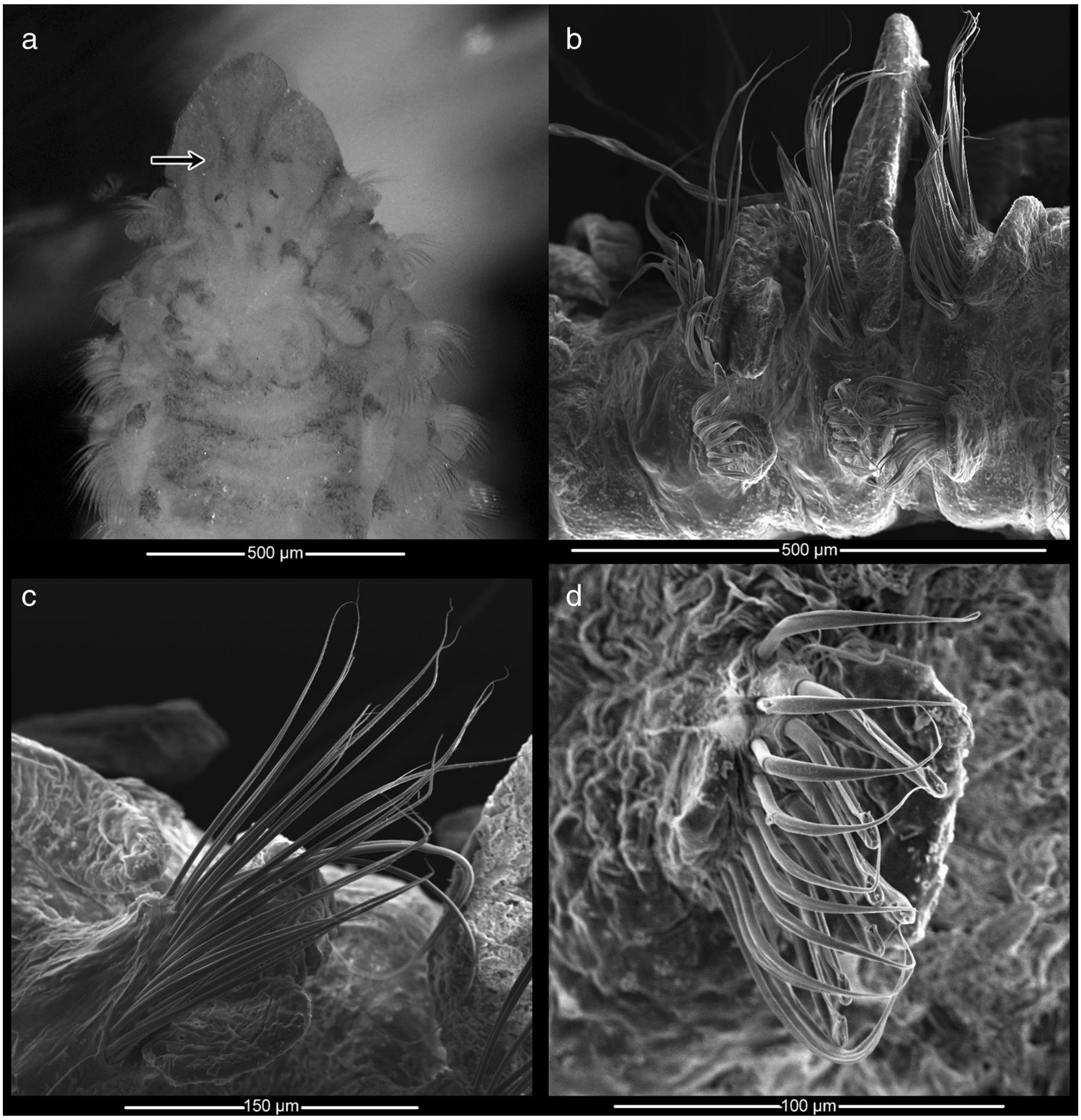


Fig. 2 *Spio symphyta* Meißner, Bick & Bastrop, 2011: **(a)** anterior end, dorsal view (stereomicroscope), black arrow indicates the fusion between the prostomium and the peristomium; **(b)** anterior end, lateral view, chaetigers 3 to 5 (SEM); **(c)** notopodium from chaetiger 16 (SEM); **(d)** neuropodium from chaetiger 14 (SEM)

Nuchal organs U-shaped, extending to the end of chaetiger 2 (Figs. 2a and 3a, b); metameric dorsal ciliated organs double-paired, clearly detectable first from between transversal ciliated band on chaetigers 6 and 7, and the posterior extension (for example, up to chaetiger 27 in specimens with about 30 chaetigers) often observable until the end of fragment; first as very short double-paired ciliated bands, longer in more posterior chaetigers (from about chaetiger 10).

Branchiae from chaetiger l, continuing to end of the fragment (incomplete specimens); branchiae on first chaetiger slightly shorter and narrower than those on the following chaetigers (Fig. 3b), reaching midline dorsally, touching on first chaetigers and becoming thinner and shorter more posteriorly (from about chaetiger 25); branchiae with narrow base, tapering distally, inner branchial ciliation present; on anterior chaetigers, branchiae basally fused with notopodial postchaetal lamellae, distinctly separated from lamellae in median and posterior chaetigers.

Ventral glands, indicated by the presence of white dots after methyl green staining and the presence of pores depictable with SEM (see Meißner et al. 2011), present from about chaetiger 6 to at least chaetiger 20, at maximum, 3 or 4 pairs of white dots per chaetiger detectable in different specimens (number of white dots highest in widest specimens); number of pairs of white dots highest in chaetigers 10-18; difficult to detect.

First notopodium slightly shifted dorsally. Notopodial postchaetal lamellae on anterior chaetigers oval, becoming

Fig. 3 Pigmentation pattern in *Spio symphyta* Meißner, Bick & Bastrop, 2011: **(a)** anterior end, dorsal view; **(b)** anterior end, dorsal view; **(c)** anterior end, lateral view; **(d)** anterior end, ventral view. Scale bar=200 μm

less wide and elongated on middle and posterior chaetigers. Neuropodial postchaetal lamellae in anterior chaetigers small, with of postchaetal lamellae shorter than the transverse row of corresponding chaetae in anteriormost chaetigers (Fig. 2b); in posterior chaetigers, the neuropodial postchaetal lamellae large and oval (Fig. 2d).

Notopodial chaetae all capillaries (Fig. 2b, c); capillaries of anterior chaetigers arranged in two rows: chaetae of anterior row limbate, distinctly granulated; chaetae of posterior row longer, thinner, lacking granulations; additional superior fascicle of capillaries present but inconspicuous; capillaries of posterior chaetigers arranged in irregular rows (Fig. 2c) of thin, long, non-granulated capillaries. Neurochaetae in anterior chaetigers arranged in two rows: chaetae of anterior row bilimbate and granulated, chaetae of the posterior row limbate without granulations. The posterior row of neurochaetae is replaced by 5–8 hooded hooks from chaetiger 11 (Figs. 2d 5a); these hooks slightly narrowed subdistally, with short hood, tridentate, main fang well developed, two uppermost teeth situated one above the other, third tooth minute (Fig. 5a); anterior row of limbate chaetae without granulations from chaetiger 15-18; two sabre chaetae in inferiormost position present from middle chaetigers.

Pigmentation: faintly pigmented; intensity of pigmentation varies among specimens. Palp with light brown pigment anteriorly on the base (Fig. 3a). Light brown pigment dorsally on prostomium and peristomium, more intense close to the narrowest part of the prostomium just before the fusion of peristomium and prostomium (Fig. 3b); longitudinal stripe of pigment between pairs of eyes (Fig. 3a, b); longitudinal stripes ventrally around mouth opening (Fig. 3d). Light brown pigment anteriorly in the median part of the branchiae from chaetiger 1 to chaetiger 9 (pigment completely surrounds the branchial basis on chaetigers 1 to 3) (Fig. 3b). Branchiae of chaetigers 1 and 2 with pigmented tips. Light brown transversal stripe behind nuchal organs (Fig. 3b); thin transversal stripes of the same color in front of and after the transversal ciliated bands on chaetigers 4 to 10 (Fig. 3a, b); pigmented patches dorsolaterally on chaetigers 3 to 7. Transverse stripes of brown pigment on the ventrum between segmental margins up to about chaetiger 14 (Fig. 3d). Laterally on the neuropodial base, small patches of light brown pigment extend from chaetiger 1 to about 11 (Fig. 3c). Laterally pigmented patches between neuropodium and notopodium from chaetiger 1 to about chaetiger 8.

Methyl green staining pattern: no distinct staining pattern. Anterior part of prostomium and peristomium, as well as elevated posterior part of the caruncle stain intensely; branchiae and margins of postchaetal lamellae of anterior and medium chaetigers also stain intensely.

Pygidium unknown.

Biology In the North Sea, *Spio symphyta* was found in fine and coarse sand areas without silt, in subtidal regions (Meißner et al. 2011). In contrast, in Arcachon Bay, specimens were found in muddy environments both in intertidal and subtidal stations (Table 1), sometimes associated with biogenic habitats (*Zostera marina* meadow, slipper limpet beds).

Distribution North Sea (Meißner et al. 2011), Arcachon Bay, France (this study).

Type locality North Sea.

Remarks In the original description of *S. symphyta* by Meißner et al. (2011), the authors forgot to explain the etymology. Since the first author of that paper is also a co-author of the present paper, we would like to make up for this mistake and mention here that the name "*symphyta*" refers to the fusion of the prostomium and peristomium just in front of the eyes.

There are only few differences between specimens of *Spio symphyta* from the North Sea and from Arcachon Bay: hooded hooks in Arcachon Bay specimens appear always from chaetiger 11 and never from chaetiger 10, as it has been rarely observed in North Sea specimens, with seven hooks in one row (instead of the usual eight). Both characters underline ontogenetic variation in *Spio* (Meißner et al. 2011) and hence, interpretation of this observation should be done with caution. Moreover, specimens from Arcachon seem to be more pigmented.

Spio martinensis Mesnil, 1896
(Fig. 4)
Spio martinensis Mesnil 1896: 122-128, VII, 1-20 – Dauvin 1989: 170-172 – Bick et al. 2010: 173-175, Figs. 7, 9.

Material examined Northeast Atlantic Ocean: France: Arcachon Bay; 10 specimens (Table 1).

Description (based on specimens from Arcachon Bay) One complete specimen (without palp), with 42 chaetigers, about 7.4 mm in length and 0.37 mm wide. Other specimens examined with 15 to 35 chaetigers (incomplete anterior fragment), 2.2 to 6.8 mm in length and 0.4 to 0.5 mm in width.

Prostomium narrow, anteriorly rounded, without median incision, posteriorly extending to chaetiger 1, and not fused with the peristomium (Fig. 4a); two pairs of black eyes arranged in trapezoid, anterior pair further apart and crescent-shaped, posterior pair closer together and eyes rounded (Fig. 4a).

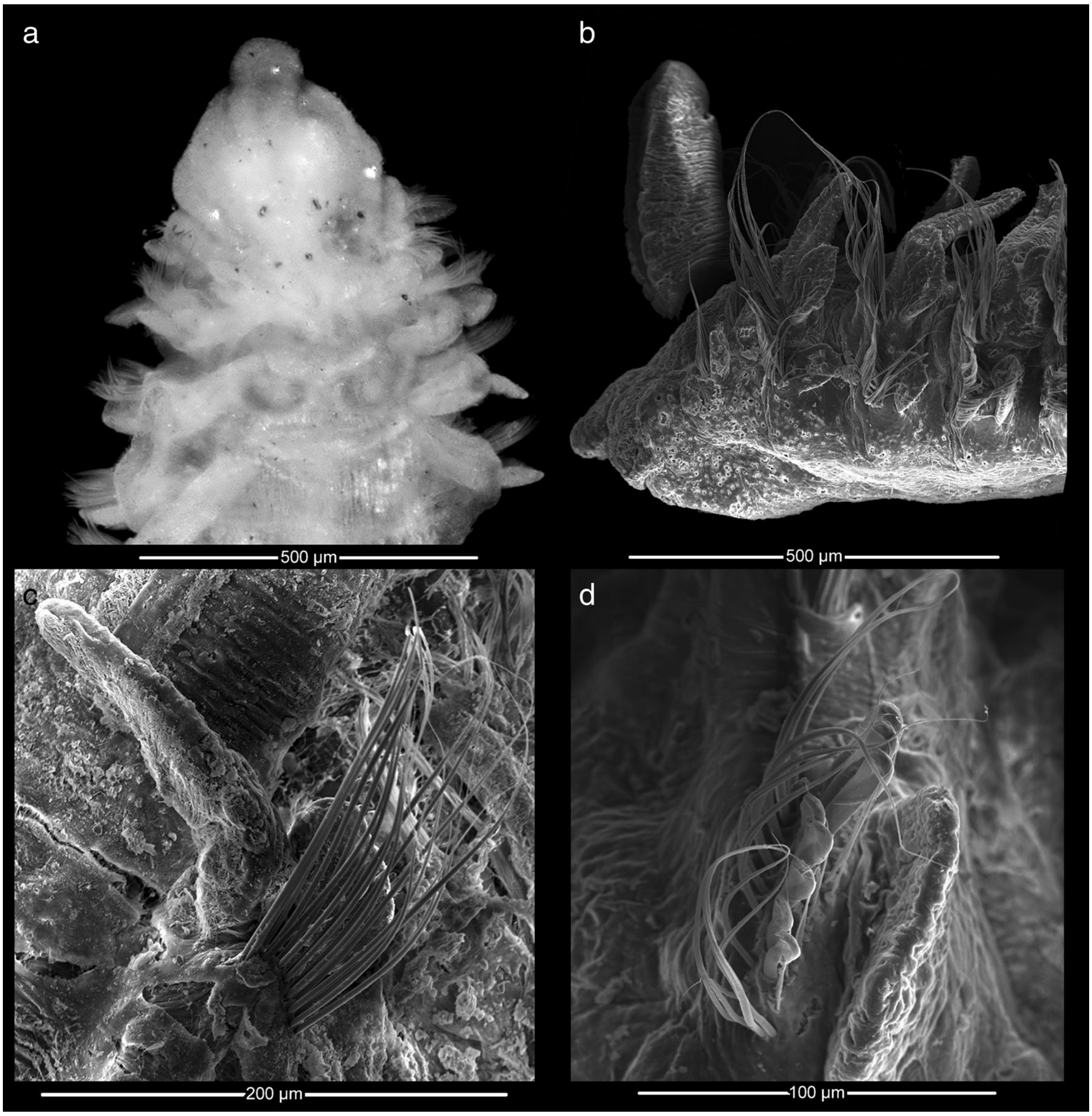


Fig. 4 *Spio martinensis* Mesnil, 1896: **(a)** anterior end, dorsal view (stereomicroscope); **(b)** anterior end, lateral view (SEM); **(c)** notopodium from chaetiger 16 (SEM); **(d)** neuropodium from chaetiger 14 (SEM)

Nuchal organs J-shaped, lateral ciliary bands extend posteriorly to the middle of chaetiger 3 (Fig. 4a); evident interruption of median ciliary band by the transversal ciliary band of chaetiger 2 (Fig. 4a); metameric dorsal ciliated organs double-paired, visible from chaetiger 5.

Branchiae from chaetiger 1, continuing almost end of the body, only the last four chaetigers without branchiae; branchiae on first chaetiger slightly shorter than those on the following chaetigers; branchiae cirriform with broad base in the anterior chaetiger, slightly tapered distally, becoming thinner and shorter posteriorly; branchiae on the anterior chaetigers almost reaching the dorsal midline; branchiae on the anterior chaetigers basally fused with notopodial postchaetal lamellae (Fig. 4c), distinctly separated from the postchaetal lamellae from chaetiger 20 until the last branchiate chaetiger.

First notopodium slightly shifted dorsally. Notopodial postchaetal lamellae on anterior chaetigers oval (Fig. 4b), becoming shorter thereafter (Fig. 4c), elongated in posterior chaetigers; neuropodial postchaetal lamellae shorter than notopodial postchaetal lamellae (Fig. 4b); oval in anterior chaetigers, becoming shorter thereafter, and rounded in posterior chaetigers.

Notopodial chaetae all limbate capillaries; chaetae of anterior chaetigers arranged in two rows of about the same length (Fig. 4b): capillaries of anterior row uniformly granulated, capillaries of posterior row thinner, lacking granulations; additional superior fascicle of very long thin capillaries granulations; capillaries of posterior chaetigers arranged in irregular rows with thin, non-granulated capillaries (Fig. 4c). Neuropodia with rows of capillaries and hooks as well as in inferior fascicle of capillaries; chaetae of anterior neuropodia arranged in two rows as notopodial chaetae; posterior row replaced by a single row of 8 hooded hooks (range 5–8) from chaetiger 13 (exceptionally from chaetiger 14), accompanied by capillaries (Fig. 4d); hooks with visible hood, narrowed subdistally, tridentate, third tooth clearly visible (Fig. 5b); inferior fascicle with two or three long, thin capillaries without granulations, replaced by two or three sabre chaetae from chaetiger 19.

Pygidium with four anal cirri; dorsal pair slender and widely spaced; ventral pair broad and cone-shaped, closely spaced, and touching each other at the base; dorsal pair and ventral pair of the same length.

Pigmentation: highly variable (some specimens without pigmentation); pigmented patches dorsolaterally on anterior chaetigers before and behind transverse ciliary bands; pigment indicates end of nuchal organs; lateral ciliary and median ciliary bands orange; median pigmented patch between the neuro- and notopodia from chaetiger 3 to 9; pigmented patch behind the anterior pair of eyes; indistinct pigment at margin of notopodial lamellae close to the branchiae.

Biology This species is present in different coastal sublittoral habitats, such as fine to medium sands or muddy sands (Dauvin 1989; Bick et al. 2010). In Arcachon Bay, it was found in small to large tidal channels with medium to strong tidal currents, associated to muddy sediments (Table 1).

Distribution *Spio martinensis* is well-represented in European marine waters. This species was recorded from Swedish and Danish fjords (Hannerz 1956; Rasmussen 1973) and from the Dutch coast (Wolff 1973). *S. martinensis* was also found in French coastal waters, from the North Sea to the Atlantic coast (Mesnil 1896; Cabioch et al. 1968; Dauvin 1989), in the Irish Sea (Southern 1914), in British waters (Radashevsky 2012), and on the Spanish coasts (Rioja 1918). Finally, specimens were sampled in the Baltic and North Seas (Bergfeld and Kröncke 2003; Bick et al. 2010).

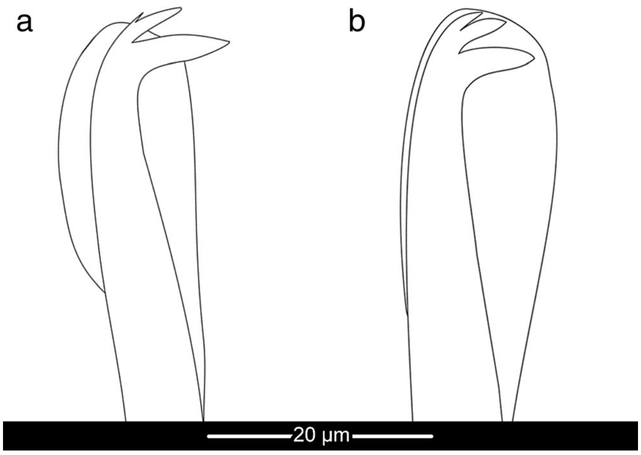


Fig. 5 Drawings of neuropodial hooded hook of **(a)** *Spio symphyta* (chaetiger 13) and **(b)** *Spio martinensis* (chaetiger 16)

Remarks The specimens from Arcachon Bay are in good agreement with the original description.

Discussion

This study presents the first record of *Spio martinensis* in Arcachon Bay, and most importantly, the first record of *S. symphyta* outside the North Sea, where the type locality of the species is situated.

From 1960 to 1990, all *Spio* spp. sampled in Arcachon Bay were identified as *Spio filicornis* (Boisseau 1962; Cazaux 1973; Auby 1991) until the publication of Dauvin (1989), who confirmed the probable confusion between *S. filicornis* and *S. decoratus*. In accordance with this paper, from 1990 to 2010, *Spio* specimens found in the lagoon were identified as *S. decoratus* (Bachelet and Dauvin 1993; Bachelet et al. 1996; Blanchet et al. 2005). Recent publications by Bick et al. (2010) and Meißner et al. (2011) fixed the identity of selected *Spio* spp. from European waters and now allow their safe identification. This eventually revealed the presence of three *Spio* species in the bay: *S. decoratus*, *S. martinensis* and *S. symphyta*. *Spio martinensis* is easily distinguished from other French *Spio* species by the presence of hooded hooks from chaetiger 13 or 14. In *S. symphyta*, hooded hooks start on chaetiger 11 (rarely 10), and a fusion of the prostomium and peristomium is observed. *S. decoratus* is very similar to *S. symphyta*, as tridentate hooks also start on chaetiger 11, but the prostomium and peristomium are not fused, and a furrow is instead present between the prostomium and the peristomium. The uppermost tooth of the tridentate hooded hook in *S. martinensis* and *S. decoratus* is easily discernable, but hardly visible in *S. symphyta*. Meißner et al. (2011) suggested that *S. symphyta* was not restricted to the North Sea and could be present in adjacent waters. Our results confirm that this species is probably common in coastal European waters. Due to the similarity of this species with *S. decoratus*, its absence in other areas could be more related to its non-detection by marine biologists than to its real absence in other ecosystems. *S. martinensis* shows a large biogeographic repartition along the French coasts, except in the Mediterranean Sea (Dauvin 1989; RESOMAR database).

Two additional *Spio* spp. are reported to occur in French waters: *S. multioculata* (Dauvin and Gentil 1980; RESOMAR database) and *S. filicornis* (Auby 1991; Hily and Bouteille 1999; Thorin et al. 2001; RESOMAR database).

S. multioculata is easily distinguished from its congeners by the presence of two groups of indistinct eyes and the presence of bidentate hooded hooks from chaetigers 28-32. The presence of *S. filicornis* in French waters is highly questionable. According to the literature, *Spio filicornis* was frequently found all over Europe in the 1960-1990s, but was probably misidentified and is now subjected to taxonomic discussion (see Dauvin 1989; Meißner et al. 2011). This species could now be considered a true Arctic species, so far only reported from West Greenland (Meißner et al. 2011).

In conclusion, routine benthic surveys are an important tool for monitoring the distribution of species. However, to deal with a specimen in-depth requires time and resources, especially with complex taxa like Spionidae. The deposition of specimens in a reference collection should be considered to allow a re-evaluation of identifications if new insights into the taxonomy are gained. New articles on the taxonomy, biodiversity, or biogeography of species occurring in European waters are welcomed by a broad audience although the fauna seems well-known. In addition, in the context of climate change and change of the environment due to human activity, the faunal composition cannot be expected to be static. The present study emphasizes that it is vital for a biologist to call into question and to be up-to-date with recent literature.

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References

Auby I (1991) Contribution à l'étude des herbiers de *Zostera noltii* dans le Bassin d'Arcachon: dynamique, production et dégradation, macrofaune associée. PhD thesis, University of Bordeaux 1, France

Bachelet G, Dauvin JC (1993) Distribution quantitative de la macrofaune benthique des sables intertidaux du bassin d'Arcachon. Oceanol Acta 16:83–97

Bachelet G, de Montaudouin X, Dauvin JC (1996) The quantitative distribution of subtidal macrozoobenthic assemblages in Arcachon Bay in relation to environmental factors: a multivariate analysis. Estuar Coast Shelf Sci 42:371–391

Bergfeld C, Kröncke I (2003) *Spio martinensis* MESNIL, 1896 (Polychaeta, Spionidae): Not a new record in German coastal waters of the North Sea. Senckenbergiana Marit 32:25–33

Bick A, Otte K, Meißner K (2010) A contribution to the taxonomy of *Spio* (Spionidae, Polychaeta, Annelida) occurring in the North and Baltic Seas, with a key to species recorded in this area. Mar Biodiv 40:161–180

Bick A, Meißner K (2011) Redescription of four species of *Spio* and *Microspio* (Polychaeta, Spionidae) from the Kuril Islands and Peter the Great Bay, northwest Pacific. Zootaxa 2968:39–56

Blanchet H, de Montaudouin X, Chardy P, Bachelet G (2005) Structuring factors and recent changes in subtidal macrozoobenthic communities of a coastal lagoon, Arcachon Bay (France). Estuar Coast Shelf Sci 64:561–576

Böggemann M (1997) Polychaeten aus der Deutschen Bucht - Taxonomische Bearbeitung und Dokumentation der vom Forschungsinstitut Senckenberg hauptsächlich in der Deutschen Bucht gesammelten Polychaeten. Cour Forsch Inst Senck 202:1–315

Boisseau J (1962) Contribution à la faune du Bassin d'Arcachon. Annélides, Sipunculiens, Echiuriens. P-v Soc Linn Bordeaux 99: 113–126

Bobretzky NV (1870) Materialy dlja fauny Tschernovo Morya. Annelidy (Annelida, Polychaeta). Zapisy Kievskovo Obshestva Estestroispytatelej 1:188–274

Cabioch L, L'Hardy JP, Rullier F (1968) Inventaire de la faune marine de Roscoff. Trav Stn Biol Roscoff 17:1–95

Cazaux C (1973) Cycle et distribution des larves de Polychètes; caractères du méroplancton des différents types de masses d'eaux du Bassin d'Arcachon. Bull Ecol 4:257–275

Dauvin JC (1989) Sur la présence de *Spio decoratus* Bobretzky 1871 en Manche et remarques sur *Spio martinensis* Mesnil 1896 et *Spio filicornis* (O.F. Müller, 1776). Cah Biol Mar 30:167–180

Dauvin JC, Gentil F (1980) Nouvelles espèces pour l'Inventaire de la Faune Marine de Roscoff: annélides polychètes et crustacés amphipodes. Trav Sta Biol Roscoff 26:5–10

Hannerz L (1956) Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). Zool Bidr Uppsala 31:1–204

Hily C, Bouteille M (1999) Modifications of the specific diversity and feeding guilds in an intertidal sediment colonized by an eelgrass meadow (*Zostera marina*) (Brittany, France). CR Acad Sci Paris Sciences de la vie 322:1121–1131

Hornemann JW (1832) Flora danica. Havniae 35:2041–2060

Linnaeus C (1753) Species plantarum, exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Stockholm

Meißner K, Bick A, Bastrop R (2011) On the identity of *Spio filicornis* (O.F. Müller, 1776)—with the designation of a neotype, and the description of two new species from the North East Atlantic Ocean based on morphological and genetic studies. Zootaxa 2815:1–27

Mesnil F (1896) Etudes de morphologie externe chez les Annélides. Les Spionidiens des côtes de la Manche. Bull Sci Fr Belg 29: 110–287

Müller OF (1776) Zoologicae Dnicae Prodomus, seu Animalium Danie et Norvegiae indigenarum characters, nomina et synonyma imprimis popularium. Hallageriis, Copenhagen

Plus M, Dalloyau S, Trut G, Auby I, de Montaudouin X, Emery E, Noël C, 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

Radashevsky VI (2012) Spionidae (Annelida) from shallow waters around the British Islands: an identification guide for the NMBAQC Scheme with an overview of spionid morphology and biology. Zootaxa 3152:1–35

Rasmussen E (1973) Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11:1–507

Rioja E (1918) Adiciones a la fauna de Anélidos Poliquetos del Cantábrico. Rev R Acad Cienc Exact Fis Nat Madrid 17:54–79

Sikorski AV (2001) Spionidae Grube, 1850. In: Jirkov IA (ed) Polychaeta of the Arctic Ocean. Yanus – K Press, Moscow, pp 271–332

Southern R (1914) Archiannelida and Polychaeta. Proc R Irish Acad Dublin 31:1–160

Thorin S, Radureau A, Feuteun E, Lefeuvre JC (2001) Preliminary results on a high east-west gradient in the macrozoobenthic community structure of the macrotidal Mont Saint-Michel bay. Cont Shelf Res 21:2167–2183

Thunberg CP (1793) Tekning och Beskrifning på en stor Ostronsort ifrån Japan. Kongl Vetenskaps Acad Nya Handl 14:140–142

Wolff WJ (1973) The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zool Verh 126:1–242

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Rapid Communication CORRECTED PROOF

First record of *Naineris setosa* (Verrill, 1900) (Annelida: Polychaeta: Orbiniidae) in the Western Mediterranean Sea

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Abstract

The Polychaeta *Naineris setosa* (Verrill, 1900) is reported for the first time in the Western Mediterranen Sea. Several specimens were collected in 2012 and 2013 in Boughrara Lagoon (Tunisia). The vector of introduction of *N. setosa* likely commercial shipping because Gabes is an international harbour with dense shipping traffic. A detailed description of specimens from Boughrara Lagoon is provided in this paper.

Key words: alien species, polychaete, Tunisia, Lagoon of Boughrara

Introduction

Introduction of new species is one the major factor affecting biodiversity in the Mediterranean Sea in the past few decades. At least 986 alien species are known in the Mediterranean, 775 in the eastern basin, 308 in the western basin, 249 in the central basin, and 190 in the Adriatic Sea. These alien species represent 5.9% of the total biodiversity (Zenetos et al. 2010, 2011, 2012). In the light of its geographic position, between western and eastern basins, the coasts of Tunisia appear to be very sensitive to colonization by exotic species. To date, 124 marine invasive alien species have been recorded along the Tunisian coastline, of which 11 are polychaetes (UNEP-MAP-RAC/SPA 2013).

Six species of Orbiniidae (Polychaeta) are known to occur in the coastal waters of Tunisia. *Naineris laevigata* (Grube, 1855) was reported for the first time in 1978 in the Gulf of Tunis (Cantone et al. 1978) and in the lagoon of Monastir (Mortier, 1978). *Phylo foetida* (Claparède, 1869) was reported in 1924 in Boughrara Lagoon (Fauvel, 1924). *Orbinia sertulata* (Savigny, 1822) and *Protoaricia oerstedii* (Claparède, 1864) were found in 1978 in the Gulf of Tunis (Cantone et al. 1978). *Scoloplos (Scoloplos) armiger* (Müller, 1776) was found in the Gulf of Gabes in 1934 (Seurat 1934), and finally *Scolaricia typica* (Eisig, 1914) was described for the first time in Tunis Bay in 2003 (Ayari and Afli 2003, 2008).

The orbiniid Polychaete *Naineris setosa* (Verrill, 1900) is considered to be a subtropical-tropical American species (Blake and Giangrande 2011). The species described as *Aricia setosa* by Verrill (1900) from an intertidal beach in Bermuda is distributed in Puerto Rico (Treadwell 1901), Florida (Hartman 1951) and the Gulf of Mexico (Rioja 1960; Perkins and Savage 1975; Hernandez-Alcantara and Solis-Weiss 1989). The first Eastern Pacific record was from Acapulco (Mexico) (Hartman 1957). *N. setosa* is also present in Costa Rica, Ecuador (Galapagos Islands) (Blake and Giangrande 2011), Belize (Solis-Weiss and Fauchald 1989) and Brazil (Rizzo and Amaral 2001). Recently, *N. setosa* was reported for the first time outside its native area, in aquaculture facility near Brindisi (Adriatic Sea, Italy) (Black and Giangrande 2011). However, this species was not included in the updated list of alien species for the Mediterranean Sea

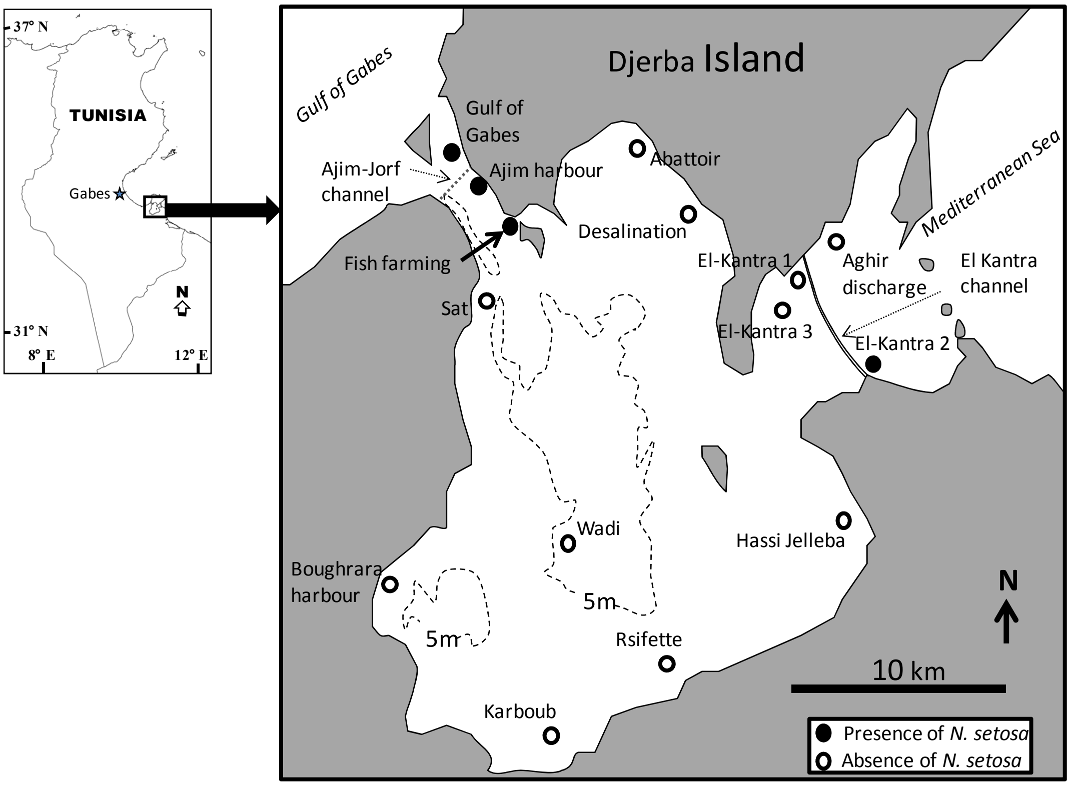

Figure 1. Presence and absence of *Naineris setosa* in Boughrara lagoon.

because, after being one of the most abundant polychaetes (500 ind.m^{-2}), this species disappeared from the area (Zenetos et al. 2012). The present paper reports the first record of *N. setosa* along the Tunisian coasts.

Material and methods

Study area

The Lagoon of Boughrara is located on the south-eastern coast of Tunisia. This small bay (about 500 km^2) is bounded on the north by the Djerba Island and on the south by the mainland. The bay connects with the Gulf of Gabes by the Ajim-Jorf channel (2.2 km wide) and by the El Kantra Channel (160 m wide) (Figure 1). The average depth is about 4 m with a maximum of 16 m in the center of the lagoon. The salinity is very high especially in summer with an average value up to 42 (Ben Aoun et al. 2007). Boughrara Lagoon is a vulnerable environment with limited access to open sea and is submitted to negative effects of aquaculture activities, fishing ports, sewage outfalls, and industrial wastes (organic matter, fluorides, cadmium, acids, etc.) (Ben Aoun et al. 2007).

This study was conducted within the framework of a National Institute of the Sciences and the Technologies of the Sea (INSTM) project and aimed to evaluate the general ecological status of the Lagoon of Boughrara.

Material examined

Benthic macrofauna was sampled from 15 stations in Boughrara Lagoon between 2012 and 2013 during summer (August) and winter (January) seasons (Figure 1, Appendix 1). Samples were collected by scuba divers with a quadrat (1 m^2, 10 cm depth) and sieved through 1 mm mesh. The remaining fraction was fixed in 7% formalin and later transferred into 70% ethanol. All specimens were examined under a Nikon SMZ1500 stereo-microscope and one specimen photographed with a Nikon DS-Fi 2 camera. Specimens were measured with the NIS-Elements Analysis software (Nikon Instruments Inc., Melville, New York, USA).

Results

Fifty specimens of *Naineris setosa* were collected in 2012–2013 from four different sites in the Boughrara Lagoon (Figure 1, Appendix 1). This species displayed highest abundances in summer at stations "Ajim Harbour" and "Gulf of Gabes" with 21 and 19 individuals m^{-2}, respectively. Abundances were lower in winter (max 6 ind.m^{-2}). *N. setosa* was always collected from in muddy sediments.

Systematics

ORBINIIDAE Hartman, 1942
Orbiniinae Hartman, 1957
Naineris Blainville, 1828
Naineris setosa (Verrill, 1900)
Figure 2

Aricia setosa Verrill, 1900: 651-653
Anthostoma latacapitata Treadwell, 1901: 203–205, figs 61–65.

Naineris setosa Hartman, 1942: 61, figs 116–118; 1951: 67–70, pl. 17, figs 1–6; Hartman 1957: 305, pl. 41, figs 1–6; Solis-Weiss and Fauchald 1989: 774–778, fig 2; Blake and Giangrande 2011: 21, figs. 1–2.

Material examined

Western Mediterranean Sea: Tunisia: lagoon of Boughrara (10°40' to 10°57' E; 33°28' to 33°45' N; station Gulf of Gabes; 12 August 2012; 1.1 m depth; 5 specimens).

Description

Incomplete specimens with 40–87 setigers and 3.6–4.7mm width. Prostomium short, broadly truncate and T-shaped (Figure 2); few eyespots, concentrated in two comma groups forming Y-shaped. Everted proboscis large and saclike. Peristomium broad and asetigerous.

Branchiae from setigers 6 in all specimens; basally broader and gradually tapering to pointed tip; anteriorly, branchiae and notopodial postsetal lobes are similar in length but posteriorly the branchiae are longer than notopodial lobes. External borders highly ciliated with blood sinus clearly visible.

Two sensory organs present from setigers 8, small, oval-shaped, located in antero margin of setiger; very close to the branchiae in anterior setigers.

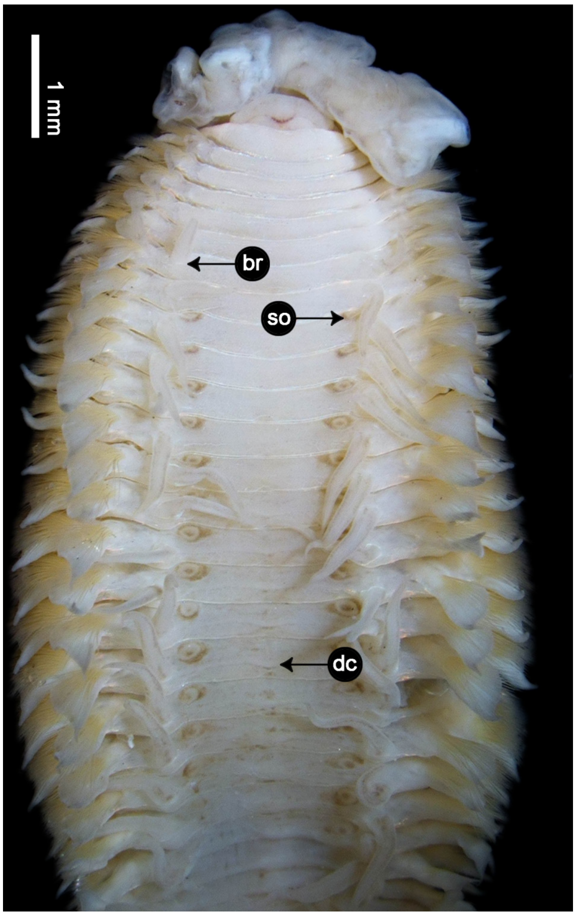

Figure 2. *Naineris setosa*: dorsal view of a specimen from Boughrara lagoon. Abbreviations: br: branchia; so: sensory organ; dc: dorsal crest. Photograph by P. Bonifácio.

Dorsal crests small, started in the thoracic region until posterior setigers, more conspicuous in abdominal region.

Thoracic region with 20–21 biramous setigers, with foliaceous and broad notopodial postsetal lobes; neuropodial postsetal shorter, broader and rounder than corresponding notopodial lobes. Neuropodial postsetal lobes with an upper digitiform papilla more evident in anterior setigers. Transitional setigers between 21 and 24.

Abdomen from setiger 25 with narrow notopodial postsetal lobes, becoming short in the posterior abdomen. In parallel, size of neuropodial postsetal lobe sharply reduced and finally tapering to narrow tips.

Thoracic notopodia with long crenulated capillaries setae arranged in 3 rows. Neuropodial thoracic setae are all crenulated capillaries arranged in two bundles: one, with about 8 rows; and two, the lower group, about 4 rows.

In abdomen, the number of setae is more reduced than in the thorax. The notopodia have crenulated capillaries and 1–2 furcate setae (hard to see). The neuropodia with crenulated capillaries and 2–3 straight, bluntly pointed uncini more posteriorly.

Distribution

North-western Atlantic: Gulf of Mexico (Perkins and Savage 1975; Hernandez-Alcantara and Solis-Weiss 1991); Puerto Rico (Treadwell 1901), Acapulco, Mexico (Hartman 1957); Belize (Solis-Weiss and Fauchald, 1989), south-eastern Brazil (Rizzo and Amaral 2001). Mediterranean: Adriatic Sea, Italy (Blake and Giangrande 2011) and western Mediterranean, lagoon of Boughrara, Tunisia (this study).

Type locality

Bermuda

Remarks:

In Mediterranean Sea, only two species of *Naineris* are recorded: *N. laevigata* (Grube, 1855) distributed apparently from Italy to south of France (Fauvel, 1927), and *N. setosa* (Verrill, 1900) from the Adriatic Sea, Italy (Blake and Giangrande, 2011). The main difference between the two species is that *N. laevigata* presents subuluncini in thoracic neuropodia, whereas *N. setosa* presents only crenulated capillaries (Fauvel 1927; Blake 1996; Solis-Weiss and Fauchald 1989; Blake and Giangrande 2011). Furthermore, the prostomium of *N. laevigata* is rounded and the branchiae appears often from setigers 7 or 8 (Fauvel, 1927). Specimens found in this study agree with description of *N. setosa* from Solis-Weiss and Fauchald (1989) and Blake and Giangrande (2011) with presence of prostomium broadly truncated, branchiae appearing on setiger 6 and presence of crenulated capillaries only in thoracic neuropodia.

Among the material examined by Solis-Weiss and Fauchald (1989), variations were found: prostomium rounded or T-shaped; eyesposts scattered or ranged in two or four sickles; 13 or 23 thoracic setigers; and thoracic neurosetae ranged in one or two bundles. All these characteristics appear to be correlated with animal age (Solis-Weiss and Fauchald 1989; Blake and Giangrande 2011). In accordance with these characteristics, animals found in this study are adults: prostomium T-shaped, few eyespots ranged in two sickles, 21 thoracic setigers and thoracic neurosetae ranged in two bundles.

Discussion

The vector of introduction of *Naineris setosa* in the Lagoon of Boughrara cannot be easily determined. According to the Mediterranean Action Plan for Invasive species (UNEP-MAP-RAC/SPA 2005) and in agreement with recent evaluation of pathways at Pan European Level (Katsanevakis et al. 2013), shipping (ballast water and sediments, anchoring, and fouling) is the second main vector of species introduction into the Mediterranean Sea after migration across the Suez Canal. *N. setosa* is probably not a Lesseptian species as this polychaeta is *a priori* not present in the Indo-Pacific region. Blake and Giangrande (2011) suggested that *N. setosa* was introduced in Italy via aquaculture. Despite the presence of two fish farms in the Boughrara Lagoon, this way of introduction may be dismissed because of the origin of the cultivated fishes: Tunisia, Republic of the Philippines, and France. As *N. setosa* was collected in four sites directly connected to the Gulf of Gabes, transport via ship hulls or ballast waters has been hypothesized. Indeed, Gabes is an international harbour with a favoured place in the middle of the Mediterranean Sea, between the oriental and occidental basins. It receives a great deal of traffic from Europe (mainly from Italy), Asia, the USA, and Mexico and is classified among the main harbours for ships carrying crude oil in the Mediterranean Sea. Indeed, there is extensive traffic of crude oil between Italy and Tunisia frequent contact between Brindisi in Italy (where *N. setosa* occurs; Blake and Giangrande 2011) and Skrika in the Gulf of Gabes. Even if maritime transport seems to be the most likely vector of introduction of this species in the Lagoon of Boughrara, it is difficult to identify the exact origin of *N. setosa* which could arrive either directly from the western Atlantic (USA, Mexico) or as a result of secondary spread from Italy.

Naineris setosa is clearly tolerant to severely degraded environmental conditions. During this study, specimens were found in four sites classified as polluted: Ajim Harbour supports many fishing activities; the Gulf of Gabes receives industrial waters charged in phosphate; the fish farming site has a heavy aquaculture influence; and El Kantra 2 is perturbed by extension of the pass of El Kantra. These four stations are characterized by high salinity (between 38.5 and 43.1) for both winter and summer seasons, muddy sediments, some areas of anoxic mud (e.g., the Ajim Harbour and fish farming stations), and by polluted waters. Blake and Giangrande (2011) indicated that the existence of the dorsal crests on the abdomen of *N. setosa* is atypical and is perhaps an adaptation, with the very vascularised branchiae, to low oxygen levels in the sediments.

With the extensive levels of intra-Mediterranean shipping traffic, *Naineris setosa* might be present in other Mediterranean harbours. As the Mediterranean Sea connects naturally with the Atlantic Ocean through the Strait of Gibraltar and with the Black Sea by the straits of Bosphorus and the Dardanelles, the presence of this species in other adjacent areas should be watched closely. Finally, the impact of non-indigenous species on the native ecosystem can be significant and may be extremely damaging to native species, local environment, and human activities (Lavesque et al. 2010). Further studies will be necessary to evaluate the major factors driving the spread of *N. setosa* in the Gulf of Gabes and to understand the consequences of its presence on the structure of benthic communities.

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References

Ayari R, Afli A (2003) Bionomie benthique du petit golfe de Tunis. *Bulletin de l'Institut National des Sciences et Technologie de la Mer de Salammbô* 30: 79–87

Ayari R, Afli A (2008) Functional groups to establish the ecological quality of soft benthic fauna within Tunis Bay (Western Mediterranean). *Vie et Milieu* 58: 67–75

Ben Aoun Z, Farhat F, Chouba L, Hadj-Ali MS (2007) Investigation on possible chemical pollution of the Boughrara lagoon, South of Tunisia, by chemical wastes. *Bulletin de l'Institut National des Sciences et Technologies de la Mer de Salammbô* 34: 119–127

Blake JA (1996) Chapter 1. Family Orbiniidae Hartman, 1942. In: Blake JA, Hilbig B, Scott PH (eds), Taxonomic atlas of the Santa Maria Basin Western Santa Barbara Channel. Vol 6. Annelida part 3. Polychaeta: Orbiniidae to Cossuridae. Santa Barbara, CA: Santa Barbara Museum of Natural History, pp 1–26, http://dx.doi.org/10.1080/11250003.2011.577982

Blake JA, Giangrande A (2011) *Naineris setosa* (Verrill) (Polychaeta, Orbiniidae), an American subtropical-tropical polychaete collected from an aquaculture facility in Brindisi (Adriatic Sea, Italy): A possible alien species. *Italian Journal of Zoology* 78: 20–26

Cantone G, Fassari G, Brigandi S (1978) Ricerche sui Polycheti della Tunisia. *Animalia* 5: 51–78

Fauvel P (1924) Sur *l'Aricia foetida Claparède et ses variétés. Bulletin de la Société Zoologique de France* 49: 518–528

Fauvel P (1927) Faune de France, Polychètes Sédentaires. Office Central de Faunistique, Paris, France, 494 pp

Hartman O (1951) The littoral marine annelids of the Gulf of Mexico. *Publications of the Institue of Marine Science* 2: 7–124

Hartman O (1957) Orbiniidae, Apistobranchidae, Paraonidae, and Longosomidae. *Allan Hancock Pacific Expeditions* 15: 183–393, plates 21-44

Hernandez-Alcantara PH, Solis-Weiss V (1991) Ecological aspects of the polychaete populations associated with the Red Mangrove *Rhizophora mangle* at Laguna de Terminos, southern part of the Gulf of Mexico. Proceedings of the 2nd International Polychaete Conference, Copenhagen 1986. *Ophelia* Supplement 5: 451–462

Katsanevakis S, Zenetos A, Belchior C, Cardoso AC (2013). Invading European Seas: assessing pathways of introduction of marine aliens. *Ocean and Coastal Management* 76: 64–74, http://dx.doi.org/10.1016/j.ocecoaman.2013.02.024

Lavesque N, Bachelet G, Béguer M, Girardin M, Lepage M, Blanchet H, Sorbe JC, Modéran J, Sauriau PG, Auby I (2010) Recent expansion of the oriental shrimp *Palameon macrodactylus* (Crustacea: Decapoda) on the western coasts of France. *Aquatic Invasions Records* 5: 103–108, http://dx.doi.org/10.3391/ai.2010.5.S1.021

Mortier M (1978) Première approche dans l'étude du macro-benthos de la lagune de Monastir, Tunisie. PhD Thesis, Université d'Aix-Marseille II, Marseille, France, 78 pp

Perkins TH, Savage T (1975) A bibliography and checklist of polychaetous annelids of Florida, the Gulf of Mexico, and the Caribbean Region. *Florida Marine Research Publications* 14: 1–62

Rioja E (1960) Estudios anelidologicos.XXIV. Adiciones a la fauna de Anelidos Poliquetos de las costas orientales de Mexico. *Anales de l Instituto de Biologica, México* 31: 289–316

Rizzo AE, Amaral AC (2001) Environmental variables and intertidal beach annelids of São Sebastião Channel (State of São Paulo, Brazil). *Revista De Biologia Tropical* 49: 849–857

Seurat LG (1934) Formations littorales et estuaires de la Syrte Mineure (Golfe de Gabès). *Bulletin de la Station Océanographique, Salammbô* 32: 1–65

Solis-Weiss V, Fauchald K (1989) Orbiniidae (Annelida: Polychaeta) from Mangrove root-mats in Belize, with a revision of the protoariciin genera. *Proceedings of the Biological Society of Washington* 102: 772–792

Treadwell AL (1901) The polychaetous annelids of Porto Rico. *Bulletin of the United States Fisheries Commission* 20: 181–210

UNEP-MAP-RAC/SPA (2005) Action Plan concerning species introductions and invasive species in the Mediterranean Sea . RAC/SPA (Ed.), Tunis, 30 pp

UNEP-MAP-RAC/SPA (2013) Marine Mediterranean Invasive Alien Species (MAMIAS), http://www.mamias.org

Verrill AE (1900) Additions to the Turbellaria, Nemertina, and Annelida of the Bermudas. *Transactions of the Connecticut Academy of Arts and Sciences* 10: 595–671

Zenetos A , Gofas S, Verlaque M, Cinar ME, Garcia Raso JE, Bianchi N, Morri C, Azzurro E, Bilecenoglu M, Froglia C, Siokou I, Violanti D, Sfriso A, San Martin G, Giangrande A, Katagan T, Ballesteros E, Ramos-Espla A, Mastrototaro F, Ocana O, Zingone A, Gambi MC, Streftaris N (2010) Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* 11: 381–493

Zenetos A, Gofas S, Verlaque M, Çinar ME, Garcia Raso JE, Bianchi CN, Morri C, Azzurro E, Bilecenoglu M, Froglia C, Siokou I, Violanti D, Sfriso A, Saint Martin G, Giangrande A, Katagan T, Ballesteros E, Ramos Espla A, Mastrototaro F, Ocana O, Zingone E, Gambi MC, Streftaris N (2011) Errata to the review article (Medit. Mar. Sci., 11 (2): 318-493). Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union’s Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science* 12: 509–514, http://dx.doi.org/10.12681/mms.87

Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, Garcia-Raso JE, Cinar ME, Almogi-Labin A, Ates AS, Azzurro E, Ballesteros E, Bianchi CN, Bilecenoglu M, Gambi MC, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle PK, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Panucci-Papadopoulou MA, Ramos Espla A, Salas C, Saint Martin G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union’s Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science* 13 (2): 328–352

Appendix 1. Records of *Naineris setosa* in the lagoon of Boughrara. N: number of individuals collected. Sites: see Figure 1.

Sites	Date	Tidal level (m)	Habitat	Latitude	Longitude	Salinity (PSU)	N
Gulf of Gabes	August 2012	1.1	Mud	33°43'N	10°44'E	41.5	19
	January 2013	1.1	Mud	33°43'N	10°44'E	41.1	1
Ajim Harbour	August 2012	1	Anoxic mud	33°42'N	10°44'E	42.3	21
	January 2013	1	Anoxic mud	33°42'N	10°44'E	41.9	1
Fish Farming	August 2012	1.5	Anoxic mud	33°41'N	10°45'E	43.1	2
El Kantra 2	January 2013	0.3	Mud	33°37'N	10°56'E	38.5	6

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Rapid Communication

Recent discovery of *Paranthura japonica* Richardson, 1909 (Crustacea: Isopoda: Paranthuridae) in European marine waters (Arcachon Bay, Bay of Biscay)

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Abstract

The Asiatic isopod *Paranthura japonica* Richardson, 1909 was collected in 2007 in Arcachon Bay (SW France), where the species occurs in a variety of habitats, both in the intertidal and at shallow depths. This species, native to the Sea of Japan, may have been accidentally introduced in Arcachon Bay with oyster transfers or as fouling on ship hulls.

Key words: *Paranthura japonica*; Isopoda; exotic species; Arcachon Bay; oyster transfers; fouling

Introduction

Only three *Paranthura* species (Crustacea: Isopoda: Paranthuridae) are known to occur in coastal Atlantic European waters: *P. costana* Bate & Westwood, 1866, from the Shetland Islands to Morocco (0–355 m depth), *P. nigropunctata* (Lucas, 1846), from the English Channel to Mauritania (0–84 m depth) (Junoy and Castelló 2003) and *P. santiparrai* Frutos, Sorbe & Junoy, 2011 recently described from the 'El Cachucho' Marine Protected Area, southern Bay of Biscay (498–817 m depth). The Asiatic species *Paranthura japonica* Richardson, 1909 was first described from a single female specimen collected in 1906 by the US steamer *Albatross* on the shore of Muroran (Hokkaido Island, Japan). At present, its known distribution includes many localities (0–15 m depth) from northern and southern coasts of Japan (Yamada et al. 2007; Nunomura, pers. comm.), eastern Russia (Nunomura 1975, 1977), and eastern China (Ong Che and Morton 1991; Li 2003; Zhang et al. 2009; Wang et al. 2010). Outside its native area, this species has been recorded in San Francisco Bay in 1993 (Cohen and Carlton 1995) and in Southern California in 2000 (Cohen et al. 2005) and is recognized as an exotic species in California (Ruiz et al. 2011). This paper reports the discovery of *P. japonica* in European marine waters (Arcachon Bay, SW France).

Material and methods

Study area

Arcachon Bay is a 180-km² macrotidal (maximum tidal range: 4.9 m) coastal lagoon situated on the south-western coast of France (Figure 1). This lagoon connects with the Atlantic Ocean by a narrow channel and receives freshwater inputs in its south-eastern part (Leyre River). It is characterised 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).

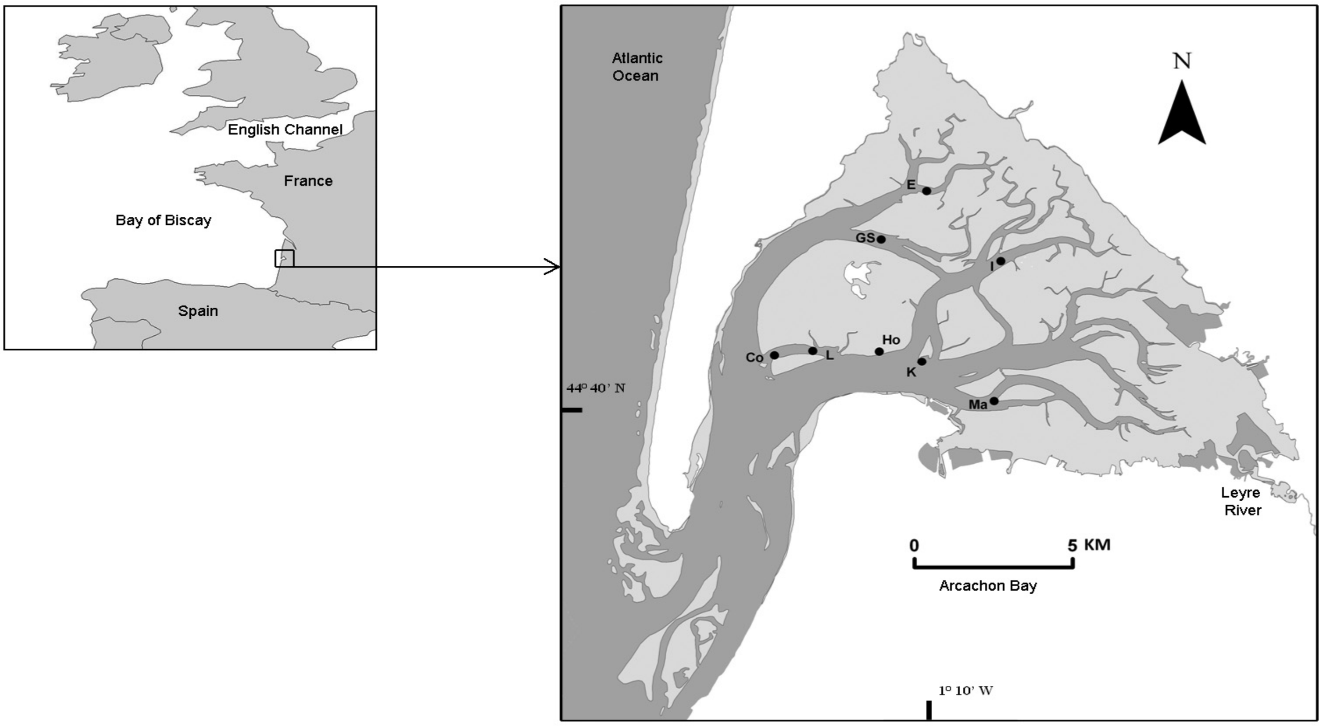

Figure 1. Stations where the benthic anthurid isopod *Paranthura japonica* was collected in Arcachon Bay.

Material examined

During surveys carried out between 2007 and 2010, *Paranthura japonica* was collected in several stations in Arcachon Bay (Figure 1). Bottom sediments were collected using a Van Veen grab in subtidal habitats or a hand-corer in intertidal habitats. These specimens (Figure 2) were compared to *P. japonica* specimens stored in the Muséum National d'Histoire Naturelle, Paris (Gurjanova leg, 1934, MNHN-IU-2009-45, Petrov Island, Sea of Japan) and in the Toyama Science Museum, Japan (Japanese specimens collected in the Toyama and Mutsu Bays, Honshu; N. Nunomura, Osaka Museum, pers. comm.). All specimens were examined under a Nikon SMZ 1500 stereomicroscope, photographed with a Nikon DS-Fi 2 camera and an image of one specimen drawn with a Wacom Intuos 5 tablet and the Inkscape software. Total length TL was measured with the NIS-Elements Analysis software from the cephalon anterior margin to the telson apex. Five specimens from Arcachon Bay (Station K) were deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN-IU-2012-1359).

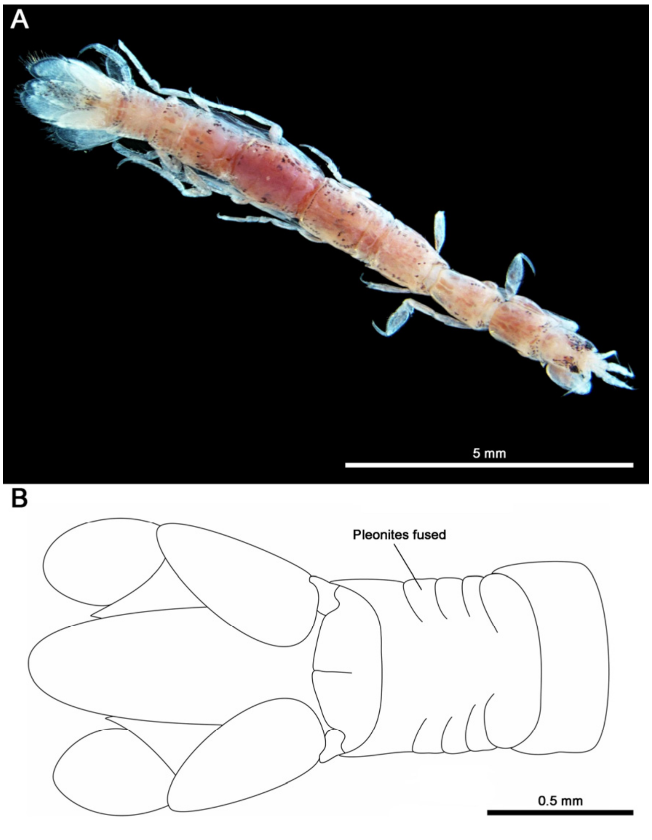

Figure 2. *Paranthura japonica*: (A) dorsal view of a specimen from Arcachon Bay, SW France (TL = 11.03 mm) (photograph by Benoit Gouillieux), (B) diagram of dorsal posterior part (setae not drawn), showing pleonites mediodorsally fused.

Results

We collected 35 specimens of *P. japonica* from a variety of habitats in Arcachon Bay: 22 individuals in mussel beds (stations Ma, Co, K), 2 individuals in intertidal oyster reefs (station Ho), 5 individuals in *Zostera marina* meadows (stations GS, L), 1 individual in a slipper limpet [*Crepidula fornicata* (Linnaeus, 1758)] bed (station I), and 5 specimens in muddy sands (station E) (Figure 1; Appendix 1).

As reported by Frutos et al. (2011), the specimens (males, females and juveniles) from Arcachon Bay can be easily separated from the European *Paranthura* species by the mid-dorsal fusion of their pleonites 1–5 (Figure 2B). Moreover, the comparison with specimens of *P. japonica* from the Sea of Japan revealed similar external morphology, characterized by the following features (and excludes other known Japanese *Paranthura* species, according to the descriptions by Nunomura (1974, 1975, 1977, 1993)): eyes composed of less than 17 ommatidia that are clumped together; short pleotelson barely exceeding the tip of uropods; pereonite 6 shorter than pereonite 5; and anterolateral angles of cephalon exceeding rostral projection. None of the other known *Paranthura* species shows such a combination of morphological characters. Therefore, we concluded that the Arcachon specimens were *P. japonica*.

At first glance, *P. japonica* could be confused with the cosmopolitan *Cyathura carinata* (Krøyer, 1847), a well-known littoral Anthuridae from European coasts, and including muddy fine sediments from Arcachon Bay (Salvat 1967). However, this last species can be distinguished by mouth appendages not acutely produced (a major morphological feature at family level), pleonites 1–5 completely fused, appendix masculina of pleopod 2 bearing distally two flat lobes and a stout anchor-shaped seta, and telson with two dorsal statocysts (see full description in Cléret 1960).

Discussion

The vector of introduction of *Paranthura japonica* in Arcachon Bay is difficult to determine. The natural spread of adult specimens from another location is unlikely for several reasons: (1) the species is known only from its native area (NE Pacific) and California; (2) as a benthic species, it does not seem able to swim over long distances; and (3) the major shipping harbours in SW France are situated far from Arcachon Bay (Bordeaux 200 km, Bayonne 150 km) and separated from the bay by highly dynamic, sandy, shores. Ship's ballast water and fouling have been hypothesized as the way of introduction of *P. japonica* on the Pacific coast of North America (Cohen and Carlton 1995; Cohen et al. 2005). In our opinion transport in ballast waters may be dismissed because of the direct development and the lack of pelagic larvae in Paranthuridae (Frutos et al. 2011), as well as the absence of large commercial ships in Arcachon Bay. Introduction with colonial organisms (e.g. sponges, hydroids, ascidians or bryozoans) fouling the hulls of sailing ships or pleasure boats is a possible vector for *P. japonica*'s entry in Arcachon Bay and was suggested for other isopods such as *Mesanthura* sp. in Italian harbours (Lorenti et al. 2009) and *Synidotea laevidorsalis* (Miers, 1881) on a world-wide scale (Chapman and Carlton 1994).

Accidental introduction with oyster transfers is a likelier hypothesis. Arcachon Bay is one of the major French oyster farming sites with a production of 7,000–8,000 t per year (Scourzic et al. 2011). In the early 1970s, the Portuguese cupped oyster *Crassostrea angulata* (Lamarck, 1819), which was farmed in the bay since the end of the 19th century, was decimated by a viral disease (Goulletquer et al. 2002). To sustain the local oyster industry, the exotic Pacific cupped oyster *C. gigas* was then massively introduced in Arcachon Bay between 1971 and 1975, as spat from Senday Bay, NE Honshu Island, Japan (1,176 t of spat collectors from 1971 to 1975) and as adults from British Columbia, Canada (137.5 t from 1971 to 1973) (Grizel and Héral 1991). Intentional oyster transfer is a well-known vector of accidental introduction for many alien species (Gruet et al. 1976; Verlaque et al. 2007), and may have been be responsible for the introduction of *P. japonica* in Arcachon Bay and was previously documented for other non-native species in this area (Bachelet et al. 2004, 2008). However, no import of cupped oyster from Japan to Arcachon has been officially reported after the 1970s. This means that *P. japonica* may have remained unnoticed in Arcachon Bay since that time, either because it was too rare or misidentified. Alternatively, it could have been introduced with an undeclared oyster transfer from Japan or from another area where this anthurid has not been identified so far.

In Japanese waters, *P. japonica* is associated with subtidal *Zostera* spp. meadows (Nakaoka et al. 2001; Yamada et al. 2007) or with colonies of brown algae *Sargassum* spp. (Nunomura 1977). In Arcachon Bay, it seems to be well established in the whole area, including different locations and habitats, but it remains a rare species with low abundances (see Appendix 1).

P. japonica might be present in other European shellfish farming areas. The transfer of *C. gigas* among regions has caused the introduction and spread of numerous alien species in northern Europe (Goulletquer et al. 2002). The lack of previous records in Europe might be due to the small size of individuals, the low abundance of local populations, or its misidentification (including a possible confusion with *Cyathura carinata*).

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References

Bachelet G, Blanchet H, Cottet M, Dang C, de Montaudouin X, de Moura Queiros A, Gouillieux B, Lavesque N (2008) A round-the-world tour almost completed: first records of the invasive mussel *Musculista senhousia* in the North-east Atlantic (southern Bay of Biscay). *Marine Biodiversity Records* 2, e119, http://dx.doi.org/10.1017/S1755267209001080

Bachelet G, Simon-Bouhet B, Desclaux C, Garcia-Meunier P, Mairesse G, de Montaudouin X, Raigné H, Randriambao K, Sauriau PG, Viard F (2004) Invasion of the eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on resident fauna. *Marine Ecology Progress Series* 276: 147–159, http://dx.doi.org/10.3354/meps276147

Chapman JW, Carlton JT (1994) Predicted discoveries of the introduced isopod *Synidotea laevidorsalis* (Miers, 1881). *Journal of Crustacean Biology* 14: 700–714, http://dx.doi.org/10.2307/1548863

Cléret JJ (1960) Etude de *Cyathura carinata* (Krøyer) (Isopode Anthuridae) 1. Redescription de l'espèce et discussion systématique. *Cahiers de Biologie Marine* 1: 433–452

Cohen AN, Carlton JT (1995) Biological Study. Nonindigenous aquatic species in a United States estuary: A case study of the biological invasions of the San Francisco Bay and Delta. US Fish and Wildlife Service, Washington, DC, 246 pp

Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2005) Rapid Assessment Survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7: 995–1002, http://dx.doi.org/10.1007/s10530-004-3121-1

Frutos I, Sorbe JC, Junoy J (2011) The first blind *Paranthura* species (Crustacea, Isopoda, Paranthuridae) from the 'El Cachucho' Marine Protected Area (Le Danois Bank, southern Bay of Biscay). *Zootaxa* 2971: 17–32

Goulletquer P, Bachelet G, Sauriau PG, Noel P (2002) Open Atlantic coast of Europe - A century of introduced species into French waters. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive aquatic species of Europe. Distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 276–290, http://dx.doi.org/10.1007/978-94-015-9956-6_30

Grizel H, Héral M (1991) Introduction into France of the Japanese oyster (*Crassostrea gigas*). *Journal du Conseil International pour l'Exploration de la Mer* 47: 399–403

Gruet Y, Héral M, Robert JM (1976) Premières observations sur l'introduction de la faune associée au naissain d'huîtres japonaises *Crassostrea gigas* (Thunberg), importé sur la côte atlantique française. *Cahiers de Biologie Marine* 17: 173–184

Junoy J, Castelló J (2003) Catálogo de las especies ibéricas y baleares de isópodos marinos (Crustacea, Isopoda). *Boletín del Instituto Español de Oceanografía* 19: 293–325

Lorenti M, Dappiano M, Gambi MC (2009) Occurrence and ecology of *Mesanthura* (Crustacea: Isopoda: Anthuridea) in two Italian harbours. *Marine Biodiversity Records* 2, e48, http://dx.doi.org/10.1017/S1755267209000542

Li L (2003) Hong Kong's isopods. In: Morton B (ed) Perspectives on marine environment change in Hong Kong and Southern China. Hong Kong University Press, pp 137–166

Nakaoka M, Toyohara T, Matsumasa M (2001) Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. *Marine Ecology* 22: 379–395, http://dx.doi.org/10.1046/j.1439-0485.2001.01726.x

Nunomura N (1974) Marine Isopoda from the coast of Hikigawa Town, Kii Peninsula, middle Japan (1). Bulletin *of the Osaka Museum of Natural History* 28: 1–12

Nunomura N (1975) Marine Isopoda from the rocky shore of Osaka Bay, middle Japan (1). *Bulletin of the Osaka Museum of Natural History* 29: 15–35

Nunomura N (1977) Marine Isopoda from Amakusa, Kyushu (I). *Publications of the Amakusa Marine Biological Laboratory* 4: 71–90

Nunomura N (1993) Marine isopod crustaceans of Seto Inland Sea deposited at the Toyama Science Museum 1. Suborder Anthuridea-1. *Bulletin of the Toyama Science Museum* 16: 15–30

Ong Che RG, Morton B (1991) Spatial and temporal variations in the subtidal macrobenthic community of Tai Tam Bay, Hong Kong. *Asian Marine Biology* 8: 193–216

Plus M, Dalloyau S, Trut G, Auby I, de Montaudouin X, Emery E, Noel C, Viala C (2010) Long-term evolution (1988–2008) of *Zostera* spp. meadows in Arcachon Bay (Bay of Biscay). *Estuarine, Coastal and Shelf Science* 87: 357–366, http://dx.doi.org/10.1016/j.ecss.2010.01.016

Ruiz G, Fofonoff P, Steves B, Dahlstrom A (2011) Marine crustacean invasions in North America: a synthesis of historical records and documented impacts. In: Galil BS, Clark PF, Carlton JT (eds), In the wrong place – Alien marine crustaceans: distribution, biology and impacts. *Invading Nature* 6. Springer, pp 215–250, http://dx.doi.org/10.1007/978-94-007-0591-3_6

Salvat B (1967) La macrofaune carcinologique endogée des sédiments meubles intertidaux (Tanaïdacés, Isopodes et Amphipodes), éthologie, bionomie et cycle biologique. Mémoires du Muséum National d'Histoire Naturelle, Série A, *Zoologie* 15: 1–275

Scourzic T, Loyen M, Fabre E, Tessier A, Dalias N, Trut G, Maurer D, Simonnet B (2011) Evaluation du stock d'huîtres sauvages et en élevage dans le Bassin d'Arcachon. Contrat Agence des Aires Marines Protégées & OCEANIDE, 70 pp

Verlaque M, Boudouresque CF, Mineur F (2007) Oyster transfers as a vector for marine species introductions: a realistic approach based on the macrophytes. In: Impact of mariculture on coastal ecosystems. CIESM Workshop Monographs 32, pp 39–47

Wang CF, Ren XQ, Xu RL (2010) Composition, abundance, and diversity of the Peracarida on different vegetation types in the Qi'ao-Dan'gan Island Mangrove Nature Reserve on Qi'ao Island in the Pearl River estuary, China. *Zoological Studies* 49: 608–615

Yamada K, Hori M, Tanaka Y, Hasegawa N, Nakaoka M (2007) Temporal and spatial macrofauna community changes along a salinity gradient in seagrass meadows of Akkeshi-ko estuary and Akkeshi Bay, northern Japan. *Hydrobiologia* 592: 345–358, http://dx.doi.org/10.1007/s10750-007-0767-6

Zhang J, Hansen PK, Fang J, Wang W, Jiang Z (2009) Assessment of the local environmental impact of intensive marine shellfish and seaweed farming – Application of the MOM system in the Sungo Bay, China. *Aquaculture* 287: 304–310, http://dx.doi.org/10.1016/j.aquaculture.2008.10.008

Appendix 1. Records of the non-indigenous benthic isopod *Paranthura japonica* in Arcachon Bay. N: number of individuals collected. Sites: see Figure 1.

Sites	Date	Habitat	Tidal level (m)	Latitude	Longitude	N
Ho	June 2007	oyster reef	+1	44°40' N	01°10' W	1
Ho	December 2007	oyster reef	+1	44°40' N	01°10' W	1
Ma	October 2008	mussel bed	-3	44°39' N	01°07' W	12
Co	June 2009	mussel bed	-4.7	44°40' N	01°12' W	2
E	September 2009	muddy sands	-3.8	44°43' N	01°09' W	5
GS	September 2009	*Zostera* meadow	-3.9	44°42' N	01°10' W	1
I	September 2009	slipper limpet bed	-4.3	44°42' N	01°07' W	1
K	September 2009	mussel bed	-7.8	44°40' N	01°09' W	5
L	September 2009	*Zostera* meadow	-3.9	44°40' N	01°11' W	4
Ma	October 2010	mussel bed	-3	44°39' N	01°07' W	3