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**ECOLOGIE DES FORAMINIFERES BENTHIQUES
DANS LE PRODELTA DU RHONE
DETERMINATION DE BIO-INDICATEURS
ENVIRONNEMENTAUX ET RECONSTITUTION
HISTORIQUE D'UNE ANTHROPISATION RECENTE**

Aurélie Goineau

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** COLOGIE DES FORAMINIFERES BENTHIQUES DANS LE
PRODELTA DU RHONE
DETERMINATION DE BIO-INDICATEURS ENVIRONNEMENTAUX
ET RECONSTITUTION HISTORIQUE D'UNE ANTHROPISATION
RECENTE**

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Devant le jury ci-dessous :

Gerhard SCHMIEDL	Rapporteur	Professeur, Universit� de Hambourg
J�r�me BONNIN	Rapporteur	MdC, EPOC, Universit� Bordeaux I
Christophe RABUILLE	Examineur	Directeur de Recherche (HDR), LSCE
Antoine GREMARE	Examineur	Professeur, EPOC, Universit� Bordeaux I
Maria-Angela BASSETTI	Examineur	MdC, IMAGES, Universit� de Perpignan
Directeur de th�se : Frans JORISSEN		Professeur, BIAF, Universit� d'Angers
Co-directeur de th�se : Christophe FONTANIER		MdC (HDR), BIAF, Universit� d'Angers

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INTRODUCTION

Cette thèse intitulée « Ecologie des foraminifères benthiques dans le prodelta du Rhône – Détermination de bio-indicateurs environnementaux et reconstitution historique d'une anthropisation récente » s'inscrit dans le cadre de deux grands projets, l'ANR CHACCRA (Climate and Human-induced Alterations in Carbon Cycling at the River-seA connection, 2007–2010) ainsi que l'ANR EXTREMA (Episodes météo-climatiques extrêmes et redistribution des masses sédimentaires et des polluants associés au sein d'un système côtier, 2007–2010). Ces deux programmes ont pour but l'élaboration et la validation d'outils capables de prévoir les modifications possibles dans le cycle du carbone et les transferts de polluants au débouché du Rhône et sur le plateau continental adjacent en réponse au changement climatique (hausse des émissions de CO₂ atmosphérique et des phénomènes climatiques extrêmes). Ces travaux sont intégrés au grand programme national « Vulnérabilité : Milieux et Climat » financé par l'Agence Nationale de la Recherche. Au sein de ces projets, l'objectif principal de ce travail de thèse est de définir les caractéristiques écologiques des faunes de foraminifères benthiques peuplant actuellement les sédiments de la plate-forme continentale sous l'influence directe du fleuve Rhône, dans le but d'utiliser les faunes benthiques en tant que bio-indicateurs des caractéristiques environnementales actuelles et passées. Cette étude s'oriente donc autour de deux grands axes :

(1) Dans un premier temps, décrire la variabilité spatiale et temporelle des faunes vivantes de foraminifères benthiques en réponse à l'ensemble des paramètres environnementaux prévalant sur la zone d'étude, tels que les processus hydro-sédimentaires à l'interface eau – sédiment, la nature des sédiments, ainsi que la qualité et la quantité de matière organique détritique et les conditions d'oxygénation dans le sédiment.

(2) Dans un second temps, définir un outil basé sur les assemblages fossiles de foraminifères benthiques afin de reconstruire les changements environnementaux passés du prodelta du Rhône, changements liés aux variations naturelles de l'hydrosystème rhodanien mais aussi à la pression anthropique croissante au cours du dernier siècle.

1. LES FORAMINIFERES BENTHIQUES

1.1. Généralités

Les foraminifères benthiques sont des organismes unicellulaires eucaryotes (classe FORAMINIFERA, règne PROTOCTISTA GRANULORETICULOSA ; Sen Gupta, 1999) produisant un test autour de leur unique cellule. Ce test peut être de nature organique, agglutinée (agglomération de particules biogènes ou terrigènes), ou carbonatée (cristaux d'aragonite ou de calcite minéralisés par l'organisme). Cette coquille confère aux foraminifères une capacité importante de fossilisation dépendant de la nature propre de leur test, mais aussi des conditions physico-chimiques du milieu sédimentaire où ils meurent. Les tests de foraminifères benthiques préservés dans les archives sédimentaires constituent donc un outil micropaléontologique majeur dans les reconstitutions paléo-environnementales ainsi que dans l'établissement des échelles biostratigraphiques.

À ce jour, près de 2455 genres et 40000 espèces (vivantes ou fossiles) sont répertoriées depuis les environnements littoraux (marais, estuaires,...) jusqu'aux fosses marines (Murray, 1991a). La classification taxonomique actuelle est essentiellement basée sur la morphologie du test (Loeblich et Tappan, 1988; Sen Gupta, 1999). La composition et les microstructures du test sont de première importance pour classer les foraminifères en divers ordres. La composition chimique et les arrangements granulaires des cristaux sont utilisés comme critères discriminants secondaires afin de définir et de distinguer les sous-ordres et les super-familles. Le mode d'addition des chambres d'habitation (i.e., forme et arrangement des chambres), la nature des cloisons et les ouvertures ainsi que la nature sessile ou vagile des organismes sont également considérés (Sen Gupta, 1999). Dans la mesure où cette classification ne tient pas compte des analyses génétiques indispensables aujourd'hui pour classer les organismes vivants en espèces dites biologiques, les espèces de foraminifères actuellement répertoriées sont des espèces dites morphologiques, hiérarchisées dans une classification purement phénétique. L'établissement d'une classification phylogénétique des foraminifères (basée sur la reconnaissance de séquences de gènes) est en cours depuis plus d'une dizaine d'années (e.g., Pawlowski et al., 1994; Pawlowski, 2000; Schweizer et al., 2005, 2008; Longet et Pawlowski, 2007; Piña-Ochoa et al., 2010) et tend à démontrer une diversité spécifique beaucoup plus grande que le laisse supposer la classification morphologique actuellement en vigueur, plus particulièrement pour les foraminifères planctoniques.

1.2. Caractéristiques biologiques

La cellule d'un foraminifère est constituée d'un cytoplasme dont la partie interne, l'endoplasme, constitue la plus grande partie de la masse cytoplasmique à l'intérieur du test. Le test (squelette intra-cytoplasmique) est synthétisé dans la partie externe du cytoplasme appelée ectoplasme. L'ectoplasme peut se ramifier afin de former des pseudopodes pouvant s'étendre via l'ouverture principale du test jusqu'à 1 cm de long (Murray, 2002). Ces pseudopodes permettent au foraminifère de se déplacer sur et dans le sédiment (0.01 à 0.5 mm par minute ; Kitazato, 1988; Wetmore, 1988; Travis et Bowser, 1991), mais aussi d'appréhender dans l'environnement extérieur la nourriture ainsi que les particules organiques (e.g., spicules d'éponges, tests d'autres espèces de foraminifères) ou inorganiques (e.g., grains de quartz, micas) nécessaires à la construction de leur test (foraminifères agglutinés) (e.g., Lipps, 1983).

Les foraminifères benthiques sont des organismes organo-hétérotrophes, c'est-à-dire trouvant leur source de carbone dans la matière organique suivant plusieurs stratégies telles que l'assimilation de débris déposés sur et dans le sédiment (dépositivore), de particules en suspension (suspensivore) mais aussi de bactéries présentes dans les sédiments (bactériophage) (Debenay et al., 1996). Certaines espèces de foraminifères benthiques sembleraient présenter des relations endosymbiotiques afin de s'affranchir des apports en carbone organique, soit avec des algues (e.g., Lee et Anderson, 1991; Lee et al., 1995; Bernhard et Bowser, 1999), soit avec des bactéries (e.g., Bernhard, 1996).

La reproduction des foraminifères benthiques peut alterner entre un mode sexué et asexué, donnant naissance à des individus libérés dans l'environnement par l'abandon ou la dissolution du test parental (Murray, 2006). Lors de la reproduction sexuée (gamogonie), la fusion de deux gamètes à n chromosomes génère des individus diploïdes présentant une loge initiale (proloculus) de petite taille (individus microsphériques). Au contraire, les organismes issus de la reproduction asexuée (schizogonie) héritent d'un noyau ainsi que d'une partie du cytoplasme parental, présentant un proloculus de grande taille (individus mégalosphériques). Dans le second cas, le foraminifère meurt en se reproduisant.

2. LES ECOSYSTEMES BENTHIQUES DES ENVIRONNEMENTS MARINS DE PLATE-FORME SOUMIS À UNE INFLUENCE FLUVIATILE

Le plateau continental est défini comme le prolongement physique du continent dans le domaine marin, s'étendant de la côte jusqu'à la rupture de pente vers 200 m de profondeur.

D'un point de vue sédimentaire, la zone s'étendant entre 0 et 20 m de profondeur correspond au domaine côtier composé essentiellement de sédiments grossiers (sables). Au-delà, de 20 m jusqu'à 200 m de profondeur, s'étend le plateau continental constitué de dépôts fins argileux. Cependant, l'apport de sédiments relativement grossiers (silts, sables) sous l'influence d'un fleuve modifie en partie la structure et la morphologie de la côte et du plateau continental. Ainsi, ces apports fluviaux peuvent former au débouché du fleuve un édifice deltaïque, formation contrôlée par le débit du fleuve, la quantité et la granularité (i.e., taille des grains) des sédiments apportés, la morphologie de la côte mais aussi l'intensité des processus liés à la houle et à la marée. Un delta se compose d'une partie émergée appelée plaine deltaïque parcourue par un réseau de chenaux fluviaux, et d'une partie sous-marine appelée prodelta se déposant sous la forme d'un lobe sédimentaire. Les dépôts silto-argileux du prodelta constituent une zone de transition entre les sédiments sableux observés près de l'embouchure du fleuve et les dépôts fins (argiles) du plateau continental. Le prodelta, situé à l'interface entre le domaine continental (fleuve, plaine deltaïque) et le domaine marin (plateau), constitue donc un environnement potentiellement très sensible aux risques naturels (e.g., tempêtes, crues) mais aussi aux risques liés aux activités humaines (e.g., pollution).

2.1. Rôle des plates-formes continentales dans le cycle du carbone

Les écosystèmes marins de plate-forme continentale sont caractérisés par une très forte productivité jouant un rôle majeur dans le cycle du carbone (Walsh et al., 1981; Hargrave, 1985; Smith et MacKenzie, 1987; Walsh, 1988, 1991; Jahnke et al., 1990; Wollast, 1991; Hedges et Keil, 1995; Bauer et Druffel, 1998) (Fig. 1). Ainsi, malgré la surface limitée que représentent ces environnements (10% de la surface océanique totale), environ 25% de la production primaire océanique mondiale a lieu dans les zones côtières (Smith et Hollibaugh, 1993). Les apports conséquents de nutriments dissous via le panache des fleuves sont notamment à l'origine de cellules locales de forte productivité et d'importants flux de production exportée vers le sédiment (Lohrenz et al., 1990, 1997; Dagg et Breed, 2003). Les rivières sont également la source d'importants apports de matière organique d'origine terrestre (e.g., composés organiques de sol, débris végétaux) et fluviale (production primaire fluviale) sous forme particulaire (Mopper et Degens, 1979; Eppley, 1984; Romankevich, 1984). Par la suite, l'ensemble du matériel organique particulaire exporté (production primaire d'origine terrestre, fluviale et marine) peut être soit enfoui dans les sédiments, soit reminéralisé via les processus diagénétiques (Froelich et al., 1979; Canfield et al., 1993). Au

total, 80% de l'enfouissement du carbone organique se produirait dans les zones côtières (Smith et Hollibaugh, 1993; Hedges et Keil, 1995). Cet enfouissement dépend essentiellement (1) du flux de matière organique (quantité et qualité) vers l'interface eau – sédiment, (2) de l'intensité de la minéralisation dans la colonne d'eau mais aussi à l'interface eau – sédiment (couche néphéloïde de fond) et dans le sédiment, (3) ainsi que des processus hydro-sédimentaires (suspension – resuspension) (McKee et al., 2004).

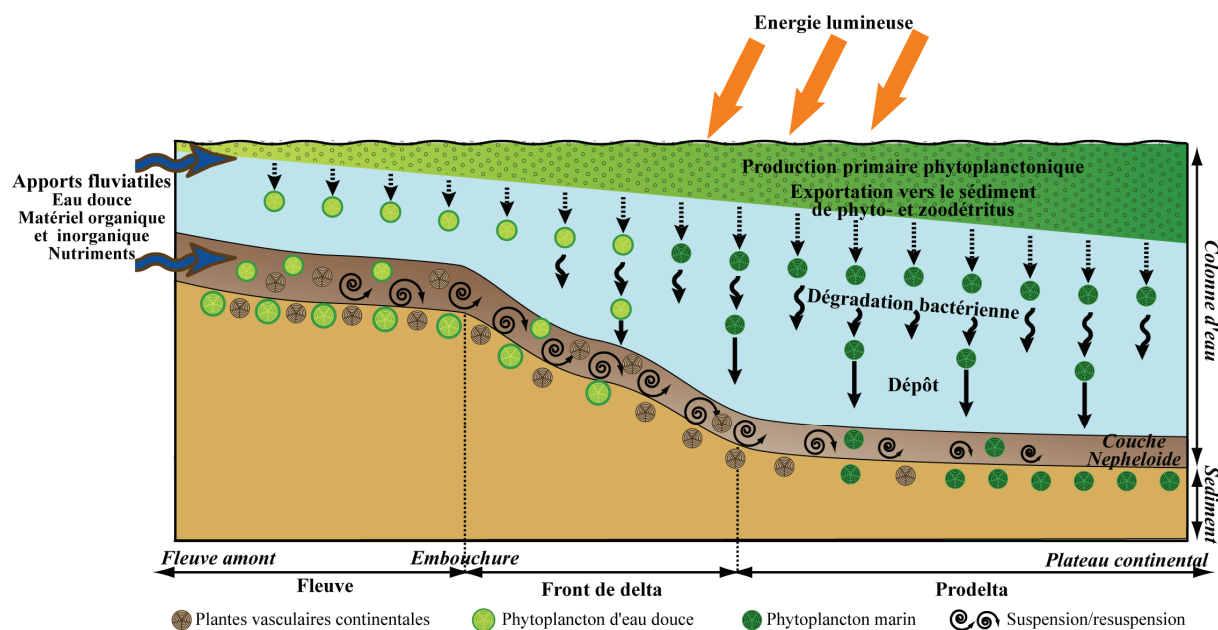


Figure 1 : Schéma synthétique des différentes sources de carbone organique et de son devenir dans les environnements de plateau continentale soumis à une influence fluviale (modifié d'après Mojtahid, 2007).

Un fort apport de matière organique vers le sédiment peut avoir à la fois des effets positifs et négatifs sur les communautés benthiques. Au débouché des fleuves, d'importants flux de matière organique vers le sédiment peuvent augmenter la biomasse de la macrofaune benthique (Mann, 1988; Largier, 1993; Danovaro et al., 2000; Manini et al., 2002; Salen-Picard et al., 2002; Salen-Picard et al., 2003; Darnaude et al., 2004). Néanmoins, un trop fort apport peut également conduire à une eutrophisation du système benthique, conduisant à l'apparition de phénomènes d'hypoxie à l'interface eau – sédiment et dans les eaux de fond (Van der Zwaan et Jorissen, 1991; Jorissen et al., 1992; Donnici et Serandrei Barbero, 2002). Ces conditions ont alors un impact désastreux sur les communautés benthiques, entraînant une mortalité accrue et une baisse de la biodiversité (e.g., Kemp et Boynton, 1992; Diaz et Rosenberg, 1995, 2008; Heip, 1995; Rabalais et al., 2002; McAllen et al., 2009). Ce phénomène reflète la complexité des interactions entre les processus physiques (stratification

de la colonne d'eau, circulation des eaux de fonds, régime des vents) et les processus biogéochimiques (minéralisation de la matière organique) (Buscail et al., 1995; Guidi-Guilvard et Buscail, 1995; Rowe, 2001; Rabouille et al., 2008).

2.2. La matière organique détritique : sources, caractérisation et dégradation

Les environnements de plate-forme continentale soumis à l'influence d'un fleuve sont alimentés par trois sources majeures de matière organique :

- (1) le continent lessivé par le fleuve et ses affluents, apportant des fragments de plantes vasculaires ainsi que du matériel issu du lessivage des sols.
- (2) la production primaire d'eau douce au sein du fleuve, source de phytodétritus fluviaux.
- (3) la production primaire marine sur le plateau adjacent au débouché du fleuve, source de phyto- et zoodétritus marins.

Ces débris organiques de natures variées possèdent une dégradabilité différente. Ainsi, une matière récemment synthétisée, dite « labile » (e.g., phytoplancton), est dégradée plus rapidement qu'une matière ayant déjà subi un ou plusieurs cycles de dégradation (e.g., matière organique en suspension).

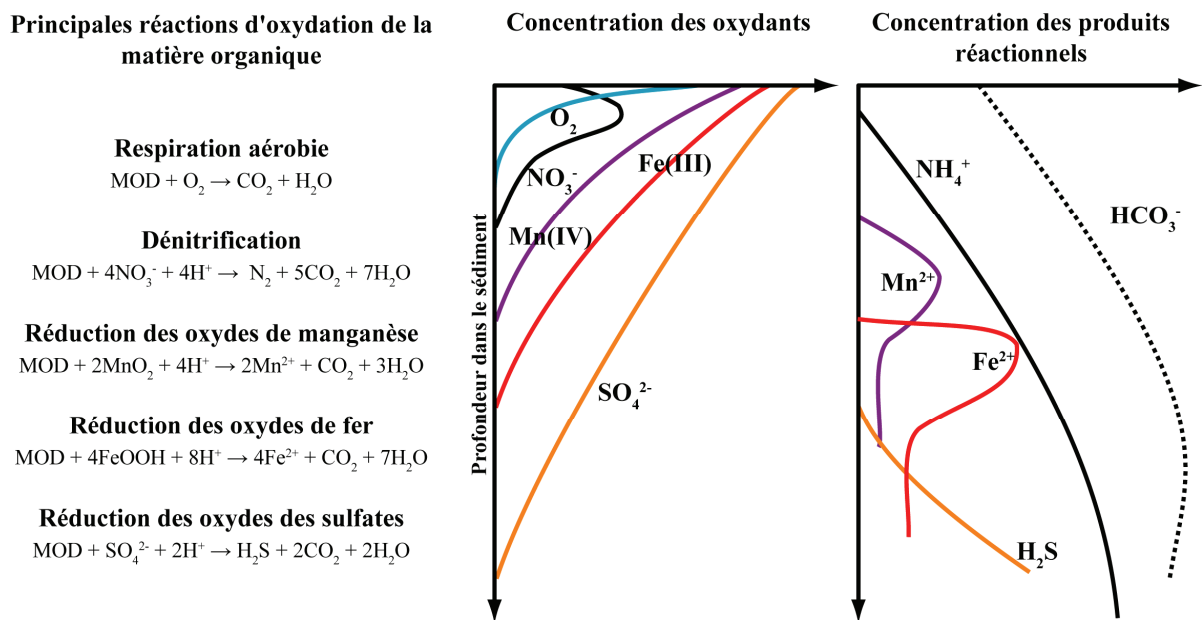


Figure 2 : Principales réactions de dégradation de la matière organique (MO) ayant lieu dans les sédiments, et représentations schématiques dans ces mêmes sédiments des concentrations des accepteurs d'électrons (oxydants) et des produits issus de la dégradation (produits réactionnels) (d'après Froelich et al., 1979).

La dégradation de la matière organique est un processus catabolique, c'est-à-dire permettant à un organisme uni- ou pluricellulaire d'acquérir de l'énergie. La minéralisation correspond à l'étape finale de cette dégradation, consistant en l'oxydation du carbone organique en phase inorganique (minérale) (Canfield, 1993; Kristensen et Holmer, 2001). Cette oxydation nécessite un accepteur d'électrons ou oxydant. Chaque oxydant possède son enthalpie propre, libérant donc plus ou moins d'énergie lors de l'oxydation du carbone organique. Selon Froelich et al. (1979), l'oxydant fournissant le plus d'énergie est utilisé en premier. Dès lors que cet oxydant est épuisé, la minéralisation se poursuit par l'utilisation des autres accepteurs d'électrons. Dans un milieu dit stationnaire, ne variant donc pas au cours du temps, la séquence typique d'utilisation des oxydants est l'oxygène (O₂), les nitrates (NO₃⁻), les oxydes métalliques (manganèse – Mn, fer – Fe), et enfin les sulfates (SO₄²⁻) (Fig. 2). Ces processus, pouvant se produire dans les sédiments et dans la colonne d'eau, contribuent à diminuer la labilité de la matière organique (Berner, 1980; Middelburg, 1989) mais aussi la concentration en oxygène dissous dans les eaux de fonds et les eaux interstitielles. Ainsi, les sédiments marins sont des environnements réducteurs recouverts d'une couche oxique superficielle dont l'épaisseur peut varier de quelques millimètres à plusieurs dizaines de centimètres selon l'intensité de la dégradation. Néanmoins, la bio-irrigation induite par l'action des organismes benthiques perturbe cette interface oxique – anoxique en générant des microenvironnements plus ou moins oxygénés, et en alimentant en oxygène les sédiments plus profonds.

La dégradabilité de la matière organique dépend de son origine, mais aussi des biomolécules qui la composent. Les acides aminés, les lipides et les glucides hydrosolubles sont considérés comme les composés organiques les plus facilement dégradables (i.e., labiles). L'origine et/ou l'état de dégradation de la matière organique peuvent être retracés grâce à plusieurs outils biogéochimiques. D'après Redfield et al. (1963), une molécule de matière organique issue de la photosynthèse est constituée des éléments carbone (C), hydrogène (H), oxygène (O), azote (N), phosphore (P) et soufre (S) selon le rapport suivant : (CH₂O)₁₀₆(NH₃)₁₆(H₃PO₄). Les proportions C:N:P = 106:16:1 varient d'une espèce de phytoplancton à une autre, donc selon son origine marine ou fluviatile. Ainsi, le phytoplancton marin « frais » présente un rapport carbone vs azote (C:N) compris entre 6 et 9, alors que la matière organique d'origine terrestre (plantes vasculaires) présente des valeurs > 20 (Redfield et al., 1963; Gordon et Goñi, 2003 ; Tableau 1). Lors de la dégradation du phytoplancton marin, le rapport C:N augmente et tend vers des valeurs > 10 proches de celui des végétaux terrestres. De ce fait, la mesure du rapport C:N de la matière organique

particulaire ne permet pas à elle seule d'isoler les effets de source et de dégradation de la matière organique (Savoye et al., 2003). L'analyse des isotopes stables du carbone ($\delta^{13}\text{C}$) peut aider à préciser ces effets. Ainsi, le phytoplancton d'origine marine ou estuarien est caractérisé par un $\delta^{13}\text{C}$ compris entre -25‰ et -20‰ , alors que les végétaux terrestres présentent des valeurs $< -27\text{‰}$. La dégradation tend à légèrement augmenter ces valeurs isotopiques. L'analyse complémentaire du C:N et du $\delta^{13}\text{C}$ permet de retracer éventuellement la/les source(s) de la matière organique particulaire (Tableau 1). Certaines biomolécules peuvent également servir à retracer l'origine d'un matériel organique. Par exemple, la lignine, molécule très peu dégradée contenue exclusivement dans les plantes vasculaires, sert à retracer la matière organique d'origine terrestre, alors que la chlorophylle-*a* est généralement admise comme indicatrice de la production phytoplanctonique.

Source de matière organique	C:N	$\delta^{13}\text{C}$
Plantes vasculaires terrestres	~20 à 50	-29 à -24‰
Matériel organique issu du lessivage des sols	~7.5 à 17	-29 à -27‰
Phytoplancton d'eau douce	~5.5 à 8	-29 à -22‰
Phytoplancton marin	~5.5 à 8	-23 à -18‰

Tableau 1 : Composition en isotopes stables du carbone ($\delta^{13}\text{C}$) et rapport C/N des sources potentielles de matière organique des sédiments d'environnement marin sous influence fluviale (d'après Gordon et Goñi, 2003; Tesi et al., 2007).

2.2. Les foraminifères benthiques dans les environnements marins soumis à une influence fluviale

Les foraminifères benthiques occupent des niches écologiques très variées, depuis les environnements littoraux (marais, estuaires,...) jusqu'aux fosses marines. Afin d'expliquer la répartition spatiale de ces organismes dans le domaine marin, les premières études écologiques ont porté l'accent sur une répartition bathymétrique des faunes de foraminifères benthiques (e.g., Streeter, 1973; Schnitker, 1974, 1976; Gofas, 1978; Lohman, 1978; Murray et al., 1986, 1988). Néanmoins, il est apparu rapidement que de nombreux autres paramètres environnementaux entraînent en jeu, notamment les facteurs physico-chimiques (e.g., production primaire exportée, conditions redox dans les sédiments, processus hydro-sédimentaires) (e.g., Pujos, 1972; Streeter, 1973; Schnitker, 1974; Pujos, 1976; Blanc-Vernet, 1988). Dans les environnements de plate-forme continentale soumis à une influence fluviale,

la dynamique temporelle et la répartition spatiale des foraminifères benthiques sont fortement contrôlées par la matière organique détritique disponible dans le sédiment ainsi que la quantité d'oxygène à/sous l'interface eau – sédiment (e.g., Sen Gupta et Machain–Castillo, 1993; Alve et Murray, 1994; Jorissen et al., 1995; Gustafsson et Nordberg, 2000, 2001; Duijnsteet et al., 2003; Suhr et al., 2003; Langezaal et al., 2006; Hyams–Kaphzan et al., 2009). À ce titre, les foraminifères benthiques pourraient constituer un maillon important des réseaux trophiques des écosystèmes benthiques en participant amplement à la fixation et au recyclage du carbone, de l'azote ou du phosphore issus de la matière organique détritique (e.g., Altenbach et Sarntheim, 1989; Gooday et al., 1992; Moodley et al., 2000, 2002). Il est également admis que la composition, la densité et les microhabitats (répartition verticale dans le sédiment) des communautés de foraminifères benthiques sont influencés par la qualité de la matière organique exportée au sédiment (e.g., Altenbach et Sarntheim, 1989; Corliss et Emerson, 1990; Rathburn et Corliss, 1994; Jorissen et al., 1995, 1998; De Rijk et al., 2000). Cependant, en l'absence d'oxygène, certaines espèces de foraminifères benthiques sont capables d'accumuler et/ou d'utiliser les nitrates afin d'oxyder la matière organique (Risgaard–Petersen et al., 2006; Høgslund et al., 2008; Piña–Ochoa et al., 2010). Cette capacité, retrouvée notamment chez des espèces typiques d'environnements sous influence fluviale (e.g., *Nonionella stella*, *Valvulineria bradyana*), leur confère la possibilité de survivre dans des environnements hypoxiques à totalement anoxiques.

En parallèle, d'autres facteurs physico-chimiques participent à la distribution spatiale des foraminifères benthiques dans de tels environnements tels que le pH, la salinité et la température des eaux de fond, ainsi que les processus hydro-sédimentaires. Les foraminifères benthiques possèdent une gamme de tolérance très large concernant les paramètres température et salinité. Ces organismes sont observés des eaux douces aux eaux fortement hypersalines (0 à ~ 70‰) (Murray, 2006), et des eaux polaires aux eaux tropicales. La salinité influence les organismes principalement à travers l'osmose cellulaire, c'est-à-dire la diffusion de molécules à travers leur membrane cytoplasmique. En dessous d'une salinité de 10–12‰, une cellule peut s'arrêter de fonctionner sauf si l'organisme maintient une importante composition ionique interne (McLusky et Elliott, 2004). Cette condition explique pourquoi la majorité des espèces, ainsi que les plus fortes biodiversités, sont rencontrées dans les eaux de salinité normale (33–37‰). Vers les environnements hypersalins (> 37‰), la diversité et le nombre d'espèces diminuent progressivement (Murray, 2006). Dans les environnements soumis à l'influence d'un fleuve, ces deux paramètres peuvent varier sensiblement, dépendant des variations saisonnières des températures continentales et du débit du fleuve. Par ailleurs,

au niveau de la zone côtière (0 à 20 m de profondeur), les sédiments sont susceptibles d'être remobilisés sous l'action combinée de la houle et de la marée. Dans ces environnements à forte courantologie vit généralement une épifaune de foraminifères attachée au substrat (Murray, 2006). Au-delà de 20 m de profondeur, les sédiments peuvent être remobilisés sous l'action des houles de tempête jusqu'à des profondeurs de 100 m lors d'évènements exceptionnels (Reineck et Singh, 1975). Par ailleurs, le dépôt de matériel fluviatile au débouché des fleuves peut également perturber sensiblement l'environnement benthique en détruisant totalement ou partiellement l'écosystème préexistant. La recolonisation de ce nouveau milieu par les organismes benthiques peut se faire sur des périodes de temps très variables, allant de quelques jours à plusieurs années selon l'étendue de la perturbation. Ces organismes peuvent être soit allochtones, transportés en même temps que le dépôt perturbateur, soit voisins de l'environnement perturbé (Alve, 1999).

Cette gamme très étendue de tolérances environnementales, combinée à une très forte richesse spécifique, un cycle de vie court (1 à 3 mois en moyenne, 1 an maximum ; Murray, 1991b), et des demandes écologiques caractéristiques à chaque espèce, font des foraminifères benthiques de bons bio-indicateurs de leur environnement.

3. CONTEXTE DE L'ETUDE

3.1. Contexte actuel

Le fleuve Rhône s'étend sur 832 km de long depuis sa source en Suisse au pied du Mont de Fourche (1735 m d'altitude) jusqu'à son double exutoire en Mer Méditerranée. Son vaste bassin versant (97800 km²) présente une grande diversité géologique, le Rhône charriant les terrains calcaires et cristallins du Jura, des Alpes externes et des contreforts méridionaux du Massif Central (Fig. 3). Le Rhône est la principale source d'eau douce (80%) et de matériel terrigène (90%) du Golfe du Lion (Durrieu de Madron et al., 2000, 2003). Son débit moyen annuel est de 1700 m³.s⁻¹, atteignant des valeurs supérieures à 3000 m³.s⁻¹ lors d'épisodes de crues majeures au printemps et en automne (Pont et al., 2002). Lors d'une crue exceptionnelle en décembre 2003, le débit du fleuve a atteint plus de 12000 m³.s⁻¹, le maximum connu à ce jour. Le fleuve se divise en deux branches au niveau de Arles : le Petit Rhône et le Grand Rhône. Le Grand Rhône se déverse en Méditerranée via l'embouchure de Roustan, concentrant 85 à 90% des flux solides et liquides totaux du Rhône. Le Petit Rhône se déverse plus à l'Est via l'exutoire d'Orgon, ne représentant que 10 à 15% de la décharge totale du Rhône.

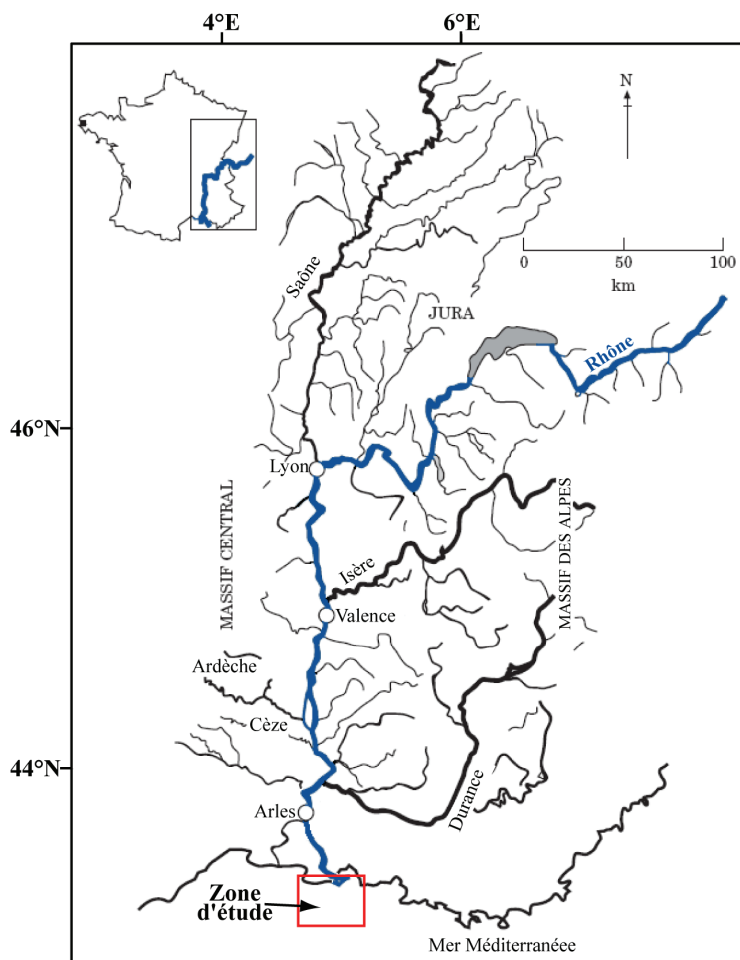


Figure 3 : Contextes géographique et hydrographique du Rhône (bassin versant et principaux affluents), et situation de la zone d'étude.

Le mélange des eaux douces du Rhône avec les eaux marines de la Mer Méditerranée génère un coin salé typique des estuaires microtidaux en amont de l'embouchure. Les eaux denses marines pénètrent dans le fleuve au-dessus du fond, pendant que les eaux douces du fleuve restent en surface. La position de ce coin salé dépend essentiellement du débit du Rhône, poussé vers l'embouchure lors de forts débits ($> 2000 \text{ m}^3 \cdot \text{s}^{-1}$) mais pouvant aussi remonter jusqu'à 20 km en amont en période d'étiage (i.e., bas débit $\sim 500 \text{ m}^3 \cdot \text{s}^{-1}$) (Eisma, 1993).

Le matériel (inorganique et organique) rhodanien est transféré vers l'environnement marin essentiellement via la couche néphéloïde benthique (e.g., Aloïsi et al., 1982; Naudin et al., 1992, 1997). Néanmoins, le panache de dilution du fleuve se formant dans les eaux de surface constitue aussi un vecteur de transfert notable de ce matériel. L'extension et la forme du panache dépendent de l'intensité du Courant Nord-Méditerranéen, des régimes de vents de secteurs nord (Mistral) ou nord-ouest (Tramontane), mais aussi du débit du fleuve. En

moyenne, ce panache est dévié vers le sud-ouest (Naudin et al., 1997 ; Fig. 4). Si 30% des apports rhodaniens sont transférés vers la pente continentale et les bassins profonds via la couche néphéloïde et les canyons sous-marins (Millot et Monaco, 1984; Durrieu de Madron, 1994; Berné et Loubrieu, 1999; Droz et al., 2001), la plus grande partie se dépose près de l'embouchure du Rhône entre 0 et 60 m de profondeur et jusqu'à 6 km de l'embouchure, générant de très forts taux de dépôt des sédiments de l'ordre de 50 cm.an^{-1} (Calmet et Fernandez, 1990; Charmasson et al., 1998; Rabineau et al., 2005). Cette zone est composée d'un front de delta jusqu'à 20 m de profondeur, caractérisé par une forte pente ($> 4^\circ$), puis d'une zone prodeltaïque moins pentue jusqu'à environ 60 m de profondeur. Au-delà de cette zone prodeltaïque, la pente et les taux de sédimentation diminuent sensiblement, atteignant des valeurs pouvant varier entre 0.2 et 0.6 cm.an^{-1} (Zuo et al., 1997; Miralles et al., 2005).



Figure 4 : Image satellitale MODIS du Golfe du Lion au 15 septembre 2002 présentant l'extension marine vers le sud-ouest du panache du Rhône (d'après Ulses, 2005).

Grâce aux apports rhodaniens, le Golfe du Lion est l'une des zones les plus productives de Méditerranée (Diaz, 2000), le Rhône apportant 50% des nutriments nécessaires à la production primaire totale de la zone (Lochet et Leveau, 1990). La production phytoplanctonique est maximale de mars à mai, les concentrations en chlorophylle-*a* des eaux de surface atteignant 1 mg.m^{-3} . Un bloom du phytoplancton fluvial est également observé en cette saison dans les eaux de surface du Rhône, cette production pouvant être transportée via le panache du fleuve jusqu'au domaine marin (Harmelin-Vivien et al., 2008). La saison estivale est la plus oligotrophique avec seulement $0.1\text{--}0.2 \text{ mg Chl-}a.\text{m}^{-3}$ dans les eaux de surface du Golfe du Lion (Bosc et al., 2004).

3.2. Changements historiques

L'évolution historique du système Rhône a été étudiée à travers de nombreux outils tels que la palynologie, la sédimentologie mais aussi l'étude des sites archéologiques (e.g., L'Homer et al., 1981; Arnaud-Fassetta et Provansal, 1999; Provansal et al., 1999, 2003; Arnaud-Fassetta, 2000, 2002; Bruneton et al., 2001; Vella et al., 2005; Sabatier et al., 2006; Berné et al., 2007; Rey et al., 2009; Arnaud-Fassetta et al., 2010).

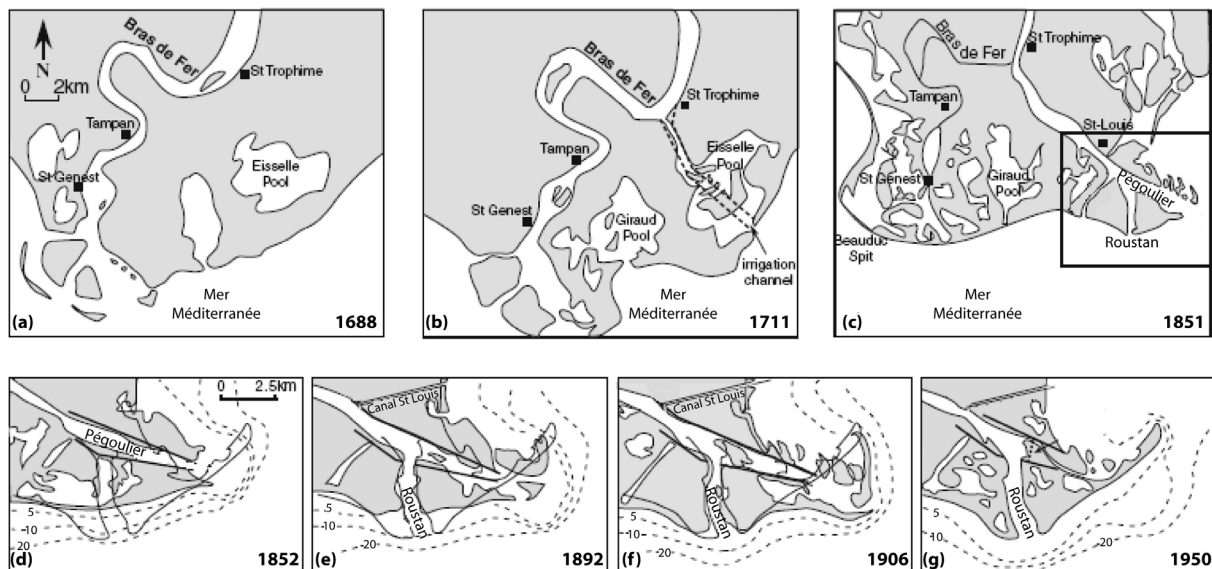


Figure 5 : Evolution historique (18^{ème}–21^{ème} siècle) des embouchures du Rhône. (d'après Maillet et al., 2005).
(a–b) Migration naturelle du chenal de Bras de Fer vers le chenal de Pégoulie en 1711 ; (c–g) Evolution de l'embouchure du Rhône depuis 1850 sous l'influence des travaux d'ingénierie, ouvrant et fermant artificiellement les chenaux de Pégoulie et de Roustan.

Les premières preuves de l'existence du Rhône remontent à la crise messinienne (entre –5.96 et –5.33 Ma) lorsque le niveau de la Mer Méditerranée descendit d'environ 1500 m (Clauzon, 1974). Depuis la fin du dernier maximum glaciaire (~18000 ans Before Present – BP), les variations du niveau marin puis l'influence croissante des activités humaines ont fortement contraint les flux sédimentaires et les processus érosifs contrôlant la morphologie du système deltaïque et prodeltaïque (Berendsen et Stouthamer, 2000; Stouthamer, 2001). Depuis 4000 ans BP, le Rhône a changé de cours à plusieurs reprises au gré des migrations de ses chenaux, formant une série de lobes deltaïques dont les vestiges sont encore visibles de la plaine deltaïque actuelle à la plate-forme continentale (Vella et al., 2005). Après la migration naturelle du chenal de Bras de Fer vers le chenal de Pégoulie en 1711 (Fig. 5a–b), la fixation de l'embouchure et des chenaux par des travaux d'ingénierie (stabilisation des berges,

construction de barrages hydro-électriques, travaux de dragage des fonds) ont stoppé l'évolution naturelle du Rhône (Sabatier et al., 2006) (Fig. 5d–g). Ce forçage anthropique, couplé à une réduction constante de la fréquence des crues majeures (Pichard, 1995), a entraîné une réduction significative de la charge solide du Rhône, passant de 22 Mt.an⁻¹ au cours du 18^{ème} siècle à ~8 Mt.an⁻¹ aujourd'hui (Antonelli, 2002; Pont et al., 2002; Provansal et al., 2003). Actuellement, le budget sédimentaire négatif entraîne une érosion massive de la côte sous l'action de courants côtiers puissants, ainsi qu'une migration de l'embouchure vers l'est. La hausse des fréquences des tempêtes et la montée du niveau marin ont accentué ce phénomène de migration au cours des dernières décennies (Suanez et Provansal, 1998; Sabatier, 2001; Sabatier et Suanez, 2003; Sabatier et al., 2009).

3.3. Les programmes CHACCRA et EXTREMA : Etudier et prédire l'influence des changements climatiques sur l'écosystème côtier au débouché du Rhône

Les projets CHACCRA (Climate and Human-induced Alterations in Carbon Cycling at the River-seA connection) et EXTREMA (Episodes météo-climatiques extrêmes et redistribution des masses sédimentaires et des polluants associés au sein d'un système côtier) sont intégrés au programme national « Vulnérabilité : Milieux et Climat » (VMC) financé par l'Agence Nationale de la Recherche (ANR). Ce programme a pour but l'élaboration et la validation d'outils d'évaluation et de prévision de la vulnérabilité des écosystèmes naturels (terrestres ou marins) ou anthropisés dans un contexte de changement climatique.

Le projet CHACCRA est une composante de l'initiative internationale RiOMar (River-dominated Ocean Margins). Le but de ce projet est d'étudier les variations du flux de carbone liées aux modifications du climat et de l'hydrologie au débouché du Rhône, fleuve majeur de la Méditerranée occidentale. Le milieu côtier joue un rôle prépondérant dans le cycle du carbone organique. De par ce rôle, il entre également en jeu dans le cycle du carbone global en agissant comme une source de CO₂ vers l'atmosphère lors de la minéralisation du carbone organique, mais aussi comme puits de CO₂ lorsque ce carbone organique est enfoui dans les sédiments. Il est aujourd'hui admis que le plateau continental agit globalement comme un puits de CO₂ d'environ 0.4 Pg C.an⁻¹. Malheureusement, dans un contexte de changement climatique, il est difficile de prédire comment vont évoluer ces environnements en terme de bilan de carbone.

Pour se faire, le projet fait appel aux compétences de nombreux laboratoires français se répartissant le travail en différentes tâches :

– **Tâche 1** : étudier les apports (nutriments dissous et particulaires) du Rhône dans le Golfe du Lion.

– **Tâche 2** : étudier les processus biogéochimiques liés à la production de matière organique et à sa minéralisation dans le panache du Rhône.

– **Tâche 3** : étudier les processus biogéochimiques liés à la préservation et à la minéralisation de la matière organique dans les sédiments.

– **Tâche 4** : concevoir un modèle couplé physique-biogéochimie combinant l'ensemble des données acquises par les équipes des Tâches 1, 2 et 3, et simulant le devenir des composés fluviaux en Méditerranée.

La conception de ce modèle constitue le but ultime du programme CHACCRA. En effet, celui-ci permettra d'extrapoler les variations des bilans de carbone au débouché du Rhône liées aux modifications du climat ainsi qu'à la pression anthropique croissante.

Le projet EXTREMA est, quant à lui, dédié à l'impact des épisodes climatiques extrêmes (crues, tempêtes) sur la redistribution des masses sédimentaires et des polluants associés au sein d'un environnement côtier sous une influence fluviale majeure, le Rhône. Tout comme le projet CHACCRA, ce travail se divise en plusieurs grands volets :

– **Volet A** : étudier l'apport de contaminants atmosphériques (précipitations météoriques, aérosols, poussières sahariennes).

– **Volet B** : étudier l'apport de contaminants lors des phénomènes de crue du fleuve Rhône et de la rivière Têt.

– **Volet C** : étudier l'impact des tempêtes sur le remaniement des sédiments, et donc des contaminants associés, déposés sur le plateau continental.

– **Volet D** : quantifier l'export de sédiment et de contaminants associés vers le milieu marin profond.

– **Volet E** : concevoir un modèle simulant les transports sédimentaires sur le plateau continental suite à des événements climatiques extrêmes.

3.4. Ecologie des foraminifères benthiques dans le prodelta du Rhône – Détermination de bio-indicateurs environnementaux et reconstitution historique d'une anthropisation récente

Ce projet de thèse s'intègre dans la Tâche 3 du programme CHACCRA ayant pour but l'étude des processus biogéochimiques dans les sédiments. Les foraminifères benthiques semblent jouer un rôle important dans les écosystèmes benthiques de par leur participation dans la minéralisation du carbone organique. De ce fait, il semble indispensable de comprendre comment la variété des sources de matière organique alimentant les sédiments du prodelta, ainsi que les processus de reminéralisation de cette matière (i.e., conditions redox dans les sédiments), peuvent influencer sur la distribution de ces organismes. Par ailleurs, la détermination de faunes définissant des conditions environnementales précises au sein du prodelta permettrait d'utiliser les foraminifères benthiques en tant que bio-indicateurs afin de reconstruire l'évolution des conditions environnementales passées du prodelta, mais aussi de prévoir éventuellement son évolution future. Aussi, cet aspect s'intègre parfaitement au sein du Volet D du projet EXREMA dont le but de quantifier les transferts de sédiment vers le milieu marin profond nécessite une connaissance des volumes sédimentaires stockés dans les lobes deltaïques du Rhône, et donc une reconstruction précise des conditions passées dans ces environnements. Les faunes de foraminifères benthiques du prodelta du Rhône ont déjà été étudiées par le passé (Kruit, 1955; Blanc-Vernet, 1969; Bizon et Bizon, 1984). Si les travaux de Kruit (1955) ont apporté une vision préliminaire de la distribution de ces faunes dans la zone d'étude, Blanc-Vernet (1969) et Bizon et Bizon (1984) ont en revanche étudié de façon plus précise la taxonomie des assemblages morts et vivants. Néanmoins, les méthodes d'échantillonnage (carottier boîte) ainsi que l'absence d'analyses des paramètres environnementaux au cours de ces travaux ont rendu impossible une définition précise de l'influence des conditions environnementales au sein du prodelta sur l'écologie des foraminifères vivants. En comparaison avec ces études préliminaires, l'intérêt de ce projet de thèse réside notamment dans son approche pluridisciplinaire faisant appel à de multiples notions telles que l'écologie des foraminifères benthiques, mais aussi les processus géochimiques entrant en jeu dans le cycle de la matière organique exportée vers les sédiments. Ainsi, cette thèse s'articule autour de 5 chapitres.

Dans un premier temps, le but est de préciser la répartition spatiale dans l'ensemble de la zone d'étude des faunes de foraminifères benthiques lors d'une période d'échantillonnage (Campagne BEHEMOTH, Septembre 2006 ; Fig. 6a).

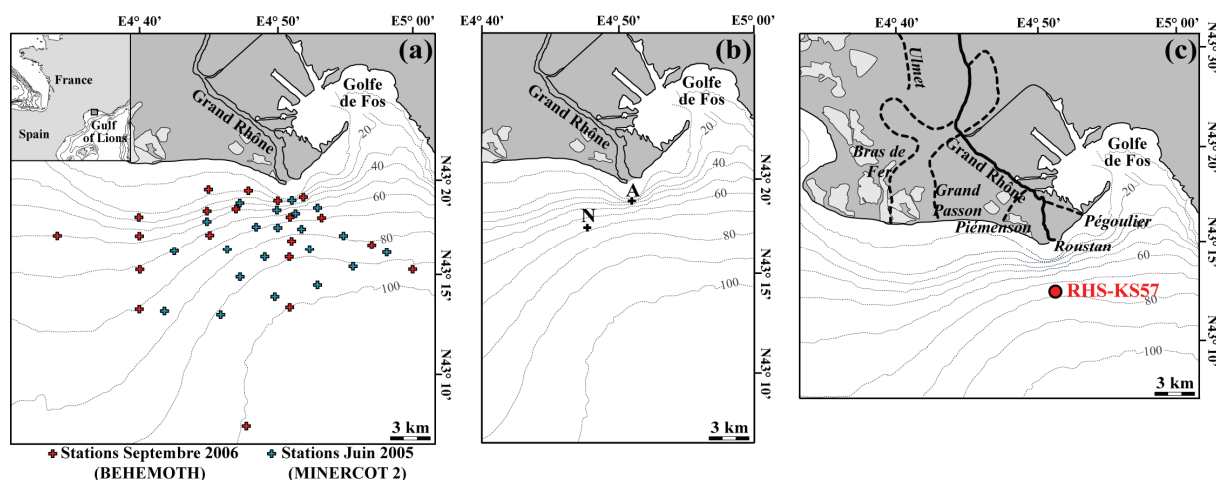


Figure 6 : Localisation de la zone d'étude et des stations étudiées au cours de ce travail. (a) 20 stations échantillonnées en Septembre 2006 (mission BEHEMOTH ; Chapitres 1 et 3) et 19 stations échantillonnées en Juin 2005 (mission MINERCOT 2 ; Chapitre 3) ; (b) Stations A et N étudiées dans le cadre du programme CHACCRA afin de préciser la variabilité spatiale à petite échelle (décimétrique ; mission RIOTECH, Septembre 2007 ; Chapitre 2) ainsi que la variabilité temporelle des faunes vivantes de foraminifères benthiques (missions RiOMar 1, RIOTECH, CHACCRA-bent 1 et CHACCRA-bent 2 ; Avril 2007, Septembre 2007, Mai 2008, Décembre 2008 ; Chapitre 3) ; et (c) Carotte RHS-KS57 étudiée dans le but de retracer l'évolution historique du Rhône (mission RHOSOS, Septembre 2008, programme EXTREMA ; Chapitre 5).

L'environnement prodeltaïque au débouché du Rhône présente des environnements très contrastés en termes de processus hydro-sédimentaires à l'interface eau – sédiment, d'accumulation de matière organique et de conditions redox dans les sédiments. Le but de cette étude est d'estimer si la distribution et la structure des faunes de foraminifères benthiques sont contraintes par ces conditions environnementales. Pour cela, les faunes vivantes de foraminifères benthiques provenant de 20 stations échantillonnées en Septembre 2006 ont été étudiées (mission BEHEMOTH). Ces stations couvrent l'ensemble de la zone d'étude, de 15 à 100 m de profondeur et de 1 à ~22 km de l'embouchure du Rhône. L'intérêt est plus particulièrement porté sur la structure (densité, diversité, composition) et la répartition spatiale des faunes de foraminifères afin de les comparer par la suite à des bases de données environnementales très larges. Le but de ce chapitre est d'éprouver si les faunes de foraminifères benthiques sont des bio-indicateurs pertinents des conditions environnementales variées prévalant dans la zone du prodelta, et plus particulièrement des apports complexes de matière organique.

Dans un second chapitre, la variabilité pouvant exister dans les faunes de foraminifères benthiques à l'échelle décimétrique à un même site d'échantillonnage est

étudiée puis discutée. Une distribution hétérogène des dépôts de matière organique à la surface du sédiment peut engendrer une variabilité spatiale à très petite échelle (infra métrique) des faunes vivantes de foraminifères benthiques en favorisant les espèces les plus opportunistes. Si cette variabilité spatiale à petite échelle (i.e., patchiness) existe dans notre zone d'étude, celle-ci pourrait biaiser non seulement la variabilité estimée à l'échelle kilométrique dans le 1^o chapitre, mais aussi la variabilité temporelle des faunes de foraminifères. Dans ces conditions, l'échantillonnage d'une seule carotte par station pourrait ne plus être réellement représentatif de la zone étudiée. Ainsi, deux stations A et N (20 et 68 m de profondeur) sont étudiées, 4 carottes ayant été échantillonnées à chacune d'elle (Fig. 6b). Les répliquas de chaque station sont comparés à travers la composition faunistique de chaque carotte exprimée en abondances absolues et relatives (pourcentages) des différentes espèces. Par la suite, cette base de données est comparée à celle établie dans le Chapitre 1 à l'échelle du prodelta. Cette comparaison, basée sur une analyse statistique, a pour but de préciser si la variabilité spatiale enregistrée à petite échelle est plus importante que celle observée à une échelle kilométrique.

Dans une troisième partie, les variations temporelles des faunes vivantes de foraminifères benthiques sont décrites à ces deux mêmes stations A et N (Fig. 6b). Au cours du projet CHACCRA, celles-ci ont été échantillonnées à quatre reprises en Avril 2007, Septembre 2007, Mai 2008 et Décembre 2008 (missions RiOMar 1, RIOTECH, CHACCRA-bent 1 et CHACCRA-bent 2). Ces quatre périodes correspondent à des conditions environnementales très variées, de bas (Avril et Septembre 2007) à fort débit du Rhône (crue ; Mai et Décembre 2008), mais aussi de faible (Septembre 2007 et Décembre 2008) à forte productivité primaire (bloom de printemps dans le Golfe du Lion et dans le fleuve Rhône ; Avril 2007 et Mai 2008). Le but de ce chapitre est de comprendre comment la mise en place de conditions environnementales très contrastées (processus hydro-sédimentaires, qualité/quantité de matière organique) à un même site peut impacter les faunes de foraminifères du point de vue de leur structure (composition faunistique, densités, diversité).

Dans une quatrième partie, l'intérêt se porte sur l'enregistrement des faunes mortes de foraminifères dans les archives sédimentaires récentes. Ainsi, les thanatocénoses (i.e., faunes mortes en cours de fossilisation dans les sédiments de sub-surface) de foraminifères sont décrites à 39 stations échantillonnées en Juin 2005 et Septembre 2006 au cours des missions MINERCOT 2 et BEHEMOTH (Fig. 6a). Ces faunes mortes sont comparées aux faunes

vivantes observées à ces mêmes sites afin de mettre en évidence des différences potentielles en terme de composition faunistique, mais aussi de déterminer les processus taphonomiques (e.g., dissolution des tests, fragmentation mécanique, contamination, remobilisation) éventuellement responsables de ces différences. Cette comparaison permettra d'apprécier si la signification environnementale portée par les faunes vivantes (Chapitres 1 et 3) est conservée par les faunes mortes lors de la fossilisation. Par la suite, une calibration de ces assemblages morts récemment permettra de définir des thanatofacies caractéristiques de conditions environnementales précises au sein du prodelta, constituant un outil essentiel à la reconstruction des conditions paléo-environnementales au débouché du Rhône.

Enfin, le cinquième chapitre est consacré à l'étude des faunes fossiles de foraminifères préservées depuis 400 ans dans la carotte RHS-KS57 (79 m de profondeur, mission RHOSOS, programme EXTREMA) prélevée en face de l'embouchure actuelle du Rhône (Fig. 6c). Grâce à leur capacité de fossilisation importante, les foraminifères benthiques constituent un outil majeur des reconstructions paléo-environnementales. Au cours des chapitres précédents, les assemblages vivants de foraminifères benthiques ont pu être observés dans leur milieu naturel, apportant des connaissances majeures concernant leurs préférences écologiques actuelles au sein du prodelta du Rhône (Chapitres 1, 2 et 3). A partir de ces connaissances, les faunes sub-fossiles (i.e., mortes récemment) ont pu être calibrées en tant qu'indicateurs des conditions environnementales passées (i.e., thanatofacies ; Chapitre 4). Grâce à ces thanatofacies définis au sein même du prodelta du Rhône, les faunes fossiles de foraminifères benthiques enregistrées dans la carotte RHS-KS57 vont permettre de retracer les grandes étapes dans l'évolution du Rhône, notamment en termes d'apports sédimentaires et de matière organique.

Les grandes conclusions tirées de ce travail ainsi que des axes de recherche possibles pour le futur seront présentés dans une dernière partie.

CHAPITRE 1

LIVE (STAINED) BENTHIC FORAMINIFERA FROM THE RHONE PRODELTA (GULF OF LIONS, NW MEDITERRANEAN): ENVIRONMENTAL CONTROLS ON A RIVER-DOMINATED SHELF

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CHAPITRE 1

LIVE (STAINED) BENTHIC FORAMINIFERA FROM THE

RHÔNE PRODELTA (GULF OF LIONS, NW

MEDITERRANEAN)

ENVIRONMENTAL CONTROLS ON A

RIVER-DOMINATED SHELF

Goineau A.^{a,b}, Fontanier C.^{a,b}, Jorissen F.J.^{a,b}, Lansard B.^c, Buscail R.^d, Mouret A.^e, Kerhervé P.^d, Zaragosi S.^e, Ernoult E.^{a,b,e}, Artéro C.^d, Anschutz P.^e, Metzger E.^{a,b}, Rabouille C.^f

^a Laboratory of Recent and Fossil Bio-Indicators (BIAF), University of Angers,
UPRES EA 2644, 2 Boulevard Lavoisier, 49045 Angers Cedex 01, France

^b Laboratory for the Study of Marine Bio-Indicators (LEBIM), Ker Châlon, 85350 Ile d'Yeu,
France

^c Department of Earth and Planetary Sciences, McGill University and GEOTOP,
3450 University Street, Montreal, Quebec H3A 2A7, Canada

^d Centre de Formation et de Recherche sur l'Environnement Marin, University of Perpignan,
UMR 5110 CNRS, 52 Avenue Paul Alduy, 66860 Perpignan Cedex, France

^e UMR 5805 Environnements et Paléoenvironnements Océaniques (EPOC – OASU),
University of Bordeaux I, Avenue des Facultés, 33405 Talence Cedex, France

^f Laboratoire des Sciences du Climat et de l'Environnement (LSCE),
UMR 1572 CEA – CNRS – UVSQ, F-91198 Gif-sur-Yvette Cedex, France

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ABSTRACT

In this chapter, we investigate the ecology of live (Rose Bengal-stained) benthic foraminifera collected at 20 stations ranging from 15 to 100 m depth in the Rhône prodelta (Gulf of Lions, NW Mediterranean). These sites were sampled in September 2006, five months after the Rhône River annual flood. Statistical analyses based on foraminiferal communities ($> 150 \mu\text{m}$) divide our study area into six main biofacies directly related to environmental conditions. Miliolid species are abundant in the relict prodeltaic lobe which is characterised by sand with low organic matter content. Close to the river mouth, the limited oxygen penetration in the sediment combined with important hydrosedimentary processes constitute stressful conditions for foraminiferal faunas dominated by opportunistic species (e.g., *Leptohalysis scottii*). With increasing distance from the river mouth, foraminiferal faunas (e.g., *Nonionella turgida*, *Eggerella scabra*) adapted to thrive in sediments enriched in Rhône-derived organic matter under more stable hydrosedimentary conditions appear. In the distal part of the Rhône River influence, benthic species (e.g., *Valvulineria bradyana*, *Textularia agglutinans*) living in fine sediment enriched in both continental and marine organic compounds emerge. At the deepest stations located in the south-eastern part of our study area, benthic foraminiferal faunas (e.g., *Bulimina aculeata*, *Melonis barleeanus*, *Bigenerina nodosaria*) are highly diverse, underlining stable environmental conditions characterised by marine-derived organic matter supplies and relatively deep oxygen penetration depth in the sediment. We also compare foraminiferal faunas sampled in September 2006 with communities sampled in June 2005, one month after the Rhône River annual flood (Mojtahid et al., 2009). This comparison suggests that opportunistic species (e.g., *B. aculeata*, *Cassidulina carinata*, *V. bradyana*) have responded to organic matter inputs related to marine primary production in June 2005.

Key words: Live benthic foraminifera; Rhône prodelta; Ecology; Organic matter.

1.1. INTRODUCTION

Marine ecosystems from continental shelves constitute highly productive areas playing a major role in the organic carbon cycle (Walsh et al., 1981; Hargrave, 1985; Smith and MacKenzie, 1987; Walsh, 1988, 1991; Jahnke et al., 1990; Wollast, 1991; Hedges and Keil, 1995; Bauer and Druffel, 1998). In river-dominated ocean margins, the timing, kinetics and extent of important biogeochemical processes, in the water column as well as in the

superficial sediment, are greatly influenced by large riverine inputs of dissolved and particulate terrestrial material (Hedges et al., 1997; McKee et al., 2004). Dissolved nutrients transported in the river plume off the river mouth result in localised high primary production cells and in a high exported production to the sea floor (Lohrenz et al., 1990, 1997; Dagg and Breed, 2003). In addition, river runoff carries a large amount of particulate organic matter originating from continental areas (Mopper and Degens, 1979; Eppley, 1984; Romankevich, 1984). In coastal sediments, the overall particulate organic matter (terrestrial organic matter and exported production) is degraded via diagenetic processes (Froelich et al., 1979; Canfield et al., 1993). The efficiency of the organic burial depends mainly on (1) the organic matter flux (quantity and quality) at the sediment – water interface, (2) the mineralisation at the sediment – water interface and within the sediment and (3) the hydro-sedimentary processes characterising the benthic ecosystems (McKee et al., 2004). High organic matter deposition rate induces both positive and negative effects on benthic communities. Under the river plume influence, high organic input to the sea floor enhances benthic macrofaunal biomass (Mann, 1988; Largier, 1993; Danovaro et al., 2000; Manini et al., 2002; Salen–Picard et al., 2002, 2003; Darnaude et al., 2004). However, enhanced deposition of terrestrial organic matter can also induce eutrophication of the benthic ecosystems leading to disastrous oxygen depletion at the sediment – water interface and in the bottom waters (Van der Zwaan and Jorissen, 1991; Jorissen et al., 1992; Donnici and Serandrei Barbero, 2002). These phenomena reflect the complex interaction between physical (water column stratification, bottom water currents, wind regime) and biogeochemical processes (organic matter mineralisation; Buscail et al., 1995; Guidi–Guilvard and Buscail, 1995; Rowe, 2001; Rabouille et al., 2008). Oxygen depleted bottom waters have a strong impact on benthic communities with massive mortality and decreasing biodiversity (e.g., Kemp and Boynton, 1992; Diaz and Rosenberg, 1995, 2008; Heip, 1995; Rabalais et al., 2002; McAllen et al., 2009). Benthic foraminiferal faunas constitute relevant proxies to study present and past environments since their faunal composition, spatial distribution and density are controlled by numerous physico-chemical parameters such as water depth, exported organic matter flux, oxygen availability and substrate (e.g., Gooday, 2003; Murray, 2006; Jorissen et al., 2007; Gooday et al., 2009). Notably, temporal dynamics and spatial distribution of living benthic foraminifera are largely controlled by the quantity and quality of the organic matter at the sediment – water interface, and by oxygen concentration in the bottom waters and in the superficial sediment (Alve and Murray, 1994; Gustafsson and Nordberg, 2000, 2001; Duijnsteet et al., 2003; Suhr et al., 2003; Langezaal et al., 2006; Hyams–Kaphzan et al., 2009).

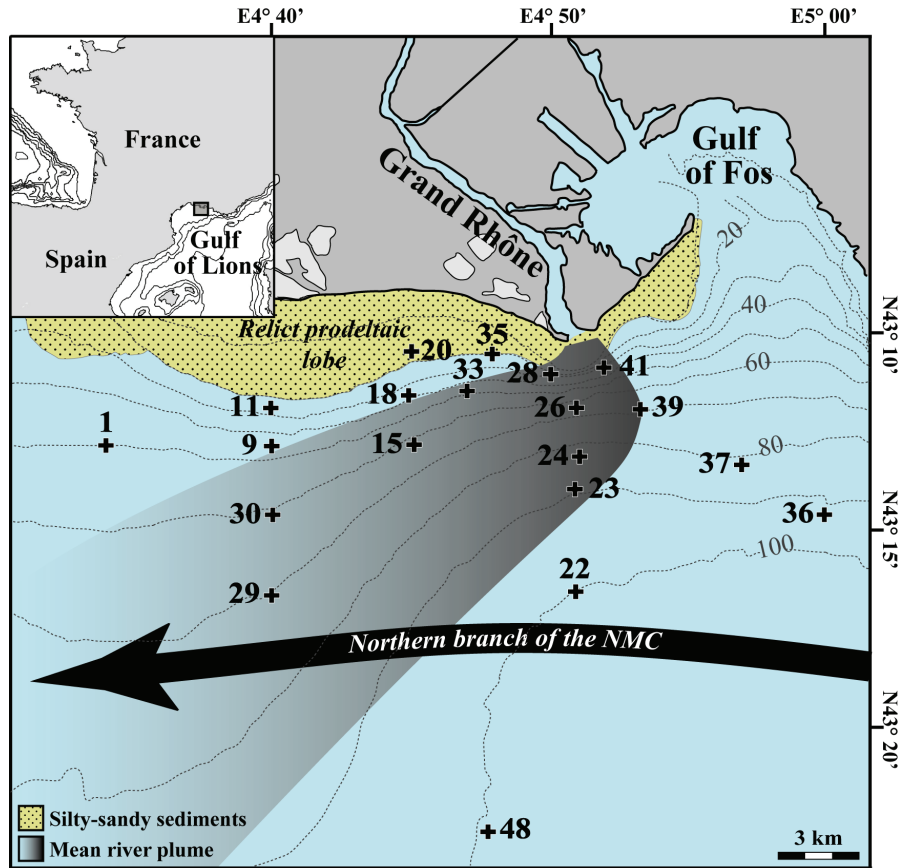


Figure 1 : Bathymetry, study area and location of the 20 investigated stations; NMC: North Mediterranean Current.

In this paper, we investigate live (stained) benthic foraminiferal assemblages from the Rhône River prodelta (Gulf of Lions, NW Mediterranean). The prodelta shows contrasted environments characterised by various physico-chemical conditions in terms of organic matter deposits, redox conditions in the sediment and substrate. We examine to what extent living foraminiferal communities are relevant and reliable environmental bio-indicators of organic matter supplies in a river-dominated shelf (Fig. 1). Benthic foraminiferal assemblages have been investigated earlier in the Rhône prodelta (Kruit, 1955; Blanc–Vernet, 1969; Bizon and Bizon, 1984). Kruit (1955) gives only a preliminary view of the distribution of foraminiferal faunas, focusing on sedimentary features. Conversely, Blanc–Vernet (1969) and Bizon and Bizon (1984) performed more precise studies providing a good preliminary taxonomic investigation of both dead and living benthic foraminifera from the prodelta. However, sampling methods (grab sampler) and the lack of measured environmental parameters did not permit them to define precisely the role of the prodelta environment on living foraminifera ecology. Mojtahid et al. (2009) studied the distribution and the ecology of live (stained) benthic foraminifera in the Rhône prodelta at 23 stations sampled in spring 2005. This work

showed that benthic foraminiferal faunas were mainly controlled by the Rhône River organic matter supplies and the oxygen penetration depth in the sediment. However, numerous studies have shown that other important parameters such as sedimentary features (granularity), and composition of the organic matter or diagenetic processes, not considered in detail by Mojtabid et al. (2009), can also have a strong impact foraminiferal faunas (e.g., Colom, 1974; Murray, 1991b; Jorissen, 1999). Therefore, for the present study, porewater chemistry (oxygen, nitrate, nitrite and ammonia), sedimentary particulate organic matter quantity (organic carbon content) and quality (amino acids and lipids contents, carbon and nitrogen stable isotopes), and sedimentary features (granularity) were analysed.

The aims of our study are (1) to describe the structure (density, diversity and composition) and spatial variability of benthic foraminiferal faunas in the Rhône prodelta, (2) to compare these data with a long environmental dataset (see above) and (3) to compare our observations with previous ones in order to appreciate the impact of organic matter quality and to investigate whether there are differences between spring (highly productive period) and the end of summer (our sampling period, less productive).

Station	Lat. (°N)	Long. (°E)	Water depth (m)	Distance from the river mouth (km)
1	43°16.992'	4°33.989'	49	22.2
9	43°17.020'	4°39.991'	44	14.6
11	43°17.973'	4°39.959'	26	14.0
15	43°17.055'	4°45.148'	60	8.9
18	43°18.288'	4°44.950'	37	7.5
20	43°19.366'	4°45.057'	15	7.8
22	43°13.250'	4°51.000'	98	11.4
23	43°15.941'	4°50.971'	86	5.7
24	43°16.757'	4°51.143'	79	4.4
26	43°17.979'	4°51.028'	62	2.8
28	43°18.816'	4°50.130'	18	1.0
29	43°13.285'	4°39.989'	68	17.9
30	43°15.301'	4°40.028'	60	16.5
33	43°18.397'	4°47.068'	47	5.4
35	43°19.324'	4°47.978'	20	3.1
36	43°15.305'	5°00.003'	89	14.4
37	43°16.550'	4°57.010'	80	9.6
39	43°17.940'	4°53.340'	69	4.1
41	43°18.998'	4°52.000'	30	1.5
48	43°07.374'	4°47.827'	100	22.4

Table 1: Location and characteristics of the 20 stations sampled during the BEHEMOTH cruise in September 2006.

1.2. MATERIALS AND METHODS

1.2.1. Study area

The Gulf of Lions is a large crescent-shaped continental shelf in the North Western Mediterranean Sea, its continental slope being incised by submarine canyons (Berné and Gorini, 2005). The oceanographic circulation is characterised by the cyclonic North Mediterranean Current (NMC) which flows south-westwards along the Gulf of Lions continental margin (Béthoux and Prieur, 1983; Millot, 1990). The general circulation is also strongly influenced by north and north-western winds, respectively the Mistral and the Tramontane (Millot, 1999). In winter, these wind regimes induce a strong mixing of the water column and surface dense water cascading (Millot, 1990; Bethoux et al., 2002; Canals et al., 2006; Ulses et al., 2008a, 2008b). In summer, weaker winds induce seasonal thermocline formation linked to water column stratification (Millot, 1990). At a basin scale, the annual primary production is moderate, with values of 78 to 204 g C.m⁻².year⁻¹ (Lefevre et al., 1997; Conan et al., 1998; Bosc et al., 2004). Bosc et al. (2004) determined a clear bloom from late winter to late spring (March, April and May) after a period of intense vertical mixing of the surface layers in winter. During the spring bloom, Chl-*a* concentrations in surface waters are above 1 mg Chl-*a*.m⁻³, contrasting with minimal Chl-*a* concentrations in summer (0.1–0.2 mg Chl-*a*.m⁻³). Nutrient inputs from the Rhône River support 50% of the total nutrient stock needed for primary production in the whole Gulf of Lions (Lochet and Leveau, 1990). The Rhône River is also the main source of freshwater and terrestrial materials in this area (respectively 90% and 80%; Durrieu de Madron et al., 2000, 2003). With an annual mean flow of 1.700 m³.s⁻¹ (Pont et al., 2002), it supplies 6.2 Mt.year⁻¹ of particles to the Gulf (Thill et al., 2001). These particulate inputs are partly mediated by a river plume that flows generally south-westward, with a marine extension and shape that depend on Rhône river outflow, wind regime and the strength of the North Mediterranean Current (Naudin et al., 1997). Flood events occur in autumn and spring with discharge values reaching 10.000 m³.s⁻¹ (Pont et al., 2002). A part of the terrestrial input of the Rhône River forms at the outlet of the river a delta front and a prodeltaic zone. This prodeltaic zone extends between 0 and 60 m water depth and from 0 to 6 km off the river mouth (Rabineau et al., 2005). High sedimentation rates ranging between 30 to 50 cm.year⁻¹ have been recorded in this area (Calmet and Fernandez, 1990; Charmasson et al., 1998; Rabineau et al., 2005). A significant part of the suspended particulate material is also transported in the bottom nepheloid layer (BNL), the main pathway for detrital transfer to the coastal area in river-dominated ocean

margins (Naudin and Cauwet, 1997). According to Got and Aloisi (1990), 70% of the introduced particles are deposited on the shelf and 30% are transferred to the slope and the deeper basin.

1.2.2. Sediment sampling

Between 26 August and 3 September 2006, twenty stations were sampled in the Rhône prodelta during the BEHEMOTH cruise on board the *R.V. Tethys II*. Stations were located at a distance of about 1 to 22 km from the river mouth, between 15 and 100 m depth (Fig. 1, Table 1). At each station, 8 sediment cores (72 cm² surface area) were recovered with a classical Barnett multicorer (Barnett et al., 1984) allowing the sampling of relatively undisturbed sediment – water interface. All geochemical and faunal analyses were performed on cores collected from the same multicorer deployment.

1.2.3. Environmental and foraminiferal faunal analyses

For almost each station (Fig. 2, Appendix A), grain sizes, total Nitrogen and Organic Carbon concentrations (TN and OC, respectively), total amino acids (AA) and lipids contents, and carbon and nitrogen stable isotopic ratios of organic matter ($\delta^{13}\text{C}_{\text{OM}}$ and $\delta^{15}\text{N}_{\text{OM}}$) were measured for the first centimetre of the sediment. For 12 stations (1, 11, 15, 18, 23, 26, 29, 35, 36, 37, 41, 48), a core was sliced in thin horizontal sections (every 0.5 cm for the top 2 cm, 1 cm below down to 10 cm depth, and every 2 cm below 10 cm) for further pore waters analyses of dissolved nitrate, nitrite and ammonia. In parallel, for almost each station (Fig. 2a,b, Appendix B), profiles of O₂ in the pore water were performed on board, and bottom free waters were collected immediately after core recovery for dissolved O₂ concentration measurements. Detailed protocols of all these parameters measurements are described in Fontanier et al. (2008b).

For faunal analysis, a sediment core was sliced on board at each station; every 0.5 cm from the sediment – water interface down to 2 cm depth, and every 1 cm from 2 to 5 cm depth. Each sample was preserved in 95% ethanol containing 1 g.l⁻¹ of Rose Bengal, a commonly used stain for live foraminifera identification (Walton, 1952; Murray and Bowser, 2000). Benthic foraminifera analyses were performed on the > 150 μm size fraction. All stained specimens from the surface to 5 cm depth were hand-sorted under wet conditions. Total foraminiferal densities (D), i.e. the total number of individuals counted on the whole 5 cm of sediment, were normalised for a surface area of 100 cm². Shannon index H and Evenness

index E (Hayek and Buzas, 1997; Murray, 2006) were calculated in order to describe the diversity of foraminiferal faunas. Cluster analyses were performed on the 20 stations (Q-mode) and the 22 major species (R-mode). These analyses were based on the arcsinus values of square root “ p_i ” for all taxa recorded in each core (J. Hohenegger, personal communication). “ p_i ” is the relative frequency of the i species in one core. We constructed tree diagrams using Ward’s method based on Euclidian distance. For Q-mode clustering, we applied the Indicator Value (IV) Method with major species (Dufrêne and Legendre, 1997) following Baldi and Hohenegger (2008) to determine indicative species in each cluster of stations. A taxon is considered as indicative when its IV is greater than 30%.

1.3. RESULTS

1.3.1. Sedimentary features

At Stations 11, 20 and 35 located close to the shore line, grain size frequencies Q_{50} and D_{90} describe silty to sandy sediments ($Q_{50} > 38 \mu\text{m}$ and $D_{90} > 110 \mu\text{m}$, Fig. 2c,d and Appendix A). The surficial sediments contain numerous gastropods (mostly *Turitella* spp.) and mollusc bioclasts. Stations 18, 26, 28, 33, 39 and 41 (between 18 and 69 m depth) are characterised by silt rich in plant remains ($D_{90} > 42 \mu\text{m}$). Stations 1, 9, 15, 22, 23, 24, 29, 30, 36 and 37 (from 44 to 98 m depth) are equally characterised by silty sediment, but with few plant remains ($Q_{50} < 10 \mu\text{m}$ and $D_{90} < 47 \mu\text{m}$).

1.3.2. Bottom and pore water oxygenation

Bottom waters exhibit high oxygen concentration at all investigated stations ($> 200 \mu\text{mol.l}^{-1}$) (Fig. 2a and Appendix B). The highest O_2 concentrations are measured close to the Rhône River mouth with a value of $293 \mu\text{mol.l}^{-1}$ (92.8% O_2 saturation) at Station 26 (62 m). The lowest concentrations are recorded at the deeper stations 23 (86 m) and 48 (100 m) with respective values of 204 and $210 \mu\text{mol.l}^{-1}$ (63.5 and 64.5% O_2 saturation, respectively). Oxygen penetration depth (OPD) increases with distance from the river mouth (Fig. 2b and Appendix B). The OPD is only 1.5 mm at Station 28 (18 m depth) and it increases to 6.7 and 8.4 mm offshore (Stations 1, 29, 30, 48).

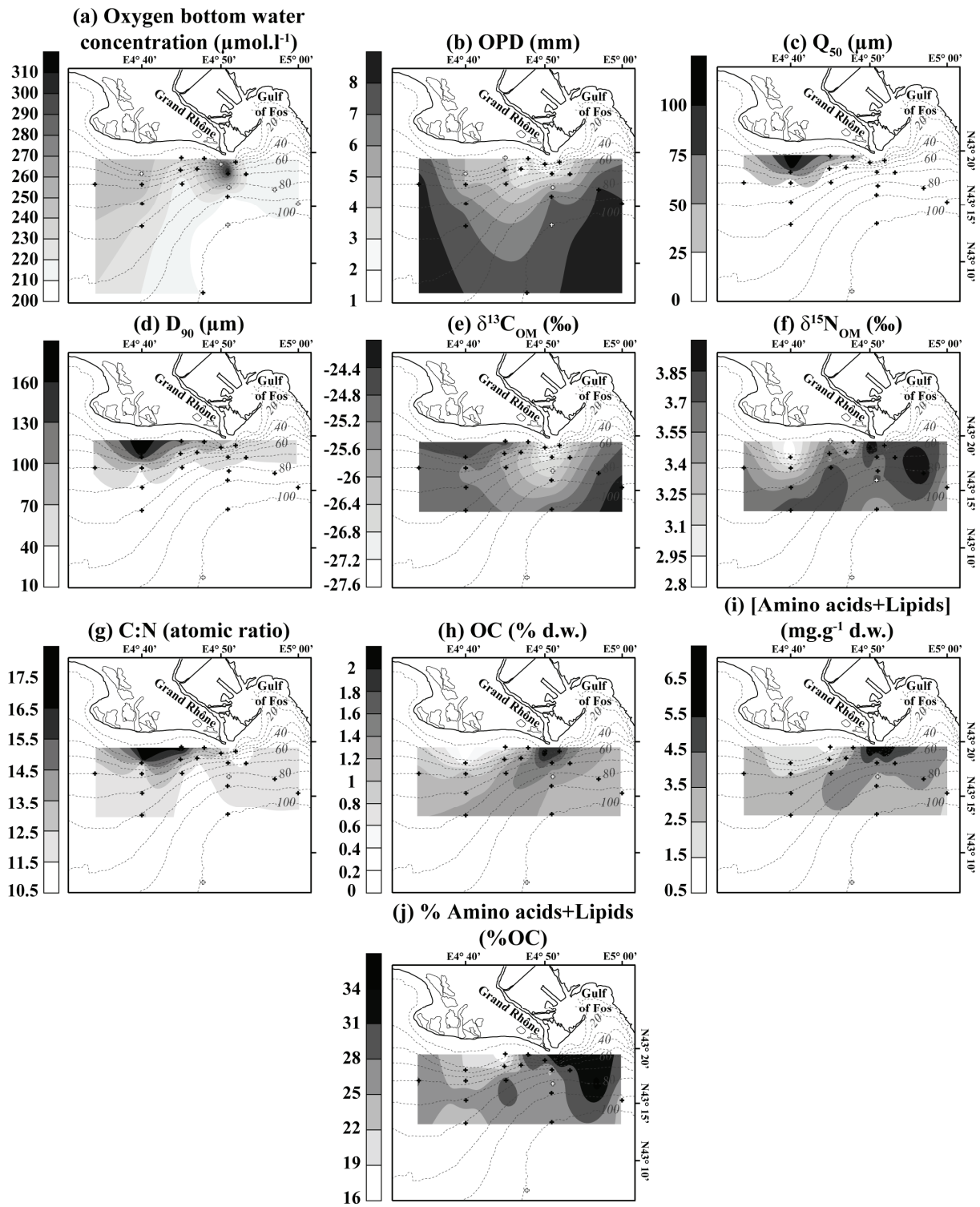


Figure 2: Spatial distribution of the different analysed environmental parameters; measurements were performed at stations represented by a black cross. (a–b) Dissolved oxygen concentration in bottom water and oxygen penetration depth in the sediment; (c–d) Grain size frequencies Q_{50} and D_{90} ; (e–g) Isotopic and atomic signatures of particulate organic matter from the first centimetre of sediment ($\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$); (h–i) Total organic carbon content (long-term precision: $\pm 0.02\%$) and sum of amino acids (precision: $\pm 15\%$) and lipids concentration (precision: $\pm 10\%$) for dry-weight sediment (d.w.); and (j) Percentage of amino acids and lipids in OM in the first centimetre of sediment.

1.3.3. Nitrate, nitrite and ammonia

At Stations 35 and 41 (respectively 20 and 30 m depth), close to the river mouth, ΣNH_3 (ammonium + ammonia) concentration exhibits a strong increase with sediment depth, with values of 500–1000 $\mu\text{mol.l}^{-1}$ in the 8–9 cm depth interval (Table 2, Appendix C). At the other stations, the downcore increase is moderate with values ranging from 0 at the sediment water – interface to 40–220 $\mu\text{mol.l}^{-1}$ in the deeper levels. ΣNO_3 (nitrate + nitrite) concentration decreases with sediment depth at all stations. A peak of ΣNO_3 concentration is always recorded in the oxygenated part of the sediment (first centimetre) and an additional maximum is frequently present in the anoxic part of the sediment (between 2 and 9 cm depth), i.e. Stations 41, 26, 35, 23 and 1.

Station	41	26	35	23	18	15	37	36	29	1	48
Distance from the river mouth (km)	1.5	2.8	3.1	5.7	7.5	8.9	9.6	14.4	17.9	22.2	22.4
Sediment depth (cm)		ΣNH_3 ($\mu\text{mol.l}^{-1}$)									
0	2.8	6.2	10.6	5.5	9.5	3.9	5.4	6.8	6.8	5.1	5.8
0.25	148.7	28.9	56.9	14.8	13.9	8.7	9.2	6.1	5.7	2.9	6.5
0.75	207.5	64.0	157.7	31.2	20.5	7.8	9.2	6.8	10.4	18.9	21.8
1.25	322.2	70.2	188.0	57.7	28.6	21.4	10.8	11.4	10.2	25.5	10.9
1.75	371.1	93.6	202.3	67.9	30.0	31.1	27.0	18.2	24.8	37.1	19.6
2.5	542.4	106.9	315.0	87.4	45.4	54.4	38.5	12.9	22.6	53.8	17.5
3.5	710.3	109.2	404.5	116.2	64.5	73.9	64.7	7.6	47.3	80.8	17.5
4.5	796.6	135.0	429.2	119.1	108.5	80.7	76.3	19.7	70.7	116.4	29.1
5.5	854.0	161.5	471.4	117.0	123.8	101.1	98.6	13.6	80.6	117.9	38.6
6.5	919.2	177.1	492.5	119.1	160.5	98.2	133.3	17.4	88.5	125.9	36.4
7.5	941.1	194.2	485.3	104.4	167.8	139.0	125.6	23.5	94.4	–	41.5
8.5	1006.3	153.7	513.6	93.3	–	158.4	144.1	37.9	104.9	156.4	37.1
9.5	942.5	202.8	478.7	110.7	224.2	144.8	145.6	44.0	96.0	174.6	36.4
Sediment depth (cm)		ΣNO_3 ($\mu\text{mol.l}^{-1}$)									
0	3.0	1.8	2.1	4.7	2.4	2.1	5.1	4.5	2.4	1.3	5.0
0.25	–	1.8	3.2	2.6	6.8	7.3	8.4	6.9	4.9	4.6	5.9
0.75	–	1.3	1.5	2.6	2.1	1.9	5.1	5.2	1.2	0.8	3.4
1.25	0.9	1.4	1.5	1.9	1.4	0.9	1.4	1.7	1.0	0.6	1.7
1.75	–	2.1	2.1	2.8	1.1	0.8	1.6	1.5	1.3	0.8	1.1
2.5	1.9	1.0	2.7	3.5	1.4	1.2	1.0	1.7	1.1	0.4	1.3
3.5	2.3	1.2	1.9	5.4	1.1	1.4	0.6	1.5	0.8	0.9	0.8
4.5	0.9	1.3	0.7	1.5	1.6	1.1	0.6	0.9	0.7	1.1	0.8
5.5	1.3	1.2	0.5	2.2	0.6	–	2.0	0.7	1.0	1.2	1.3
6.5	1.6	1.4	0.6	1.7	1.2	1.6	1.0	1.9	1.3	1.9	0.4
7.5	1.0	1.0	0.7	1.3	1.4	1.4	0.8	1.1	0.9	–	0.4
8.5	0.5	1.1	0.7	1.5	–	1.4	0.7	0.9	0.7	2.6	0.6
9.5	0.7	1.2	0.7	1.7	1.4	1.2	–	0.7	0.6	0.7	0.6

Table 2: Geochemical analyses performed at 11 stations from the closest (Station 41) to the farthest station (Station 48) from the Rhône River mouth: ΣNO_3 and ΣNH_3 profiles in the porewater. Bold values indicate maximal concentrations at each station. Precisions are $\pm 5\%$ for ΣNH_3 and $\pm 0.5 \mu\text{mol l}^{-1}$ for ΣNO_3 .

1.3.4. Sedimentary Organic Matter

In the study area, OC content in the first cm of the sediment ranges between 0.43 and 2.10% (dry weight) (Fig. 2h). Lower values are recorded at sandy stations (Stations 11, 20, 35) and at the sites (Stations 1, 22, 36) farthest from the river mouth. Higher values are measured in the vicinity of the river mouth at Stations 26, 28 and 41. $\delta^{13}\text{C}_{\text{OM}}$ ranges from -27.51‰ at the Rhone River mouth to -24.21‰ south-eastwards, with a corridor of low values along a south-western axis (Fig. 2e). The spatial distribution of $\delta^{15}\text{N}_{\text{OM}}$ is more heterogeneous, with data ranging from 2.83 to 4.01‰ (Fig. 2f). The highest $\delta^{15}\text{N}_{\text{OM}}$ value is recorded close to the river mouth but no obvious spatial trend is observed with the other data. High values of C:N ratio (> 13.1) are recorded at sandy stations 20, 35 and 18 (Fig. 2g). Sediment at Stations 28 and 41 (in the vicinity of the river mouth) is obviously enriched in amino acids and lipids with concentrations $> 6 \text{ mg.g}^{-1}$ (Fig. 2i), that contribute to 28.9 and 35.7% of OC (Fig. 2j). The spatial distribution of both compounds shows also a corridor of high values in a south-western direction. Minimal values are observed in sandy sediments of Stations 11 and 20 ($< 1.5 \text{ mg.g}^{-1}$).

1.3.5. Foraminiferal faunas ($> 150 \mu\text{m}$)

1.3.5.1 Foraminiferal density, diversity and equitability

A total number of 133 taxa was identified in the Rhône prodelta composed of 70 hyaline, 35 agglutinated and 28 porcellaneous taxa. Twenty-two species present a relative abundance higher than 5% at least at one station (Appendices D and E). They are considered as major species. The distribution of these taxa is pictured in Figure 3.

Living foraminiferal density (D) tends to increase with distance from the river mouth. The highest value is recorded at Station 30 with 2580 individuals/100 cm². High foraminiferal densities are also recorded at Stations 18, 22, 35, 36 and 37 with values ranging between 1650 and 1850 ind./100 cm² (Fig. 4a). Species richness (S) ranges from 9 (Station 28, 18 m) to 69 (Station 48, 100 m) (Fig. 4b), and increases with distance from the river mouth towards the deepest stations. The Shannon index (H) shows a similar trend with increasing values from the river mouth at Station 41 (1.30) to the deeper stations 48, 22 and 36 (H between 3.22 and 3.5) (Fig. 4c). The Evenness index (E) also increases with depth and values range from 0.18 (Station 33) to 0.48 (Station 36) (Fig. 4d). Because of the very low density recorded at Station 28 (46 ind./100 cm²), this station was not taken into account for Shannon and Evenness indices and for the distribution of the major species. In a study of replicate cores from the

Rhône prodelta, the authors demonstrate that absolute densities may vary significantly between replicate cores at a same station, without significant changes of the percentages of dominant taxa (Goineau et al., Submitted – see Chapter 2 in this thesis). Consequently, we have decided to use percentage data for our statistics and to picture foraminiferal distributional patterns (Fig. 3).

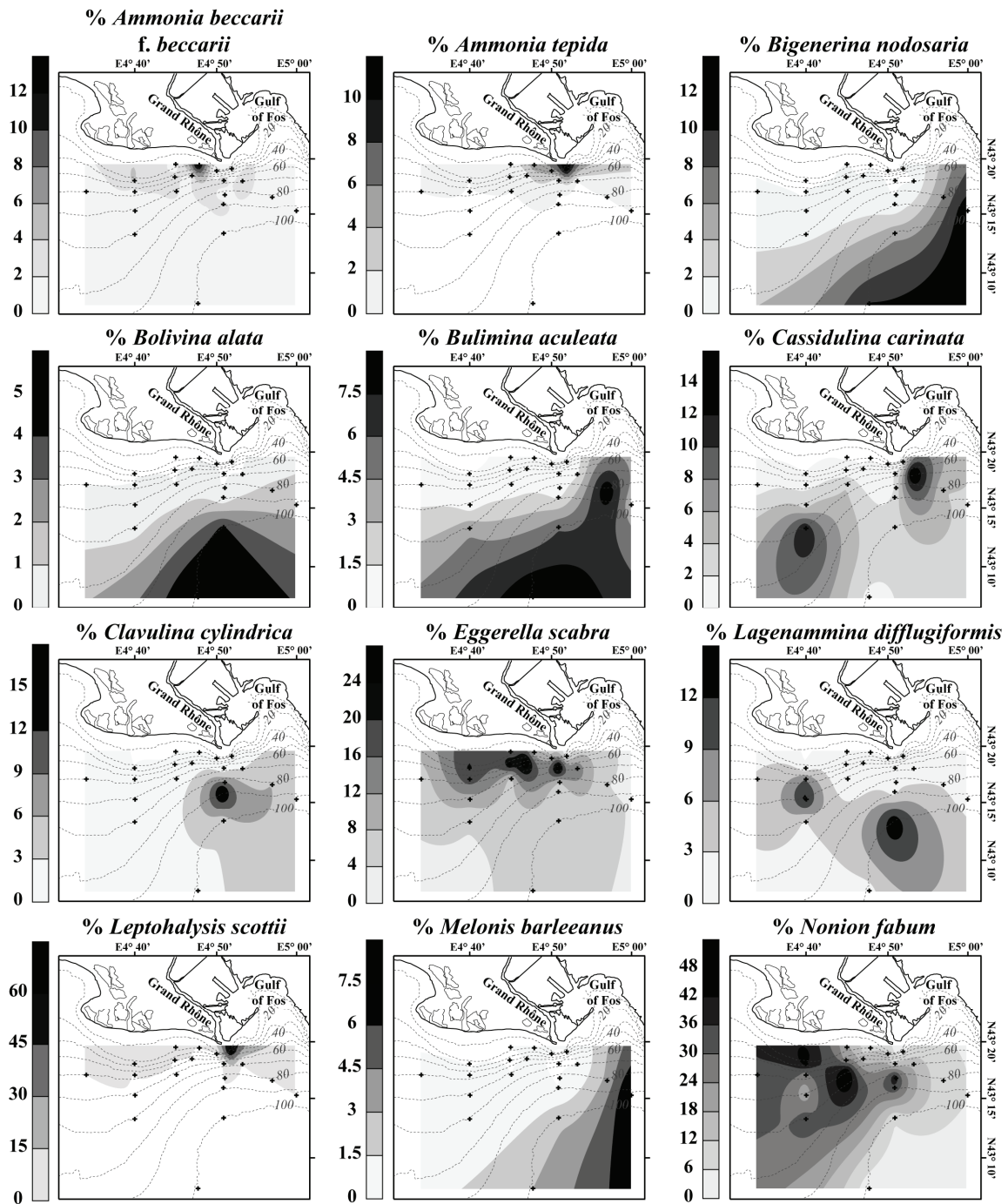


Figure 3: Relative abundances and spatial distribution of the 22 major species (> 5% in at least one station) of the > 150 μm size fraction.

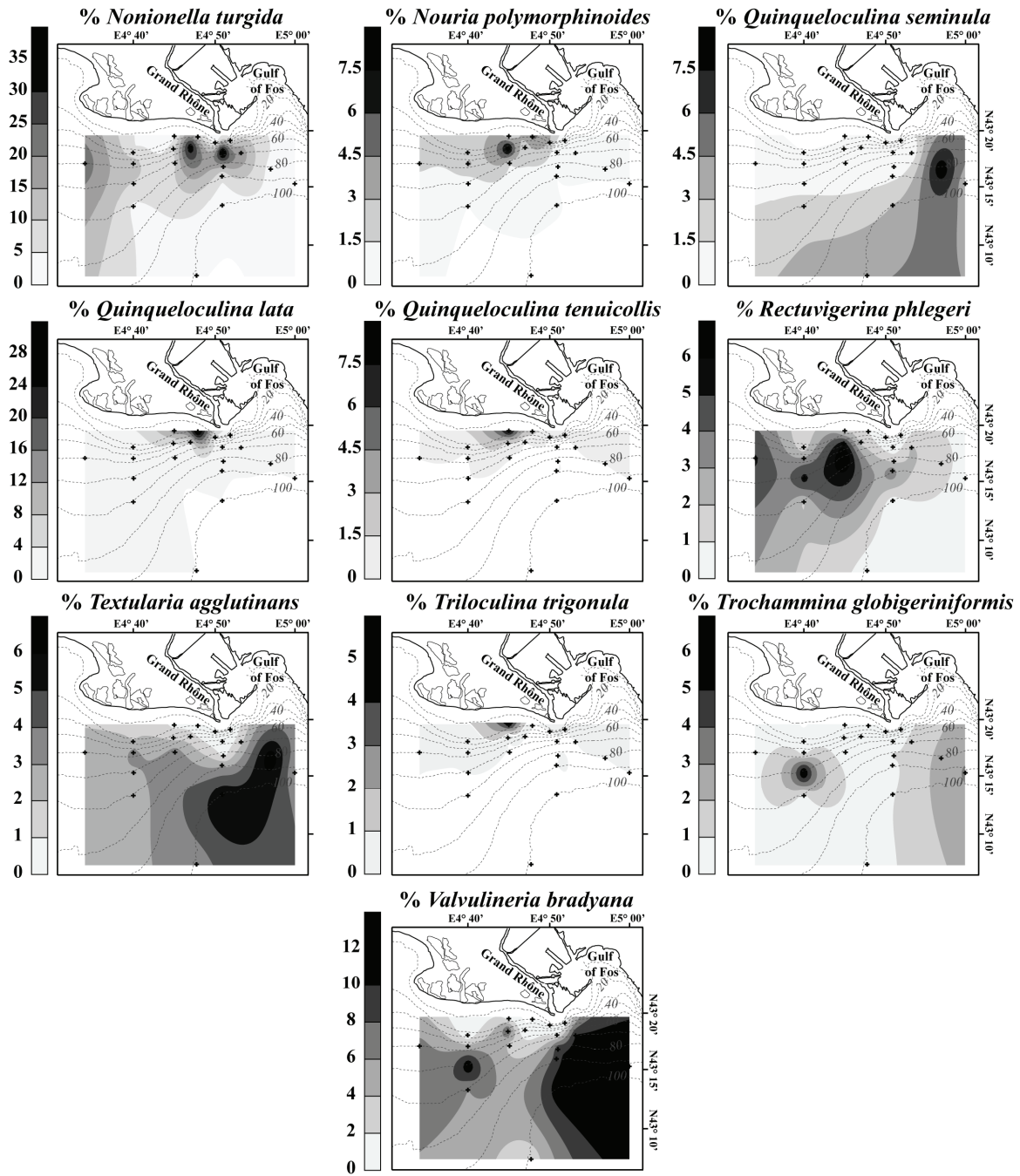


Figure 3 (continued)

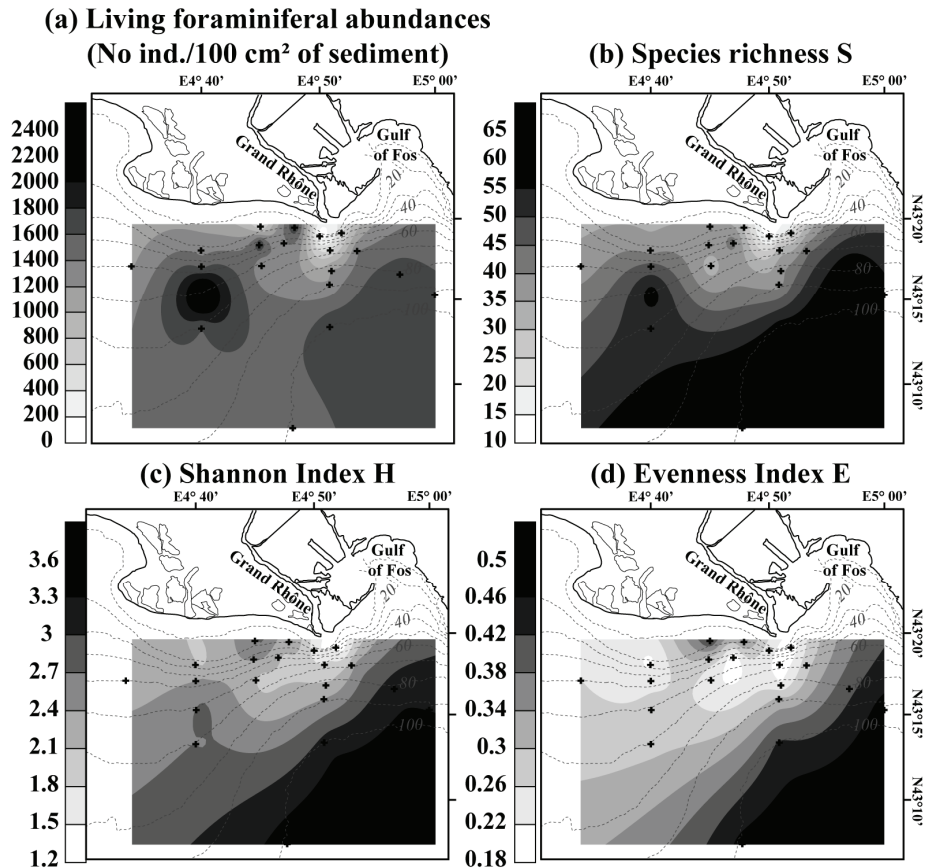


Figure 4: Ecological indices describing foraminiferal assemblages from the top 5 cm of sediment. Station 28 is not represented because of its very low faunal density ($<< 300$ ind./ 100 cm^2). (a) Foraminiferal densities normalised for a surface area of 100 cm^2 of sediment; (b) Number of species S ; and (c–d) Biodiversity (H) and Evenness (E) indices.

1.3.5.2. Cluster analyses

1.3.5.2.1. R-mode clustering

When a cut-off level of 0.8 is applied, R-mode cluster analysis allows us to distinguish 4 groups of species and 3 single ones (Fig. 5): Group T1 composed of *Ammonia beccarii* forma *beccarii* (sensu Jorissen, 1988), *Nouria polymorphinoides*, *Quinqueloculina lata*, *Quinqueloculina tenuicollis* and *Triloculina trigonula*; Group T2 composed of *Bolivina alata*, *Melonis barleeanus*, *Bigenerina nodosaria*, *Bulimina aculeata* and *Quinqueloculina seminula*; Group T3 with *Cassidulina carinata*, *Rectuvigerina phlegeri*, *Textularia agglutinans*, *Trochammina globigeriniformis*, *Clavulina cylindrica*, *Lagenammina difflugiformis* and *Valvulineria bradyana*; Group T4 with *Nonionella turgida* and *Eggerella scabra*.

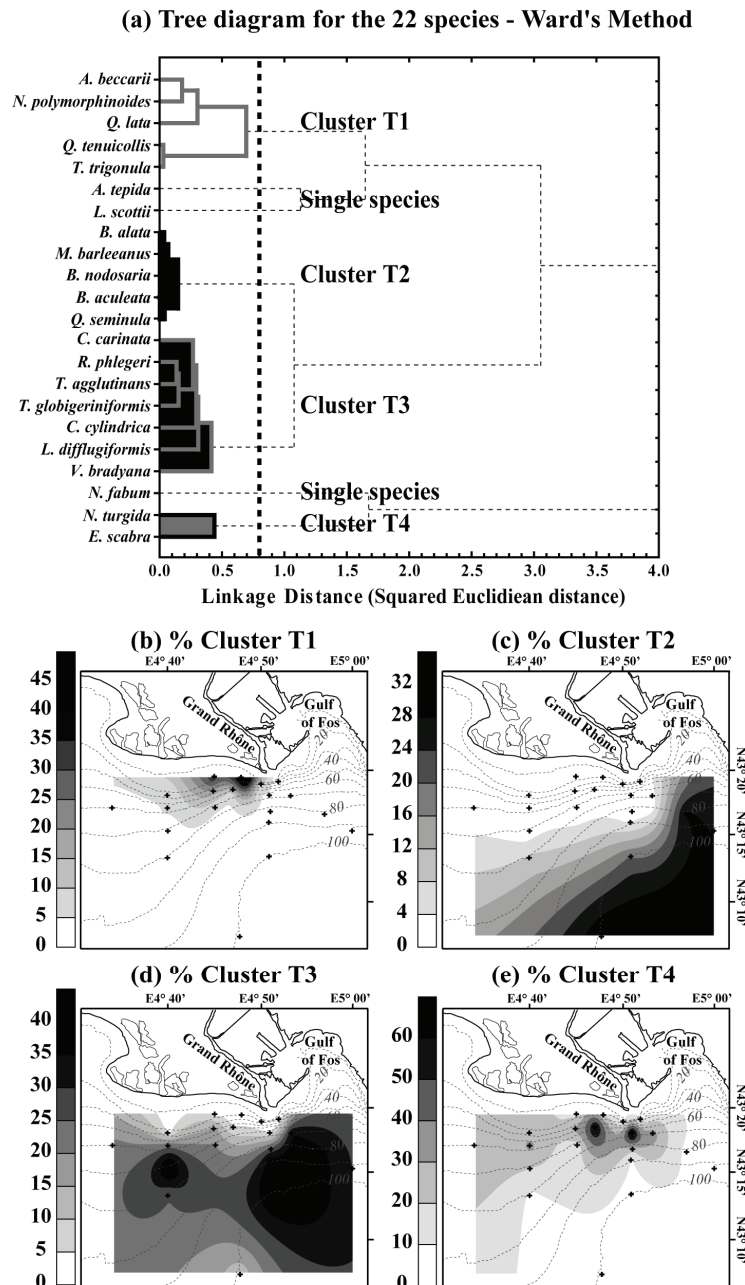


Figure 5: (a) R-mode cluster analysis of the 22 major species (> 5% in at least one station) according to Ward's method, based on standardised percentages P_i of these species. (b–e) Relative abundance and spatial distribution of the four groups of species defined by R-mode clustering.

1.3.5.2.2. Q-mode clustering

A cut-off level of 0.8 is applied to the Q-mode cluster analysis, dividing our stations into four main groups plus two single stations (Fig. 6). Calculation of the Indicator Value allowed us to determine indicative species in each cluster ($IV > 30\%$) (Table 3).

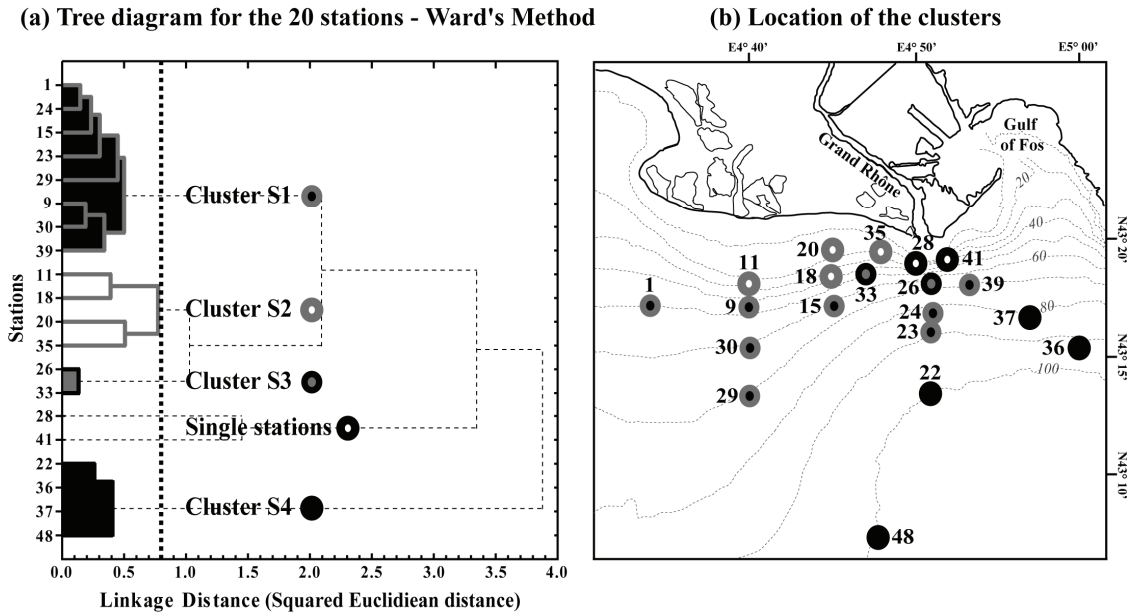


Figure 6: (a) Q-mode cluster analysis of the 20 stations according to Ward's method, based on standardised percentages P_i of total foraminiferal assemblages of the $> 150 \mu\text{m}$ size fraction; (b) Location of the groups of stations defined by Q-mode clustering.

Cluster S1 corresponds to stations 1, 9, 15, 23, 24, 29, 30 and 39 (44–86 m) under the mean position of the river plume, *C. carinata*, *R. phlegeri*, *T. globigeriniformis* and *Nonion fabum* are the most indicative species, associated with secondary species *C. cylindrica*, *L. difflugiformis* and *V. bradyana*. Cluster S2 groups Stations 11, 18, 20 and 35 (15–37 m) located in the sandy sediment. *Q. tenuicollis*, *Q. lata*, *N. polymorphinoides*, *A. beccarii* f. *beccarii* and *T. trigonula* are the most characteristic species of this cluster, associated in a less extent with *E. scabra*, *N. fabum* and *R. phlegeri*. Cluster S3 corresponds to Stations 26 and 33 (47–62 m), farther from the river mouth, with *N. turgida* and *E. scabra*. Species defined as secondary taxa in Cluster S1 (*C. cylindrica*, *L. difflugiformis* and *V. bradyana*) are more developed in cluster S4 that corresponds to the deepest and farthest Stations 22, 36, 37 and 48 (80 to 100 m depth), where *B. alata*, *B. nodosaria*, *M. barleeanus*, *Q. seminula*, *B. aculeata* and *T. agglutinans* are the most characteristic taxa. *T. globigeriniformis* and *C. carinata* are still indicative species but less so than in cluster S1. At single Stations 28 (18 m) and 41 (30 m) located at the immediate vicinity of the river mouth, *Ammonia tepida* and *Leptohalysis scottii* are the indicative species of benthic foraminiferal faunas.

Clusters or Single stations Major species (> 5%)	28	41	Cluster S1	Cluster S2	Cluster S3	Cluster S4
<i>Ammonia beccarii</i> f. <i>beccarii</i>	0	1	15	62	13	9
<i>Ammonia tepida</i>	20	48	0	18	8	0
<i>Bigenenerina nodosaria</i>	0	0	2	0	0	96
<i>Bolivina alata</i>	0	0	2	0	0	96
<i>Bulimina aculeata</i>	0	0	13	1	5	81
<i>Cassidulina carinata</i>	0	0	57	0	4	38
<i>Clavulina cylindrica</i>	0	0	40	0	6	53
<i>Eggerella scabra</i>	1	1	19	32	37	11
<i>Lagenammia difflugiformis</i>	0	1	38	0	2	53
<i>Leptohalysis scottii</i>	0	97	0	1	1	0
<i>Melonis barleeanus</i>	0	0	1	0	0	95
<i>Nonion fabum</i>	1	1	45	32	11	10
<i>Nonionella turgida</i>	0	4	26	15	50	5
<i>Nouria polymorphinoides</i>	1	3	11	68	7	0
<i>Quinqueloculina lata</i>	1	2	8	76	13	0
<i>Quinqueloculina seminula</i>	0	1	12	0	1	84
<i>Quinqueloculina tenuicollis</i>	0	0	0	99	0	0
<i>Rectuvigerina phlegeri</i>	0	0	49	31	10	10
<i>Textularia agglutinans</i>	0	0	26	10	8	56
<i>Triloculina trigonula</i>	0	0	2	46	0	0
<i>Trochammina globigeriniformis</i>	0	0	46	4	7	44
<i>Valvulineria bradyana</i>	0	0	37	3	1	50

Table 3: Indicator values (IV; Dufrêne and Legendre, 1997) of the major species for each group of stations defined by Q-mode cluster analysis. For each species, IV > 30% are indicated by light grey shades, and the maximum IV by dark grey boxes.

1.4. DISCUSSION

1.4.1. Environmental settings

The spatial distribution of quantitative and qualitative descriptors of sedimentary organic matter show a south-westward trend from the river mouth in agreement with the yearly mean position of the Rhône River plume over the shelf (Naudin et al., 1997). In Figure 7, $\delta^{13}\text{C}_{\text{OM}}$ versus $\delta^{15}\text{N}_{\text{OM}}$ of sedimentary organic matter for all stations are plotted. We compare our data with the isotopic signatures of different sources of particulate organic matter (POM) potentially contributing to the organic matter supply to the sea floor in our study area (Darnaude et al., 2004; Harmelin-Vivien et al., 2008; P. Kerhervé, personal communication). All the stations spread between the three end-members (Rhône River POM, marine POM and Terrestrial plant detritus). Stations 28 and 41, which are located in the delta front, are characterised by the lowest $\delta^{13}\text{C}_{\text{OM}}$ values ($\delta^{13}\text{C}_{\text{OM}} < -27\text{‰}$), suggesting the strongest contribution of the Rhône River. Stations 9, 15, 18, 23, 26, 33, 35 and 39 are characterised by a mixing between both marine and terrestrial POM with, nevertheless, a dominant influence

of continental source. $\delta^{13}C_{OM}$ values at the deeper and farther stations 1, 11, 22, 29, 30, 36 and 37 show a more pronounced marine influence. A noticeable observation is the lack of stations with a strongly dominant marine influence (offshore seawater POM).

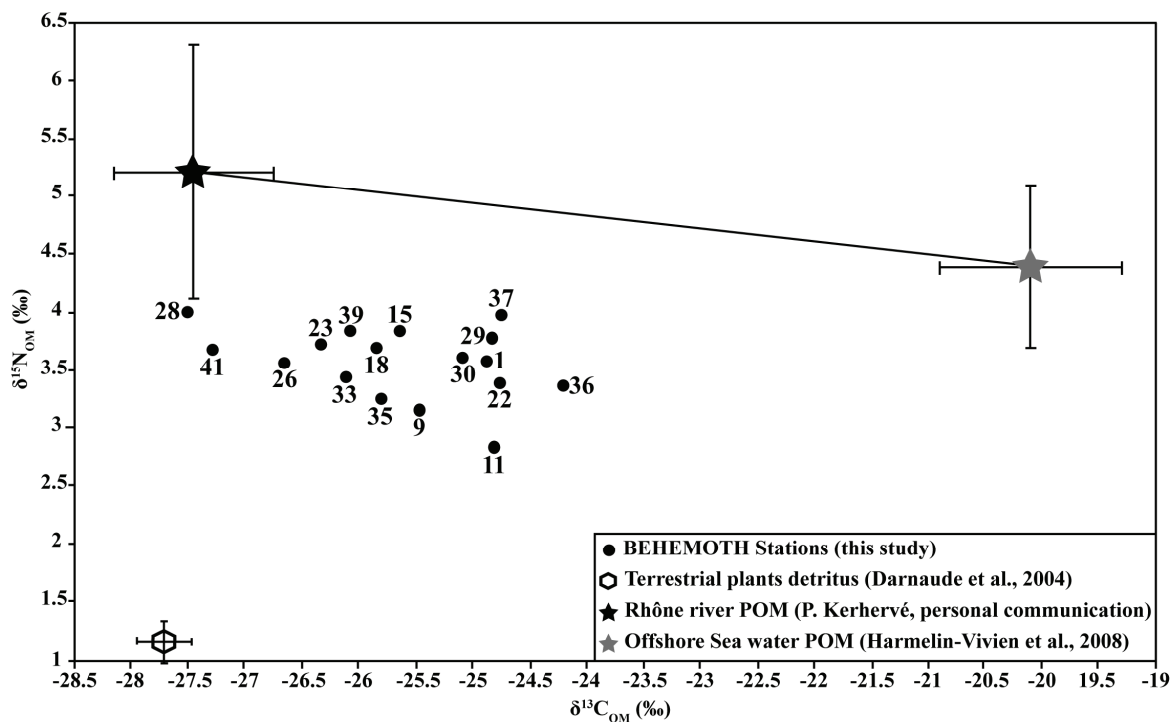


Figure 7: Stable isotopic composition of the organic matter ($\delta^{13}C_{OM}$ vs $\delta^{15}N_{OM}$) from the first centimetre of sediment. The composition of three possible OC sources (Terrestrial plant detritus, Rhône River POM, and offshore seawater POM) are also plotted to illustrate the relative influence of each source.

The overall contribution of marine POM in the prodeltaic area is obviously related to primary production which is largely determined by the spring bloom (Bosc et al., 2004) and the Rhône River discharge (Lochet and Leveau, 1990). For instance, Sea WiFS images (“Ocean Color” website, <http://marine.jrc.ec.europa.eu/>) reveal that in 2006 the spring bloom started at the end of March ($> 1 \text{ mg Chl-}a.m^{-3}$), following a high Rhône River discharge period ($> 2000 \text{ m}^3.s^{-1}$, Compagnie Nationale du Rhône; Fig. 8a) and especially two Rhône River floods in March–April ($> 3000 \text{ m}^3.s^{-1}$, until $3700 \text{ m}^3.s^{-1}$; Fig. 8a). This episode of high primary production ended in May, with Chl-*a* concentration remaining low ($< 0.5 \text{ mg Chl-}a.m^{-3}$) until our sampling period (August/September 2006). This temporary context could explain the fairly moderate contribution of marine-derived OM in surface sediment in September 2006 (our sampling period). However, we can also not exclude the occurrence of degradation processes in surface sediments that tend to decrease $\delta^{13}C_{OM}$ values of fresh and labile marine OM (Lehmann et al., 2002). Nevertheless, even though previous studies pointed

out the strong continental signature of the organic detritus exported to the Rhône prodelta (Durrieu de Madron et al., 2000; Darnaude et al., 2004; Tesi et al., 2007; Lansard et al., 2009; Mojtahid et al., 2009), other studies reported that sedimentary OM occasionally has a strong marine signature (Tesi et al., 2007; Lansard et al., 2009).

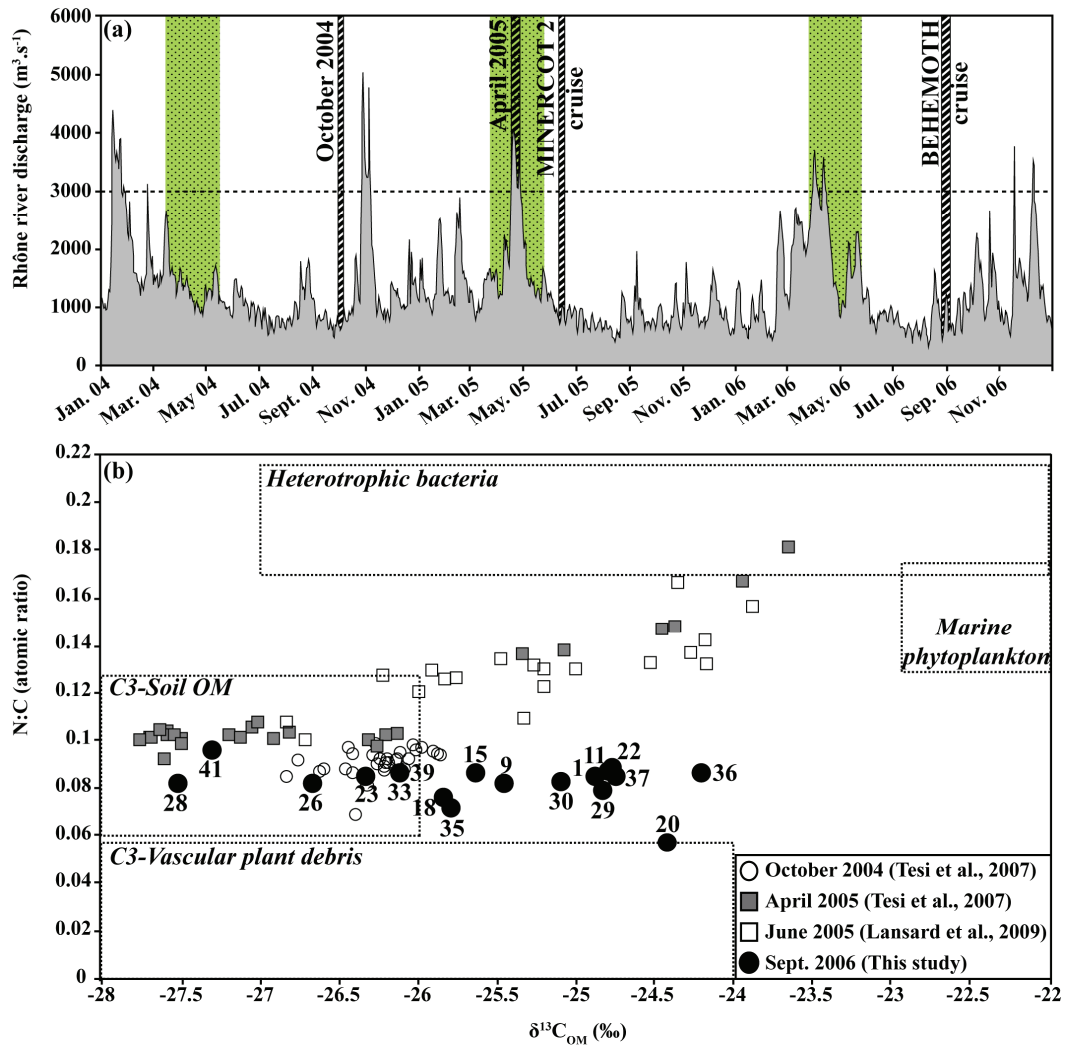


Figure 8: (a) Mean daily discharge of the Rhône River recorded at Beaucaire, located 65 km upstream from the river mouth from January 2004 to December 2006 (Compagnie Nationale du Rhône). Different sampling campaigns are represented by black hatched areas; the black dotted line indicates the minimum discharge value defining a Rhône River flood; green dotted areas represent spring blooms in the Gulf of Lions (SeaWiFS images); (b) Stable isotopic composition of the organic carbon ($\delta^{13}C_{OM}$) vs N:C atomic ratio for the first centimetre of sediment. Data represented were collected in September 2006 (this study), October 2004 and April 2005 (Tesi et al., 2007), and June 2005 (Lansard et al., 2009). The composition of four possible OC sources (C_3 vascular plant detritus, C_3 soil OM, marine phytoplankton detritus and heterotrophic bacteria) is also plotted to illustrate the relative influence of each source. The N:C ratio was used rather than the classical C:N ratio because the former are more robust statistically and behave linearly in a mixing model (Gordon and Goñi, 2003).

In Figure 8b, $\delta^{13}\text{C}_{\text{OM}}$ and N:C atomic ratio are plotted in order to compare our geochemical measurements (September 2006) with those performed in October 2004 and April 2005 by Tesi et al. (2007), and in June 2005 by Lansard et al. (2009). In October 2004 and in September 2006, sedimentary OM was characterised by a mixture of soil-derived OM, vascular plant debris and degraded marine OM. Conversely, N:C ratio recorded in April and June 2005 suggest a larger contribution of fresh marine POM at the distal stations (high N:C ratio and $\delta^{13}\text{C}_{\text{OM}}$). This marine contribution may be related to high Chl-*a* concentration ($> 1 \text{ mg Chl-}a \cdot \text{m}^{-3}$) in marine surface waters from the mid of March to the end of May, with a maximum after the annual Rhône River flood (up to $4000 \text{ m}^3 \cdot \text{s}^{-1}$ on 04/20/2005). This spring bloom period ended few weeks before the sampling campaign of June 2005.

During our sampling period, the highest values of OC and available organic matter concentration (AA and lipids; Grémare et al., 2003, 2005) are recorded at the river mouth with a corridor of high contents in the south-western direction (Fig. 2 and Appendix A). In many studies, terrestrial organic matter is considered as strongly refractory (Keil et al., 1997; Burdige, 2007). However, the Rhône River organic supplies are remarkably important in the proximal prodelta ($53 \text{ to } 318 \pm 79 \text{ g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$; Lansard et al., 2009) and a part of the organic compounds is available for mineralisation by benthic organisms (Grémare et al., 2003, 2005). Consequently, the OPD is minimal at the proximal stations ($< 3.2 \text{ mm}$ at Stations 26 and 41) and increases with distance from the river mouth (8.1 mm at Station 37). The very shallow OPD into the sediment (Fig. 2 and Appendix B) indicates an intense sedimentary OC mineralisation close to the river mouth (Lansard et al., 2009). Moreover, low concentration of $\sum\text{NO}_3$ and a high $\sum\text{NH}_3$ gradient from deep to surficial sediments recorded at the shallowest sites plead for intense denitrification and ammonification processes, indicative of important additional degradation of the organic matter through anaerobic pathways (Froelich et al., 1979). Oxygen consumption decreases with depth/distance from the river mouth and anaerobic processes become less important (lower $\sum\text{NO}_3$ consumption and lower $\sum\text{NH}_3$ production). Finally, the low OC contents ($< 1\%$) and high C:N ratio (> 17) recorded at the sandy stations (Stations 11 and 20) (Fig. 2 and Appendix A) may be related to hydrodynamical reworking of fine-grained material onto which OM is generally adsorbed (Mayer, 1994; Keil et al., 1998). Consequently, only coarse-grained material and plants debris remain, increasing C:N values (or decreasing N:C ratio) (Buscail et al., 1995; Keil et al., 1998; Leithold and Hope, 1999; Tesi et al., 2007).

1.4.2. Benthic foraminiferal biofacies.

R-mode and Q-mode cluster analyses processed on benthic foraminifera are synthesised in Table 4. Clusters of species (R-mode) and indicative species determined within clusters of stations (Q-mode) define the same groups of species, enabling us to identify five clear biofacies (single species and Biofacies A, B, C D). However, four species (*Clavulina cylindrica*, *Lagenammina difflugiformis*, *Textularia agglutinans* and *Valvulineria bradyana*) are grouped either with Biofacies C (i.e. under the Rhône River influence with R-mode clustering) or with Biofacies D (i.e. out of the Rhône River influence with Q-mode clustering and IV method). Therefore, we decide to define a sixth Biofacies E composed by these four species. Spatial distribution of the six biofacies is represented in Figure 9.

Major species (> 5%)	Clusters		T4				T3				T2				Biofacies	Location in the Rhône prodelta
	Single species	Single stations	S3	S1	S2	S4	S1	S2	S3	S4	S1	S2	S3	S4		
<i>Ammonia tepida</i> <i>Leptohalysis scottii</i>	■	■													Single species	At the immediate vicinity of the Rhône River mouth
<i>Eggerella scabra</i> <i>Nonionella turgida</i>			■	■				■							Biofacies A	Close to the Rhône River mouth
<i>Ammonia beccarii</i> f. <i>beccarii</i> <i>Nouria polymorphinoides</i> <i>Quinqueloculina lata</i> <i>Quinqueloculina tenuicollis</i> <i>Triloculina trigonula</i>					■	■		■							Biofacies B	Sandy substrate
<i>Eggerella scabra</i> <i>Nonion fabum</i> <i>Rectuvigerina phlegeri</i>	■		■					■			■					
<i>Cassidulina carinata</i> <i>Nonion fabum</i> <i>Rectuvigerina phlegeri</i> <i>Trochammina globigeriniformis</i>	■							■			■			■	Biofacies C	Under the Rhône River influence
<i>Bigenerina nodosaria</i> <i>Bolivina alata</i> <i>Bulimina aculeata</i> <i>Melonis barleeanus</i> <i>Quinqueloculina seminula</i>												■		■	Biofacies D	Out of the Rhône River influence
<i>Cassidulina carinata</i> <i>Trochammina globigeriniformis</i>											■			■		
<i>Clavulina cylindrica</i> <i>Lagenammina difflugiformis</i> <i>Textularia agglutinans</i> <i>Valvulineria bradyana</i>											■	■		■	Biofacies E	At the edge of river/marine influence

Table 4: Synthesis of R-mode and Q-mode cluster analyses and definition of the different biofacies. For Clusters T1, T2, T3 and T4 (R-mode), dark grey shades indicate the clustered species. For Clusters S1, S2, S3 and S4 (Q-mode), dark grey boxes correspond to maximum IV of the species (i.e., the most indicative species of the cluster), whereas light grey shades indicate IV between 30 and 40% (i.e., secondary species of the cluster).

The single Stations 28 and 41 are characterised by live faunas dominated by *Leptohalysis scottii* and *Ammonia tepida* (Fig. 9a). As indicated by ΣNH_3 concentration in the sediment and OPD, aerobic and anaerobic degradation of the organic matter is very intense, due to high amounts of available organic matter supplied by the Rhône River. Moreover, sediment deposition rate may vary drastically through time in relation to the riverine discharge, the dynamics of the bottom nepheloid layer and the intensity of wave-induced sediment reworking (Calmet and Fernandez, 1990; Naudin and Cauwet, 1997; Charmasson et al., 1998; Rabineau et al., 2005; Durrieu de Madron et al., 2008). In these conditions, foraminiferal faunas are poorly diverse. Low Evenness index is related to the strong dominance of *L. scottii*. This opportunistic species may respond to episodic input of labile OM (Diz and Francés, 2008; Mojtahid et al., 2009). It is obviously able to tolerate highly turbid environments (Scott et al., 2005; Diz and Francés, 2008). *A. tepida* is related to the shallow-water conditions prevailing at the vicinity of river mouths (Jorissen, 1987; Donnici and Serandrei Barbero, 2002; Rossi and Vaiani, 2008; Frezza and Carboni, 2009). In our study area, the relative abundances of these two species show a positive correlation with the concentration of available organic matter ($r = 0.85$; Table 5) and a negative correlation with $\delta^{13}\text{C}_{\text{OM}}$ ($r = -0.65$). The strong dominance of both species suggests the presence of non-equilibrium communities living in shallow-water environments under a strong riverine influence in terms of inorganic and organic inputs.

Biofacies A (Fig. 9b) is located close to the river mouth. OC and available organic matter in surficial sediment are high. Organic detritus is largely from terrestrial origin. The benthic recycling of OC is intense as depicted by low OPD and high ΣNH_3 concentration in the sediment. We assume that the hydro-sedimentary conditions at these stations are less variable compared to Stations 28 and 41. H and E indices are very low, and *Nonionella turgida* and *Eggerella scabra* are both indicative species. As observed in other studies (Jorissen, 1987; Van der Zwaan and Jorissen, 1991; Barmawidjaja et al., 1992; Donnici and Serandrei Barbero, 2002; Diz and Francés, 2008; Duchemin et al., 2008; Rossi and Vaiani, 2008), *N. turgida* is able to respond to important supplies of relatively low-quality OM in hypoxic sediments by increased densities in the uppermost oxygenated sediment. At our stations, it can be considered as an opportunistic and stress-tolerant taxon thriving in hypoxic and eutrophic conditions. *E. scabra* lives also in muddy to sandy sediments enriched in low-quality OM (Donnici and Serandrei Barbero, 2002; Diz and Francés, 2008; Duchemin et al., 2008). According to Diz et al. (2006), *E. scabra* would be a better competitor for space and food in organic matter-enriched and hypoxic sediments.

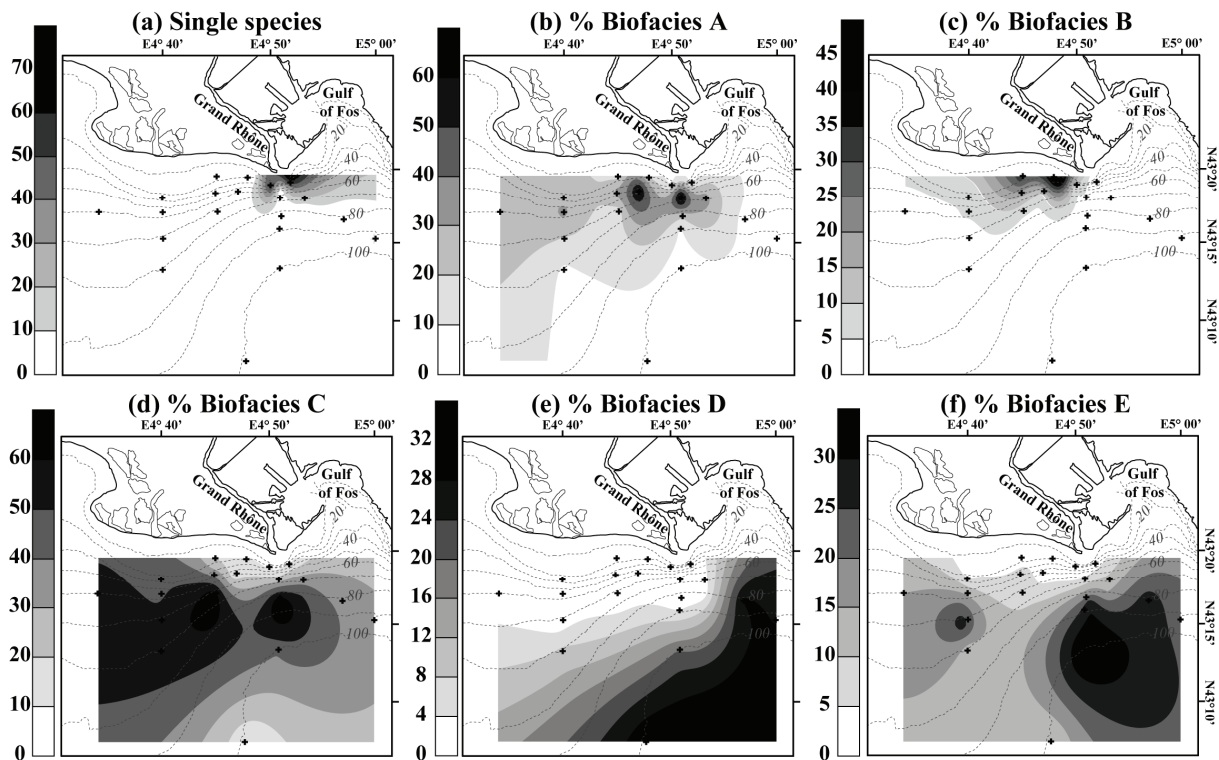


Figure 9: Spatial distribution of the five biofacies determined by R-mode and Q-mode cluster analyses. (a) Single species: *L. scotti* and *A. tepida*; (b) Biofacies A: *N. turgida* and *E. scabra*; (c) Biofacies B: *A. beccarii* f. *beccarii*, *Q. lata*, *Q. tenuicollis*, *T. trigonula* and *N. polymorphinoides*; (d) Biofacies C: *C. carinata*, *N. fabum*, *R. phlegeri* and *T. globigeriniformis*; (e) Biofacies D: *B. alata*, *B. aculeata*, *M. barleeanus*, *Q. seminula* and *B. nodosaria*; and (f) Biofacies E: *V. bradyana*, *C. cylindrica*, *L. difflugiformis* and *T. agglutinans*.

Biofacies B (Fig. 9c) groups sandy stations (Stations 11, 18, 20 and 35) located in the relict prodeltaic lobe of Bras de Fer (Vella et al., 2005). Low OC content and available organic matter concentration may be explained by winnowing related to strong bottom currents prevailing at these stations. The OPD (3.4–4.5 mm) is slightly higher compared to previous stations, but anaerobic processes in the sediment are still important. *Ammonia beccarii* forma *beccarii*, *Quinqueloculina lata*, *Quinqueloculina tenuicollis*, *Triloculina trigonula* and *Nouria polymorphinoides* are characteristic taxa, associated to *Nonion fabum*, *Rectuvigerina phlegeri* and *Eggerella scabra*. As observed by other authors, *A. beccarii* f. *beccarii*, *R. phlegeri*, *Q. seminula* and *E. scabra* are characteristic of very shallow-water and prodeltaic environments (Jorissen, 1987; Donnici and Serandrei Barbero, 2002; Mendes et al., 2004; Rossi and Vaiani, 2008; Frezza and Carboni, 2009). Furthermore, the high abundances of miliolids (*Q. lata*, *Q. tenuicollis*, *T. trigonula*) at Stations 20 and 35 is probably related to sandy substrates with low OM content (Jorissen, 1988; Donnici and Serandrei Barbero, 2002; Rossi and Vaiani, 2008). *N. fabum*, *R. phlegeri*, *N. polymorphinoides* and *E. scabra* are

frequently observed in sandy sediment supplied with terrestrial OM (Debenay and Redois, 1997; Redois and Debenay, 1999; Mendes et al., 2004; Diz and Francés, 2008; Duchemin et al., 2008; Mojtahid et al., 2009). In the Rhône prodelta, the cumulative percentages of these species show a strong positive correlation with sandy sediment enriched in continental and/or degraded OM ($r = 0.72$ with C:N ratio) (Table 5). The association of the indicative species belonging to Biofacies B is characteristic of sandy environments subjected to strong hydrodynamic processes.

	Single species	Biofacies A	Biofacies B	Biofacies C	Biofacies D	Biofacies E
Distance/river mouth (km)	-0.46 <i>p</i> =0.048	-0.19 <i>p</i> =0.425	-0.27 <i>p</i> =0.255	0.44 <i>p</i> =0.056	0.28 <i>p</i> =0.234	0.39 <i>p</i> =0.093
Depth (m)	-0.43 <i>p</i> =0.067	-0.14 <i>p</i> =0.562	-0.58 <i>p</i> =0.009	0.16 <i>p</i> =0.514	0.65 <i>p</i> =0.003	0.83 <i>p</i> =0.000
Clay (%)	-0.22 <i>p</i> =0.375	-0.11 <i>p</i> =0.643	-0.71 <i>p</i> =0.001	0.2 <i>p</i> =0.415	0.46 <i>p</i> =0.048	0.74 <i>p</i> =0.000
Silt (%)	0.05 <i>p</i> =0.828	0.04 <i>p</i> =0.872	-0.6 <i>p</i> =0.006	0.03 <i>p</i> =0.897	0.25 <i>p</i> =0.298	0.47 <i>p</i> =0.045
Sand (%)	0.02 <i>p</i> =0.943	0.00 <i>p</i> =0.999	0.64 <i>p</i> =0.003	-0.08 <i>p</i> =0.756	-0.31 <i>p</i> =0.191	-0.55 <i>p</i> =0.015
[AA+Lipids] (mg.g ⁻¹ d.w.)	0.85 <i>p</i> =0.000	-0.19 <i>p</i> =0.446	-0.12 <i>p</i> =0.630	-0.41 <i>p</i> =0.083	-0.15 <i>p</i> =0.537	-0.28 <i>p</i> =0.240
%AA+Lipids (% OC)	0.53 <i>p</i> =0.020	-0.26 <i>p</i> =0.281	-0.15 <i>p</i> =0.545	-0.19 <i>p</i> =0.430	0.07 <i>p</i> =0.782	0.04 <i>p</i> =0.879
δ ¹³ C _{OM} (‰)	-0.65 <i>p</i> =0.003	-0.24 <i>p</i> =0.317	0.06 <i>p</i> =0.818	0.23 <i>p</i> =0.339	0.54 <i>p</i> =0.017	0.39 <i>p</i> =0.102
δ ¹⁵ N _{OM} (‰)	0.27 <i>p</i> =0.268	-0.2 <i>p</i> =0.418	-0.27 <i>p</i> =0.256	0.01 <i>p</i> =0.953	0.1 <i>p</i> =0.689	0.12 <i>p</i> =0.636
C:N (atomic ratio)	-0.23 <i>p</i> =0.335	-0.01 <i>p</i> =0.957	0.72 <i>p</i> =0.001	-0.05 <i>p</i> =0.833	-0.2 <i>p</i> =0.418	-0.3 <i>p</i> =0.218
OC (%)	0.69 <i>p</i> =0.001	0.04 <i>p</i> =0.855	-0.36 <i>p</i> =0.134	-0.29 <i>p</i> =0.236	-0.16 <i>p</i> =0.522	-0.16 <i>p</i> =0.504
OPD (mm)	-0.52 <i>p</i> =0.023	-0.4 <i>p</i> =0.090	-0.36 <i>p</i> =0.110	0.29 <i>p</i> =0.220	0.66 <i>p</i> =0.002	0.82 <i>p</i> =0.000

Table 5: Correlation matrix between biofacies and environmental parameters. Dark grey areas indicate correlation coefficients with $p \leq 0.001$, and light grey shades with $p \leq 0.01$.

Biofacies C (Fig. 9d) groups stations under the yearly mean direction of the river plume (Stations 1, 9, 15, 23, 24, 29, 30 and 39) (Naudin et al., 1997). The ratio between Rhône River-derived OM and marine POM decreases with distance from the river mouth. The concentrations of OC and available organic compounds are low compared with values recorded at shallow stations close to the river mouth. OPD (3.2 to 8.4 mm) and $\sum\text{NH}_3$ concentration in the sediment suggest relatively moderate OM degradation compared with other shallower stations close to the river mouth. *Cassidulina carinata*, *N. fabum*, *R. phlegeri*, and *Trochammina globigeriniformis* are indicative species. Low E and H reflect the strong dominance of *N. fabum*. As previously explained, *N. fabum* and *R. phlegeri* may be found in

poorly oxygenated sediments with low-quality OM supplied from continental areas (Fontanier et al., 2002; Langezaal et al., 2006; Diz and Francés, 2008; Duchemin et al., 2008; Mojtahid et al., 2009). However, previous studies (Fontanier et al., 2003; Langezaal et al., 2004; Duchemin et al., 2008) observed a clear response of *N. fabum* and *C. carinata* after marine phytoplankton blooms, suggesting their ability to feed on labile phytodetritus. Therefore, the above-mentioned group of species lives in environments where marine influence in terms of organic inputs is slightly more important compared to shallower stations.

Biofacies D (Fig. 9e) corresponds to the deepest area of the Rhône prodelta, far away from the river mouth (Stations 22, 36, 37 and 48). OM degradation in the sediment is relatively moderate as depicted by the relatively high OPD (> 7.3 mm) and the low $\sum\text{NH}_3$ concentration. Sedimentary OM is a mixing between Rhône River and marine POM. The indicative species in this area are *Bolivina alata*, *Bulimina aculeata*, *Melonis barleeanus*, *Quinqueloculina seminula* and *Bigenerina nodosaria* associated with *C. carinata* and *T. globigeriniformis*. S, H and E are very high, indicating equilibrium faunas. *B. aculeata* is commonly reported in fine-grained sediment from the continental shelf and the open slope (Murray, 1991a; Jorissen et al., 1998; Mendes et al., 2004). This species can feed on phytodetritus, and is probably able to quickly ingest fresh OM derived from marine primary production (Kitazato et al., 2003; Nomaki et al., 2005a, 2005b, 2006; Eberwein and Mackensen, 2006). Duchemin et al. (2008) observed such an opportunistic behaviour for *B. nodosaria*, which grows after a phytoplankton bloom in the outer shelf of the Bay of Biscay. This taxon is also observed in the upper slope of the Gulf of Lions and from the Bay of Biscay suggesting its dependence to marine phytodetritus (Fontanier et al., 2008b). *B. alata* and *M. barleeanus* both thrive in organic-matter enriched and well-oxygenated sediment from the upper continental slope (Murray, 1991a; Fontanier et al., 2002, 2003, 2005, 2006, 2008a, 2008b). They are commonly found in intermediate infaunal microhabitats (Fontanier et al., 2003, 2008a). In our study area, all these species present a strong positive correlation with water depth ($r = 0.65$; Table 5) and OPD into the sediment ($r = 0.66$). All dominant species of Biofacies D describe environments of a river-influenced outer shelf with relatively unstressed conditions and increasing marine influence.

Biofacies E (Fig. 9f) is characterised by *Valvulineria bradyana*, *Clavulina cylindrica*, *Lagenammia difflugiformis* and *Textularia agglutinans*. It is distributed at the border between Biofacies C and Biofacies D. Fontanier et al. (2002) reported *V. bradyana* and *C. cylindrica* at an outer shelf station from the Bay of Biscay (140 m deep), where both species were considered as bio-indicators of eutrophic environments under marine influence. In the

Rhône prodelta, this biofacies is strongly positively correlated with water depth ($r = 0.83$; Table 5) and well oxygenated ($r = 0.82$ with OPD) clayey sediments ($r = 0.74$). Therefore, these species constitute a transitional biofacies where the continental OM contribution is still recorded but in a minor degree, and is gradually replaced by more marine-derived OM.

1.4.3. Temporal variability of benthic foraminiferal faunas: a comparison with previous results

Benthic environments from the Rhône prodelta were investigated during MINERCOT 2 Cruise (10 to 17 June 2005). Geochemical features and foraminiferal ecology are described in Lansard et al. (2009) and Mojtahid et al. (2009). In the next paragraph, we will investigate how the environmental characteristics and foraminiferal faunas change between the strongly productive season (MINERCOT 2 cruise) and the much less productive summer situation (our sampling period). Analyses on living (rose Bengal stained) benthic foraminiferal faunas collected in June 2005 were processed on the $> 150 \mu\text{m}$ fractions by Mojtahid et al. (2009). In our study area, species absolute densities (raw data) can present important small-scale (decimetric) spatial heterogeneity, whereas species relative abundances (normalised data) are statistically less patchy (Goineau et al., Submitted – see Chapter 2 in this thesis). Consequently, the following comparison is based on species relative abundances (percentages). Note that the locations of the stations were different between June 2005 and September 2006 and thereafter we will only consider stations from September 2006 situated in the June 2005 study area. We will not take into account stations M1 (from June 2005, MINERCOT 2) and BT28 (from September 2006, BEHEMOTH) because of their very low densities ($\ll 300 \text{ ind./100 cm}^2$).

Ecological indices show similar trends for both sampling periods. Density, species richness, biodiversity and Evenness index are low at the river mouth and in the mean direction of the river plume. Maximal values are recorded in the farther and deeper stations out of the river influence. However, densities, species richness and Shannon index are higher in September 2006 ($S = 9$ to 61 ; $H = 1.30$ to 3.22) compared with June 2005 ($S = 11$ to 42 ; $H = 0.95$ to 2.91). We performed a Principal Component Analysis (PCA) based on relative abundances of the 17 major species observed during both sampling campaigns at the 37 considered stations (Fig. 10). In Figures 10a and 10b, we have plotted stations sampled in June 2005 (M2, M3...) and those sampled in September 2006 (BT9, BT11...). Axes 1, 2 and

3 account respectively for 26.0, 14.3 and 14.2% of the total variability, and divide our stations into different groups.

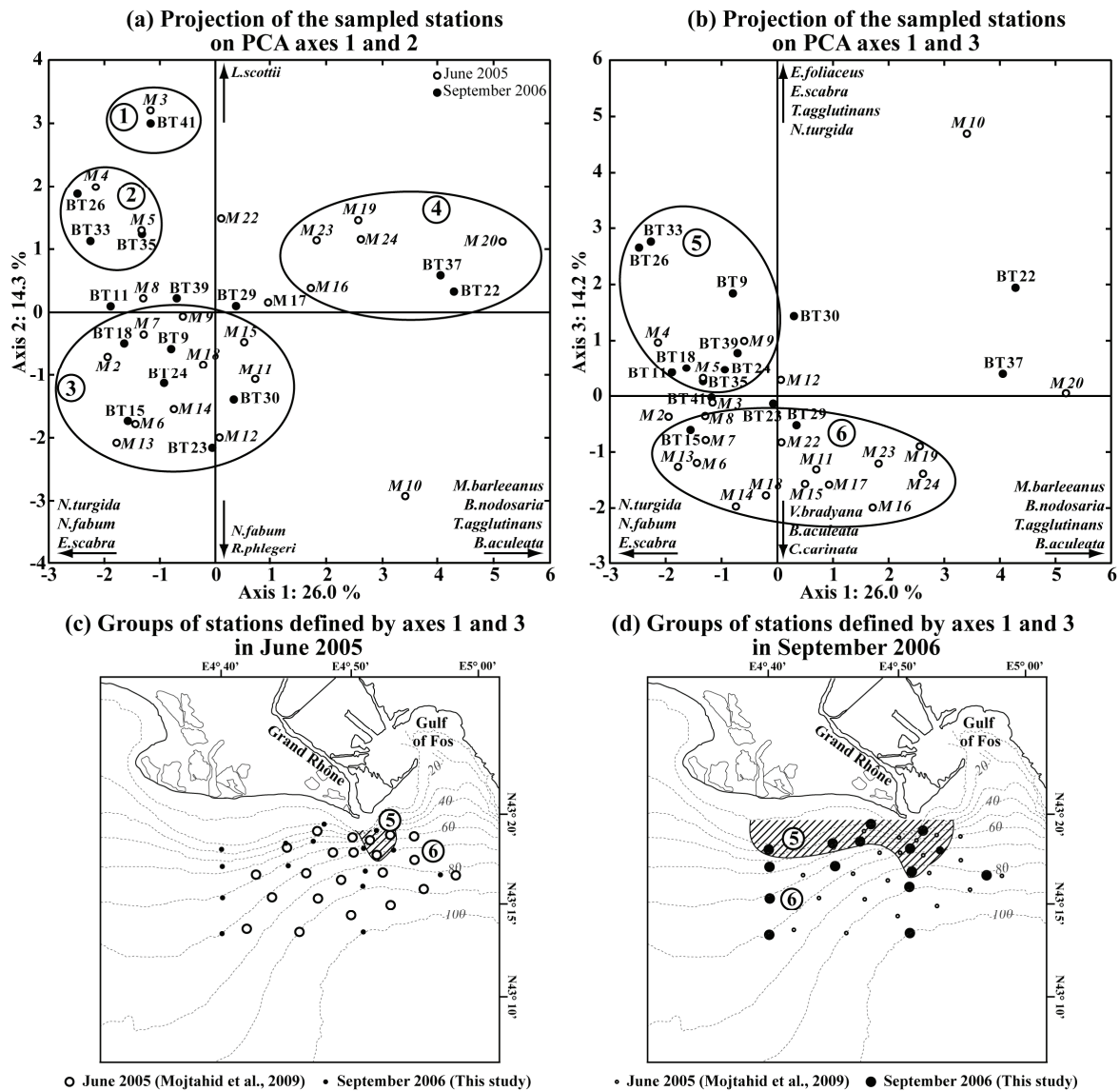


Figure 10: PCA based on the relative abundances of the 17 chosen major species in June 2005 and September 2006. (a) Projection of the 37 stations on the factor-plane defined by PCA axes 1 and 2, and indication of the highest loading species on each axis. The circles indicate four groups of stations; (b) Projection of the 37 stations on the factor-plane defined by PCA axes 1 and 3; and (c–d) Location of the Groups of stations 5 (hatched area) and 6, defined by the PCA axes 1 and 3, for June 2005 and September 2006 sampling periods.

Group 1 is constituted by the two stations located in the immediate vicinity of the river mouth (Fig. 10a). There, faunas are dominated by *L. scotti* (68 and 78%). The second group (Group 2) is composed of two stations sampled in June 2005 and three stations sampled in September 2006. These stations are located close to the river mouth but farther than the previous ones.

They are characterised by *N. turgida*, *N. fabum* and *E. scabra*. Group 3 groups stations located under the mean position of the river plume. They are enriched in *N. fabum* and *R. phlegri*. The last group (Group 4) identified with PCA axes 1 and 2 is mainly constituted by stations from June 2005 (5 stations against 2 stations from September 2006), located outside the Rhône river-influenced area, and dominated by *M. barleeanus*, *B. nodosaria*, *T. agglutinans* and *B. aculeata*. Therefore, no clear differences between faunas collected in June 2005 and in September 2006 are highlighted by the two first PCA axes. However, the position of the stations on Axis 3 gives some additional information (Fig. 10b). Group 5 plots on the positive side of this axis where the faunas are loaded by *E. scabra* and *N. turgida*. In this group, Stations of September 2006 have much higher scores on this axis than stations from June 2005, due to the high abundances of *N. turgida* and *E. scabra* close to the river mouth in September 2006. Group 6 has a negative score on the axis which is loaded by *V. bradyana*, *B. aculeata* and *C. carinata*. Stations from June 2005 are dominant in this group, suggesting that these three species are more abundant during this sampling period.

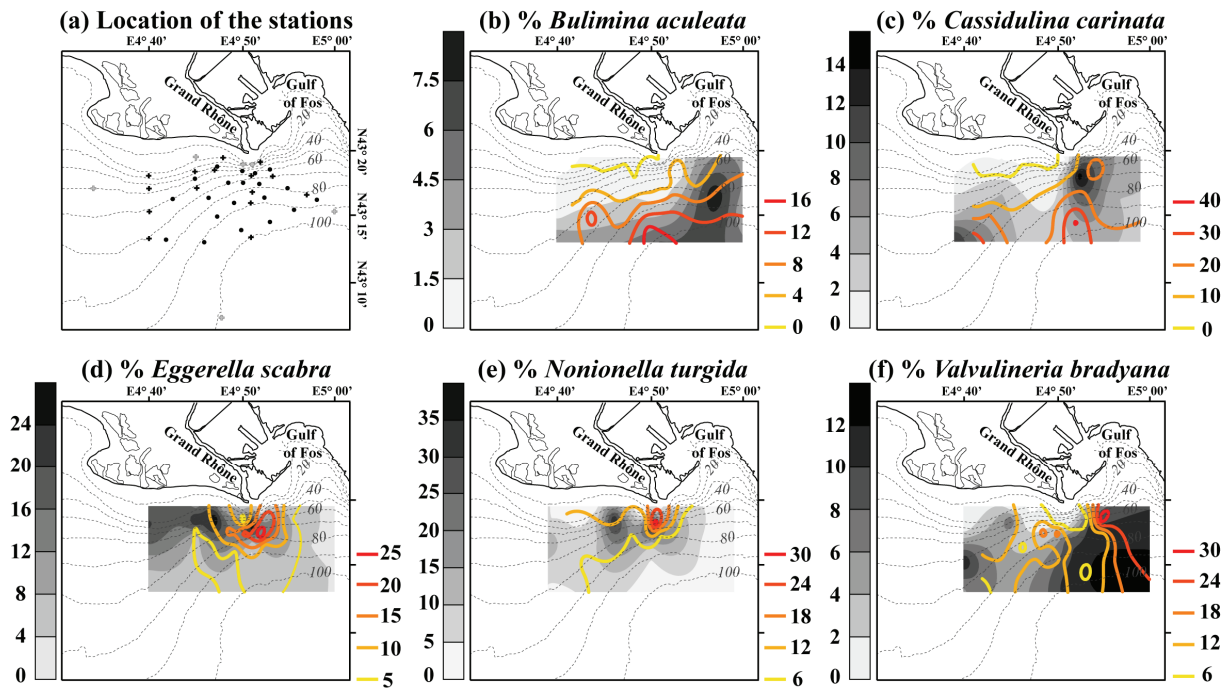


Figure 11: Relative abundance and spatial distribution of the five major species (> 5% in at least one station/season) highlighted by the PCA in June 2005 (yellow to red shaded-lines; Mojtahid et al., 2009) and September 2006 (grey areas, this study).

Therefore, two main differences in foraminiferal assemblages between June 2005 and September 2006 are highlighted (Fig. 10c–d and Fig. 11): (1) an extended area dominated by *N. turgida* and *E. scabra* (Group 5) at stations close to the river mouth in September 2006; and (2) in June 2005, a more limited distribution area of faunas dominated by *N. turgida* and *E. scabra*, restricted to the immediate vicinity of the Rhône River mouth, but a more extended zone with high abundances of *B. aculeata*, *C. carinata* and *V. bradyana* (Group 6). *N. turgida* and *E. scabra* were found in September 2006 close to the river mouth in a strongly river-impacted area with high amounts of terrestrial OM (this study). At the same sampling period, the relative abundances of *C. carinata*, *B. aculeata* and *V. bradyana* increased with distance from the river mouth and enhanced marine OM input from sea surface primary production to the sea floor. In June 2005, fresh marine OM was more abundant in the whole studied area compared to September 2006. These environmental conditions would (1) favour the development of the opportunistic species *B. aculeata*, *C. carinata* and *V. bradyana*, and (2) restrict high abundances of *N. turgida* and *E. scabra* to the immediate vicinity of the Rhône River mouth.

1.5. CONCLUSIONS

Live (rose Bengal stained) benthic foraminifera data from the Rhône prodelta show a clear link with environmental parameters. Sediments in the whole area are largely enriched in organic carbon, especially at the river mouth where available organic compounds of terrestrial origin concentrate, and efficient organic matter degradation processes (both aerobic and anaerobic pathways) take place. However, variable conditions such as deposition rates or hydrodynamic conditions prevail in this area, constituting stressful conditions for benthic foraminiferal faunas. Consequently, despite abundant available food, species richness is very low in this area and opportunistic species dominate foraminiferal assemblages. With increasing distance from the river mouth, the continental footprint and stress related to hydro-sedimentary processes decreases. In the south-western part, foraminiferal faunas dwell on sediment with organic matter derived from the Rhône River. As the marine contribution increases (more marine-derived OM signature), foraminiferal faunas become dominated by species that tolerate both weak continental influence and more marine conditions. In the south-eastern area, when the continental influence diminishes and environmental conditions become less stressed and more stable, the abundance of these species increases considerably, highlighting their preference for fresher OM. New taxa appear and dwell exclusively in this

environment. A peculiar area in the north-western part corresponding to a relict prodeltaic lobe, mainly composed of sandy sediments and poorly enriched in organic material, is inhabited by a fauna composed of many miliolid species. The comparison between the sampling campaigns of June 2005 and September 2006 shows that in June 2005, few weeks after the end of the spring bloom, benthic foraminiferal faunas are still responding to the increased marine primary production, with an extended area dominated by the opportunistic species *B. aculeata*, *C. carinata* and *V. bradyana*.

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APPENDICES

Appendix A

Environmental analyses performed on the first centimetre of sediment: Sedimentary features (grain size frequencies Q_{50} and D_{90}); Analyses of particulate organic matter: Organic Carbon, Amino-acids, Lipids, Available organic matter contents (lipids + amino acids, Grémare et al., 2003, 2005), Stable isotopic ratios $\delta^{13}C_{OM}$ and $\delta^{15}N_{OM}$, and atomic ratio C:N. Empty cases correspond to unmeasured parameters at the corresponding station.

Appendix B

Bottom water temperature and oxygenation and oxygen penetration depth into the sediment. Empty cases correspond to unmeasured parameters at the corresponding station.

Appendix C

Geochemical analyses performed at 11 stations from the closest (Station 41) to the farthest station (Station 48) from the Rhône River mouth: oxygen, ΣNO_3 and ΣNH_3 profiles in the porewater.

Appendix D

Taxonomical list of the 22 benthic foraminiferal taxa presenting a relative abundance higher than 5% at least at one station, with references to plates and figures in literature.

Appendix E

Total benthic foraminiferal counts. “Tot.” corresponds to the non-standardised total number of specimens counted for each species at each station; “%” indicates the relative abundance of each species at each station. Grey boxes indicate percentages and species > 5%.

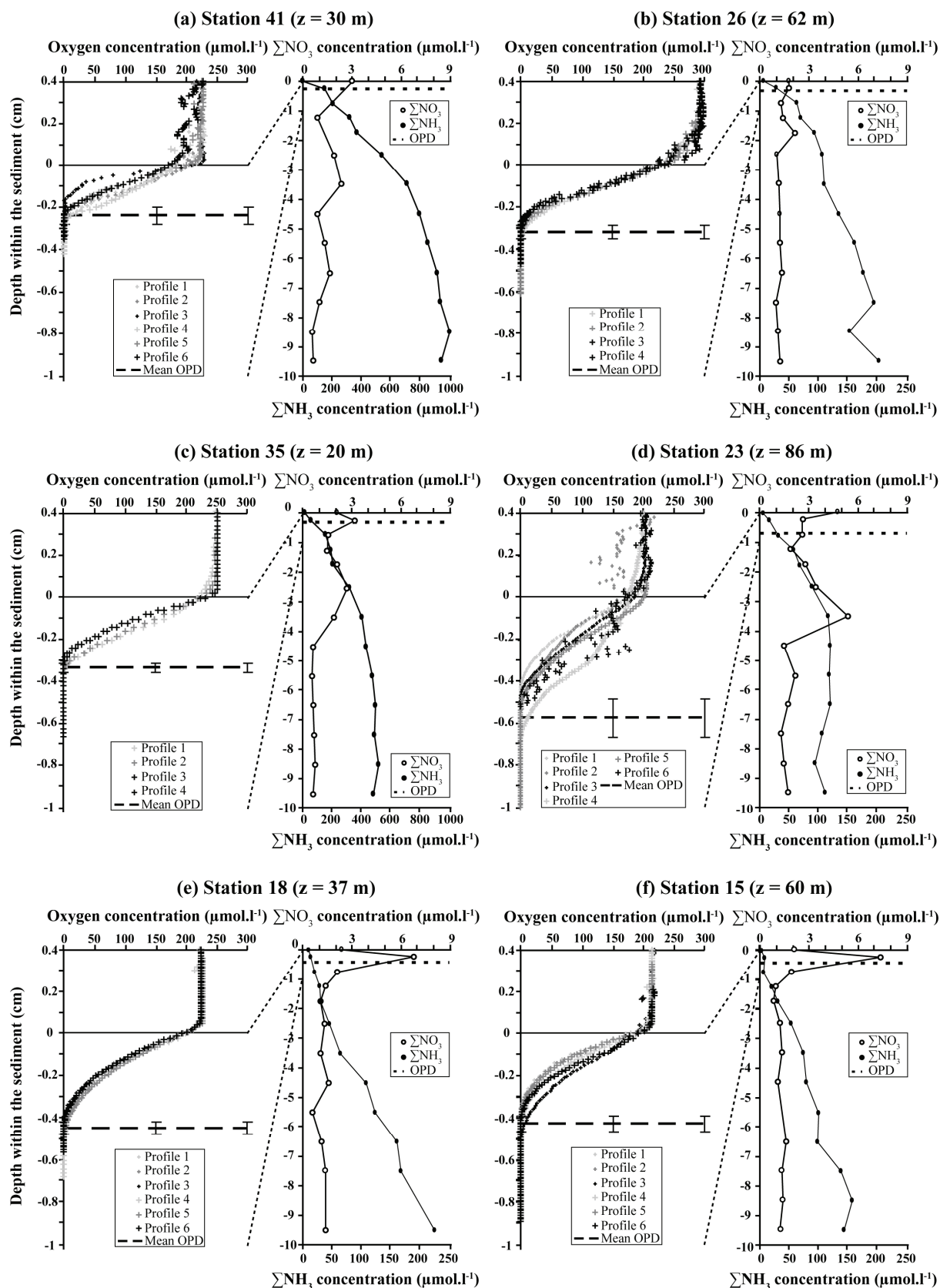
Appendix A

Station	Water depth (m)	Distance from the river mouth (km)	Sediment grain size		Organic Carbon (% d.w.)	Amino-acids		Lipids		Amino-acids +Lipids		$\delta^{13}\text{C}_{\text{OM}}$ (‰)	$\delta^{15}\text{N}_{\text{OM}}$ (‰)	C:N (atomic ratio)
			Q_{50} (μm)	D_{90} (μm)		mg.g ⁻¹ d.w.	% of OC	mg.g ⁻¹ d.w.	% of OC	mg.g ⁻¹ d.w.	% of OC			
1	49	22.2	9.7	43.1	1.08	2.66	24.6	0.39	3.7	3.06	28.3	-24.88	3.58	11.77
9	44	14.6	10.5	47.1	1.17	2.17	18.6	0.39	3.4	2.57	22.0	-25.46	3.15	12.28
11	26	14.0	66.7	153.2	0.56	1.09	19.6	0.22	4.0	1.32	23.6	-24.8	2.83	11.47
15	60	8.9	9.3	35.7	1.33	3.52	26.5	0.51	3.8	4.03	30.3	-25.63	3.84	11.64
18	37	7.5	12.1	55.4	1.14	1.94	17.0	0.41	3.6	2.35	20.6	-25.84	3.69	13.16
20	15	7.8	85.9	139.3	0.43	0.62	14.5	0.09	2.0	0.70	16.5	-24.43	-	17.68
22	98	11.4	7.4	25.2	1.09	2.50	23.0	0.35	3.2	2.85	26.1	-24.77	3.39	11.31
23	86	5.7	8.2	33.5	1.19	2.79	23.4	0.45	3.8	3.24	27.2	-26.33	3.72	11.86
24	79	4.4	8.9	33.8	-	-	-	-	-	-	-	-	-	-
26	62	1.8	11.5	54.6	1.49	3.04	20.4	0.57	3.9	3.62	24.3	-26.66	3.59	12.26
28	18	1.0	12.8	69.4	2.10	4.92	23.4	1.16	5.5	6.08	28.9	-27.51	4.01	12.21
29	68	17.9	8.0	29.0	1.24	2.21	17.9	0.40	3.2	2.62	21.1	-24.83	3.79	12.66
30	60	16.5	9.0	34.8	1.15	2.64	22.8	0.47	4.0	3.10	26.9	-25.09	3.6	12.1
33	47	5.4	11.8	51.8	1.37	2.82	20.6	0.49	3.6	3.31	24.1	-26.11	3.47	11.57
35	20	3.1	38.0	110.4	1.01	2.80	27.7	0.40	3.9	3.20	31.6	-25.79	3.25	13.94
36	89	14.4	8.2	29.7	1.02	2.08	20.4	0.32	3.2	2.40	23.6	-24.21	3.37	11.61
37	80	9.6	9.0	34.3	1.13	3.57	31.6	0.37	3.3	3.94	34.9	-24.75	3.98	11.8
39	69	4.1	10.3	41.8	1.33	3.34	25.0	0.52	3.9	3.86	29.0	-26.07	3.82	11.6
41	30	1.5	13.7	63.5	1.88	5.78	30.7	0.94	5.0	6.72	35.7	-27.29	3.68	10.44
48	100	22.4	-	-	-	-	-	-	-	-	-	-	-	-

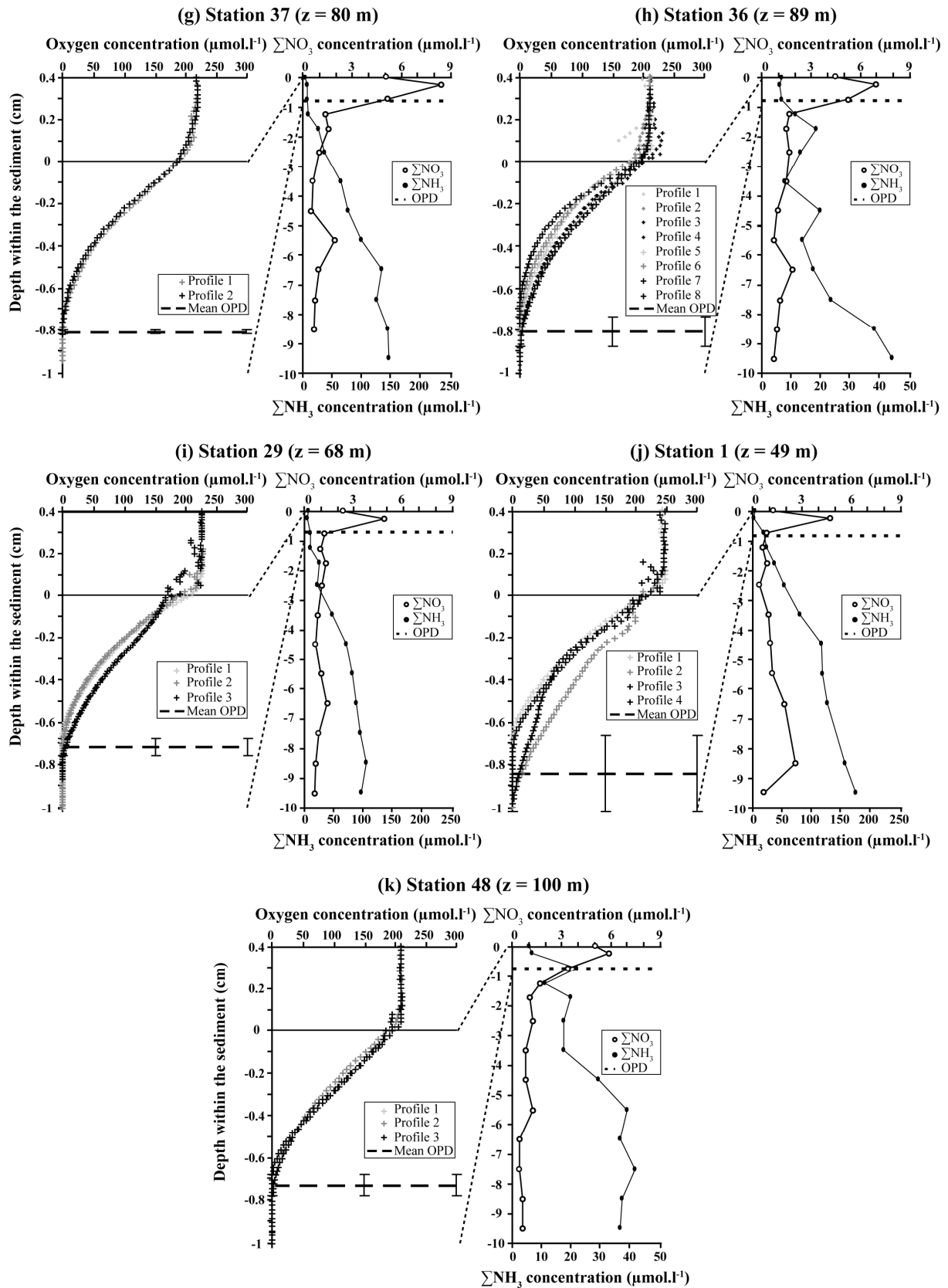
Appendix B

Station	Water depth (m)	Distance from the river mouth (km)	Bottom water temperature (°C)	Bottom water oxygenation		Oxygen Penetration Depth (mm)
				$\mu\text{mol.l}^{-1}$	% Saturation	
1	49	22.2	14.6	246.5 ± 1.7	77.3	8.4 ± 1.8
9	44	14.6	14.6	245.7 ± 1.4	77.1	4.9 ± 0.1
11	26	14.0	–	–	–	–
15	60	8.9	13.6	214.2 ± 2.3	65.9	4.3 ± 0.4
18	37	7.5	14.3	224.3 ± 1.8	70.4	4.5 ± 0.3
20	15	7.8	15.1	252.9 ± 0.9	80.1	–
22	98	11.4	–	–	–	–
23	86	5.7	13.8	204.5 ± 1.4	63.5	7.0 ± 1.8
24	79	4.4	–	–	–	–
26	62	1.8	14.8	292.9 ± 2.9	92.8	3.2 ± 0.3
28	18	1.0	–	–	–	1.5 ± 0.2
29	68	17.9	13.8	225.9 ± 3.5	70.2	7.2 ± 0.4
30	60	16.5	14.0	236.5 ± 2.3	73.5	6.7 ± 0.3
33	47	5.4	14.9	235.5 ± 2.0	74.6	2.3 ± 0.1
35	20	3.1	15.1	250.1 ± 1.2	79.2	3.4 ± 0.2
36	89	14.4	–	–	–	8.1 ± 0.7
37	80	9.6	–	–	–	8.1 ± 0.1
39	69	4.1	14.1	219.2 ± 3.3	68.1	4.2 ± 0.2
41	30	1.5	14.2	224.0 ± 0.6	69.6	2.4 ± 0.4
48	100	22.4	13.4	209.7 ± 0.6	64.5	7.3 ± 0.5

Appendix C



Appendix C



Appendix D

- Ammonia beccarii* f. *beccarii* (Linnaeus) = *Nautilus beccarii* Linnaeus f. *beccarii* Linnaeus, 1758; in Jorissen, 1988, Plate 2, Fig. 5a–b
- Ammonia beccarii* f. *inflata* (Seguenza) = *Nautilus beccarii* Linnaeus f. *inflata* Seguenza, 1862; in Jorissen, 1988, Plate 6, Figs. 1–4
- Ammonia tepida* (Cushman) = *Rotalia beccarii* Linnaeus var. *tepida* Cushman, 1926; in Jorissen, 1988, Plate 2, Fig. 8a–b (as *Ammonia parkinsoniana* f. *tepida*)
- Bigenerina nodosaria* d'Orbigny, 1826; in Jorissen, 1988, Plate 1, Fig. 10
- Bolivina alata* (Seguenza) = *Vulvulina alata* Seguenza, 1862; in Mojtahid et al., 2009, Plate 2, Fig. 15
- Bulimina aculeata* d'Orbigny, 1826; in Jorissen, 1988, Plate 4, Fig. 5
- Cassidulina carinata* Silvestri, 1896 = *Cassidulina laevigata* d'Orbigny var. *carinata* Silvestri, 1896; in Mojtahid et al., 2009, Plate 1, Fig. 3
- Clavulina cylindrica* d'Orbigny, 1952; in Jones, 1994, Plate 44, Figs. 19–24
- Eggerella scabra* (Williamson) = *Bulimina scabra* Williamson, 1858; in Jones, 1994, Plate 47, Figs. 15–17
- Lagenammina difflugiformis* (Brady) = *Reophax difflugiformis* Brady, 1879; in Mojtahid et al., 2009, Plate 3, Fig. 46
- Leptohalysis scottii* (Chaster) = *Reophax scottii* Chaster, 1892; in Sgarella and Montcharmont Zei, 1993, Plate 2, Fig. 5
- Melonis barleeanus* (Williamson) = *Nonionina barleeana* Williamson, 1858; in Jorissen, 1988, Plate 4, Fig. 8 (as *Nonion barleeenum*)
- Nonion fabum* (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798; in Jones, 1994, Plate 109, Figs. 12–13
- Nonionella turgida* (Williamson) = *Rotalina turgida* Williamson, 1858; in Jorissen, 1988, Plate 4, Figs. 11–13
- Nouria polymorphinoides* Heron–Allen and Earland, 1914; in Barmawidjaja et al., 1992, Plate 4, Fig. 4
- Quinqueloculina lata* Terquem, 1876; in Murray, 2003, Plate 4, Figs. 9–10
- Quinqueloculina seminula* (Linnaeus) = *Serpula seminulum* Linnaeus, 1758; in Murray, 2003, Plate 4, Figs. 11–12
- Quinqueloculina tenuicollis* (Wiesner) = *Miliolina tenuicollis* Wiesner, 1923; in Cimerman and Langer, 1991, Plate 28, Figs. 5–6 (as *Cycloforina tenuicollis*)

Rectuvigerina phlegeri Le Calvez, 1959; in Schiebel, 1992, Plate 3, Fig. 10a–d

Textularia agglutinans d'Orbigny, 1839; in Mojtahid et al., 2009, Plate 2, Figs. 43–44

Triloculina trigonula (Lamarck) = *Miliolites trigonula* Lamarck, 1804; in Jorissen, 1988,
Plate 2, Fig. 13

Trochammina globigeriniformis (Parker & Jones) = *Lituola nautiloidea* Lamarck var.
globigeriniformis Parker and Jones, 1865; in Timm, 1992, Plate 4, Fig. 2a–b

Valvulineria bradyana (Fornasini) = *Discorbina bradyana* Fornasini, 1900; in Jorissen, 1988,
Plate 4, Figs. 1–2

Appendix E

Station	BT 1		BT 9		BT 11		BT 15		BT 18		BT 20		BT 22	
	49		44		30		60		37		15		98	
Water depth (m)														
Taxa	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Perforates														
Indet.	–		–		6	0.6	–		1	0.1	1	0.4	–	
<i>Ammonia beccarii</i> f. <i>beccarii</i>	5	0.6	13	1.2	41	4.2	20	2.3	34	2.6	3	1.1	8	0.6
<i>Ammonia beccarii</i> f. <i>inflata</i>	6	0.7	7	0.7	8	0.8	9	1.0	1	0.1	–		10	0.8
<i>Ammonia tepida</i>	–		–		–		–		14	1.1	1	0.4	–	
<i>Amphicoryna scalaris</i>	1	0.1	1	0.1	–		1	0.1	2	0.2	–		6	0.5
<i>Astacolus crepidulus</i>	–		–		–		–		–		–		–	
<i>Bolivina</i> sp.	–		–		9	0.9	–		1	0.1	–		–	
<i>Bolivina alata</i>	–		–		–		–		–		–		56	4.4
<i>Bolivina dilatata</i>	–		1	0.1	–		–		–		3	1.1	–	
<i>Bolivina spathulata</i>	–		–		–		–		–		–		–	
<i>Bolivina striatula</i>	–		1	0.1	–		–		1	0.1	–		–	
<i>Bolivina subaenariensis</i>	–		2	0.2	–		–		–		–		4	0.3
<i>Bulimina</i> sp.	–		–		–		–		–		–		–	
<i>Bulimina aculeata</i>	5	0.6	2	0.2	–		5	0.6	1	0.1	2	0.7	75	5.9
<i>Bulimina costata</i>	–		–	0.0	–		–		–		–		12	0.9
<i>Bulimina elongata</i>	–		4	0.4	30	3.1	–		4	0.3	9	3.3	–	
<i>Bulimina gibba</i>	–		1	0.1	–		–		–		–		9	0.7
<i>Bulimina marginata</i>	4	0.5	3	0.3	–		1	0.1	–		1	0.4	14	1.1
<i>Cassidulina carinata</i>	9	1.1	18	1.7	–		34	3.9	2	0.2	–		37	2.9
<i>Cassidulina crassa</i>	–		–		–		–		–		–		–	
<i>Cassidulina oblonga</i>	–		–		–		–		–		–		3	0.2
<i>Chilostomella oolina</i>	–		–		–		–		–		–		11	0.9
<i>Cibicides</i> sp.	–		–		–		–		–		–		–	
<i>Cibicides lobatulus</i>	–		–		1	0.1	–		–		–		5	0.4
<i>Dentalina</i> sp.1	–		–		–		–		–		–		–	
<i>Dentalina</i> sp.2	–		–		–		–		–		–		2	0.2
<i>Dentalina</i> sp.3	–		–		–		–		–		–		–	
<i>Dentalina bradyensis</i>	–		–		–		–		–		–		1	0.1
<i>Dentalina filiformis</i>	–		–		–		1	0.1	–		–		–	
<i>Elphidium</i> sp.1	–		–		1	0.1	–		–		5	1.8	–	
<i>Elphidium advenum</i>	6	0.7	–		4	0.4	2	0.2	2	0.2	3	1.1	–	
<i>Elphidium crispum</i>	–		–		8	0.8	–		25	1.9	6	2.2	1	0.1
<i>Elphidium granosum</i> f. <i>lidoense</i>	–		–		1	0.1	–		–		7	2.5	–	
<i>Elphidium poeyanum</i> f. <i>decipiens</i>	–		–		1	0.1	–		–		2	0.7	–	
<i>Epistominella</i> sp.	–		–		–		–		–		–		–	
<i>Epistominella vitrea</i>	–		–		–		–		–		–		–	
<i>Fursenkoina acuta</i>	1	0.1	1	0.1	1	0.1	–		1	0.1	1	0.4	–	
<i>Gavelinopsis praegeri</i>	1	0.1	8	0.8	8	0.8	–		2	0.2	–		–	
<i>Glandulina ovula</i>	–		–		–		–		–		–		–	
<i>Globobulimina affinis</i>	–		–		–		–		–		–		3	0.2
<i>Globobulimina pyrula</i>	–		–		–		–		–		–		3	0.2
<i>Globobulimina pyrula</i> var. <i>pseudospinescens</i>	–		–		–		–		–		–		–	
<i>Globocassidulina subglobosa</i>	1	0.1	–		–		–		–		–		4	0.3
<i>Gyroidina umbonata</i>	1	0.1	1		–		1	0.1	–		–		9	0.7
<i>Hanzawaia boueana</i>	–		–		–		–		–		–		1	0.1
<i>Hyalinea balthica</i>	–		–		–		1	0.1	–		–		24	1.9
<i>Lagena</i> spp.	–		–		–		–		–		–		–	
<i>Lenticulina atlantica</i>	–		–		–		–		–		–		–	
<i>Lenticulina peregrina</i>	–		–		–		–		–		–		5	0.4
<i>Melonis barleeanus</i>	1	0.1	–		–		–		–		–		33	2.6
<i>Neolenticulina variabilis</i>	–		–		–		–		–		–		–	

Appendix E (continued)

Station Taxa	BT 1		BT 9		BT 11		BT 15		BT 18		BT 20		BT 22	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
<i>Nonion fabum</i>	297	35.0	293	27.7	442	45.7	448	51.3	286	21.9	56	20.4	82	6.4
<i>Nonionella bradii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella turgida</i>	195	23.0	152	14.4	51	5.3	81	9.3	106	8.1	6	2.2	12	0.9
<i>Polymorphinidae</i>	–	–	–	–	–	–	–	–	–	–	–	–	2	0.2
<i>Pseudoeponides falsobeccarii</i>	12	1.4	17	1.6	1	0.1	20	2.3	7	0.5	–	–	39	3.1
<i>Pullenia quinqueloba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rectuvigerina phlegeri</i>	44	5.2	34	3.2	12	1.2	62	7.1	74	5.7	4	1.5	3	0.2
<i>Reussella spinulosa</i>	–	–	–	–	1	0.1	–	–	–	–	1	0.4	–	–
<i>Robertina translucens</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>	–	–	–	–	1	0.1	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>	2	0.2	–	–	6	0.6	2	0.2	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia complanata</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Uvigerina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina bifurcata</i>	–	–	–	–	–	–	–	–	–	–	–	–	4	0.3
<i>Uvigerina elongatastriata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>	–	–	–	–	–	–	–	–	–	–	–	–	7	0.5
<i>Uvigerina peregrina</i>	–	–	–	–	–	–	1	0.1	–	–	–	–	1	0.1
<i>Valvulineria bradyana</i>	56	6.6	42	4.0	–	–	28	3.2	108	8.3	–	–	142	11.1
<i>Valvulineria complanata</i>	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
Miliolids														
Indet.	–	–	–	–	2	0.2	–	–	–	–	–	–	–	–
<i>Adelosina</i> spp.	5	0.6	5	0.5	–	–	11	1.3	9	0.7	2	0.7	–	–
<i>Biloculinella</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Biloculinella labiata</i>	30	3.5	3	0.3	–	–	1	0.1	1	0.1	–	–	9	0.7
<i>Cornuspira foliacea</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Miliolinella</i> spp.	–	–	–	–	–	–	–	–	–	–	1	0.4	–	–
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	–	5	1.8	–	–
<i>Pseudotriloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Pyrgo</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo depressa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo elongata</i>	–	–	–	–	–	–	–	–	2	0.2	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	–	–	–	–	–	14	1.1	–	–	–	–
<i>Pyrgo subsphaerica</i>	–	–	1	0.1	–	–	4	0.5	1	0.1	–	–	–	–
<i>Quinqueloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>	–	–	–	–	4	0.4	–	–	–	–	–	–	–	–
<i>Quinqueloculina badenensis</i>	1	0.1	–	–	–	–	–	–	–	–	–	–	8	0.6
<i>Quinqueloculina lata</i>	4	0.5	4	0.4	5	0.5	17	1.9	37	2.8	–	–	–	–
<i>Quinqueloculina milletti</i>	–	–	–	–	–	–	–	–	–	–	2	0.7	–	–
<i>Quinqueloculina seminula</i>	5	0.6	2	0.2	–	–	3	0.3	1	0.1	41	14.9	39	3.1
<i>Quinqueloculina stalkerii</i>	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	1	0.1	1	0.1	5	0.4	24	8.7	–	–
<i>Sigmoilinita tenuis</i>	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	1	0.1	2	0.2	–	–	–	–	–	–	–	–	3	0.2
<i>Siphonaperta</i> sp.	–	–	2	0.2	–	–	–	–	–	–	–	–	–	–
<i>Siphonaperta aspera</i>	–	–	–	–	–	–	–	–	–	–	11	4.0	–	–
<i>Spiroloculina excavata</i>	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–	2	0.2
<i>Triloculina trigonula</i>	1	0.1	2	0.2	–	–	–	–	1	0.1	15	5.5	–	–

Appendix E (continued)

Station Taxa	BT 1		BT 9		BT 11		BT 15		BT 18		BT 20		BT 22	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Fossilising agglutinated														
<i>Bigenerina nodosaria</i>	2	0.2	–	–	–	–	–	–	2	0.2	–	–	70	5.5
<i>Textularia</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia agglutinans</i>	20	2.4	36	3.4	19	2.0	31	3.5	20	1.5	2	0.7	76	6.0
<i>Textularia porecta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia saggitula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated														
Indet.	3	0.4	2	0.2	14	1.4	–	–	13	1.0	–	–	1	0.1
Epilithe Indet.	1	0.1	–	–	27	2.8	–	–	–	–	–	–	–	–
Agglutinate sp.333	–	–	6	0.6	–	–	–	–	–	–	–	–	18	1.4
<i>Adercotryma</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	2	0.2	–	–	–	–	–	–	–	–	4	0.3
<i>Ammoscalaria foliacea</i>	5	0.6	12	1.1	–	–	–	–	6	0.5	–	–	25	2.0
<i>Clavulina cylindrica</i>	19	2.2	14	1.3	–	–	8	0.9	2	0.2	–	–	43	3.4
<i>Cribrostomoides</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides subglobosus</i>	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	3	0.4	1	0.1	–	–	–	–	41	3.1	1	0.4	1	0.1
<i>Eggerella</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–	5	0.4
<i>Eggerella</i> sp.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Eggerella scabra</i>	50	5.9	194	18.4	198	20.5	55	6.3	316	24.2	39	14.2	67	5.2
<i>Haplophragmoides</i> spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lagenammina difflugiformis</i>	28	3.3	94	8.9	2	0.2	–	–	–	–	2	0.7	188	14.7
<i>Leptohalysis scottii</i>	–	–	–	–	9	0.9	–	–	–	–	3	1.1	–	–
<i>Nouria polymorphinoides</i>	14	1.6	37	3.5	15	1.5	14	1.6	116	8.9	3	1.1	1	0.1
<i>Psammosphaera bowmani</i>	–	–	4	0.4	28	2.9	5	0.6	38	2.9	1	0.4	–	–
<i>Recurvoides scitulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax bilocularis</i>	–	–	–	–	1	0.1	–	–	–	–	–	–	2	0.2
<i>Reophax dentaliniformis</i>	–	–	–	–	–	–	–	–	1	0.1	–	–	–	–
<i>Reophax fusiformis</i>	–	–	23	2.2	6	0.6	–	–	3	0.2	5	1.8	2	0.2
<i>Reophax scorpiurus</i>	5	0.6	1	0.1	1	0.1	1	0.1	–	–	–	–	47	3.7
<i>Technitella legumen</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Technitella melo</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina globigeriniformis</i>	5	0.6	5	0.3	1	0.1	5	0.6	4	0.3	1	0.4	12	0.9
<i>Trochammina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina</i> cf. <i>fissuraperta</i>	–	–	–	–	2	0.2	–	–	–	–	6	2.2	–	–
Organic foraminifera	–	–	–	–	–	–	–	–	–	–	–	–	23	1.8
Total number of living individuals	849		1057		968		874		1305		275		1277	

Appendix E (continued)

Station	BT 23		BT 24		BT 26		BT 28		BT 29		BT 30		BT 33	
Water depth (m)	86		78		62		18		68		60		47	
Taxa	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Perforates														
Indet.	–		1	0.1	–		–		–		2	0.1	–	
<i>Ammonia beccarii</i> f. <i>beccarii</i>	25	2.9	6	0.7	12	3.3	–		15	1.3	10	0.5	16	1.6
<i>Ammonia beccarii</i> f. <i>inflata</i>	21	2.4	–		–		–		50	4.3	15	0.8	1	0.1
<i>Ammonia tepida</i>	–		–		3	0.8	18	54.5	–		–		12	1.2
<i>Amphicoryna scalaris</i>	–		1	0.1	1	0.3	–		1	0.1	4	0.2	–	
<i>Astacolus crepidulus</i>	–		–		–		–		–		–		–	
<i>Bolivina</i> sp.	–		–		–		–		–		–		–	
<i>Bolivina alata</i>	2	0.2	–		–		–		7	0.6	4	0.2	–	
<i>Bolivina dilatata</i>	–		–		–		–		–		–		2	0.2
<i>Bolivina spathulata</i>	–		–		–		–		–		–		–	
<i>Bolivina striatula</i>	2	0.2	–		–		–		1	0.1	–		–	
<i>Bolivina subaenariensis</i>	8	0.9	–		–		–		3	0.3	2	0.1	–	
<i>Bulimina</i> sp.	–		–		–		–		1	0.1	–		1	0.1
<i>Bulimina aculeata</i>	11	1.3	6	0.7	4	1.1	–		48	4.2	11	0.6	6	0.6
<i>Bulimina costata</i>	1	0.1	–		–		–		–		–		–	
<i>Bulimina elongata</i>	–		–		–		–		–		–		3	0.3
<i>Bulimina gibba</i>	7	0.8	2	0.2	–		–		–		2	0.1	2	0.2
<i>Bulimina marginata</i>	–		–		2	0.5	–		33	2.9	23	1.2	1	0.1
<i>Cassidulina carinata</i>	20	2.3	18	2.1	6	1.6	–		139	12.0	50	2.7	1	0.1
<i>Cassidulina crassa</i>	–		–		4	1.1	–		–		–		–	
<i>Cassidulina oblonga</i>	–		–		–		–		–		–		–	
<i>Chilostomella oolina</i>	6	0.7	–		–		–		–		1	0.1	–	
<i>Cibicides</i> sp.	–		–		–		–		–		–		–	
<i>Cibicides lobatulus</i>	–		–		–		–		–		1	0.1	–	
<i>Dentalina</i> sp.1	–		–		–		–		–		–		–	
<i>Dentalina</i> sp.2	–		–		–		–		–		–		–	
<i>Dentalina</i> sp.3	–		–		–		–		–		–		–	
<i>Dentalina bradyensis</i>	–		–		–		–		1	0.1	–		–	
<i>Dentalina filiformis</i>	–		–		–		–		–		2	0.1	–	
<i>Elphidium</i> sp.1	–		–		–		–		–		–		–	
<i>Elphidium advenum</i>	1	0.1	1	0.1	3	0.8	–		2	0.2	3	0.2	7	0.7
<i>Elphidium crispum</i>	–		–		–		–		23	2.0	4	0.2	1	0.1
<i>Elphidium granosum</i> f. <i>lidoense</i>	–		–		–		–		–		–		–	
<i>Elphidium poeyanum</i> f. <i>decipiens</i>	–		–		–		–		–		–		–	
<i>Epistominella</i> sp.	–		–		–		–		–		–		–	
<i>Epistominella vitrea</i>	–		–		–		–		–		–		–	
<i>Fursenkoina acuta</i>	–		–		–		–		–		1	0.1	2	0.2
<i>Gavelinopsis praegeri</i>	1	0.1	–		–		–		3	0.3	12	0.6	–	
<i>Glandulina ovula</i>	–		–		–		–		–		–		–	
<i>Globobulimina affinis</i>	–		–		–		–		1	0.1	1	0.1	–	
<i>Globobulimina pyrula</i>	–		–		–		–		–		–		–	
<i>Globobulimina pyrula</i> var. <i>pseudospinescens</i>	–		–		1	0.3	–		1	0.1	–		–	
<i>Globocassidulina subglobosa</i>	9	1.0	–		–		–		20	1.7	1	0.1	–	
<i>Gyroidina umbonata</i>	11	1.3	3	0.3	–		–		9	0.8	3	0.2	–	
<i>Hanzawaia boueana</i>	–		–		–		–		2	0.2	1	0.1	–	
<i>Hyalinea balthica</i>	6	0.7	–		–		–		7	0.6	8	0.4	–	
<i>Lagena</i> spp.	1	0.1	1	0.1	–		–		1	0.1	1	0.1	–	
<i>Lenticulina atlantica</i>	–		–		1	0.3	–		–		–		–	
<i>Lenticulina peregrina</i>	–		–		–		–		–		–		–	
<i>Melonis barleeanus</i>	–		–		–		–		6	0.5	9	0.5	–	
<i>Neolenticulina variabilis</i>	–		–		–		–		–		–		–	

Appendix E (continued)

Station Taxa	BT 23		BT 24		BT 26		BT 28		BT 29		BT 30		BT 33	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
<i>Nonion fabum</i>	305	35.0	356	40.6	34	9.3	4	12.1	379	32.8	370	19.9	127	12.9
<i>Nonionella bradii</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Nonionella turgida</i>	49	5.6	133	15.2	150	41.1	–	–	47	4.1	173	9.3	350	35.7
<i>Polymorphinidae</i>	–	–	–	–	–	–	–	–	6	0.5	9	0.5	–	–
<i>Pseudoepionides falsobeccarii</i>	16	1.8	7	0.8	1	0.3	–	–	19	1.6	15	0.8	–	–
<i>Pullenia quinqueloba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rectuvigerina phlegeri</i>	33	3.8	15	1.7	1	0.3	–	–	22	1.9	101	5.4	16	1.6
<i>Reussella spinulosa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia complanata</i>	–	–	–	–	–	–	–	–	3	0.3	1	0.1	–	–
<i>Uvigerina</i> sp.	–	–	–	–	–	–	–	–	1	0.1	–	–	–	–
<i>Uvigerina bifurcata</i>	–	–	–	–	–	–	–	–	1	0.1	1	0.1	–	–
<i>Uvigerina elongatastriata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>	–	–	–	–	–	–	–	–	2	0.2	–	–	–	–
<i>Uvigerina peregrina</i>	3	0.3	–	–	–	–	–	–	–	–	–	–	–	–
<i>Valvulineria bradyana</i>	75	8.6	83	9.5	3	0.8	–	–	69	6.0	219	11.8	1	0.1
<i>Valvulineria complanata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Miliolids														
Indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelosina</i> spp.	–	–	10	1.1	2	0.5	–	–	1	0.1	5	0.3	10	1.0
<i>Biloculinella</i> sp.1	–	–	–	–	–	–	–	–	–	–	3	0.2	–	–
<i>Biloculinella labiata</i>	10	1.1	1	0.1	–	–	–	–	9	0.8	19	1.0	–	–
<i>Cornuspira foliacea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella</i> spp.	–	–	–	–	–	–	1	3.0	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudotriloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo</i> sp.	–	–	–	–	1	0.3	–	–	–	–	–	–	–	–
<i>Pyrgo depressa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo elongata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	–	–	–	–	–	2	0.2	–	–	8	0.6
<i>Pyrgo subsphaerica</i>	1	0.1	1	0.1	1	0.3	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> sp.	–	–	–	–	1	0.3	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>	1	0.1	–	–	1	0.3	1	3.0	–	–	–	–	2	0.2
<i>Quinqueloculina badenensis</i>	1	0.1	–	–	–	–	–	–	1	0.1	–	–	–	–
<i>Quinqueloculina lata</i>	5	0.6	2	0.2	9	2.5	1	3.0	45	3.9	7	0.4	33	3.4
<i>Quinqueloculina milletti</i>	–	–	–	–	–	–	4	12.1	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	10	1.1	2	0.2	–	–	–	–	28	2.4	12	0.6	3	0.3
<i>Quinqueloculina stalkerii</i>	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilinita tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	–	2	0.2
<i>Sigmoilopsis</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	1	0.1	–	–	–	–	1	0.1	3	0.2	–	–
<i>Siphonaperta</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Siphonaperta aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroloculina excavata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix E (continued)

Station Taxa	BT 23		BT 24		BT 26		BT 28		BT 29		BT 30		BT 33	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Fossilising agglutinated														
<i>Bigenerina nodosaria</i>	3	0.3	–	–	–	–	–	–	18	1.6	1	0.1	–	–
<i>Textularia</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1
<i>Textularia agglutinans</i>	25	2.9	5	0.6	2	0.5	–	–	27	2.3	52	2.8	14	1.4
<i>Textularia porecta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia saggitula</i>	1	0.1	–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated														
Indet.	4	0.5	1	0.1	–	–	–	–	1	0.1	4	0.2	2	0.2
Epilithe Indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Agglutinate sp.333	–	–	4	0.5	–	–	–	–	–	–	31	1.7	4	0.4
<i>Adercotryma</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	3	0.3	2	0.5	–	–	1	0.1	7	0.4	1	0.1
<i>Ammoscalaria foliacea</i>	4	0.5	9	1.0	2	0.5	–	–	4	0.3	34	1.8	14	1.4
<i>Clavulina cylindrica</i>	144	16.5	77	8.8	1	0.3	–	–	1	0.1	12	0.6	10	1.0
<i>Cribrostomoides</i> sp.	–	–	–	–	2	0.5	–	–	–	–	–	–	–	–
<i>Cribrostomoides subglobosus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	–	–	1	0.1	2	0.5	–	–	–	–	3	0.2	6	0.6
<i>Eggerella</i> sp.1	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
<i>Eggerella</i> sp.2	–	–	–	–	–	–	–	–	–	–	–	–	5	0.5
<i>Eggerella scabra</i>	32	3.7	69	7.9	108	29.6	3	9.1	52	4.5	186	10.0	277	28.2
<i>Haplophragmoides</i> spp.	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–
<i>Lagenammina difflugiformis</i>	13	1.5	22	2.5	1	0.3	–	–	29	2.5	239	12.9	4	0.4
<i>Leptohalysis scottii</i>	–	–	1	0.1	2	0.5	–	–	–	–	–	–	1	0.1
<i>Nouria polymorphinoides</i>	–	–	9	1.0	1	0.3	1	3.0	–	–	7	0.4	20	2.0
<i>Psammosphaera bowmani</i>	–	–	1	0.1	–	–	–	–	–	–	2	0.1	7	0.7
<i>Recurvoides scitulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax</i> sp.	–	–	2	0.2	–	–	–	–	–	–	4	0.2	–	–
<i>Reophax bilocularis</i>	–	–	–	–	–	–	–	–	1	0.1	–	–	–	–
<i>Reophax dentaliniformis</i>	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Reophax fusiformis</i>	–	–	7	0.8	–	–	–	–	3	0.3	23	1.2	1	0.1
<i>Reophax scorpiurus</i>	–	–	2	0.2	–	–	–	–	1	0.1	16	0.9	–	–
<i>Technitella legumen</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Technitella melo</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina</i> sp.	–	–	–	–	–	–	–	–	–	–	2	0.1	–	–
<i>Trochammina</i> sp.1	–	–	–	–	–	–	–	–	–	–	5	0.3	–	–
<i>Trochammina globigeriniformis</i>	5	0.6	10	1.1	1	0.3	–	–	6	0.5	118	6.4	5	0.5
<i>Trochammina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina</i> cf. <i>fissuraperta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Organic foraminifera	–	–	2	0.2	–	–	–	–	–	–	2	0.1	–	–
Total number of living individuals	872		877		365		33		1154		1858		981	

Appendix E (continued)

Station Water depth (m) Taxa	BT 35 20		BT 36 89		BT 37 80		BT 39 69		BT 41 30		BT 48 100	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Perforates												
Indet.	–		–		–		1	0.1	–		1	0.1
<i>Ammonia beccarii</i> f. <i>beccarii</i>	181	13.5	13	1.1	11	0.9	28	2.8	1	0.3	6	0.6
<i>Ammonia beccarii</i> f. <i>inflata</i>	–		55	4.6	24	2.0	–		–		18	1.8
<i>Ammonia tepida</i>	70	5.2	–		–		–		44	12.0	–	
<i>Amphicoryna scalaris</i>	–		17	1.4	12	1.0	1	0.1	–		39	3.9
<i>Astacolus crepidulus</i>	–		1	0.1	–		–		–		–	
<i>Bolivina</i> sp.	5	0.4	1	0.1	–		–		4	1.1	–	
<i>Bolivina alata</i>	–		19	1.6	15	1.2	–		–		55	5.5
<i>Bolivina dilatata</i>	–		–		–		4	0.4	–		–	
<i>Bolivina spathulata</i>	–		–		–		1	0.1	–		–	
<i>Bolivina striatula</i>	–		3	0.3	3	0.2	–		–		1	0.1
<i>Bolivina subaenariensis</i>	–		20	1.7	7	0.6	1	0.1	–		8	0.8
<i>Bulimina</i> sp.	–		–		–		–		1	0.3	–	
<i>Bulimina aculeata</i>	1	0.1	38	3.2	109	8.9	12	1.2	–		90	9.0
<i>Bulimina costata</i>	–		2	0.2	3	0.2	–		–		3	0.3
<i>Bulimina elongata</i>	22	1.6	–		–		2	0.2	5	1.4	–	
<i>Bulimina gibba</i>	–		–		–		1	0.1	–		–	
<i>Bulimina marginata</i>	1	0.1	8	0.7	19	1.6	11	1.1	1	0.3	42	4.2
<i>Cassidulina carinata</i>	–		46	3.9	50	4.1	152	15.3	–		14	1.4
<i>Cassidulina crassa</i>	–		–		–		–		–		–	
<i>Cassidulina oblonga</i>	–		1	0.1	3	0.2	–		–		3	0.3
<i>Chilostomella oolina</i>	–		10	0.8	15	1.2	–		–		24	2.4
<i>Cibicides</i> sp.	–		–		–		–		–		2	0.2
<i>Cibicides lobatulus</i>	–		–		–		–		–		1	0.1
<i>Dentalina</i> sp.1	–		–		–		–		–		1	0.1
<i>Dentalina</i> sp.2	–		–		–		–		–		2	0.2
<i>Dentalina</i> sp.3	–		–		–		–		–		1	0.1
<i>Dentalina bradyensis</i>	–		–		–		–		–		–	
<i>Dentalina filiformis</i>	–		–		–		–		–		–	
<i>Elphidium</i> sp.1	–		–		–		–		–		–	
<i>Elphidium advenum</i>	9	0.7	–		1	0.1	2	0.2	–		–	
<i>Elphidium crispum</i>	35	2.6	2	0.2	2	0.2	–		–		2	0.2
<i>Elphidium granosum</i> f. <i>lidoense</i>	14	1.0	–		–		–		–		–	
<i>Elphidium poeyanum</i> f. <i>decepiens</i>	–		–		–		–		–		–	
<i>Epistominella</i> sp.	–		–		–		–		–		1	0.1
<i>Epistominella vitrea</i>	–		–		–		1	0.1	–		–	
<i>Fursenkoina acuta</i>	2	0.1	–		–		2	0.2	–		–	
<i>Gavelinopsis praegeri</i>	–		1	0.1	2	0.2	1	0.1	–		–	
<i>Glandulina ovula</i>	–		1	0.1	–		–		–		–	
<i>Globobulimina affinis</i>	–		12	1.0	5	0.4	–		–		10	1.0
<i>Globobulimina pyrula</i>	–		–		2	0.2	–		–		20	2.0
<i>Globobulimina pyrula</i> var. <i>pseudospinescens</i>	–		6	0.5	2	0.2	–		–		32	3.2
<i>Globocassidulina subglobosa</i>	–		8	0.7	3	0.2	–		–		42	4.2
<i>Gyroidina umbonata</i>	–		10	0.8	5	0.4	1	0.1	–		4	0.4
<i>Hanzawaia boueana</i>	–		5	0.4	2	0.2	–		–		3	0.3
<i>Hyalinea balthica</i>	–		13	1.1	16	1.3	–		–		7	0.7
<i>Lagena</i> spp.	–		3	0.3	1	0.1	–		–		1	0.1
<i>Lenticulina atlantica</i>	–		–		–		–		–		–	
<i>Lenticulina peregrina</i>	–		6	0.5	1	0.1	–		–		2	0.2
<i>Melonis barleeanus</i>	2	0.1	95	8.0	41	3.4	–		–		30	3.0
<i>Neolenticulina variabilis</i>	–		–		1	0.1	–		–		–	

Appendix E (continued)

Station Taxa	BT 35		BT 36		BT 37		BT 39		BT 41		BT 48	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
<i>Nonion fabum</i>	131	9.8	76	6.4	105	8.6	158	15.9	8	2.2	23	2.3
<i>Nonionella bradii</i>	–		–		–		–		–		–	
<i>Nonionella turgida</i>	144	10.8	46	3.9	38	3.1	190	19.1	20	5.5	2	0.2
<i>Polymorphinidae</i>	–		1	0.1	11	0.9	–		–		–	
<i>Pseudoepionides falsobeccarii</i>	–		27	2.3	22	1.8	6	0.6	–		16	1.6
<i>Pullenia quinqueloba</i>	–		–		–		–		–		1	0.1
<i>Rectuvigerina phlegeri</i>	14	1.0	8	0.7	16	1.3	21	2.1	–		5	0.5
<i>Reussella spinulosa</i>	–		–		–		–		–		–	
<i>Robertina translucens</i>	–		–		2	0.2	–		–		–	
<i>Rosalina bradyi</i>	–		–		–		–		–		–	
<i>Rosalina vilardeboana</i>	–		–		–		–		–		–	
<i>Saidovina karreriana</i>	–		–		1	0.1	–		–		–	
<i>Stainforthia complanata</i>	–		4	0.3	4	0.3	–		–		1	0.1
<i>Uvigerina</i> sp.	–		–		–		–		–		–	
<i>Uvigerina bifurcata</i>	–		13	1.1	1	0.1	–		–		5	0.5
<i>Uvigerina elongatastriata</i>	–		1	0.1	–		–		–		–	
<i>Uvigerina mediterranea</i>	–		10	0.8	1	0.1	–		–		45	4.5
<i>Uvigerina peregrina</i>	–		4	0.3	2	0.2	1	0.1	–		5	0.5
<i>Valvulineria bradyana</i>	–		147	12.4	144	11.8	99	10.0	–		26	2.6
<i>Valvulineria complanata</i>	–		–		–		–		–		–	
Miliolids												
Indet.	1	0.1	–		–		–		–		1	0.1
<i>Adelosina</i> spp.	–		7	0.6	4	0.3	3	0.3	–		1	0.1
<i>Biloculinella</i> sp.1	–		–		–		4	0.4	–		–	
<i>Biloculinella labiata</i>	–		18	1.5	15	1.2	1	0.1	–		19	1.9
<i>Cornuspira foliacea</i>	–		–		–		–		–		1	0.1
<i>Miliolinella</i> spp.	–		–		–		–		–		1	0.1
<i>Miliolinella subrotunda</i>	–		–		–		–		–		1	0.1
<i>Pseudotriloculina</i> sp.	–		–		–		–		–		–	
<i>Pyrgo</i> sp.	–		–		–		–		–		–	
<i>Pyrgo depressa</i>	–		–		–		–		–		2	0.2
<i>Pyrgo elongata</i>	–		–		–		–		–		–	
<i>Pyrgo oblonga</i>	–		–		–		7	0.7	–		–	
<i>Pyrgo subsphaerica</i>	–		4	0.3	1	0.1	1	0.1	–		–	
<i>Quinqueloculina</i> sp.	–		–		–		–		–		–	
<i>Quinqueloculina aspera</i>	2	0.1	–		–		1	0.1	–		–	
<i>Quinqueloculina badenensis</i>	–		7	0.6	13	1.1	–		–		–	
<i>Quinqueloculina lata</i>	408	30.5	–		3	0.2	19	1.9	3	0.8	–	
<i>Quinqueloculina milletti</i>	–		–		–		–		16	4.4	–	
<i>Quinqueloculina seminula</i>	–		38	3.2	108	8.9	1	0.1	1	0.3	44	4.4
<i>Quinqueloculina stalkerii</i>	2	0.1	–		–		–		–		–	
<i>Quinqueloculina tenuicollis</i>	28	2.1	–		–		–		–		–	
<i>Sigmoilinita tenuis</i>	–		–		–		–		–		–	
<i>Sigmoilopsis</i> sp.	–		–		–		–		–		–	
<i>Sigmoilopsis schlumbergeri</i>	–		–		2	0.2	–		–		3	0.3
<i>Siphonaperta</i> sp.	–		–		–		–		–		–	
<i>Siphonaperta aspera</i>	–		–		–		–		1	0.3	–	
<i>Spiroloculina excavata</i>	–		–		–		–		–		–	
<i>Triloculina tricarinata</i>	–		–		1	0.1	–		–		1	0.1
<i>Triloculina trigonula</i>	–		–		–		–		–		–	

Appendix E (continued)

Station Taxa	BT 35		BT 36		BT 37		BT 39		BT 41		BT 48	
	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%	Tot	%
Fossilising agglutinated												
<i>Bigenerina nodosaria</i>	–		139	11.7	72	5.9	–		–		102	10.2
<i>Textularia</i> sp.	–		–		–		–		–		–	
<i>Textularia agglutinans</i>	1	0.1	34	2.9	83	6.8	17	1.7	–		33	3.3
<i>Textularia porecta</i>	–		–		–		–		2	0.5	–	
<i>Textularia saggitula</i>	–		–		–		–		–		–	
Non-fossilising agglutinated												
Indet.	4	0.3	–		4	0.3	1	0.1	1	0.3	10	1.0
Epilithe Indet.	–		1	0.1	4	0.3	–		–		5	0.5
Agglutinate sp.333	–		–		–		3	0.3	–		2	0.2
<i>Adercotryma</i> sp.	–		–		1	0.1	–		–		5	0.5
<i>Adercotryma glomerata</i>	–		1	0.1	2	0.2	2	0.2	–		1	0.1
<i>Ammoscalaria foliacea</i>	–		11	0.9	9	0.7	11	1.1	–		19	1.9
<i>Clavulina cylindrica</i>	–		59	5.0	73	6.0	27	2.7	–		23	2.3
<i>Cribrostomoides</i> sp.	–		–		–		–		–		–	
<i>Cribrostomoides subglobosus</i>	–		–		–		–		–		–	
<i>Cribrostomoides wiesneri</i>	31	2.3	1	0.1	–		7	0.7	2	0.5	–	
<i>Eggerella</i> sp.1	–		–		–		–		–		–	
<i>Eggerella</i> sp.2	–		–		–		–		–		–	
<i>Eggerella scabra</i>	111	8.3	47	4.0	50	4.1	152	15.3	5	1.4	58	5.8
<i>Haplophragmoides</i> spp.	–		–		–		–		–		2	0.2
<i>Lagenammina difflugiformis</i>	–		23	1.9	34	2.8	8	0.8	1	0.3	16	1.6
<i>Leptohalysis scottii</i>	4	0.3	–		–		7	0.7	248	67.8	–	
<i>Nouria polymorphinoides</i>	69	5.2	–		1	0.1	4	0.4	2	0.5	–	
<i>Psammosphaera bowmani</i>	38	2.8	–		–		–		–		–	
<i>Recurvoides scitulus</i>	–		7	0.6	1	0.1	–		–		6	0.6
<i>Reophax</i> sp.	–		–		–		–		–		–	
<i>Reophax bilocularis</i>	–		–		–		–		–		6	0.6
<i>Reophax dentaliniformis</i>	–		–		1	0.1	–		–		4	0.4
<i>Reophax fusiformis</i>	5	0.4	1	0.1	–		–		–		–	
<i>Reophax scorpiurus</i>	–		18	1.5	8	0.7	–		–		38	3.8
<i>Technitella legumen</i>	–		–		–		–		–		1	0.1
<i>Technitella melo</i>	–		1	0.1	–		–		–		1	0.1
<i>Trochammina</i> sp.	–		–		–		–		–		–	
<i>Trochammina</i> sp.1	–		–		–		–		–		–	
<i>Trochammina globigeriniformis</i>	1	0.1	37	3.1	27	2.2	14	1.4	–		4	0.4
<i>Trochammina</i> sp.	–		–		–		–		–		–	
<i>Trochammina</i> cf. <i>fissuraperta</i>	–		–		–		–		–		–	
Organic foraminifera												
	–		–		–		7	0.7	–		–	
Total number of living individuals	1336		1187		1219		993		366		1004	

CHAPITRE 2

SPATIAL VARIABILITY (DECIMETRIC-SCALE) OF LIVE (STAINED) BENTHIC FORAMINIFERA FROM A RIVER-DOMINATED SHELF (GULF OF LIONS): APPLICATIONS FOR FORAMINIFERAL STUDIES

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CHAPITRE 2

**SPATIAL VARIABILITY (DECIMETRIC-SCALE) OF LIVE
(STAINED) BENTHIC FORAMINIFERA FROM A RIVER-
DOMINATED SHELF (GULF OF LIONS)**

APPLICATIONS FOR FORAMINIFERAL STUDIES

Goineau A.^{a,b}, Fontanier C.^{a,b}, Jorissen F.J.^{a,b}, Hunault G.^c, Buscail R.^d, Kerhervé P.^d,
Metzger, E.^{a,b}

^a Laboratory of Recent and Fossil Bio-Indicators (BIAF), University of Angers,
UPRES EA 2644, 2 Boulevard Lavoisier, 49045 Angers Cedex 01, France,

^b Laboratory for the Study of Marine Bio-Indicators (LEBIM), Ker Châlon, 85350 Ile d'Yeu,
France

^c Hémodynamique Interaction Fibrose et Invasivité Tumorales Hépatiques (HIFITH),
University of Angers, UPRES 3859, IFR 132, Pavillon Ollivier, Rue Haute de Reculée, 49045
Angers Cedex, France

^d Centre de Formation et de Recherche sur l'Environnement Marin, University of Perpignan,
UMR 5110 CNRS, 52 Avenue Paul Alduy, 66860 Perpignan Cedex, France

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ABSTRACT

Live (Rose Bengal-stained) benthic foraminifera were investigated at two stations (24 and 67 m depth) in the Rhône prodelta (NW Mediterranean, Gulf of Lions). At each site, four replicate cores were sampled to precise whether small-scale (decimetric) spatial variability of foraminiferal faunas exists in our study area. Both sites are strongly impacted by Rhône River inputs (high contents of continental organic matter). In these dynamic environments, foraminiferal faunas of the 63–150 and >150 μm size fractions are dominated by *Ammonia tepida*, *Leptohalysis scottii* and *Psammosphaera fusca* at 1.9 km from the river mouth (Station A, 24 m deep) and by *Nonionella turgida*, *Nonion fabum*, *Valvulineria bradyana* and *Eggerella scabra* at 5.5 km from the mouth (Station N, 67 m). Foraminiferal faunas show more or less important absolute density variations at each site. At Station N, the significant dissimilarity between replicate cores is probably caused by the opportunistic behaviour of Bolivinids and *N. turgida*. This heterogeneous distribution of foraminiferal faunas in such dynamic environment can result from a patchy distribution of the organic matter. However, foraminiferal faunas are not significantly different between replicate cores at both sites when species relative abundances are considered. We also compared our present data with those described by Goineau et al. (In Press – see Chapter 1 in this thesis) for 20 stations sampled in the Rhône prodelta in September 2006. As expected, spatial variability observed at this larger geographical scale is too important to be hidden by potential small-scale (decimetric) variability existing with species relative abundances at one site. These conclusions confirm the reliability of foraminiferal biofacies analysis in a river-dominated environment, determined with only one replicate core per site. Finally, our data also imply the preferable use of species relative abundances to compare benthic foraminiferal communities in temporal surveys.

Keywords: Live benthic foraminifera; Patchiness; Decimetric scale; Rhône prodelta.

2.1. INTRODUCTION

Continental shelves constitute key environments in terms of primary production and transfer of organic and inorganic matter (Walsh et al., 1981; Hargrave, 1985; Smith and MacKenzie, 1987; Walsh, 1988, 1991; Jahnke et al., 1990; Wollast, 1991; Hedges and Keil, 1995; Bauer and Druffel, 1998). Notably, in river-dominated shelves, rivers play a major role in the transfer of particulate organic matter from continental to marine areas (Mopper and

Degens, 1979; Eppley, 1984; Romankevich, 1984). Moreover, dissolved nutrients supplied by river can enhance local primary production inducing deposition of fresh marine organic matter at the seafloor (Lohrenz et al., 1990, 1997; Van der Zwaan and Jorissen, 1991; Dagg and Breed, 2003). Such important organic matter inputs to the sea floor can either lead to increased benthic macrofaunal biomass (Mann, 1988; Largier, 1993; Danovaro et al., 2000; Manini et al., 2002; Salen-Picard et al., 2002, 2003; Darnaude et al., 2004), or to eutrophication of the benthic ecosystems with hypoxic to anoxic conditions at the sediment-water interface and in the bottom waters (Van der Zwaan and Jorissen, 1991; Jorissen et al., 1992; Donnici and Serandrei Barbero, 2002). Thus, in such shelf environments, the spatial distribution (on a kilometric scale) and temporal dynamics of living benthic foraminifera are controlled by (1) the availability of organic detritus at and below the sediment-water interface, (2) oxygen concentration in bottom and sediment pore waters, and (3) hydro-sedimentary processes prevailing at the sea floor (Alve and Murray, 1994; Gustafsson and Nordberg, 2000, 2001; Duijnsteet et al., 2003; Suhr et al., 2003; Langezaal et al., 2006; Diz and Francés, 2008; Duchemin et al., 2008; Mojtahid et al., 2009; Goineau et al., In Press). In the shelf area under influence of the Rhône River (Gulf of Lions), distinct benthic foraminiferal faunas inhabit contrasted benthic environments (Goineau et al., In Press – see Chapter 1 in this thesis). For instance, miliolid species (e.g., *Quinqueloculina lata*, *Triloculina trigonula*) characterise a sandy coastal area submitted to winnowing by strong bottom currents. *Leptohalysis scottii* and *Ammonia tepida* dominate an organic matter-enriched and flood-influenced area close to the Rhône River mouth. Faunas dominated by *Nonionella turgida*, *Cassidulina carinata*, *Nonion fabum*, and *Clavulina cylindrica* inhabit ecosystems off the river mouth characterised by a decreasing Rhône influence in terms of organic and inorganic supplies (Goineau et al., In Press – see Chapter 1). Unfortunately, foraminiferal datasets from ecological studies are usually established on the basis of one sample (i.e., core) per investigated station. Few studies performed in deep-sea (Bernstein et al., 1978; Bernstein and Meador, 1979; Barras et al., 2010; Griveaud et al., In press) and shelf environments (Buzas, 1968; Hohenegger et al., 1989, 1993; Buzas and Gibson, 1990; Silva et al., 1996; Swallow, 2000; Buzas et al., 2002; Morvan et al., 2006) have investigated the spatial dynamics of benthic foraminifera at a smaller spatial scale (<1 km). In these studies, small-scale (decimetric to decametric) spatial variability of benthic foraminiferal faunas exists and is explained by a patchy distribution of organic detritus at the seafloor, potentially of heterogeneous quality and/or origin, favouring the growth of some species by pulsating reproduction rates and/or increasing competition. Some works performed on the macro- and meiofaunas also put into evidence that patchiness

depends on the studied spatial scale (centimetric, decimetric, metric or kilometric) (Underwood and Chapman, 1996; Middelboe et al., 2003; Frascchetti et al., 2005; Balata et al., 2006; Smale, 2008). Physical and biological processes (e.g., food availability, food quality, substrate, inter- and intra specific competition) explain spatial variability at these different scales in shallow environments (Underwood and Petraitis, 1993; Underwood, 1996; Legendre et al., 1997; Benedetti-Cecchi, 2001; Coleman, 2002). Nevertheless, Barras et al. (2010) showed at a shallow station in the Bay of Biscay that if micro- to meso-scale patchiness exists, it is less important than maximal temporal variability of foraminiferal faunas. In our paper, we will try to highlight if such a patchy distribution of benthic foraminiferal faunas exists at a decimetric scale in the Rhône prodelta, by considering both their absolute and relative densities (i.e., percentages). Investigating this key feature will allow us understanding two other important questions. At first, are spatial patterns observed at a large scale (i.e., kilometric-scale) overshadowed by a higher patchy distribution of benthic foraminifera at a smaller scale (i.e., decimetric-scale)? Furthermore, as evoked by Barras et al. (2010), can temporal variability of foraminiferal communities, sampled at one site at different periods, be hidden or obscured by small-scale spatial variability (patchiness) recorded during only one sampling period?

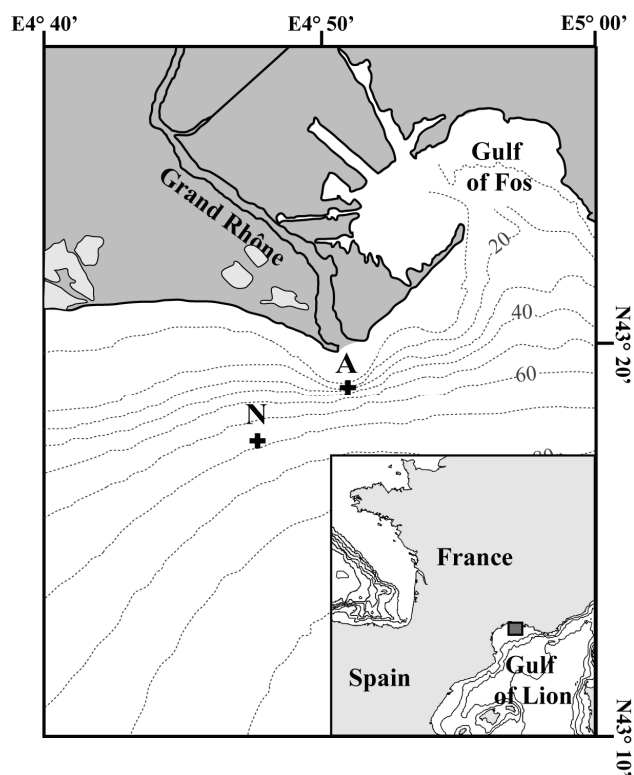


Figure 1: Study area and location of both Stations A and N.

Therefore, we present here a decimetric-scale spatial variability study of live (stained) benthic foraminiferal faunas sampled at two stations A and N in the Rhône prodeltaic area (RIOTECH cruise, September 2007; Fig. 1). Environmental conditions prevailing at each site differ one from the other (Cathalot et al., 2009; Pastor et al., In press). Station A (24 m depth) is located close to the Rhône River mouth in the proximal prodelta (1.9 km far from the river mouth). It is characterised by a strong continental imprint in terms of organic and inorganic inputs. Station N (67 m depth), 5.5 km far away from the river mouth, is characterised by a weaker riverine influence. We have investigated both the 63–150 μm and $>150 \mu\text{m}$ size fractions in four replicate cores at each site. Foraminiferal faunal variability is studied through faunal composition, expressed by the absolute and relative densities of the various species. It is sustained by statistical analyses (Friedman test). Afterwards, we compare the spatial variability determined in this study at a decimetric-scale with the spatial variability recorded in the whole prodelta (“kilometric” scale; Goineau et al., In Press – see Chapter 1) in order to judge the importance of small-scale patchiness compared to the foraminiferal distribution determined at a larger scale.

2.2. MATERIAL AND METHODS

2.2.1. Study area

The Gulf of Lion (North-Western Mediterranean Sea) is a large crescent-shaped continental shelf incised by submarine canyons (Berné and Gorini, 2005). The general oceanographic circulation is dominated by the cyclonic Liguro-Provençal Current (LPC) flowing to the west from the Provence to the Catalonia coast (Béthoux and Prieur, 1983; Millot, 1990). This circulation is under the strong influence of the Northern and North-Western Mistral and Tramontane wind regimes (Millot, 1999). With an annual primary production of 78 to 204 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at the basin scale (Lefevre et al., 1997; Conan et al., 1998; Bosc et al., 2004), the Gulf of Lions is one the most productive areas of the Mediterranean Sea (Diaz, 2000). Chl-*a* concentrations in surface waters vary from 1 $\text{mg Chl-}a\cdot\text{m}^{-3}$ from March to May, the most productive season, to 0.1–0.2 $\text{mg Chl-}a\cdot\text{m}^{-3}$ in summer (Bosc et al., 2004). 50% of the total nutrients needed for primary production in the Gulf of Lions are introduced by the Rhône river (Lochet and Leveau, 1990). With an annual mean flow of 1.700 $\text{m}^3\cdot\text{s}^{-1}$ (Pont et al., 2002), reaching 10.000 $\text{m}^3\cdot\text{s}^{-1}$ during flood events in autumn and spring (Pont et al., 2002), the Rhône River carries 90% of terrigenous material and 80% of fresh water introduced into the Gulf of Lions (Durrieu de Madron et al., 2000, 2003),

supplying as much as 6.2 Mt.an^{-1} of particles to this area (Thill et al., 2001). This terrigenous material is transferred to the marine environment via two different ways: in sea surface water within the river plume, flowing south-westward, and above the sea floor in a benthic nepheloid layer (Naudin et al., 1997). 70% of these introduced particles are deposited on the shelf and 30% are transferred to the slope and the deeper basin (Got and Aloisi, 1990). On the continental shelf, at the outlet of the river mouth, a part of the terrigenous input forms a delta front and a prodelta. This prodelta extends from 0 to 60 m depth, to a distance of above to 6 km far from the river mouth (Rabineau et al., 2005). High deposition rates ranging between 30 and 50 cm.year^{-1} are recorded in this area (Calmet and Fernandez, 1990; Charmasson et al., 1998; Rabineau et al., 2005).

2.2.2. Sediment sampling

Stations A and N were sampled on the 13th and 14th of September 2007 during the RIOTECH cruise on board the *R/V Téthys II*. Stations were respectively located at 24 and 67 m depth in the Rhône prodelta (Fig. 1, Table 1). Sediment cores of 72 cm^2 surface area were recovered with a multicorer MUC 8/100 (Oktopus GmbH) that permits to collect simultaneously eight cores with a preserved sediment-water interface.

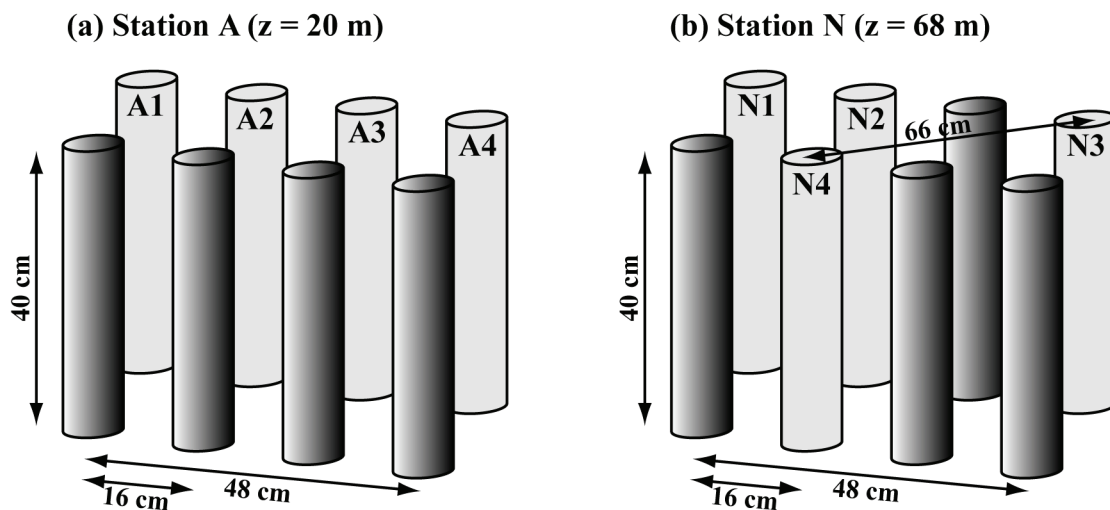


Figure 2: Relative location of replicate cores sampled at both Stations A (a) and N (b) on the multicorer after deployments.

At each station, four replicate cores from the same multicorer deployment were sampled for foraminiferal analyses. This sampling method permits the assessment of micro-scale

patchiness (distance between replicates from 16 to 66 cm; Fig. 2). Three supplementary cores were collected on another multicorer deployment for organic matter analyses.

2.2.3. Environmental analyses

For both stations, Total Organic Matter, Total Nitrogen and Organic Carbon concentrations (TOM, TN and OC, respectively), total hydrolysable amino acids (THAA) and total lipids contents, and carbon and nitrogen stable isotopic ratios of organic matter ($\delta^{13}\text{C}_{\text{OM}}$ and $\delta^{15}\text{N}_{\text{OM}}$) were measured on milled and freeze-dried sediment samples from the top 0–0.5 cm of one sediment core. All protocols are precisely detailed in Fontanier et al. (2008b).

In situ profiles of O_2 in the pore water were obtained by a benthic microprofiler using Clark micro-electrodes (Rabouille et al., 2003; Cathalot et al., 2009). Bottom-waters were sampled at 2 m above the sea floor by a Niskin bottle for determination of temperature (T_{BW}) and dissolved oxygen ($[\text{O}_2]_{\text{BW}}$) (Table 1).

2.2.4. Foraminiferal analysis

For foraminiferal faunal analysis, each replicate core was sliced on board, every 0.5 cm from the sediment-water interface down to 2 cm depth, and every 1 cm from 2 to 5 cm depth. These samples were stored in 500 cm³ pots with 95% ethanol containing 1 g.l⁻¹ Rose Bengal and shaken for several seconds. Rose Bengal staining is a coloration method commonly used for the identification of live foraminifera (Walton, 1952; Murray and Bowser, 2000). In the laboratory, samples were sieved through 63 and 150 μm mesh screens and then preserved in 95% ethanol. All stained specimens of the >150 μm size fraction were handpicked down to 2 cm depth under wet conditions under a binocular microscope and stored in micropaleontological slides. Foraminifera belonging to the 63–150 μm size fraction were investigated down to 1 cm depth. Samples of this size fraction were dried and split with an Ottomicrosplitter because of faunal richness, and foraminifera from complete splits were wet-picked until a minimum of 300 individuals was counted. Despite the easy and rapid way of Rose Bengal technique, an important methodological problem is that protoplasm of dead foraminifera may be preserved in anoxic sediment, and may still be stained by Rose Bengal (Bernhard, 1988; Corliss and Emerson, 1990; Bernhard, 2000). Consequently, only specimens with all chambers (except the last one) brightly stained pink were counted, and doubtful individuals were compared with perfectly stained individuals of the same species found in more superficial and oxygenated sediment layers. Total living foraminiferal density was

calculated for the >150 μm (0–2 cm depth) and 63–150 μm size fractions (0–1 cm) in each replicate core. These absolute density values are normalised for a sediment surface area of 100 cm^2 (D_{100}). Species relative densities (i.e., percentages) calculated for each replicate core permits to define major species (i.e., species >5% in at least one core). In the 63–150 μm size fraction, since total absolute densities were extrapolated (splits), resulting estimated absolute and relative density values are approximated and preceded by a “~”. We calculated mean absolute (MD_{100}) and relative densities of each major species, with standard deviation (Sd), defining a mean foraminiferal faunal composition for each station. To assess the biodiversity of foraminiferal faunas, Shannon (H) and Evenness (E) indices were calculated in each replicate cores for both size fractions (Hayek and Buzas, 1997; Murray, 2006).

2.2.5. Statistical analyses

We performed statistical analyses with the R software on major species of: (1) Station A, 63–150 μm size fraction; (2) Station A, >150 μm size fraction; (3) Station N, 63–150 μm size fraction; and (4) Station N, >150 μm size fraction. Each database was investigated for absolute (D_{100}) and relative (%) abundances, i.e., a total of eight analysed files. Normality and sphericity of each database were tested with the classical Shapiro and Mauchly tests. Since none of the eight databases were both normal and spherical at the same time, we used the non-parametric Friedman's test to highlight any significant difference between replicates. Absolute and relative densities of major species within each replicate core were the dependant variables. For all computations, the level of signification was 0.05.

2.3. RESULTS

2.3.1. Environmental data

In the top half cm of sediment, OC contents of 1.2% d.w and 1.4% d.w. are measured at Station N and Station A, respectively. Total hydrolysable amino acids and lipids contents exhibit values of 2.7 mg.g^{-1} d.w. (Station N) and 3.7 mg.g^{-1} d.w. (Station A), and represent 22.4 and 26.4% of OC, respectively. $\delta^{13}\text{C}_{\text{OM}}$ values are -26.64‰ at Station A and -25.82‰ at Station N. $\delta^{15}\text{N}$ is constant, with values of 3.92‰ and 3.90‰ at Station A and N, respectively. Both stations exhibit high bottom water oxygen concentrations ($> 200 \mu\text{mol.l}^{-1}$), with oxygen saturation values of 82% at Station A and 68% at Station N (Table 1). Oxygen penetration depth (OPD) into the sediment is very shallow, with 1.6 mm at Station A and 4.8 mm at Station N.

		Station	A	N
Stations characteristics	Lat. (°N)		43°18'47"	43°17'27"
	Long. (°E)		4°51'05"	4°47'50"
	Water depth (m)		24	67
	Distance/river mouth (km)		1.9	5.5
Bottom water analyses	T _{BW} (°C)		17.7	14.5
	[O ₂] _{BW} (µmol.l ⁻¹)		244	217
	(%Saturation)		82	68
Sediment analyses	OPD (mm)		1.6	4.8
	TOM (mg.g ⁻¹ d.w.)		25.2	21.6
	OC (% d.w.)		1.4	1.2
	TN (% d.w.)		0.131	0.106
	Lipids (mg.g ⁻¹ d.w.)		1.1	0.6
	THAA (mg.g ⁻¹ d.w.)		2.6	2.1
	Lipids + THAA (mg.g ⁻¹ d.w.)		3.7	2.7
	(%TOM)		14.7	12.5
	(%OC)		26.4	22.5
	(C:N) _{OM} (Atomic ratio)		12.5	13.2
δ ¹³ C _{OM} (‰)		-26.64	-25.82	
δ ¹⁵ N (‰)		3.92	3.90	

Table 1: Stations characteristics (latitude, longitude, water depth and distance from the river mouth) and overall analyses performed at these sites: bottom waters temperature (T_{BW}) and oxygenation ($[O_2]_{BW}$), oxygen penetration depth (OPD) into the sediment, and particulate organic matter from the top half-centimetre of sedimen, i.e., total organic matter (TOM), organic carbon (OC), total nitrogen (TN), lipids and total hydrolysable amino-acids (THAA) contents for dry-weight sediment (d.w.) and contribution to TOM (%TOM) and OC (%OC).

2.3.2. Foraminiferal faunas

2.3.2.1. Station A (24 m)

In the 63–150 µm size fraction, foraminiferal density (D_{100}) ranges between ~960 (core A1) and ~1570 ind./100 cm² (core A2) (mean total density $MD_{100} = 1314$ ind./100 cm² ± 13%; Fig. 3a, Table 2). The lowest species richness (S) is recorded in core A4 with 13 taxa, whereas highest value of 18 taxa is identified in core A2 (Fig. 3b). The Shannon index (H) varies from 1.75 to 1.98. The Evenness index (E) ranges between 0.39 and 0.46 (Fig. 3c–d). Foraminiferal faunas are dominated by non-fossilising agglutinated (~66 to 75%) and perforate taxa (~12 to 19%; Appendix A). *Psammosphaera fusca* (~41 to 45%) and *Leptohalysis scottii* (~17 to 27%) strongly dominate the faunas in all replicate cores (Fig. 4a). *Bolivina dilatata*, *Stainforthia fusiformis* and *Quinqueloculina pygmaea* are found in all cores but are less abundant. *Quinqueloculina pygmaea* accounts for ~3 to 6% of total living faunas,

and is a major taxon in core A2. *Bolivina dilatata* and *S. fusiformis* constitute between ~1–6% and ~1–5% of the total faunas, respectively. The highest variability in absolute densities is observed for *S. fusiformis* ($MD_{100} = 42 \text{ ind./100 cm}^2 \pm 48\%$), *B. dilatata* ($39 \text{ ind./100 cm}^2 \pm 43\%$) and *Q. pygmaea* ($53 \text{ ind./100 cm}^2 \pm 40\%$) with standard deviations >40% (Fig. 5a, Table 2).

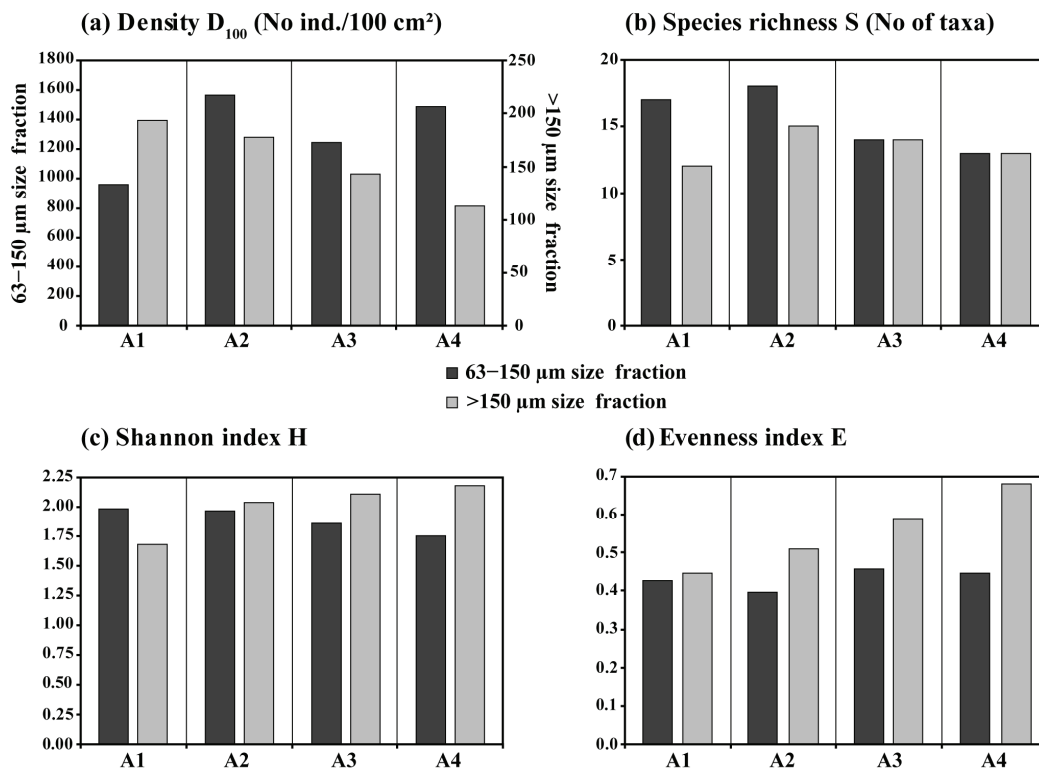
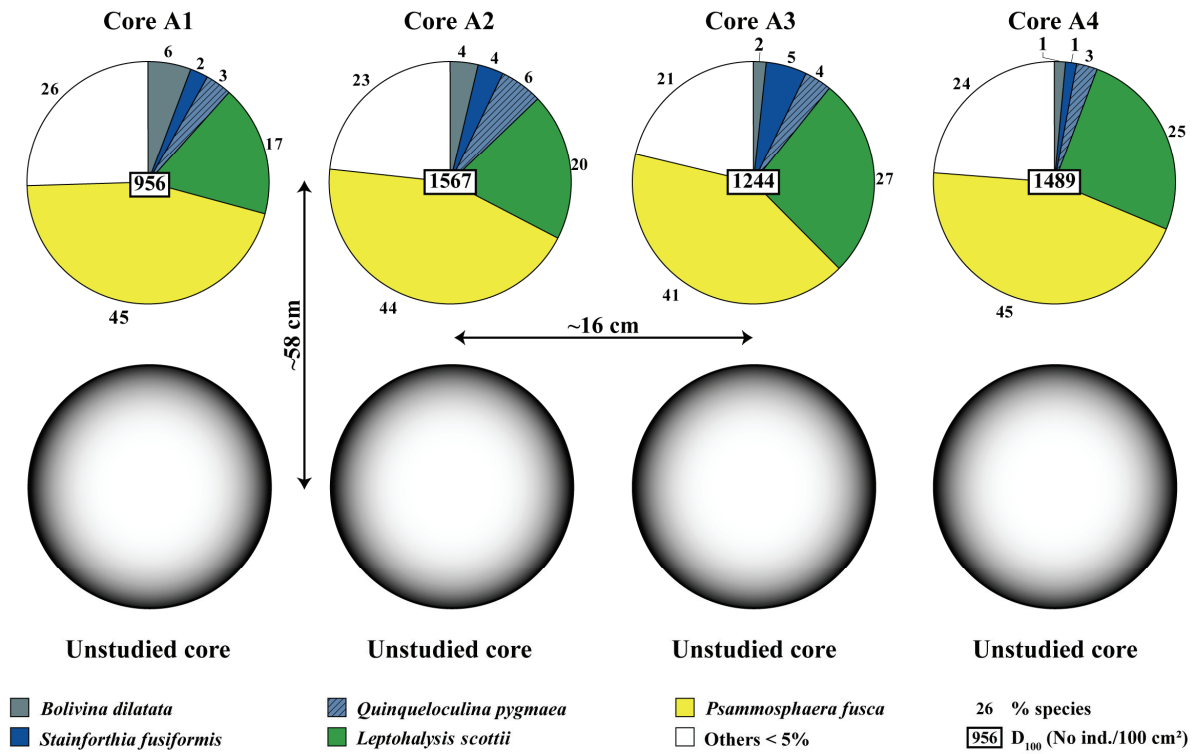


Figure 3: Ecological indices describing foraminiferal assemblages at Station A of the 63–150 µm (top first centimetre of sediment, dark grey histograms) and >150 µm size fractions (0–2 cm of sediment, light grey histograms). (a) Foraminiferal densities normalised for a surface area of 100 cm² of sediment; (b) Number of species S; (c–d) Biodiversity (H) and Evenness (E) indices.

In the >150 µm fauna, total foraminiferal density varies between 113 in core A4 and 193 ind./100 cm² in core A1 ($MD_{100} = 158 \text{ ind./100 cm}^2 \pm 20\%$; Fig. 3a, Table 2). Species richness ranges from 12 to 15 (Fig. 3b). The Shannon index varies from 1.7 to 2.2 (Fig. 3c), whereas the Evenness index E ranges between 0.45 (core A1) and 0.68 (core A4) (Fig. 3d). The faunas are mainly composed of perforate (43.2 to 67.9%) and non-fossilising agglutinated taxa (21.2 to 43.4%; Appendix B). *Ammonia tepida* dominates the faunas in all replicates, with relative abundances ranging between 25.4 and 53.6%.

(a) 63–150 μm size fraction



(b) >150 μm size fraction

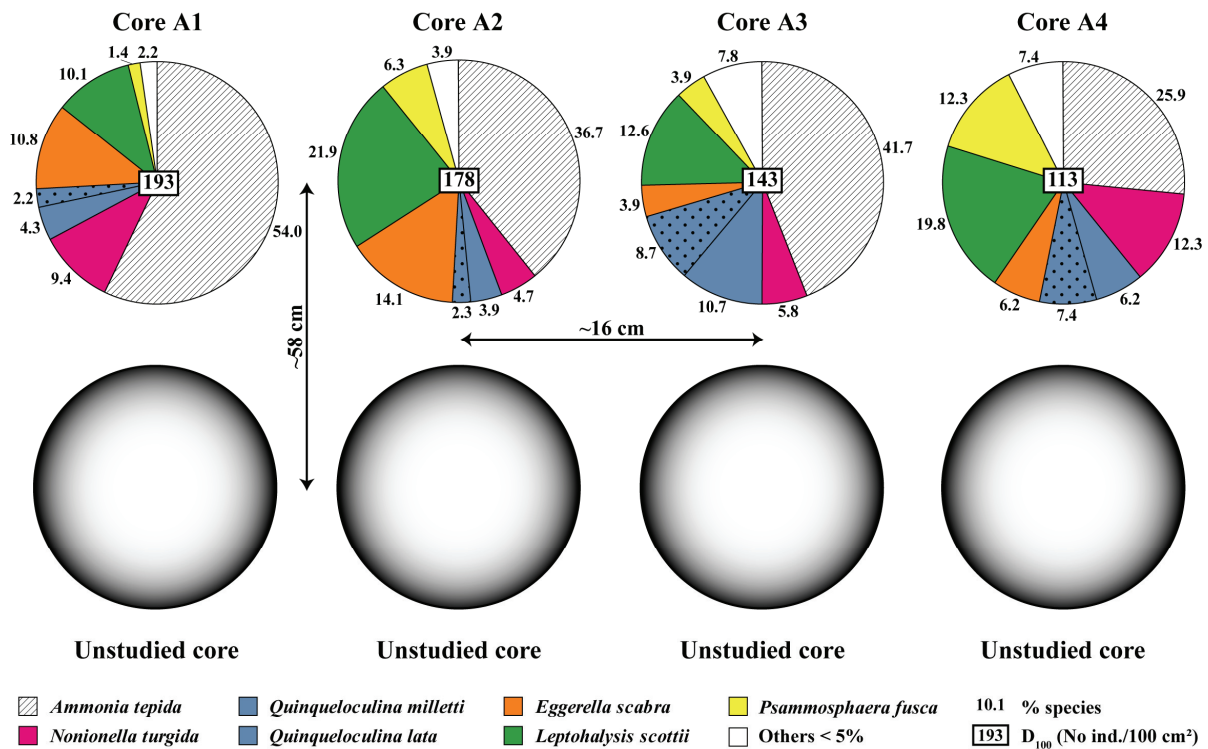


Figure 4: Relative abundances of major species ($\geq 5\%$ in at least one core) of living faunas in the 63–150 μm (a) and > 150 μm size fractions (b) for the four replicate cores of Station A. The organisation of circular diagrams follows the position of the cores (studied and unstudied) on the multicorer.

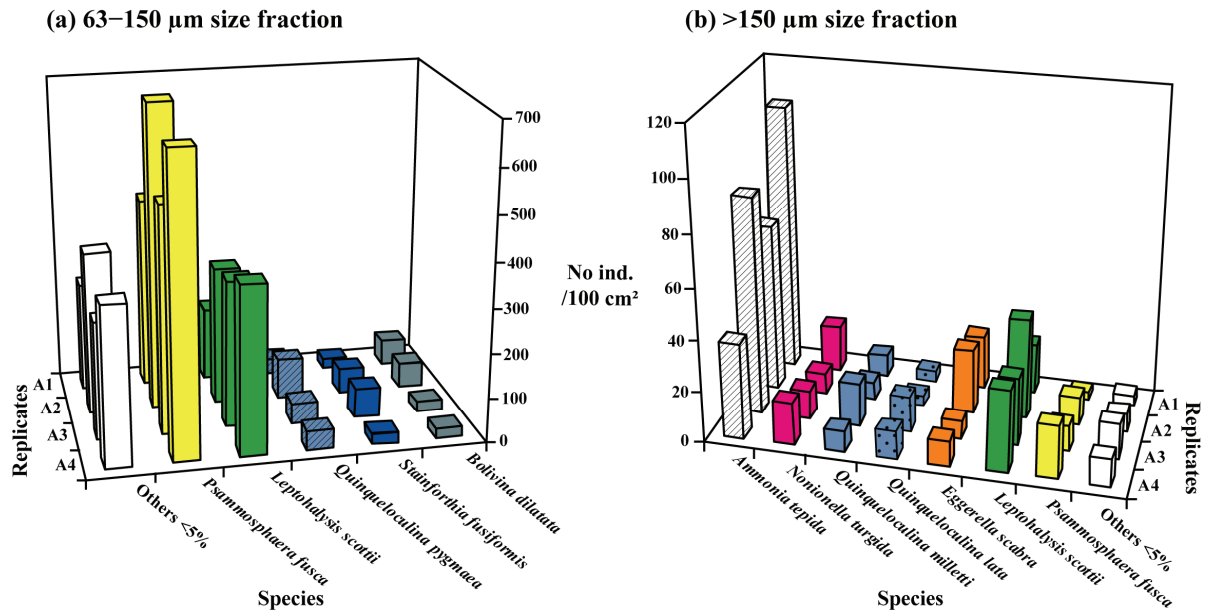


Figure 5: Foraminiferal densities of the major species ($\geq 5\%$ in at least on core) in the 63–150 μm (A) and >150 μm size fractions (b) for the four replicates of Station A. Values are standardised for a surface area of 100 cm^2 (core surface: 72 cm^2 ; sediment depth: 2 cm).

Station A	MD ₁₀₀ (ind./ 100 cm^2)	Sd (ind./ 100 cm^2)	% (%)	Sd
63–150 μm size fraction				
<i>Bolivina dilatata</i>	39	17	43%	3.2 1.7
<i>Leptohalysis scottii</i>	297	79	27%	22.4 3.8
<i>Psammosphaera fusca</i>	575	107	19%	43.8 1.6
<i>Quinqueloculina pygmaea</i>	53	21	40%	3.9 1.0
<i>Stainforthia fusiformis</i>	42	20	48%	3.2 1.5
Total No living individuals	1314	172	13%	
>150 μm size fraction				
<i>Ammonia tepida</i>	65	27	41%	39.3 9.9
<i>Eggerella scabra</i>	15	8	58%	8.7 3.9
<i>Leptohalysis scottii</i>	25	8	34%	16.0 4.9
<i>Nonionella turgida</i>	12	4	34%	8.0 3.0
<i>Psammosphaera fusca</i>	8	4	53%	6.0 4.1
<i>Quinqueloculina lata</i>	7	3	47%	5.1 2.9
<i>Quinqueloculina milletti</i>	9	3	37%	6.2 2.7
Total No living individuals	158	32	20%	

Table 2: Mean absolute (MD₁₀₀) and relative densities (%) calculated with replicate cores of Station A. “Sd” is the standard deviation of the calculated mean value. Dark-grey boxes indicate standard deviation values >40%.

The second most abundant species is *Leptohalysis scottii* which composes from 10 to 21.7% of total living faunas. *Eggerella scabra*, *Nonionella turgida*, *Quinqueloculina milletti*, *Quinqueloculina lata* and *Psammosphaera fusca* are less abundant. *Nonionella turgida* composes from 4.7 to 12.3% of total living faunas. *Quinqueloculina milletti* and *Q. lata* are major species in replicate cores A3 and A4, with a maximum relative abundance in core A4 of 10.6 and 8.7%, respectively. *Psammosphaera fusca* presents low relative abundances in cores A1 and A3 (<5%), but maximum values in cores A2 and A4 where it represents respectively 6.2 and 12.3% of total fauna. Absolute densities of *E. scabra* (15 ind./100 cm² ± 58%), *P. fusca* (8 ind./100 cm² ± 53%), *Q. lata* (7 ind./100 cm² ± 47%) and *A. tepida* (65 ind./100 cm² ± 41%) are most variable (Fig. 5a, Table 2).

2.3.2.2. Station N (67 m)

In the 63–150 µm fauna, total absolute density D_{100} ranges between ~6380 and ~10370 ind./100 cm² ($MD_{100} = 8190$ ind./100 cm² ± 31%; Fig. 6a, Table 3). Foraminiferal densities in cores N1 and N4 are quite similar (~9700 and 10370 ind./100 cm², respectively) and almost two times higher than in cores N2 and N3 (respectively ~6380 and ~5070 ind./100 cm²) (Fig. 6a, Appendix A). The standard deviation among these four replicates is of 31%. Species richness ranges between 35 (core N3) and 56 taxa (core N1) (Fig. 6b). The Shannon index H is relatively high with values varying between 2.4 and 3.1 (Fig. 6c). The Evenness index E ranges between 0.33 and 0.42 (Fig. 6d). Perforate (~61 to 70%) and non-fossilising agglutinated taxa (~26 to 33%) compose foraminiferal assemblages (Appendix A).

Eight species present relative abundances >5% in at least one replicate core: *Bolivina dilatata*, *Bolivina spathulata*, *Hopkinsina atlantica*, *Nonionella turgida*, *Rectuvigerina phlegeri*, *Stainforthia fusiformis*, *Eggerella scabra* and *Leptohalysis scottii* (Fig. 7a). The most abundant species is *N. turgida* with a maximum of ~31% in core N3. Its relative abundance is lower in the other cores with values of ~8 to 10%. *Eggerella scabra* presents relative densities between ~12% and 17%. *Bolivina dilatata* is relatively abundant in all cores (~12 to 17%) except in core N3 where it represents only ~6% of total assemblages. *Hopkinsina atlantica* is also a major species in all replicates, accounting for ~5 to 10% of the total living faunas. *Leptohalysis scottii* is a major species in almost all replicates (~5 to 11%), except in core N1 where it accounts for ~4% of the total living fauna. *Rectuvigerina phlegeri* presents relative abundances around ~7 to 8% in cores N1 and N4, but only ~2 to 5% in the two other replicates.

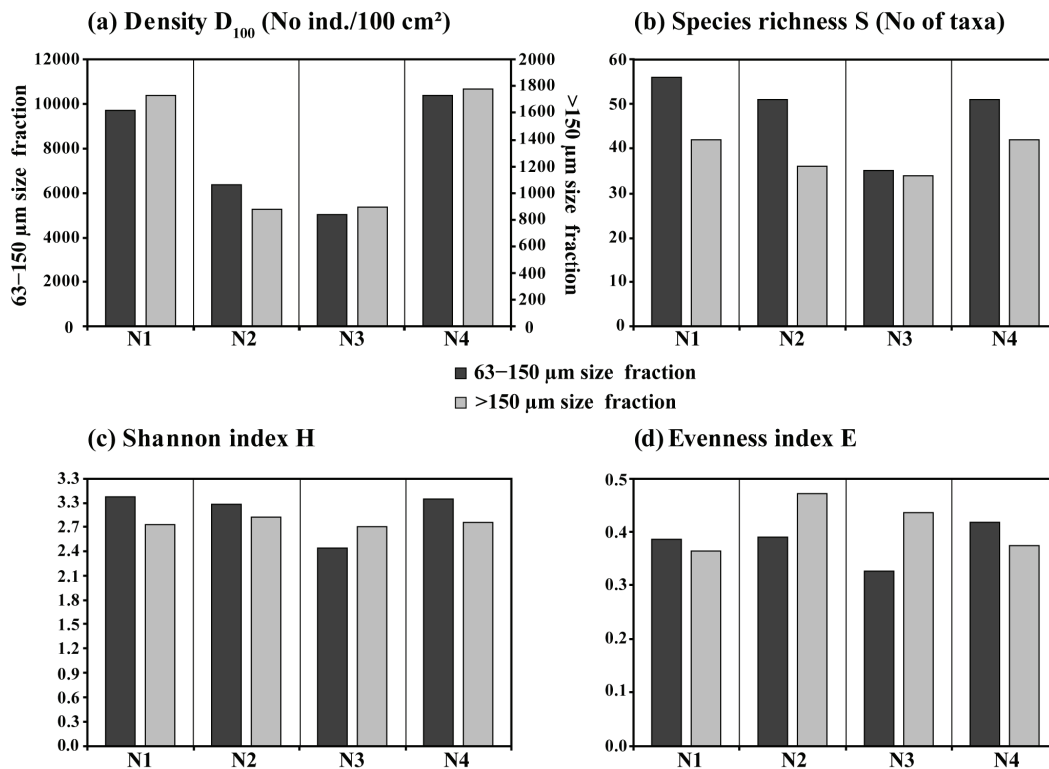
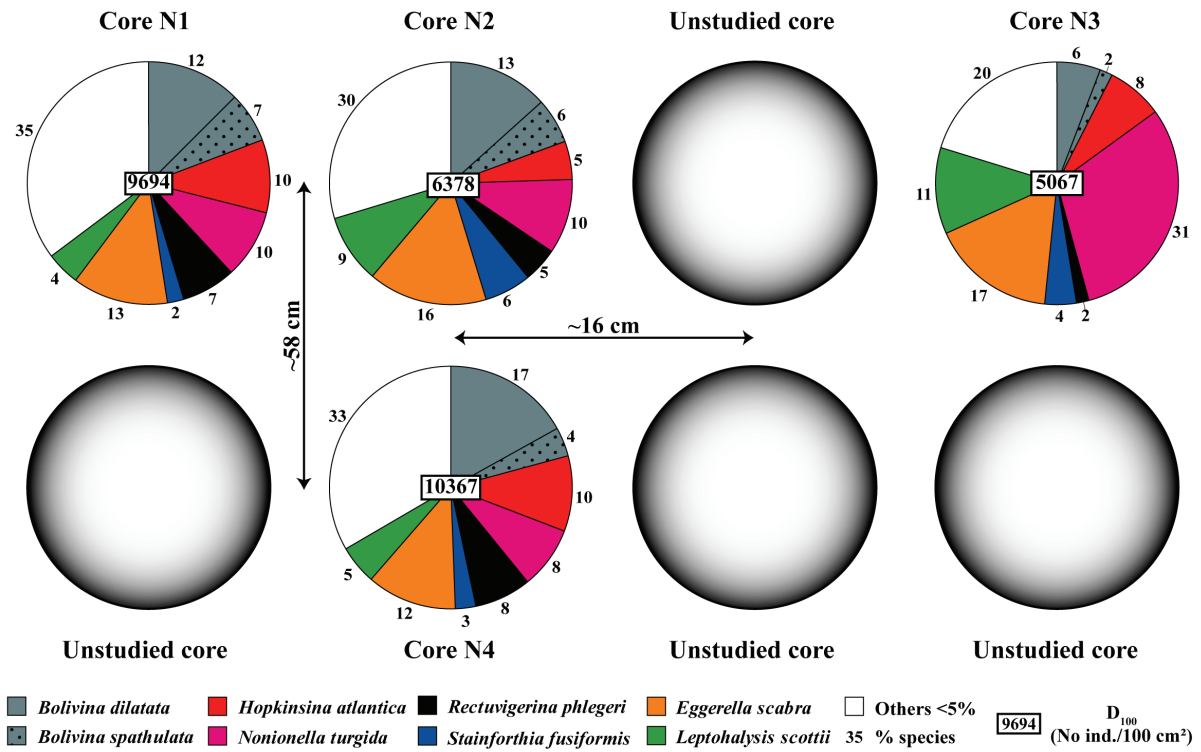


Figure 6: Ecological indices describing foraminiferal assemblages at Station N of the 63–150 µm (top first centimetre of sediment, dark grey histograms) and >150 µm size fractions (0–2 cm of sediment, light grey histograms). (a) Foraminiferal densities normalised for a surface area of 100 cm² of sediment; (b) Number of species S; (c–d) Biodiversity (H) and Evenness (E) indices.

Bolivina spathulata composes between ~6 and 7% of the total living faunas in cores N1 and N2, and accounts only for ~2 to 4% of the total living faunas in replicates N3 and N4. Finally, *S. fusiformis* is a minor taxa (<5%) in almost all replicates, except in core N2 where its relative abundance reaches ~6% of the total living fauna. Concerning absolute densities, *B. dilatata* presents a minimum density of ~290 ind./100 cm² in core N3 compared to ~850–1760 ind./100 cm² in the other cores (Fig. 8a). *Bolivina spathulata* presents the same trend with ~90 ind./100 cm² in N3 versus ~390 to 660 ind./100 cm² in N1, N2 and N4. The absolute density of *R. phlegeri* is ten times higher in replicates N1 and N4 compared to N3 (from ~80 to ~720 to 790 ind./100 cm²). *Nonionella turgida* is the only taxon presenting higher abundances in core N3, with ~1560 ind./100 cm² versus ~630 to 960 ind./100 cm² in the three other cores. Thus, *R. phlegeri* (475 ind./100 cm² ± 62%), *B. dilatata* (1025 ind./100 cm² ± 52%), *B. spathulata* (~380 ind./100 cm² ± 52%) and *H. atlantica* (~670 ind./100 cm² ± 48%) present the most important absolute densities variation (Table 3).

(a) 63–150 μm size fraction



(b) >150 μm size fraction

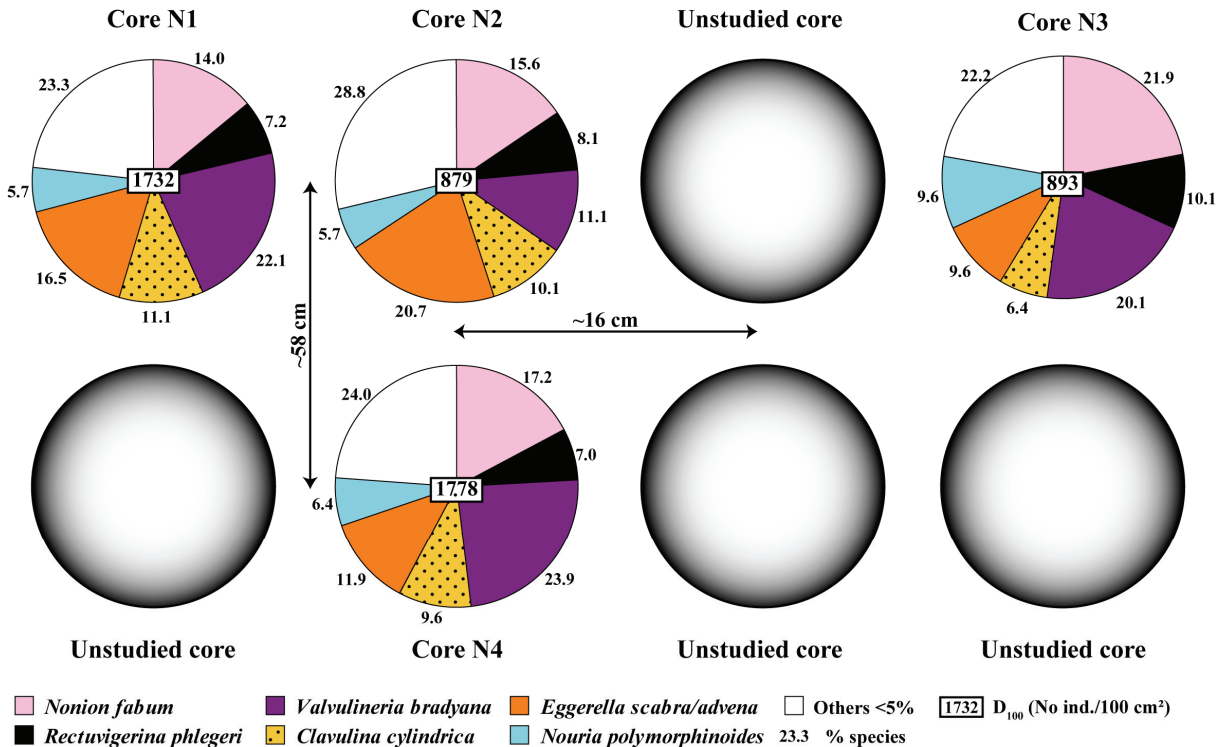


Figure 7: Relative abundances of major species ($\geq 5\%$ in at least one core) of living faunas in the 63–150 μm (a) and >150 μm size fractions (b) for the four replicates of Station N. The organisation of circular diagrams follows the position of the cores (studied and unstudied) on the multicorer.

Station N	MD ₁₀₀ (ind./ 100 cm ²)	Sd (ind./ 100 cm ²)	%	Sd
63–150 µm size fraction				
<i>Bolivina dilatata</i>	1025	534	52%	12.1 4.1
<i>Bolivina spathulata</i>	383	201	52%	4.6 2.0
<i>Eggerella scabra</i>	1090	177	16%	14.4 1.9
<i>Hopkinsina atlantica</i>	671	319	48%	8.1 2.0
<i>Leptohalysis scotti</i>	531	74	14%	7.5 2.9
<i>Nonionella turgida</i>	1000	341	34%	14.7 9.3
<i>Rectuvigerina phlegeri</i>	475	293	62%	5.4 2.5
<i>Stainforthia fusiformis</i>	271	70	26%	3.8 1.5
Total No living individuals	8190	2519	31%	
>150 µm size fraction				
<i>Clavulina cylindrica</i>	127	56	44%	9.3 1.8
<i>Eggerella scabra</i>	191	72	37%	14.7 4.3
<i>Nonion fabum</i>	220	62	28%	17.2 3.0
<i>Nouria polymorphinoides</i>	88	24	27%	6.9 1.6
<i>Rectuvigerina phlegeri</i>	103	23	23%	8.1 1.2
<i>Valvulineria bradyana</i>	271	137	50%	19.3 4.9
Total No living individuals	1320	435	33%	

Table 3: Mean absolute (MD₁₀₀) and relative densities (%) calculated with replicate cores of Station N. “Sd” is the standard deviation of the calculated mean value. Dark-grey boxes indicate standard deviation values >40%.

In the >150 µm size fraction, total foraminiferal standing stocks in replicate cores at Station N vary from 879 (core N2) to 1778 (core N4) ind./100 cm² (MD₁₀₀ = 1320 ind./100 cm² ± 33%; Fig. 6a, Table 3). Cores N2 and N3 present comparable foraminiferal densities (879 and 893 ind./100 cm², respectively). Cores N1 and N4 show also similar densities but two times higher than replicate cores N2 and N3 (respectively 1732 and 1778 ind./100 cm²) (Fig. 6a, Appendix B). From 34 to 42 taxa were recognised in the cores with the highest species richness recorded in cores N1 and N4 (Fig. 6b). Diversity index H is ~2.8 in all cores (Fig. 6c). The Evenness index E ranges from 0.36 and 0.47 (Fig. 6d). Foraminiferal assemblages are composed by perforate (47.4 to 63.6%) and agglutinated taxa (34.5 to 51%) (Appendix B). The most abundant species *Valvulineria bradyana* accounts for 11.1 to 23.9% of total faunas. *Nonion fabum* and *Eggerella scabra* are also abundant, with percentages ranging between 14.0 and 21.9% and from 9.6 to 20.7%, respectively. *Rectuvigerina phlegeri* and *Clavulina cylindrica* show comparable relative abundances, with 7.0 to 10.1% and 6.4 to 11.1%, respectively. *Nouria polymorphinoides* is somewhat less abundant with relative abundances varying from 5.7 to 9.6%. As in the 63–150 µm size fraction, absolute densities

present differences between replicates (Fig. 8b). The highest absolute densities variations are calculated for *V. bradyana* (241 ind./100 cm² ± 50%), *C. cylindrica* (127 ind./100 cm² ± 44%) and, in a lesser extent, *E. scabra* (191 ind./100 cm² ± 37%) (Table 3). *Valvulineria bradyana* reaches a minimum of 97 ind./100 cm² in core N2, with a maximal density of 425 ind./100 cm² in N4. In core N2, *C. cylindrica* and *E. scabra* have a minimum density of 57 and 86 ind./100 cm², respectively. They attain densities as high as 192 and 286 ind./100 cm² in core N1.

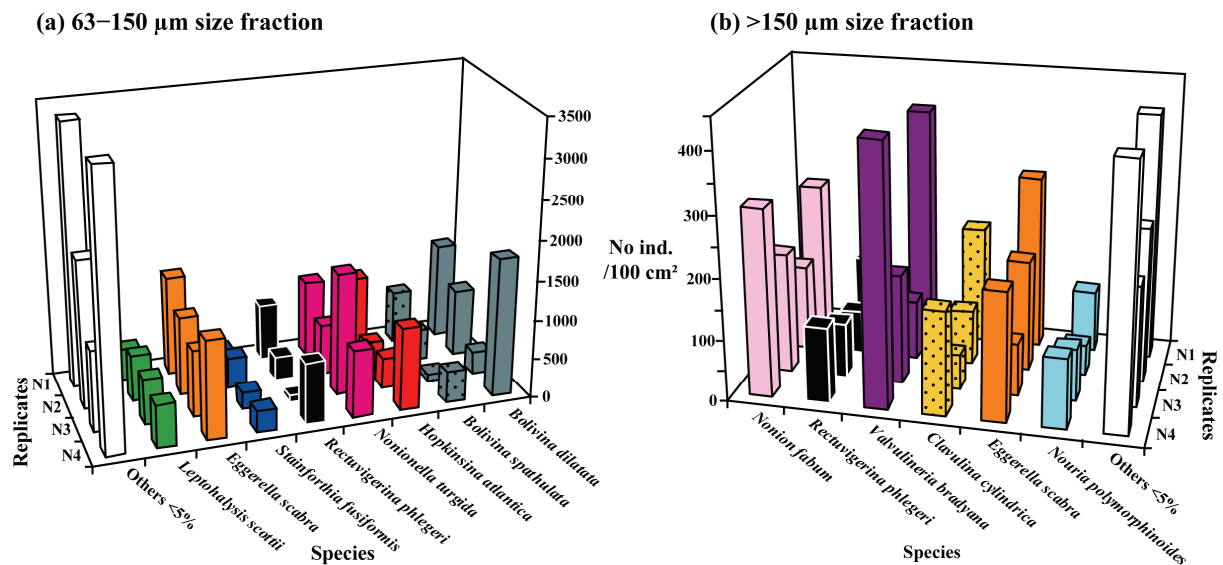


Figure 8: Foraminiferal densities of the major species ($\geq 5\%$ in at least on core) in the 63–150 μm (0–1 cm of sediment; a) and $>150 \mu\text{m}$ size fractions (0–2 cm of sediment; b) for the four replicates of Station N. Values are standardised for a surface area of 100 cm² (core surface: 72 cm²).

2.3.2.3. Statistical analyses

For Station A, Friedman’s test shows no significant differences ($p > 0.05$) among the four replicates, for both size fractions and both data treatments (i.e., absolute and relative densities) (Table 4). For Station N, no significant differences between replicates are found for both size fractions when percentage data are considered. However, when absolute densities D_{100} are used, some significant differences show up in both size fractions ($p < 0.05$).

Station	Size fraction	Data	Normality (Shapiro test)	Sphericity (Mauchly test)	Friedman's test (p-value)
A	63–150 μm	D ₁₀₀	No	No	0.2496
		%	No	No	0.8935
	>150 μm	D ₁₀₀	No	No	0.9644
		%	No	No	0.7530
N	63–150 μm	D ₁₀₀	No	No	0.0206
		%	No	No	0.8630
	>150 μm	D ₁₀₀	Yes	No	0.0003
		%	Yes	No	0.5561

Table 4: Statistical analyses performed on the 8 databases. Dark-grey boxes indicate p-values <0.05.

2.4. DISCUSSION

2.4.1. Contrasted environments

Environmental conditions prevailing at both Stations A and N in September 2007 were investigated by Cathalot et al. (2009). High oxygen concentrations were measured in bottom waters at both stations, indicating an efficient ventilation of the benthic environment. Station A (24 m depth) is characterised by shallower sediment oxygen penetration depth (<2 mm) than Station N (~5 mm, 67 m depth). The shallow OPD at Station A is related to important oxygen consumption in the topmost sediment layer (dissolved oxygen uptake of 15.3 ± 1.5 mmol O₂.m⁻².d⁻¹) due to the high amounts of available organic compounds observed in our study (lipids and THAA: 3.7 mg.g⁻¹ d.w.; 26.4% of OC). At Station N, the concentration of available organic compounds is lower (2.7 mg.g⁻¹ d.w.; 22.5% OC), explaining the lower oxygen consumption estimated by Cathalot et al. (2009) (dissolved oxygen uptake of 6.6 ± 0.9 mmol O₂.m⁻².d⁻¹). Carbon and nitrogen stable isotopic values exhibit an organic material mainly originating from the Rhône River (means of $d^{13}\text{C}_{\text{OM}} = -27.4 \pm 0.7\text{‰}$ and $d^{15}\text{N}_{\text{OM}} = 5.2 \pm 1.1\text{‰}$ over the period 2006–2009; P. Kerhervé, personal communication) with however a more pronounced terrestrial influence at the shallowest station A, as described in Cathalot et al. (2009).

2.4.2. Spatial variability at a decimetric scale

2.4.2.1. Station A

At Station A, statistical analyses do not put into evidence significant spatial variability ($p \gg 0.05$) between the four replicate cores, for both size fractions and both data treatments (absolute and relative densities of major species). A rather limited variability of total absolute densities (i.e., standing stocks) is observed for the four replicate cores (Fig. 5, Appendix A and 2). Previous studies pointed out the opportunistic behaviour of *Leptohalysis scottii*, *Psammosphaera fusca*, *Bolivina dilatata* and *Stainforthia fusiformis* which would be able to thrive in episodically disturbed environments (episodic hypoxia, high bottom currents) (Kaminski, 1985; Alve, 1995; Kaminski et al., 1995; Langezaal et al., 2006; Duchemin et al., 2007; Mojtahid et al., 2009). *Ammonia tepida*, *Nonionella turgida* and *Eggerella scabra* characterise hypoxic sediments enriched in Rhône-derived organic matter (Goineau et al., In Press – see Chapter 1). Consequently, foraminiferal faunas observed in the four replicates testify of important physical environmental constraints, with huge amounts of continental organic detritus transported by episodic floods and sea-floor hydro-sedimentary processes (sediment input, strong bottom currents; Cathalot et al., 2009).

2.4.2.2. Station N

At Station N, statistical analyses put in evidence some significant differences ($p < 0.05$) between replicate cores when the absolute densities D_{100} of major species are considered (Table 4). In both size fractions, total standing stocks present indeed significant variations among replicates, with values two times higher in cores N1 and N4 than in replicates N2 and N3 (Fig. 8, Appendix A and 2). This significant dissimilarity seems to be due to D_{100} variations ($Sd > 40\%$) of *Rectuvigerina phlegeri*, Bolivinids (*Bolivina dilatata* and *Bolivina spathulata*), *Hopkinsina atlantica* and *Nonionella turgida* in the 63–150 μm size fraction. For example, standing stocks of Bolivinids and *R. phlegeri* are three to ten times smaller in core N3 than in the three other replicates, whereas the number of specimens of *Nonionella turgida* increases in this last core. Bolivinids, *H. atlantica*, *N. turgida* and *R. phlegeri* are commonly observed in river-impacted areas, thriving in sediments enriched in continental OM (Barmawidjaja et al., 1992; Jorissen et al., 1992; Diz et al., 2006; Diz and Francés, 2008; Mojtahid et al., 2009). More precisely, Bolivinids, *H. atlantica*, *N. turgida* would preferentially or occasionally feed on freshly deposited organic phytodetritus, with even a potential opportunistic response for *B. dilatata* (Fontanier et al., 2003; Duijnsteet et al., 2005;

Langezaal et al., 2006; Duchemin et al., 2007) and *N. turgida* (Jorissen, 1987; Van der Zwaan and Jorissen, 1991; Barmawidjaja et al., 1992; Donnici and Serandrei Barbero, 2002; Diz and Francés, 2008; Duchemin et al., 2008; Rossi and Vaiani, 2008). In the >150 µm size fraction, faunas are dominated by e.g., *Valvulineria bradyana* (11.1–23.9%), *Nonion fabum* (14–21.9%), *Eggerella scabra* (9.6–20.7%) and *Clavulina cylindrica* (6.4–11.1%), with highest D₁₀₀ variations of *C. cylindrica* and *V. bradyana*. All these taxa were notably described in shelf environments enriched in continental and/or low-quality organic detritus (Fontanier et al., 2002; Langezaal et al., 2006; Duchemin et al., 2007, 2008; Diz and Francés, 2008). In the Rhône prodelta, these species characterise sediments under the river influence in terms of organic matter inputs, but with an increasing contribution of marine material and a deepening of sediment oxygenation (Goineau et al., In Press – see Chapter 1). Therefore, foraminiferal faunas observed in both size fractions depict a typical river-influenced environment with a clear continental influence but weaker than at Station A (e.g., hydro-sedimentary processes). Sediments are supplied by high organic matter inputs from various origins (continental, riverine, marine) and of heterogeneous quality (fresh or degraded) (Darnaude et al., 2004; Harmelin-Vivien et al., 2008). Thus, organic matter patches of different compositions (marine/riverine phytoplankton, terrestrial plant debris,...) may be spread on the sea floor, generating local food sources for benthic communities. Foraminiferal faunas present different food preferences between species. For instance, we already mentioned the food preference of Boliviniids, *H. atlantica* and *N. turgida* for fresh OM, especially diatoms (e.g., Barmawidjaja et al., 1992; Jorissen et al., 1992; Hohenegger et al., 1993; Gustafsson and Nordberg, 2001; Ernst et al., 2002; Duijnsteet et al., 2005; Duchemin et al., 2007, 2008; Diz and Francés, 2008). Local accumulation of specific food in decimetric depressions could favour the growth of the most reactive and specialised taxa by enhanced reproduction and growth. Therefore, inter-specific competition between Boliviniids and *N. turgida* in the small size fraction could explain their significantly different absolute densities in replicate cores (inverse evolution of their absolute densities), induced by their common food preference for diatoms and fresh OM (competition for food resource). Nevertheless, major species relative densities (i.e., percentages) from all cores are not significantly dissimilar ($p \gg 0.05$) despite these important standing stock differences. Since D₁₀₀ variations are comparable among species, relative abundances are not significantly different between replicate cores for both 63–150 and >150 µm size fractions.

2.4.3. Kilometric-scale versus decimetric-scale spatial variability

Living benthic foraminifera (>150 μm size fraction) were investigated in the whole Rhône prodelta and the adjacent outer shelf (surface area $\sim 28 \text{ km}^2$ vs 18 km^2) during BEHEMOTH cruise (Goineau et al., In Press – see Chapter 1). The cruise took place in September 2006 during a period of low riverine discharge ($< 2000 \text{ m}^3 \cdot \text{s}^{-1}$ for the last 3 months before the cruise) and low sea surface primary production. Both Stations A and N were sampled in September 2007 (RIOTECH cruise) with similar conditions prevailing in terms of productivity and riverine outflow (Cathalot et al., 2009).

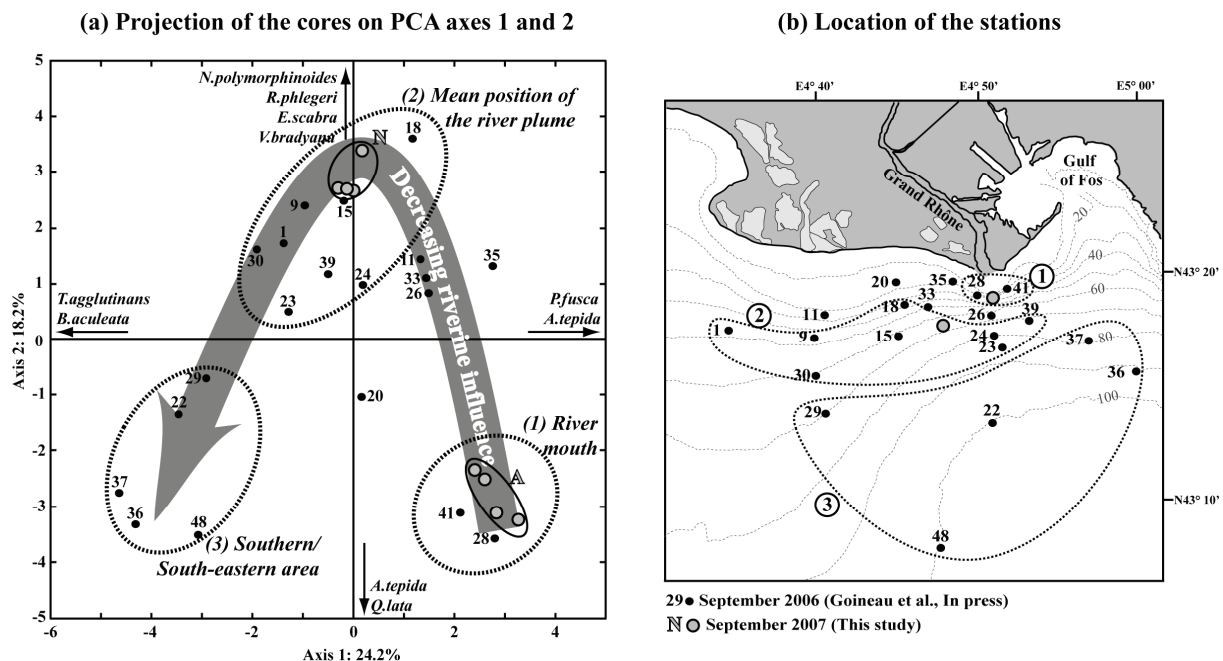


Figure 9: PCA based on the relative abundances of the 21 species representing more than 5% of total living faunas in at least one core in the top 0–2 cm of sediment in September 2006 (Goineau et al., In Press) and September 2007 (this study). (a) Projection of the 20 stations of September 2006 and the 8 replicate cores of Stations A and N on the factor-plane defined by PCA axes 1 and 2. Species with the highest loading are precised on each axis. The circles point out three groups of stations; (b) Location of the groups of stations (dotted lines) defined by PCA axes 1 and 2.

We performed a Principal Component Analysis (PCA) to compare foraminiferal faunas of the >150 μm size fraction observed at both Stations A and N in September 2007 (decimetric-scale variability) with foraminiferal faunas of September 2006 (kilometric-scale variability). This analysis is based on relative abundances (non-normalised) of the 21 species representing more than 5% of total living faunas in at least one core in the top 0–2 cm of sediment (Fig. 9). In figure 9a, we have plotted all the stations sampled during the

BEHEMOTH cruise (20 stations) on Axes 1 and 2. These two axes account for 24.2 and 18.2% of the total variability, respectively. The distribution of the stations on the plot highlights a “horse-shoe” gradient (Hill and Gauch Jr, 1980; Digby and Kempton, 1987) related to a decreasing Rhône River influence from the lower left to the upper centre, to the lower right of the plot. Replicate cores of Station A plot close to each other (i.e., maximum distance of 1.1 units between A1 and A4), and are grouped with BEHEMOTH stations close to the river mouth (Group 1; Fig. 9a–b). In this area, foraminiferal faunas are dominated by *Ammonia tepida*, *Quinqueloculina lata* and *Psammosphaera fusca*. Considering Station N, the replicates plot also close to each other (i.e., maximum distance of 0.7 units between N3 and N4) and are all grouped with stations under the mean position of the river plume (Group 2; Figs. Fig. 9a–b), enriched in *Nouria polymorphinoides*, *Rectuvigerina phlegeri*, *Eggerella scabra* and *Valvulineria bradyana*. This analysis confirms that spatial variability of foraminiferal faunal composition induced by the wide range of environmental conditions at the scale of the Rhône prodelta is more important than the rather limited decimetric-scale patchiness observed at one station.

2.5. CONCLUSIONS

Live (stained) benthic foraminiferal faunas were investigated in two groups of four replicate cores each sampled at two stations (24 and 67 m depth) in the Rhône prodelta. Both sites are impacted by Rhône River inputs in terms of organic matter content and origin. At the station closest to the river mouth (Station A, 1.9 km from the mouth, 19m water depth), foraminiferal faunas in both size fractions (63–150 and >150 μm) are dominated by *Leptohalysis scottii*, *Psammosphaera fusca* and *Ammonia tepida*. At the farther Station N (5.5 km from the river mouth, 67 m water depth), benthic faunas (both size fractions) are mainly composed by *Nonionella turgida*, *Eggerella scabra*, *Valvulineria bradyana* and *Nonion fabum*. Statistical analyses put in evidence a significantly patchy distribution of absolute foraminiferal densities among replicate cores, especially at Station N. This significant dissimilarity may be due to the opportunistic behaviour of Bolivinids and *Nonionella turgida*. In such dynamic environments, the patchy distribution of organic matter from various origins may control a part of foraminiferal patchiness in terms of standing stocks, favouring heterogeneous growth of the most reactive taxa according to their food preferences. Nevertheless, species relative abundances (i.e., percentages) are not significantly different between replicate cores for both 63–150 and >150 μm size fractions and at both Stations A

and N. Furthermore, the large foraminiferal composition variations observed at the scale of the Rhône prodelta is too high to be overshadowed by potential small-scale (decimetric) variability existing with species relative abundances at one site. Considering these important conclusions, determination of foraminiferal biofacies at a kilometric-scale in such river-dominated environment is reliable by using species relative abundances, even when only one replicate core is sampled at one site. Consequently, temporal surveys of benthic foraminiferal communities at a single site should preferably be based on percentage data, and not on absolute density data, especially when only one core is investigated per sampling period.

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APPENDICES

Appendix A

Total benthic foraminiferal counts on the 63–150 μm size fraction. For each species in each replicate core, “r.d.” and “D₁₀₀” correspond to non-standardized (raw data) and standardised (for a surface area of 100 cm^2) total absolute densities, respectively, and “%” indicates relative abundance. Grey boxes indicate percentages and species > 5%.

Appendix B

Total benthic foraminiferal counts on the > 150 μm size fraction. For each species in each replicate core, “r.d.” and “D₁₀₀” correspond to non-standardised (raw data) and standardised (for a surface area of 100 cm^2) total absolute densities, respectively, and “%” indicates relative abundance. Grey boxes indicate percentages and species > 5%.

Appendix C

Taxonomic reference list for major taxa.

Appendix A

Replicate cores : Station A Taxa 63–150 µm size fraction	A1			A2			A3			A4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Perforates												
Indet.	8	11	1	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	24	33	3	–	–	–	–	–	–	–	–	–
<i>Ammonia tepida</i>	24	33	3	40	56	4	32	44	4	48	67	4
<i>Amphicoryna scalaris</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>	40	56	6	40	56	4	16	22	2	16	22	1
<i>Bolivina seminuda</i>	–	–	–	–	–	–	–	–	–	16	22	1
<i>Bolivina spathulata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>	–	–	–	8	11	1	–	–	–	–	–	–
<i>Bulimina aculeata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>	8	11	1	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>	–	–	–	–	–	–	16	22	2	32	44	3
<i>Buliminella elegantissima</i>	–	–	–	8	11	1	–	–	–	–	–	–
<i>Cancris auriculus</i>	8	11	1	–	–	–	–	–	–	–	–	–
<i>Cassidulina carinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina crassa</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina minuta</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium poeyanum</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Epistominella vitrea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fissurina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fursenkoina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hanzawaia boueana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hopkinsina atlantica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina atlantica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonion</i> sp.1	–	–	–	8	11	1	–	–	–	–	–	–
<i>Nonion fabum</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella iridea</i>	–	–	–	16	22	1	–	–	–	–	–	–
<i>Nonionella stella</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella turgida</i>	–	–	–	8	11	1	–	–	–	–	–	–
<i>Rectuvigerina phlegeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia complanata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia concava</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia fusiformis</i>	16	22	2	40	56	4	48	67	5	16	22	1
<i>Valvulineria bradyana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Virgulinea fragilis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Virgulopsis</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–

Appendix A (continued)

Replicate cores : Station A Taxa 63–150 µm size fraction	A1			A2			A3			A4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Miliolids												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelosina</i> spp.	–	–	–	–	–	–	16	22	2	–	–	–
<i>Biloculinella labiata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	24	33	3	–	–	–	32	44	4	16	22	1
<i>Quinqueloculina milletti</i>	24	33	3	32	44	3	16	22	2	48	67	4
<i>Quinqueloculina pygmaea</i>	24	33	3	64	89	6	32	44	4	32	44	3
<i>Quinqueloculina seminula</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina stalkerii</i>	–	–	–	8	11	1	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroloculina excavata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated												
<i>Textularia agglutinans</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia porrecta</i>	24	33	3	32	44	3	16	22	2	32	44	3
Non-fossilising agglutinated												
Indet.	8	11	1	8	11	1	–	–	–	–	–	–
Agglutinate sp.333	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Clavulina cylindrica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Eggerella scabra</i>	–	–	–	–	–	–	16	22	2	–	–	–
<i>Eratidus foliaceus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lagenammina difflugiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Leptohalysis scotti</i>	120	167	17	224	311	20	240	333	27	272	378	25
<i>Nouria polymorphinoides</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Psammosphaera bowmani</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Psammosphaera fusca</i>	312	433	45	496	689	44	368	511	41	480	667	45
<i>Pseudobolivina fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax nana</i>	8	11	1	48	67	4	16	22	2	48	67	4
<i>Trochammina globigeriniformis</i>	8	11	1	8	11	1	–	–	–	–	–	–
Organic foraminifera	8	11	1	40	56	4	32	44	4	16	22	1
No perforate individuals	128	178	19	168	233	15	112	156	13	128	178	12
No miliolid individuals	72	100	10	104	144	9	96	133	11	96	133	9
No fossilising agglutinated individuals	24	33	3	32	44	3	16	22	2	32	44	3
No non-fossilising agglutinated ind.	456	633	66	784	1089	70	640	889	71	800	1111	75
No organic individuals	8	11	1	40	56	4	32	44	4	16	22	1
Total No living individuals	688	956		1128	1567		896	1244		1072	1489	

Appendix A (continued)

Replicate cores : Station N Taxa 63–150 µm size fraction	N1			N2			N3			N4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Perforates												
Indet.	16	22	0	–	0	–	–	0	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	32	44	0	24	33	1	8	11	0	16	22	0
<i>Ammonia tepida</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphicoryna scalaris</i>	8	11	0	–	0	–	–	0	–	40	56	1
<i>Astacolus crepidulus</i>	8	11	0	–	0	–	–	0	–	–	–	–
<i>Bolivina dilatata</i>	868	1206	12	612	850	13	208	289	6	1264	1756	17
<i>Bolivina seminuda</i>	68	94	1	24	33	1	16	22	0	168	233	2
<i>Bolivina spathulata</i>	472	656	7	280	389	6	64	89	2	288	400	4
<i>Bolivina striatula</i>	100	139	1	84	117	2	–	0	–	104	144	1
<i>Bulimina aculeata</i>	32	44	0	24	33	1	–	0	–	8	11	0
<i>Bulimina elongata</i>	36	50	1	20	28	0	32	44	1	56	78	1
<i>Bulimina marginata</i>	20	28	0	–	0	–	16	22	0	64	89	1
<i>Buliminella elegantissima</i>	–	0	–	4	6	0	–	0	–	–	–	–
<i>Cancris auriculus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina carinata</i>	80	111	1	28	39	1	–	0	–	96	133	1
<i>Cassidulina crassa</i>	16	22	0	–	0	–	8	11	0	–	–	–
<i>Cassidulina minuta</i>	–	0	–	16	22	0	–	0	–	16	22	0
<i>Elphidium advenum</i>	–	0	–	–	0	–	8	11	0	–	–	–
<i>Elphidium poeyanum</i>	8	11	0	–	0	–	–	0	–	–	–	–
<i>Epistominella vitrea</i>	236	328	3	172	239	4	64	89	2	208	289	3
<i>Fissurina</i> sp.	–	0	–	–	0	–	–	0	–	16	22	0
<i>Fursenkoina</i> sp.	16	22	0	–	0	–	48	67	1	56	78	1
<i>Gavelinopsis praegeri</i>	16	22	0	8	11	0	–	0	–	8	11	0
<i>Gyroidina umbonata</i>	16	22	0	8	11	0	16	22	0	48	67	1
<i>Hanzawaia boueana</i>	–	0	–	8	11	0	–	0	–	–	–	–
<i>Hopkinsina atlantica</i>	668	928	10	232	322	5	280	389	8	752	1044	10
<i>Hyalinea balthica</i>	4	6	0	8	11	0	–	0	–	8	11	0
<i>Lenticulina atlantica</i>	20	28	0	8	11	0	8	11	0	8	11	0
<i>Nonion</i> sp.1	60	83	1	40	56	1	–	–	–	16	22	0
<i>Nonion fabum</i>	88	122	1	32	44	1	16	22	0	72	100	1
<i>Nonionella bradyi</i>	8	1264	0	4	6	0	–	–	–	16	22	0
<i>Nonionella iridea</i>	36	50	1	16	22	0	136	189	4	96	133	1
<i>Nonionella stella</i>	220	306	3	76	106	2	112	156	3	152	211	2
<i>Nonionella turgida</i>	688	956	10	456	633	10	1120	1556	31	616	856	8
<i>Rectuvigerina phlegeri</i>	520	722	7	224	311	5	56	78	2	568	789	8
<i>Robertina transluscens</i>	24	33	0	8	11	0	–	–	–	–	–	0
<i>Saidovina karreriana</i>	68	94	1	32	44	1	–	–	–	64	89	1
<i>Stainforthia complanata</i>	12	17	0	8	11	0	–	–	–	–	–	–
<i>Stainforthia concava</i>	48	67	1	68	94	1	–	–	–	16	22	0
<i>Stainforthia fusiformis</i>	152	211	2	276	383	6	152	211	4	200	278	3
<i>Valvulineria bradyana</i>	208	289	3	12	17	0	32	44	1	176	244	2
<i>Virgulinea fragilis</i>	4	6	0	8	11	0	–	–	–	–	–	–
<i>Virgulopsis</i> sp.	4	6	0	–	–	–	–	–	–	–	–	–

Appendix A (continued)

Replicate cores : Station N Taxa 63–150 µm size fraction	N1			N2			N3			N4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Miliolids												
Indet.	8	11	0	–	–	–	–	–	–	–	–	–
<i>Adelosina</i> spp.	8	11	0	8	11	0	8	11	0	48	67	1
<i>Biloculinella labiata</i>	–	–	–	–	–	–	–	–	–	8	11	0
<i>Miliolinella subrotunda</i>	–	–	–	8	11	0	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	4	6	0	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	24	33	0	–	–	–	–	–	–	24	33	0
<i>Quinqueloculina milletti</i>	8	11	0	–	–	–	–	–	–	8	11	0
<i>Quinqueloculina pygmaea</i>	–	–	–	–	–	–	–	–	–	8	11	0
<i>Quinqueloculina seminula</i>	–	–	–	16	22	0	8	11	0	–	0	–
<i>Quinqueloculina stalkerii</i>	16	22	0	64	89	1	16	22	0	32	44	0
<i>Sigmoilopsis schlumbergeri</i>	12	17	0	12	17	0	8	11	0	–	–	–
<i>Spiroloculina excavata</i>	4	6	0	–	–	–	–	–	–	–	–	–
<i>Triloculina</i> sp.	–	–	–	8	11	0	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	8	11	0
Fossilising agglutinated												
<i>Textularia agglutinans</i>	–	–	–	–	–	–	8	11	0	56	78	1
<i>Textularia porrecta</i>	72	100	1	116	161	3	16	22	0	136	189	2
Non-fossilising agglutinated												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
Agglutinate sp.333	104	144	1	104	144	2	16	22	0	120	167	2
<i>Adercotryma glomerata</i>	8	11	0	16	22	0	8	11	0	–	–	–
<i>Clavulina cylindrica</i>	92	128	1	36	50	1	40	56	1	104	144	1
<i>Cribrostomoides wiesneri</i>	48	67	1	48	67	1	8	11	0	72	100	1
<i>Eggerella scabra</i>	908	1261	13	720	1000	16	608	844	17	904	1256	12
<i>Eratidus foliaceus</i>	–	–	–	8	11	0	–	–	–	–	–	–
<i>Lagenammia difflugiformis</i>	–	–	–	–	–	–	–	–	–	16	22	0
<i>Leptohalysis scotti</i>	292	406	4	428	594	9	416	578	11	392	544	5
<i>Nouria polymorphinoides</i>	60	83	1	16	22	0	–	–	–	16	22	0
<i>Psammosphaera bowmani</i>	192	267	3	48	67	1	16	22	0	88	122	1
<i>Psammosphaera fusca</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudobolivina fusiformis</i>	16	22	0	12	17	0	–	–	–	24	33	0
<i>Reophax fusiformis</i>	8	11	0	–	–	–	8	11	0	40	56	1
<i>Reophax nana</i>	16	22	0	44	61	1	–	–	–	40	56	1
<i>Trochammina globigeriniformis</i>	204	283	3	56	78	1	64	89	2	104	144	1
Organic foraminifera	–	–	–	–	–	–	–	–	–	–	–	–
No perforate individuals	4880	8031	70	2820	3917	61	2400	3333	66	5216	7244	70
No miliolid individuals	80	111	1	120	167	3	40	56	1	136	189	2
No fossilising agglutinated individuals	72	100	1	116	161	3	24	33	1	192	267	3
No non-fossilising agglutinated ind.	1948	2706	28	1536	2133	33	1184	1644	32	1920	2667	26
No organic individuals	–	–	–	–	–	–	–	–	–	–	–	–
Total No living individuals	6980	10947		4592	6378		3648	5067		7464	10367	

Appendix B

Replicate cores : Station A Taxa > 150 µm size fraction	A1			A2			A3			A4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Perforates												
Indet.	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ammonia beccarii</i> f. <i>beccarii</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ammonia tepida</i>	75	104	53.6	47	65	36.4	43	60	41.3	21	29	25.9
<i>Amphicoryna scalaris</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Astacolus crepidulus</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Astacolus insolitus</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina alata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina dilatata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina spathulata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina striatula</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bolivina subaenariensis</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulimina</i> sp.	-	-	-	1	1	0.8	1	1	1.0	-	-	-
<i>Bulimina aculeata</i>	-	-	-	1	1	0.8	-	-	-	-	-	-
<i>Bulimina costata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulimina elongata</i>	4	6	2.9	4	6	3.1	3	4	2.9	-	-	-
<i>Bulimina gibba</i>	1	1	0.7	-	-	-	-	-	-	-	-	-
<i>Bulimina marginata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassidulina carinata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassidulina crassa</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chilostomella ovoidea</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Elphidium advenum</i>	-	-	-	-	-	-	1	1	1.0	2	3	2.5
<i>Elphidium crispum</i>	-	-	-	-	-	-	-	-	-	1	1	1.2
<i>Fursenkoina</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fursenkoina acuta</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gavelinopsis praegeri</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Globobulimina pyrula</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Globocassidulina subglobosa</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gyroidina umbonata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyalinea balthica</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lagena</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lenticulina atlantica</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nonion fabum</i>	2	3	1.4	1	1	0.8	5	7	4.8	1	1	1.2
<i>Nonionella turgida</i>	13	18	9.3	6	8	4.7	6	8	5.8	10	14	12.3
<i>Pseudoepionides falsobeccarii</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rectuvigerina phlegeri</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Robertina transluscens</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Saidovina karreriana</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Valvulineria bradyana</i>	-	-	-	-	-	-	-	-	-	-	-	-
Miliolids												
Indet.	-	-	-	-	-	-	1	1	1.0	-	-	-
<i>Adelosina longirostra</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Biloculinella labiata</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cornuspira foliacea</i>	-	-	-	-	-	-	-	-	-	-	-	-

Appendix B (continued)

Replicate cores : Station A Taxa > 150 µm size fraction	A1			A2			A3			A4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
<i>Pyrgo elongata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>	4	6	2.9	4	6	3.1	2	3	1.9	2	3	2.5
<i>Quinqueloculina lata</i>	3	4	2.1	3	4	2.3	9	13	8.7	6	8	7.4
<i>Quinqueloculina milletti</i>	6	8	4.3	5	7	3.9	11	15	10.6	5	7	6.2
<i>Quinqueloculina seminula</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroloculina excavata</i>	–	–	–	1	1	0.8	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated												
<i>Bigenerina nodosaria</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia agglutinans</i>	–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
Agglutinate sp.333	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammoscalaria foliacea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Clavulina cylindrica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Eggerella scabra</i>	15	21	10.7	18	25	14.0	4	6	3.8	5	7	6.2
<i>Haplophragmoides</i> spp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lagenammina difflugiformis</i>	–	–	–	–	–	–	–	–	–	1	–	1.2
<i>Leptohalysis scottii</i>	14	19	10.0	28	39	21.7	13	18	12.5	16	22	19.8
<i>Nouria polymorphinoides</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Psammosphaera fusca</i>	2	3	1.4	8	11	6.2	4	6	3.8	10	14	12.3
<i>Reophax</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax dentaliniformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroplectammina</i> sp.1	1	1	0.7	1	1	0.8	1	1	1.0	1	1	1.2
<i>Trochammina globigeriniformis</i>	–	–	–	1	1	0.8	–	–	–	–	–	–
Organic foraminifera	–	–	–	–	–	–	–	–	–	–	–	–
No perforate individuals	95	132	67.9	60	83	46.5	59	82	56.7	35	49	43.2
No miliolid individuals	13	18	9.3	13	18	10.1	23	32	22.1	13	18	16.0
No fossilising agglutinated individuals	–	–	–	–	–	–	–	–	–	–	–	–
No non-fossilising agglutinated ind.	32	44	22.9	56	78	43.4	22	31	21.2	33	46	40.7
No organic individuals	–	–	–	–	–	–	–	–	–	–	–	–
Total No living individuals	140	194		129	179		104	144		81	113	

Appendix B (continued)

Replicate cores : Station N Taxa > 150 µm size fraction	N1			N2			N3			N4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Perforates												
Indet.	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Ammonia beccarii</i> f. <i>beccarii</i>	22	31	1.8	10	14	1.6	9	13	1.4	25	35	2.0
<i>Ammonia tepida</i>	–	–	–	2	3	0.3	–	–	–	–	–	–
<i>Amphicoryna scalaris</i>	–	–	–	–	–	–	1	1	0.2	1	1	0.1
<i>Astacolus crepidulus</i>	1	1	0.1	1	1	0.2	1	1	0.2	–	–	–
<i>Astacolus insolitus</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Bolivina</i> sp.	2	3	0.2	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>	–	–	–	–	–	–	1	1	0.2	–	–	–
<i>Bolivina spathulata</i>	–	–	–	–	–	–	–	–	–	2	3	0.2
<i>Bolivina striatula</i>	1	1	0.1	2	3	0.3	–	–	–	1	1	0.1
<i>Bolivina subaenariensis</i>	2	3	0.2	–	–	–	–	–	–	–	–	–
<i>Bulimina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>	1	1	0.1	–	–	–	–	–	–	2	3	0.2
<i>Bulimina costata</i>	–	–	–	1	1	0.2	–	–	–	1	1	0.1
<i>Bulimina elongata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina gibba</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>	1	1	0.1	2	3	0.3	–	–	–	–	–	–
<i>Cassidulina carinata</i>	23	32	1.8	29	40	4.6	13	18	2.0	29	40	2.3
<i>Cassidulina crassa</i>	4	6	0.3	1	1	0.2	–	–	–	1	1	0.1
<i>Chilostomella ovoidea</i>	–	–	–	–	–	–	15	21	2.3	–	–	–
<i>Elphidium advenum</i>	1	1	0.1	–	–	–	–	–	–	1	1	0.1
<i>Elphidium crispum</i>	1	1	0.1	–	–	–	1	1	0.2	–	–	–
<i>Fursenkoina</i> sp.	–	–	–	1	1	0.2	–	–	–	–	–	–
<i>Fursenkoina acuta</i>	–	–	–	–	–	–	1	1	0.2	–	–	–
<i>Gavelinopsis praegeri</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>	–	–	–	1	1	0.2	–	–	–	–	–	–
<i>Globocassidulina subglobosa</i>	–	–	–	1	1	0.2	–	–	–	1	1	0.1
<i>Gyroidina umbonata</i>	4	6	0.3	1	1	0.2	2	3	0.3	–	–	–
<i>Hyalinea balthica</i>	2	3	0.2	–	–	–	1	1	0.2	4	6	0.3
<i>Lagena</i> spp.	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Lenticulina atlantica</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Nonion fabum</i>	175	243	14.0	99	138	15.6	141	196	21.9	220	306	17.2
<i>Nonionella turgida</i>	29	40	2.3	22	31	3.5	22	31	3.4	23	32	1.8
<i>Pseudoeponides falsobeccarii</i>	2	3	0.2	3	4	0.5	6	8	0.9	8	11	0.6
<i>Rectuvigerina phlegeri</i>	90	125	7.2	51	71	8.1	65	90	10.1	90	125	7.0
<i>Robertina translucens</i>	1	1	0.1	1	1	0.2	1	1	0.2	–	–	–
<i>Saidovina karreriana</i>	–	–	–	2	3	0.3	–	–	–	1	1	0.1
<i>Valvulineria bradyana</i>	275	382	22.1	70	97	11.1	129	179	20.1	306	425	23.9
Miliolids												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelosina</i> spp.	7	10	0.6	3	4	0.5	6	8	0.9	9	13	0.7
<i>Biloculinella labiata</i>	1	1	0.1	–	–	–	1	1	0.2	2	3	0.2
<i>Cornuspira foliacea</i>	–	–	–	–	–	–	–	–	–	1	1	0.1

Appendix B (continued)

Replicate cores : Station N	N1			N2			N3			N4		
	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%	r.d.	D ₁₀₀	%
Taxa > 150 µm size fraction												
<i>Pyrgo elongata</i>	3	4	0.2	–	–	–	–	–	–	13	18	1.0
<i>Pyrgo oblonga</i>	7	10	0.6	3	4	0.5	4	6	0.6	–	–	–
<i>Quinqueloculina aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	–	–	–	–	–	–	–	–	–	2	3	0.2
<i>Quinqueloculina milletti</i>	1	1	0.1	–	–	–	–	–	–	6	8	0.5
<i>Quinqueloculina seminula</i>	6	8	0.5	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis</i> sp.	–	–	–	–	–	–	–	–	–	2	3	0.2
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	4	6	0.6	–	–	–	–	–	–
<i>Spiroloculina excavata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	1	1	0.2	–	–	–
Fossilising agglutinated												
<i>Bigenerina nodosaria</i>	–	–	–	1	1	0.2	–	–	–	–	–	–
<i>Textularia agglutinans</i>	23	32	1.8	14	19	2.2	3	4	0.5	22	31	1.7
Non-fossilising agglutinated												
Indet.	2	3	0.2	–	–	–	–	–	–	2	3	0.2
Agglutinate sp.333	42	58	3.4	17	24	2.7	13	18	2.0	45	63	3.5
<i>Adercotryma glomerata</i>	6	8	0.5	–	–	–	5	7	0.8	11	15	0.9
<i>Ammoscalaria foliacea</i>	19	26	1.5	19	26	3.0	3	4	0.5	29	40	2.3
<i>Clavulina cylindrica</i>	138	192	11.1	64	89	10.1	41	57	6.4	123	171	9.6
<i>Cribrostomoides wiesneri</i>	16	22	1.3	7	10	1.1	9	13	1.4	16	22	1.3
<i>Eggerella scabra</i>	206	286	16.5	131	182	20.7	62	86	9.6	152	211	11.9
<i>Haplophragmoides</i> spp.	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Lagenammina difflugiformis</i>	9	13	0.7	7	10	1.1	3	4	0.5	11	15	0.9
<i>Leptohalysis scottii</i>	1	1	0.1	–	–	–	1	1	0.2	–	–	–
<i>Nouria polymorphinoides</i>	73	101	5.9	36	50	5.7	62	86	9.6	82	114	6.4
<i>Psammosphaera bowmani</i>	5	7	0.4	1	1	0.2	2	3	0.3	2	3	0.2
<i>Reophax</i> sp.	–	–	–	3	4	0.5	–	–	–	–	–	–
<i>Reophax dentaliniformis</i>	–	–	–	1	1	0.2	1	1	0.2	–	–	–
<i>Reophax fusiformis</i>	17	24	1.4	5	7	0.8	5	7	0.8	15	21	1.2
<i>Spiroplectammina</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina globigeriniformis</i>	25	35	2.0	17	24	2.7	12	17	1.9	14	19	1.1
Organic foraminifera	1	1	0.1	–	–	–	–	–	–	–	–	–
No perforate individuals	639	888	51.2	300	417	47.4	409	568	63.6	720	1000	56.3
No miliolid individuals	25	35	2.0	10	14	1.6	12	17	1.9	35	49	2.7
No fossilising agglutinated individuals	23	32	1.8	15	21	2.4	3	4	0.5	22	31	1.7
No non-fossilising agglutinated individuals	559	776	44.8	308	428	48.7	219	304	34.1	503	699	39.3
No organic individuals	1	1	0.1	–	–	–	–	–	–	–	–	–
Total No living individuals	1247	1732		633	879		643	893		1280	1778	

Appendix C

- Ammonia tepida* (Cushman) = *Rotalia beccarii* Linnaeus var. *tepida* Cushman, 1926; in Jorissen, 1988, Plate 2, Fig. 8a–b (as *Ammonia parkinsoniana* f. *tepida*)
- Bolivina dilatata* (Reuss) = *Brizalina dilatata* Reuss, 1850; in Colom, 1974, Fig. 18j–n
- Bolivina spathulata* (Williamson) = *Textularia variabilis* Williamson var. *spathulata* Williamson, 1858; in Jorissen, 1988, Plate 1, Fig. 5
- Clavulina cylindrica* d’Orbigny, 1952; in Jones, 1994, Plate 44, Figs. 19–24
- Eggerella scabra* (Williamson) = *Bulimina scabra* Williamson, 1858; in Jones, 1994, Plate 47, Figs. 15–17
- Hopkinsina atlantica* (Cushman) = *Hopkinsina pacifica* Cushman var. *atlantica* Cushman, 1944; in Diz and Francès, 2008, Plate II, Fig. 8
- Leptohalysis scottii* (Chaster) = *Reophax scottii* Chaster, 1892; in Sgarella and Montcharmont Zei, 1993, Plate 2, Fig. 5
- Nonion fabum* (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798; in Jones, 1994, Plate 109, Figs. 12–13
- Nonionella turgida* (Williamson) = *Rotalina turgida* Williamson, 1858; in Jorissen, 1988, Plate 4, Figs. 11–13
- Nouria polymorphinoides* Heron–Allen and Earland, 1914; in Barmawidjaja et al., 1992, Plate 4, Fig. 4
- Psammosphaera fusca* Schulze, 1875; in Höglund, 1947, Plate 4, Figs. 9–10
- Quinqueloculina lata* Terquem, 1876; in Murray, 2003, Plate 4, Figs. 9–10
- Quinqueloculina milletti* (Wiesner) = *Miliolina milletti* Wiesner, 1912; in Boltovskoy et al., 1980, Plate 28, Figs. 13–17
- Quinqueloculina pygmaea* Reuss, 1850; in Sgarella and Montcharmont Zei, 1993, Plate 7, Fig. 2
- Rectuvigerina phlegeri* Le Calvez, 1959; in Schiebel, 1992, Plate 3, Fig. 10a–d
- Stainforthia fusiformis* (Williamson) = *Bulimina pupoides* d’Orbigny var. *fusiformis* Williamson, 1858; in Gooday and Alve, 2001, Plate 3, Figs. A–B–C
- Valvulineria bradyana* (Fornasini) = *Discorbina bradyana* Fornasini, 1900; in Jorissen, 1988, Plate 4, Figs. 1–2

CHAPITRE 3

TEMPORAL VARIABILITY OF LIVE (STAINED) BENTHIC FORAMINIFERAL FAUNAS IN A RIVER-DOMINATED SHELF: FAUNAL RESPONSE TO CHANGES OF THE RIVER INFLUENCE (RHÔNE PRODELTA, NW MEDITERRANEAN)

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CHAPITRE 3

**TEMPORAL VARIABILITY OF LIVE (STAINED) BENTHIC
FORAMINIFERAL FAUNAS IN A RIVER-DOMINATED
SHELF**

**FAUNAL RESPONSE TO RAPID CHANGES
OF THE RIVER INFLUENCE
(RHÔNE PRODELTA, NW MEDITERRANEAN)**

Goineau A.^{a,b}, Fontanier C.^{a,b}, Jorissen F.^{a,b}, Buscail R.^c, Kerhervé P.^c, Cathalot C.^d, Pruski A.^e, Bourgeois S.^e, Metzger E.^{a,b}, Rabouille C.^d

^a Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), University of Angers,
UPRES EA 2644, 2 Boulevard Lavoisier, 49045 Angers Cedex 01, France

^b Laboratoire d'Etude des Bio-Indicateurs Marins (LEBIM), Ker Châlon, 85350 Ile d'Yeu,
France

^c Centre de Formation et de Recherche sur l'Environnement Marin, University of Perpignan,
UMR 5110 CNRS, 52 Avenue Paul Alduy, 66860 Perpignan Cedex, France

^d Laboratoire des Sciences du Climat et de l'Environnement (LSCE),
UMR 1572 CEA–CNRS–UVSQ, F-91198 Gif-sur-Yvette Cedex, France

^e Laboratoire d'Océanographie Biologique de Banyuls (LOBB) – Laboratoire Arago,
UMR 7621 (CNRS, UPMC), 18 avenue Fontaulé, 66650 Banyuls sur mer, France

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l'ANR CHACCRA*

ABSTRACT

Living (rose Bengal-stained) benthic foraminifera were investigated at two stations (24 and 67 m depth) in the Rhône prodelta (NW Mediterranean, Gulf of Lions). At each site, one core was sampled in April 2007, September 2007, May 2008 and December 2008, permitting to observe foraminiferal faunas of the 63–150 and >150 µm size fractions under a wide range of environmental conditions. Significantly different foraminiferal faunas were observed during the four investigated periods at the shallowest Station A located in the close vicinity of the Rhône River mouth. Different colonisation stages are observed after major Rhône River flood events. Thousands living individuals of *Leptohalysis scottii* had colonised a freshly deposited sediment only few days after the beginning of a flood (May 2008), whereas species more typical of river-dominated shelves (*Ammonia tepida*) and high-energy environments (*Psammosphaera fusca*) constituted a more advanced colonisation stage few weeks after the deposit of riverine material enriched in organic matter (December 2008). Under more stable conditions (i.e., no sediment deposit), relatively diverse and equilibrated faunas grew in the sediments. Noticeable input of riverine phytoplankton to the sediment during spring bloom conditions (April 2007) benefited to species able to feed on fresh phytodetritus (e.g., *Bolivina dilatata*, *Nonionella stella*, *Stainforthia fusiformis*). High energy conditions did not prevent the establishment of relatively diverse faunas (September 2007) but favoured taxa specialised to such environmental conditions (*A. tepida*, *P. fusca*). The reduced influence of the Rhône River input at the farther Station N led to less contrasted environmental conditions during the four sampling periods, and so to less obvious variations in foraminiferal faunal composition. During reduced riverine influence (i.e., low Rhône discharge and/or weak bottom currents), species able to feed on fresh phytodetritus (e.g., *Clavulina cylindrica*, *Hopkinsina atlantica*, *Nonionella iridea* and *Nonionella turgida*) benefited from eutrophic conditions of the spring bloom (April 2007, May 2008). Conversely, the occurrence of *Nouria polymorphinoides* (September 2007, December 2008) was indicative of a high riverine influence (high river discharge and/or stronger bottom currents). This study put into evidence the extremely rapid response (days to weeks) of benthic foraminiferal faunas to strong variations in environmental conditions, especially close to the river mouth (Station A), response noticeably reduced farther from the mouth (Station N) due to a weaker impact of riverine input.

Key words: Living benthic foraminifera; Rhône prodelta; Temporal variability; Riverine influence.

3.1. INTRODUCTION

River-dominated shelves constitute dynamic environments at the interface between the continent and the ocean. In these areas, dissolved nutrients supplied by the river induce a local increase in primary production and in fresh organic matter export to the sea floor (Lohrenz et al., 1990, 1997; Dagg and Breed, 2003). Moreover, the high variability over time of riverine discharge leads to contrasted environmental conditions in the coastal ocean. In the Rhône River prodelta, high sediment input (continental organic and inorganic material) related to flood events disturbs the benthic environment by modifying geochemical processes (Cathalot et al., 2009; Pastor, 2010) and macrofaunal activity (Salen-Picard et al., 2002; Hermand et al., 2008). In such a dynamic environment, benthic foraminiferal faunas may also vary significantly in space and in time. Small-scale spatial variability has been investigated at two stations (24 and 67 m depth) sampled on the shelf under the influence of the Rhône River in September 2007 (Goineau et al., Submitted – see Chapter 2 in this thesis). In that study, the authors show that significant patchiness exists in absolute foraminiferal abundances of replicate cores at one site, but much less in major species relative abundances (i.e., percentages). Consequently, the authors recommend using preferentially species relative abundances to compare benthic foraminiferal communities in temporal surveys. Benthic foraminiferal assemblages have also been analysed at a larger scale in the Rhône prodelta (15 to 100 m depth, 1 to 22.4 km off the mouth) during two sampling seasons (Mojtahid et al., 2009; Goineau et al., In Press – see Chapter 1 in this thesis). These studies put into evidence a bio-zonation of the area depending on hydro-sedimentary processes, sediment grainsize, and on the quality and quantity of sedimentary organic matter. A preliminary comparison based on major species relative abundances observed the two sampling seasons shows a positive response of the most opportunistic species (e.g., *Bulimina aculeata*, *Cassidulina carinata*, *Valvulineria bradyana*) to fresher and/or more marine phytodetritus input related to spring bloom conditions (June 2005). Unfortunately, no long-term temporal survey for a single site has been performed in the Rhône prodelta until now. Such an investigation would allow us to better define what is the impact of changing environmental conditions (e.g., hydro-sedimentary processes, quality/quantity of the organic matter) on the foraminiferal faunas. Furthermore, in case temporal variability of faunal composition is observed, it would be important to know how fast such faunal changes can take place and how far offshore such variability can be observed.

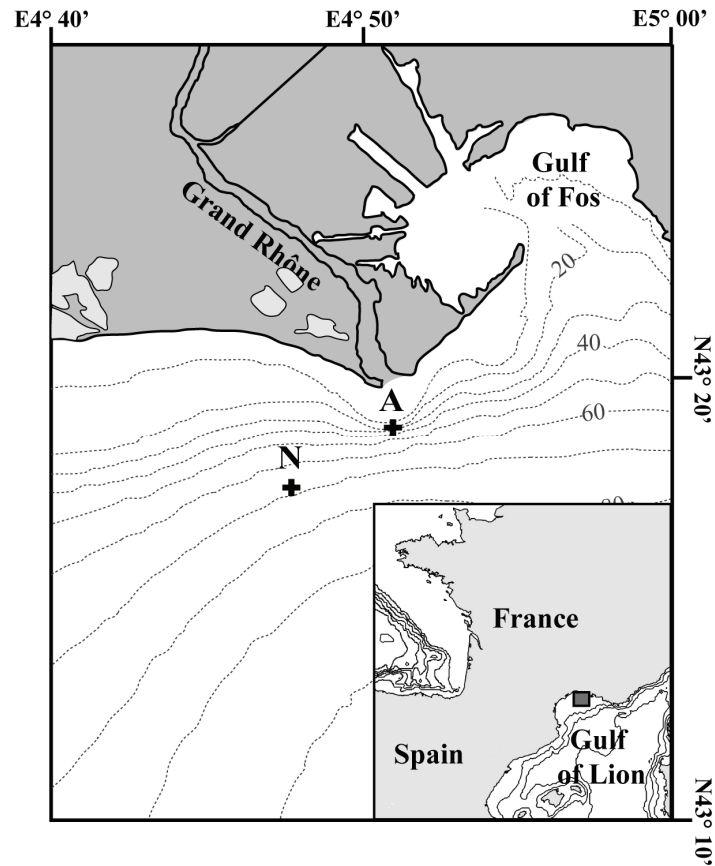


Figure 1: Study area and location of both investigated Stations A and N.

In this chapter, we will try to obtain new insights into the temporal variability of live (stained) benthic foraminiferal faunas from the Rhône prodelta by investigating two sites sampled during four periods with contrasted environmental conditions. Sites A and N (24 and 67 m depth, respectively) were both visited in April 2007, September 2007, May 2008 and December 2008, these sampling dates cover a wide range of environmental conditions from low to high discharge (flood), and from oligotrophic to spring bloom conditions. We have analysed both 63–150 μm and $> 150 \mu\text{m}$ size fractions of one core per site for each sampling period. These analyses are combined with various environmental measurements such as sediment oxygenation (oxygen penetration depth, oxygen uptake) and sedimentary organic matter quantity (organic carbon content) and quality (Chl-*a*, amino acids and lipids contents, carbon and nitrogen stable isotopes). The aim of this study is to describe the structure (standing stocks, diversity, composition) and temporal variability of benthic foraminiferal faunas in the Rhône prodelta, and to link our observations with environmental conditions prevailing in the water column (low/high river discharge, low/high primary production) and within the sediment at the time of sampling.

3.2. MATERIAL AND METHODS

3.2.1. Study area

The Rhône River flows into the Gulf of Lions, a large crescent-shaped continental shelf located in the North-Western Mediterranean Sea (Berné and Gorini, 2005). At the river mouth, a turbid river plume spreads out. According to Naudin et al. (1997), its offshore extension and shape depend on the Rhône outflow (low/high discharge), wind regime (Mistral and Tramontane; Millot, 1999) and the intensity of the North Mediterranean Current flowing westward along the continental slope (Béthoux and Prieur, 1983; Millot, 1990). The mixing between riverine (low salinity) and marine waters (high salinity) in the Rhône channel is typical of a microtidal saltwedge estuary. The salt water forms a wedge in the river bed underneath the freshwater layer. The landward extension of this wedge is mainly controlled by the river discharge. During low water discharge periods (about $500 \text{ m}^3 \cdot \text{s}^{-1}$), the salt intrusion can extend up to 20 km inland, whereas marine waters are pushed seaward to the river mouth during high water discharge ($> 3000 \text{ m}^3 \cdot \text{s}^{-1}$), without any influence on bottom water salinity off the river mouth (Eisma, 1993). The Rhône River carries 90% of the terrigenous material and 80% of the fresh water introduced into the Gulf of Lions (Durrieu de Madron et al., 2000, 2003). Thanks to these riverine supplies, the Gulf of Lions is one of the most productive areas of the Mediterranean Sea (Diaz, 2000), the Rhône River supplying 50% of the total nutrients needed for primary production into the Gulf (Lochet and Leveau, 1990). Phytoplankton primary production is maximal from March to May with Chl-*a* concentrations in sea-surface waters of $1 \text{ mg Chl-}a \cdot \text{m}^{-3}$ (Bosc et al., 2004). The summer season is the most oligotrophic period with $0.1\text{--}0.2 \text{ mg Chl-}a \cdot \text{m}^{-3}$ in surface waters. In the Rhône River, riverine phytoplankton blooms also during spring. This riverine production can be exported to the open sea in the surface waters of the river plume (Harmelin-Vivien et al., 2008).

The mean annual flow of the Rhône River is about $1700 \text{ m}^3 \cdot \text{s}^{-1}$, with maximum discharge values $> 3000 \text{ m}^3 \cdot \text{s}^{-1}$ in autumn and spring during major flood events (Pont et al., 2002). The terrigenous material carried during these events is transferred to the marine environment essentially in a bottom nepheloid layer above the sea floor, but also in suspension in the surface waters of the river plume (Naudin et al., 1997). Although 30% of the introduced particles are transferred to the slope and to the deeper basin (Got and Aloisi, 1990), a major part of the riverine terrigenous input is deposited close to the river outlet, from 0 to 60 m depth and from 0 to 6 km off the mouth, thus forming a delta front and a

prodeltaic area (Rabineau et al., 2005). This zone is subject to very high deposition rates ranging from 30 to 50 cm.year⁻¹ (Calmet and Fernandez, 1990; Charmasson et al., 1998; Rabineau et al., 2005).

3.2.2. Sediment sampling

Stations A and N were sampled on the *R/V Téthys II* in April 2007 (RiOMar 1 cruise), September 2007 (RIOTECH cruise), May 2008 (CHACCRA-bent 1 cruise) and December 2008 (CHACCRA-bent 2 cruise). The two stations were respectively located at 24 and 67 m depth in the Rhône prodelta (Fig. 1, Table 1). At each station and during each sampling period, one core (72 cm² surface area) was recovered with a multicorer MUC 8/100 (Oktopus GmbH) that permits to collect cores with an undisturbed sediment – water interface. We studied live benthic foraminiferal faunas in all cores. Various environmental parameters were also analysed at each site for the different sampling periods.

Station	Lat. (°N)	Long. (°E)	Water depth (m)	Dist./river mouth (km)	Period	Q_{mean} (m ³ .s ⁻¹ .d ⁻¹)	Δt /last major flood (d)	SM_{mean} (mg.l ⁻¹ .d ⁻¹)	T_{BW} (°C)	$[O_2]_{BW}$ (μmol.l ⁻¹)
A	43° 18' 47"	4° 51' 4"	24	1.9	Apr.07	1018	42	5	14.9	259
					Sept.07	768	188	13	17.7	244
					May.08	1718	2	115	16.8	238
					Dec.08	1461	27	17	14.8	237
N	43° 17' 33"	4° 47' 59"	67	5.5	Apr.07	1018	42	5	14.5	253
					Sept.07	768	188	13	14.5	217
					May.08	1718	38	115	16.3	240
					Dec.08	1461	27	17	–	–

Table 1: Location and environmental characteristics of both Stations A and N over the four sampling campaigns. Q_{mean} and SM_{mean} are mean Rhône River discharge and suspended material load, respectively, calculated over the 15 days prior to sampling. Δt /last major flood is the time interval since the last Rhône River flood > 3000 m³.s⁻¹. T_{BW} and $[O_2]_{BW}$ correspond to bottom water temperature and oxygenation, respectively.

3.2.3. Rhône River discharge and supplies

Daily Rhône River discharge (Q in m³.s⁻¹) and suspended material (SM in mg.l⁻¹) concentrations were measured by the Institut de Radioprotection et de Sûreté Nucléaire (IRSN) and the Compagnie Nationale du Rhône (CNR) at the SORA station located at Arles. For each sampling period, we calculated the mean Rhône River discharge (Q_{mean}) and the

mean suspended material load (SM_{mean}) for the 15 days prior to sampling. We also determined the time lapse since the last major flood, i.e. $> 3000 \text{ m}^3 \cdot \text{s}^{-1}$, expressed in days.

3.2.4. Geochemical analyses

For both stations, Total Nitrogen and Organic Carbon concentrations (TN and OC, respectively), total hydrolysable amino acids (THAA) and total lipids contents, and carbon and nitrogen stable isotopic ratios of organic matter ($\delta^{13}\text{C}_{\text{OC}}$ and $\delta^{15}\text{N}$) were measured on milled and freeze-dried sediment samples from the top 0–0.5 cm of one sediment core (Buscail et al., In prep). Chlorophyll-*a* (Chl-*a*) concentrations were also analysed on thawed sediment sampled in the top half-centimetre of one core.

In situ profiles of O_2 in the pore water were obtained by a benthic microprofiler using Clark micro-electrodes (Rabouille et al., 2003; Cathalot et al., 2009). Bottom waters were sampled 2 m above the sea floor by a Niskin bottle, for determination of temperature (T_{BW}) and dissolved oxygen ($[\text{O}_2]_{\text{BW}}$) (Table 1).

3.2.5. Benthic foraminiferal faunas

For foraminiferal faunal analysis, each replicate core was sliced on board, every 0.5 cm until 2 cm depth, and every 1 cm from 2 to 5 cm depth. Each sample was preserved in a plastic bottle with a solution of 95% ethanol and $1 \text{ g} \cdot \text{L}^{-1}$ Rose Bengal stain. In the laboratory, samples were sieved through 63 and 150 μm mesh screens and the sieve residue were again preserved in 95% ethanol. All stained specimens of the $> 150 \mu\text{m}$ size fraction were handpicked down to 5 cm depth under wet conditions under a binocular microscope and stored in micropaleontological slides. Foraminifera belonging to the 63–150 μm size fraction were only investigated in the topmost 0.5 cm. Samples of this size fraction were dried and split with an Ottomicrosplitter because of the high standing stocks. All living foraminifera from complete splits were wet-picked until a minimum of 300 individuals was counted. Rose Bengal stain (Walton, 1952; Murray and Bowser, 2000) is commonly used in living foraminiferal studies because of the easy and rapid way of this technique. However, an important methodological problem is that protoplasm of dead foraminifera may be preserved in anoxic sediments, and may still be stained by Rose Bengal (Bernhard, 1988, 2000; Corliss and Emerson, 1990). Consequently, only specimens with all chambers (except the last one) brightly stained pink were counted, and doubtful individuals were compared with perfectly stained individuals of the same species found in more superficial and oxygenated sediment

layers. Total living foraminiferal standing stocks were calculated for the $> 150 \mu\text{m}$ (0–5 cm depth) and $63\text{--}150 \mu\text{m}$ size fractions (0–0.5 cm) for each core. These absolute density values are normalised for a sediment surface area of 100 cm^2 (D). Species relative abundances (i.e. percentages, %) calculated for each core allow to define major species (i.e. species $> 5\%$ in at least one core). To quantify the diversity patterns of the foraminiferal faunas, Shannon (H) and Evenness (E) indices were calculated in each core for both size fractions (Hayek and Buzas, 1997; Murray, 2006).

3.3. RESULTS

3.3.1. Rhône River discharge and supplies

The four sampling campaigns were characterised by different Rhône River regimes (Fig. 2, Table 1).

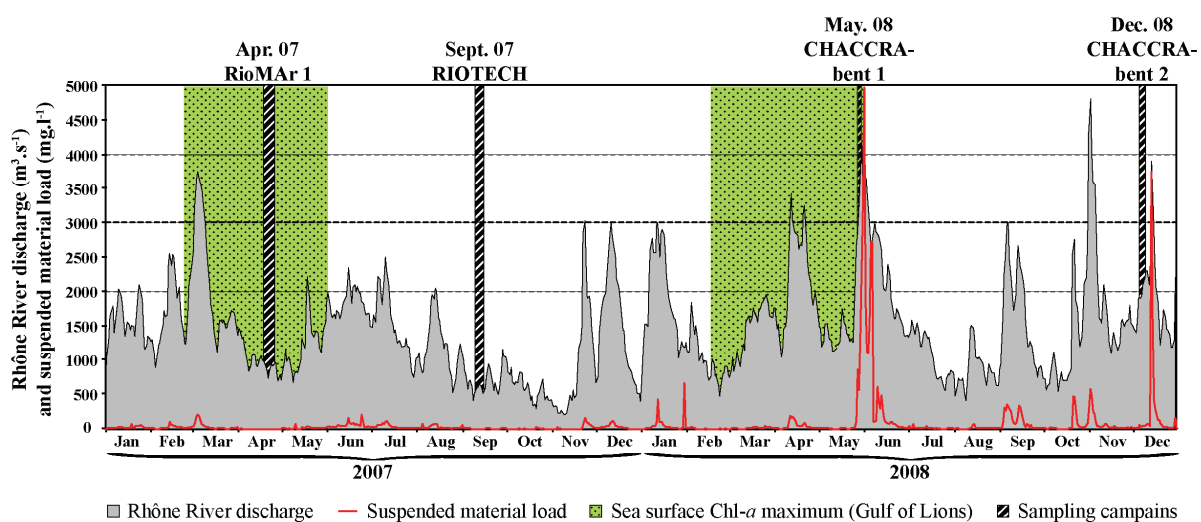


Figure 2: Mean daily discharge (light-grey area) and suspended material load (red curve) of the Rhône River recorded by the Compagnie Nationale du Rhône and the IRSN at SORA station (Arles), located $\sim 45 \text{ km}$ upstream from the river mouth from January 2007 to December 2008. Different sampling campaigns are represented by black-dashed areas; green dotted areas represent spring blooms in the Gulf of Lions (SeaWiFS images).

The time interval since the last major flood (i.e., Rhône discharge $> 3000 \text{ m}^3 \cdot \text{s}^{-1}$) ranged from 2 (May 2008) to 188 days (September 2007). In April 2007, the last major flood was recorded ~ 50 days before sampling. In September 2007, the mean Rhône River discharge in the 15 days before sampling (Q_{mean}) was minimal with a value of $\sim 770 \text{ m}^3 \cdot \text{s}^{-1}$. In May 2008, sampling was performed 2 days after the beginning of a major flood (from $\sim 1730 \text{ m}^3 \cdot \text{s}^{-1}$ on the 27th of May, 2008 to $\sim 3820 \text{ m}^3 \cdot \text{s}^{-1}$ during sampling on the 29th of May, 2008). Finally, in

December 2008, sampling took place 27 days after a late fall major flood (until $\sim 4800 \text{ m}^3 \cdot \text{s}^{-1}$). Q_{mean} values were maximal during the latter sampling period, with $\sim 1700 \text{ m}^3 \cdot \text{s}^{-1}$ (May 2008) and $\sim 1450 \text{ m}^3 \cdot \text{s}^{-1}$ (December 2008). A minimal mean suspended material load (SM_{mean}) was recorded in April 2007, with only $5 \text{ mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$. In May 2008, SM_{mean} was maximal reaching $115 \text{ mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$.

3.3.2. Bottom water characteristics – Sediment oxygenation and oxygen uptake

At Station A, bottom water temperature (T_{bw}) varied between 14.8 (December 2008) and 17.7 °C (September 2007) (Table 1). Bottom waters were well-oxygenated, with values $> 200 \text{ } \mu\text{mol} \cdot \text{l}^{-1}$ ($237\text{--}259 \text{ } \mu\text{mol} \cdot \text{l}^{-1}$). Oxygen penetration depth (OPD) was minimal and exhibited minor variation between April 2007, September 2007 and December 2008, with values ranging from 1.4 to 1.7 mm (Table 1). A deepening of the OPD was observed in May 2008 when a 5.8 mm-thick oxygenated level was observed. Dissolved oxygen uptake (DOU) was maximal in April 2007 and December 2008 with 21.5 and $20.6 \text{ mmol O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, respectively. A minimal uptake was measured in May 2008 with $9.2 \text{ mmol O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

For Station N, no data are available for December 2008. At the other three sampling periods, bottom water temperature ranged from 14.5 to 16.3 °C. Bottom water oxygen concentration was also high, with values varying between 217 and $253 \text{ } \mu\text{mol} \cdot \text{l}^{-1}$. OPD was deeper than at Station A, with values ranging from 3.3 to 3.8 in April 2007 and May 2008 to 4.9 mm in September 2007. DOU was lower than at Station A, with similar values of 9.2 and $9.5 \text{ mmol O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in April 2007 and May 2008. DOU was minimal in September 2007 with $6.6 \text{ mmol O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

3.3.3. Sedimentary particulate organic matter and chlorophyll-*a* concentrations

At Station A, lowest organic carbon (OC) contents in the top half-centimetre of sediment were recorded in May and December 2008, with values of 1.13% d.w. and 1.22% d.w., respectively (Fig. 3a, Table 2). The highest concentration was measured in April 2007, with a content of 2.05% d.w.. Lowest concentrations of the sum of amino acids and lipids were observed in December and May 2008, with values of 1.8 and $1.9 \text{ mg} \cdot \text{g}^{-1}$ d.w. (i.e., 14.7 and 16.7% of the OC, respectively). The highest content ($4.2 \text{ mg} \cdot \text{g}^{-1}$ d.w., 20.4% of the OC.) was recorded in April 2007. $\delta^{13}\text{C}_{\text{OC}}$ ranged from -27.18‰ in April 2007 to -24.79‰ in December 2008. Intermediate values of -26.64 to -26.30‰ were recorded in September 2007 and May 2008. The C:N ratio showed important variations, with values ranging between 12.5

in September 2007 and 28.1 in December 2008. Unfortunately, no $\delta^{15}\text{N}$ value is available for December 2008. During the three other sampling periods, $\delta^{15}\text{N}$ was less variable than $\delta^{13}\text{C}_{\text{OC}}$, values ranging between 2.90 and 3.92‰. Chl-*a* concentrations in the top first centimetre of the sediment varied between 2.14 and 9.78 $\mu\text{g}\cdot\text{g}^{-1}$ d.w., with minimal values in April 2007 and maximum contents in December 2008.

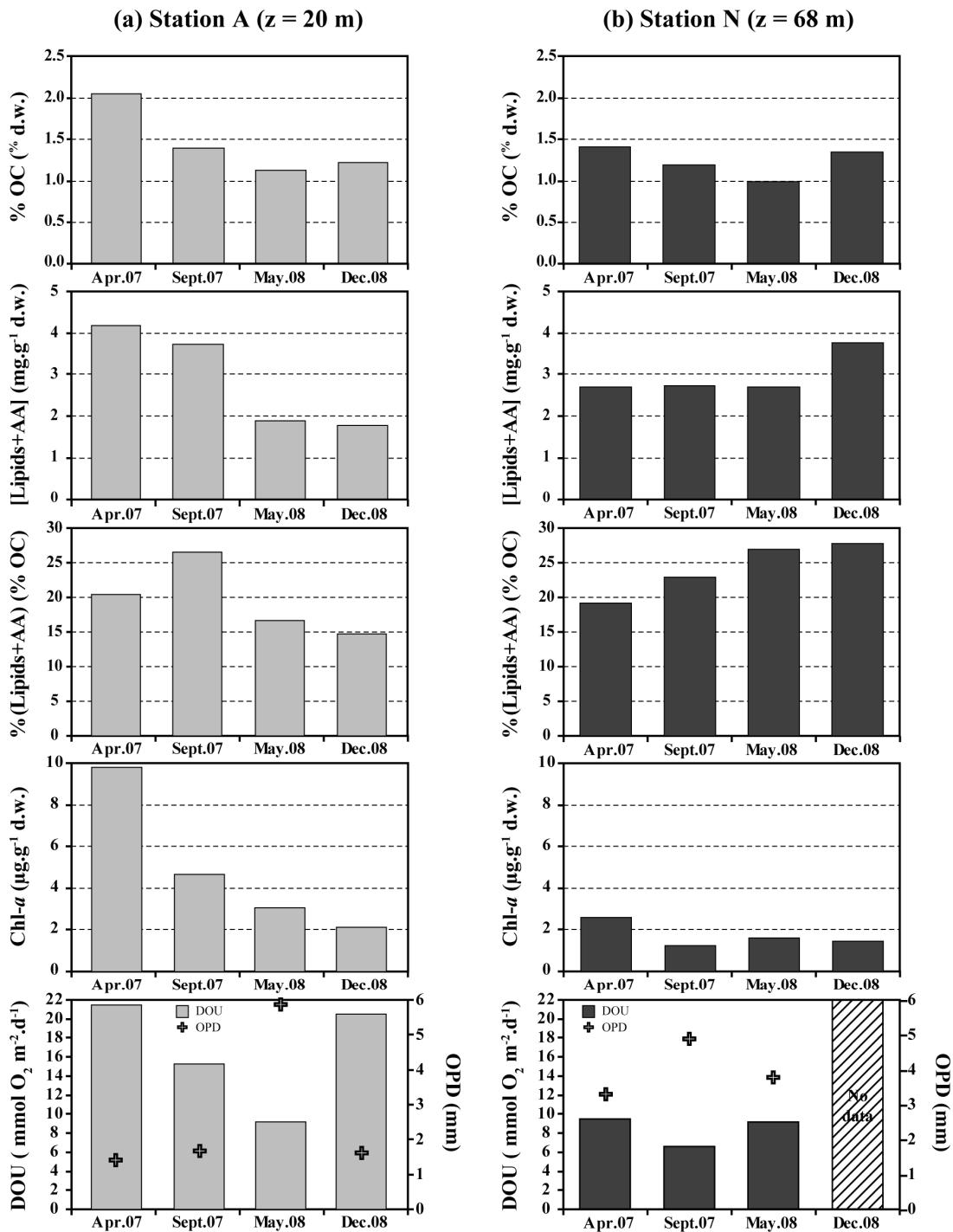


Figure 3: Descriptors of the organic matter and oxygen parameters measured at both Stations A (a) and N (b).

At Station N, OC content was minimal in May 2008 with only 1.00% d.w., and reached its maximum value in April 2007 and December 2008 with 1.4% d.w. (Fig. 3b, Table 2). The sum of amino acids and lipids had comparable concentrations in April 2007, September 2007 and May 2008, with values of 2.7 mg.g⁻¹ d.w. (from 19.2 to 27.0% of the OC). The highest concentrations were recorded in December 2008 with 3.8 mg.g⁻¹ d.w. (27.8% of the OC). Also $\delta^{13}\text{C}_{\text{OC}}$ and $\delta^{15}\text{N}$ were very constant, ranging from -26.12 to -25.82‰ and from 3.46 to 3.90‰, respectively. The lowest C:N ratio was measured in May 2008 with a value of 12.0. Maximal values were recorded in December 2008 and April 2007, with 16.2 and 17.4, respectively. Sedimentary Chl-*a* content showed small variations between the investigated sampling dates. The highest concentration was measured in April 2007 with 2.57 $\mu\text{g.g}^{-1}$ d.w., whereas values were fairly similar for the three other sampling periods, ranging between 1.23 and 1.62 $\mu\text{g.g}^{-1}$ d.w.

Station	Period	OPD (mm)	DOU (mmol O ₂ . m ⁻² .d ⁻¹)	OC (% d.w.)	C:N (Atomic ratio)	$\delta^{13}\text{C}_{\text{OC}}$ (‰)	$\delta^{15}\text{N}$ (‰)	Lipids+THAA (mg.g ⁻¹ d.w.)	(% OC)	Chl- <i>a</i> ($\mu\text{g.g}^{-1}$)
A	Apr.07	1.4 ± 0.2	21.5 ± 3.9	2.05	15.2	-27.18	3.58	4.2	20.4	9.78
	Sept.07	1.7 ± 0.1	15.3 ± 1.5	1.40	12.5	-26.64	3.92	3.7	26.5	4.66
	May.08	5.8 ± 0.8	9.2 ± 3.1	1.13	14.8	-26.3	2.90	1.9	16.7	3.07
	Dec.08	1.6 ± 0.3	20.6 ± 2.6	1.22	28.1	-24.79	-	1.8	14.7	2.14
N	Apr.07	3.3 ± 0.6	9.5 ± 1.2	1.42	17.4	-25.94	3.89	2.7	19.2	2.57
	Sept.07	4.9 ± 1.1	6.6 ± 0.9	1.20	13.2	-25.82	3.90	2.7	22.9	1.23
	May.08	3.8 ± 0.6	9.2 ± 1.9	1.00	12.0	-26.115	3.46	2.7	27.0	1.62
	Dec.08	-	-	1.36	16.2	-25.88	3.67	3.8	27.8	1.47

Table 2: Results of the different environmental parameters analysed within sediments of both Stations A and N over the four sampling campaigns. Oxygen penetration depth (OPD), dissolved oxygen uptake (DOU) and analyses on particulate organic matter from the top half-centimetre of sediment: organic carbon (OC), carbon and nitrogen stable isotopic ratios ($\delta^{13}\text{C}_{\text{OC}}$ and $\delta^{15}\text{N}$), sum of lipids and total hydrolysable amino-acids (THAA) contents for dry-weight sediment (d.w.) and contribution to the OC (%OC).

3.3.4. Foraminiferal faunas

3.3.4.1. Station A (24 m)

In the >150 μm fauna, total foraminiferal standing stocks in the 0 to 5 cm sediment interval varied from 286 (September 2007) to 7767 ind./100 cm² (May 2008) (Fig. 4a). The species richness S varied from 8 (May 2008) to 19 (April 2007) (Fig. 4b). The Shannon index H ranged from 0.11–0.33 in May and December 2008 to 1.47–1.77 in April and September

2007 (Fig. 4c). The Evenness index followed the same trend with minimum values of 0.10–0.12 in May and December 2008 and maximal index in September 2007 (0.35) (Fig. 4d). The faunal composition was characterised by a strongly variable contribution of perforate and non-fossilising agglutinated species. In May 2008, non-fossilising agglutinated taxa accounted for 98.4% of the faunas, whereas in December 2008 perforates contributed to 97.1% of the total assemblage. During the other two sampling periods, perforate species represented from 34.1 to 62.6% of the total fauna, and non-fossilising agglutinated taxa from 26.7 to 65.0% of the total assemblage (Appendix A).

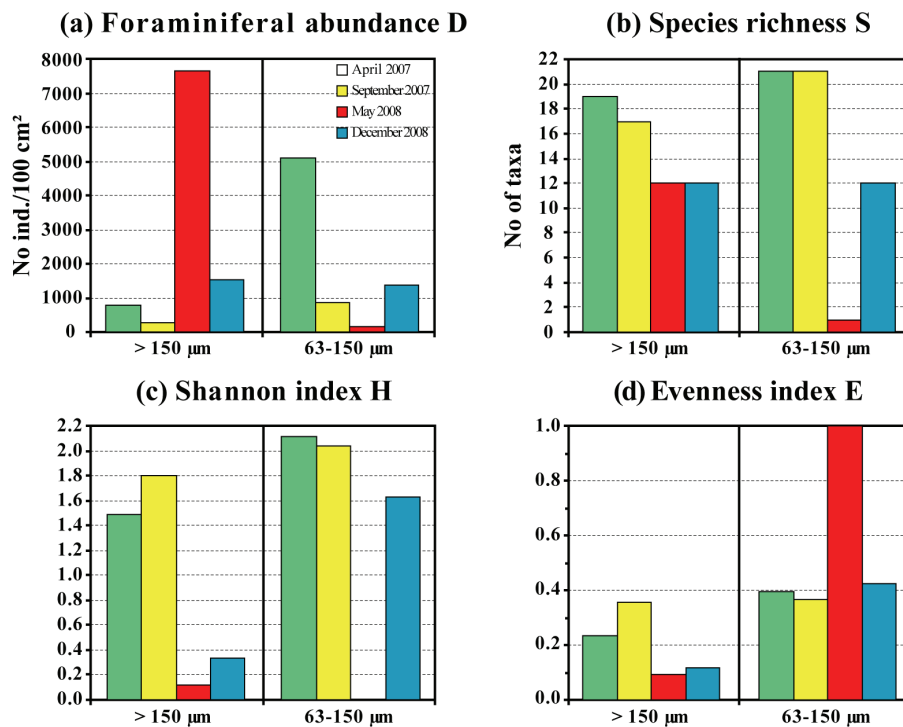
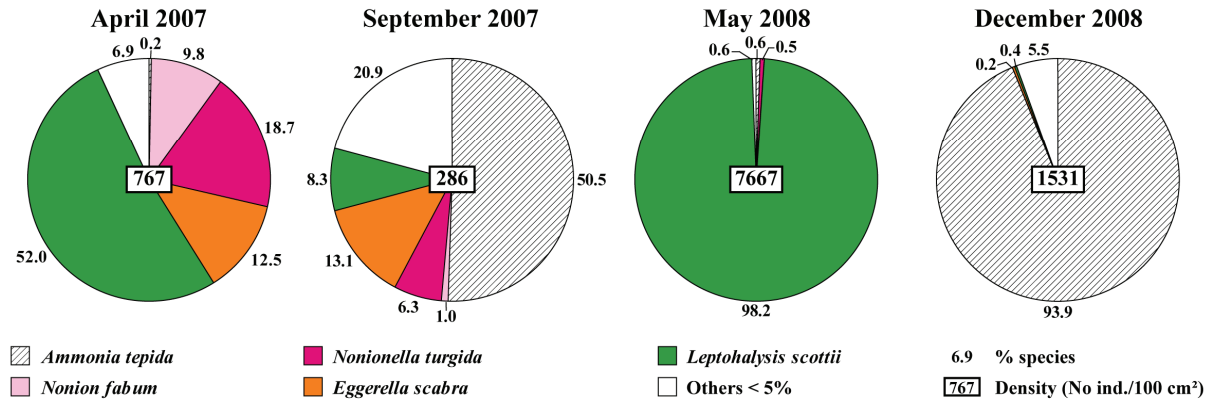


Figure 4: Foraminiferal abundance D standardised for a surface area of 100 cm^2 (core surface: 72 cm^2 ; sediment depth: 0.5 cm for the $63\text{--}150 \mu\text{m}$ size fraction and 5 cm for the $> 150 \mu\text{m}$ size fraction) (a), species richness S (b), Shannon index H (c) and Evenness index E (d) of the total living foraminiferal faunas in the $> 150 \mu\text{m}$ and $63\text{--}150 \mu\text{m}$ size fractions at Station A for the four sampling periods.

A total of 31 taxa were recognised at Station A, with 5 major species: *Ammonia tepida*, *Nonion fabum*, *Nonionella turgida*, *Eggerella scabra* and *Leptohalysis scottii* (Fig. 5a). In April 2007, the fauna was characterised by elevated percentages of *L. scottii* ($> 50\%$), *N. turgida* (18.7%), *E. scabra* (12.5%) and *N. fabum* (9.8%). In September 2007, the contribution of *L. scottii* was much lower (8.3%), whereas *A. tepida* accounted for 50.5% of the total fauna. In May 2008, the abundance of *L. scottii* reached $7538 \text{ ind./}100 \text{ cm}^2$, i.e.,

98.2% of the total assemblage. In December 2008, this species was absent whereas *A. tepida* strongly dominated the fauna, with 1438 ind./100 cm² or 93.9% of the total assemblage.

(a) > 150 µm size fraction



(b) 63-150 µm size fraction

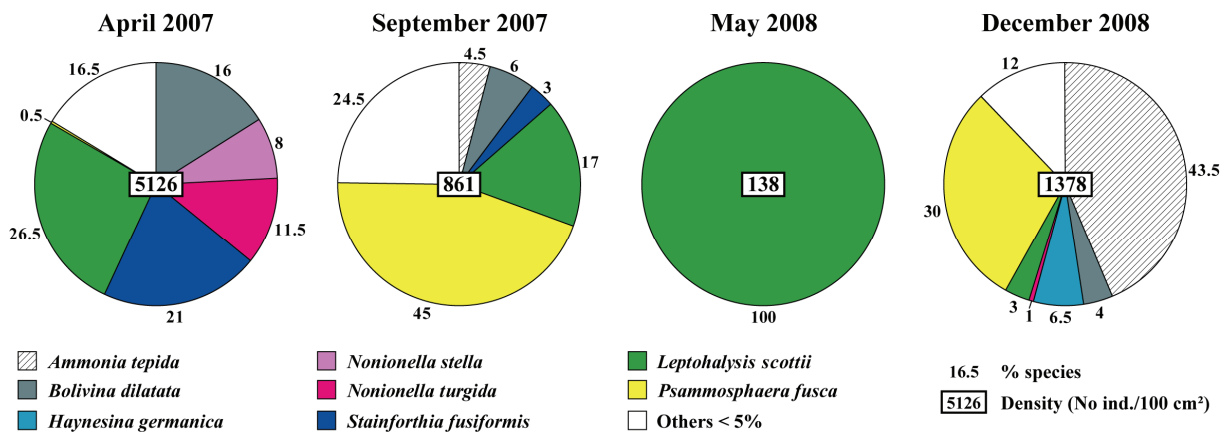


Figure 5: Relative abundances of the major species in the > 150 µm (a) and the 63–150 µm size fractions (b) at Station A for the four sampling periods.

In the 63–150 µm size fraction, the foraminiferal abundances in the top most 0.5 cm ranged from ~140 (May 2008) to ~5120 ind./100 cm² (April 2007) (Fig. 4a). The species richness S varied from 1 (May 2008) to 21 (April 2007) (Fig. 4b). A maximal Shannon index was recorded in April and September 2007, with values of 2.11 and 2.04, respectively. The lowest diversity was observed in May 2008 when only one species was identified (H = 0) (Fig. 4c). Except for the peculiar period of May 2008, the Evenness index was fairly constant with values ranging between 0.37 and 0.43 (Fig. 4d).

The foraminiferal faunal composition was quite variable (Appendix B). In May 2008, *Leptohalysis scottii*, a non-fossilising agglutinated taxon, accounted for 100% of the faunas. During the three other sampling periods, the relative contribution of perforate taxa ranged

from ~20 (September 2007) to 68.5% (April 2007), whereas non-fossilising agglutinated species accounted for ~27 to 68% of the total fauna. A total of 29 taxa were recognised, with 8 species presenting relative abundances > 5% in at least one core: *Ammonia tepida*, *Bolivina dilatata*, *Haynesina germanica*, *Nonionella stella*, *Nonionella turgida*, *Stainforthia fusiformis*, *Leptohalysis scottii* and *Psammosphaera fusca* (Fig. 5b). In April 2007, foraminiferal faunas were characterised by *L. scottii* (~26.5%), *S. fusiformis* (~21%) and *B. dilatata* (~16%). We noted the presence of *N. turgida* (~11.5%) and *N. stella* (~8%). In September 2007, *P. fusca* accounted for ~45% of total living faunas, and *L. scottii* was relatively abundant (~17%). In May 2008, foraminiferal faunas were totally dominated by *L. scottii* which composed 100% of the total living assemblage. In December 2008, *L. scottii* was low frequent (~3%), whereas *A. tepida* dominated the fauna (~43.5%). *P. fusca* was the second most abundant species with a relative abundance of ~30%. *H. germanica* accounted for ~6.5% of the total living fauna.

3.3.4.2. Station N (67 m)

In the >150 μm size fraction, foraminiferal abundances varied between 1092 (April 2007) and 2753 ind./100 cm^2 (May 2008) (Fig. 6a). The number of taxa varied between 37 (May 2008) and 59 (April 2007) (Fig. 6b). The Shannon and Evenness indices were quite similar, with values ranging from 2.13 to 2.63 and from 0.23 to 0.29, respectively (Fig. 6c–d). Non-fossilising agglutinated (32–64%) and perforate taxa (31–63%) dominated the assemblages (Appendix A).

A total of 72 species was recognised, with 9 major species: *Nonion fabum*, *Nonionella turgida*, *Rectuvigerina phlegeri*, *Valvulineria bradyana*, *Clavulina cylindrica*, *Cribrostomoides wiesneri*, *Eggerella scabra*, *Leptohalysis scottii* and *Nouria polymorphinoides* (Fig. 7a). In April 2007, agglutinated taxa were dominant (64.4%) with *E. scabra* (45.9%), *C. cylindrica* (7.4%) and *C. wiesneri* (5.1%). In September 2007, *C. cylindrica* (10.7%) and *E. scabra* (18.3%) were abundant, together with *V. bradyana* (21.2%), *N. fabum* (13.7%), *R. phlegeri* (7.1%) and *N. polymorphinoides* (5.6%). In May 2008, high percentages of *E. scabra* (20.0%), *V. bradyana* (19.2%), but also *N. turgida* (14.7%) were observed. In December 2008, high contributions of *N. polymorphinoides* (15.2%), *R. phlegeri* (11.1%) and *L. scottii* (5.3%) were noticed.

In the 63–150 μm fauna, foraminiferal standing stocks ranged between ~2580 (December 2008) and ~11640 ind./100 cm^2 May 2008) (Fig. 6a). The species richness S varied from 40 (April 2007, May and December 2008) to 59 (September 2007) (Fig. 6b). Comparable Shannon index H values were measured during the four periods, between 2.90

and 3.11 (Fig. 6c). The Evenness index showed quite similar values in April 2007, May and December 2008 (0.45–0.53), and a minimum of 0.38 recorded in September 2007 (Fig. 6d). Perforate (~67.5–74%) and non-fossilising agglutinated taxa (~18.5–28%) dominated the foraminiferal faunas (Appendix B).

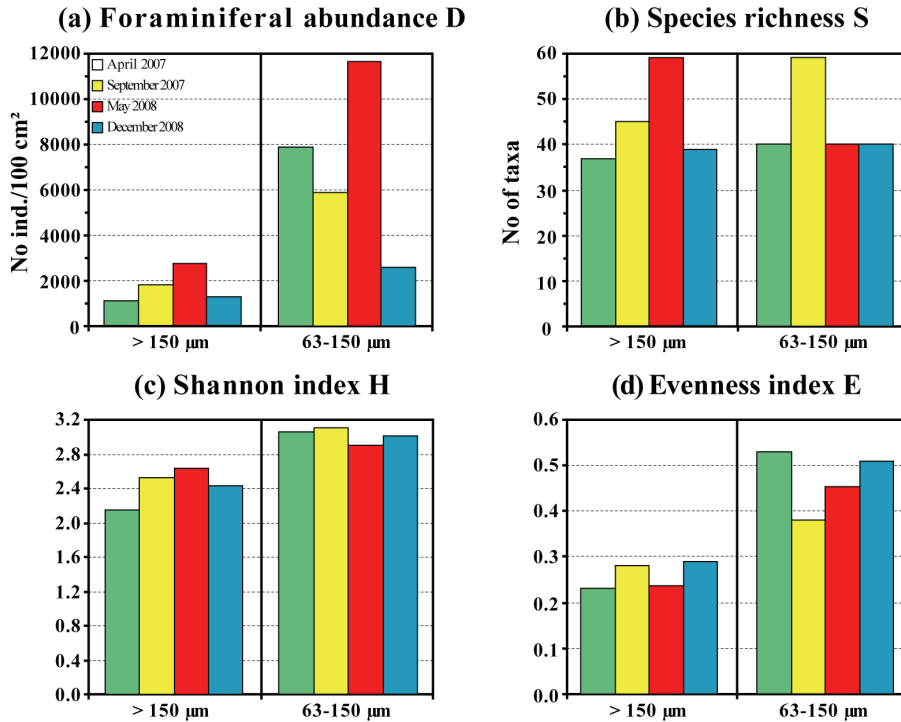
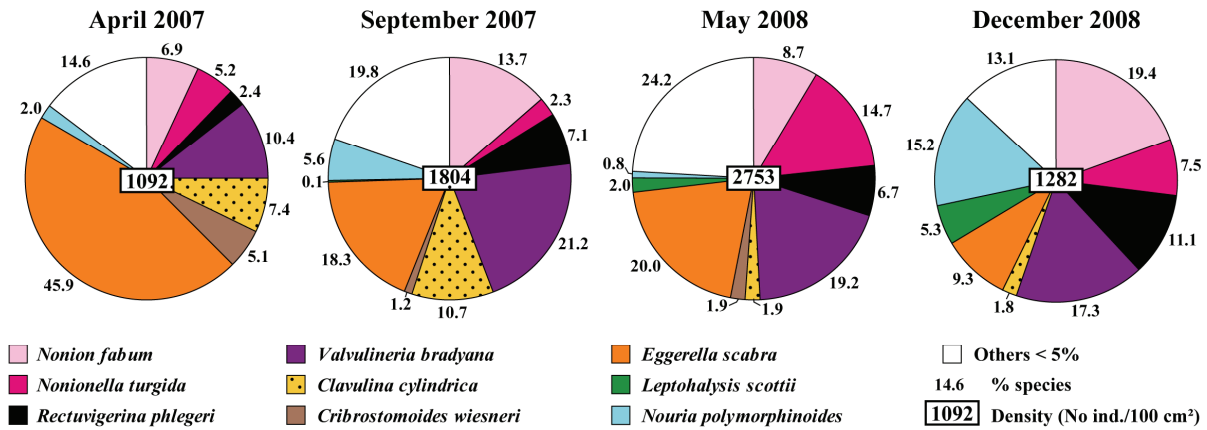


Figure 6: Foraminiferal abundance D standardised for a surface area of 100 cm^2 (core surface: 72 cm^2 ; sediment depth: 0.5 cm for the $63\text{--}150 \mu\text{m}$ size fraction and 5 cm for the $> 150 \mu\text{m}$ size fraction) (a), species richness S (b), Shannon index H (c) and Evenness index E (d) of the total living foraminiferal faunas in the $> 150 \mu\text{m}$ and $63\text{--}150 \mu\text{m}$ size fractions at Station N for the four sampling periods.

A total of 57 taxa were recognised at this station, with 10 species accounting for more than 5% of total living faunas in at least one core: *Bolivina dilatata*, *Bolivina seminuda*, *Bolivina spathulata*, *Hopkinsina atlantica*, *Nonionella iridea*, *Nonionella turgida*, *Rectuvigerina phlegeri*, *Textularia porrecta*, *Eggerella scabra* and *Leptohalysis scottii* (Fig. 7b). In April 2007, foraminiferal faunas were characterised by a high contribution of *B. dilatata* (~21%), *N. turgida* (~7.5%) and *H. atlantica* (~7%). In September 2007, *H. atlantica* (~8.5%) and *N. turgida* (~6.5%) were associated with *B. spathulata* (~8%), *R. phlegeri* (~8%) and *E. scabra* (~13.5%). In May 2008, *N. turgida* (~16%) and *L. scottii* (~12%) were the most abundant species, together with *N. iridea* (~11.5%) and *T. porrecta* (~7%). Finally, in December 2008, high abundances of *B. seminuda* (~5.5%) and *T. porrecta* (~12%) were recorded.

(a) > 150 µm size fraction



(b) 63-150 µm size fraction

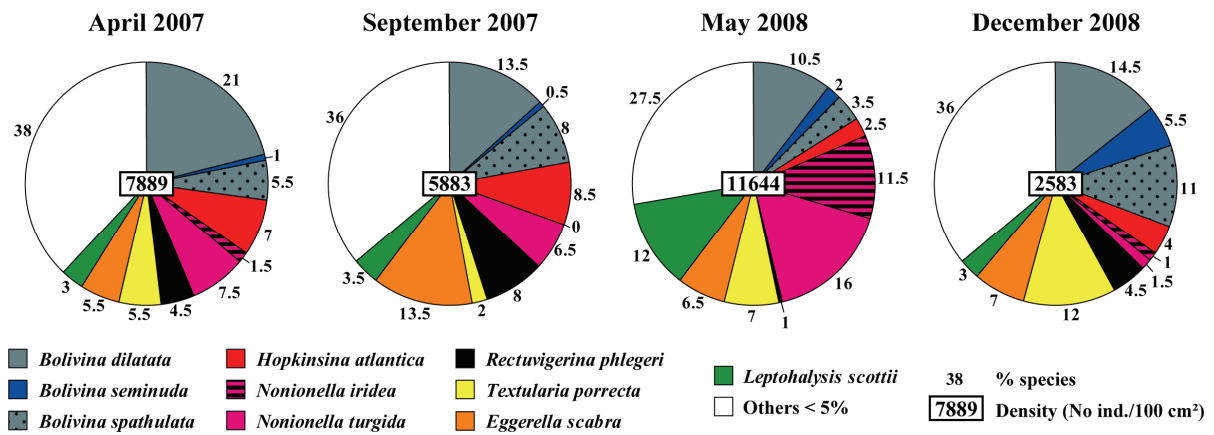


Figure 7: Relative abundances of the major species in the > 150 µm (a) and the 63–150 µm size fractions (b) at Station N for the four sampling periods.

3.4. DISCUSSION

3.4.1. Environmental setting

The overall environmental dataset shows contrasted conditions for the four sampling periods and between the two investigated stations. In all investigated periods, the sediment at Station A (24 m depth) presented a high content in OC, lipids, amino acids and Chl-*a* in comparison with the deeper Station N (67 m depth). This highlighted a concentration of organic-rich deposits close to the Rhône River mouth, in agreement with observations presented in previous studies (Cathalot et al., 2009; Lansard et al., 2009; Goineau et al., In Press – see Chapter 1 in this thesis).

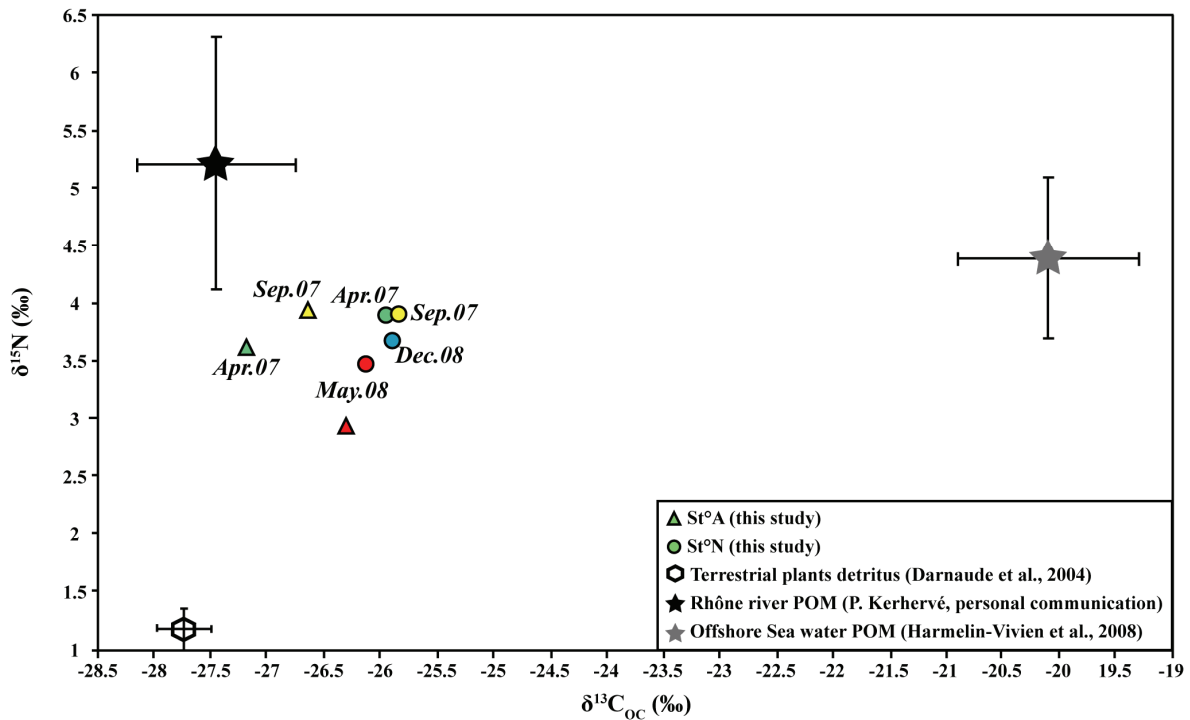


Figure 8: Stable isotopic composition of the organic matter ($\delta^{13}C_{OC}$ vs $\delta^{15}N$) from the first half-centimetre of sediment. The composition of three possible OC sources (Terrestrial plant detritus, Rhône River POM, and offshore seawater POM) are also plotted to illustrate the relative influence of each source.

In figure 8, $\delta^{13}C_{OC}$ has been plotted versus $\delta^{15}N$ for both stations and all sampling periods, together with isotopic signatures of different potential particulate organic matter (POM) sources in our study area (Darnaude et al., 2004; Harmelin-Vivien et al., 2008; P. Kerhervé, personal communication). Both Stations A and N plot between Rhône River and Offshore sea water POM, but much closer to the Rhône source (low $\delta^{13}C_{OC}$). However, important isotopic variations were recorded at Station A, with measures plotting either close to “Rhône POM” or to “terrestrial detritus” end members. In April and September 2007, both sampled during low Rhône discharge conditions ($Q_{mean} < 1000 \text{ m}^3 \cdot \text{s}^{-1}$; $SM_{mean} < 15 \text{ mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$), sedimentary organic matter (OM) measured at Station A plotted close to the Rhône POM end-member, possibly with a contribution of riverine phytoplankton. Therefore, the maximal sediment Chl-*a* contents measured during these sampling periods suggest a major contribution of continental OM and riverine phytoplankton. On the contrary, May and December 2008, sampled after and during a flood ($Q_{mean} > 1400 \text{ m}^3 \cdot \text{s}^{-1}$; $SM_{mean} = 17 \text{ to } 115 \text{ mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$), showed a stronger contribution of terrestrial plant detritus. According to Cathalot et al. (2009) and P. Kerhervé (personal communication), the slightly higher $\delta^{13}C_{OC}$ values ($> -26.5\text{‰}$) recorded after the floods also pointed out the contribution of soil-derived organic material brought by the river. Station N also received an organic matter with a strong contribution of the Rhône-

derived organic detritus. The isotopic signatures were comparable for the four sampling periods, suggesting a weaker impact of fluctuating Rhône River discharge compared to Station A.

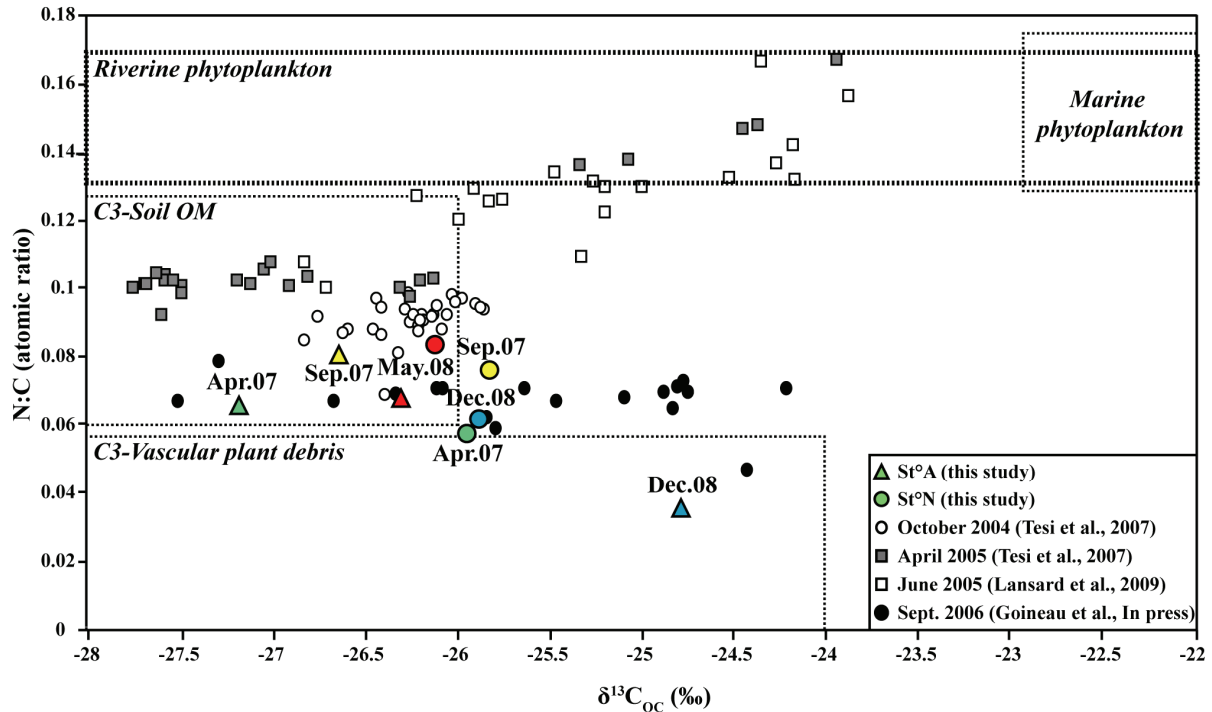


Figure 9: Stable isotopic composition of the organic carbon ($\delta^{13}C_{OM}$) vs N:C atomic ratio for the first half-centimetre of sediment measured at Stations A and N during the four sampling periods. The four other databases represented were collected in September 2006 (Goineau et al., In Press – see Chapter 1 in this thesis), October 2004 and April 2005 (Tesi et al., 2007), and June 2005 (Lansard et al., 2009). The composition of four possible OC sources (C_3 -vascular plant detritus, C_3 -soil OM, marine and riverine phytoplankton detritus) is also plotted to illustrate the relative influence of each source. The N:C ratio was used rather than the classical C:N ratio because the former are more robust statistically and behave linearly in a mixing model (Gordon and Goñi, 2003).

$\delta^{13}C_{OC}$ versus N:C atomic ratio is presented on figure 9 together with complementary measurements performed in the Rhône prodelta in October 2004, April 2005 (23–68 m depth, ~1 to 8 km off the river mouth; Tesi et al., 2007), June 2005 (20–98 m depth, ~2 to 16 km off the mouth; Lansard et al., 2009) and September 2006 (18–100 m depth, ~1 to 22 km off the mouth; Goineau et al., In Press – see Chapter 1). The $\delta^{13}C_{OC}$ and N:C ratios of sedimentary organic material collected in April and June 2005 were indicative of a clear marine contribution. Stations A and N were both characterised by a mixture of soil and plant-derived OM in all four sampling periods, and plotted close to the samples collected in October 2004 and September 2006 conditions. Consequently, no clear marine influence was recorded at our

two stations, in none of the four sampling periods. It appears that variations in Chl-*a* contents between sampling periods were mainly due to changes in the Rhône River regime (high/low discharge) and riverine phytoplankton dynamics which appears to bloom at the same time as marine phytoplankton (Harmelin-Vivien et al., 2008). At both stations, the accumulation of labile (i.e. bioavailable) Rhône-derived material at the river mouth and in the proximal prodelta led to an important sediment oxygen consumption, due to organic carbon mineralisation (high DOU, shallow OPD), during the four investigated periods (Table 1).

3.4.2. Temporal dynamics of benthic foraminiferal faunas

Small-scale spatial variability of benthic foraminiferal faunas have been investigated through the study of four replicate cores sampled at the same Stations A and N (Goineau et al., Submitted– see Chapter 2 in this thesis). In that study, the authors have shown that absolute foraminiferal abundances (i.e., D) may present significant differences between replicate cores at a same station. However, variations of the major taxa percentages were not significantly different. Since our temporal survey of benthic foraminiferal faunas was performed on only one core per investigated site and per sampling period, the following discussion is based on percentage data of the major species.

3.4.2.1. Station A

The foraminiferal faunas observed at Station A, dominated by *Ammonia tepida*, *Bolivina dilatata*, *Eggerella scabra*, *Haynesina germanica*, *Leptohalysis scottii*, *Nonion fabum*, *Nonionella stella*, *Nonionella turgida*, *Psammosphaera fusca* and *Stainforthia fusiformis*, are typical of river-dominated shelves (e.g., Jorissen, 1987; Van der Zwaan and Jorissen, 1991; Barmawidjaja et al., 1992; Jorissen et al., 1992; Donnici and Serandrei Barbero, 2002; Diz et al., 2006; Diz and Francés, 2008; Frezza and Carboni, 2009), and especially of the Rhône prodelta (Mojtahid et al., 2009; Goineau et al., In Press– see Chapter 1 in this thesis).

In April 2007, sampling is performed during a low Rhône discharge and spring bloom conditions in the Gulf of Lions (SeaWifs images: “Ocean Colour” website, <http://marine.jrc.ec.europa.eu/>). The very rich foraminiferal faunas are dominated by *Bolivina dilatata*, *Nonionella stella*, *Nonionella turgida*, *Stainforthia fusiformis* and *Leptohalysis scottii* in the 63–150 µm size fraction, and *Nonion fabum*, *Nonionella turgida*, *Eggerella scabra* and *Leptohalysis scottii* in the > 150 µm size fraction (Fig. 5). Both size fractions

present well diversified faunas with a maximal biodiversity (Shannon index) and standing stocks in the 63–150 μm size fraction (Fig. 4). In the Rhône prodelta, *N. fabum* seems to be adapted to a wide range of environments, thriving preferentially in sediments enriched in both continental and more marine OM under the river plume (Mojtahid et al., 2009; Goineau et al., In Press— see Chapter 1). *B. dilatata*, *N. turgida* and *E. scabra* are abundant in a restricted area close to the Rhône River mouth, receiving important amounts of continental OM (Mojtahid et al., 2009; Goineau et al., In Press— see Chapter 1). However, these species would also be able to feed on fresh phytodetritus inputs, especially diatoms (Hohenegger et al., 1993; Gustafsson and Nordberg, 2001; Diz et al., 2006; Diz and Francés, 2008; Duchemin et al., 2008; Hyams-Kaphzan et al., 2009). *B. dilatata* is known to proliferate, due to an opportunistic behaviour after fresh phytodetritus inputs in river-influenced environments (Barmawidjaja et al., 1992; Jorissen et al., 1992; Duchemin et al., 2007; Duchemin et al., 2008). Therefore, its occurrence in April 2007 could be related to a recent deposition of fresh riverine phytoplankton. This hypothesis is corroborated by the occurrence of *N. stella*, *N. turgida* and *S. fusiformis* which have also been reported in the Ría de Vigo (Spain) and in the Bay of Biscay responding to fresh OM inputs by enhanced reproduction (Gustafsson and Nordberg, 2001; Diz et al., 2006; Diz and Francés, 2008). At Station A, we observe specimens of *N. turgida* and *L. scottii* in both size fractions, showing the presence of both adult and juvenile forms, probably as a result of reproduction shortly before sampling. *S. fusiformis* has been observed close to the Rhône River mouth during late spring bloom conditions (June 2005; Mojtahid et al., 2009). It appears therefore that the above-mentioned group of taxa constitutes a highly reactive and diverse fauna responding to the eutrophic conditions in the vicinity of the Rhône River mouth, following riverine phytoplankton blooms.

In September 2007, no major flood had occurred for the last 6 months, and the last significant phytoplankton bloom ended more than 3 months before sampling. The much poorer foraminiferal fauna is mainly composed of *B. dilatata*, *L. scottii* and *Psammosphaera fusca* in the 63–150 μm size fraction, and *Ammonia tepida*, *N. turgida*, *E. scabra* and *L. scottii* in the larger size fraction (Fig. 5). *A. tepida* is a very common taxon in shallow open marine environments, especially at the vicinity of river mouths (e.g., Jorissen, 1987, 1988; Donnici and Serandrei Barbero, 2002; Rossi and Vaiani, 2008; Frezza and Carboni, 2009). *P. fusca* is a monothalamous agglutinated taxon observed from deep-sea (Kaminski, 1985; Jones, 1988; Kaminski et al., 1995; Harloff and Mackensen, 1997) to shelf environments (Canadian fjord, Antarctic coast, Laptev Sea; Lukina, 2001; Gaździcki and Majewski, 2003;

Vázquez Riveiros and Patterson, 2007). *P. fusca* has been reported as a pioneer opportunistic species in high energy environment (Kaminski, 1985; Kaminski et al., 1995). Thus, the dominance (~50%) of *P. fusca* in the 63–150 µm sized-fauna could suggest a possible disturbance of the benthic environment by moderate to strong currents. In parallel, the association of *B. dilatata*, *N. turgida*, *E. scabra* and *L. scottii* contributing to diverse ($H > 1.8$) and relatively equilibrated faunas ($E \approx 0.35$) could be linked to the important amounts of labile organic compounds (lipids, THAA, Chl-*a*; Table 2) measured in the sediment. To summarise, the low-abundant but well-diversified fauna observed in September 2007 suggests an environment which is still characterised by high amounts of still bio-available organic matter, possibly influenced by more or less high energy conditions.

Sampling of Station A in May 2008 took place during very peculiar conditions. A major Rhône River flood characterised by very high SM load (until $867 \text{ mg.l}^{-1}.\text{d}^{-1}$; IRSN) started two days before sampling. A 4 cm-thick flood deposit constituted by very light liquid mud (mean particle diameter: 6.74 µm ; Cathalot et al., 2009) was observed at the surface of all cores sampled at this station. The huge accumulation rate induced by the flood led to a strong dilution of OM and much lower OC, labile organic compounds and Chl-*a* contents (Fig. 3). These extreme conditions were probably responsible for the almost monospecific foraminiferal faunas, constituted by almost 100% of *L. scottii* in both size fractions (Fig. 5). In the $> 150 \text{ µm}$ size fraction, *L. scottii* reached huge abundances of $\sim 7500 \text{ ind./100 cm}^2$, and the densities increased with sediment depth (Fig. 6a). This virtually monospecific *L. scottii* assemblage can be explained in two different ways: (1) the specimens present at the site or in surrounding areas before the flood responded to the disturbance induced by the flood deposit by an extremely fast reproduction (strongly opportunistic behaviour); (2) individuals were transported together with terrigenous material from the Rhône River during the flood (allochthonous origin). The first scenario implies that massive reproduction had to take place in less than 2 days, the time-lapse between the beginning of the flood and sediment sampling. In culture experiments performed on sediments sampled in the northern Adriatic Sea near the Po outlet (32 m water depth), Ernst et al. (2002) showed that *L. scottii* could enlarge its population by 80% in the three weeks following a simulated physical disturbance consisting in a gentle mixing of the sediment. It seems therefore unlikely that more than 7000 individuals/100 cm², most of them adults or pre-adults found in the $> 150\text{µm}$ size fraction, were produced in only 2 days, in an environment impoverished in OM. The second assumption of an allochthonous origin of *L. scottii* would imply a massive transport from the continental part of the Rhône River to the proximal prodelta. *L. scottii* has earlier been

reported from estuarine environments living in turbid and high-energy waters (Scott et al., 2005; Diz and Francés, 2008). Unfortunately, we have no data on the foraminiferal community living upstream from the Rhône River mouth. However, the hypothesis of an allochthonous origin of the thousands of individuals of *L. scottii* seems most probable. Whatever the way this taxon arrived at the sampling site, it is evident that it is a very early recoloniser of a newly deposited sediment surface. Such a behaviour has earlier been described in the Oslofjord where individuals of *L. scottii* rapidly immigrated from neighbouring environments to massively colonise newly deposited sediments.

In December 2008, a major flood occurred 3 weeks before sampling, responsible for a new terrigenous deposit close to the river mouth (Cathalot et al., 2009). At Station A, we observe an approximately 3 cm-thick surficial deposit of silty sediments (R. Buscail, personal communication). Foraminiferal faunas are essentially composed by *A. tepida*, *Haynesina germanica* and *P. fusca* (Fig. 5). The low diversity ($H < 0.4$) but high abundances observed in the $> 150 \mu\text{m}$ size fraction went together with a strong dominance ($E \approx 0.1$) of *A. tepida* in both absolute ($\sim 1400 \text{ ind./100 cm}^2$) and relative abundances ($\sim 94\%$). The associated species *H. germanica* is a typical estuarine species, thriving in intertidal and subtidal areas (e.g., Alve and Murray, 1999; Debenay et al., 2000; Diz and Francés, 2008). It appears therefore that the association of *A. tepida*, *H. germanica* and *P. fusca* is indicative of a very high riverine influence. The flood recorded 3 weeks before (Q until $\sim 4800 \text{ m}^3 \cdot \text{s}^{-1}$; Compagnie Nationale du Rhône) may have significantly disturbed the benthic environment by the deposit of organic-rich terrigenous material close to the river mouth (OC content = 6% d.w.; Cathalot et al., 2009). Since *H. germanica* is typical of brackish water environments, it can be supposed that juvenile specimens of this taxon have been transported by the flood from habitats in the inner part of the Rhône River channel to our study site. At a slightly later stage, *A. tepida* and *P. fusca* may have colonised the newly deposited organic-rich flood deposit, profiting from their high tolerance for high-energy conditions.

To synthesise, foraminiferal faunas observed at this shallow Station A were obviously influenced by the Rhône River in some way during all four periods (Fig. 10). Sedimentary disturbance appears to be periodically disturbing the benthic environment. Stable environmental conditions, without major sediment input, which prevailed in April and September 2007, allowed the establishment of diverse and equilibrated faunas.

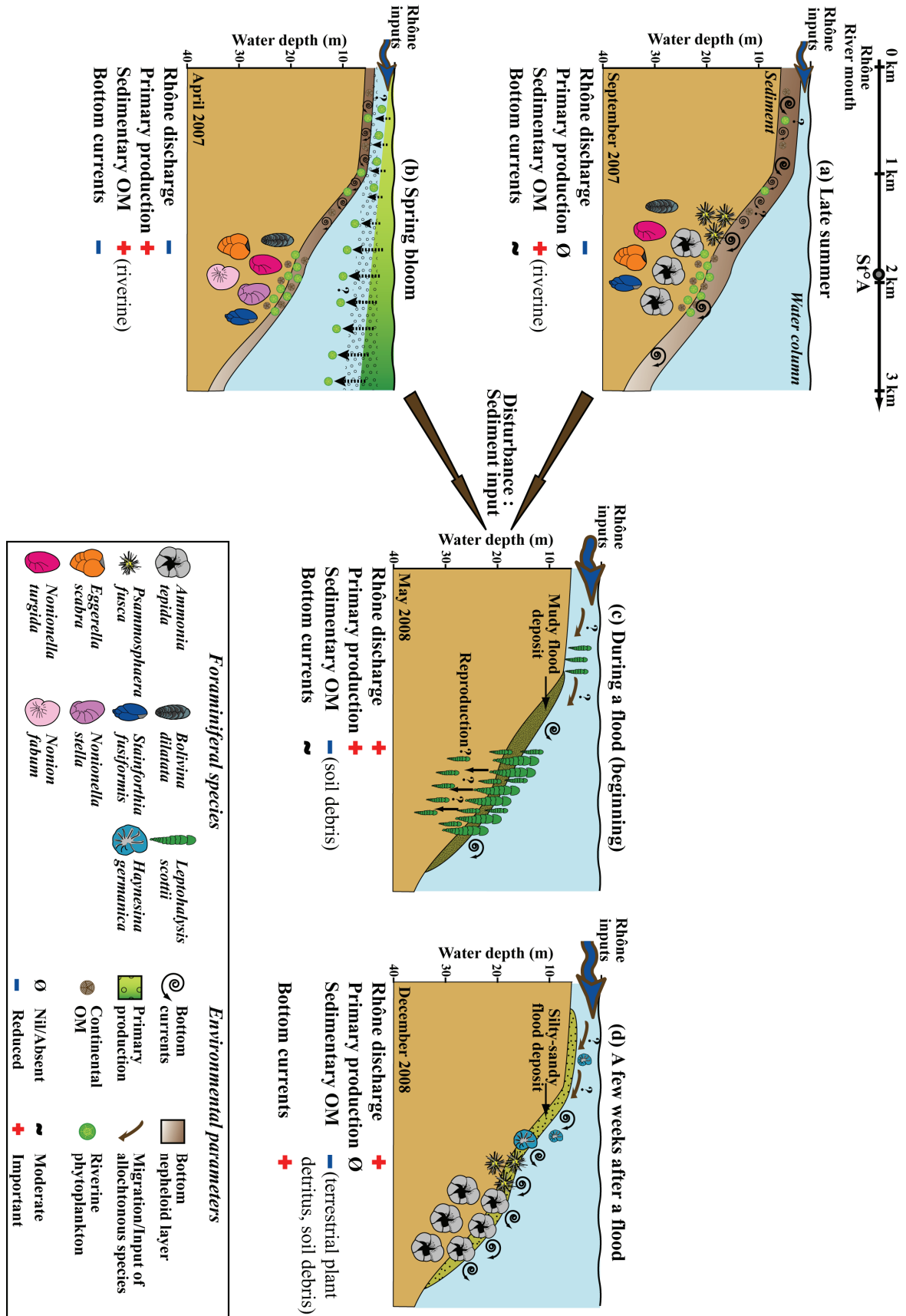


Figure 10: Synthetic picture of the processes influencing the foraminiferal faunal composition during the four investigated periods at the shallowest Station A.

The availability of fresh OM and the hydrodynamic conditions above the sea floor were the main factors influencing foraminiferal faunal composition. Conversely, highly unstable conditions with massive sediment input characterise the environment in May and December 2008. The particular conditions led to the presence of faunas typical for the early stages of ecosystem colonisation. In these faunas, the foraminiferal composition appears to depend on the time lapse since the last flood deposit, and on the OM content of the recently deposited sediments. A few days after such a massive sediment input (May 2008), an extremely rich monospecific assemblage of pioneer species already inhabited the newly deposited flood layer impoverished in labile OM. Conversely, an input of OM enriched sediments in December 2008 led to the observation, a few weeks later, of a more advanced colonisation stage. In both cases, foraminiferal faunas responded with an opportunistic strategy to the creation of an azoic sedimentary environment (*Leptohalysis scottii*, May 2008) and/or to the high amounts of OM supplied by the river flood (*Ammonia tepida*, December 2008).

3.4.2.2. Station N

At Station N, environmental conditions are much less contrasted than at the shallower Station A (see above § 3.4.2.1.). Foraminiferal faunas of both size fractions were diverse (Shannon index $H > 2$) and relatively equilibrated ($E > 0.2$) during the four investigated periods, depicting the absence of opportunistic behaviour and/or recolonisation phenomena. Four taxa were abundant in all assemblages: *Bolivina dilatata*, *Eggerella scabra*, *Nonion fabum* and *Valvulineria bradyana*. These four taxa are common in the Rhône prodeltaic area, present in sediments close to the Rhône River mouth with important continental OM supplies (Station A, see above), but also at sites more offshore, under the Rhône River plume (Mojtahid et al., 2009; Goineau et al., In Press— see Chapter 1 in this thesis). *B. dilatata* is described as an ubiquitous taxon adapted to a wide range of environmental conditions in the Ría de Vigo (Spain) and in the Bay of Biscay (Diz and Francés, 2008; Duchemin et al., 2008), also able to respond to fresh phytodetritus input (Barmawidjaja et al., 1992; Jorissen et al., 1992; Duchemin et al., 2007; Duchemin et al., 2008).

As for Station A, sampling in April 2007 took place during the early spring bloom and under low Rhône discharge conditions. At Station N, these conditions led to relatively high OC (1.42% d.w.) and Chl-*a* contents in surficial sediments ($2.57 \mu\text{g}\cdot\text{g}^{-1}$; Table 2). The small-sized (63–150 μm) benthic foraminiferal fauna of the topmost 0.5 cm was very abundant and highly diverse compared to the $> 150 \mu\text{m}$ size fraction of the upper 5 cm (Fig. 6). These faunas were characterised by high relative abundances of *Clavulina cylindrica*,

Cribrostomoides wiesneri and *Hopkinsina atlantica*. As suggested for Station A at the same sampling period, the very high contribution of *Eggerella scabra* in the > 150 µm sized-fauna (> 40%) would be due to its ability to respond to fresh phytodetritus inputs. *C. cylindrica* was considered typical of eutrophic conditions on the continental shelf of the Bay of Biscay (Fontanier et al., 2002). *H. atlantica* has been described in river-influenced shelves (Barmawidjaja et al., 1992; Jorissen et al., 1992; Diz and Francés, 2008; Mojtahid et al., 2009), where it was usually considered as an opportunistic taxon responding to fresh OM input (Ernst et al., 2002; Duijnsteet et al., 2005). When considering the moderate enrichment in Chl-*a* of the top half centimetre of sediment at this period, we assume that this association of foraminiferal species would benefit from an input of fresh phytodetritus, such as has been suggested for the shallower Station A at the same period.

In September 2007, high percentages of *Bolivina spathulata*, *C. cylindrica*, *H. atlantica*, *Rectuvigerina phlegeri*, and especially of *Nouria polymorphinoides* were noticed (Fig. 7). Goineau et al. (In Press— see Chapter 1) reported *N. polymorphinoides* during another sampling period (September 2006) in coarse sediments from the coast west of the Rhône River mouth which was submitted to strong bottom currents. At Station A, the foraminiferal faunas observed in September 2007 suggested possibly high energy conditions. Therefore, the contribution of *N. polymorphinoides* in September 2007 could be indicative of a non-negligible Rhône River influence, with also the possible action of bottom currents as at Station A.

In May 2008, Station N was sampled 3 days after the beginning of a major flood carrying important amounts of organic and inorganic terrestrial material close to the river mouth. However, contrary to Station A, no flood deposit was observed at the surface of any of the sampled cores. Consequently, we assumed that Station N had not been impacted by the deposits of terrigenous material. Therefore, just as in April 2007, the late spring bloom conditions prevailing in the Gulf of Lions at the time of sampling (SeaWifs images) would have been the main controlling parameter at the study site. In May 2008, the foraminiferal faunas were characterised by a high contribution of *Nonionella iridea*, *Nonionella turgida* and *Leptohalysis scottii* in the 63–150 µm size fraction, and of *N. turgida* in the large-sized fauna (Fig. 7). Gustafsson and Nordberg (2001) demonstrated that *N. turgida* could reproduce and grow from juvenile to adult form in less than 1 month after a fresh OM deposit. In the present study, high abundances of *N. turgida* in both size fractions (~15%), together with the occurrence of *N. iridea*, which was rare to totally absent during the three other seasons, suggest the recent input of fresh OM at the study site (Gooday, 1986; Mackensen et al., 1990;

Gooday and Hughes, 2002; Duchemin et al., 2007; Duchemin et al., 2008). At the same Station N, Goineau et al. (Submitted – see Chapter 2 in this thesis) showed that local accumulation of food particles in decimetric depressions could favour the growth of the most reactive and specialised taxa (e.g., *N. turgida*) by enhanced reproduction and growth. In May 2008, surficial sediments were enriched in fresher OM (C:N = 12, labile OM = 27.0% OC; Table 2) than in April 2007 under similar spring bloom conditions (C:N = 17.4, labile OM = 19.2% OC; Table 2).

In December 2008, sediment samples were recovered 3 weeks after a major Rhône flood. The high amounts of fresh water and organic-rich suspended material ($Q > 2000 \text{ m}^3 \cdot \text{s}^{-1}$ and $\text{SM}_{\text{mean}} \sim 172 \text{ mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$ during 12 days) carried to the Gulf of Lions during this flood would explain the high contents in labile OM measured in the surficial sediments of Station N (Table 2). In the foraminiferal faunas, *B. spathulata*, *R. phlegeri* and *N. polymorphinoides* were abundant, but a high contribution of *Bolivina seminuda* and *Textularia porrecta* was also observed in the 63–150 μm size fraction (Fig. 7). The occurrence of *N. polymorphinoides*, just as in September 2007, would plead for a noticeable riverine influence as reported at the shallower Station A during the same period (see above § 3.4.2.1.). In the Mediterranean Sea, the association of *B. seminuda* and *B. spathulata* has frequently been reported in meso- to eutrophic environments (e.g., Barmawidjaja et al., 1992; Jorissen et al., 1995; De Rijk et al., 2000; Schmiedl et al., 2000; Duijnste, 2001). In the Bay of Biscay, this association of bolivinid species characterised spring bloom conditions after phytodetritus input (Fontanier et al., 2003; Langezaal et al., 2006). Therefore, the occurrence of these species is coherent with the high labile OM content of the sediment resulting from a recent input of riverine organic material deposited by a major Rhône River flood.

To summarise, slight variations noticed in the foraminiferal faunas of Station N would be linked either to fresh OM supplies from sea surface primary production and/or to the Rhône River regime. In April 2007 and May 2008, spring bloom conditions allowed the growth of species able to feed on fresh phytodetritus (e.g., *Clavulina cylindrica*, *Hopkinsina atlantica*, *Nonionella iridea*, *Nonionella turgida*). In September 2007 and December 2008, the establishment of the taxon *Nouria polymorphinoides* was indicative of a higher riverine influence. The additional input of riverine organic matter after a major flood in December 2008 was beneficial for taxa visibly able to thrive in environments submitted to a noticeable riverine influence (e.g., *Bolivina seminuda*, *Bolivina spathulata*, *Textularia porrecta*). Despite these putative environmental forcing, the recurrent occurrence of the four same taxa (i.e.,

Bolivina dilatata, *Eggerella scabra*, *Nonion fabum*, *Valvulineria bradyana*) in relatively high abundances at any period in diverse and equilibrated faunas depicts the relatively stable state of the environment at this site.

3.5. CONCLUSIONS

Sampling sediments from the Rhône prodelta in April 2007, September 2007, May 2008 and December 2008 permitted us to observe foraminiferal faunas under a wide range of environmental conditions. The location of the shallowest Station A in the close vicinity of the Rhône River mouth led to very contrasted environmental conditions between the four sampling periods, permitting us to observe significantly different foraminiferal faunas. Major disturbance of the benthic environment induced by massive sediment deposits at this shallow site after Rhône River floods allowed the development of opportunistic species. Two days after a major flood event, thousands of individuals of *Leptohalysis scottii* were observed in a newly deposited flood sediment, constituting an assemblage of very early recolonisers. A few weeks after another major flood (December 2008), typical species of river-dominated shelves (*Ammonia tepida*) and high-energy environments (*Psammospaera fusca*) benefited from the high amounts of continental organic matter supplied by the flood. More stable conditions (i.e., no sediment deposit) allowed the growth of diverse and quite equilibrated faunas. Under the eutrophic conditions resulting from the spring phytoplankton bloom (April 2007), abundant and diverse fauna were composed of species feeding on fresh phytodetritus (e.g., *Bolivina dilatata*, *Nonionella stella*, *Stainforthia fusiformis*). Also in September 2007, diverse faunas were observed despite the oligotrophic conditions in surface water and/or the assumed high energy conditions prevailing above the sea floor. At Station N, variations in environmental conditions as well as faunal composition are much less important than at Station A. At this site farther off the river mouth, *Clavulina cylindrica*, *Hopkinsina atlantica*, *Nonionella iridea* and *Nonionella turgida* are indicative of fresh OM input during eutrophic spring bloom conditions (April 2007, May 2008). On the contrary, the occurrence of *Nouria polymorphinoides* (September 2007, December 2008) was indicative of a higher riverine influence (i.e., high river discharge and/or oligotrophic conditions).

This study showed that foraminiferal faunas were able to respond extremely quickly (days to weeks) to strong variations in environmental conditions, especially close to the river mouth (Station A). This response was noticeable but significantly reduced ~5 km off the mouth

(Station N), probably due to a reduced impact of riverine input out of the proximal prodeltaic area.

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APPENDICES

Appendix A

Total benthic foraminiferal counts on the > 150 µm size fraction. For each species in each core, “r.d.” and “D” correspond to non-standardised (raw data) and standardised (for a surface area of 100 cm²) total absolute abundances, respectively, and “%” indicates relative abundance. Grey boxes indicate percentages and species > 5%.

Appendix B

Total benthic foraminiferal counts on the 63–150 µm size fraction. For each species in each core, “r.d.” and “D” correspond to non-standardised (raw data) and standardised (for a surface area of 100 cm²) total absolute abundances, respectively, and “%” indicates relative abundance. Grey boxes indicate percentages and species > 5%.

Appendix C

Taxonomic reference list for major taxa.

Appendix A

Station Sampling period Taxa	Station A											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
Perforates												
<i>Ammonia beccarii</i> f. <i>beccarii</i>	3	4	0.5	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia parkinsoniana</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Ammonia tepida</i>	1	1	0.2	104	144	50.5	32	44	0.6	1035	1438	93.9
<i>Amphicoryna scalaris</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>	1	1	0.2	–	–	–	5	7	0.1	1	1	0.1
<i>Bolivina striatula</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Bolivina subaenariensis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Buccella granulata</i>	–	–	–	1	1	0.5	–	–	–	–	–	–
<i>Bulimina aculeata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>	11	15	2.0	6	8	2.9	4	6	0.1	–	–	–
<i>Bulimina gibba</i>	–	–	–	1	1	0.5	–	–	–	–	–	–
<i>Bulimina marginata</i>	–	–	–	1	1	0.5	–	–	–	2	3	0.2
<i>Cancris oriculus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina carinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina crassa</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina filiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>	1	1	0.2	–	–	–	–	–	–	–	–	–
<i>Elphidium crispum</i>	–	–	–	1	1	0.5	–	–	–	–	–	–
<i>Elphidium poeyanum</i> f. <i>decipiens</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Epistominella vitrea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fursenkoina</i> sp.	3	4	0.5	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Haynesina</i> spp.	–	–	–	–	–	–	–	–	–	30	42	2.7
<i>Hopkinsina atlantica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina atlantica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina peregrina</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonion fabum</i>	54	75	9.8	2	3	1.0	5	7	0.1	–	–	–
<i>Nonionella iridea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella stella</i>	9	13	1.6	–	–	–	11	15	0.2	–	–	–
<i>Nonionella turgida</i>	103	143	18.7	13	18	6.3	28	39	0.5	–	–	–
<i>Pseudoepionides falsobeccarii</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rectuvigerina phlegeri</i>	1	1	0.2	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthiaconcava</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Valvulineria bradyana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Virgullinella fragilis</i>	1	1	0.2	–	–	–	–	–	–	–	–	–
Miliolids												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelosina longirostra</i>	2	3	0.4	–	–	–	–	–	–	–	–	–
<i>Biloculinella labiata</i>	–	–	–	–	–	–	–	–	–	–	–	–

Appendix A (continued)

Station Sampling period Taxa	Station A											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Pseudotriloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo elongata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>	1	1	0.2	10	14	4.9	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	2	3	0.4	4	6	1.9	3	4	0.1	4	6	0.4
<i>Quinqueloculina milletti</i>	–	–	–	7	10	3.4	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	–	–	–	1	1	0.5	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina stalkerii</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilinita tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated												
<i>Textularia agglutinans</i>	–	–	–	–	–	–	–	–	–	–	–	–
Non fossilising agglutinated												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
Agglutinate sp.333	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammoscalaria foliacea</i>	1	1	0.2	–	–	–	–	–	–	–	–	–
<i>Clavulina cylindrica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	1	–	0.2	–	–	–	–	–	–	–	–	–
<i>Eggerella scabra</i>	69	96	12.5	27	38	13.1	–	–	–	2	3	0.2
<i>Haplophragmoides</i> spp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lagenammina difflugiformis</i>	–	–	–	1	1	0.5	–	–	–	3	4	0.3
<i>Leptohalysis scottii</i>	287	399	52.0	17	24	8.3	5427	7538	98.2	4	6	0.4
<i>Nouria polymorphinoides</i>	1	1	0.2	–	–	–	3	4	0.1	–	–	–
<i>Psammosphaera bowmani</i>	–	–	–	9	13	4.4	1	1	0.0	18	25	1.6
<i>Pseudobolivina fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax nana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroplectamina</i> sp.1	–	–	–	1	1	0.5	1	1	0.0	–	–	–
<i>Trochammina globigeriniformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
Organic foraminifera	–	–	–	–	–	–	–	–	–	–	–	–
Total No Perforates	188	261	34.1	129	179	62.6	85	118	1.5	1070	1486	97.1
Total No Miliolids	5	7	0.9	22	31	10.7	3	4	0.1	5	7	0.5
Tot. No Fossilising Agglutinates	–	–	–	–	–	–	–	–	–	–	–	–
Tot. No Non-fossilising Agglutinates	359	499	65.0	55	76	26.7	5432	7544	98.4	27	38	2.5
Total No Organic	–	–	–	–	–	–	–	–	–	–	–	–
Total No individuals	552	767		206	286		5520	7667		1102	1531	

Appendix A (continued)

Station Sampling period Taxa	Station N											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
Perforates												
<i>Ammonia beccarii</i> f. <i>beccarii</i>	1	1	0.1	23	32	1.8	15	21	0.8	–	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	19	26	2.4	–	–	–	10	14	0.5	38	53	4.1
<i>Ammonia parkinsoniana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia tepida</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Amphicoryna scalaris</i>	–	–	–	–	–	–	1	1	0.1	3	4	0.3
<i>Astacolus crepidulus</i>	2	3	0.3	1	1	0.1	1	1	0.1	–	–	–
<i>Bolivina</i> sp.	–	–	–	2	3	0.2	–	–	–	1	1	0.1
<i>Bolivina alata</i>	–	–	–	1	1	0.1	1	1	0.1	–	–	–
<i>Bolivina dilatata</i>	–	–	–	1	1	0.1	–	–	–	–	–	–
<i>Bolivina striatula</i>	–	–	–	1	1	0.1	3	4	0.2	5	7	0.5
<i>Bolivina subaenariensis</i>	–	–	–	2	3	0.2	1	1	0.1	–	–	–
<i>Buccella granulata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>	1	1	0.1	1	1	0.1	5	7	0.3	–	–	–
<i>Bulimina elongata</i>	2	3	0.3	–	–	–	1	1	0.1	3	4	0.3
<i>Bulimina gibba</i>	1	1	0.1	–	–	–	5	7	0.3	2	3	0.2
<i>Bulimina marginata</i>	3	4	0.4	1	1	0.1	21	29	1.1	3	4	0.3
<i>Cancris oriculus</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Cassidulina carinata</i>	6	8	0.8	24	33	1.8	86	119	4.4	1	1	0.1
<i>Cassidulina crassa</i>	–	–	–	4	6	0.3	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>	–	–	–	–	–	–	1	1	0.1	1	1	0.1
<i>Dentalina filiformis</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>	4	6	0.5	1	1	0.1	11	15	0.6	4	6	0.4
<i>Elphidium crispum</i>	–	–	–	1	1	0.1	3	4	0.2	–	–	–
<i>Elphidium poeyanum</i> f. <i>decipiens</i>	–	–	–	–	–	–	6	8	0.3	2	3	0.2
<i>Epistominella vitrea</i>	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Fursenkoina</i> sp.	–	–	–	–	–	–	1	1	0.1	4	6	0.4
<i>Gavelinopsis praegeri</i>	–	–	–	1	1	0.1	–	–	–	–	–	–
<i>Globobulimina pyrula</i>	–	–	–	–	–	–	–	–	–	1	1	0.1
<i>Gyroidina umbonata</i>	–	–	–	4	6	0.3	1	1	0.1	–	–	–
<i>Haynesina</i> spp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hopkinsina atlantica</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>	1	1	0.1	2	3	0.2	3	4	0.2	–	–	–
<i>Lenticulina atlantica</i>	2	3	0.3	–	–	–	5	7	0.3	–	–	–
<i>Lenticulina peregrina</i>	–	–	–	1	1	0.1	–	–	–	–	–	–
<i>Nonion fabum</i>	54	75	6.9	178	247	13.7	172	239	8.7	179	249	19.4
<i>Nonionella iridea</i>	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Nonionella stella</i>	–	–	–	–	–	–	45	63	2.3	–	–	–
<i>Nonionella turgida</i>	41	57	5.2	30	42	2.3	291	404	14.7	69	96	7.5
<i>Pseudoepionides falsobeccarii</i>	–	–	–	2	3	0.2	–	–	–	3	4	0.3
<i>Rectuvigerina phlegeri</i>	19	26	2.4	92	128	7.1	132	183	6.7	102	142	11.1
<i>Robertina translucens</i>	3	4	0.4	1	1	0.1	3	4	0.2	–	–	–
<i>Rosalina vilardeboana</i>	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	1	1	0.1	1	1	0.1
<i>Stainforthia concava</i>	–	–	–	–	–	–	3	4	0.2	–	–	–
<i>Valvulineria bradyana</i>	82	114	10.4	275	382	21.2	380	528	19.2	160	222	17.3
<i>Virgullinella fragilis</i>	–	–	–	–	–	–	–	–	–	–	–	–
Miliolids												
Indet.	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Adelosina longirostra</i>	8	11	1.0	7	10	0.5	11	15	0.6	4	6	0.4
<i>Biloculinella labiata</i>	–	–	–	1	1	0.1	1	1	0.1	1	1	0.1

Appendix A (continued)

Station Sampling period Taxa	Station N											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	2	3	0.1	–	–	–
<i>Pseudotriloculina</i> sp.	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Pyrgo elongata</i>	–	–	–	3	4	0.2	–	–	–	–	–	–
<i>Pyrgo oblonga</i>	–	–	–	7	10	0.5	2	3	0.1	2	3	0.2
<i>Quinqueloculina aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	1	1	0.1	–	–	–	3	4	0.2	1	1	0.1
<i>Quinqueloculina milletti</i>	–	–	–	1	1	0.1	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	4	6	0.5	6	8	0.5	2	3	0.1	3	–	0.3
<i>Quinqueloculina stalkerii</i>	–	–	–	–	–	–	–	–	–	1	0	0.1
<i>Sigmoilinita tenuis</i>	–	–	–	–	–	–	–	–	–	1	0	0.1
<i>Sigmoilopsis schlumbergeri</i>	3	4	0.4	–	–	–	1	0	0.1	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	1	0	0.1	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	2	0	0.1	1	0	0.1
Fossilising agglutinated												
<i>Textularia agglutinans</i>	19	–	2.4	23	0	1.8	69	0	3.5	11	0	1.2
Non fossilising agglutinated												
Indet.	–	–	–	2	3	0.2	1	1	0.1	–	–	–
Agglutinate sp.333	–	–	–	42	58	3.2	5	7	0.3	–	–	–
<i>Adercotryma glomerata</i>	3	4	0.4	6	8	0.5	33	46	1.7	1	1	0.1
<i>Ammoscalaria foliacea</i>	11	15	1.4	20	28	1.5	18	25	0.9	6	8	0.7
<i>Clavulina cylindrica</i>	58	81	7.4	139	193	10.7	38	53	1.9	17	24	1.8
<i>Cribrostomoides wiesneri</i>	40	56	5.1	16	22	1.2	38	53	1.9	–	–	–
<i>Eggerella scabra</i>	361	501	45.9	238	331	18.3	396	550	20.0	86	119	9.3
<i>Haplophragmoides</i> spp.	3	4	0.4	1	1	0.1	1	1	0.1	4	6	0.4
<i>Lagenammina difflugiformis</i>	1	1	0.1	10	14	0.8	1	1	0.1	1	1	0.1
<i>Leptohalysis scottii</i>	–	–	–	1	1	0.1	39	54	2.0	49	68	5.3
<i>Nouria polymorphinoides</i>	16	22	2.0	73	101	5.6	16	22	0.8	140	194	15.2
<i>Psammosphaera bowmani</i>	9	13	1.1	6	8	0.5	14	19	0.7	3	4	0.3
<i>Pseudobolivina fusiformis</i>	–	–	–	–	–	–	1	1	0.1	–	–	–
<i>Reophax fusiformis</i>	1	1	0.1	17	24	1.3	12	17	0.6	2	3	0.2
<i>Reophax nana</i>	1	1	0.1	–	–	–	–	–	–	–	–	–
<i>Spiroplectammina</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochammina globigeriniformis</i>	2	3	0.3	30	42	2.3	22	31	1.1	7	10	0.8
Organic foraminifera	–	–	–	1	1	0.1	40	56	2.0	–	–	–
Total No Perforates	245	340	31.2	649	901	50.0	1211	1682	61.3	582	808	63.1
Total No Miliolids	16	22	2.0	25	35	1.9	27	38	1.4	14	19	1.5
Tot. No Fossilising Agglutinates	19	26	2.4	23	32	1.8	69	96	3.5	11	15	1.2
Tot. No Non-fossilising Agglutinates	506	703	64.4	601	835	46.3	635	882	32.1	316	439	34.2
Total No Organic	–	–	–	1	1	0.1	40	56	2.0	–	–	–
Total No individuals	786	1092		1299	1804		1982	2753		923	1282	

Appendix B

Station Sampling period Taxa	Station A											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
Perforates												
Indet.	–	–	–	4	6	0.9	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	11	15	0.3	12	17	2.6	–	–	–	24	33	2.4
<i>Ammonia tepida</i>	–	–	–	28	39	4.3	–	–	–	432	600	43.5
<i>Amphicoryna scalaris</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>	597	830	16.2	36	50	6.0	–	–	–	40	56	4.0
<i>Bolivina seminuda</i>	96	133	2.6	–	–	–	–	–	–	–	–	–
<i>Bolivina spathulata</i>	21	30	0.6	–	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>	11	15	0.3	4	6	0.5	–	–	–	–	–	–
<i>Bulimina aculeata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>	21	30	0.6	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>	11	15	0.3	–	–	–	–	–	–	–	–	–
<i>Buliminella elegantissima</i>	11	15	0.3	4	6	0.5	–	–	–	–	–	–
<i>Cancris oriculus</i>	–	–	–	4	6	0.9	–	–	–	16	22	1.6
<i>Cassidulina carinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina crassa</i>	11	15	0.3	–	–	–	–	–	–	–	–	–
<i>Cassidulina minuta</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina oblonga</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium poeyanum</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Epistominella vitrea</i>	11	15	0.3	–	–	–	–	–	–	–	–	–
<i>Fissurina</i> sp.	–	–	–	–	–	–	–	–	–	8	11	0.8
<i>Fursenkoina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hanzawaia boueana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Haynesina germanica</i>	–	–	–	–	–	–	–	–	–	64	89	6.5
<i>Hopkinsina atlantica</i>	139	193	3.8	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina atlantica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonion</i> sp.1	–	–	–	4	6	0.5	–	–	–	–	–	–
<i>Nonion fabum</i>	11	15	0.3	–	–	–	–	–	–	–	–	–
<i>Nonionella</i> sp.1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella iridea</i>	75	104	2.0	4	6	0.5	–	–	–	–	–	–
<i>Nonionella stella</i>	415	576	8.1	–	–	–	–	–	–	–	–	–
<i>Nonionella turgida</i>	593	823	11.6	–	–	–	–	–	–	8	11	0.8
<i>Rectuvigerina phlegeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia complanata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia concava</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia fusiformis</i>	1081	1502	21.1	20	28	3.3	–	–	–	–	–	–
<i>Valvulineria bradyana</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Virgulinea fragilis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Virgulopsis</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
Miliolids												
Indet.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adelosina longirostra</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cornuspira involvens</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	–	–	–

Appendix B (continued)

Station Sampling period Taxa	Station A											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
<i>Quinqueloculina lata</i>	–	–	–	4	6	0.9	–	–	–	–	–	–
<i>Quinqueloculina milletti</i>	–	–	–	24	33	3.8	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	44	62	0.9	28	39	4.3	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina stalkerii</i>	–	–	–	4	6	0.5	–	–	–	–	–	–
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Siphonaperta aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated												
<i>Textularia agglutinans</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia porrecta</i>	128	178	3.5	4	6	0.5	–	–	–	–	–	–
Non fossilising agglutinated												
Indet.	–	–	–	8	11	1.4	–	–	–	40	56	4.0
Agglutinate sp.333	–	–	–	–	–	–	–	–	–	–	–	–
<i>Adercotryma glomerata</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammoscalaria foliacea</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Clavulina cylindrica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribrostomoides wiesneri</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Eggerella scabra</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Leptohalysis scottii</i>	971	1348	26.3	104	144	16.9	99	138	100	32	44	3.2
<i>Nouria polymorphinoides</i>	–	–	–	–	–	–	–	–	–	24	33	2.4
<i>Psammosphaera bowmani</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Psammosphaera fusca</i>	11	15	0.3	276	383	44.9	–	–	–	296	411	29.8
<i>Pseudobolivina fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Reophax nana</i>	21	30	0.6	24	33	3.4	–	–	–	–	–	–
<i>Trochammina globigeriniformis</i>	–	–	–	8	11	1.4	–	–	–	8	11	0.8
Organic foraminifera	–	–	–	16	22	2.1	–	–	–	–	–	–
Total No Perforates	2528	3511	68.5	120	167	20.0	–	–	–	592	822	59.7
Total No Miliolids	32	44	0.9	60	83	9.5	–	–	–	–	–	–
Tot. No Fossilising Agglutinates	128	178	3.5	4	6	0.5	–	–	–	–	–	–
Tot. No Non-fossilising Agglutinates	1003	1393	27.2	420	583	68.0	99	138	100	400	556	40.3
Total No Organic	–	–	–	16	22	2.1	–	–	–	–	–	–
Total No individuals	3691	5126		620	861		99	138		992	1378	

Appendix B (continued)

Station Sampling period Taxa	Station N											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
Perforates												
Indet.	48	67	0.8	8	11	0.2	208	289	2.5	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	16	22	0.3	28	39	0.7	–	–	–	24	33	1.3
<i>Ammonia tepida</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphicoryna scalaris</i>	48	67	0.8	4	6	0.1	–	–	–	4	6	0.2
<i>Astacolus crepidulus</i>	32	44	0.6	4	6	0.1	16	22	0.2	–	–	–
<i>Bolivina dilatata</i>	1200	1667	21.1	556	772	13.4	880	1222	10.5	268	372	14.4
<i>Bolivina seminuda</i>	48	67	0.8	28	39	0.6	176	244	2.1	104	144	5.6
<i>Bolivina spathulata</i>	304	422	5.4	348	483	8.1	288	400	3.4	200	278	10.8
<i>Bolivina striatula</i>	272	378	4.8	84	117	2.0	80	111	1.0	76	106	4.1
<i>Bulimina aculeata</i>	–	–	–	20	28	0.5	–	–	–	–	–	–
<i>Bulimina elongata</i>	32	44	0.6	24	33	0.6	48	67	0.6	16	22	0.9
<i>Bulimina marginata</i>	64	89	1.1	8	11	0.2	80	111	1.0	8	11	0.4
<i>Buliminella elegantissima</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cancris oriculus</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina carinata</i>	–	–	–	48	67	1.1	48	67	0.6	4	6	0.2
<i>Cassidulina crassa</i>	–	–	–	8	11	0.2	32	44	0.4	8	11	0.4
<i>Cassidulina minuta</i>	–	–	–	8	11	0.2	16	22	0.2	–	–	–
<i>Cassidulina oblonga</i>	16	22	0.3	–	–	–	16	22	0.2	–	–	–
<i>Elphidium poeyanum</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Epistominella vitrea</i>	208	289	3.7	172	239	4.1	240	333	2.9	60	83	3.2
<i>Fissurina</i> sp.	–	–	–	–	–	–	–	–	–	16	22	0.9
<i>Fursenkoina</i> sp.	–	–	–	4	6	0.1	–	–	–	16	22	0.9
<i>Gavelinopsis praegeri</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	–	–	–	12	17	0.3	–	–	–	–	–	–
<i>Hanzawaia boueana</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Haynesina germanica</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hopkinsina atlantica</i>	416	578	7.3	380	528	8.5	208	289	2.5	72	100	3.9
<i>Hyalinea balthica</i>	16	22	0.3	4	6	0.1	–	–	–	–	–	–
<i>Lenticulina atlantica</i>	48	67	0.8	12	17	0.3	32	44	0.4	28	39	1.5
<i>Nonion</i> sp.1	–	–	–	28	39	0.7	–	–	–	–	–	–
<i>Nonion fabum</i>	–	–	–	36	50	0.8	112	156	1.3	12	17	0.6
<i>Nonionella</i> sp.1	–	–	–	–	–	–	240	333	2.9	16	22	0.9
<i>Nonionella bradyi</i>	224	311	3.9	4	6	0.1	–	–	–	–	–	–
<i>Nonionella iridea</i>	80	111	1.4	–	–	–	944	1311	11.3	20	28	1.1
<i>Nonionella stella</i>	240	333	4.2	72	100	1.6	304	422	3.6	–	–	–
<i>Nonionella turgida</i>	432	600	7.6	272	378	6.4	1360	1889	16.2	28	39	1.5
<i>Rectuvigerina phlegeri</i>	256	356	4.5	344	478	7.8	64	89	0.8	88	122	4.7
<i>Robertina translucens</i>	–	–	–	16	22	0.4	–	–	–	–	–	–
<i>Saidovina karreriana</i>	–	–	–	48	67	1.1	–	–	–	8	11	0.4
<i>Stainforthia complanata</i>	80	111	1.4	8	11	0.2	96	133	1.1	–	–	–
<i>Stainforthia concava</i>	–	–	–	56	78	1.4	–	–	–	88	122	4.7
<i>Stainforthia fusiformis</i>	32	44	0.6	148	206	4.0	192	267	2.3	72	100	3.9
<i>Valvulineria bradyana</i>	80	111	1.4	96	133	1.9	16	22	0.2	16	22	0.9
<i>Virgulineria fragilis</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Virgulopsis</i> sp.	16	22	0.3	–	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–	–	–	–	–
Miliolids												
Indet.	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Adelosina longirostra</i>	16	22	0.3	4	6	0.1	–	–	–	4	6	0.2
<i>Cornuspira involvens</i>	–	–	–	–	–	–	–	–	–	16	22	0.9
<i>Miliolinella subrotunda</i>	–	–	–	4	6	0.1	32	44	0.4	–	–	–

Appendix B (continued)

Station Sampling period Taxa	Station N											
	Apr.07			Sept. 07			May.08			Dec.08		
	r.d.	D	%	r.d.	D	%	r.d.	D	%	r.d.	D	%
<i>Quinqueloculina lata</i>	32	44	0.6	12	17	0.2	16	22	0.2	–	–	–
<i>Quinqueloculina milletti</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	32	44	0.6	–	–	–	–	–	–	8	11	0.4
<i>Quinqueloculina seminula</i>	–	–	–	8	11	0.2	–	–	–	4	6	0.2
<i>Quinqueloculina stalkerii</i>	48	67	0.8	40	56	1.1	112	156	1.3	4	6	0.2
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	16	22	0.2	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	–	8	11	0.2	–	–	–	–	–	–
<i>Siphonaperta aspera</i>	–	–	–	–	–	–	–	–	–	4	6	0.2
<i>Triloculina</i> sp.	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	16	22	0.2	–	–	–
Fossilising agglutinated												
<i>Textularia agglutinans</i>	–	–	–	–	–	–	16	22	0.2	–	–	–
<i>Textularia porrecta</i>	304	422	5.4	80	111	2.1	608	844	7.3	228	317	12.3
Non fossilising agglutinated												
Indet.	48	67	0.8	–	–	–	–	–	–	–	–	–
Agglutinate sp.333	96	133	1.7	104	144	2.5	64	89	0.8	84	117	4.5
<i>Adercotryma glomerata</i>	32	44	0.6	8	11	0.2	48	67	0.6	4	6	0.2
<i>Ammoscalaria foliacea</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Clavulina cylindrica</i>	96	133	1.7	44	61	1.0	96	133	1.1	–	–	–
<i>Cribrostomoides wiesneri</i>	112	156	2.0	40	56	1.0	32	44	0.4	–	–	–
<i>Eggerella scabra</i>	304	422	5.4	552	767	13.3	528	733	6.3	128	178	6.9
<i>Leptohalysis scottii</i>	176	244	3.1	144	200	3.6	1008	1400	12.0	52	72	2.8
<i>Nouria polymorphinoides</i>	–	–	–	32	44	0.7	–	–	–	8	11	0.4
<i>Psammosphaera bowmani</i>	64	89	1.1	96	133	2.1	16	22	0.2	4	6	0.2
<i>Psammosphaera fusca</i>	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudobolivina fusiformis</i>	32	44	0.6	4	6	0.1	32	44	0.4	16	22	0.9
<i>Reophax fusiformis</i>	–	–	–	4	6	0.1	–	–	–	–	–	–
<i>Reophax nana</i>	48	67	0.8	28	39	0.7	48	67	0.6	8	11	0.4
<i>Trochammina globigeriniformis</i>	32	44	0.6	104	144	2.2	–	–	–	36	50	1.9
Organic foraminifera	–	–	–	–	–	–	–	–	–	–	–	–
Total No Perforates	4208	5844	74.1	2904	4033	67.9	5696	7911	67.9	1252	1739	67.3
Total No Miliolids	128	178	2.3	88	122	2.2	192	267	2.3	40	56	2.2
Tot. No Fossilising Agglutinates	304	422	5.4	80	111	2.1	624	867	7.4	228	317	12.3
Tot. No Non–fossilising Agglutinates	1040	1444	18.3	1164	1617	27.8	1872	2600	22.3	340	472	18.3
Total No Organic	–	–	–	–	–	–	–	–	–	–	–	–
Total No individuals	5680	7889		4236	5883		8384	11644		1860	2583	

Appendix C

- Ammonia tepida* (Cushman) = *Rotalia beccarii* Linnaeus var. *tepida* Cushman, 1926; in Jorissen, 1988, Plate 2, Fig. 8a–b (as *Ammonia parkinsoniana* f. *tepida*)
- Bolivina dilatata* (Reuss) = *Brizalina dilatata* Reuss, 1850; in Colom, 1974, Fig. 18j–n
- Bolivina seminuda* Cushman, 1911; in Mojtahid et al., 2008, Plate 1, Fig. 5
- Bolivina spathulata* (Williamson) = *Textularia variabilis* Williamson var. *spathulata* Williamson, 1858; in Jorissen, 1988, Plate 1, Fig. 5
- Clavulina cylindrica* d'Orbigny, 1952; in Jones, 1994, Plate 44, Figs. 19–24
- Cribrostomoides wiesneri* (Parr) = *Labrospira wiesneri* Parr, 1950; in Jones, 1994, Plate 40, Figs. 14–15
- Eggerella scabra* (Williamson) = *Bulimina scabra* Williamson, 1858; in Jones, 1994, Plate 47, Figs. 15–17
- Haynesina germanica* (Ehrenberg) = *Nonionina germanica* Ehrenberg, 1840; in Diz and Francès, 2008, Plate II, Fig. 5
- Hopkinsina atlantica* (Cushman) = *Hopkinsina pacifica* Cushman var. *atlantica* Cushman, 1944; in Diz and Francès, 2008, Plate II, Fig. 8
- Leptohalysis scottii* (Chaster) = *Reophax scottii* Chaster, 1892; in Sgarella and Montcharmont Zei, 1993, Plate 2, Fig. 5
- Nonion fabum* (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798; in Jones, 1994, Plate 109, Figs. 12–13
- Nonionella iridea* Heron–Allen and Earland, 1932; in "Discovery" Rept., v. 4, p. 438, Plate 16, Figs. 14–16
- Nonionella stella* Cushman and Moyer, 1930; in Diz and Francès, 2008, Plate 2, Fig. 6
- Nonionella turgida* (Williamson) = *Rotalina turgida* Williamson, 1858; in Jorissen, 1988, Plate 4, Figs. 11–13
- Nouria polymorphinoides* Heron–Allen and Earland, 1914; in Barmawidjaja et al., 1992, Plate 4, Fig. 4
- Psammosphaera fusca* Schulze, 1875; in Höglund, 1947, Plate 4, Figs. 9–10
- Rectuvigerina phlegeri* Le Calvez, 1959; in Schiebel, 1992, Plate 3, Fig. 10a–d
- Stainforthia fusiformis* (Williamson) = *Bulimina pupoides* d'Orbigny var. *fusiformis* Williamson, 1858; in Gooday and Alve, 2001, Plate 3, Figs. A–B–C
- Textularia porrecta* (Brady) = *Textularia agglutinans* d'Orbigny var. *porrecta* Brady, 1884; in Rept. Challenger Expedition, London, England, p. 364, Plate 43, Fig. 4

Valvulineria bradyana (Fornasini) = *Discorbina bradyana* Fornasini, 1900; in Jorissen, 1988,
Plate 4, Figs. 1–2

CHAPITRE 4
LIVING – DEAD COMPARISON OF BENTHIC
FORAMINIFERAL FAUNAS FROM THE RHÔNE
PRODELTA: DETERMINATION OF THANATOFACIES FOR
PALEOENVIRONMENTAL RECONSTRUCTIONS

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CHAPITRE 4

**LIVING – DEAD COMPARISON OF BENTHIC
FORAMINIFERAL FAUNAS FROM THE RHÔNE
PRODELTA**

**DETERMINATION OF THANATOFACIES FOR
PALEOENVIRONMENTAL RECONSTRUCTIONS**

A. Goineau, C. Fontanier, M. Mojtahid and F. Jorissen

Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), Université d'Angers
UPRES EA 2644, 2 Boulevard Lavoisier, 49045 Angers Cedex 01, France

and

Laboratoire d'Etude des Bio-Indicateurs Marins (LEBIM)
Ker Châlon, 85350 Ile d'Yeu, France

ABSTRACT

Dead foraminiferal faunas (> 150 µm) were studied at 39 stations sampled in September 2006 (BEHEMOTH cruise) and June 2005 (MINERCOT 2 cruise). Stations were located between 15 and 100 m depth in the Rhône prodelta (Gulf of Lions, NW Mediterranean). The comparison between dead and living assemblages permitted better understanding of taphonomical processes acting on benthic foraminiferal faunas in this area. Both physic-co chemical (transport, fragmentation/dissolution) and biological processes modify the composition of the sub-fossil faunas. The fragility of the test (e.g., *Bolivina alata*, *Quinqueloculina tenuicollis*, *Triloculina trigonula*) explains the loss of individuals from the living to the dead faunas. Strong bottom currents acting at the shallowest sites (i.e., from the river mouth to the western coast) may result in a redistribution of dead faunas (i.e., input of allochthonous individuals or redistribution of the fauna; e.g., *Bulimina elongata*, *Quinqueloculina lata*). Farther from these shallow environments, biological processes such as high production rates may explain higher relative abundances of opportunistic species in the dead fauna (e.g., *Bulimina marginata*, *Cassidulina carinata*, *Nonionella turgida*, *Valvulineria bradyana*). Thereafter, cluster analyses based on dead foraminiferal assemblages divide our study area into four main thanatofacies directly related to precise environmental conditions. Close to the river mouth, *A. beccarii* f. *beccarii* and *Ammonia tepida* were found in sediments submitted to a high riverine influence (i.e., bottom currents, organic and inorganic material input). *Elphidium* species are abundant in the silty-sandy relict deltaic lobe west of the river mouth which is characterised by strong longshore currents disturbing the benthic environment. In the “river plume” thanatofacies, *N. turgida* is indicative of a zone submitted to important riverine sediment input, whereas *N. fabum*, *Rectuvigerina phlegeri* and *V. bradyana* are found along the coast west of the Rhône River mouth. In the more stable and deeper southern to south-eastern prodeltaic area, species able to feed on fresh phytodetritus dominate the faunas (e.g., *Bulimina aculeata/marginata*, *Hyalinea balthica*), whereas *Cassidulina carinata* benefits from both riverine and marine influences on the northern border of this outer shelf thanatofacies. This study, which put into evidence minor variations between the living and the dead faunas, improves the use of benthic foraminiferal faunas to investigate the paleo-Rhône prodelta through the study of fossil foraminiferal archives.

Key words: Dead benthic foraminifera; Rhône prodelta; Taphonomical processes; Thanatofacies.

4.1. INTRODUCTION

Because of their widespread distribution in various environmental settings (i.e., mud flats, shallow coastal areas, continental slope, deep-sea...) and their adaptability to various ecological conditions (i.e., substrate, oxygen and food availability), benthic foraminifera across make them a very useful tool for recent environmental studies. The preservation in sediments of their carbonate tests makes them also a perfect proxy for paleoenvironmental reconstructions. The use of benthic foraminiferal assemblages (composition, density) in these studies requires a good knowledge of modern faunas. Unfortunately, taphonomical processes may cause large differences between living faunas present at a certain time and place and dead faunas preserved in the sedimentary record. Transport of small-sized specimens by bottom currents, and dissolution or disintegration of the most fragile taxa (e.g., some agglutinated species) may change the composition of dead faunas compared with the living ones (Murray, 1991; de Stigter et al., 1999; Jorissen and Wittling, 1999). Moreover, some biological factors linked to population dynamics such as interspecific differences in reproduction rates or seasonal variability in standing stocks may cause considerable differences between the living fauna at one time and the fossil fauna forming at the same site (de Stigter et al., 1999; Jorissen and Wittling, 1999). In principle, in environments submitted to important seasonal and/or interannual variations of organic matter fluxes and sediment/bottom water oxygenation (e.g., continental shelves), dead foraminiferal faunas reflect a time-averaged mixture of the assemblages succeeding each other in time, giving an integrated picture of the population dynamics and of the functioning of the ecosystem as a whole (Murray, 1991; Jorissen and Wittling, 1999). Living faunas from the Rhône prodelta were investigated in June 2005 (Mojtahid et al., 2009) and September 2006 (Goineau et al., In Press – see Chapter 1 in this thesis). In both studies, foraminiferal faunal composition and distribution in the prodelta were essentially controlled by hydro-sedimentary processes, sediment grain size, and also the quality (fresh, degraded), quantity and origin (continental, marine) of sedimentary organic matter. Furthermore, the intensity of aerobic (i.e., sediment oxygen penetration depth) and anaerobic degradation of organic matter (nitrate/nitrite consumption) depended also on the quality and quantity of this material. As we showed in Chapter 3, these parameters may vary over the year in function of the Rhône River discharge and the intensity of riverine and marine primary production. The highly variable panel of environmental conditions prevailing in the Rhône prodelta over the year is responsible for rapidly changing faunas, even at a single site.

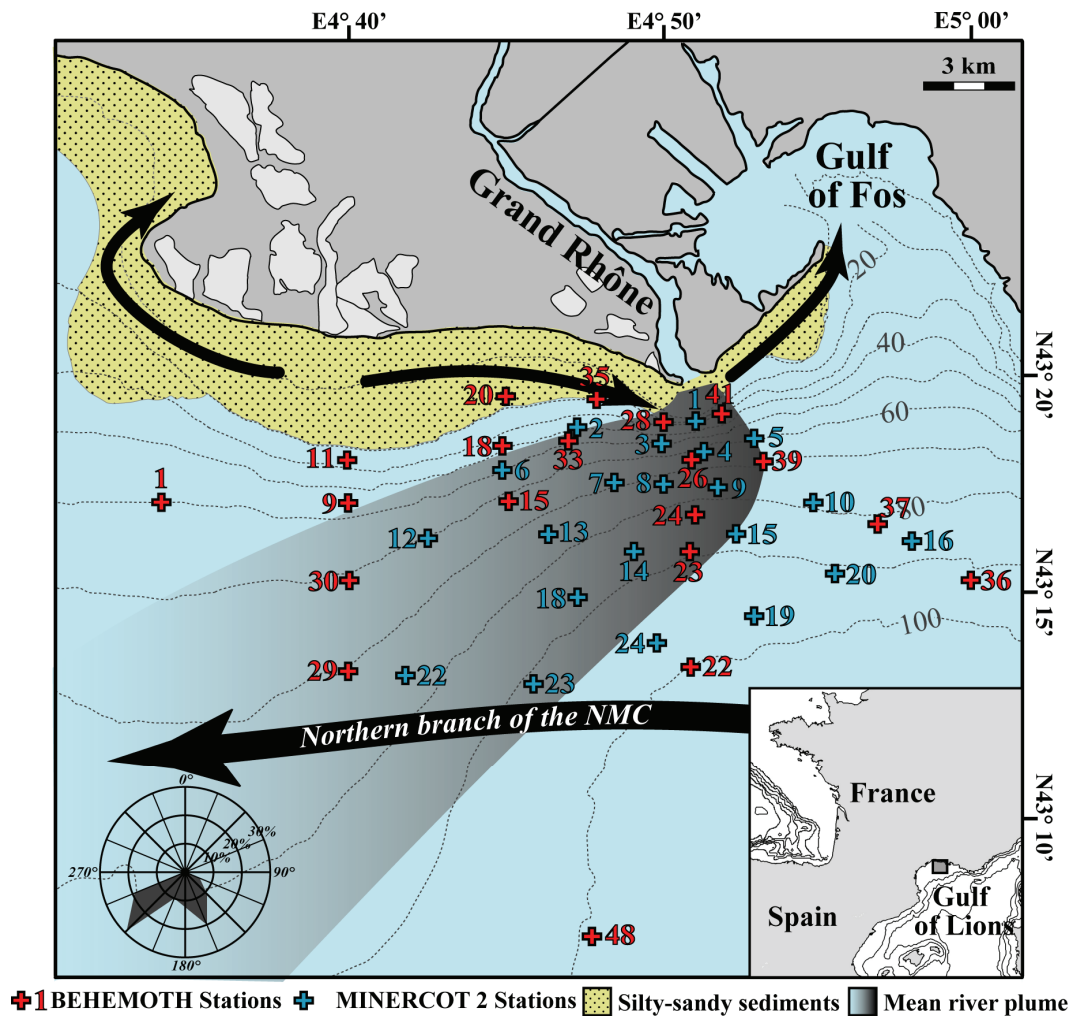


Figure 1: Study area and location of the 41 investigated stations. The yellow-dotted area corresponds to the silty-sandy sediments of the relict prodeltaic lobes of Grand Passon – Bras de Fer and Pégoulie (Vella et al., 2005); the circle diagram indicates mean swells frequency and direction (Brunel, 2010), and black arrows longshore currents (Sabatier and Suanes, 2003). NMC: North Mediterranean Current.

The aim of the present chapter is to calibrate the present-day distribution of sub-fossil foraminiferal faunas to make them a useful tool for paleo-environmental reconstructions in the Rhône prodelta. In order to do so, we will compare the living and dead foraminiferal faunas from the Rhône prodelta. We will describe dead foraminiferal faunas in terms of diversity and composition, and identify differences between living and sub-fossil faunas due to taphonomical and biological processes. Next, we will determine sub-fossil foraminiferal thanatofacies and compare their spatial distribution with biofacies determined with the living fauna in Chapter 1. This comparison will provide us with a powerful tool to reconstruct the Quaternary history of the Rhône prodelta on the basis of sediment core material.

4.2. MATERIAL AND METHODS

20 stations (e.g., BT1, BT9) were sampled in September 2006 during the BEHEMOTH cruise on board the *R/V Téthys II* (INSU). Sediment cores of 72 cm² surface area were collected using a Barnett multicorer (Barnett et al., 1984) between 15 and 100 m depth (Fig. 1, Table 1). At each station, one core was sliced on board for benthic foraminiferal analyses into 0.5 cm levels from the surface down 2 cm depth, and 1 cm levels down to 5 cm depth, and preserved in 95% ethanol with 1 g.l⁻¹ Rose Bengal. Sediment samples were sieved in the laboratory using sieves of 63 and 150 µm mesh size. All living (Rose Bengal stained) specimens from the > 150 µm size fraction were hand-picked under wet conditions from the surface down to 5 cm depth (Goineau et al., In Press – see Chapter 1 in this thesis). We also analysed dead (unstained) foraminifera in the 3–4 cm level of the same size fraction. The dead faunas from this slightly deeper sediment level give a good overview of fossilising species since rapidly decomposing taxa (e.g., agglutinated species with organic cement) are noticeably reduced (Bizon and Bizon, 1984), and also deep infaunal species which may be under-represented in surface levels (Loubere, 1989) should be well represented. Samples were dried and in some cases, when faunal richness was too important, splitted with an Ottomicrosplitter. Foraminifera from complete samples or splits were hand-sorted until a minimum of 300 individuals was counted. Dead faunas of the > 150 µm size fraction were also investigated in samples from the Rhône prodelta collected during the MINERCOT 2 cruise in June 2005 at 21 stations (M1, M2,...) in the 3–4 cm or 2–5 cm sediment levels (Mojtahid, 2007). We combined our database with the one of (Mojtahid, 2007) to obtain a more detailed geographical overview of dead fossilising faunas in the prodelta. Since taphonomic processes induce important loss of foraminifera especially in the group of non-fossilising agglutinated taxa (Bizon and Bizon, 1984), we will consider only fossilising species (perforates, miliolids and fossilising agglutinates) in the following analyses. Moreover, we will not take into account two stations (M1 and BT41) because of their very low number of fossilising individuals (< 10 specimens). For the 39 other stations, Shannon (H) and Evenness (E) indices were calculated and total abundances for the fossilising part of the foraminiferal faunas (D) were normalised for a 100 cm³ sediment volume. The relative contribution (%) of each species to the total fossilising fauna was calculated for each core. Cluster analyses based on major species relative abundances were applied for the 39 stations (Q-mode) and the 23 major fossilising species (R-mode). We constructed tree diagrams using unweighted pair-group (average) method based on Pearson correlation coefficient.

BEHEMOTH cruise – September 2006					MINERCOT 2 cruise – June 2005				
Station	Lat. (°N)	Long. (°E)	Water depth (m)	Distance from the river mouth (km)	Station	Lat. (°N)	Long. (°E)	Water depth (m)	Distance from the river mouth (km)
BT1	43°16.992'	4°33.989'	49	22.2	M1	43°18.9'	4°51.2'	20	1.9
BT9	43°17.020'	4°39.991'	44	14.6	M2	43°18.6'	4°47.4'	40	5.0
BT11	43°17.973'	4°39.959'	26	14.0	M3	43°18.3'	4°50.1'	53	3.0
BT15	43°17.055'	4°45.148'	60	8.9	M4	43°18.2'	4°51.5'	60	3.2
BT18	43°18.288'	4°44.950'	37	7.5	M5	43°18.4'	4°53.1'	63	4.2
BT20	43°19.366'	4°45.057'	15	7.8	M6	43°17.7'	4°45.0'	40	8.6
BT22	43°13.250'	4°51.000'	98	11.4	M7	43°17.4'	4°48.6'	65	5.3
BT23	43°15.941'	4°50.971'	86	5.7	M8	43°17.4'	4°50.2'	65	4.5
BT24	43°16.757'	4°51.143'	79	4.4	M9	43°17.3'	4°52.0'	65	4.9
BT26	43°17.979'	4°51.028'	62	2.8	M10	43°17.0'	4°55.0'	80	7.8
BT28	43°18.816'	4°50.130'	18	1.0	M12	43°16.2'	4°42.6'	58	12.8
BT29	43°13.285'	4°39.989'	68	17.9	M13	43°16.3'	4°46.5'	75	8.7
BT30	43°15.301'	4°40.028'	60	16.5	M14	43°15.9'	4°49.3'	85	7.6
BT33	43°18.397'	4°47.068'	47	5.4	M15	43°16.3'	4°52.5'	89	6.9
BT35	43°19.324'	4°47.978'	20	3.1	M16	43°16.1'	4°58.1'	83	12.0
BT36	43°15.305'	5°00.003'	89	14.4	M18	43°14.9'	4°47.4'	85	10.1
BT37	43°16.550'	4°57.010'	80	9.6	M19	43°14.5'	4°53.1'	98	10.3
BT39	43°17.940'	4°53.340'	69	4.1	M20	43°15.4'	4°55.7'	92	10.6
BT41	43°18.998'	4°52.000'	30	1.5	M22	43°13.2'	4°41.8'	74	17.1
BT48	43°07.374'	4°47.827'	100	22.4	M23	43°13.0'	4°46.0'	90	14.1
					M24	43°13.9'	4°50.0'	95	10.9

Table 1: Location and characteristics of the 41 stations sampled during the BEHEMOTH (September 2006) and MINERCOT 2 (June 2005) cruises.

In order to appreciate differences between living and dead faunas, we calculated the $L/(L+D)$ ratio ($\%Living/(\%Living+\%Dead)$; Jorissen and Wittling, 1999) for all species $> 5\%$ in either living fossilising or dead fossilising assemblages from September 2006 (BEHEMOTH cruise) and June 2005 (MINERCOT 2 cruise) databases. We first calculated corrected relative abundances for all taxa in the living assemblage after removing all non-fossilising agglutinated species. Next, we compared these corrected percentages with the percentages in the dead faunas, again considering fossilising taxa only. When the $L/(L+D)$ ratio ranges between 0 and 0.5, the taxon is relatively more abundant in the dead than in the living assemblage. On the contrary, a $L/(L+D)$ value above 0.5 characterises a species richer in the living fauna.

4.3. RESULTS

4.3.1. Density, diversity and equitability of fossilising foraminiferal faunas

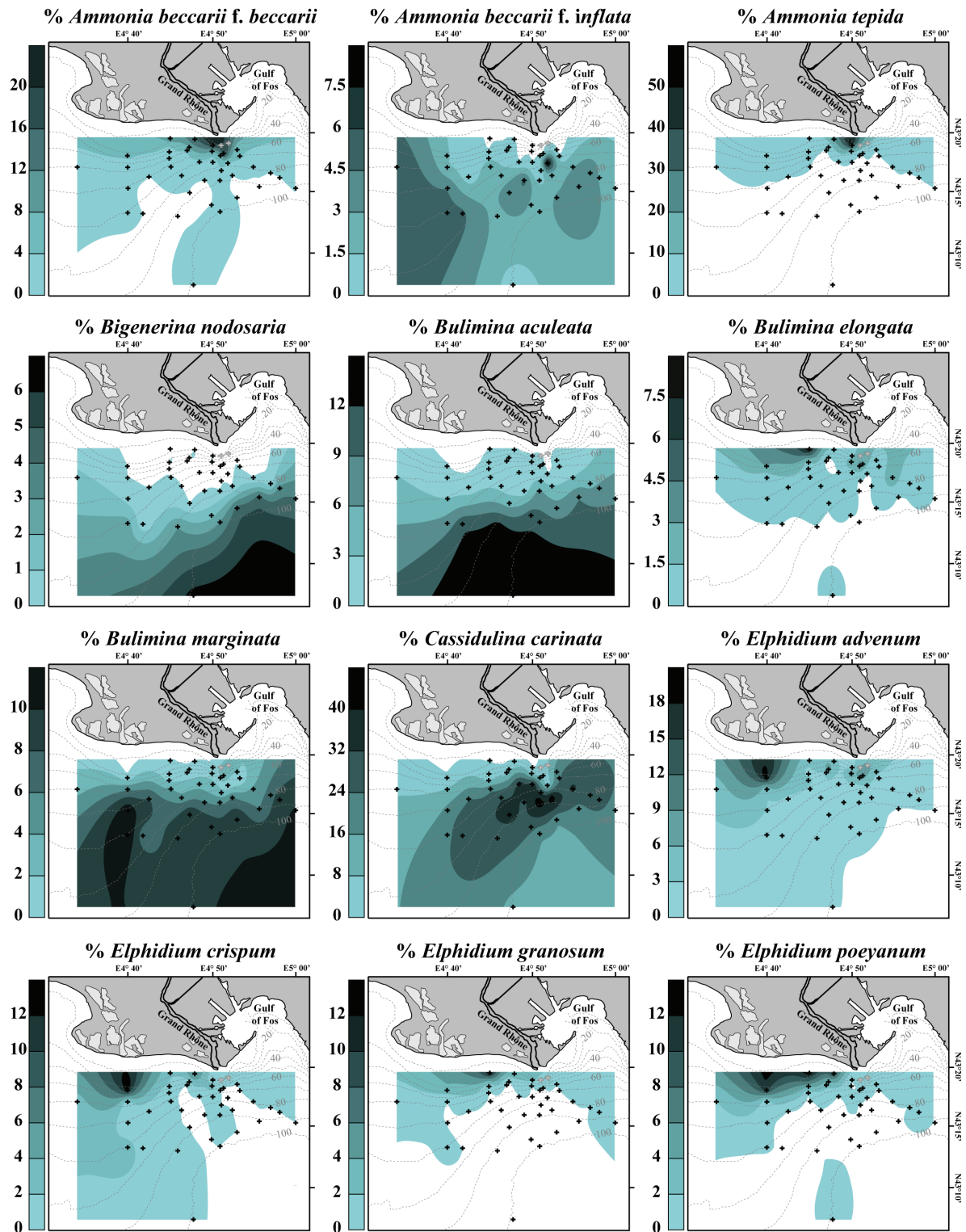


Figure 2: Relative abundances and spatial distribution of the 23 fossilising major species (> 5% in at least one station) of the > 150 μm size fraction. Light grey stations correspond to Stations BT41 and M1 excluded from all analyses because of their very low foraminiferal densities (< 10 observed individuals).

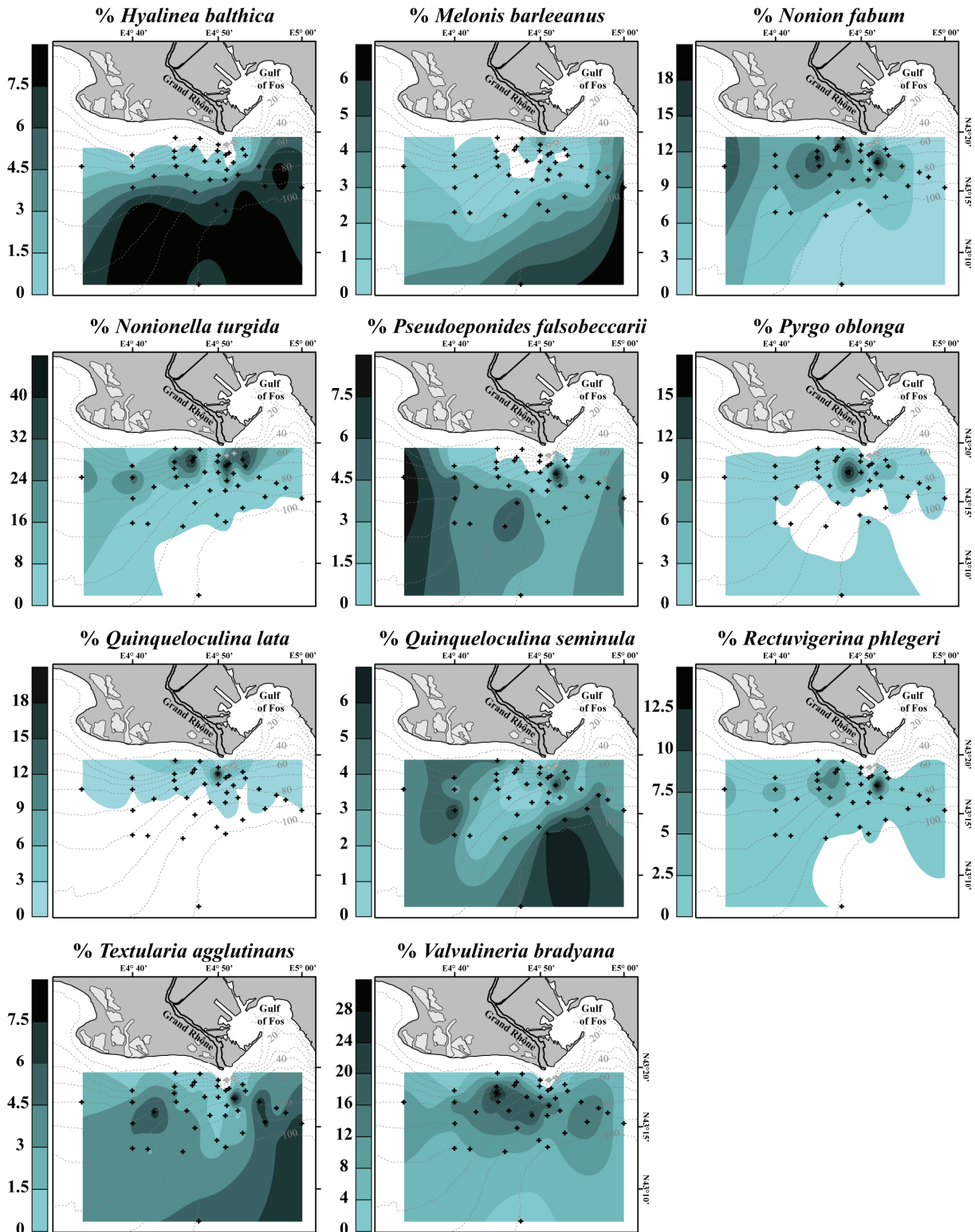


Figure 2 (continued)

A total of 88 fossilising species (63 perforates, 22 miliolids and 3 fossilising agglutinates) plus 16 non-fossilising agglutinated taxa were identified in the dead faunas of the 3–4 cm level (Appendix A). When considering total dead faunas, non-fossilising agglutinated species compose until ~30% of total foraminiferal faunas. 4 non-fossilising

agglutinated species show percentages > 5% in at least one core: *Clavulina cylindrica*, *Cribrostomoides wiesneri*, *Eggerella scabra* and *Lagenammina difflugiformis*. However, as explained in the “Material and Methods” section, we removed all non-fossilising agglutinated taxa and recalculated percentages using only fossilising species (perforates, miliolids and fossilising agglutinates). 23 species present a relative contribution to the fossilising fauna > 5% in at least one core. The spatial distribution of these major species was mapped using the surface mapping software Surfer (Golden Software, version 7.04) (Fig. 2).

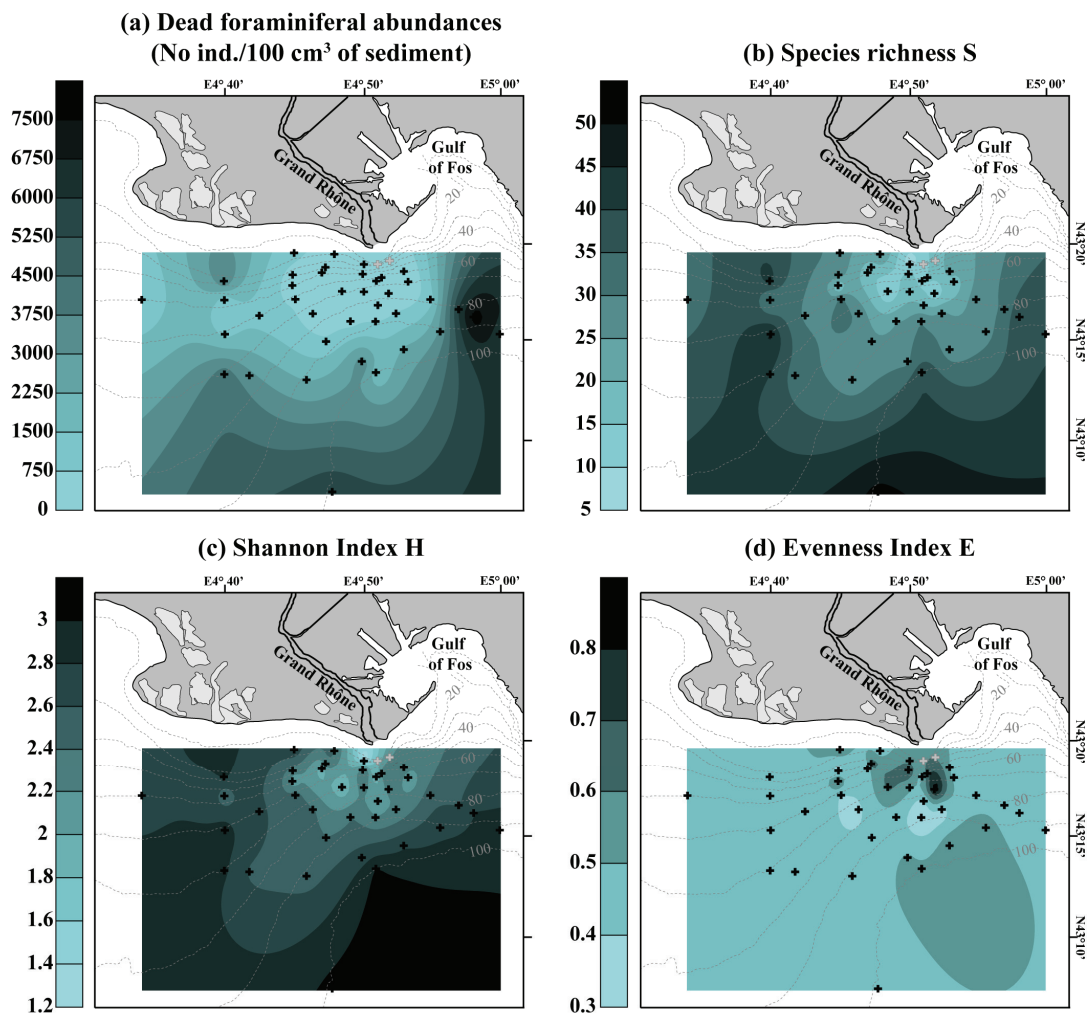


Figure 3: Ecological indices describing fossilising foraminiferal assemblages from the top 5 cm of sediment. (a) Foraminiferal densities (D) normalised for a volume of sediment of 100 cm³; (b) Number of species S; (c)–(d) Biodiversity (H) and Evenness (E) indices.

Fossilising foraminiferal abundances (D) present lowest values ($D < 1000$ ind./100 cm³) from 0 to ~10 km far from the river mouth and along the western coast (Fig. 3a). Species richness (S) and the Shannon index (H) shows a similar spatial pattern, with lowest values ($S < 30$, $H < 2.5$) in a ~10 km wide area around the river mouth. Two corridors of low

biodiversity values appear from the river mouth in south-western direction and along the western coast, in an east-west transect (Fig. 3b,c). Species richness ranges from 6 (Station BT28, 18 m) to 52 (Station BT48, 100 m), whereas the Shannon index (H) varies between 1.19 (Station BT 28) and 3.06 (Station BT48). The Evenness index (E) presents an irregular spatial distribution, with high values close to the river mouth (0.89 at Station M9) and at deeper Stations M19, M20 and M24 (from 0.52 to 0.60). Minimal values (from 0.30 to 0.39) are recorded at intermediate stations (e.g., BT23, BT18, M15) located between 4.4 and 8.9 km far from the mouth (Fig. 3d).

4.3.2. Living – dead comparison

In September 2006 (BEHEMOTH cruise) and June 2005, a total of 26 species present a relative abundance > 5% in the living and/or the dead fossilising faunas (Tables 2 and 3).

Quinqueloculina tenuicollis and *Triloculina trigonula* are observed only in the September 2006 sampling period, these species being relatively more abundant in the living fauna (L/(L+D) values of 1.00 and 0.66, respectively; Table 4). The distinction between *Ammonia tepida* and *Ammonia beccarii* f. *beccarii* was made only in the living and dead faunas of September 2006. *A. tepida* shows higher relative abundances in the dead fauna (L/(L+D) < 0.40; Table 4), whereas more heterogeneous living/dead ratios are recorded for *A. beccarii* f. *beccarii*. Dead individuals of *A. beccarii* f. *beccarii* are relatively more abundant at stations close to the river mouth (Stations BT20, BT24, BT26, BT33, BT39), with L/(L+D) values ranging from 0.11 to 0.41, contrary to stations along the western coast (Stations BT11, BT15, BT18, BT23, BT35) where a higher relative abundance in the living fauna is recorded (L/(L+D) values from 0.51 to 0.79). In June 2005, *Ammonia* spp., grouping *A. beccarii* f. *beccarii* and *A. tepida*, follows the same trend as *A. beccarii* f. *beccarii* in September 2006 (Table 5).

Bulimina marginata, *Elphidium* spp. (i.e., *Elphidium advenum*, *Elphidium crispum*, *Elphidium granosum*, *Elphidium poeyanum*), *Hyalinea balthica* and *Pyrgo oblonga* are relatively more abundant in the dead fauna of both September 2006 (L/(L+D) values from 0 to 0.36; Table 4) and June 2005 (L/(L+D) values from 0 to 0.59; Table 5). On the contrary, living specimens of *Bolivina alata* and *Nonion fabum* show higher relative abundances during both sampling periods (L/(L+D) > 0.45; Tables 4 and 5).

Living-dead comparison of benthic foraminiferal faunas in the Rhône prodelta

Stations	BT1		BT9		BT11		BT15		BT18		BT20		BT22		BT23		BT24	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Ammonia beccarii</i> f. <i>beccarii</i>	0.7	2.3	2.0	0.6	6.2	5.7	2.5	2.1	4.4	1.2	1.4	11.4	1.0	1.5	3.7	1.1	0.9	3.8
<i>Ammonia beccarii</i> f. <i>inflata</i>	0.8	6.0	1.1	1.6	1.2	1.7	1.1	2.6	0.1	–	–	–	1.2	2.4	3.1	0.9	–	–
<i>Ammonia tepida</i>	–	–	–	0.3	0.0	3.4	–	0.2	1.8	2.7	0.5	5.7	–	–	–	–	–	–
<i>Bolivina alata</i>	–	–	–	–	–	–	–	–	–	–	–	–	6.7	2.3	0.3	–	–	–
<i>Bulimina aculeata</i>	0.7	3.2	0.3	0.3	–	0.1	0.6	1.5	0.1	0.6	0.9	–	8.9	10.9	1.6	6.5	0.9	3.1
<i>Bulimina elongata</i>	0.0	0.2	0.6	0.3	4.5	3.2	–	0.6	0.5	0.9	4.2	9.0	–	–	–	–	–	–
<i>Bulimina marginata</i>	0.6	3.3	0.5	5.5	–	0.1	0.1	4.1	–	0.6	0.5	0.3	1.7	8.1	0.0	5.4	–	2.3
<i>Cassidulina carinata</i>	1.3	7.1	2.7	8.4	–	0.7	4.3	21.4	0.3	0.9	–	0.3	4.4	17.3	3.0	43.9	2.7	29.0
<i>Elphidium</i> spp.	0.8	9.8	0.0	4.5	2.1	48.1	0.3	3.2	3.5	9.1	8.4	33.2	0.1	0.3	0.1	1.5	0.2	0.0
<i>Hyalinea balthica</i>	–	0.7	–	–	–	–	0.1	1.9	–	–	–	–	2.9	7.0	0.9	3.4	–	–
<i>Melonis barleeanus</i>	0.1	1.2	–	0.6	–	–	–	0.4	–	–	–	–	3.9	2.4	–	0.4	–	1.5
<i>Nonion fabum</i>	41.5	14.8	44.3	9.4	66.6	6.9	57.1	12.8	37.4	12.5	26.2	4.1	9.8	2.9	45.5	7.9	54.4	1.5
<i>Nonionella turgida</i>	27.2	17.4	23.0	30.0	7.7	5.3	10.3	16.9	13.9	33.7	2.8	2.2	1.4	0.5	7.3	4.3	20.3	25.2
<i>Pseudoepionides falsobeccarii</i>	1.7	9.3	2.6	5.2	0.2	0.3	2.5	2.1	0.9	–	–	–	4.7	2.8	2.4	1.1	1.1	0.8
<i>Rectuvigerina phlegeri</i>	6.1	2.8	5.1	4.8	1.8	0.6	7.9	2.8	9.7	2.7	1.9	0.3	0.4	0.2	4.9	1.5	2.3	1.5
<i>Valvulineria bradyana</i>	7.8	9.5	6.3	14.8	–	1.4	3.6	15.8	14.1	18.5	–	–	16.9	5.7	11.2	10.1	12.7	19.1
<i>Pyrgo oblonga</i>	–	0.2	–	1.0	–	0.1	–	0.2	1.8	0.9	–	–	–	0.3	–	–	–	0.8
<i>Quinqueloculina lata</i>	0.6	–	0.6	–	0.8	1.9	2.2	0.2	4.8	2.1	19.2	8.2	–	–	0.7	0.4	0.3	1.5
<i>Quinqueloculina seminula</i>	0.7	3.3	0.3	2.3	0.0	4.5	0.4	1.3	0.1	1.2	0.0	5.2	4.7	6.3	1.5	1.9	0.3	1.5
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	0.2	0.1	0.1	–	0.7	0.9	11.2	0.0	–	–	–	–	–	–
<i>Triloculina trigonula</i>	0.1	–	0.3	–	–	2.0	–	–	0.1	–	7.0	3.5	–	–	–	–	–	–
<i>Bigenerina nodosaria</i>	0.3	1.2	–	–	–	–	–	–	0.3	–	–	–	8.4	3.1	0.4	–	–	–
<i>Textularia agglutinans</i>	2.8	2.7	5.4	3.9	2.9	1.3	3.9	2.1	2.6	2.1	0.9	–	9.1	3.2	3.7	1.9	0.8	–

Stations	BT26		BT29		BT30		BT33		BT35		BT36		BT37		BT39		BT48	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Ammonia beccarii</i> f. <i>beccarii</i>	4.9	7.7	1.4	0.4	0.9	0.4	2.6	4.4	16.9	16.2	1.3	0.2	1.1	–	3.7	5.5	0.7	0.6
<i>Ammonia beccarii</i> f. <i>inflata</i>	–	–	4.7	5.0	1.3	4.4	0.2	–	–	–	5.6	1.9	2.4	4.3	–	–	2.2	0.7
<i>Ammonia tepida</i>	1.2	1.5	–	–	–	–	1.9	–	6.5	21.2	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	–	–	0.7	0.1	0.3	0.2	–	–	–	–	1.9	1.9	1.5	0.7	–	–	6.8	1.3
<i>Bulimina aculeata</i>	1.6	1.5	4.5	7.3	0.9	2.9	1.0	0.6	0.1	0.2	3.9	8.6	10.9	4.7	1.6	–	11.2	15.0
<i>Bulimina elongata</i>	0.0	3.1	–	–	–	0.7	0.5	–	2.1	1.0	–	–	–	–	0.3	–	–	0.2
<i>Bulimina marginata</i>	0.8	1.5	3.1	12.0	2.0	11.5	0.2	0.6	0.1	–	0.8	10.1	1.9	6.8	1.5	–	5.2	9.3
<i>Cassidulina carinata</i>	2.5	7.7	13.2	21.6	4.3	18.1	0.2	3.1	–	0.2	4.7	21.1	5.0	29.4	20.3	21.9	1.7	13.6
<i>Elphidium</i> spp.	1.2	6.2	2.4	5.3	0.6	4.4	1.3	6.3	5.4	24.7	0.2	0.4	0.3	0.4	0.3	1.4	0.2	0.7
<i>Hyalinea balthica</i>	–	–	0.7	8.4	0.7	4.0	–	–	–	–	1.3	6.1	1.6	8.6	–	–	0.9	6.7
<i>Melonis barleeanus</i>	–	–	0.6	1.8	0.8	0.4	–	–	0.2	–	9.7	7.0	4.1	2.5	–	–	3.7	6.0
<i>Nonion fabum</i>	14.0	4.6	35.9	3.1	31.8	5.5	20.4	5.0	12.2	8.5	7.8	1.4	10.5	1.1	21.1	5.5	2.9	0.9
<i>Nonionella turgida</i>	61.7	50.8	4.5	2.3	14.9	11.5	56.1	49.1	13.4	13.0	4.7	0.0	3.8	1.1	25.3	35.6	0.2	–
<i>Pseudoepionides falsobeccarii</i>	0.4	–	1.8	4.0	1.3	4.6	–	–	–	–	2.8	5.1	2.2	2.9	0.8	–	2.0	2.1
<i>Rectuvigerina phlegeri</i>	0.4	–	2.1	0.3	8.7	0.9	2.6	7.5	1.3	–	0.8	0.3	1.6	1.8	2.8	0.0	0.6	–
<i>Valvulineria bradyana</i>	1.2	–	6.5	6.6	18.8	8.6	0.2	13.2	–	0.7	15.0	5.1	14.3	14.7	13.2	8.2	3.2	2.2
<i>Pyrgo oblonga</i>	–	–	0.2	–	–	–	1.3	1.9	–	–	–	–	–	–	0.9	6.8	–	0.2
<i>Quinqueloculina lata</i>	3.7	0.0	4.3	0.0	0.6	–	5.3	2.5	38.0	4.0	–	–	0.3	–	2.5	0.0	–	–
<i>Quinqueloculina seminula</i>	0.0	3.1	2.7	3.7	1.0	6.0	0.5	–	–	1.3	3.9	2.9	10.8	4.3	0.1	2.7	5.5	5.0
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	2.6	0.0	–	–	–	0.4	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	0.2	–	–	–	0.3	–	–	–	0.4	–	–	–	–
<i>Bigenerina nodosaria</i>	–	–	1.7	2.4	0.1	0.7	–	–	–	–	14.2	4.1	7.2	0.4	–	–	12.7	6.4
<i>Textularia agglutinans</i>	0.8	–	2.6	4.4	4.5	4.6	2.2	0.6	0.1	0.2	3.5	6.4	8.3	2.9	2.3	1.4	4.1	5.2

Table 2: Relative abundances of fossilising species > 5% in the living and/or the dead faunas of September 2006. Grey boxes correspond to percentages > 2.5%, whereas bold values indicate percentages > 5%.

Stations	M2		M3		M4		M5		M6		M7		M8		M9		M10		M12	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Ammonia</i> spp.	9.9	10.2	7.0	12.9	9.1	22.2	12.6	3.8	1.5	2.7	1.0	3.2	1.9	3.2	0.5	3.1	0.0	0.5	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	0.0	0.4	–	–	–	–	–	–	0.2	1.1	–	–	–	–	1.9	9.4	1.9	2.9	5.3	0.5
<i>Bolivina alata</i>	–	–	–	–	0.2	0.0	0.2	0.0	–	–	–	–	–	–	0.5	0.0	0.2	0.0	0.1	0.0
<i>Bulimina aculeata</i>	0.0	0.8	0.3	1.6	0.2	0.0	0.0	0.8	0.6	0.0	0.1	0.0	0.0	1.4	3.2	0.0	5.2	2.9	4.5	1.0
<i>Bulimina elongata</i>	0.2	0.0	9.2	3.2	2.1	3.2	2.6	0.8	0.1	1.1	–	–	0.5	0.5	0.5	0.0	0.7	2.9	0.0	0.5
<i>Bulimina marginata</i>	0.1	0.4	1.3	1.6	0.0	4.8	0.0	2.3	0.0	1.1	0.9	3.2	0.7	2.3	0.9	0.0	2.5	4.3	1.6	8.1
<i>Cassidulina carinata</i>	0.2	7.0	1.0	1.6	2.1	6.3	13.8	21.8	0.6	4.8	5.1	35.5	8.7	37.0	23.1	3.1	22.3	33.3	3.1	23.8
<i>Elphidium</i> spp.	4.6	13.9	3.2	11.3	1.1	9.5	0.7	5.3	1.4	4.3	0.7	0.0	1.6	2.7	0.5	3.1	0.2	1.0	2.0	2.9
<i>Hyalinea balthica</i>	–	–	–	–	–	–	0.0	0.8	–	–	0.1	0.0	0.1	0.5	0.5	0.0	0.5	5.2	0.2	2.9
<i>Melonis barleeanus</i>	0.8	0.0	1.0	0.0	–	–	–	–	–	–	0.3	0.0	–	–	–	–	–	–	0.5	0.5
<i>Nonion fabum</i>	53.2	18.9	34.1	6.5	28.5	9.5	33.0	3.0	55.2	17.0	54.6	9.7	42.5	6.8	25.0	21.9	16.3	7.1	41.4	10.5
<i>Nonionella turgida</i>	15.5	17.6	31.5	22.6	47.6	27.0	21.9	36.8	11.7	11.7	7.6	3.2	12.4	9.6	10.6	0.0	2.9	1.4	9.3	6.7
<i>Pseudoepionides falsobeccarii</i>	–	–	–	–	0.2	0.0	–	–	0.2	0.0	0.1	0.0	–	–	2.8	9.4	1.2	3.3	0.9	3.3
<i>Rectuvigerina phlegeri</i>	5.7	3.7	–	–	0.2	0.0	0.7	0.0	6.4	6.4	1.2	1.6	0.8	0.9	4.2	15.6	3.8	1.0	6.7	1.4
<i>Valvulineria bradyana</i>	7.1	13.9	–	–	1.6	1.6	5.2	3.8	18.7	31.9	24.6	16.1	25.1	13.7	13.4	12.5	7.1	12.4	17.6	14.8
<i>Pyrgo oblonga</i>	0.0	3.7	0.0	1.6	0.0	1.6	0.0	1.5	0.0	0.5	0.4	17.7	0.0	8.2	3.7	6.3	0.5	0.5	0.1	0.0
<i>Quinqueloculina lata</i>	1.0	1.2	10.5	22.6	6.6	4.8	6.2	4.5	0.8	1.1	1.7	0.0	2.2	1.8	0.9	0.0	0.0	1.4	–	–
<i>Quinqueloculina seminula</i>	0.0	3.3	0.0	3.2	0.0	1.6	0.0	3.0	0.1	2.1	0.1	1.6	0.5	0.9	1.4	6.3	8.0	1.4	1.6	2.4
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	0	0.4	–	–	0	1.6	–	–	0	0.5	–	–	–	–	–	–	–	–	–	–
<i>Bigenerina nodosaria</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.0	–	–
<i>Textularia agglutinans</i>	0.6	1.6	–	–	–	–	0.2	1.5	1.8	3.7	0.1	1.6	0.4	0.9	3.7	9.4	18.1	7.1	2.8	6.7

Stations	M13		M14		M15		M16		M18		M19		M20		M22		M23		M24	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
<i>Ammonia</i> spp.	0.0	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	1.4	2.1	2.7	5.0	5.6	1.6	3.0	2.8	1.6	3.7	3.3	3.3	5.8	4.4	6.0	4.7	13.1	2.7	8.1	2.7
<i>Bolivina alata</i>	0.1	0.0	–	–	0.2	0.0	3.2	0.6	0.3	0.7	0.7	1.1	2.4	1.1	0.1	0.8	4.3	0.5	4.5	1.0
<i>Bulimina aculeata</i>	3.5	2.1	8.5	1.4	10.4	3.1	11.6	6.7	6.9	4.7	16.2	7.0	11.8	8.9	5.5	11.1	10.0	13.5	19.9	10.5
<i>Bulimina elongata</i>	0.3	1.0	0.0	0.9	–	–	0.0	0.9	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>	1.0	4.5	0.7	6.0	0.6	6.2	1.1	9.2	0.7	10.0	0.4	10.0	1.0	5.9	1.2	6.4	0.4	8.9	0.0	9.2
<i>Cassidulina carinata</i>	2.1	31.1	14.5	29.8	24.5	44.6	18.6	27.3	17.6	34.2	47.7	17.0	15.8	21.1	38.3	30.6	22.9	28.3	17.5	26.5
<i>Elphidium</i> spp.	0.5	1.7	0.5	0.9	0.1	0.0	0.2	1.2	0.0	0.7	0.2	0.4	–	–	3.1	2.2	0.7	0.8	0.4	0.0
<i>Hyalinea balthica</i>	0.1	2.8	0.3	3.2	1.2	5.2	1.7	7.7	0.8	4.3	3.2	8.5	3.5	5.9	1.8	9.2	1.7	7.8	2.0	7.1
<i>Melonis barleeanus</i>	–	–	–	–	0.1	0.5	1.7	1.8	0.1	0.3	0.5	2.6	7.2	1.1	0.4	0.3	3.0	1.3	2.4	2.7
<i>Nonion fabum</i>	66.0	9.0	48.3	8.3	29.5	5.2	7.4	0.9	42.0	5.3	1.3	5.9	3.1	3.7	17.0	5.8	8.0	2.4	7.1	1.0
<i>Nonionella turgida</i>	10.1	4.5	4.9	1.8	2.9	1.6	3.1	0.9	4.0	2.0	1.4	0.4	0.7	1.5	16.9	1.4	1.7	0.3	1.8	0.7
<i>Pseudoepionides falsobeccarii</i>	0.2	2.1	0.1	1.8	0.6	3.1	1.5	3.1	0.8	5.6	0.6	2.2	2.1	2.2	2.3	3.6	4.2	5.1	0.3	2.4
<i>Rectuvigerina phlegeri</i>	8.2	4.2	8.0	1.8	4.6	1.0	2.5	0.9	4.6	0.7	0.2	0.0	1.0	0.4	0.4	0.6	1.0	0.0	0.7	0.0
<i>Valvulineria bradyana</i>	4.3	19.7	7.9	21.1	13.4	10.9	27.0	9.2	15.6	12.6	4.6	11.8	19.4	14.1	2.7	7.8	15.2	8.1	18.3	7.8
<i>Pyrgo oblonga</i>	0.0	0.7	0.1	0.5	–	–	0.0	0.3	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina lata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	0.0	0.3	0.7	0.5	0.5	0.5	7.6	2.5	1.5	1.3	3.5	5.5	1.4	4.8	0.8	0.8	1.8	2.4	2.5	3.1
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bigenerina nodosaria</i>	–	–	–	–	0.1	0.0	0.2	3.4	–	–	0.9	4.4	4.9	4.4	0.1	0.3	0.9	3.0	1.2	1.7
<i>Textularia agglutinans</i>	1.1	3.1	0.2	0.9	2.0	1.0	0.5	5.5	0.7	3.7	7.3	2.6	10.8	6.3	0.7	2.8	2.7	3.2	2.1	1.4

Table 3: Relative abundances of fossilising species > 5% in the living and/or the dead faunas of June 2005. Grey boxes correspond to percentages > 2.5%, whereas bold values indicate percentages > 5%.

Quinqueloculina seminula and *Pseudoeponides falsobeccarii* show similar to higher relative abundances in the dead than in the living faunas (L/(L+D) values from 0.18 to 0.57 and from 0.15 to 0.54, respectively; Tables 4 and 5). Some exceptions are recorded at Station BT37, M10, M16 and BT22 where living specimens present higher relative abundances (L/(L+D) > 0.63). On the contrary, *Rectuvigerina phlegeri* present higher abundances in the living fauna (L/(L+D) values from 0.50 to 0.62; Tables 4 and 5), except at both Stations BT33 and M9 where this species is better represented in the sub-fossil fauna (L/(L+D) \approx 0.2).

Nonionella turgida and *Valvulineria bradyana* tend to be equally to more abundant in the sub-fossil than in the living fauna from the river mouth to the south-western part of the prodelta (L/(L+D) values from 0.29 to 0.59 and from 0.01 to 0.59, respectively; Tables 4 and 5). However, at eastern and southern stations, living individuals of *N. turgida* (Stations BT1, BT23, BT29, BT36, BT37) and *V. bradyana* (BT22, BT30, BT36, BT39, M16, M23 and M24) are more abundant (L/(L+D) values from 0.61 to 1.00 and from 0.60 to 0.75, respectively; Tables 4 and 5).

Different trends in living/dead ratios are noticed for *Bigenerina nodosaria*, *Bulimina aculeata* and *Cassidulina carinata* in September 2006 and June 2005. *B. nodosaria* is better represented in the living assemblage of September 2006 (L/(L+D) > 0.45; Table 4) whereas dead individuals are relatively more abundant in June 2005 (L/(L+D) values ranging from 0.06 to 0.52; Table 5). *C. carinata* and *B. aculeata* are relatively more abundant in the dead fauna in September 2006 (L/(L+D) values from 0.00 to 0.59 and from 0.18 to 0.57, respectively). Conversely, in June 2005, living specimens of *B. aculeata* (L/(L+D) values from 0.57 to 1.00) and *C. carinata* (L/(L+D) from 0.56 to 0.88) have a much higher relative contribution, especially at stations located from the southern to the south-eastern prodeltaic area (e.g., Stations M9, M10, M19, M20, M23, M24).

The 6 remaining species, i.e., *Ammonia beccarii* f. *inflata*, *Bulimina elongata*, *Melonis barleeanus*, *Quinqueloculina lata* and *Textularia agglutinans*, present more variable L/(L+D) values, i.e., either higher relative abundance in the dead or in the living faunas without clear spatial trend (heterogeneous distribution of living/dead ratios in the prodelta) and/or temporal continuity (i.e., different trends between September 2006 and June 2005 faunas).

Station	BT1	BT9	BT11	BT15	BT18	BT20	BT22	BT23	BT24	BT26	BT29	BT30	BT33	BT35	BT36	BT37	BT39	BT48
Water depth	49	44	26	60	37	15	98	86	79	62	68	60	47	20	89	80	69	100
Distance/River mouth	22.2	14.6	14.0	8.9	7.5	7.8	11.4	5.7	4.4	2.8	17.9	16.5	5.4	3.1	14.4	9.6	4.1	22.4
<i>Ammonia beccarii</i> f. <i>beccarii</i>	-	-	0.52	0.54	0.79	0.11	-	0.77	0.19	0.39	-	-	0.37	0.51	-	-	0.41	-
<i>Ammonia beccarii</i> f. <i>inflata</i>	0.12	-	-	0.31	-	-	-	0.77	-	-	0.49	0.23	-	-	0.74	0.36	-	-
<i>Ammonia tepida</i>	-	-	0.00	-	0.40	0.08	-	-	-	-	-	-	-	0.24	-	-	-	-
<i>Bolivina alata</i>	-	-	-	-	-	-	0.75	-	-	-	-	-	-	-	-	-	-	0.84
<i>Bulimina aculeata</i>	0.18	-	-	-	-	-	0.45	0.20	0.23	-	0.38	0.25	-	-	0.31	0.70	-	0.43
<i>Bulimina elongata</i>	-	-	0.59	-	-	0.32	-	-	-	0.00	-	-	-	-	-	-	-	-
<i>Bulimina marginata</i>	0.14	0.08	-	0.03	-	-	0.17	0.00	-	-	0.21	0.15	-	-	0.07	0.22	-	0.36
<i>Cassidulina carinata</i>	0.15	0.24	-	0.17	-	-	0.20	0.06	0.09	0.24	0.38	0.19	0.05	-	0.18	0.14	0.48	0.11
<i>Elphidium</i> spp.	0.1	0.0	0.04	0.1	0.28	0.20	-	-	-	0.2	0.3	0.1	0.17	0.18	-	-	-	-
<i>Hyalinea balthica</i>	-	-	-	-	-	-	0.29	0.21	-	-	0.07	0.15	-	-	0.18	0.16	-	0.11
<i>Melonis barleeanus</i>	-	-	-	-	-	-	0.62	-	-	-	-	-	-	-	0.58	0.62	-	0.38
<i>Nonion fabum</i>	0.74	0.83	0.91	0.82	0.75	0.86	0.77	0.85	0.97	0.75	0.92	0.85	0.80	0.59	0.85	0.91	0.79	0.75
<i>Nonionella turgida</i>	0.61	0.43	0.59	0.38	0.29	0.56	-	0.63	0.45	0.55	0.66	0.56	0.53	0.51	1.00	0.78	0.42	-
<i>Pseudoepionides falsobeccarii</i>	0.15	0.33	-	0.54	-	-	0.63	-	-	-	0.31	0.22	-	-	0.35	0.43	-	-
<i>Rectivigerina phlegeri</i>	0.69	0.51	-	0.74	0.78	-	-	0.77	-	-	-	0.91	0.25	-	-	-	1.00	-
<i>Vahvulineria bradyana</i>	0.45	0.30	-	0.18	0.43	-	0.75	0.53	0.40	-	0.50	0.69	0.01	-	0.75	0.49	0.62	0.59
<i>Pyrgo oblonga</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.12	-
<i>Quinqueloculina lata</i>	-	-	-	0.69	0.70	-	-	-	-	1.00	1.00	-	0.68	0.90	-	-	1.00	-
<i>Quinqueloculina seminula</i>	0.17	-	0.00	-	-	0.00	0.42	-	-	0.00	0.42	0.15	-	-	0.57	0.71	0.05	0.52
<i>Quinqueloculina tenuicollis</i>	-	-	-	-	-	1.00	-	-	-	-	-	-	-	1.00	-	-	-	-
<i>Triloculina trigonula</i>	-	-	-	-	-	0.66	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bigenerina nodosaria</i>	-	-	-	-	-	-	0.73	-	-	-	-	-	-	-	0.78	0.95	-	0.67
<i>Textularia agglutinans</i>	0.51	0.58	0.58	0.65	0.55	-	0.74	0.67	-	-	0.37	0.49	-	-	0.35	0.74	-	0.44

Table 4: L/(L+D) ratios of fossilising major taxa when the species relative abundance is > 2.5% in the living and/or the dead faunas of September 2006. Blue boxes correspond to L/(L+D) < 0.4 (higher % in dead faunas), pink boxes to values > 0.6 (higher % in living faunas), and black areas to ratios ranging between 0.4 and 0.6.

Station	M2	M3	M4	M5	M6	M7	M8	M9	M10	M12	M13	M14	M15	M16	M18	M19	M20	M22	M23	M24	
Water depth	40	53	60	63	40	65	65	65	80	58	75	85	89	83	85	98	92	74	90	95	
Distance/River mouth	5.0	3.0	3.2	4.2	8.6	5.3	4.5	4.9	7.8	12.8	8.7	7.6	6.9	12.0	10.1	10.3	10.6	17.1	14.1	10.9	
<i>Ammonia</i> spp.	0.49	0.35	0.29	0.77	0.36	0.25	0.37	0.13	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Ammonia beccarii</i> f. <i>inflata</i>	-	-	-	-	-	-	-	0.16	0.40	0.92	-	0.35	0.78	0.52	0.31	0.50	0.57	0.56	0.83	0.75	
<i>Bolivina alata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	0.84	-	-	-	-	-	0.89	0.81
<i>Bulimina aculeata</i>	-	-	-	-	-	-	-	1.00	0.65	0.82	0.63	0.86	0.77	0.63	0.60	0.70	0.57	0.33	0.43	0.65	
<i>Bulimina elongata</i>	-	0.74	0.39	0.78	-	-	-	-	0.19	-	-	-	-	-	-	-	-	-	-	-	
<i>Bulimina marginata</i>	-	-	0.00	-	-	0.22	-	-	0.37	0.16	0.18	0.10	0.09	0.11	0.07	0.04	0.14	0.16	0.05	0.00	
<i>Cassidulina carinata</i>	0.03	-	0.24	0.39	0.11	0.13	0.19	0.88	0.40	0.11	0.06	0.33	0.36	0.41	0.34	0.74	0.43	0.56	0.45	0.40	
<i>Elphidium</i> spp.	0.25	0.22	0.11	0.12	0.25	-	0.37	0.13	-	0.41	-	-	-	-	-	-	-	0.59	-	-	
<i>Hyalinea balthica</i>	-	-	-	-	-	-	-	-	0.09	0.07	0.03	0.08	0.19	0.18	0.16	0.27	0.37	0.17	0.18	0.22	
<i>Melonis barleeanus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.16	0.87	-	0.69	0.46	
<i>Nonion fabum</i>	0.74	0.84	0.75	0.92	0.76	0.85	0.86	0.53	0.70	0.80	0.88	0.85	0.85	0.89	0.89	0.18	0.45	0.74	0.77	0.87	
<i>Nonionella turgida</i>	0.47	0.58	0.64	0.37	0.50	0.70	0.56	1.00	0.67	0.58	0.69	0.73	0.65	0.77	0.67	-	-	-	-	-	
<i>Pseudoepionides falsobeccarii</i>	-	-	-	-	-	-	-	0.23	0.26	0.21	-	-	0.16	0.32	0.12	-	-	0.39	0.45	-	
<i>Rectuvigerina phlegeri</i>	0.61	-	-	-	0.50	-	-	0.21	0.80	0.82	0.66	0.81	0.82	0.73	0.87	-	-	-	-	-	
<i>Vaubulineria bradyana</i>	0.34	-	-	0.58	0.37	0.60	0.65	0.52	0.36	0.54	0.18	0.27	0.55	0.75	0.55	0.28	0.58	0.25	0.65	0.70	
<i>Pyrgo oblonga</i>	0.00	-	-	-	-	0.02	0.00	0.37	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Quinqueloculina lata</i>	-	0.32	0.58	0.58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Quinqueloculina seminula</i>	0.00	0.00	-	0.00	-	-	-	0.18	0.85	-	-	-	-	0.76	-	0.39	0.23	-	-	0.45	
<i>Quinqueloculina tenuicollis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Triloculina trigonula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Bigenerina nodosaria</i>	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-	-	0.16	0.52	-	0.23	-	
<i>Textularia agglutinans</i>	-	-	-	-	0.33	-	-	0.28	0.72	0.30	0.27	-	-	0.08	0.15	0.74	0.63	0.20	0.45	-	

Table 5: L/(L+D) ratios of fossilising major taxa when the species relative abundance is > 2.5% in the living and/or the dead faunas of June 2005. Blue boxes correspond to L/(L+D) < 0.4 (higher % in dead faunas), pink boxes to values > 0.6 (higher % in living faunas), and black areas to ratios ranging between 0.4 and 0.6.

4.3.3. Cluster analyses

Q-mode clustering divides our 39 stations into one isolated station (M9) plus 4 main groups which can be considered as distinct thanatofacies (Fig. 4a). Thanatofacies A groups Stations BT28 and BT35, located in the immediate vicinity of the Rhône River mouth (18–20 m depth, 1–3.1 km from the mouth; Fig. 4b). Thanatofacies B corresponds to Stations BT11 and BT20 along the coast west of the river mouth, and characterised by silty to sandy sediments (15–26 m depth, ~8–14 km from the mouth). Stations BT1, BT9, BT18, BT26, BT33, BT39, M2, M3, M4, M5 and M6 (37–69 m depth, 2.8–22.2 km from the mouth) constitute Thanatofacies C extending from the prodeltaic area (< 60 m depth) to a WSW narrow corridor along the northern border of the Rhône River plume (Fig. 1). The remaining 23 stations constitute Thanatofacies D which extends from the southern border of the prodeltaic area to the outer shelf (58–100 m depth, 4.4–22.4 km far from the mouth).

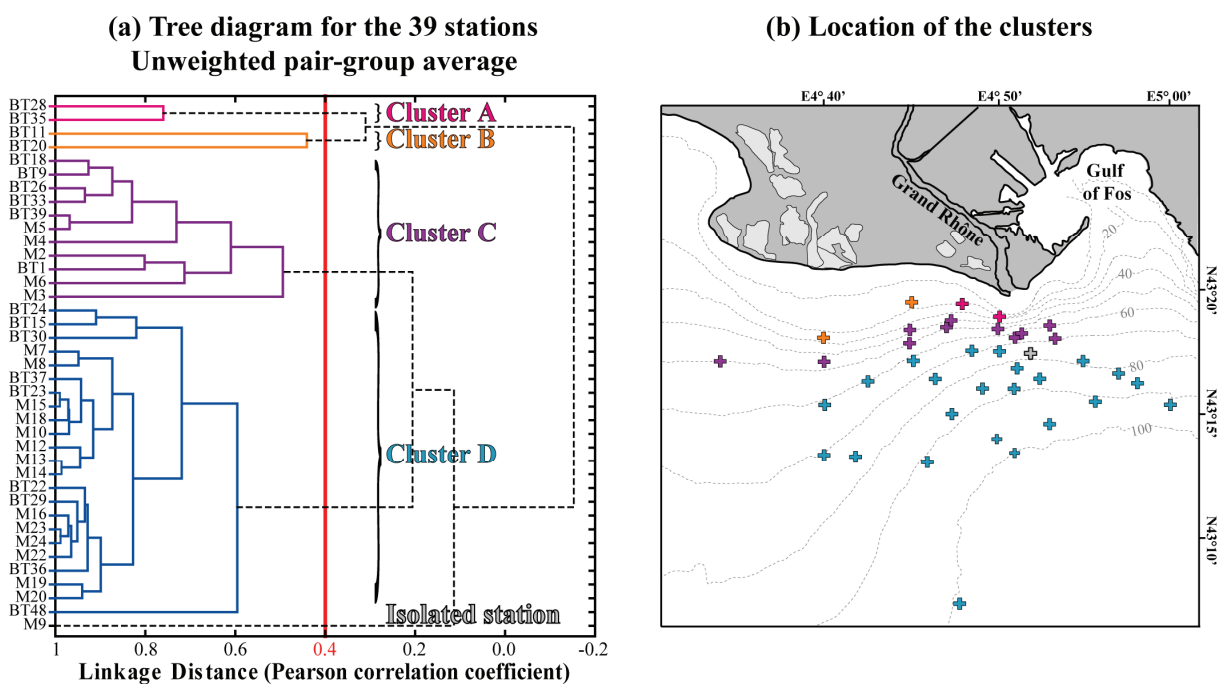


Figure 4: Q-mode cluster analysis of the 39 stations using unweighted pair-group average method, based on percentages of major species (> 5% in at least one station) of the > 150 μm size fraction (a), and location of the groups of stations defined by Q-mode clustering (b).

R-mode cluster analysis performed on the 23 major fossilising species puts in evidence 4 groups of taxa and 3 single species (Fig. 5). Cluster 1 is composed of *Ammonia beccarii* forma *beccarii* and *Ammonia tepida*; Cluster 2 is constituted by *Elphidium advenum*, *Elphidium crispum*, *Bulimina elongata*, *Elphidium granosum*, *Elphidium poeyanum* and

Quinqueloculina lata; Cluster 3 contains *Rectuvigerina phlegeri*, *Nonion fabum*, and *Valvulineria bradyana*; Cluster 4 is composed of *Ammonia beccarii* forma *inflata*, *Pseudoeponides falsobeccarii*, *Textularia agglutinans*, *Quinqueloculina seminula*, *Bigenerina nodosaria*, *Melonis barleeanus*, *Bulimina aculeata*, *Hyalinea balthica*, and *Bulimina marginata*. *Cassidulina carinata*, *Nonionella turgida* and *Pyrgo oblonga* constitute the three single taxa. The spatial distribution of the cumulative percentages in the living (September 2005 and June 2005) and the dead faunas of these species and species groups is pictured in figure 6.

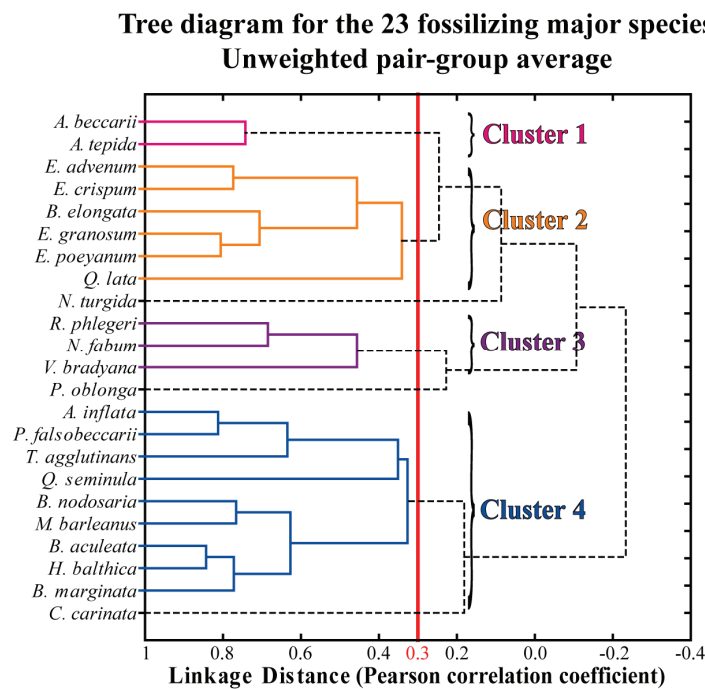


Figure 5: R-mode cluster analyses of the 23 fossilizing species using unweighted pair-group average method, based on percentages of major species (> 5% in at least one station) of the > 150 μm size fraction.

4.4. DISCUSSION

4.4.1. Living – dead comparison

The use of foraminiferal faunas in paleoenvironmental studies is generally based on the comparison of the fossil record with modern sub-fossil and/or living assemblages. However, important differences in faunal composition may be observed between living and dead faunas at the same site (Murray, 1991; Jorissen and Wittling, 1999). Therefore, identifying these differences and the responsible taphonomical (e.g., transport, dissolution)

and biological processes (e.g., population dynamics) is a key condition before applying the benthic foraminiferal tool to paleoenvironmental reconstructions.

In the Rhône prodelta, sub-fossil and living foraminiferal assemblages were studied during two contrasted periods. In September 2006 (BEHEMOTH cruise), sampling took place during low discharge and low primary production conditions, whereas high primary production prevailed in surface waters of the Gulf of Lions in June 2005 (MINERCOT 2). The comparison of living and dead foraminiferal faunas observed during these two sampling periods put into evidence three groups of species: (1) species more abundant in the living fauna; (2) taxa with higher relative abundances in the sub-fossil fauna; (3) taxa without a clear pattern presenting both compartments. For some species, the pattern even changed depending on the studied sampling period. These three different patterns may be explained in three possible ways: (1) transport processes leading to an export/input of autochthonous/allochthonous individuals, (2) seasonal variability in the production of individuals, and/or (3) post-mortem physico-chemical destruction of the test (i.e., fossilisation rate).

4.4.1.1. Transport processes

Transport processes are important at shallowest stations from the river mouth to the western coast. The coast west of the Rhône River mouth is an erosional area where wave-generated longshore currents laterally redistribute the sediments (Fig. 1; Sabatier and Suanez, 2003). This erosional pattern leads to an outcrop of the sediments of the relict deltaic lobe of Bras de Fer (Blanc, 1977; L'Homer, 1993; Sabatier et al., 2006). When this deltaic lobe was active (365–239 yr Before Present, i.e., 1585–1711 Anno Domini; Colomb et al., 1975; Vella et al., 2005), foraminiferal faunas from these sediments were dominated by *Elphidium* species (A.-S. Fanget, personal communication). Therefore, higher relative abundances of *Elphidium* species observed in the dead faunas from this area may be related to a mixing of a relict fossil assemblage with modern sub-fossil faunas. The redistribution of the sediments in this shallow area may also affect benthic foraminiferal faunas, leading to a heterogeneous distribution of both living and dead specimens of the species thriving in this area. It would so explain the absence of clear trend in the living/dead ratio of *Bulimina elongata* and *Quinqueloculina lata*.

Transport processes may also bring allochthonous species from surrounding environments. For example, *Ammonia beccarii* f. *beccarii* is a taxon adapted to a wide range of environmental conditions. In the present study area, living and dead specimens have been reported from the interdistributaries of the Rhône deltaic system (i.e., inner shore

environments) to shallow coastal marine areas (i.e., from 0 to ~60 m depth) (Kruit, 1955; Blanc-Vernet, 1969; Goineau et al., In Press – see Chapter 1 in this thesis). Therefore, allochthonous input from these environments either during Rhône flood events or under the action of longshore currents would explain the relatively higher abundances of dead specimens of *A. beccarii* f. *beccarii* recorded in the vicinity of the Rhône River mouth.

4.4.1.2. Biological processes

Biological processes depend on the ecology of the considered foraminiferal species, particularly on differences in production rates between species. Production rate may also vary both in time and space for one considered species.

Seasonal variability in the production rate of living *Ammonia tepida*, *Bulimina aculeata*, *Bulimina marginata*, *Cassidulina carinata*, *Hyalinea balthica*, *N. turgida* and *Valvulineria bradyana* has been well illustrated in previous works. A temporal study performed at a shallow station in the vicinity of the Rhône River mouth (see Chapter 3 in this thesis) put into evidence important temporal changes in the absolute and relative abundances of *A. tepida*, depending on the Rhône River influence (i.e., Rhône discharge). Similarly, *B. aculeata*, *B. marginata*, *C. carinata*, *H. balthica*, *N. turgida* and *V. bradyana* are reported as opportunistic species able to respond to fresh organic phytodetritus input by increased reproduction (e.g., Jorissen, 1987; Van der Zwaan and Jorissen, 1991; Barmawidjaja et al., 1992; Jorissen et al., 1992; Levy et al., 1995; De Rijk et al., 2000; Donnici and Serandrei Barbero, 2002; Fontanier et al., 2003, 2008a; Kitazato et al., 2003; Nomaki et al., 2005a, 2005b, 2006; Eberwein and Mackensen, 2006; Langezaal et al., 2006; Diz and Francés, 2008; Duchemin et al., 2008; Rossi and Vaiani, 2008). In the present study, low primary production conditions prevailed in September 2006 whereas June 2005 was characterised by late spring bloom conditions. Therefore, the higher relative contribution of *A. tepida*, *B. aculeata/marginata*, *C. carinata*, *H. balthica*, *N. turgida* and *V. bradyana* to the dead faunas would be related to a larger production of living individuals during another period. For *B. aculeata*, *C. carinata* and *N. turgida*, this period would correspond to the late spring bloom conditions as proved by the higher relative abundance of living individuals at stations located in the southern to south-eastern prodeltaic area in June 2005 (Goineau et al., In Press – see Chapter 1). For *N. turgida*, this stronger production rate has been put into evidence at a station located in the prodeltaic area (68 m depth, 4.5 km far from the mouth) where higher absolute and relative abundances of living individuals of *N. turgida* were reported during productive conditions of May 2008 (see Chapter 3). Nevertheless, the observation of moderate

abundances of *N. turgida* in sub-fossil faunas also supposes a loss of information from the living fauna to sub-fossil record, linked either to the fragility of its test and/or to the supposed high deposition rates prevailing in this part of the Rhône prodelta.

These opportunistic species, producing punctually numerous living individuals, have a noticeable influence on the living/dead ratios of less opportunistic taxa. The production of numerous individuals by opportunistic species decreases the relative contribution in the sub-fossil fauna of species with a lower or a more constant production rate over the year. This hypothesis can be assumed for *Nonion fabum*. This taxon has a significantly reduced relative abundance in the sub-fossil assemblage despite its relatively high percentages in the living fauna of the Rhône prodelta under a wide range of environmental conditions (i.e., from productive spring bloom to more oligotrophic conditions of the late summer; Mojtahid et al., 2009; Goineau et al., In Press – see Chapters 1 and 3).

4.4.1.3. Fossilisation rate

Fossilisation rates of benthic foraminifera depend on the fragility of the test. The dissolution/fragmentation of a test during taphonomical processes leads to a loss of individuals in the sub-fossil faunas. Miliolids are known to be particularly fragile species, their test being easily dissolvable. In the Rhône prodelta, two miliolids (i.e., *Quinqueloculina tenuicollis* and *Triloculina trigonula*) are particularly affected by this phenomenon, individuals being almost totally absent in the dead faunas. Perforate species such as *Bolivina alata* and *Rectuvigerina phlegeri* present thin and fragile tests which chambers are easily broken (see Appendix 1, Plates 1–2, Photos 6, 9 and 16 at the end of this manuscript,), leading to their possible destruction during fossilisation processes.

4.4.2. Foraminiferal thanatofacies

In the Rhône prodelta, cluster analyses performed on dead assemblages put in evidence four groups of stations and species (thanatofacies) (Fig. 6). The spatial distribution of these thanatofacies defines four distinct areas in the Rhône prodelta (Fig. 4b).

Thanatofacies A (Stations BT28 and BT35) is located in the vicinity of the river mouth. In this area, foraminiferal faunas are dominated by species of Cluster 1 grouping *Ammonia tepida* and *Ammonia beccarii* f. *beccarii* (Fig. 6a). The correlation matrix calculated between the relative abundances of *A. beccarii* f. *beccarii* and *A. tepida* in the living and the dead faunas put into evidence their significantly similar spatial distribution in both

assemblages (correlation coefficient $r = 0.74$ in September 2006 and 0.89 in June 2005; $p < 0.001$; Table 6). The association of these species is typical of shallow coastal environments in the vicinity of river mouths (Jorissen, 1987; Donnici and Serandrei Barbero, 2002; Mendes et al., 2004; Rossi and Vaiani, 2008; Frezza and Carboni, 2009). As assumed above (see § 4.4.1.1.), allochthonous living and/or dead individuals of *A. beccarii* f. *beccarii* might be supplied from the river and/or from shallower environments during Rhône River flood and/or under the action of longshore currents.

Taxa	September 2006		June 2005	
	r	p	r	p
<i>A. beccarii</i> f. <i>beccarii</i>	0.75	0.0003		
<i>A. tepida</i>	0.91	0.0000		
Total Cluster 1	0.89	0.0000	0.74	0.0002
<i>B. elongata</i>	0.78	0.0002	0.66	0.0015
<i>Elphidium</i> spp.	0.69	0.0017	0.78	0.00005
<i>Q. lata</i>	0.70	0.0012	0.89	0.0000
Total Cluster 2	0.67	0.0023	0.96	0.0000
<i>N. fabum</i>	0.52	0.0258	0.53	0.0168
<i>R. phlegeri</i>	0.38	0.1167	0.42	0.0683
<i>V. bradyana</i>	0.43	0.0765	0.36	0.1238
Total Cluster 3	0.63	0.005	0.62	0.0038
<i>A. beccarii</i> f. <i>inflata</i>	0.46	0.0554	0.30	0.2004
<i>B. nodosaria</i>	0.87	0.0000	0.71	0.0005
<i>B. aculeata</i>	0.80	0.00006	0.73	0.0003
<i>B. marginata</i>	0.66	0.003	0.06	0.7986
<i>H. balthica</i>	0.81	0.00004	0.82	0.00001
<i>M. barleeanus</i>	0.90	0.0000	0.46	0.0396
<i>P. falscobeccarii</i>	0.51	0.0324	0.72	0.0003
<i>Q. seminula</i>	0.42	0.082	0.12	0.6195
<i>T. agglutinans</i>	0.54	0.022	0.57	0.0088
Total Cluster 4	0.86	0.00001	0.88	0.0000
<i>C. carinata</i>	0.44	0.0708	0.29	0.2193
<i>N. turgida</i>	0.91	0.0000	0.80	0.0000
<i>P. oblonga</i>	0.51	0.0299	0.30	0.1993

Table 6: Correlation coefficients between living and dead fossilising faunas of September 2006 and June 2005.

Dark-grey boxes indicate correlation coefficients with $p > 0.05$.

In September 2006, the association of living *A. beccarii* f. *beccarii* and *A. tepida* was related to low-oxygenated sediments enriched in continental organic matter (Goineau et al., In Press

– see Chapter 1). In a study of temporal variability performed in the vicinity of the Rhône River mouth, *A. tepida* was reported under high Rhône discharge conditions and after a major input of riverine sediments (see Chapter 3). Therefore, the presence of *A. beccarii* f. *beccarii* and *A. tepida* in sub-fossil assemblages is characteristic of very high riverine influence in terms of organic inputs and hydro-sedimentary processes (i.e., bottom currents, sediment input).

Thanatofacies B corresponds to the silty-sandy coastal area located west of the river mouth (Stations BT11 and BT20). This area is characterised by maximal abundances of Cluster 2 taxa (i.e., *Bulimina elongata*, *Elphidium* spp and *Quinqueloculina lata*; Fig. 6b). *B. elongata*, *Elphidium* spp and *Q. lata* follow the same spatial distribution pattern in both living and dead faunas of June 2005 and September 2006 ($r = 0.96$ and 0.67 , respectively; $p < 0.01$; Table 6). In September 2006, this area is characterised by low sedimentary organic carbon and labile organic matter (i.e., lipids, amino-acids) contents of continental origin. In this area, bottom currents may significantly disturb the benthic environment. *B. elongata* and *Elphidium* spp. have already been reported thriving in silty to sandy substrates from shallow marine sediments under riverine influence (Jorissen, 1988; Barmawidjaja et al., 1992; Bellotti et al., 1994; Frezza and Carboni, 2009). Therefore, species belonging to Thanatofacies 2 depict coastal silty to sandy environments submitted to strong bottom currents.

The single taxon *Nonionella turgida* and species belonging to Cluster 3 (*Nonion fabum*, *Rectuvigerina phlegeri* and *Valvulineria bradyana*) present highest relative abundances at stations from Thanatofacies C (Fig. 6c,f). *N. turgida* and the association of *N. fabum*, *R. phlegeri* and *V. bradyana* are negatively correlated with foraminiferal abundances ($r = -0.47$ and -0.38 , respectively, with $p < 0.01$; Table 7). Important sediment inputs lead to a dilution of dead faunas, traduced by the observation of low foraminiferal abundances. Consequently, *N. turgida*, *N. fabum*, *R. phlegeri* and *V. bradyana* would be indicative of high sediment deposition rates in the prodelta. *N. turgida* is also negatively correlated with species richness (S) and biodiversity index (H) ($r = -0.48$ to -0.42 ; Table 7). These two indices are closely related to foraminiferal abundances D. Since Cluster 3 species do not present such high correlation with S and H, *N. turgida* would tolerate a more important riverine pressure (deposition rate) than *N. fabum*, *R. phlegeri* and *V. bradyana*. This is in agreement with studies performed in the vicinity of river mouths (e.g., Po River, Ría de Vigo; (Jorissen, 1987; Van der Zwaan and Jorissen, 1991; Barmawidjaja et al., 1992; Donnici and Serandrei Barbero, 2002; Diz and Francés, 2008; Rossi and Vaiani, 2008), where *N. turgida* was

reported as an opportunistic and stress-tolerant taxon living in hypoxic sediments enriched in low-quality OM.

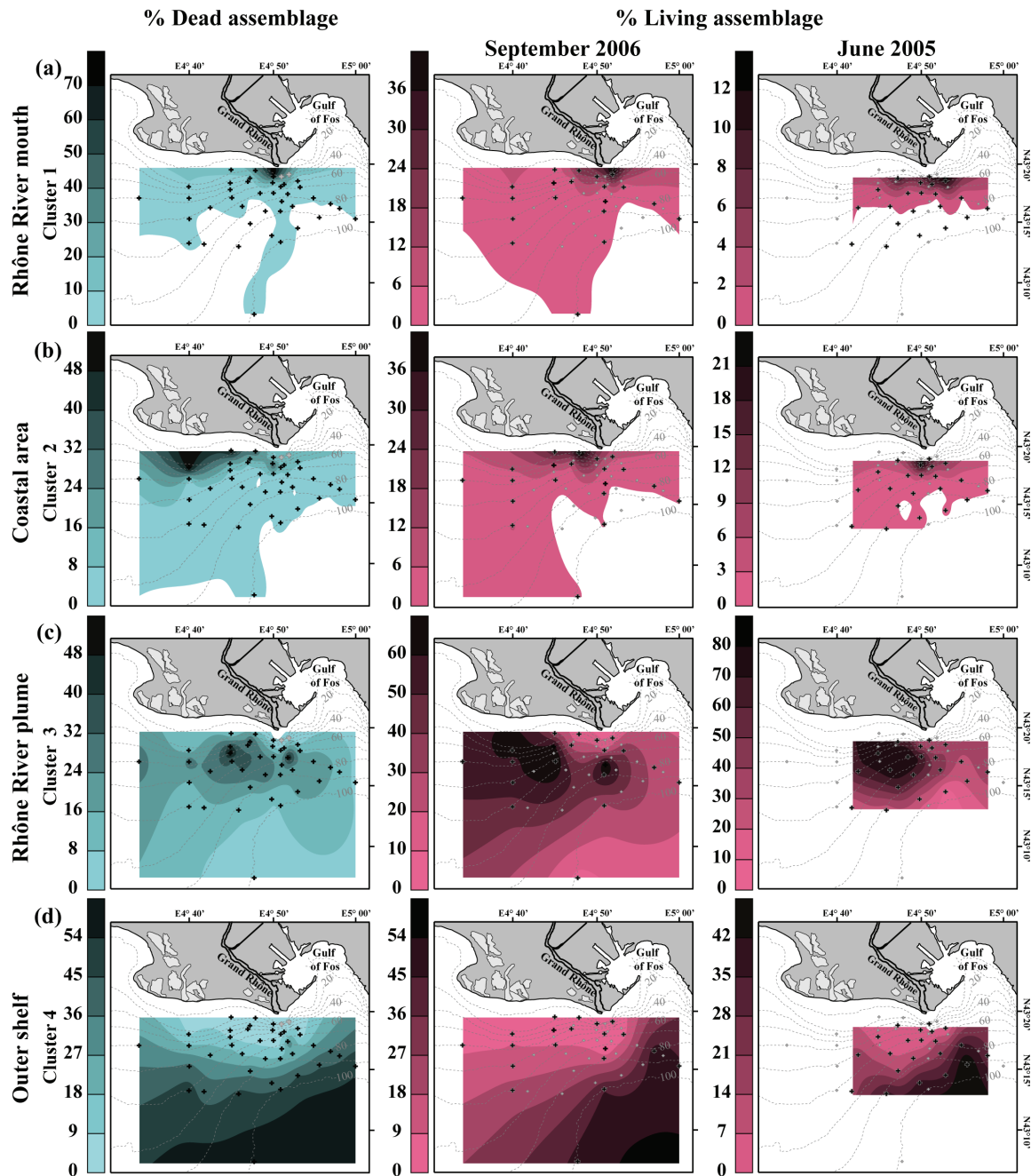


Figure 6: Spatial distribution in the dead and the living faunas of September 2006 and June 2005 of the groups of species determined by R-mode cluster analysis. Cluster 1: *A. beccarii* f. *beccarii*, *A. tepida*; Cluster 2: *B. elongata*, *Elphidium* spp., *Q. lata*; Cluster 3: *N. fabum*, *R. phlegeri*, *V. bradyana*; Cluster 4: *A. beccarii* forma *inflata*, *B. nodosaria*, *B. aculeata*, *B. marginata*, *H. balthica*, *M. barleeanus*, *P. falsobeccarii*, *Q. seminula* and *T. agglutinans*.

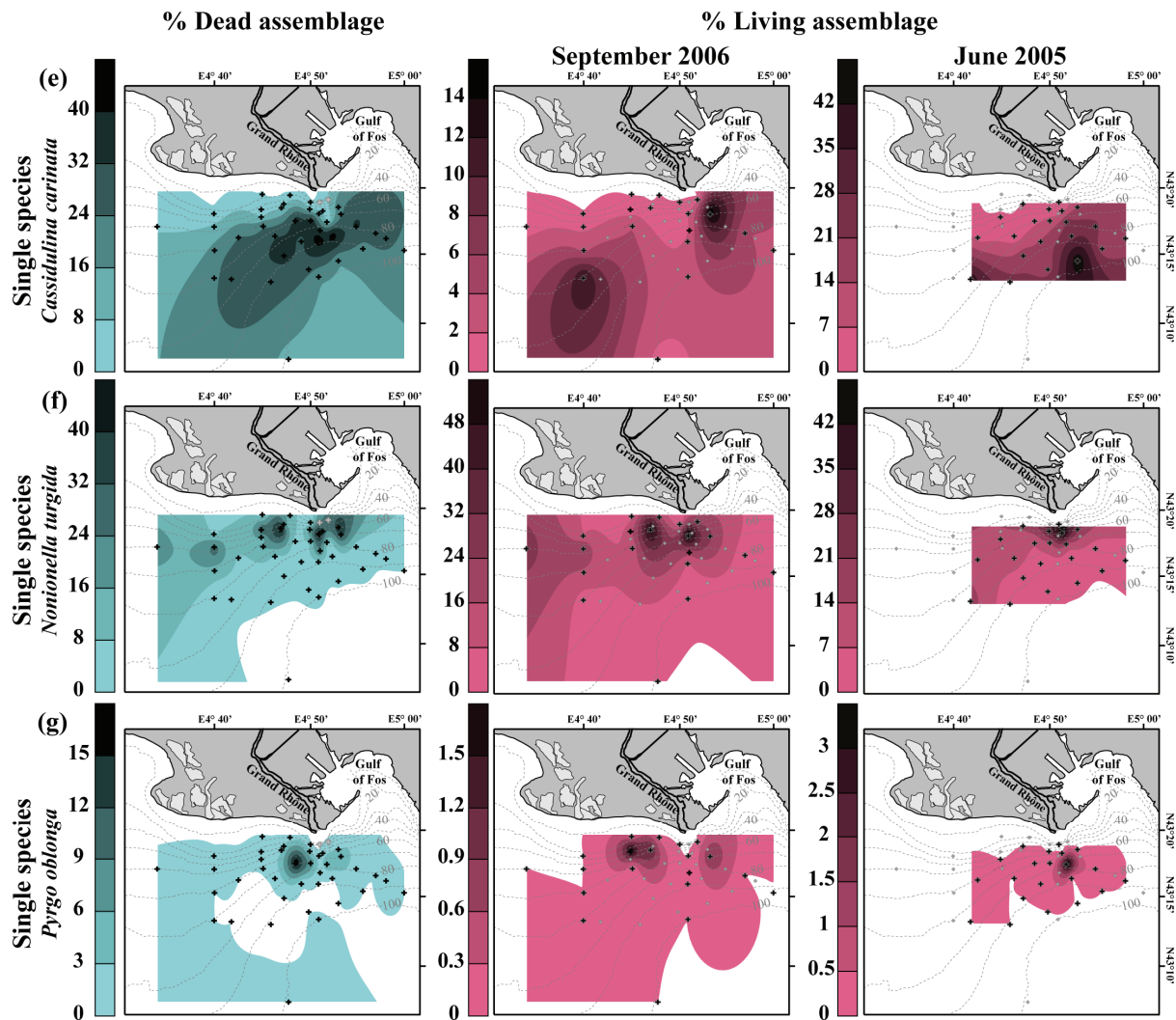


Figure 6 (continued)

N. turgida and the association of *N. fabum*, *R. phlegeri* and *V. bradyana* present a similar spatial distribution in the Rhône prodelta in both living and sub-fossil faunas of June 2005 and September 2006 ($r > 0.62$, $p < 0.01$; Table 6). However, if we focus on each species, *R. phlegeri* and *V. bradyana* do not show significant positive correlations ($p > 0.05$). *R. phlegeri* is observed closer to the coast in the sub-fossil (Station BT33, M6, M13; 40–75 m depth) than in the living fauna (Stations BT30 and M12; > 13 km far from the mouth; Tables 2 and 3). Concerning *V. bradyana*, maximal abundances of living individuals in September 2006 and June 2005 are found at farther stations than in sub-fossil record, i.e., in areas submitted to both riverine and marine influences (Tables 2 and 3). The distribution of *N. fabum*, *R. phlegeri* and *V. bradyana* into a south-western direction in the living faunas of June 2005 and September 2006 is in agreement with the yearly mean position of the river plume suggested by Naudin et al. (1997). The distribution of these species closer to the coast in sub-fossil faunas can be explained in two different ways. The first hypothesis is that the Rhône River

plume would spread along an east-west transect most of the year. Since the marine extension and shape of the Rhône River plume depend on Rhône River outflow, wind regime and the strength of the North Mediterranean Current (Naudin et al., 1997), it would only occasionally extend far offshore along a south-western corridor. However, this is apparently not in agreement with the south-western yearly mean position described by Naudin et al. (1997). A second hypothesis supposes a westward transport of dead foraminiferal faunas. The Rhône prodelta is under the influence of south-eastern to south-western swells (Fig. 1) remobilising efficiently sediment from the continental shelf, especially during storms events (Brunel, 2010). Mojtahid et al. (2010) showed that *R. phlegeri* and *V. bradyana* were thriving in shallower sediment levels than *N. turgida* and *N. fabum* at stations located under the river plume. Therefore, the sedimentary transport induced by storm swells may obviously have an impact on the composition of dead foraminiferal faunas, especially on *R. phlegeri* and *V. bradyana* thriving in the top most centimetre of sediment in this area. Individuals of these two species would be transported from the east (living assemblages) to the west (sub-fossil faunas) along isobaths.

	<i>C.carinata</i>	<i>N.turgida</i>	<i>P.oblonga</i>	Cluster 1	Cluster 2	Cluster 3	Cluster 4
Cluster 1	-0.48 <i>p</i> =0.002	0.04 <i>p</i> =0.816	-0.05 <i>p</i> =0.777	/			
Cluster 2	-0.59 <i>p</i> =0.000	0.16 <i>p</i> =0.335	-0.10 <i>p</i> =0.533				
Cluster 3	-0.01 <i>p</i> =0.970	0.06 <i>p</i> =0.728	0.27 <i>p</i> =0.101				
Cluster 4	0.33 <i>p</i> =0.040	-0.60 <i>p</i> =0.000	-0.32 <i>p</i> =0.049				
D	0.17 <i>p</i> =0.310	-0.47 <i>p</i> =0.002	-0.31 <i>p</i> =0.056	-0.26 <i>p</i> =0.114	-0.12 <i>p</i> =0.453	-0.38 <i>p</i> =0.017	0.72 <i>p</i> =0.000
S	0.13 <i>p</i> =0.437	-0.42 <i>p</i> =0.008	-0.46 <i>p</i> =0.003	-0.41 <i>p</i> =0.010	0.00 <i>p</i> =0.995	-0.20 <i>p</i> =0.215	0.65 <i>p</i> =0.000
H	0.03 <i>p</i> =0.850	-0.48 <i>p</i> =0.002	-0.31 <i>p</i> =0.053	-0.52 <i>p</i> =0.001	0.13 <i>p</i> =0.439	-0.07 <i>p</i> =0.652	0.67 <i>p</i> =0.000
E	-0.35 <i>p</i> =0.028	-0.04 <i>p</i> =0.798	0.42 <i>p</i> =0.007	0.20 <i>p</i> =0.219	0.19 <i>p</i> =0.257	0.12 <i>p</i> =0.476	-0.10 <i>p</i> =0.541

Table 7: Correlation matrix between single species, biofacies and ecological indices describing dead foraminiferal faunas. Dark-grey boxes indicate correlation coefficients with *p* > 0.05.

The last Thanatofacies D corresponds to stations located in the south-eastern part of the study area. This outer shelf thanatofacies is inhabited by *Ammonia beccarii* f. *inflata*, *Bigenerina nodosaria*, *Bulimina aculeata*, *Bulimina marginata*, *Hyalinea balthica*, *Melonis*

barleeanus, *Pseudoeponides falsobeccarii*, *Quinqueloculina seminula* and *Textularia agglutinans* (Cluster 4; Fig. 6d). This foraminiferal fauna presents significant positive correlations with foraminiferal abundances D ($r = 0.72$), species richness S ($r = 0.65$) and diversity index H ($r = 0.67$) (Table 7), describing faunas living out of the main riverine influence (low deposition rate; see above). In June 2005 and September 2006, living specimens of Cluster 4 species are also observed in this outer shelf area ($r = 0.88$ and 0.86 , respectively; $p < 0.001$; Table 6 and Fig. 6d). However, the spatial distribution of *A. beccarii* f. *inflata*, *B. marginata* and *Q. seminula* do not present significant positive correlations between living and sub-fossil faunas ($p > 0.05$; Table 6). Living individuals of these species are restricted to the south-eastern part of the study area, whereas sub-fossil specimens are observed as far as Stations BT1 and M12 along the western coast (~13 to 22.2 km far from the mouth; Fig. 2). As assumed for Cluster 3 species, dead individuals of *A. beccarii* f. *inflata*, *B. marginata* and *Q. seminula* could have been transported westward by south-western swells. However, the action of storm swells may be reduced in this area when considering the deeper location of Thanatofacies D compared to Thanatofacies C. An alternative explanation is that *A. beccarii* f. *inflata*, *B. marginata* and *Q. seminula* would be able to thrive in sediments located far western during minimal extension of the Rhône River plume.

The single species *Cassidulina carinata* presents maximal percentages at stations located on the northern border of the outer shelf area (i.e., Thanatofacies D), from Stations M15, BT23, M8, M7 to Station M22 (Fig. 6e, Tables 2 and 3). However, living specimens of *C. carinata* occupy more sporadically the Rhône prodelta, with patches of maximal abundances (e.g., Stations BT39, BT29, M19, M22; from 4.1 to ~18 km far from the mouth; Fig. 6e, Tables 2 and 3), leading to the significantly different spatial distribution pattern between the living and the sub-fossil faunas of September 2006 and June 2005 ($r = 0.44$ and 0.29 , respectively, $p > 0.05$; Table 6). The opportunistic response of *C. carinata* ($r = -0.35$ with the Evenness index, $p < 0.05$; Table 7) to fresh phytodetritus input would lead to heterogeneous growth of this species both in space and time, explaining the significantly different distribution patterns in the living and the sub-fossil faunas. Nevertheless, the homogeneous time-averaged dead fauna of *C. carinata* concentrates in an area submitted to both riverine and marine influences, where this species would respond with an opportunistic behaviour (low Evenness index) to fresh organic matter inputs during eutrophic conditions (i.e., spring bloom).

4.5. CONCLUSIONS

Investigating dead benthic foraminiferal faunas preserved in the Rhône prodelta permitted us better understanding taphonomical processes acting on benthic foraminiferal assemblages in this area. Some taxa suffer important loss from living to dead assemblages (e.g., *Bolivina alata*, *Quinqueloculina tenuicollis*, *Triloculina trigonula*) due to the possible fragility of their test. From the river mouth to the shallow western coast, transport processes induced by strong bottom currents would explain either higher concentration due to an input of allochthonous individuals (e.g., *Ammonia beccarii* f. *beccarii*) or a heterogeneous distribution (e.g., *Bulimina elongata*, *Quinqueloculina lata*) in the sub-fossil fauna of species thriving in this area. Farther from these shallow environments, biological processes explain differences observed in the living/dead ratios of the species. Potentially opportunistic species producing numerous individuals, notably during eutrophic periods, are better represented in the dead fauna when sampling is performed out of their main production period (e.g., *Bulimina aculeata*, *Bulimina marginata*, *Hyalinea balthica*, *Nonionella turgida*, *Valvulineria bradyana*). The heterogeneous temporal and spatial growth of such opportunistic species would also lead to a patchy distribution in the living faunas over the whole prodelta (e.g., *Bulimina aculeata*, *Cassidulina carinata*). As a result, less opportunistic taxa producing fewer individuals (e.g., *Nonion fabum*, *Rectuvigerina phlegeri*) are under-represented in the sub-fossil faunas.

In parallel, the time-averaged foraminiferal fauna investigated through sub-fossil assemblages divides the study area into four thanatofacies. The river mouth thanatofacies is inhabited by *Ammonia beccarii* f. *beccarii* and *Ammonia tepida*. It constitutes the most Rhône River-impacted area of the whole prodelta. *Bulimina elongata*, *Elphidium* spp. and *Quinqueloculina lata* dominate the faunas in the sandy-silty coast west of the river mouth submitted to strong bottom currents. *Nonionella turgida* dominates foraminiferal faunas in a zone supplied by important sediment input. Typical “river plume” faunas are found along the coast west of the Rhône River mouth, whereas the living specimens of these taxa are slightly more abundant in a south-western corridor. It suggests a westward shift of the dead individuals under the action of south-eastern storm swells. In the more stable and unstressed outer shelf thanatofacies extending from the south-eastern to the south-western part of the study area, species able to feed on fresh phytodetritus with a supposedly opportunistic life strategy dominate the faunas (e.g., *Bigenerina nodosaria*, *Bulimina aculeata/marginata*, *Hyalinea balthica*, *Textularia agglutinans*). In sediments influenced by both riverine and marine influences, i.e., on the

northern border of the outer shelf thanatofacies, the opportunistic taxon *Cassidulina carinata* benefits from fresh organic matter supplied to the seafloor during the most productive seasons. For all investigated stations, the differences observed in the relative abundances and also the distributional patterns of these foraminiferal assemblages in the living and the dead faunas constitute minor variations which do not prevent interpreting well the sub-fossil archive. Therefore, the definition of these thanatofacies, characterised by clear foraminiferal assemblages reflecting accurately local environmental conditions, gives us a precious tool to investigate the paleo-Rhône prodelta through the study of fossil foraminiferal archives.

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APPENDICES

Appendix A

Total dead benthic foraminiferal counts (level 3–4 cm depth within the sediment) for the September 2006 sampling campaign (*BEHEMOTH* cruise). “D” corresponds to the normalised absolute abundance (No ind./100 cm³ of sediment) for each species at each station; “%Tot” indicates the relative abundance in the total fauna of each species at each station, whereas “%Fos” correspond to the relative abundance of each species in the fossilising fauna (i.e., perforates, miliolids and fossilising agglutinated taxa). Grey boxes indicate percentages and species > 5%.

Appendix B

Taxonomic reference list for major taxa.

Appendix A

Taxa	Station		BT1		BT9		BT11		BT15		BT18		BT20	
	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
Perforates														
Indet.	–	–	–	–	–	–	–	–	1	0.2	1	0.3	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	19	2.3	6	0.6	222	5.7	14	2.1	6	1.2	117	11.4	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	50	6.0	14	1.6	67	1.7	17	2.6	–	–	–	–	–	–
<i>Ammonia perlucida</i>	–	–	–	–	–	–	–	–	–	–	–	–	8	0.8
<i>Ammonia tepida</i>	–	–	3	0.3	133	3.4	1	0.2	13	2.7	58	5.7	–	–
<i>Ammonia parkinsoniana</i>	–	–	–	–	44	1.1	–	–	–	–	–	–	31	3.0
<i>Amphicoryna scalaris</i>	21	2.5	14	1.6	11	0.3	15	2.4	8	1.8	3	0.3	–	–
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>	–	–	–	–	22	0.6	–	–	–	–	–	–	–	–
<i>Bolivina spathulata</i>	–	–	–	–	11	0.3	1	0.2	–	–	–	–	–	–
<i>Bolivina striatula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina subaenariensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Buccella granulata</i>	–	–	–	–	11	0.3	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>	26	3.2	3	0.3	6	0.1	10	1.5	3	0.6	–	–	–	–
<i>Bulimina costata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>	1	0.2	3	0.3	122	3.2	4	0.6	4	0.9	92	9.0	–	–
<i>Bulimina gibba</i>	–	–	–	–	–	–	3	0.4	–	–	–	–	–	–
<i>Bulimina marginata</i>	28	3.3	47	5.5	6	0.1	26	4.1	3	0.6	3	0.3	–	–
<i>Cassidulina carinata</i>	60	7.1	72	8.4	28	0.7	139	21.4	4	0.9	3	0.3	–	–
<i>Cassidulina oblonga</i>	1	0.2	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulinoides bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides lobatulus</i>	1	0.2	–	–	17	0.4	–	–	–	–	–	–	–	–
<i>Cibicidoides pachydermus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina</i> sp.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina bradyensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina filiformis</i>	–	–	–	–	–	–	–	–	1	0.3	–	–	–	–
<i>Elphidium</i> sp.A	–	–	–	–	–	–	–	–	–	–	–	–	42	4.1
<i>Elphidium advenum</i>	35	4.1	31	3.5	756	19.5	17	2.6	8	1.8	47	4.6	–	–
<i>Elphidium crispum</i>	26	3.2	6	0.6	522	13.5	4	0.6	8	1.8	25	2.5	–	–
<i>Elphidium excavatum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium granosum</i>	6	0.7	–	–	133	3.4	–	–	–	–	128	12.5	–	–
<i>Elphidium poeyanum</i>	15	1.8	3	0.3	450	11.6	–	–	25	5.5	139	13.6	–	–
<i>Fursenkoina acuta</i>	–	–	–	–	–	–	–	–	1	0.3	–	–	–	–
<i>Gavelinopsis praegeri</i>	3	0.3	6	0.6	94	2.4	1	0.2	–	–	–	–	–	–
<i>Globobulimina affinis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	3	0.3	–	–	–	–	3	0.4	–	–	–	–	–	–
<i>Hanzawaia boueana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Haynesina</i> spp.	–	–	3	0.3	106	2.7	–	–	10	2.1	28	2.7	–	–
<i>Hyalinea balthica</i>	6	0.7	–	–	–	–	13	1.9	–	–	–	–	–	–
<i>Lagena</i> spp.	1	0.2	–	–	6	0.1	1	0.2	–	–	–	–	–	–
<i>Lenticulina atlantica</i>	3	0.3	–	–	–	–	–	–	1	0.3	–	–	–	–
<i>Lenticulina gibba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina peregrina</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Melonis barleeanus</i>	10	1.2	6	0.6	–	–	3	0.4	–	–	–	–	–	–
<i>Nonion fabum</i>	124	14.8	81	9.4	267	6.9	83	12.8	57	12.5	42	4.1	–	–
<i>Nonionella turgida</i>	146	17.4	258	30.0	206	5.3	110	16.9	154	33.7	22	2.2	–	–
<i>Planorbulina mediterraneensis</i>	–	–	–	–	6	0.1	–	–	–	–	–	–	–	–
Polymorphinidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudoepionides falsobeccarii</i>	78	9.3	44	5.2	11	0.3	14	2.1	–	–	–	–	–	–
<i>Rectuvigerina phlegeri</i>	24	2.8	42	4.8	22	0.6	18	2.8	13	2.7	3	0.3	–	–
<i>Reussella spinulosa</i>	–	–	–	–	6	0.1	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	3	0.3
<i>Rosalina vilardeboana</i>	–	–	–	–	–	–	–	–	–	–	–	–	3	0.3

Appendix A (continued)

Taxa	Station	BT1		BT9		BT11		BT15		BT18		BT20	
		D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Saidovina karreriana</i>		–	–	14	1.6	–	–	8	1.3	3	0.6	–	–
<i>Stainforthia concava</i>		–	–	3	0.3	–	–	–	–	1	0.3	–	–
<i>Uvigerina</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina bifurcata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina peregrina</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Valvulineria bradyana</i>		79	9.5	128	14.8	56	1.4	103	15.8	85	18.5	–	–
<i>Valvulineria minuta</i>		–	–	–	–	–	–	–	–	–	–	–	–
Miliolids													
Indet.		–	–	–	–	–	–	–	–	4	0.9	–	–
<i>Adelosina longirostra</i>		1	0.2	–	0.6	33	0.9	10	1.5	4	0.9	11	1.1
<i>Bilocolinella labiata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Cornuspira involvens</i>		–	–	–	–	11	0.3	–	–	3	0.6	–	–
<i>Miliolinella subrotunda</i>		–	–	–	–	33	0.9	3	0.4	–	–	25	2.5
<i>Pseudotriloculina rotunda</i>		–	–	–	–	–	–	–	–	–	–	8	0.8
<i>Pyrgo depressa</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>		1	0.2	8	1.0	6	0.1	1	0.2	4	0.9	–	–
<i>Pyrgo subsphaerica</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> sp.1		–	–	–	–	6	0.1	–	–	1	0.3	–	–
<i>Quinqueloculina aspera</i>		–	–	–	–	6	0.1	–	–	–	–	6	0.5
<i>Quinqueloculina badenensis</i>		6	0.7	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina lata</i>		–	–	–	–	72	1.9	1	0.2	10	2.1	83	8.2
<i>Quinqueloculina milletti</i>		–	–	–	–	11	0.3	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>		1	0.2	–	–	6	0.1	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>		28	3.3	19	2.3	172	4.5	8	1.3	6	1.2	53	5.2
<i>Quinqueloculina stalkerii</i>		–	–	3	0.3	–	–	–	–	–	–	–	–
<i>Quinqueloculina tenuicollis</i>		–	–	–	–	6	0.1	–	–	4	0.9	–	–
<i>Sigmoilinita tenuis</i>		–	–	6	0.6	33	0.9	1	0.2	1	0.3	–	–
<i>Sigmoilopsis schlumbergeri</i>		3	0.3	3	0.3	–	–	1	0.2	–	–	–	–
<i>Siphonaperta aspera</i>		–	–	–	–	–	–	–	–	–	–	3	0.3
<i>Spiroloculina excavata</i>		–	–	–	–	6	0.1	–	–	–	–	–	–
<i>Triloculina tricarinata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>		–	–	–	–	78	2.0	–	–	–	–	36	3.5
Fossilising agglutinated													
<i>Bigenerina nodosaria</i>		10	1.7	–	–	–	–	–	–	–	–	–	–
<i>Textularia agglutinans</i>		22	2.7	33	3.9	50	1.3	14	2.1	10	2.1	–	–
<i>Textularia saggitula</i>		–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated													
Indet.		10		22		6		–		4		–	
Agglutinate sp.333		–		–		–		–		3		–	
<i>Adercotryma glomerata</i>		–		6		6		–		–		–	
<i>Ammoscalaria foliacea</i>		–		–		–		4		–		–	
<i>Charoides</i>		–		–		–		–		–		–	
<i>Clavulina cylindrica</i>		–		17		6		18		7		–	
<i>Cribrostomoides subglobosus</i>		–		–		–		–		–		–	
<i>Cribrostomoides wiesneri</i>		–		6		11		1		8		–	
<i>Eggerella scabra</i>		11		147		289		82		96		122	
<i>Haplophragmoides</i> spp.		–		–		–		3		–		–	
<i>Lagennamina difflugiformis</i>		8		44		44		15		42		3	
<i>Nouria polymorphinoides</i>		–		–		11		–		7		–	
<i>Recurvoides</i> sp.		–		–		–		–		–		–	
<i>Recurvoides scitulus</i>		–		–		–		–		–		–	
<i>Reophax</i> sp.		–		3		–		–		–		–	
<i>Reophax dentaliniformis</i>		–		–		–		–		–		–	

Appendix A (continued)

Taxa	Station		BT1		BT9		BT11		BT15		BT18		BT20	
	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Reophax fusiformis</i>	–		42		–		6		22		6			
<i>Reophax nanus</i>	–		–		6		–		–		–		–	
<i>Reophax scoriurus</i>	–		–		–		1		–		–		–	
<i>Trochammina globigeriniformis</i>	–		28		28		8		4		–		–	
<i>Trochammina cf. fissuraperta</i>	–		–		–		–		1		–		–	
Tot. dead individuals	867		1175		4272		789		651		1150			
Tot. Fossilising individuals	838		861		3867		650		457		1019			
Taxa	Station		BT22		BT23		BT24		BT26		BT28		BT29	
	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
Perforates														
Indet.	3	0.2	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	25	1.5	8	1.1	7	3.8	7	7.7	11	24.2	17	0.4		
<i>Ammonia beccarii</i> f. <i>inflata</i>	42	2.4	7	0.9	–	–	–	–	–	–	217	5.0		
<i>Ammonia perlucida</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia tepida</i>	–	–	–	–	–	–	1	1.5	25	54.5	–	–	–	–
<i>Ammonia parkinsoniana</i>	–	–	–	–	–	–	–	–	1	3.0	–	–	–	–
<i>Amphicoryna scalaris</i>	72	4.2	13	1.7	7	3.8	–	–	–	–	–	–	100	2.3
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	39	2.3	–	–	–	–	–	–	–	–	–	–	6	0.1
<i>Bolivina dilatata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina spathulata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina subaenariensis</i>	47	2.8	–	–	–	–	–	–	–	–	–	–	–	–
<i>Buccella granulata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>	186	10.9	49	6.5	6	3.1	1	1.5	–	–	317	7.3		
<i>Bulimina costata</i>	8	0.5	1	0.2	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>	–	–	–	–	–	–	3	3.1	–	–	–	–	–	–
<i>Bulimina gibba</i>	22	1.3	6	0.7	1	0.8	–	–	–	–	–	–	39	0.9
<i>Bulimina marginata</i>	139	8.1	40	5.4	4	2.3	1	1.5	–	–	517	12.0		
<i>Cassidulina carinata</i>	297	17.3	326	43.9	53	29.0	7	7.7	–	–	933	21.6		
<i>Cassidulina oblonga</i>	33	1.9	4	0.6	1	0.8	–	–	–	–	78	1.8		
<i>Cassidulinoides bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>	19	1.1	3	0.4	1	0.8	–	–	–	–	11	0.3		
<i>Cibicides lobatulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides pachydermus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina</i> sp.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina bradyensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina filiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium</i> sp.A	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>	6	0.3	10	1.3	–	–	6	6.2	–	–	94	2.2		
<i>Elphidium crispum</i>	–	–	1	0.2	–	–	–	–	–	–	117	2.7		
<i>Elphidium excavatum</i>	–	–	–	–	–	–	–	–	–	–	6	0.1		
<i>Elphidium granosum</i>	–	–	–	–	–	–	–	–	1	3.0	11	0.3		
<i>Elphidium poeyanum</i>	–	–	–	–	–	–	–	–	–	–	6	0.1		
<i>Fursenkoina acuta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>	–	–	1	0.2	–	–	–	–	–	–	6	0.1		
<i>Globobulimina affinis</i>	3	0.2	–	–	–	–	–	–	–	–	6	0.1		
<i>Globobulimina pyrula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>	53	3.1	6	0.7	–	–	–	–	–	–	128	3.0		
<i>Hanzawaia boueana</i>	3	0.2	–	–	–	–	–	–	–	–	6	0.1		
<i>Haynesina</i> spp.	–	–	–	–	–	–	1	1.5	6	12.1	–	–	–	–
<i>Hyalinea balthica</i>	119	7.0	25	3.4	–	–	–	–	–	–	361	8.4		
<i>Lagena</i> spp.	6	0.3	3	0.4	–	–	–	–	–	–	11	0.3		
<i>Lenticulina atlantica</i>	–	–	–	–	–	–	–	–	–	–	6	0.1		

Appendix A (continued)

Taxa	Station		BT22		BT23		BT24		BT26		BT28		BT29	
	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Lenticulina gibba</i>	–	–	–	–	–	–	–	–	–	–	–	–	6	0.1
<i>Lenticulina peregrina</i>	3	0.2	–	–	–	–	–	–	1	1.5	–	–	–	–
Melonis barleeanus	42	2.4	3	0.4	3	1.5	–	–	–	–	1	3.0	78	1.8
Nonion fabum	50	2.9	58	7.9	3	1.5	4	4.6	–	–	–	–	133	3.1
Nonionella turgida	8	0.5	32	4.3	46	25.2	46	50.8	–	–	–	–	100	2.3
<i>Planorbulina mediterraneensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Polymorphinidae</i>	3	0.2	–	–	–	–	–	–	–	–	–	–	11	0.3
Pseudoepionides falsobecarii	47	2.8	8	1.1	1	0.8	–	–	–	–	–	–	172	4.0
Rectuvigerina phlegeri	3	0.2	11	1.5	3	1.5	–	–	–	–	–	–	11	0.3
<i>Reussella spinulosa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>	19	1.1	17	2.2	–	–	–	–	–	–	–	–	11	0.3
<i>Stainforthia concava</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina</i> sp.	3	0.2	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina bifurcata</i>	8	0.5	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>	8	0.5	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina peregrina</i>	8	0.5	1	0.2	–	–	–	–	–	–	–	–	–	–
Valvulineria bradyana	97	5.7	75	10.1	35	19.1	–	–	–	–	–	–	283	6.6
<i>Valvulineria minuta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Miliolids														
Indet.	17	1.0	–	–	–	–	–	–	8	9.2	–	–	–	–
<i>Adelosina longirostra</i>	–	–	–	–	1	0.8	–	–	–	–	–	–	6	0.1
<i>Biloculinella labiata</i>	8	0.5	1	0.2	1	0.8	–	–	–	–	–	–	6	0.1
<i>Cornuspira involvens</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudotriloculina rotunda</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo depressa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pyrgo oblonga	6	0.3	–	–	1	0.8	–	–	–	–	–	–	–	–
<i>Pyrgo subsphaerica</i>	–	–	–	–	1	0.8	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> sp.1	–	–	1	0.2	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina badenensis</i>	36	2.1	–	–	–	–	–	–	–	–	–	–	11	0.3
Quinqueloculina lata	–	–	3	0.4	3	1.5	–	–	–	–	–	–	–	–
<i>Quinqueloculina milletti</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Quinqueloculina seminula	108	6.3	14	1.9	3	1.5	3	3.1	–	–	–	–	161	3.7
<i>Quinqueloculina stalkerii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina tenuicollis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilinita tenuis</i>	–	–	–	–	–	–	–	–	–	–	–	–	11	0.3
<i>Sigmoilopsis schlumbergeri</i>	8	0.5	1	0.2	–	–	–	–	–	–	–	–	28	0.6
<i>Siphonaperta aspera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroloculina excavata</i>	–	–	–	–	–	–	–	–	–	–	–	–	11	0.3
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated														
Bigenerina nodosaria	53	3.1	–	–	–	–	–	–	–	–	–	–	106	2.4
Textularia agglutinans	56	3.2	14	1.9	–	–	–	–	–	–	–	–	189	4.4
<i>Textularia saggitula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated														
Indet.	8		–		–		–		1		–		–	
Agglutinate sp.333	–		–		–		–		–		–		–	
<i>Adercotryma glomerata</i>	19		1		–		–		–		–		–	
<i>Ammoscalaria foliacea</i>	11		–		–		–		–		–		–	

Appendix A (continued)

Taxa	Station	BT22		BT23		BT24		BT26		BT28		BT29	
		D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Charoides</i>		3		–		–		–		–		–	
<i>Clavulina cylindrica</i>		64		17		6		–		–		39	
<i>Cribrostomoides subglobosus</i>		6		–		–		–		–		–	
<i>Cribrostomoides wiesneri</i>		–		–		1		–		–		–	
<i>Eggerella scabra</i>		131		40		13		13		–		211	
<i>Haplophragmoides</i> spp.		14		4		–		–		–		–	
<i>Lagennamina difflugiformis</i>		50		6		7		–		–		172	
<i>Nouria polymorphinoides</i>		–		–		–		–		–		–	
<i>Recurvoides</i> sp.		–		–		–		1		–		–	
<i>Recurvoides scitulus</i>		11		–		–		–		–		–	
<i>Reophax</i> sp.		3		–		–		–		–		–	
<i>Reophax dentaliniformis</i>		–		–		–		–		–		–	
<i>Reophax fusiformis</i>		6		7		3		–		–		22	
<i>Reophax nanus</i>		–		–		–		–		–		–	
<i>Reophax scorpiurus</i>		6		–		–		–		–		–	
<i>Trochammina globigeriniformis</i>		33		4		1		–		–		17	
<i>Trochammina</i> cf. <i>fissuraperta</i>		–		–		–		–		–		–	
Tot. dead individuals		2078		822		213		106		47		4783	
Tot. Fossilising individuals		1714		743		182		90		46		4322	

Taxa	Station	BT30		BT33		BT35		BT36		BT37		BT39	
		D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
Perforates													
Indet.		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>		6	0.4	10	4.4	135	16.2	11	0.2	–	–	6	5.5
<i>Ammonia beccarii</i> f. <i>inflata</i>		56	4.4	–	–	–	–	122	1.9	267	4.3	–	–
<i>Ammonia perlucida</i>		–	–	–	–	3	0.3	–	–	–	–	–	–
<i>Ammonia tepida</i>		–	–	–	–	176	21.2	–	–	–	–	–	–
<i>Ammonia parkinsoniana</i>		–	–	–	–	7	0.8	–	–	–	–	–	–
<i>Amphicoryna scalaris</i>		19	1.5	–	–	–	–	239	3.8	178	2.9	1	1.4
<i>Astacolus crepidulus</i>		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>		3	0.2	–	–	–	–	117	1.9	44	0.7	–	–
<i>Bolivina dilatata</i>		–	–	–	–	1	0.2	–	–	–	–	1	1.4
<i>Bolivina spathulata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina subaenariensis</i>		3	0.2	–	–	–	–	44	0.7	22	0.4	1	1.4
<i>Buccella granulata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>		36	2.9	1	0.6	1	0.2	539	8.6	289	4.7	–	–
<i>Bulimina costata</i>		–	–	–	–	–	–	22	0.4	–	–	–	–
<i>Bulimina elongata</i>		8	0.7	–	–	8	1.0	–	–	–	–	–	–
<i>Bulimina gibba</i>		6	0.4	–	–	–	–	61	1.0	89	1.4	–	–
<i>Bulimina marginata</i>		144	11.5	1	0.6	–	–	633	10.1	422	6.8	–	–
<i>Cassidulina carinata</i>		228	18.1	7	3.1	1	0.2	1328	21.1	1822	29.4	22	21.9
<i>Cassidulina oblonga</i>		3	0.2	–	–	–	–	144	2.3	89	1.4	–	–
<i>Cassidulinoides bradyi</i>		–	–	1	0.6	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>		3	0.2	–	–	–	–	6	0.1	22	0.4	–	–
<i>Cibicides lobatulus</i>		–	–	–	–	–	–	6	0.1	22	0.4	–	–
<i>Cibicidoides pachydermus</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina</i> sp.3		–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina bradyensis</i>		–	–	–	–	–	–	6	0.1	–	–	–	–
<i>Dentalina filiformis</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium</i> sp.A		–	–	–	–	4	0.5	–	–	–	–	–	–
<i>Elphidium advenum</i>		39	3.1	7	3.1	31	3.7	–	–	22	0.4	1	1.4
<i>Elphidium crispum</i>		8	0.7	–	–	57	6.8	–	–	–	–	–	–
<i>Elphidium excavatum</i>		–	–	–	–	1	0.2	–	–	–	–	–	–

Appendix A (continued)

Taxa	Station	BT30		BT33		BT35		BT36		BT37		BT39	
		D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Elphidium granosum</i>		–	–	–	–	32	3.8	22	0.4	–	–	–	–
<i>Elphidium poeyanum</i>		8	0.7	7	3.1	86	10.3	–	–	–	–	–	–
<i>Fursenkoina acuta</i>		3	0.2	–	–	1	0.2	–	–	–	–	3	2.7
<i>Gavelinopsis praegeri</i>		8	0.7	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina affinis</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>		–	–	–	–	–	–	6	0.1	–	–	–	–
<i>Gyroidina umbonata</i>		3	0.2	–	–	–	–	39	0.6	67	1.1	–	–
<i>Hanzawaia boueana</i>		3	0.2	–	–	–	–	11	0.2	–	–	–	–
<i>Haynesina</i> spp.		–	–	3	1.3	39	4.7	–	–	–	–	–	–
<i>Hyalinea balthica</i>		50	4.0	–	–	–	–	383	6.1	533	8.6	–	–
<i>Lagena</i> spp.		–	–	–	–	–	–	11	0.2	22	0.4	–	–
<i>Lenticulina atlantica</i>		–	–	1	0.6	–	–	–	–	–	–	–	–
<i>Lenticulina gibba</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina peregrina</i>		–	–	–	–	–	–	33	0.5	–	–	–	–
<i>Melonis barleeanus</i>		6	0.4	–	–	–	–	439	7.0	156	2.5	–	–
<i>Nonion fabum</i>		69	5.5	11	5.0	71	8.5	89	1.4	67	1.1	6	5.5
<i>Nonionella turgida</i>		144	11.5	108	49.1	108	13.0	–	–	67	1.1	36	35.6
<i>Planorbulina mediterraneensis</i>		–	–	–	–	–	–	–	–	–	–	–	–
Polymorphinidae		8	0.7	–	–	–	–	–	–	–	–	–	–
<i>Pseudoepionides falsobecarii</i>		58	4.6	–	–	–	–	322	5.1	178	2.9	–	–
<i>Rectuvigerina phlegeri</i>		11	0.9	17	7.5	–	–	17	0.3	111	1.8	–	–
<i>Reussella spinulosa</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Rutherfordoides</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–
<i>Saidovina karreriana</i>		3	0.2	–	–	–	–	–	–	44	0.7	–	–
<i>Stainforthia concava</i>		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina bifurcata</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>		–	–	–	–	–	–	11	0.2	–	–	–	–
<i>Uvigerina peregrina</i>		3	0.2	–	–	–	–	56	0.9	–	–	–	–
<i>Valvulineria bradyana</i>		108	8.6	29	13.2	6	0.7	322	5.1	911	14.7	8	8.2
<i>Valvulineria minuta</i>		–	–	–	–	–	–	–	–	22	0.4	–	–
Miliolids													
Indet.		11	0.9	6	2.5	3	0.3	83	1.3	133	2.2	–	–
<i>Adelosina longirostra</i>		6	0.4	–	–	6	0.7	67	1.1	–	–	–	–
<i>Biloculinella labiata</i>		3	0.2	–	–	–	–	17	0.3	–	–	1	1.4
<i>Cornuspira involvens</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>		3	0.2	–	–	3	0.3	11	0.2	–	–	1	1.4
<i>Pseudotriloculina rotunda</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo depressa</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>		–	–	4	1.9	–	–	–	–	–	–	7	6.8
<i>Pyrgo subsphaerica</i>		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> sp.1		–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina aspera</i>		–	–	–	–	1	0.2	–	–	–	–	–	–
<i>Quinqueloculina badenensis</i>		8	0.7	–	–	–	–	117	1.9	22	0.4	–	–
<i>Quinqueloculina lata</i>		–	–	6	2.5	33	4.0	–	–	–	–	–	–
<i>Quinqueloculina milletti</i>		–	–	–	–	3	0.3	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>		75	6.0	–	–	11	1.3	183	2.9	267	4.3	3	2.7
<i>Quinqueloculina stalkerii</i>		3	0.2	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina tenuicollis</i>		–	–	–	–	–	–	–	–	22	0.4	–	–
<i>Sigmoilinita tenuis</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>		17	1.3	–	–	–	–	78	1.2	67	1.1	–	–
<i>Siphonaperta aspera</i>		–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroloculina excavata</i>		–	–	–	–	–	–	28	0.4	–	–	–	–

Appendix A (continued)

Taxa	Station	BT30		BT33		BT35		BT36		BT37		BT39	
		D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos	D	%Fos
<i>Triloculina tricarinata</i>		3	0.2	–	–	–	–	6	0.1	–	–	1	1.4
<i>Triloculina trigonula</i>		3	0.2	–	–	3	0.3	–	–	22	0.4	–	–
Fossilising agglutinated													
<i>Bigenerina nodosaria</i>		8	0.7	–	–	–	–	256	4.1	22	0.4	–	–
<i>Textularia agglutinans</i>		58	4.6	1	0.6	1	0.2	406	6.4	178	2.9	1	1.4
<i>Textularia saggitula</i>		–	–	–	–	–	–	–	–	–	–	–	–
Non-fossilising agglutinated													
Indet.		22		–		3		44		133		1	
Agglutinate sp.333		–		–		–		–		–		–	
<i>Adercotryma glomerata</i>		3		–		–		6		–		–	
<i>Ammoscalaria foliacea</i>		3		–		–		22		111		–	
<i>Charoides</i>		–		–		–		–		–		–	
<i>Clavulina cylindrica</i>		69		–		–		44		44		7	
<i>Cribrostomoides subglobosus</i>		3		–		–		–		–		–	
<i>Cribrostomoides wiesneri</i>		6		6		17		–		–		7	
<i>Eggerella scabra</i>		100		11		192		150		311		7	
<i>Haplophragmoides</i> spp.		11		–		–		17		–		–	
<i>Lagennamina difflugiformis</i>		100		–		–		200		311		3	
<i>Nouria polymorphinoides</i>		–		3		6		–		–		1	
<i>Recurvoides</i> sp.		–		–		–		–		–		–	
<i>Recurvoides scitulus</i>		–		–		–		–		–		–	
<i>Reophax</i> sp.		–		–		–		–		–		–	
<i>Reophax dentaliniformis</i>		–		–		–		–		–		1	
<i>Reophax fusiformis</i>		14		–		–		11		–		1	
<i>Reophax nanus</i>		–		–		–		–		–		–	
<i>Reophax scorpiurus</i>		3		–		–		50		–		–	
<i>Trochammina globigeriniformis</i>		28		–		–		33		–		–	
<i>Trochammina cf. fissuraperta</i>		–		–		–		–		–		–	
Tot. dead individuals		1619		240		1050		6867		7111		131	
Tot. Fossilising individuals		1258		221		833		6289		6200		101	

Taxa	Station	BT41		BT48	
		D	%Fos	D	%Fos
Perforates					
Indet.		–	–	11	0.2
<i>Ammonia beccarii</i> f. <i>beccarii</i>		–	–	33	0.6
<i>Ammonia beccarii</i> f. <i>inflata</i>		–	–	44	0.7
<i>Ammonia perlucida</i>		–	–	–	–
<i>Ammonia tepida</i>		1	11.1	–	–
<i>Ammonia parkinsoniana</i>		–	–	–	–
<i>Amphicoryna scalaris</i>		–	–	167	2.8
<i>Astacolus crepidulus</i>		–	–	–	–
<i>Bolivina alata</i>		–	–	78	1.3
<i>Bolivina dilatata</i>		–	–	–	–
<i>Bolivina spathulata</i>		–	–	–	–
<i>Bolivina striatula</i>		–	–	11	0.2
<i>Bolivina subaenariensis</i>		–	–	11	0.2
<i>Buccella granulata</i>		–	–	–	–
<i>Bulimina aculeata</i>		–	–	889	15.0
<i>Bulimina costata</i>		–	–	22	0.4
<i>Bulimina elongata</i>		–	–	11	0.2
<i>Bulimina gibba</i>		–	–	89	1.5
<i>Bulimina marginata</i>		1	11.1	556	9.3

Appendix A (continued)

Taxa	Station	BT41		BT48	
		D	%Fos	D	%Fos
<i>Cassidulina carinata</i>		6	44.4	811	13.6
<i>Cassidulina oblonga</i>		1	11.1	167	2.8
<i>Cassidulinoides bradyi</i>		–	–	–	–
<i>Chilostomella ovoidea</i>		–	–	22	0.4
<i>Cibicides lobatulus</i>		–	–	22	0.4
<i>Cibicidoides pachydermus</i>		–	–	22	0.4
<i>Dentalina</i> sp.3		–	–	11	0.2
<i>Dentalina bradyensis</i>		–	–	–	–
<i>Dentalina filiformis</i>		–	–	–	–
<i>Elphidium</i> sp.A		–	–	–	–
<i>Elphidium advenum</i>		–	–	11	0.2
<i>Elphidium crispum</i>		–	–	11	0.2
<i>Elphidium excavatum</i>		–	–	–	–
<i>Elphidium granosum</i>		–	–	–	–
<i>Elphidium poeyanum</i>		–	–	22	0.4
<i>Fursenkoina acuta</i>		–	–	–	–
<i>Gavelinopsis praegeri</i>		–	–	–	–
<i>Globobulimina affinis</i>		–	–	22	0.4
<i>Globobulimina pyrula</i>		–	–	11	0.2
<i>Gyroidina umbonata</i>		–	–	100	1.7
<i>Hanzawaia boueana</i>		–	–	22	0.4
<i>Haynesina</i> spp.		1	11.1	–	–
<i>Hyalinea balthica</i>		–	–	400	6.7
<i>Lagenella</i> spp.		–	–	33	0.6
<i>Lenticulina atlantica</i>		–	–	–	–
<i>Lenticulina gibba</i>		–	–	–	–
<i>Lenticulina peregrina</i>		–	–	11	0.2
<i>Melonis barleeanus</i>		–	–	356	6.0
<i>Nonion fabum</i>		–	–	56	0.9
<i>Nonionella turgida</i>		–	–	–	–
<i>Planorbulina mediterraneensis</i>		–	–	–	–
<i>Polymorphinidae</i>		–	–	–	–
<i>Pseudoepionides falsobecarii</i>		–	–	122	2.1
<i>Rectuvigerina phlegeri</i>		–	–	–	–
<i>Reussella spinulosa</i>		–	–	–	–
<i>Rosalina bradyi</i>		–	–	–	–
<i>Rosalina vilardeboana</i>		–	–	–	–
<i>Rutherfordoides</i> sp.		–	–	–	–
<i>Saidovina karreriana</i>		–	–	11	0.2
<i>Stainforthia concava</i>		–	–	11	0.2
<i>Uvigerina</i> sp.		–	–	44	0.7
<i>Uvigerina bifurcata</i>		–	–	11	0.2
<i>Uvigerina mediterranea</i>		–	–	22	0.4
<i>Uvigerina peregrina</i>		–	–	67	1.1
<i>Valvulineria bradyana</i>		–	–	133	2.2
<i>Valvulineria minuta</i>		–	–	11	0.2
Miliolids					
Indet.		–	–	133	2.2
<i>Adelosina longirostra</i>		–	–	22	0.4
<i>Biloculinella labiata</i>		–	–	11	0.2
<i>Cornuspira involvens</i>		–	–	–	–
<i>Miliolinella subrotunda</i>		–	–	11	0.2
<i>Pseudotriloculina rotunda</i>		–	–	–	–
<i>Pyrgo depressa</i>		–	–	11	0.2
<i>Pyrgo oblonga</i>		–	–	11	0.2
<i>Pyrgo subsphaerica</i>		–	–	–	–

Appendix A (continued)

Taxa	Station	BT41		BT48	
		D	%Fos	D	%Fos
<i>Quinqueloculina</i> sp.1		–	–	–	–
<i>Quinqueloculina aspera</i>		–	–	–	–
<i>Quinqueloculina badenensis</i>		–	–	89	1.5
<i>Quinqueloculina lata</i>		–	–	–	–
<i>Quinqueloculina milletti</i>		–	–	–	–
<i>Quinqueloculina pygmaea</i>		–	–	–	–
<i>Quinqueloculina seminula</i>		–	–	300	5.0
<i>Quinqueloculina stalkerii</i>		–	–	–	–
<i>Quinqueloculina tenuicollis</i>		–	–	–	–
<i>Sigmoilinita tenuis</i>		–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>		–	–	144	2.4
<i>Siphonaperta aspera</i>		–	–	–	–
<i>Spiroloculina excavata</i>		–	–	44	0.7
<i>Triloculina tricarinata</i>		–	–	–	–
<i>Triloculina trigonula</i>		1	11.1	–	–
Fossilising agglutinated					
<i>Bigenerina nodosaria</i>		–	–	378	6.4
<i>Textularia agglutinans</i>		–	–	311	5.2
<i>Textularia saggitula</i>		–	–	11	0.2
Non-fossilising agglutinated					
Indet.		–		122	
Agglutinate sp.333		–		–	
<i>Adercotryma glomerata</i>		–		–	
<i>Ammoscalaria foliacea</i>		–		11	
<i>Charoides</i>		–		–	
<i>Clavulina cylindrica</i>		–		33	
<i>Cribrostomoides subglobosus</i>		–		–	
<i>Cribrostomoides wiesneri</i>		–		–	
<i>Eggerella scabra</i>		–		100	
<i>Haplophragmoides</i> spp.		–		11	
<i>Lagennamina difflugiformis</i>		–		44	
<i>Nouria polymorphinoides</i>		–		–	
<i>Recurvoides</i> sp.		–		–	
<i>Recurvoides scitulus</i>		–		–	
<i>Reophax</i> sp.		–		44	
<i>Reophax dentaliniformis</i>		–		–	
<i>Reophax fusiformis</i>		–		11	
<i>Reophax nanus</i>		–		–	
<i>Reophax scorpiurus</i>		–		33	
<i>Trochammina globigeriniformis</i>		–		–	
<i>Trochammina</i> cf. <i>fissuraperta</i>		–		–	
Tot. dead individuals		13		6356	
Tot. Fossilising individuals		13		5944	

Appendix B

- Ammonia beccarii* f. *beccarii* (Linnaeus) = *Nautilus beccarii* Linnaeus f. *beccarii* Linnaeus, 1758; in Jorissen, 1988, Plate 2, Fig. 5a–b
- Ammonia beccarii* f. *inflata* (Seguenza) = *Nautilus beccarii* Linnaeus f. *inflata* Seguenza, 1862; in Jorissen, 1988, Plate 6, Figs. 1–4
- Ammonia tepida* (Cushman) = *Rotalia beccarii* Linnaeus var. *tepida* Cushman, 1926; in Jorissen, 1988, Plate 2, Fig. 8a–b (as *Ammonia parkinsoniana* f. *tepida*)
- Bigenerina nodosaria* d'Orbigny, 1826; in Jorissen, 1988, Plate 1, Fig. 10
- Bolivina alata* (Seguenza) = *Vulvulina alata* Seguenza, 1862; in Mojtahid et al., 2009, Plate 2, Fig. 15
- Bulimina aculeata* d'Orbigny, 1826; in Jorissen, 1988, Plate 4, Fig. 5
- Bulimina elongata* d'Orbigny, 1826; in Jones, 1994, Plate 50, Figs. 3–4
- Bulimina marginata* d'Orbigny, 1826; in Colom, 1974, Fig. 16d'–h', k'–o'
- Cassidulina carinata* Silvestri, 1896 = *Cassidulina laevigata* d'Orbigny var. *carinata* Silvestri, 1896; in Mojtahid et al., 2009, Plate 1, Fig. 3
- Elphidium advenum* (Cushman) = *Polystomella advena* Cushman, 1922; in Jorissen, 1988, Plate 24, Fig. 3a–b
- Elphidium crispum* (Linnaeus) = *Nautilus crispus* Linnaeus, 1758; in Jorissen, 1988, Plate 3, Fig. 8
- Elphidium granosum* f. *lidoense* (Cushman) = *Nonionina granosa* d'Orbigny f. *lidoense* Cushman, 1936; in Jorissen, 1988, Plate 2, Fig. 3
- Elphidium poeyanum* f. *decipiens* (Costa) = *Polystomella poeyana* d'Orbigny f. *decipiens* Costa, 1856; in Jorissen, 1988, Plate 2, Fig. 6
- Hyalinea balthica* (Schroeter) = *Nautilus balthicus* Schroeter, 1793; in Mojtahid et al., 2009, Plate 2, Fig. 7
- Melonis barleeanus* (Williamson) = *Nonionina barleeana* Williamson, 1858; in Jorissen, 1988, Plate 4, Fig. 8 (as *Nonion barleeanum*)
- Nonion fabum* (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798; in Jones, 1994, Plate 109, Figs. 12–13
- Nonionella turgida* (Williamson) = *Rotalina turgida* Williamson, 1858; in Jorissen, 1988, Plate 4, Figs. 11–13
- Pseudoeponides falsobeccarii* Rouvillois, 1974; in Jorissen, 1988, Plate 4, Fig. 3a–b

Pyrgo oblonga (d'Orbigny) = *Biloculina oblonga* d'Orbigny, 1839; in Rasmussen, 2005, Plate 5, Fig. 2

Quinqueloculina lata Terquem, 1876; in Murray, 2003, Plate 4, Figs. 9–10

Quinqueloculina seminula (Linnaeus) = *Serpula seminulum* Linnaeus, 1758; in Murray, 2003, Plate 4, Figs. 11–12

Quinqueloculina tenuicollis (Wiesner) = *Miliolina tenuicollis* Wiesner, 1923; in Cimerman and Langer, 1991, Plate 28, Figs. 5–6 (as *Cycloforina tenuicollis*)

Rectuvigerina phlegeri Le Calvez, 1959; in Schiebel, 1992, Plate 3, Fig. 10a–d

Textularia agglutinans d'Orbigny, 1839; in Mojtahid et al., 2009, Plate 2, Figs. 43–44

Triloculina trigonula (Lamarck) = *Miliolites trigonula* Lamarck, 1804; in Jorissen, 1988, Plate 2, Fig. 13

Valvulineria bradyana (Fornasini) = *Discorbina bradyana* Fornasini, 1900; in Jorissen, 1988, Plate 4, Figs. 1–2

CHAPITRE 5

HISTORICAL EVOLUTION OF THE RHÔNE PRODELTA RECORDED BY BENTHIC FORAMINIFERAL FAUNAS

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CHAPITRE 5

HISTORICAL EVOLUTION OF THE RHÔNE PRODELTA RECORDED BY BENTHIC FORAMINIFERAL FAUNAS

A. Goineau¹, C. Fontanier¹, F. Jorissen¹, A.-S. Fanget², M.-A. Bassetti², S. Berné^{2,3}, G. Jouet³,
D. Cossa⁴, M. Arnaud⁵, R. Buscaïl⁶, G. Maillet⁷, B. Dennielou³ and M. Jouffreau¹

¹ Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), Université d'Angers, France
and

Laboratoire d'Etude des Bio-Indicateurs Marins (LEBIM), Ile d'Yeu, France

² Institut de Modélisation et d'Analyse en Géo-Environnement et Santé (IMAGES),
Université de Perpignan, Perpignan, France

³ Ifremer, Géosciences Marines – Laboratoire de Géochimie et de Métallogénie (GM – LES),
Centre de Brest, Plouzané, France

⁴ Ifremer, Laboratoire Biogéochimie des contaminants métalliques (LBCM), Centre de
Nantes, Nantes, France

⁵ Institut de Radioprotection et de Sécurité Nucléaire (IRSN), La Seyne-sur-Mer, France

⁶ Centre de Formation et de Recherche sur l'Environnement Marin (CEFREM), Université de
Perpignan, France

⁷ Laboratoire d'Etudes Environnementales des Systèmes Anthropisés (LEESA), Université
d'Angers, Angers, France

*Les résultats présentés dans ce chapitre feront l'objet d'un article écrit en collaboration par
A.-S. Fanget (Laboratoire IMAGES, Université de Perpignan)*

ABSTRACT

The evolution of the Rhône deltaic system over the last 400 years was investigated using benthic foraminiferal faunas from a core recovered in the Rhône prodeltaic lobe of Roustan (79 m depth, ~3.8 km off the Roustan mouth). Statistics (Principal component and cluster analyses) performed on benthic foraminiferal faunas permit to distinguish well-defined periods (i.e., biozones). The base of the core is characterised by typical outer shelf faunas (e.g., *Bigenerina nodosaria*, *Melonis barleeanus*) benefiting from the gradual weakening competency and influence on the study area of the Bras de Fer channel during its last decades of activity (~250 year Before Present – BP). The shift from the Bras de Fer to the Pégoulie channel at 239 yr BP is recorded around 600 cm sediment depth with the occurrence of *Bulimina marginata* and *Pyrgo oblonga*. These species would have benefited from the sudden input of organic-rich riverine material. Thereafter, foraminiferal faunas thriving in areas subject to both riverine and marine influences (e.g., *Valvulineria bradyana*, *Cassidulina carinata*, *Hyalinea balthica*) are observed up to 160 cm depth, indicating an extension of the Rhône River plume as far as our study site. The opening of Roustan mouth at 57 yr BP is marked by the sudden occurrence at 250 cm depth of taxa thriving preferentially on the coastal prodeltaic area (*Quinqueloculina lata*). After this event, our study site was then directly supplied by riverine input leading to increased deposition rate, organic carbon and coarse sediment contents, but also of faunas tolerant to high riverine influence (e.g., *Nonionella turgida*, *Ammonia beccarii* f. *beccarii*, *Quinqueloculina lata*). The contribution of these species is maximal in 1950's (60 cm depth), pleading for a strengthening of riverine organic and terrigenous input until this period. Moreover, the replacement of *V. bradyana* by *Nonion fabum* in the top most 60 cm of the core argues for a lowering in organic matter quality supplies over the last decade(s). Therefore, foraminiferal faunas put in evidence the gradual increasing riverine influence at our study site induced by the successive migrations of its channels over the last 400 years. This investigation improved the use of fossilised benthic foraminiferal faunas for the reconstructions of past sedimentary and organic fluxes in the Rhône prodelta.

Key words: Benthic foraminifera; Rhône prodelta; Historical evolution; Organic matter input; Sediment fluxes.

5.1. INTRODUCTION

Deltaic and prodeltaic environments, located at the continent – ocean interface, are highly sensitive to natural hazards (e.g. storms, tsunamis, floods) as well as human activities (e.g. pollution). In the Mediterranean Sea, deltaic zones have particularly been described as sectors vulnerable to sea-level rise (Jeftic et al., 1992; Suanez and Provansal, 1996). The Rhône River delta, in the Gulf of Lions, is a complex hydrological system subjected to intra and interannual variability related to various factors influencing its catchment basin (e.g., ice melt, precipitation, climate; (Arnaud–Fassetta et al., 2010). With an annual mean flow of $1700 \text{ m}^3 \cdot \text{s}^{-1}$ (Pont et al., 2002), the Rhône river is the main source of freshwater, organic-inorganic material and nutrients for the Gulf of Lions (Lochet and Leveau, 1990; Durrieu de Madron et al., 2000, 2003). The historical evolution of the Rhône deltaic system has been studied through sedimentological, palynological and archaeological investigations (e.g., L’Homer et al., 1981; Arnaud–Fassetta and Provansal, 1999; Provansal et al., 1999, 2003; Arnaud–Fassetta, 2000, 2002; Bruneton et al., 2001; Vella et al., 2005; Sabatier et al., 2006; Berné et al., 2007; Rey et al., 2009; Arnaud–Fassetta et al., 2010). During the Holocene, both sea-level variations and enhanced human activities constrained sedimentary fluxes and erosional processes controlling the morphology of the deltaic and prodeltaic systems (Berendsen and Stouthamer, 2000; Stouthamer, 2001). Since 4000 yr BP (Before Present), the Rhône River has developed several successive arms and mouths, with the relict structures still visible in the modern deltaic plain and on the continental shelf (Vella et al., 2005). Engineering work (bank revetment, groynes, hydraulic deflectors, dams) processed for the last 200 years (i.e., 18th century Anno Domini – AD) has stopped this natural evolution, leading to the fixation of the mouth and channels (Sabatier et al., 2006). Until now, no studies have focused on historical benthic foraminiferal faunal changes induced by the recent evolution of the Rhône River prodelta. Previous ecological studies have focused on the modern distribution of benthic living foraminifera in relation to the Rhône prodeltaic environment (Kruit, 1955; Blanc–Vernet, 1969; Bizon and Bizon, 1984; Mojtahid et al., 2009; Goineau et al., In Press; Goineau et al., Submitted – see Chapters 1 and 2 in this thesis). Earlier in this thesis, we have studied foraminiferal thanatocoenoses and taphonomic processes acting on modern assemblages, and determined foraminiferal thanatofacies describing precise environmental conditions prevailing in different parts of the Rhône prodelta (see Chapter 4 in this thesis).

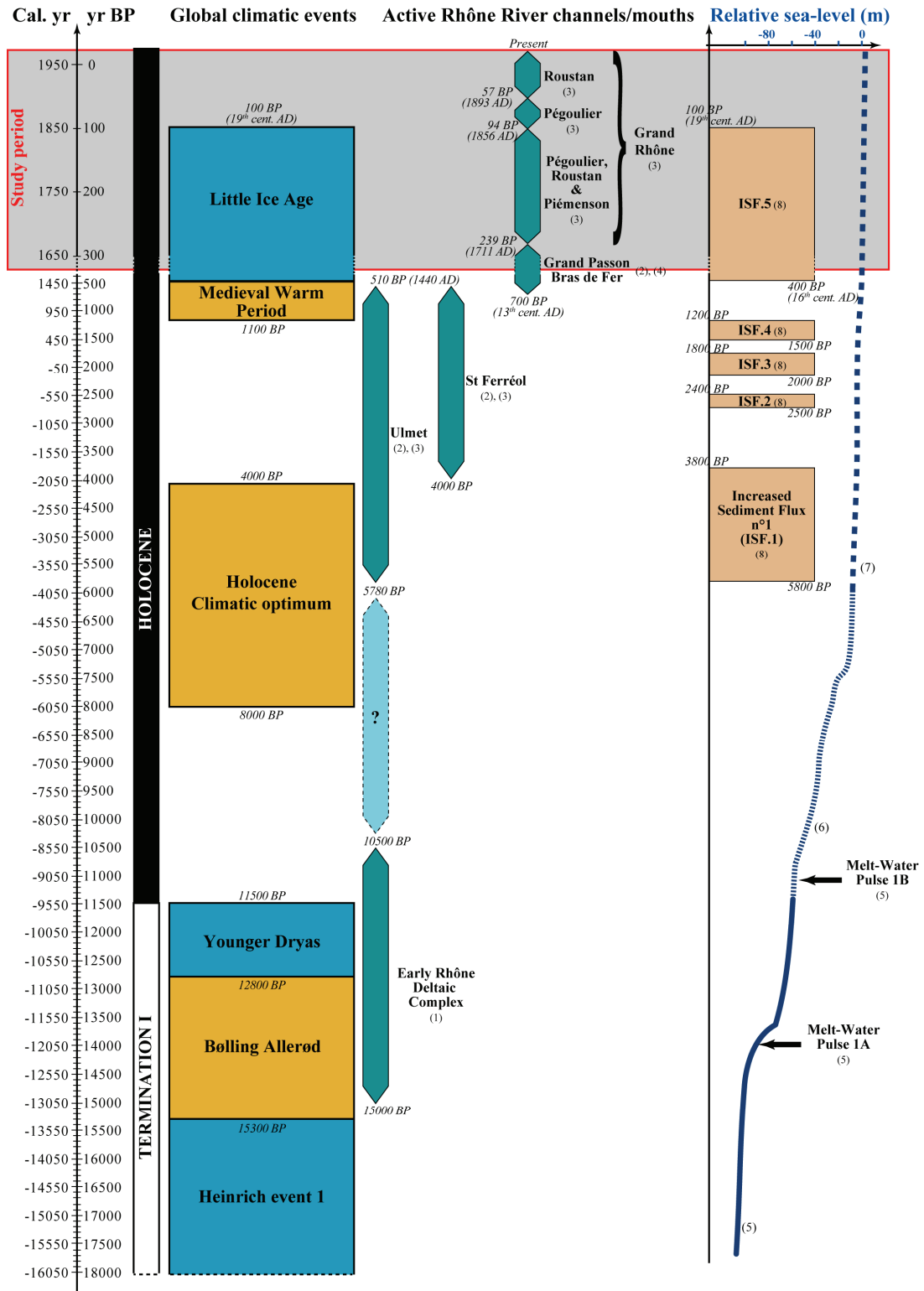


Figure 1: Synthesis of the evolution of the Rhône deltaic system from Terminaison I (18000 BP) to today. Ages are indicated in calendar year (Cal. year) and/or Before Present (year BP); AD is for “Anno Domini” (after (1) Berné et al. (2007), (2) Vella et al. (2005), (3) Russell (1942), (4) Colomb et al. (1975) and Rossiaud (1994), (5) Bard et al. (1996), (6) Aloisi et al. (1978), (7) Vella and Provansal (2000), and (8) Provansal et al. (1999, 2003) and Arnaud-Fassetta, 2000, 2002).

In this chapter, we apply the knowledge acquired in the first four chapters to a study of fossil benthic foraminifera from a long sediment core recovered in the Rhône prodelta. The multiproxy approach (lithologic description, ostracods assemblages, organic carbon content,...) combined with a robust chronostratigraphic framework (seismic reflection, $\Delta^{14}\text{C}$, ^{137}Cs , and anthropogenic Pb) allowed us to link benthic foraminiferal changes to the evolution of the prodeltaic area in the last 400 years, in terms of sedimentary patterns and organic input.

5.2. PAST AND RECENT EVOLUTION OF THE RHÔNE DELTAIC SYSTEM

The existence of the Rhône River is documented since the Messinian crisis (between – 5.96 and –5.33 Ma), when the Mediterranean sea-level fell by about 1500 m (Clauzon, 1974). Since the last deglaciation (Termination I, ~18000 yr BP; Fig. 1), sea-level fluctuations, sediment fluxes and anthropogenic forcing have controlled the construction of the Rhône delta. From 15000 to 7000 yr BP, rapid sea-level variations induced an aggradation (vertical built up) of the Rhône delta (Vella et al., 2005; Berné et al., 2007). Between 15000 and 10500 yr BP (Bølling Allerød and Younger Dryas), an early Rhône deltaic complex formed in front of the present-day Petite Camargue, during reduced sea-level rise or even stillstand (Figs. 1 and 2; Berné et al., 2007). After 7000 yr BP, the slowing down of sea-level raise favoured an increased influence of sediment fluxes, with a progradation of the system (Stanley and Warne, 1994). These sediment fluxes depend on allocyclic forcing, i.e. external to the system, especially climatic forcing and anthropogenic influence when approaching the historical period (Vella, 1999; Arnaud–Fassetta, 2000; Sabatier, 2001; Antonelli, 2002). The Ulmet and St Ferréol channels activated at 5780 and 4000 yr BP, respectively (Figs. 1 and 2). This situation lasted until 510 yr BP when these channels were artificially closed (Rossiaud, 1994). At least four Increased Sediment Flux episodes (ISF) dated between 5800–3800 yr BP, 2500–2400 yr BP, 2000–1800 yr BP, and 1500–1200 yr BP took place during the activity of these channels (Provansal et al., 1999, 2003; Arnaud–Fassetta et al., 2010). These events are thought to reflect flood dominated conditions, characterised by (1) higher flood intensity and frequency, (2) increased river sediment load, (3) a coarsening of sediment supplies, (4) increased deposition rate within channels, and/or (5) an enhanced progradation of deltaic lobes (Vella et al., 2005; Arnaud–Fassetta et al., 2010). After the closure of the Ulmet and St Ferréol channels, numerous other channels and deltaic lobes have been active. The Grand Passon channel was active from 700 to 343 yr BP (Colomb et al., 1975; Rossiaud, 1994; Vella

et al., 2005). The activity of the Bras de Fer channel (365–239 yr BP) coincided with the beginning of the Little Ice Age (LIA, ~400–100 yr BP).

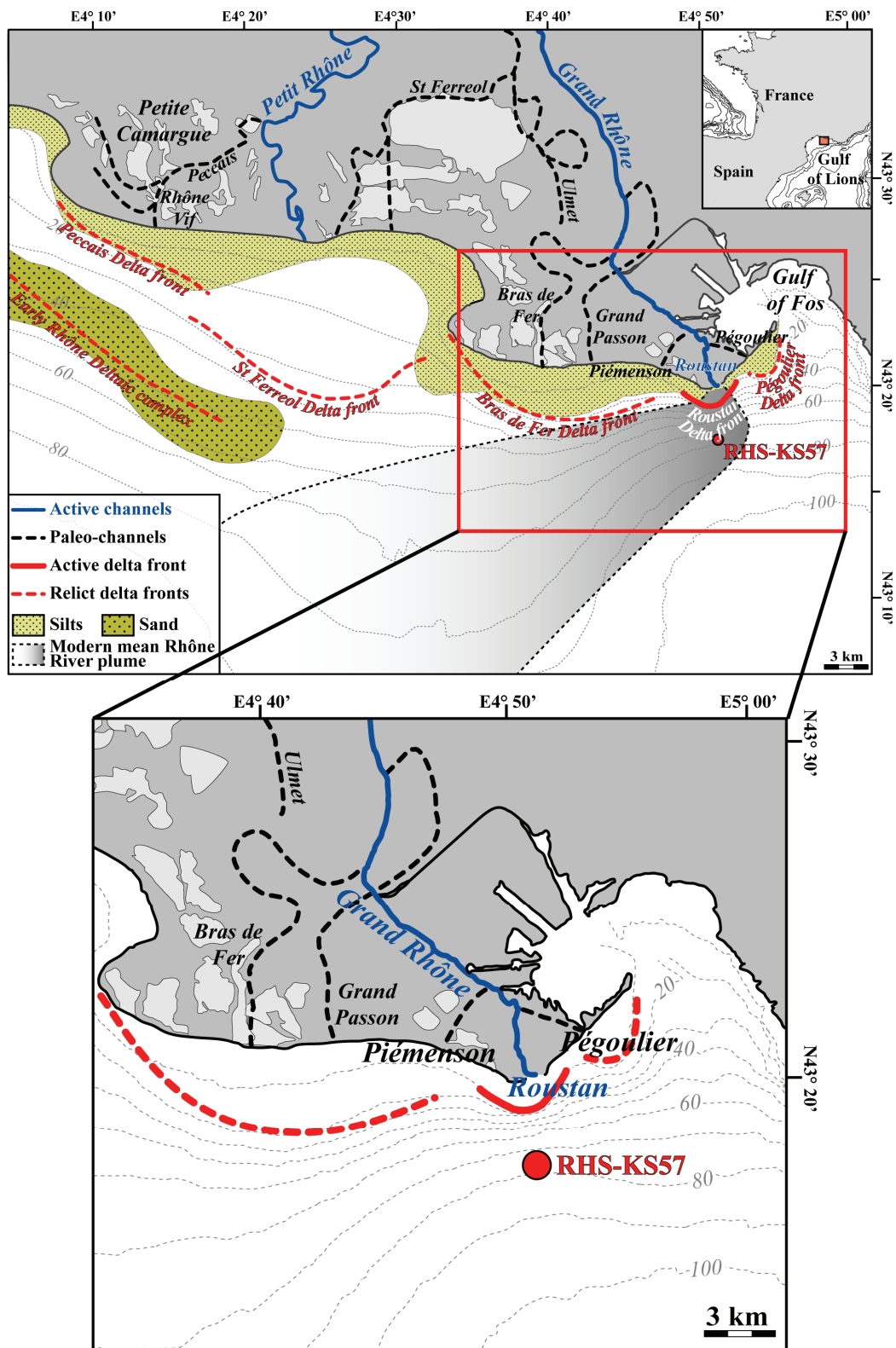


Figure 2: Present-day context of our study area and location of the investigated core RHS-KS57. Location of silty and sandy patches after Berné et al. (2007).

This climatic period is characterised by an intensification of Rhône major flood (> 5.25 m NGF – Nivellement Général de la France) frequency, a new episode of increased sediment flux to the sea, and thus an intense and rapid southward progradation of the Bras de Fer deltaic lobe by about 160 m/yr. After 290 yr BP, the deposit of riverine sediments upstream of the mouth led to a gradual instability of the channel and finally to its abandon at 239 yr BP. The newly built Pégoulie channel resulted in a more eastern river outlet. From this date to the present-day, engineering works, i.e., anthropogenic forcing, have progressively constrained the evolution of the river mouth. The higher frequency of major floods induced a strong progradation of the Pégoulie lobe, by about 35 to 60 m/yr between 238 and 57 yr BP. At 94 yr BP, the embankment of the channel caused the closing of the lateral arms of Roustan and Piémenson, and an acceleration of the Pégoulie lobe progradation (70 m/yr). At 57 yr BP, the difficulty in evacuating sediment inputs off the Pégoulie channel led to the re-opening of Roustan mouth. This last channel benefited from the progressive abandon of Pégoulie and became the unique mouth of the Rhône River since 6 yr BP until today (Provansal et al., 2003).

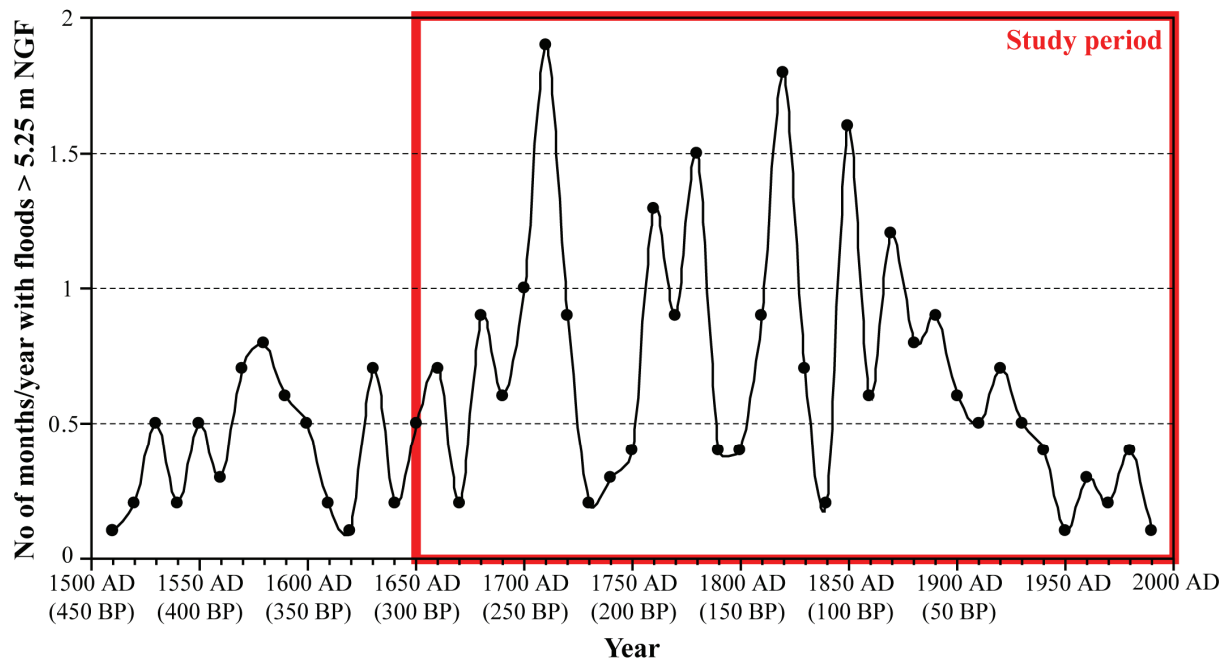


Figure 3: Number of floods per year > 5.25 m NGF (Nivellement Général de la France) in Arles (black histograms) from 450 yr BP (1500 AD) to today (after Pichard (1995)).

After 100 yr BP, the Rhône River sediment load has considerably been reduced (22 Mt/yr during the between 150 and 50 yr BP, 8–10 Mt/yr at 0 yr BP; Antonelli, 2002; Pont et al., 2002; Provansal et al., 2003) as a consequence of the constant reduction in flood

frequency (Fig. 3) and a strong anthropogenic forcing of the system (reforestation of the upper catchment basin, engineering works in the Rhône valley: embankment, dam construction, dredging,...) (Poinsard, 1992; Gautier, 1994; Pichard, 1995; Arnaud–Fassetta and Provansal, 1999; IRS, 2000; Antonelli and Provansal, 2002; Arnaud–Fassetta, 2003; Provansal et al., 2003; Antonelli et al., 2004). Nowadays, a negative sediment budget combined with the action of strong longshore currents is responsible for an erosion of the Rhône deltaic coast and a migration of the mouth to the east, enhanced during the past decades by increased storm surges and sea-level rise (Suanez and Provansal, 1998; Sabatier, 2001; Sabatier and Suanez, 2003; Sabatier et al., 2009).

5.3. MATERIAL AND METHODS

Core RHS-KS57 (N43°17.106, E4°50.965, 7.71 m long) was recovered during the RHOSOS cruise (RHOne SOurce to Sink) in September 2008 on board the *R/V Le Suroît* (Ifremer) (Fig. 2). The core was collected at 79 m depth (~3.8 km off Roustan mouth) with a Küllenberg corer in the Rhône deltaic lobe Roustan. The chronology of our core is based on seismic reflection (S. Berné, M.-A. Bassetti and A.-S. Fanget, Institut de Modélisation et d'Analyse en Géo-Environnement et Santé – IMAGES, Perpignan), anthropogenic Pb measurements ($^{206}\text{Pb}/^{208}\text{Pb}$ ratio; D. Cossa, Ifremer Nantes), ^{137}Cs analyses and one AMS radiocarbon measurement ($\Delta^{14}\text{C}$) on a gastropod shell (*Turitella* sp.) found at the 652 cm depth (M. Arnaud, Institut de Radioprotection et de Sûreté Nucléaire – IRSN; La Seyne-sur-Mer, France). Results of these analyses are presented in Table 1.

Sediment depth in the core	Age		Datation method
	year BP	year AD	
150 cm	~0	1956	^{137}Cs
370 cm	100	1850	$^{206}\text{Pb}/^{208}\text{Pb}$
652 cm	279	1671	$\Delta^{14}\text{C}$ on a single <i>Turitella</i> sp.

Table 1: Chronostratigraphic framework of core RHS-KS57: results of ^{137}Cs , anthropogenic Pb ($^{206}\text{Pb}/^{208}\text{Pb}$ ratio) and $\Delta^{14}\text{C}$ analyses.

The core was sliced on board into centimetre intervals, and sediment samples were sieved over 63 and 150 μm mesh screens. All dead specimens of benthic foraminifera from the > 150 μm size fraction were picked in 24 1 cm-thick samples between 1 and 771 cm depth in the core. When interpreting the fossil faunas, it should be kept in mind that taphonomic

processes may have destroyed an important part of the information through the destruction of the more fragile taxa (agglutinated and organic). Thus, only fossilising species (perforates, miliolids and fossilising agglutinated, see Chapter 4) are considered in the following analyses. For each level, total foraminiferal density (D) and classical ecological indices (species richness S , Rarefaction index E_{50} , Shannon index H , Evenness index E) have been calculated. We also processed R-mode clustering using unweighted pair-group method on relative densities of major taxa. We performed a Principal Component Analysis (PCA) based on the variance – covariance matrix between the 19 major species (relative abundances) observed along the core. In the discussion, our observations are completed by other analyses performed on ostracods assemblages (M.-A. Bassetti and A.-S. Fanget, IMAGES, Perpignan), sedimentary facies and granularity (B. Dennielou and G. Jouet, Ifremer Plouzané), as well as organic geochemistry (% organic carbon: R. Buscail, CEFREM, Perpignan).

5.4. RESULTS

5.4.1. Density, diversity and equitability

A total of 61 perforate, 17 miliolid and 3 fossilising agglutinated taxa are identified in the 24 analysed samples (Appendix A). Highest foraminiferal abundances D are recorded at 700 and 751 cm depth with 724 and 753 counted specimens, respectively. These densities drop to 82 individuals at 550 cm depth, followed by a new peak in foraminiferal abundances at 540 cm depth (227 ind./level). A constant decrease is observed from this level up to 380 cm depth, with total abundances of 97 and 103 ind./level at 400 and 380 cm depth, respectively. At 350 cm depth, high densities are measured with 390 ind./level, followed by a sharp decrease until 250 cm depth (57 ind./level). Along the top 250 cm of the core, foraminiferal densities remain quite constant and below ~ 100 ind./level, with a minimum of 51 individuals in level 160–161 cm and a maximum of 107 individuals at 200 cm depth (Fig. 4a). Species richness (S , Fig. 4b) follows exactly the same trend with a maximum of 51 identified species at 700 cm depth, and a minimum of 9 species at 150 cm. The rarefaction index calculated for 50 individuals (E_{50} , Fig. 4c) follows a more constant trend, with 2 maxima in level 700–701 cm (19 taxa) and from 160 cm depth to the top of the core (up to ~ 18 species) and a minimal value of ~ 8 taxa at 150 cm depth. E_{50} ranges between ~ 10 and 15 species in the rest of the core (from 680 to 200 cm depth). The Shannon diversity index (H , Fig. 4d) is maximal at 700 cm depth, with a value of ~ 2.9 . It ranges between ~ 1.7 and ~ 2.1 from 680 to 300 cm depth. From 300 cm depth to the surface, H shows erratic values varying between ~ 1.6 and ~ 2.6 .

The Evenness index (E, Fig. 4e) gradually increases towards the top of the core, from ~0.2 (level 650–651 cm) to ~0.7 (100 cm depth).

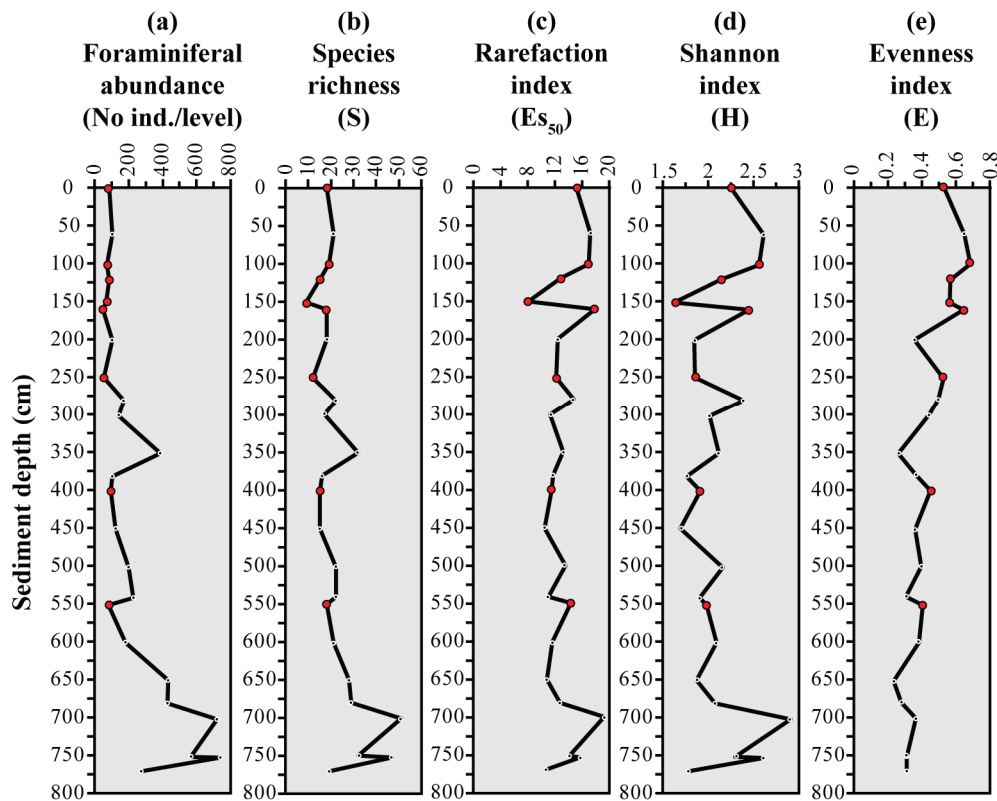


Figure 4: Ecological indices describing fossilising foraminiferal faunas along core RHS-KS57. (a) Foraminiferal abundances per investigated level; (b) Number of species S ; (c) Rarefaction index E_{50} ; (d)–(e) Biodiversity (H) and Evenness (E) indices. Red circles indicate levels with abundances < 100 counted individuals.

5.4.2. Faunal composition

19 taxa present a relative abundance > 5% in at least one sample. When a cut-off level of 0.4 is applied, R-mode clustering divides these 19 species into 5 groups plus 4 single taxa (Fig. 5a). Single species are *Pseudoeponides falsobeccarii*, *Cassidulina carinata*, *Adelosina longirostra* and *Bolivina dilatata*. *C. carinata* is abundant in the whole core (~15–8.5%), whereas *B. dilatata* is observed essentially in the top 3 m, with a maximal contribution of ~10.5% and 8.6% at 300 and 60 cm depth, respectively (Fig. 5c). *A. longirostra* has a low contribution (~0–2.5%) in most samples, with a maximal percentage of ~7% at 100 cm depth (Fig. 5c).

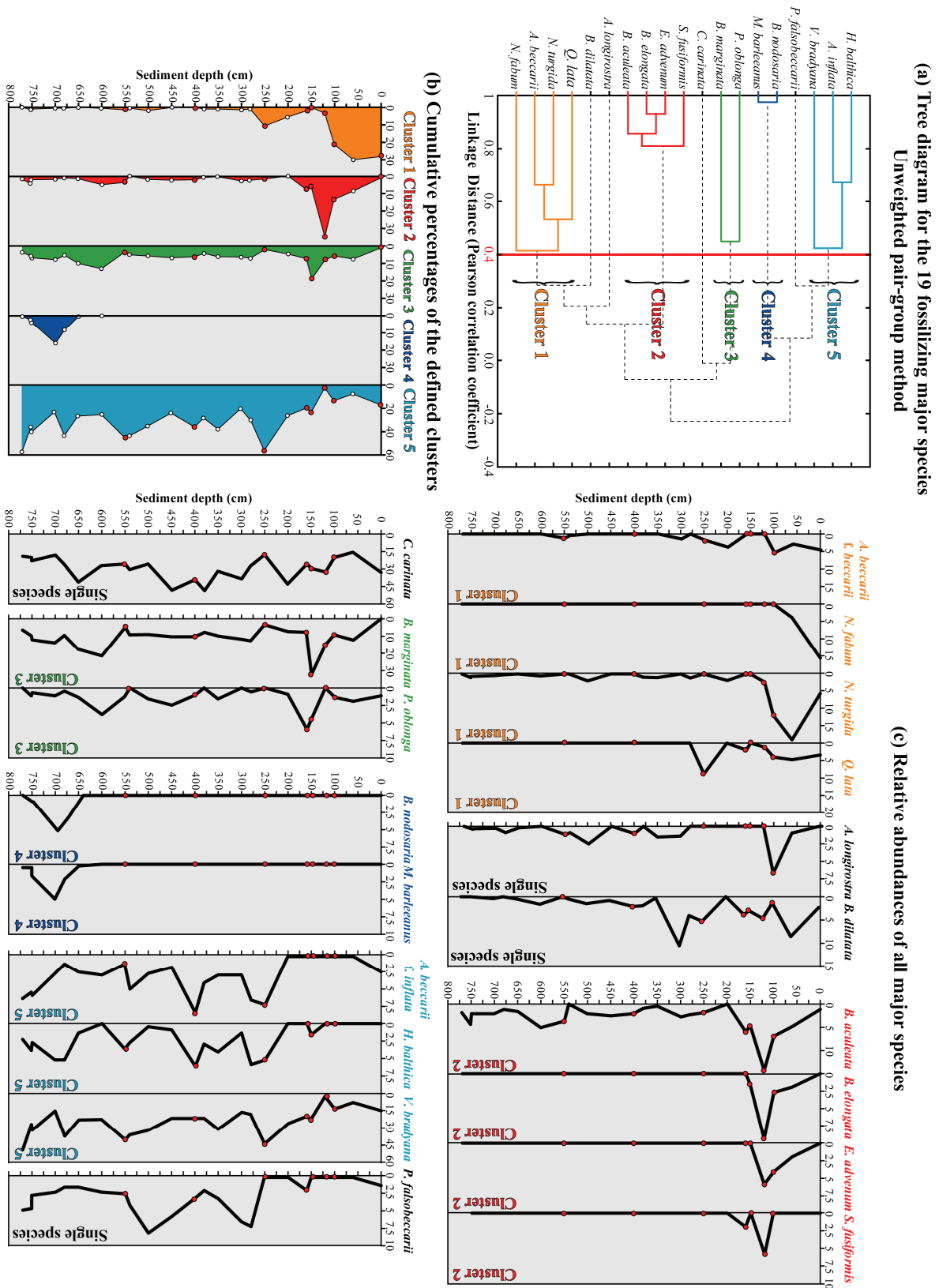


Figure 5: R-mode cluster analysis performed on the 19 fossilizing major species (> 5% in at least one of the 24 investigated samples) (a), cumulative percentages of taxa composing the defined clusters along core RHS-KS57 (b), and relative abundances of each taxon along core RHS-KS57 (c). Red circles indicate levels with abundances < 100 counted individuals.

P. falsobeccarii is essentially observed from 771 to 160 cm depth, with maximal contribution at 770 and 751 cm depth (~4.5%) and from 540 to 280 cm depth (up to ~8%) (Fig. 5c). The first Cluster 1 groups *Ammonia beccarii* f. *beccarii*, *Nonion fabum*, *Nonionella turgida* and *Quinqueloculina lata*. These species are present from 250 cm depth to the top of the core, with two maxima at 250 cm depth (10.5%) and in the topmost 100 cm (~21–30%) (Fig. 5b). Cluster 2 is composed by *Bulimina aculeata*, *Bulimina elongata*, *Elphidium advenum* and *Stainforthia fusiformis*. These taxa are only present between 160 and 60 cm depth, with a highest relative abundance of ~35% at 120 cm depth. From the base of the core until 60 cm depth, the contribution of Cluster 3 (*Bulimina marginata* and *Pyrgo oblonga*) varies between ~3.5 and ~37%. Highest percentages are observed at 600–650 cm depth (~19–25%), and from 120 to 160 cm depth (~14–37%). These taxa are almost totally absent in the topmost 1 cm of the core (~1%). Cluster 4, characterised by *Bigenerina nodosaria* and *Melonis barleeanus*, is observed between 650 and 771 cm depth, reaching a maximal contribution of ~10% at 700 cm depth. Cluster 5 groups *Ammonia beccarii* f. *inflata*, *Hyalinea balthica* and *V. bradyana*. Its highest contribution (~57.5%) is recorded in the basal part of the core (770 cm depth), followed by a sharp decrease until 700 cm depth (~23%). From 680 to 380 cm depth, its relative abundance is high (from ~24 to ~45%). A maximum occurs at 250 cm depth (~56%), followed by a decreasing trend until 120 cm depth (~2%). In the topmost 100 cm, its contribution remains fairly constant (~7.5–17%).

Principal Component analysis based on the variance – covariance matrix between the 19 major species defines three axes accounting for 84.4% of the total variability. In figure 6a, we have plotted the 24 samples on Axes 1 and 2. These two axes account for 44.4% and 27.5% of the total variability, respectively. A first group of levels (Group I) plots on the positive side of Axis 1 (350, 751, 750, 540, 680, 550, 250, 770 cm), strongly positively loaded by *V. bradyana*. On the far negative side of this axis plots level 120 cm, characterised by high relative abundances of, e.g., *C. carinata*, *B. marginata*, *B. aculeata* and *N. turgida*. Group II is constituted by levels 300, 400, 650, 200, 450 and 380 cm, with faunas dominated by *C. carinata* (negative side of Axis 2). A third group (Group III) is constituted by levels 60 and 100 cm, characterised by high abundances of *N. turgida* (positive side of Axis 2). The third axis (12.5% of the total variability; Fig. 6b) permits to separate between levels 150 and 600 cm (Group IV) dominated by, e.g., *B. marginata* (positive side of Axis 3), and the 0 cm level on the negative side of this axis because of the high contribution of, e.g., *N. fabum* and *N. turgida*.

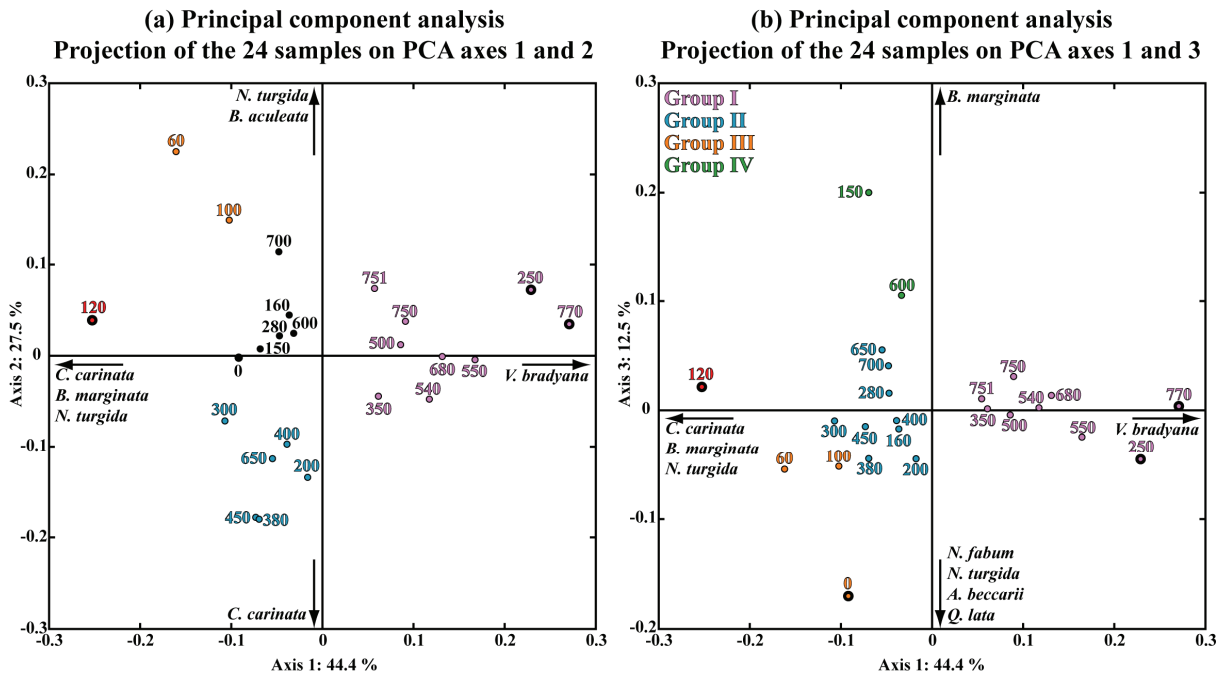


Figure 6: Principal Component Analysis based on the relative abundances of the 19 major species from core RHS-KS57: projection of the 24 samples on the factor-plane defined by PCA axes 1–3 (a) and 1–2 (b), and indication of the highest loading species on each axis. The circles indicate four groups of samples.

5.5. DISCUSSION

On the basis of the results obtained with the cluster analysis and the PCA based on benthic foraminiferal faunas, two main biozones can be distinguished in core RHS-KS57 (Fig. 7). The first Biozone A stretches from the downcore up to 160 cm depth. These levels are characterised by the domination of *Cassidulina carinata* and *Valvulineria bradyana* (PCA axes 1 and 2; Fig. 6a), and by maximal contribution of species from Cluster 5 (*Ammonia beccarii* f. *inflata*, *Hyalinea balthica*). In this sediment interval, three levels seem to record more specific environmental conditions. Levels 770 and 250 cm depth show highest abundances of *V. bradyana* (highest scores on PCA Axis 1; Fig. 6a). At 250 cm depth, a peak in Cluster 1 species is also recorded (*Q. lata*; Fig. 5b,c). Level 600 cm is isolated because of the high contribution of the Cluster 3 taxa *B. marginata* (highest score on PCA axis 3; Fig. 6b) and *P. oblonga* (Fig. 5b,c). We also can distinguish levels 700 and 680 cm depth characterised by the only occurrence of taxa belonging to Cluster 4 (*Bigennerina nodosaria* and *Melonis barleeanus*; Fig. 5b). The second main Biozone B corresponds to levels from 150 cm depth to the top of the core. In these levels, the contribution of *V. bradyana* decreases whereas *C. cassidulina* remains an important taxon (PCA axis 1; Fig. 6a). At the base of this

biozone, level 150 cm stands out because of maximal abundances of Cluster 3 species (i.e., *B. marginata* and *P. oblonga*; Figs. 5b,c and 6b), whereas level 120 cm is characterised by a peak in Cluster 2 taxa (*B. aculeata*, *B. elongata*, *E. advenum*, *S. fusiformis*; Fig. 5b). The following levels are marked by the noticeable increased influence of *N. turgida* (PCA Axis 2; Fig. 6a) and of *N. fabum* in the top most level (Fig. 6b).

Hereafter, we have used the subfossil foraminiferal thanatofacies (SFT) defined in Chapter 4 in order to facilitate and strengthen the interpretation of the foraminiferal faunas (i.e., of the biozones). Each SFT corresponds to a faunal group living under precise environmental conditions prevailing in specific parts of the recent Rhône prodelta (Fig. 8).

Biozone A, from 770 to 160 cm depth, is characterised by foraminiferal faunas dominated by *Valvulineria bradyana*, *Cassidulina carinata*, *Hyalinea balthica* and *Ammonia beccarii* f. *inflata*. Sub-fossil specimens of these species are observed from the river plume (*V. bradyana*; Fig. 8c) to the outer shelf area (*A. beccarii* f. *inflata*, *H. balthica*; Fig. 8d). *C. carinata* is considered as an opportunistic species living in areas with both riverine and marine influences, benefiting from fresh organic matter inputs of riverine (river plume) and/or marine origin (Fig. 8e). Consequently, foraminiferal faunas observed in Biozone A describe a fairly undisturbed environment (outer shelf faunas) with a noticeable riverine influence (*C. carinata*, *V. bradyana*). The very high contribution of *V. bradyana* at 770 cm depth is followed by constantly decreasing abundances up to 700 cm depth and the punctual occurrence of *B. nodosaria* and *M. barleeanus* at 700 and 680 cm depth. In modern sub-fossil faunas, the latter two species are also observed on the outer shelf, but show a lower tolerance to riverine influence than *A. beccarii* f. *inflata* and *H. balthica*. According to $\Delta^{14}\text{C}$ datation performed on a single specimen of *Turitella* sp., level 650 cm is dated around 279 ± 26 yr BP ($\Delta^{14}\text{C}$). Since the shift from the Bras de Fer to Pégoulie channel occurred around 239 yr BP, levels 700 and 680 cm would correspond to the last decades of activity of the Bras de Fer channel, located far west of our core locality (Fig. 7m). This period is marked by a significant decrease in river regime and competency, leading to a gradual lowering of the Rhône influence on the study area (Maillet, 2005). This reduced riverine input caused lower sediment deposition rates at our study site, explaining the maximal foraminiferal densities observed during this time interval (levels 751 to 680 cm) and the replacement of *V. bradyana* by species thriving preferentially in areas not influenced by riverine outflow.

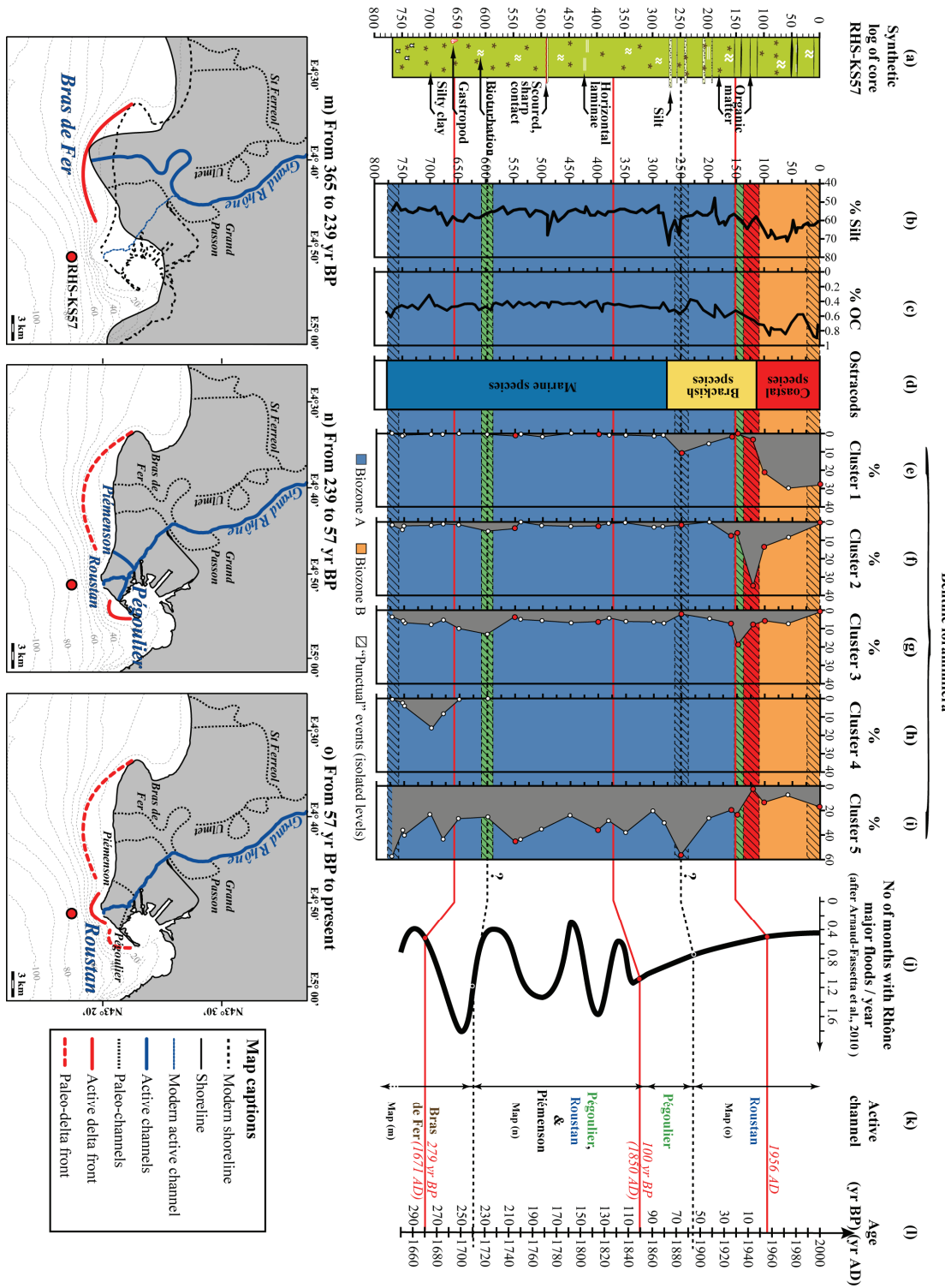


Figure 7: Synthesis of results obtained with all measured parameters on core RHS-KS57: lithologic log (a), silty sediment (b) and organic carbon contents (c), ostracods (d). For foraminiferal faunas, Cluster A: *A. beccarii* f. *beccarii*, *N. fabum*, *N. turgida* and *Q. lata* (e); Cluster B: *B. aculeata*, *B. elongata*, *E. advenum* and *S. fusiformis* (f); Cluster C: *B. marginata* and *P. oblonga* (g); Cluster D: *B. nodosaria* and *M. barleeanus* (h); Cluster E: *A. beccarii* f. *inflata*, *H. balthica* and *V. bradyana* (i). In parallel is reported the Rhône River flood regime from 290 yr BP (1650 AD) to today. Light blue, green and orange horizons correspond to the four biozones defined with benthic foraminiferal faunas. Red lines indicate datations obtained with $\Delta^{14}\text{C}$, ^{210}Pb and ^{137}Cs analyses.

At 650 cm depth, the disappearance of *B. nodosaria* and *M. barleeanus* and the re-establishment of *V. bradyana* and *C. carinata* suggest the end of this weaker riverine regime episode and an intensification of flood frequency around 250–240 yr BP (up to ~1.8 months/year with floods > 5.25 m NGF; Figs. 3 and 7j).

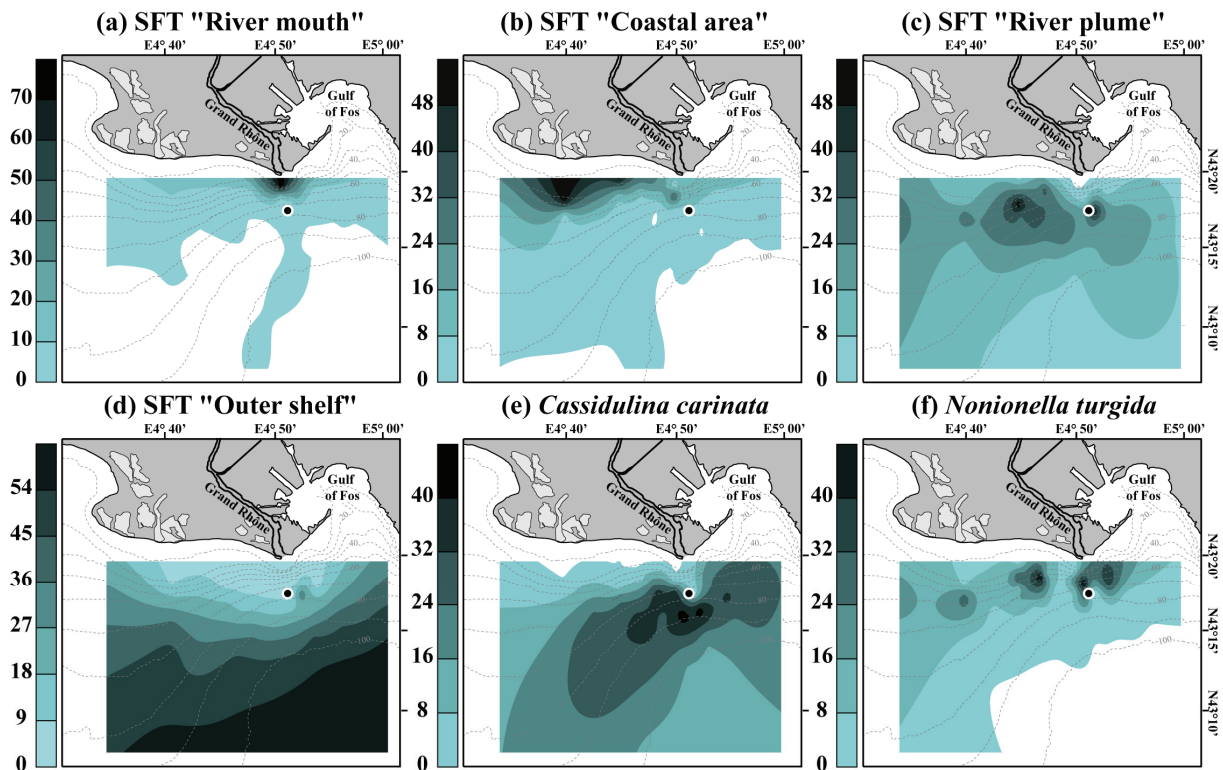


Figure 8: Today spatial distribution of the five sub-fossil thanatofacies (SFT) defined with sub-recent dead foraminiferal faunas, with the position of our core RHS-KS57 (black and white circle). (a) “Rhône River mouth”: *A. tepida* and *A. beccarii f. beccarii*; (b) “Coastal area”: *B. elongata*, *E. advenum*, *E. crispum*, *E. granosum*, *E. poeyanum* and *Q. lata*; (c) “River plume”: *N. fabum*, *R. phlegeri* and *V. bradyana*; (d) “Outer shelf”: *A. beccarii f. inflata*, *B. nodosaria*, *B. aculeata*, *B. marginata*, *H. balthica*, *M. barleeanus*, *P. falsobeccarii*, *Q. seminula* and *T. agglutinans*; (e) *Cassidulina carinata*: “Confluence between riverine and marine influences”; (f) *Nonionella turgida*

These conditions are interrupted at 600 cm depth by the noticeable increased abundances of *Bulimina marginata* and *Pyrgo oblonga* (Cluster 3; Fig. 5b). In sub-recent fossil faunas, these two species are found in very different prodeltaic areas. *B. marginata* is observed preferentially sheltered from river influence (i.e., on the outer shelf), whereas *P. oblonga* is characteristic of the most river influenced area, submitted to high sedimentary and organic material input (see Chapter 4). *B. marginata* is considered as one of the most opportunistic species in the Mediterranean sea, depending on high organic flux to the sea floor especially during phytoplankton blooms (Jorissen, 1987; Barmawidjaja et al., 1992; Jorissen et al., 1992;

De Rijk et al., 2000). Consequently, the occurrence of these taxa would indicate an input of sediments enriched in organic matter. This event could correspond to the abandon at 239 yr BP of the Bras de Fer channel for the Pégoulie arm flowing east of our core and the accessories arms of Piémenson and Roustan (Fig. 7n). Nowadays, the Rhône River plume flows generally south-westward, with a marine extension and shape that depend on the intensity of Rhône river outflow, the wind regime and the strength of the North Mediterranean Current (Naudin et al., 1997). Thus, also the river plume forming off the Pégoulie outlet was probably deviated into a south-western direction, probably impacting our study site by massive riverine supplies. At 550 cm depth, the decreased contribution of these species depicts a return to weaker riverine influence, more precisely of environmental conditions typical of areas on the border of the river plume flowing off the Pégoulie mouth, but also with a clear marine influence (see above).

Around ~370 cm depth, dated ~100 yr BP (anthropogenic Pb), the Pégoulie channel became the only active arm after the artificial closing down of accessories arms of Piémenson and Roustan, leading to a sudden increase in Pégoulie channel outflow (Maillet, 2005). Although most of the investigated parameters do not record major environmental changes at our study site (sedimentary facies, silt content, ostracods; Fig. 7a,b,d), foraminiferal faunas are characterised by the strong increase of *Bolivina dilatata* at 300 cm (Fig. 5c), which coincides with an early increase in OC content (Fig. 7c). In modern assemblages from the Rhône prodelta, the small-sized (63–150 µm) species *B. dilatata* is thriving in prodeltaic sediments enriched in continental organic matter (Mojtahid et al., 2009). In other studies, it has been reported with an opportunistic behaviour after important organic matter inputs (Barmawidjaja et al., 1992; Jorissen et al., 1992; Duchemin et al., 2007, 2008). In fact, *B. dilatata* is generally considered as a marker of increased organic matter supplies. Its presence corroborates our hypothesis of the impact of a major shift in dominant river channel at 100 yr BP, coinciding to about 350 cm sediment depth. At 250 cm depth, *Quinqueloculina lata* appears suddenly (~9%; Fig. 5c) in very low abundant (57 ind./level; Fig. 4a) and low diverse faunas (Fig. 4d). Nowadays, *Q. lata* is a typical species of silty sediments from the coastal prodeltaic area (Fig. 8b). Consequently, this very shallow taxon cohabits with faunas living preferentially under moderate riverine influence (i.e., *C. carinata*, *V. bradyana*, *H. balthica* and *A. beccarii* f. *inflata*; see above). This observation is synchronous with increases in the percentage of brackish ostracod species (Fig. 7d), organic carbon content (Fig. 7c) and the deposition of silty layers between ~270 and ~240 cm depth (Fig. 7a,b). Consequently, all measured parameters suggest a remarkable increase in riverine input at our study site around

270–250 cm depth. According to our chronostratigraphic framework, this event takes place between 100 yr BP (~370 cm depth, anthropogenic Pb) and 1956 AD (~150 cm depth, ^{137}Cs analyses), thus possibly corresponding to the re-opening of Roustan mouth at 57 yr BP. The location of our core directly in front of the Roustan mouth (~4 km; Fig. 7o) probably resulted in a sudden increased Rhône influence shown by the input of shallow/allochthonous faunas (*Q. lata*), but also of coarse and organic-rich riverine material diluting foraminiferal faunas (lower absolute abundances).

At 150 cm depth, we observe noticeable decrease in faunas indicative of weak to moderate riverine influence (*V. bradyana*, *H. balthica* and *A. beccarii* f. *inflata*) synchronous with a new occurrence of *B. marginata* and *P. oblonga*. These opportunistic taxa (see above) would benefit from increased riverine inputs enriched in organic material (from 0.41 to 0.62% OC from 280 to 170 cm depth; Fig. 7c) after the opening of Roustan mouth. This is the beginning of Biozone B. At 120 cm depth, we observe a minimal abundance of *V. bradyana*, *H. balthica*, *A. beccarii* f. *inflata*. *Q. lata* and *Nonionella turgida* (i.e., Cluster 1) start to increase, whereas the contribution of *Bulimina aculeata*, *Bulimina elongata*, *Elphidium advenum*, *Stainforthia fusiformis* (i.e., Cluster 2) and *B. marginata* is maximal. In sub-fossil faunas, these last species are found from the river mouth (*S. fusiformis*; (Mojtahid et al., 2009) to the most coastal silty area located west of the Rhône River mouth (*B. elongata*, *E. advenum*, *Q. lata*; Fig. 8b). The observation of such faunas highly tolerant to a strong riverine influence pleads for a strengthening of the Rhône input at our study site. The increase in *Q. lata* and *N. turgida* is continuous up to 60 cm depth. In this sediment interval (120 to 60 cm depth), OC and silty sediment reach maximal contents around 60 cm depth (~72% silt, ~0.87% OC; Figs. 7b,c). In sub-recent fossil faunas, *N. turgida* thrives preferentially in the most river impacted area (with highest deposition rates, see Chapter 4), in sediments enriched in riverine organic material (Goineau et al., In Press – see Chapter 1 in this thesis). Since 100 yr BP, climatic (end of the Little Ice Age) and anthropogenic forcings (engineering works on the Rhône channels) have led to a considerable reduction of the riverine discharge and sediment load, thus weakening noticeably the impact of the Rhône River outflow on its prodelta (e.g., Pichard, 1995; Arnaud-Fassetta and Provansal, 1999; Antonelli, 2002; Pont et al., 2002; Provansal et al., 2003). Surprisingly, the foraminiferal faunas as well as other environmental parameters (% OC, % silt, ostracods) suggest an opposite trend, with a gradual strengthening of the Rhône influence starting around 270 cm depth with the opening of Roustan mouth (~57 yr BP).

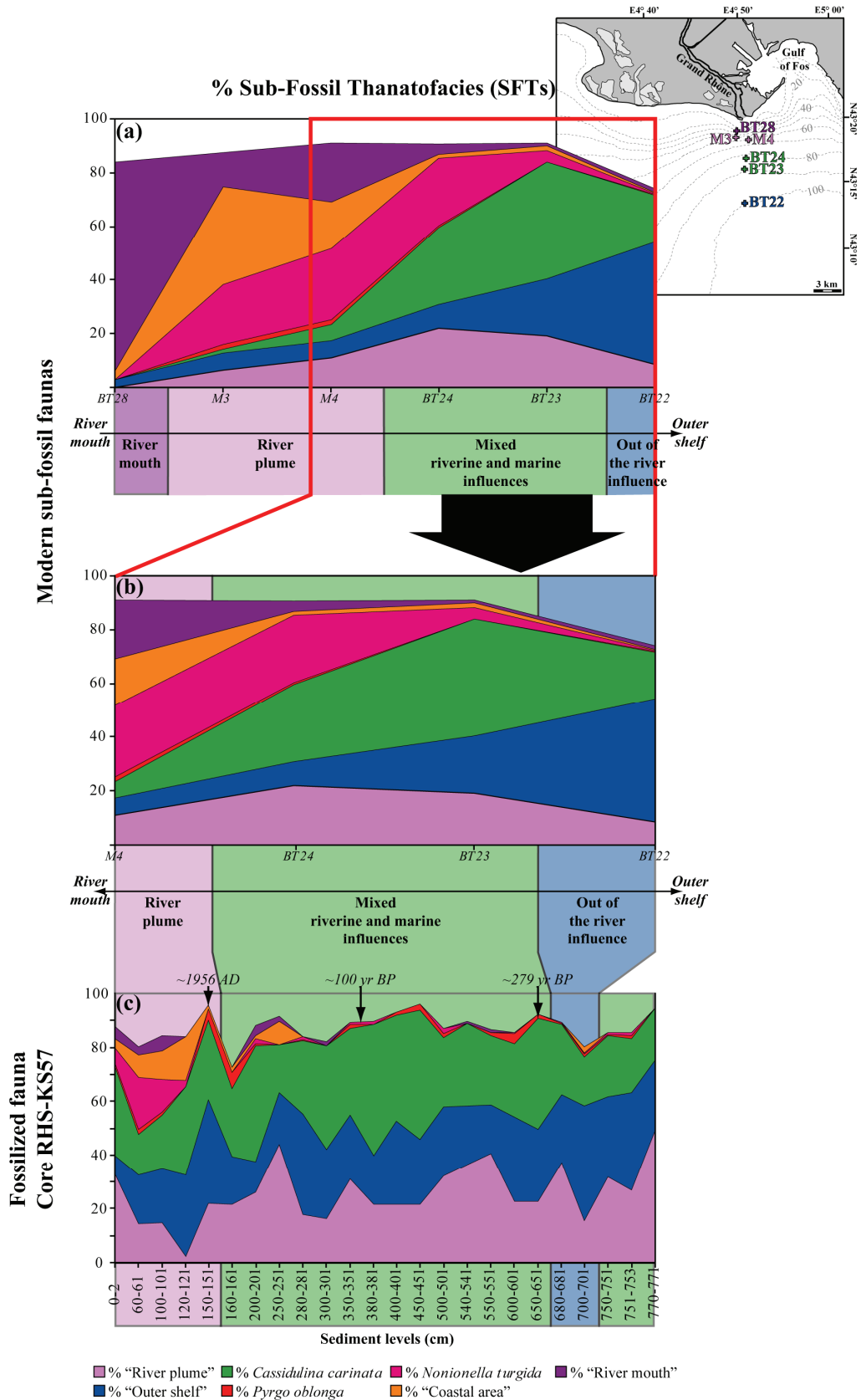


Figure 9: Comparison of Sub-Fossil Thanatofacies (SFTs) relative abundances in modern sub-fossil faunas, from the river mouth to the offshore environment, (a) with fossilised fauna from core RHS-KS57 (b). Light blue, green and red horizons correspond to the three SFTs observed in core RHS-KS57.

Moreover, we notice in the top most 60 cm of the core the sudden appearance and increase of *Nonion fabum* (Fig. 5c). Nowadays, this species thrives together with *V. bradyana* under the river plume, but would be more tolerant than *V. bradyana* to sediment enriched in low-quality organic matter (see Chapter 4). Thus, the increasing contribution of *N. fabum* could translate a decrease of organic matter quality at our study site during the last decade(s), in spite of the weakening of the Rhône influence.

To summarise, benthic foraminiferal faunas put into evidence two main periods: a first one with reduced to moderate riverine influence (Biozones A and B, from the bottom of the core until ~270 cm depth), and a second one with a more pronounced Rhône River impact (Biozone C and D, from ~270 cm depth to the top of the core). On figure 9 we present the modern succession of SFTs based on the study of subrecent (dead) faunas, with increasing distance from the river mouth (Stations BT28, M3, M4, BT26, BT24, BT23 and BT22). We observe a succession of river mouth, river plume, mixed riverine/marine influence, and finally outer shelf faunas along this transect with a minor Rhône River influence (Fig. 9a). If we plot the same SFTs in core RHS-KS57 (Fig. 9c), we observe at the base of the core typical outer shelf faunas (*B. nodosaria*, *M. barleeanus*, levels 700, 680 cm). These faunas are thereafter replaced by species thriving in areas subject to both riverine and marine influences (from 650 to 160 cm depth; e.g., *A. beccarii* f. *inflata*, *H. balthica*, *P. falsobeccarii*), and then by faunas typical of a dominantly riverine influence in the top most 100 cm (e.g., *A. beccarii* f. *beccarii*, *N. turgida*, *N. fabum*). Thus, we observe a succession from outer shelf to river plume thanatofacies similar to the offshore–onshore transect represented on figure 9b. These faunal changes depict the gradual progradation of the Roustan deltaic lobe which has advanced of ~2 km offshore since the re-opening of the Roustan mouth at 57 yr BP (Maillet, 2005).

5.6. CONCLUSIONS

Studying benthic foraminiferal faunas from core RHS-KS57, recovered in the Rhône prodeltaic lobe of Roustan, allowed us to reconstruct the main historical changes of the Rhône deltaic system for the last 400 years. Foraminiferal faunas put into evidence two well-defined periods. The base of the core corresponds to the last decades of activity of the Bras de Fer channel. Its gradual weakening competency and influence on the study area during this period allows the establishment of typical outer shelf faunas (e.g., *Bigenerina nodosaria*, *Melonis barleeanus*). After this period of weak riverine influence up to 160 cm depth, the dominance of foraminiferal faunas thriving in areas with mixed riverine/marine influence (e.g.,

Valvulineria bradyana, *Cassidulina carinata*, *Hyalinea balthica*) indicates an extension of the river plume as far as our study site. The shift from the Bras de Fer to the Pégoulie channel is marked around 600 cm sediment depth by the occurrence of *Bulimina marginata* and *Pyrgo oblonga* benefiting from the sudden input of sediments enriched in organic matter. The sudden occurrence at 250 cm depth of taxa thriving preferentially on the coastal prodeltaic area (*Quinqueloculina lata*) marks the opening of Roustan mouth at 57 yr BP. Our study site was then straight in front of the new Roustan mouth, directly supplied by riverine inputs (increasing deposition rate, organic carbon and coarse sediment contents). This event initiates the increasing contribution of faunas tolerant to high riverine influence (e.g., *Nonionella turgida*, *Ammonia beccarii* f. *beccarii*, *Quinqueloculina lata*) pleading for a strengthening of riverine organic and terrigenous inputs until 1950's (up to 60 cm depth). In the top most 60 cm of the core, the replacement of *V. bradyana* by *Nonion fabum* argues for a lowering in organic matter quality supplies over the last decade(s). Therefore, even if a higher sample resolution is necessary (every 1 to 10 cm) to study small-scale variations in the Rhône River influence, this preliminary study on benthic foraminiferal faunas put in evidence the gradual increasing Rhône River influence induced by the progradation of the Roustan lobe over the last 100 years. Consequently, fossilised archives of benthic foraminifera are a useful tool in the Rhône prodelta for the reconstruction of past sedimentary and organic fluxes.

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APPENDICES

Appendix A

Total benthic foraminiferal counts within core RHS-KS57. “r.d.” corresponds to the non-standardised total number of specimens counted for each species in each level; “%” indicates the relative abundance within the fossilising fauna for each species in each level. Grey boxes indicate percentages > 5% and major taxa.

Appendix B

Taxonomic reference list for major taxa.

Appendix A

Taxa	Level (cm)	0–2		60–61		100–101		120–121		150–151		160–161		200–201		250–251	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
Perforates																	
Indet.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>		4	4.5	3	2.9	4	5.3	–	–	–	–	–	–	4	3.7	1	1.8
<i>Ammonia beccarii</i> f. <i>inflata</i>		2	2.3	–	–	–	–	–	–	–	–	–	–	–	–	4	7.0
<i>Ammonia tepida</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphicoryna</i> spp.		3	3.4	3	2.9	1	1.3	–	–	–	–	–	–	3	2.8	–	–
<i>Astacolus crepidulus</i>		1	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astacolus insolitus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astergerinata mamilla</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Aubignyna planidorsa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina dilatata</i>		2	2.3	9	8.6	1	1.3	4	4.7	2	2.9	2	3.9	–	–	3	5.3
<i>Bolivina spathulata</i>		–	–	2	1.9	1	1.3	–	–	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>		–	–	–	–	–	–	–	–	–	–	2	3.9	2	1.9	–	–
<i>Bolivina subaenariensis</i>		1	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Buccella granulata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>		1	1.1	5	4.8	5	6.7	12	14.0	3	4.4	3	5.9	–	–	1	1.8
<i>Bulimina costata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina elongata</i>		–	–	2	1.9	2	2.7	8	9.3	1	1.5	–	–	–	–	–	–
<i>Bulimina gibba</i>		–	–	–	–	3	4.0	1	1.2	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>		–	–	13	12.4	7	9.3	13	15.1	22	32.4	4	7.8	8	7.5	2	3.5
<i>Cassidulina carinata</i>		29	33.0	16	15.2	15	20.0	28	32.6	20	29.4	13	25.5	46	43.0	10	17.5
<i>Cassidulina crassa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina minuta</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina oblonga</i>		1	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulinoides bradyi</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides lobatulus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicidoides pachydermus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Criboelphidium cuvillieri</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>		–	–	2	1.9	3	4.0	5	5.8	–	–	–	–	–	–	–	–
<i>Elphidium crispum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium poeyanum</i>		–	–	–	–	–	–	–	–	–	–	–	–	1	0.9	–	–
<i>Fissurina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fursenkoina acuta</i>		–	–	1	1.0	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis translucens</i>		–	–	–	–	–	–	1	1.2	–	–	–	–	–	–	–	–
<i>Globobulimina affinis</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globocassidulina subglobosa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroidina umbonata</i>		–	–	–	–	–	–	–	–	–	–	2	3.9	–	–	–	–
<i>Hanzawaia boueana</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Haynesina depressula</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>		–	–	–	–	–	–	–	–	1	1.5	–	–	–	–	3	5.3
<i>Lagena</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina atlantica</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina ?calcar</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina peregrina</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Melonis barleeanus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Neoconorbina terquemi</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonion fabum</i>		13	14.8	4	3.8	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella iridea</i>		–	–	–	–	–	–	–	–	–	–	2	3.9	2	1.9	–	–
<i>Nonionella stella</i>		–	–	–	–	–	–	2	2.3	–	–	1	2.0	1	0.9	–	–

Appendix A (continued)

Taxa	Level (cm)	0-2		60-61		100-101		120-121		150-151		160-161		200-201		250-251	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Nonionella turgida</i>		5	5.7	20	19.0	9	12.0	2	2.3	-	-	-	-	2	1.9	-	-
<i>Oolina</i> spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Porosonion granosum</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudoepionides falsobecarii</i>		1	1.1	-	-	-	-	-	-	-	-	1	2.0	-	-	-	-
<i>Rectuvigerina phlegeri</i>		3	3.4	3	2.9	1	1.3	-	-	-	-	1	2.0	-	-	-	-
<i>Robertina translucens</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rosalina</i> sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rosalina bradyi</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rosalina vilardeboana</i>		-	-	1	1.0	-	-	-	-	-	-	-	-	-	-	-	-
Rotalidae indet.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rutherfordoides</i> sp.1		-	-	-	-	-	-	-	-	1	1.5	-	-	1	0.9	-	-
<i>Sphaeroidina bulloides</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Stainforthia complanata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Stainforthia concava</i>		3	3.4	2	1.9	1	1.3	-	-	-	-	2	3.9	1	0.9	-	-
<i>Stainforthia fusiformis</i>		-	-	-	-	-	-	5	5.8	-	-	1	2.0	-	-	-	-
<i>Uvigerina peregrina bifurcata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Uvigerina mediterranea</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Valvulinera bradyana</i>		13	14.8	8	7.6	10	13.3	2	2.3	15	22.1	10	19.6	28	26.2	25	43.9
Miliolids																	
Indet.		-	-	-	-	-	-	1	1.2	-	-	1	2.0	-	-	-	-
<i>Adelosina longirostra</i>		-	-	1	1.0	5	6.7	-	-	-	-	-	-	-	-	-	-
<i>Biloculinella labiata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cornuspira foliacea</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cornuspira involvens</i>		-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	-	-
<i>Miliolinella</i> spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Miliolinella subrotunda</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pyrgo</i> sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pyrgo oblonga</i>		1	1.1	2	1.9	1	1.3	-	-	3	4.4	3	5.9	1	0.9	-	-
<i>Pyrgo subsphaerica</i>		-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	-	-
<i>Quinqueloculina</i> spp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quinqueloculina badenensis</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quinqueloculina lata</i>		3	3.4	5	4.8	3	4.0	1	1.2	-	-	1	2.0	-	-	5	8.8
<i>Quinqueloculina milletti</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1.8
<i>Quinqueloculina pygmaea</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quinqueloculina seminula</i>		-	-	-	-	2	2.7	-	-	-	-	1	2.0	3	2.8	-	-
<i>Quinqueloculina stalkerii</i>		-	-	2	1.9	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sigmoilinita tenuis</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sigmoilopsis schlumbergeri</i>		-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	1	1.8
<i>Spiroloculina excavata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Triloculina</i> sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Triloculina tricarinata</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Triloculina trigonula</i>		-	-	-	-	-	-	-	-	-	-	1	2.0	-	-	-	-
Fossilising agglutinated																	
Indet.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bigenerina nodosaria</i>		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spiroplectinella wrighti</i> (= <i>saggitula</i>)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Textularia agglutinans</i>		2	2.3	1	1.0	1	1.3	1	1.2	-	-	-	-	1	0.9	1	1.8
Non-fossilising agglutinated																	
Indet.		1	████	2	████	-	████	-	████	1	████	-	████	4	████	-	████
<i>Adercotryma glomerata</i>		2	████	-	████	-	████	-	████	-	████	-	████	-	████	-	████
<i>Ammoscalaria foliacea</i>		-	████	-	████	-	████	-	████	-	████	-	████	-	████	-	████
<i>Clavulina cylindrica</i>		3	████	-	████	2	████	-	████	5	████	1	████	12	████	4	████
<i>Cribrostomoides</i> sp.		-	████	-	████	-	████	-	████	-	████	-	████	-	████	-	████

Appendix A (continued)

Taxa	Level (cm)	0–2		60–61		100–101		120–121		150–151		160–161		200–201		250–251	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Cribr stomoides subglobosus</i>		–		–		–		–		–		–		–		–	
<i>Cribr stomoides wiesneri</i>		2		–		–		–		–		–		–		–	
<i>Eggerella</i> spp.		12		9		12		6		6		2		23		24	
<i>Haplophragmoides</i> spp.		3		–		–		–		–		–		–		–	
<i>Lagenammina</i> sp.		–		–		–		–		–		–		–		–	
<i>Lagenammina difflugiformis</i>		2		–		–		–		–		–		–		–	
<i>Recurvoides contortus</i>		–		–		–		–		–		–		–		–	
<i>Reophax fusiformis</i>		–		–		–		–		–		–		–		–	
<i>Techinitella legumen</i>		–		–		1		–		–		–		–		–	
<i>Trochammina</i> sp.		–		–		–		–		–		–		–		–	
<i>Trochammina globigeriniformis</i>		–		–		–		–		–		–		3		–	
Tot. non-fossilising Agglutinated		25		11		15		6		12		3		42		28	
Tot. Fossilising individuals		88		105		75		86		68		51		107		57	

Taxa	Level (cm)	280–281		300–301		350–351		380–381		400–401		450–451		500–501		540–541	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
Perforates																	
<i>Indet.</i>		3	1.7	1	0.7	–	–	–	–	–	–	1	0.8	1	0.5	3	1.3
<i>Ammonia beccarii</i> f. <i>beccarii</i>		–	–	2	1.4	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Ammonia beccarii</i> f. <i>inflata</i>		11	6.4	4	2.8	11	2.8	4	3.9	8	8.2	2	1.6	5	2.5	11	4.8
<i>Ammonia tepida</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Amphicoryna</i> spp.		5	2.9	1	0.7	3	0.8	2	1.9	1	1.0	1	0.8	7	3.5	7	3.1
<i>Astacolus crepidulus</i>		–	–	–	–	–	–	1	1.0	–	–	–	–	–	–	–	–
<i>Astacolus insolitus</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Astergerinata mamilla</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Aubignyna planidorsa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>		2	1.2	–	–	2	0.5	–	–	–	–	–	–	1	0.5	1	0.4
<i>Bolivina dilatata</i>		7	4.0	15	10.5	1	0.3	2	1.9	2	2.1	1	0.8	3	1.5	1	0.4
<i>Bolivina spathulata</i>		–	–	–	–	1	0.3	3	2.9	1	1.0	–	–	–	–	–	–
<i>Bolivina striatula</i>		1	0.6	1	0.7	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Bolivina subaenariensis</i>		2	1.2	–	–	–	–	1	1.0	1	1.0	–	–	1	0.5	–	–
<i>Buccella granulata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina aculeata</i>		4	2.3	4	2.8	2	0.5	1	1.0	2	2.1	3	2.4	4	2.0	–	–
<i>Bulimina costata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Bulimina elongata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina gibba</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>		22	12.7	17	11.9	39	10.0	8	7.8	10	10.3	13	10.4	18	9.0	21	9.3
<i>Cassidulina carinata</i>		47	27.2	55	38.5	124	31.8	50	48.5	38	39.2	60	48.0	51	25.6	69	30.4
<i>Cassidulina crassa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina minuta</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cassidulina oblonga</i>		–	–	–	–	4	1.0	–	–	–	–	–	–	–	–	–	–
<i>Cassidulinoides bradyi</i>		2	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicides lobatulus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cibicidoides pachydermus</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Cribr oelphidium cuvillieri</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dentalina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium advenum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium crispum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium poeyanum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fissurina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fursenkoina acuta</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Gavelinopsis praegeri</i>		–	–	–	–	–	–	–	–	–	–	1	0.8	–	–	–	–
<i>Gavelinopsis translucens</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix A (continued)

Taxa	Level (cm)	280–281		300–301		350–351		380–381		400–401		450–451		500–501		540–541	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Globobulimina affinis</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina pyrula</i>		–	–	–	–	2	0.5	–	–	–	–	–	–	–	–	–	–
<i>Globocassidulina subglobosa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Gyroidina umbonata</i>		2	1.2	–	–	2	0.5	1	1.0	–	–	1	0.8	–	–	1	0.4
<i>Hanzawaia boueana</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Haynesina depressula</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hyalinea balthica</i>		10	5.8	2	1.4	16	4.1	3	2.9	6	6.2	1	0.8	1	0.5	6	2.6
<i>Lagena</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina atlantica</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1.3
<i>Lenticulina ?calcar</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina peregrina</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Melonis barleeanus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Neoconorbina terquemi</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonion fabum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella iridea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella stella</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella turgida</i>		2	1.2	–	–	4	1.0	1	1.0	–	–	–	–	4	2.0	–	–
<i>Oolina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Porosonion granosum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudoepionides falsobeccarii</i>		12	6.9	9	6.3	12	3.1	2	1.9	3	3.1	7	5.6	16	8.0	9	4.0
<i>Rectuvigerina phlegeri</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>		–	–	1	0.7	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Rosalina</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina bradyi</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>		1	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotalidae indet.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rutherfordoides</i> sp.1		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Sphaeroidina bulloides</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia complanata</i>		2	1.2	–	–	–	–	–	–	–	–	–	–	–	–	2	0.9
<i>Stainforthia concava</i>		–	–	4	2.8	1	0.3	1	1.0	–	–	–	–	1	0.5	–	–
<i>Stainforthia fusiformis</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina peregrina bifurcata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Uvigerina mediterranea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Valvulineria bradyana</i>		31	17.9	23	16.1	121	31.0	22	21.4	21	21.6	27	21.6	64	32.2	82	36.1
Miliolids																	
Indet.		–	–	–	–	4	1.0	–	–	–	–	–	–	–	–	–	–
<i>Adelosina longirostra</i>		–	–	2	1.4	6	1.5	–	–	1	1.0	–	–	5	2.5	2	0.9
<i>Biloculinella labiata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cornuspira foliacea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cornuspira involvens</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Miliolinella subrotunda</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	1	0.4
<i>Pyrgo</i> sp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrgo oblonga</i>		1	0.6	–	–	6	1.5	–	–	1	1.0	3	2.4	3	1.5	–	–
<i>Pyrgo subsphaerica</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina badenensis</i>		1	0.6	1	0.7	2	0.5	–	–	–	–	–	–	3	1.5	–	–
<i>Quinqueloculina lata</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina milletti</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>		–	–	–	–	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>		3	1.7	1	0.7	7	1.8	–	–	–	–	1	0.8	3	1.5	2	0.9
<i>Quinqueloculina stalkerii</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilinita tenuis</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>		–	–	–	–	4	1.0	–	–	–	–	–	–	2	1.0	–	–

Appendix A (continued)

Taxa	Level (cm)		280–281		300–301		350–351		380–381		400–401		450–451		500–501		540–541	
	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Spiroloculina excavata</i>	–	–	–	–	2	0.5	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.5	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina trigonula</i>	–	–	–	–	–	–	–	–	–	–	1	1.0	–	–	–	–	–	–
Fossilising agglutinated																		
Indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.5	–	–
<i>Bigenerina nodosaria</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spiroplectinella wrighti</i> (= <i>saggitula</i>)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Textularia agglutinans</i>	2	1.2	–	–	6	1.5	1	1.0	1	1.0	1	1.0	3	2.4	4	2.0	1	0.4
Non-fossilising agglutinated																		
Indet.	4		2		2		1		–		–		–		–		1	
<i>Adercotryma glomerata</i>	–		–		–		–		–		–		–		–		–	
<i>Ammoscalaria foliacea</i>	–		–		1		–		–		–		–		–		–	
<i>Clavulina cylindrica</i>	7		2		3		–		–		–		–		–		4	
<i>Cribrostomoides</i> sp.	–		–		–		–		–		–		–		–		–	
<i>Cribrostomoides subglobosus</i>	–		1		–		–		–		–		–		–		–	
<i>Cribrostomoides wiesneri</i>	–		–		–		–		–		–		–		–		–	
<i>Eggerella</i> spp.	9		–		15		3		–		3		3		3		9	
<i>Haplophragmoides</i> spp.	4		–		–		–		–		–		–		–		–	
<i>Lagenammina</i> sp.	–		–		–		–		–		–		–		–		–	
<i>Lagenammina difflugiformis</i>	1		–		–		–		–		–		–		–		–	
<i>Recurvoides contortus</i>	–		–		–		–		–		–		–		–		–	
<i>Reophax fusiformis</i>	–		–		–		–		–		–		–		1		–	
<i>Technitella legumen</i>	–		–		–		–		–		–		–		–		–	
<i>Trochammina</i> sp.	–		–		–		–		–		–		–		–		–	
<i>Trochammina globigeriniformis</i>	–		–		–		–		–		–		–		–		–	
Tot. non-fossilising Agglutinated	25		5		21		4		0		3		4		4		14	
Tot. Fossilising individuals	173		143		390		103		97		125		199		227			

Taxa	Level (cm)		550–551		600–601		650–651		680–681		700–701		750–751		751–753		770–771	
	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
Perforates																		
Indet.	2	2.4	–	–	1	0.2	–	–	–	–	–	–	–	–	2	0.3	–	–
<i>Ammonia beccarii</i> f. <i>beccarii</i>	1	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammonia beccarii</i> f. <i>inflata</i>	1	1.2	5	2.7	10	2.3	5	1.2	18	2.5	32	5.6	38	5.2	17	6.2	–	–
<i>Ammonia tepida</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Amphicoryna</i> spp.	1	1.2	11	5.9	3	0.7	8	1.9	17	2.3	9	1.6	4	0.6	1	0.4	–	–
<i>Astacolus crepidulus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astacolus insolitus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Astergerinata mamilla</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Aubignyna planidorsa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bolivina alata</i>	–	–	–	–	2	0.5	–	–	11	1.5	2	0.4	8	1.1	–	–	–	–
<i>Bolivina dilatata</i>	–	–	3	1.6	2	0.5	–	–	3	0.4	–	–	–	–	–	–	–	–
<i>Bolivina spathulata</i>	–	–	1	0.5	2	0.5	–	–	1	0.1	–	–	–	–	–	–	–	–
<i>Bolivina striatula</i>	–	–	–	–	–	–	–	–	2	0.5	–	–	–	–	–	–	–	–
<i>Bolivina subaenariensis</i>	–	–	2	1.1	–	–	2	0.5	2	0.3	21	3.7	31	4.3	6	2.2	–	–
<i>Buccella granulata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.4
<i>Bulimina aculeata</i>	3	3.7	9	4.9	7	1.6	5	1.2	14	1.9	12	2.1	31	4.3	5	1.8	–	–
<i>Bulimina costata</i>	1	1.2	1	0.5	–	–	2	0.5	–	–	–	–	1	0.1	1	0.4	–	–
<i>Bulimina elongata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina gibba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Bulimina marginata</i>	4	4.9	40	21.6	77	17.7	41	9.6	101	14.0	69	12.1	71	9.8	18	6.5	–	–
<i>Cassidulina carinata</i>	21	25.6	50	27.0	178	41.0	111	25.9	130	18.0	129	22.7	145	20.0	52	18.9	–	–

Appendix A (continued)

Taxa	Level (cm)	550–551		600–601		650–651		680–681		700–701		750–751		751–753		770–771	
		r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Cassidulina crassa</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	1	0.1	–	–
<i>Cassidulina minuta</i>		–	–	–	–	–	–	1	0.2	–	–	–	–	–	–	–	–
<i>Cassidulina oblonga</i>		–	–	–	–	2	0.5	12	2.8	8	1.1	16	2.8	16	2.2	2	0.7
<i>Cassidulinoides bradyi</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Chilostomella ovoidea</i>		–	–	–	–	–	–	1	0.2	–	–	–	–	–	–	–	–
<i>Cibicides</i> sp.		–	–	–	–	–	–	–	–	–	–	1	0.2	–	–	–	–
<i>Cibicides lobatulus</i>		–	–	–	–	–	–	–	–	4	0.6	–	–	1	0.1	–	–
<i>Cibicidoides pachydermus</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cribolephidium cuvillieri</i>		–	–	–	–	–	–	–	–	12	1.7	–	–	–	–	–	–
<i>Dentalina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	2	0.3	–	–
<i>Elphidium advenum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Elphidium crispum</i>		–	–	–	–	–	–	–	–	16	2.2	–	–	–	–	–	–
<i>Elphidium poeyanum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Fissurina</i> spp.		–	–	–	–	–	–	–	–	2	0.3	–	–	–	–	–	–
<i>Fursenkoina acuta</i>		–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Gavelinopsis praegeri</i>		–	–	–	–	–	–	–	–	–	–	4	0.7	–	–	–	–
<i>Gavelinopsis translucens</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globobulimina affinis</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Globobulimina pyrula</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Globocassidulina subglobosa</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Gyroldina umbonata</i>		3	3.7	1	0.5	2	0.5	1	0.2	1	0.1	3	0.5	5	0.7	–	–
<i>Hanzawaia boueana</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Haynesina depressula</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Hyalinea balthica</i>		3	3.7	–	–	6	1.4	22	5.1	38	5.2	15	2.6	28	3.9	6	2.2
<i>Lagena</i> spp.		–	–	–	–	–	–	1	0.2	–	–	1	0.2	–	–	–	–
<i>Lenticulina</i> spp.		–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Lenticulina atlantica</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lenticulina ?calcar</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Lenticulina peregrina</i>		–	–	–	–	–	–	–	–	2	0.3	–	–	–	–	–	–
<i>Melonis barleeanus</i>		–	–	–	–	1	0.2	9	2.1	36	5.0	9	1.6	4	0.6	1	0.4
<i>Neoconorbina terquemi</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	1	0.1	–	–
<i>Nonion fabum</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella iridea</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella stella</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nonionella turgida</i>		–	–	1	0.5	–	–	1	0.2	3	0.4	4	0.7	8	1.1	–	–
<i>Oolina</i> spp.		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Porosonion granosum</i>		–	–	–	–	–	–	–	–	15	2.1	–	–	–	–	–	–
<i>Pseudoeponides falsobeccarii</i>		2	2.4	4	2.2	6	1.4	6	1.4	15	2.1	14	2.5	33	4.6	13	4.7
<i>Rectuvigerina phlegeri</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Robertina translucens</i>		–	–	1	0.5	–	–	–	–	1	0.1	3	0.5	3	0.4	1	0.4
<i>Rosalina</i> sp.		–	–	–	–	–	–	–	–	1	0.1	1	0.2	–	–	–	–
<i>Rosalina bradyi</i>		–	–	–	–	–	–	–	–	2	0.3	–	–	–	–	–	–
<i>Rosalina vilardeboana</i>		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotalidae indet.		–	–	–	–	–	–	–	–	5	0.7	–	–	–	–	–	–
<i>Rutherfordoides</i> sp.1		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sphaeroidina bulloides</i>		–	–	–	–	–	–	–	–	1	0.1	1	0.2	–	–	–	–
<i>Stainforthia complanata</i>		–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Stainforthia concava</i>		2	2.4	2	1.1	3	0.7	–	–	–	–	–	–	–	–	–	–
<i>Stainforthia fusiformis</i>		–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Uvigerina peregrina bifurcata</i>		–	–	–	–	–	–	1	0.2	1	0.1	1	0.2	–	–	–	–
<i>Uvigerina mediterranea</i>		–	–	–	–	–	–	–	–	1	0.1	–	–	–	–	–	–
<i>Valvulineria bradyana</i>		33	40.2	42	22.7	99	22.8	158	36.9	111	15.3	181	31.8	195	26.9	135	49.1
Miliolids		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Indet.		–	–	–	–	–	–	1	0.2	2	0.3	–	–	2	0.3	2	0.7
<i>Adelosina longirostra</i>		1	1.2	–	–	1	0.2	4	0.9	2	0.3	2	0.4	3	0.4	–	–

Appendix A (continued)

Taxa	Level (cm)		550–551		600–601		650–651		680–681		700–701		750–751		751–753		770–771	
	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%	r.d.	%
<i>Biloculinella labiata</i>	–	–	–	–	1	0.2	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Cornuspira foliacea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–
<i>Cornuspira involvens</i>	–	–	–	–	–	–	–	–	–	–	1	0.1	–	–	1	0.1	–	–
<i>Miliolinella</i> spp.	–	–	–	–	1	0.2	3	0.7	–	–	–	–	–	–	5	0.7	–	–
<i>Miliolinella subrotunda</i>	–	–	1	0.5	2	0.5	–	–	–	–	3	0.4	4	0.7	–	–	–	–
<i>Pyrgo</i> sp.	–	–	–	–	–	–	–	–	–	–	2	0.3	–	–	2	0.3	–	–
<i>Pyrgo oblonga</i>	1	1.2	7	3.8	6	1.4	2	0.5	8	1.1	4	0.7	8	1.1	8	1.1	–	–
<i>Pyrgo subsphaerica</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina</i> spp.	–	–	1	0.5	1	0.2	–	–	–	–	–	–	1	0.2	–	–	–	–
<i>Quinqueloculina badenensis</i>	–	–	1	0.5	4	0.9	3	0.7	11	1.5	3	0.5	6	0.8	6	0.8	1	0.4
<i>Quinqueloculina lata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina milletti</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina pygmaea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Quinqueloculina seminula</i>	1	1.2	–	–	4	0.9	2	0.5	25	3.5	5	0.9	29	4.0	9	3.3	–	–
<i>Quinqueloculina stalkerii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilinita tenuis</i>	–	–	1	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sigmoilopsis schlumbergeri</i>	–	–	1	0.5	6	1.4	4	0.9	15	2.1	5	0.9	4	0.6	1	0.4	1	0.4
<i>Spiroloculina excavata</i>	–	–	–	–	–	–	–	–	–	–	6	0.8	4	0.7	1	0.1	–	–
<i>Triloculina</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Triloculina tricarinata</i>	–	–	–	–	–	–	–	–	–	–	3	0.4	–	–	1	0.1	–	–
<i>Triloculina trigonula</i>	1	1.2	–	–	1	0.2	–	–	–	–	–	–	–	–	–	–	–	–
Fossilising agglutinated																		
Indet.	–	–	–	–	1	0.2	1	0.2	–	–	–	–	–	–	–	–	–	–
<i>Bigerina nodosaria</i>	–	–	–	–	–	–	13	3.0	36	5.0	5	0.9	6	0.8	–	–	–	–
<i>Spiroplectinella wrighti</i> (= <i>saggitula</i>)	–	–	–	–	–	–	–	–	2	0.3	1	0.2	–	–	–	–	–	–
<i>Textularia agglutinans</i>	1	1.2	–	–	5	1.2	6	1.4	27	3.7	7	1.2	21	2.9	3	1.1	–	–
Non-fossilising agglutinated																		
Indet.	1	1.2	1	1.2	–	–	–	–	–	–	–	–	2	0.7	5	0.7	1	0.4
<i>Adercotryma glomerata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ammoscalaria foliacea</i>	–	–	1	1.2	–	–	–	–	–	–	2	0.7	7	3.0	3	0.4	–	–
<i>Clavulina cylindrica</i>	–	–	–	–	4	1.2	1	0.3	–	–	–	–	–	–	3	0.4	–	–
<i>Cribrostomoides</i> sp.	–	–	–	–	1	0.3	–	–	–	–	2	0.7	4	1.2	–	–	–	–
<i>Cribrostomoides subglobosus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.3
<i>Cribrostomoides wiesneri</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Eggerella</i> spp.	–	–	3	1.2	14	4.2	3	0.9	2	0.6	10	3.0	13	3.9	1	0.3	1	0.3
<i>Haplophragmoides</i> spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0.3	–	–
<i>Lagenamma</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	2	0.6	4	1.2	–	–
<i>Lagenamma difflugiformis</i>	1	1.2	–	–	4	1.2	1	0.3	–	–	–	–	–	–	–	–	–	–
<i>Recurvoides contortus</i>	–	–	–	–	–	–	–	–	–	–	–	–	5	1.5	–	–	–	–
<i>Reophax fusiformis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Technitella legumen</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Trochamma</i> sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	0.3	–	–	–	–
<i>Trochamma globigeriniformis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Tot. non-fossilising Agglutinated	2	1.2	5	1.2	23	5.4	5	1.4	6	1.6	31	7.6	29	7.6	3	1.1	–	–
Tot. Fossilising individuals	82	19.5	185	45.5	434	108.4	428	107.0	724	181.0	569	142.3	753	188.3	275	68.8	–	–

Appendix B

- Adelosina longirostra* (d'Orbigny) = *Triloculina longirostra* d'Orbigny, 1826; in Jorissen, 1988, Plate 2, FIG. 14
- Ammonia beccarii* f. *beccarii* (Linnaeus) = *Nautilus beccarii* Linnaeus f. *beccarii* Linnaeus, 1758; in Jorissen, 1988, Plate 2, Fig. 5a–b
- Ammonia beccarii* f. *inflata* (Seguenza) = *Nautilus beccarii* Linnaeus f. *inflata* Seguenza, 1862; in Jorissen, 1988, Plate 6, Figs. 1–4
- Bigenerina nodosaria* d'Orbigny, 1826; in Jorissen, 1988, Plate 1, Fig. 10
- Bolivina dilatata* (Reuss) = *Brizalina dilatata* Reuss, 1850; in Colom, 1974, Fig. 18j–n
- Bulimina aculeata* d'Orbigny, 1826; in Jorissen, 1988, Plate 4, Fig. 5
- Bulimina elongata* d'Orbigny, 1826; in Jones, 1994, Plate 50, Figs. 3–4
- Bulimina marginata* d'Orbigny, 1826; in Colom, 1974, Fig. 16d'–h', k'–o'
- Cassidulina carinata* Silvestri, 1896 = *Cassidulina laevigata* d'Orbigny var. *carinata* Silvestri, 1896; in Mojtahid et al., 2009, Plate 1, Fig. 3
- Elphidium advenum* (Cushman) = *Polystomella advena* Cushman, 1922; in Jorissen, 1988, Plate 24, Fig. 3a–b
- Hyalinea balthica* (Schroeter) = *Nautilus balthicus* Schroeter, 1793; in Mojtahid et al., 2009, Plate 2, Fig. 7
- Melonis barleeanus* (Williamson) = *Nonionina barleeanana* Williamson, 1858; in Jorissen, 1988, Plate 4, Fig. 8 (as *Nonion barleeanum*)
- Nonion fabum* (Fichtel and Moll) = *Nautilus faba* Fichtel and Moll, 1798; in Jones, 1994, Plate 109, Figs. 12–13
- Nonionella turgida* (Williamson) = *Rotalina turgida* Williamson, 1858; in Jorissen, 1988, Plate 4, Figs. 11–13
- Pseudoeponides falsobeccarii* Rouvillois, 1974; in Jorissen, 1988, Plate 4, Fig. 3a–b
- Pyrgo oblonga* (d'Orbigny) = *Biloculina oblonga* d'Orbigny, 1839; in Rasmussen, 2005, Plate 5, Fig. 2
- Quinqueloculina lata* Terquem, 1876; in Murray, 2003, Plate 4, Figs. 9–10
- Stainforthia fusiformis* (Williamson) = *Bulimina pupoides* d'Orbigny var. *fusiformis* Williamson, 1858; in Gooday and Alve, 2001, Plate 3, Figs. A–B–C
- Valvulineria bradyana* (Fornasini) = *Discorbina bradyana* Fornasini, 1900; in Jorissen, 1988, Plate 4, Figs. 1–2

SYNTHESE

SYNTHESE

RAPPEL DES OBJECTIFS DE LA THESE

L'objectif majeur de cette étude vise à calibrer l'outil foraminifères benthiques au débouché du Rhône afin de l'utiliser en tant que bio-indicateur des changements environnementaux actuels et passés. Pour y parvenir, ce travail s'est divisé en 5 grandes étapes :

1. Etudier la répartition spatiale des faunes vivantes de foraminifères benthiques dans l'ensemble de la plate-forme continentale soumise directement à l'influence du Rhône (15 à 100 m de profondeur, jusqu'à 22 km vers le large) afin d'estimer l'impact des dépôts de matière organique, des conditions redox dans les sédiments ainsi que des processus hydro-sédimentaires dans un tel environnement.

2. Identifier des variations potentielles de composition faunistique en termes de densités et/ou de pourcentages à l'échelle décimétrique à un même site, et ainsi éprouver la validité d'un suivi temporel des faunes vivantes de foraminifères benthiques basé sur un seul échantillonnage (une carotte) par site et par période.

3. Préciser la variabilité temporelle (4 périodes, 2007–2008) des faunes vivantes de foraminifères à deux sites en réponse aux variations de débits du Rhône (apports organiques et inorganiques) et de production phytoplanctonique.

4. Etudier la thanatocénose dans l'ensemble du prodelta (Juin 2005, Septembre 2006) et la comparer aux faunes vivantes observées aux mêmes sites afin de définir des thanatofaciès caractéristiques de conditions environnementales prévalant sur la plate-forme.

5. Etudier les faunes de foraminifères fossilisées le long d'un enregistrement sédimentaire afin d'apprécier si les foraminifères benthiques permettent de retracer les grandes phases d'évolution du Rhône au cours des derniers siècles.

1. DISTRIBUTION SPATIALE DES FAUNES VIVANTES DE FORAMINIFÈRES BENTHIQUES DANS LE PRODELTA DU RHONE : IMPACT DES FACTEURS ENVIRONNEMENTAUX

En Septembre 2006 (BEHEMOTH), les conditions environnementales prévalant sur l'ensemble de la zone apparaissent fortement influencées par les apports rhodaniens. La granularité du sédiment est assez fine sur l'ensemble de la zone (sédiment silto-argileux), excepté à l'ouest de l'embouchure où un ancien lobe deltaïque (lobe de Bras de Fer) se compose de silts et de sables. De grandes quantités de matière organique labile (acides aminés, lipides) d'origine continentale sont mesurées de l'embouchure du Rhône vers le sud-ouest sur la plate-forme, c'est-à-dire sous la position moyenne du panache. En s'éloignant vers le sud-est, la matière organique présente des caractéristiques plus marines malgré l'influence encore marquée des apports du fleuve. En lien aux fortes teneurs en matière organique, d'intenses processus de minéralisation aérobie et anaérobie sont observés jusqu'aux stations situées à ~60 m de profondeur, expliquant les très faibles pénétrations d'oxygène dans le sédiment (1.5 à 4.5 mm). En s'éloignant de l'embouchure, processus aérobies et anaérobies diminuent mais la pénétration d'oxygène reste faible (< 8.4 mm).

Ces conditions environnementales très contrastées constituent autant de niches écologiques potentielles pour les foraminifères benthiques. Ainsi, les analyses cluster basées sur les faunes de foraminifères benthiques distinguent cinq grands assemblages, chacun lié à une zone et des conditions environnementales précises (Fig. 1). Les sédiments silto-sableux de l'ancien lobe deltaïque du Bras de Fer sont caractérisés par une faune particulière composée de miliolidés (*Quinqueloculina lata*, *Quinqueloculina tenuicollis*, *Triloculina trigonula*) et d'espèces typiques des environnements côtiers ou sableux (*Ammonia beccarii* f. *beccarii*, *Nouria polymorphinoides*). Ces sédiments relativement pauvres en matière organique et mal oxygénés (~4 mm) semblent soumis à de forts courants de fond. Près de l'embouchure, les conditions stressantes induites par les processus hydro-sédimentaires liés aux apports du Rhône (érosion/vannage par les forts courants de fond, dépôt de sédiment, turbidité) conduisent au développement de faunes peu diversifiées dominées par *Ammonia tepida* et *Leptohalysis scottii*. Cette zone très riche en matière organique continentale est le siège d'intenses processus de reminéralisation. En s'éloignant de l'embouchure, le facteur hydro-sédimentaire diminue mais les processus de dégradation de la matière organique demeurent importants. Des espèces opportunistes telles que *Nonionella turgida* et *Eggerella scabra* dominent la faune, notamment grâce à leur tolérance aux sédiments peu oxygénés très riches en matière organique continentale.

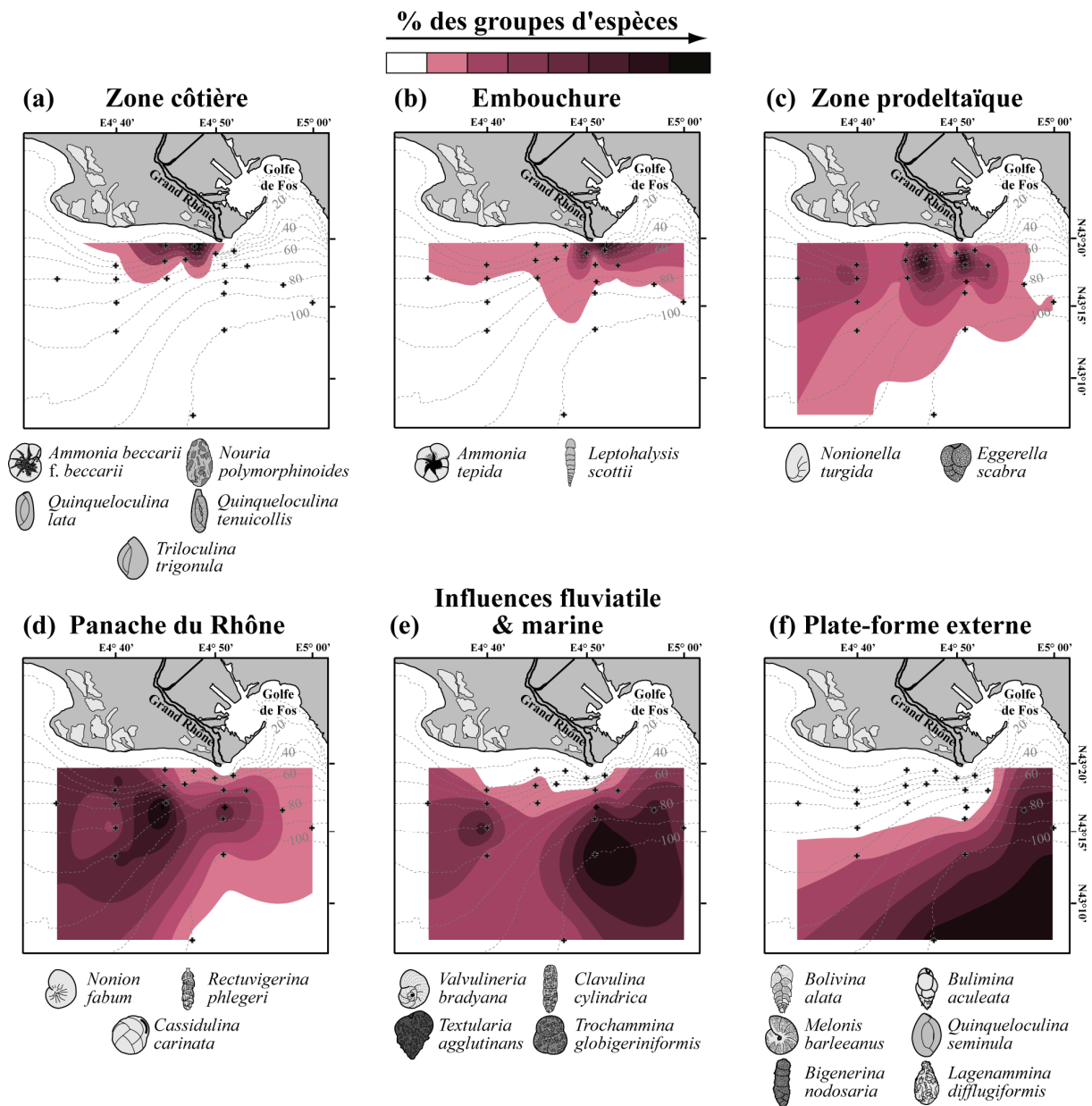


Figure 1 : Distribution spatiale des groupes d'espèces définis par l'analyse cluster basée sur les faunes vivantes de foraminifères benthiques, groupes indicateurs de conditions environnementales précises au sein du prodelta (biofaciès).

Sous la position moyenne annuelle du panache, la légère hausse de la contribution marine dans les dépôts de matière organique favorise des espèces telles que *Cassidulina carinata*, *Nonion fabum*, *Rectuvigerina phlegeri* et *Trochammina globigeriniformis*. Dans la partie sud-est de la zone (plate-forme externe), l'influence plus réduite du Rhône permet la mise en place de faunes équilibrées et diversifiées (*Bolivina alata*, *Bulimina aculeata*, *Melonis barleeanus*, *Quinqueloculina seminula* et *Bigenerina nodosaria*) bénéficiant d'une meilleure oxygénation du sédiment ainsi que d'une matière organique de plus en plus marine.

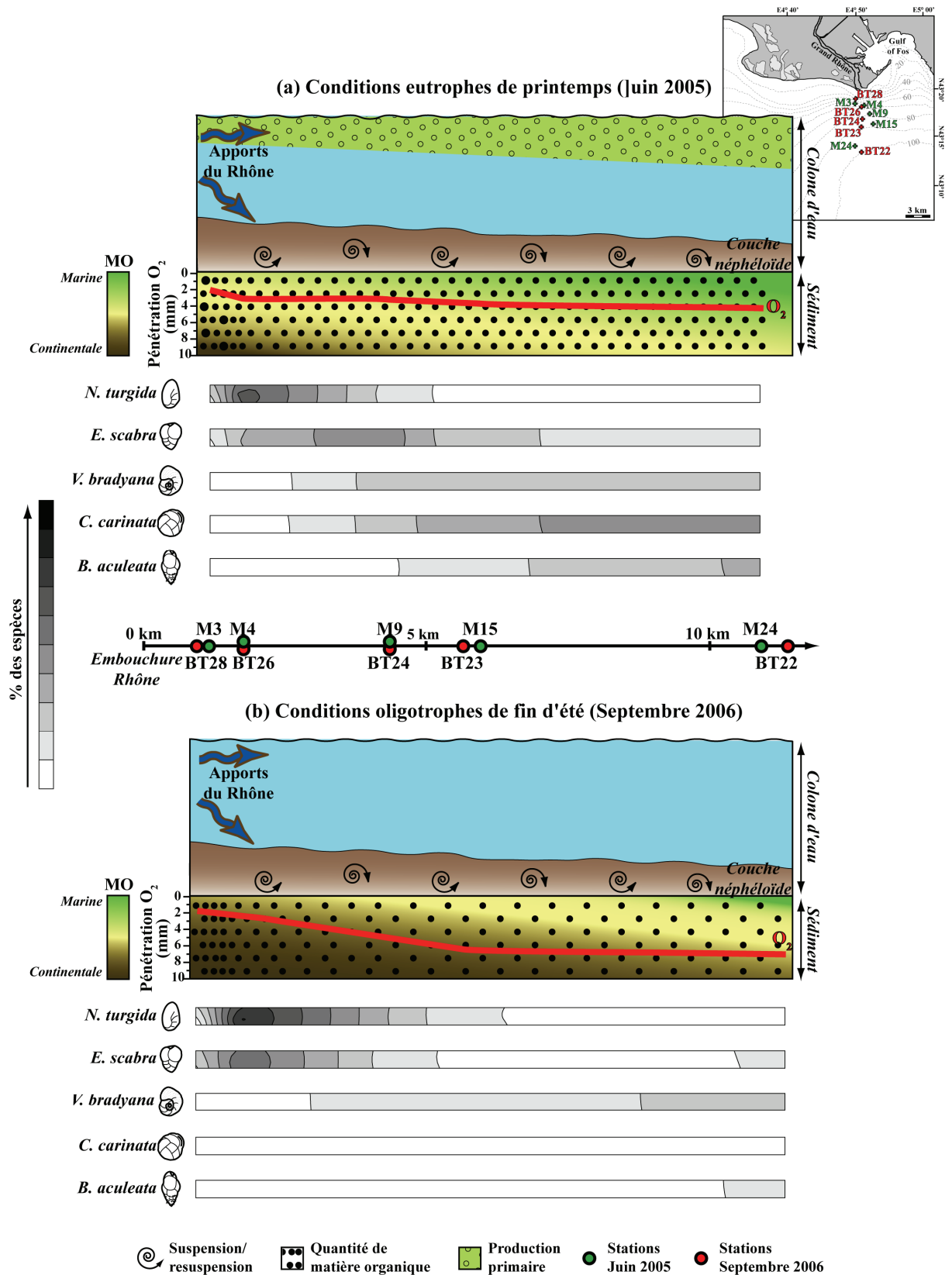


Figure 2 : Figure synthétisant les conditions environnementales et les espèces dominantes de foraminifères benthiques de l'embouchure du Rhône au plateau externe en Juin 2005 (a, MINERCOT 2) et Septembre 2006 (b, BEHEMOTH).

Certaines espèces (*Valvulineria bradyana*, *Clavulina cylindrica*, *Lagenammina difflugiformis* et *Textularia agglutinans*) semblent adaptées à vivre dans une zone de transition entre la zone d'influence réduite du Rhône et les sédiments situés sous le panache, profitant ainsi des apports fluviaux peu à peu remplacés par une matière organique plus marine.

Ces faunes décrites en Septembre 2006 caractérisent les conditions oligotrophiques de fin d'été. En revanche, en Juin 2005, Mojtabid et al. (2009) observent des faunes bénéficiant des apports de phytodétritus frais liés aux conditions de bloom phytoplanctonique de printemps (Fig. 2). L'analyse en Composante Principale (ACP) effectuée sur ces deux bases de données de foraminifères benthiques (Septembre 2006 et Juin 2005) a pu mettre en évidence une contribution plus importante de *N. turgida* et *E. scabra* en Septembre 2006 liée à l'influence fluviale plus importante et/ou l'absence de production marine dans les eaux de surface (Fig. 2b). En revanche, en Juin 2005, l'abondance d'espèces opportunistes telles que *B. aculeata*, *C. carinata* et *V. bradyana* augmente sensiblement probablement grâce aux apports de matière organique fraîche plus importants qu'en Septembre 2006 (Fig. 2b).

Pour résumer, les faunes vivantes de foraminifères benthiques montrent une forte variabilité spatiale en réponse aux conditions environnementales très contrastées prévalant à l'échelle du prodelta du Rhône. Les paramètres influant sur cette répartition semblent être, en premier lieu, la qualité et la quantité de matière organique, mais aussi l'ensemble des processus hydro-sédimentaires liés aux apports du Rhône au plus près de l'embouchure.

2. DISTRIBUTION SPATIALE A L'ECHELLE DECIMETRIQUE DES FAUNES VIVANTES DE FORAMINIFERES BENTHIQUES

La variabilité spatiale à l'échelle infra-métrique (i.e., décimétrique) des faunes de foraminifères benthiques a été étudiée à deux Stations A et N (19 et 68 m de profondeur, 1.8 et 4.5 km de l'embouchure) afin de préciser si la variabilité spatiale enregistrée à petite échelle est plus importante que celle mise en évidence à une échelle kilométrique (Chapitre 1). Les deux stations étudiées au cours de ce chapitre sont sensiblement impactées par les apports du Rhône. Ainsi, les fortes teneurs en matière organique d'origine continentale mesurées près de l'embouchure (Station A) induisent d'importants processus de minéralisation et donc une forte consommation d'oxygène (pénétration < 2 mm dans les sédiments). A la Station N, les concentrations plus faibles en matière organique labile

permettent une pénétration de l'oxygène dans les sédiments légèrement plus importante (~5 mm).

Quatre répliquas ont été échantillonnés à chaque site étudié afin d'estimer la variabilité des faunes de foraminifères benthiques à l'échelle décimétrique. Pour chaque site, les faunes des fractions 63–150 μm et $> 150 \mu\text{m}$ observées dans ces répliquas ont été comparées entre elles grâce à des analyses statistiques (test de Friedman). Ces analyses se basent, dans un premier temps, sur les abondances absolues (nombre d'individus par 100 cm^2 de sédiment) des espèces majeures ($> 5\%$ dans au moins un répliqua), puis dans un second temps sur les abondances relatives (i.e., pourcentages) de ces mêmes espèces. En Station A, les tests statistiques ne mettent pas en évidence de différences significatives entre les faunes des fractions 63–150 μm et $> 150 \mu\text{m}$ des quatre répliquas, aussi bien avec les abondances absolues que les abondances relatives. Ces faunes sont dominées par, e.g., *Ammonia tepida*, *Leptohalysis scottii* et *Psammosphaera fusca*, trois espèces caractéristiques des environnements soumis à d'importants processus hydro-sédimentaires et enrichis en matière organique continentale. Contrairement à la Station A, les faunes de foraminifères benthiques en Station N montrent des différences significatives en termes d'abondances absolues dans les fractions 63–150 μm et $> 150 \mu\text{m}$, les abondances totales pouvant passer du simple au double entre certains répliquas. Ces variations significatives d'abondances semblent dues à *Rectuvigerina phlegeri*, mais surtout au comportement opportuniste de *Bolivina* spp. (*Bolivina dilatata* et *Bolivina spathulata*), *Hopkinsina atlantica* et *Nonionella turgida*. Cette distribution hétérogène des faunes de foraminifères dans un environnement aussi dynamique pourrait être liée à une répartition irrégulière de la matière organique dans les sédiments. En effet, un dépôt hétérogène dans les sédiments de matériel organique d'origines (phytoplancton, débris de plantes terrestres) et de qualités variées (fraîche, dégradée) créeraient des sources locales de nourriture, favorisant la croissance des espèces les plus réactives selon leur préférence alimentaire. Néanmoins, les différences notées entre les répliquas de la Station N deviennent non-significatives lorsque les abondances relatives des espèces majeures (i.e., pourcentages) sont prises en compte. Ces résultats démontrent la fiabilité des abondances relatives des espèces lorsque différentes faunes de foraminifères benthiques provenant du prodelta du Rhône sont comparées entre elles, notamment lors de suivis temporels/saisonniers à un même site. En revanche, l'utilisation des abondances absolues requiert une certaine prudence compte tenu de la variabilité potentiellement importante existant pour une même espèce.

Par la suite, les abondances relatives des faunes de ces deux jeux de répliquas ont été comparées avec celles des faunes décrites à 20 stations échantillonnées dans le prodelta du

Rhône en Septembre 2006 (Chapitre 1). Cette comparaison montre que la variabilité existant potentiellement à l'échelle décimétrique (ce chapitre) est bien trop faible pour dissimuler celle enregistrée à l'échelle du prodelta (kilométrique). Ces conclusions confirment la fiabilité des biofaciès définis à partir des faunes de foraminifères benthiques à l'échelle du prodelta dans un tel environnement sous influence fluviale, et ce à partir d'un seul répliqua par site étudié.

3. VARIABILITE TEMPORELLE DES FAUNES VIVANTES DE FORAMINIFERES BENTHIQUES : REPONSE DES FAUNES A DES VARIATIONS RAPIDES DE LEUR ENVIRONNEMENT

Les faunes vivantes de foraminifères benthiques des fractions 63–150 μm et $> 150 \mu\text{m}$ ont été étudiées à deux Stations A et N (19 et 68 m de profondeur ; 1.8 et 4.5 km de l'embouchure du Rhône) échantillonnées dans le prodelta du Rhône en Avril 2007, Septembre 2007, Mai 2008 et Décembre 2008 (missions RiOMar 1, RIOTECH, CHACCRA-bent 1 et CHACCRA-bent 2). Ces quatre périodes d'échantillonnage ont permis d'étudier les faunes de foraminifères benthiques sous des conditions variées de débits du Rhône et de production primaire dans les eaux de surface. L'étude de la variabilité spatiale à petite échelle ayant validé l'utilisation des abondances relatives des espèces majeures de foraminifères dans les suivis saisonniers, la comparaison des faunes se succédant au cours de ces quatre périodes s'est basée essentiellement sur les pourcentages d'espèces.

Les sédiments superficiels de la Station A sont caractérisés par de fortes teneurs en carbone organique et matière organique labile (acides aminés, lipides) supérieures à celles mesurées à la Station N à toutes les périodes étudiées. Les isotopes stables du carbone et de l'azote ($\delta^{13}\text{C}$ et $\delta^{15}\text{N}$) indiquent une origine principalement fluviale de cette matière organique à ces deux stations. Néanmoins, les sédiments de la Station A sont également marqués par une influence notable de la matière organique continentale (débris végétaux).

En Station A, les conditions environnementales et les faunes vivantes de foraminifères présentent une variabilité relativement importante au cours des quatre périodes étudiées (Fig. 3). Malgré le bas débit du Rhône mesuré en Septembre 2007, l'absence de production primaire dans les eaux de surface induit une influence relativement importante du fleuve comme le suggèrent les faibles densités de foraminifères ainsi que la forte dominance d'*Ammonia tepida* et de *Psammosphaera fusca*. Néanmoins, les concentrations élevées en matière organique d'origine fluviale permettent également l'établissement de faunes diversifiées composées d'espèces typiques d'environnement sous influence fluviale, e.g., *Bolivina dilatata*, *Nonionella turgida* et *Eggerella scabra* (Fig. 3a). En Avril 2007, une faune

abondante et diversifiée, composée d'espèces hautement réactives aux apports de matière organique fraîche liés aux conditions de bloom de printemps (e.g., *B. dilatata*, *Nonionella stella*, *N. turgida*, *Stainforthia fusiformis*, *E. scabra*, *L. scottii*), est mise en place dans les deux fractions (Fig. 3b). En Mai 2008, un assemblage quasi monospécifique composé de milliers de spécimens de *L. scottii* est retrouvé dans les sédiments apportés par une crue majeure du Rhône initiée deux jours plus tôt (Fig. 3c). Cette faune visiblement allochtone proviendrait soit du fleuve amont, contenue dans les sédiments apportés par la crue, soit d'autres environnements adjacents, migrant et colonisant le nouvel habitat ainsi créé. Dans chacune des hypothèses avancées, cet assemblage constitue un stade précurseur de recolonisation. En Décembre 2008, une crue majeure du Rhône a été enregistrée trois semaines avant l'échantillonnage. L'association d'*A. tepida* et de *P. fusca* avec une espèce typique des environnements estuariens (*Haynesina germanica*) confirme l'influence fluviale notable en cette période. L'origine allochtone des spécimens de *H. germanica* semble évidente, *A. tepida* et *P. fusca* colonisant par la suite le dépôt de crue dans lequel ces espèces bénéficieraient de fortes teneurs en carbone organique (6%) (Fig. 3d).

En résumé, l'influence du Rhône à cette Station A est évidente au cours des quatre périodes étudiées, les apports de sédiments liés aux crues du Rhône semblant constituer la perturbation majeure de l'environnement benthique. Dans ces conditions instables (Mai et Décembre 2008), les faunes de foraminifères apparaissent en déséquilibre, leur composition dépendant du temps écoulé depuis l'apport de sédiment de crues, mais aussi de la quantité de matière organique contenue dans ces sédiments. Quelques jours après une telle perturbation (Mai 2008), les premières espèces recolonisent déjà un dépôt pourtant appauvri en matière organique. En revanche, un apport de sédiments riches en matière organique permet d'observer quelques semaines plus tard un stade plus avancé de recolonisation par les foraminifères (Décembre 2008). Dans ces deux cas de figure, une stratégie de vie opportuniste liée à la destruction de l'environnement (*Leptohalysis scottii*, Mai 2008) et/ou à un apport conséquent de matière organique lors de la crue (*Ammonia tepida*, Décembre 2008) est mise en évidence. A l'opposé, les conditions prévalant en Avril et Septembre 2007 permettent la mise en place de faunes diversifiées et relativement équilibrées. Dans ces cas de figure, la fraîcheur de la matière organique constitue le principal facteur influençant la composition des faunes de foraminifères.

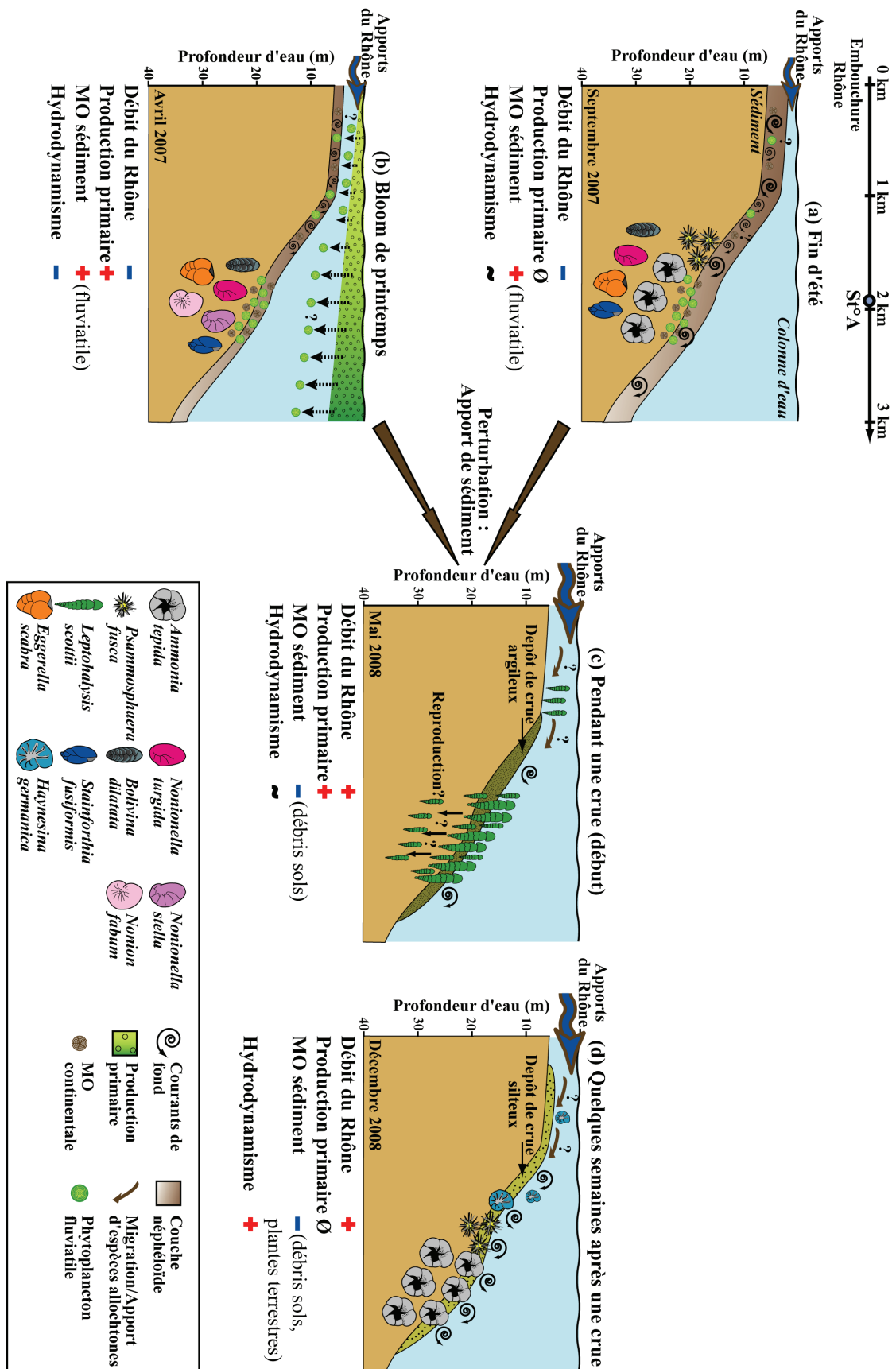


Figure 3 : Figure synthétisant les principaux processus influençant la composition des faunes de foraminifères benthiques en Station A au cours des quatre périodes étudiées.

En Station N, les légères variations de composition faunistique enregistrées seraient principalement liées aux apports de matière organique fraîche provenant de la production marine de surface, mais aussi au débit du Rhône. En Avril 2007 et Mai 2008, les conditions de bloom de printemps survenant en période de bas débits du fleuve profitent aux espèces connues pour se nourrir de phytodétritus frais (e.g., *Clavulina cylindrica*, *Hopkinsina atlantica*, *Nonionella iridea*, *Nonionella turgida*). En Septembre 2007 et Décembre 2008, la présence de *Nouria polymorphinoides* traduit une hausse de l'influence du Rhône/baisse de l'influence « marine ». En Décembre 2008, *Bolivina seminuda*, *Bolivina spathulata* et *Textularia porrecta* profiteraient d'un apport de matière organique d'origine fluviale lié à une crue survenue quelques semaines plus tôt. Néanmoins, malgré l'impact supposé de ces facteurs environnementaux (i.e., production de surface, débit du Rhône), la présence récurrente au cours des quatre périodes étudiées de *Bolivina dilatata*, *Eggerella scabra*, *Nonion fabum*, *Valvulineria bradyana* en abondance relativement importante, de plus dans des faunes diversifiées et équilibrées, met en évidence le caractère relativement stable (comparé à la Station A) de l'environnement benthique à ce site.

En conclusion, cette étude a pu montrer la capacité de réponse très rapide des faunes de foraminifères benthiques (quelques jours à quelques semaines) à des variations importantes des conditions environnementales, notamment près de l'embouchure (Station A). Cette réponse est également visible mais significativement réduite à environ 5 km de l'embouchure (Station N), probablement en raison de l'impact plus faible des apports du Rhône hors de la zone prodeltaïque (> 60 m de profondeur).

4. COMPARAISON DES FAUNES VIVANTES ET DES FAUNES MORTES DE FORAMINIFÈRES BENTHIQUES

Les faunes mortes de foraminifères benthiques (> 150 μm) ont été étudiées à 39 stations échantillonnées en Septembre 2006 (BEHEMOTH) et en Juin 2005 (MINERCOT 2) dans l'ensemble du prodelta du Rhône (15 à 100 m de profondeur). La comparaison de ces faunes aux assemblages vivants observés à ces mêmes stations a pour but d'identifier et de mieux comprendre les processus taphonomiques entrant en jeu dans cet environnement particulièrement dynamique.

Les processus taphonomiques mis en évidence dans le prodelta du Rhône se divisent en deux sous-catégories : les processus physico-chimiques (i.e., transport,

dissolution/fragmentation du test) et les processus biologiques. L'apparente fragilité du test de *Bolivina alata*, *Quinqueloculina tenuicollis* et *Triloculina trigonula* semble expliquer la perte d'individus notée dans la faune morte. Aux stations les moins profondes situées de l'embouchure du Rhône à la côte sableuse plus à l'ouest, l'action de forts courants générés par la houle induit un transport des faunes mortes. Ce transport se traduit soit par un enrichissement de certaines espèces dans la faunes morte suite à un apport d'individus allochtones (e.g., *Ammonia beccarii* f. *beccarii*), soit par une redistribution des faunes mortes conduisant à une répartition hétérogène (e.g., *Bulimina elongata*, *Quinqueloculina lata*). En s'éloignant de ces sites peu profonds, les processus biologiques tendent à expliquer une part importante des différences notées entre faunes mortes et vivantes. En effet, les taux de reproduction élevés caractérisant les espèces opportunistes (e.g., *Bulimina marginata*, *Cassidulina carinata*, *Nonionella turgida*, *Valvulineria bradyana*) expliqueraient leurs très fortes abondances relatives notées dans la faune morte. De ce fait, les espèces moins opportunistes (i.e., produisant moins d'individus) voient leur contribution diminuée dans les faunes mortes (e.g., *Nonion fabum*, *Rectuvigerina phlegeri*).

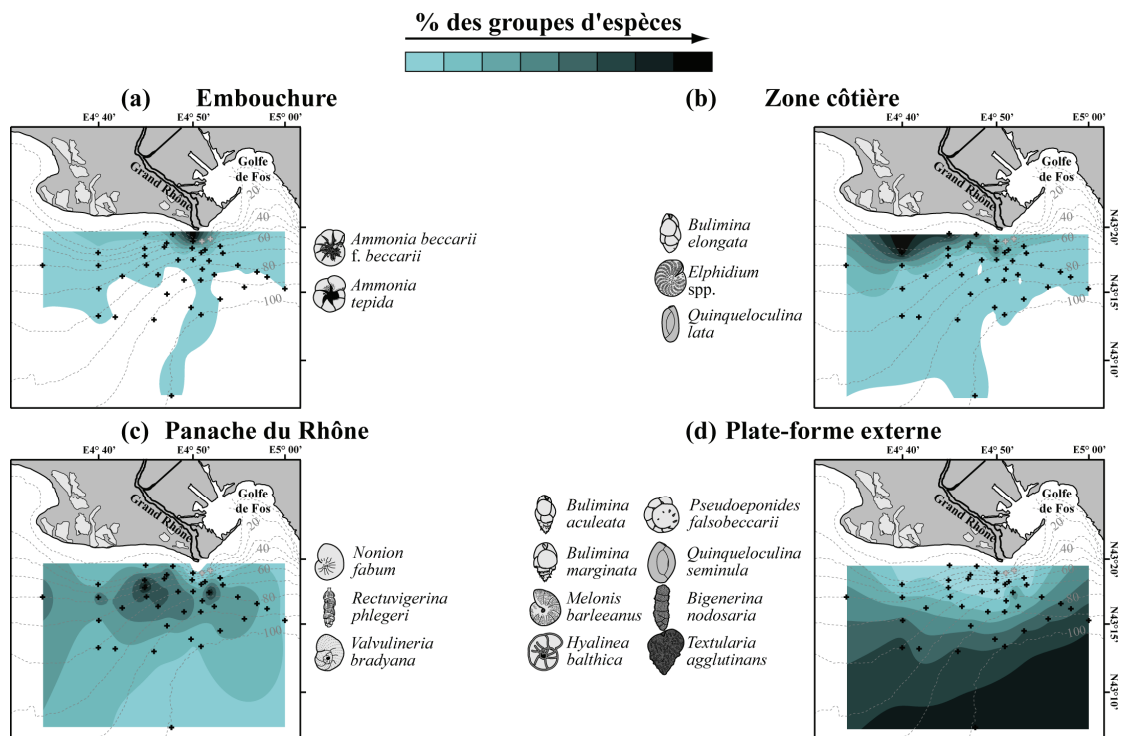


Figure 4 : Distribution spatiale des groupes d'espèces définis par l'analyse cluster basée sur les faunes mortes, groupes indicateurs de conditions environnementales précises au sein du prodelta (thanathofaciès).

Les analyses cluster effectuées sur cette base de données permettent de diviser le prodelta du Rhône en quatre grandes zones (thanatofaciès) caractérisées par des assemblages de foraminifères benthiques et des conditions environnementales précises (Fig. 4). Près de l'embouchure (Fig. 4a), *Ammonia beccarii* f. *beccarii* et *Ammonia tepida* vivent dans des sédiments soumis à une très forte influence fluviale (i.e., courants de fond, apport de matériel fluviale inorganique et organique). Les espèces d'*Elphidium*, associées à *Bulimina elongata* et *Quinqueloculina lata*, dominent les faunes dans les sédiments sablo-silteux de l'ancien lobe deltaïque de Bras de Fer à l'ouest de l'embouchure (Fig. 4b). Cette zone est soumise à de forts courants pouvant perturber l'environnement benthique. *Nonionella turgida* caractérise la partie proximale du panache du Rhône (i.e., entre 30 et 60 m de profondeur), zone soumise à de forts taux de sédimentation. Les faunes observées dans la partie plus distale du panache sont dominées par *Nonion fabum*, *Rectuvigerina phlegeri* et *Valvulineria bradyana* (Fig. 4c). Dans la faune morte, ces espèces sont distribuées le long de la côte à l'ouest de l'embouchure du Rhône, alors que les spécimens vivants se concentrent vers le sud-ouest du prodelta. Cette légère différence de répartition spatiale pourrait être due au transport induit par l'action des houles de tempête provenant du sud-est. Enfin, dans la partie la plus profonde et stable située au sud-est du prodelta (i.e., plate-forme externe ; Fig. 4d), des espèces répondant à des apports de phytodétritus frais dominent les faunes (e.g., *Bulimina aculeata/marginata*, *Hyalinea balthica*). *Cassidulina carinata* profiterait à la fois de l'influence marine et de l'influence fluviale en vivant préférentiellement entre cette zone stable et le panache du Rhône.

En résumé, cette étude a mis en évidence des différences mineures entre les assemblages morts et vivants de foraminifères benthiques, aussi bien dans leur distribution spatiale que dans leur composition faunistique. Ainsi, malgré les processus taphonomiques, le message écologique porté par les faunes vivantes serait préservé après leur mort, les faunes fossiles de foraminifères benthiques reflétant donc fidèlement les conditions environnementales prévalant localement dans le prodelta du Rhône. De ce fait, les thanatofaciès définis dans cette étude constituent un outil précieux dans la reconstruction des conditions paléo-environnementales au sein du système prodeltaïque du Rhône à travers l'étude des archives fossiles de foraminifères benthiques.

5. EVOLUTION HISTORIQUE DU PRODELTA DU RHONE ENREGISTREE PAR LES FAUNES DE FORAMINIFERES BENTHIQUES

L'évolution du système prodeltaïque du Rhône au cours des 400 dernières années a pu être retracée à travers l'étude des assemblages fossiles de foraminifères benthiques. Ces faunes proviennent de la carotte RHS-KS57 (7.70 m de long) prélevée dans le lobe deltaïque de Roustan à environ 3.8 km de l'embouchure (79 m de profondeur ; Fig. 5). Grâce aux analyses statistiques basées sur ces assemblages (analyses en composante principale et cluster) ainsi qu'aux thanatofaciès définis à partir des faunes mortes récentes préservées dans le prodelta du Rhône (Chapitre 4), il a été possible de reconstituer les grandes étapes dans l'évolution du Rhône en termes d'apports sédimentaires et de matière organique.

A la base de la carotte, vers 700 cm de profondeur, la présence d'espèces actuellement typiques du plateau externe bordant le prodelta (i.e., *Bigenerina nodosaria* et *Melonis barleeanus*) correspondrait à la baisse sensible de compétence du chenal de Bras de Fer, et donc de l'influence du Rhône sur la zone, quelques années avant son abandon en 239 BP (1711 AD) (Fig. 5a). L'abandon du chenal de Bras de Fer marque l'activation plus à l'est du chenal de Pégoulie ainsi que des distributaires secondaires de Roustan et Piémenson (Fig. 5b). Cet événement est enregistré vers 600 cm de profondeur par l'augmentation de *Bulimina marginata* et *Pyrgo oblonga*. Ces deux espèces bénéficieraient d'un apport soudain de matière organique, le débouché du fleuve s'effectuant alors plus proche du site d'étude.

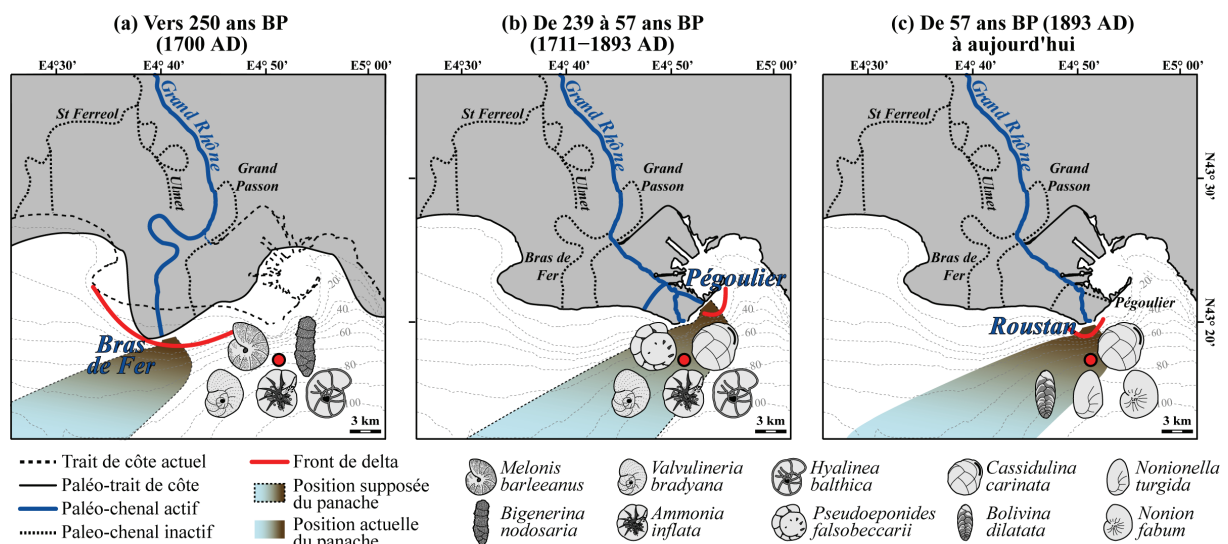


Figure 5 : Figure synthétique résumant les grandes étapes dans l'évolution du système deltaïque et prodeltaïque du Rhône enregistrées par les faunes de foraminifères au cours des 400 dernières années. Le point rouge localise la carotte RHS-KS57.

Par la suite, la contribution majeure de *Cassidulina carinata*, *Valvulineria bradyana*, *Ammonia beccarii* f. *inflata* et *Hyalinea balthica* jusqu'à 160 cm de profondeur atteste d'un environnement relativement stable, situé à la limite de l'influence marine (*A. beccarii* f. *inflata* et *H. balthica*) et de celle du Rhône (*C. carinata* et *V. bradyana*) (Fig. 5b). En effet, le panache fluvial se formant au débouché du chenal principal de Pégoulie devait s'étendre vers le sud-ouest jusqu'au site d'étude sous l'action des vents, de la circulation océanique générale et du débit du Rhône (Fig. 5b).

Suite à la fermeture de Roustan et Piémenson vers 100 BP (1852 AD), la concentration des apports rhodaniens dans l'unique chenal de Pégoulie entraîne une hausse soudaine de sa compétence (effet de « chasse ») et donc des apports de matériel fluvial vers le domaine marin. L'apparition de l'espèce opportuniste *Bolivina dilatata* vers 370 cm de profondeur marque cet apport massif de matériel fluvial riche en matière organique sur le site d'étude. La réouverture de l'embouchure de Roustan en 57 BP (1893 AD) est enregistrée vers 250 cm de profondeur par l'apparition soudaine de *Quinqueloculina lata*, une espèce vivant actuellement dans les sédiments sableux de la zone côtière du prodelta. L'emplacement du site d'étude directement en face de l'embouchure de Roustan explique la hausse significative des apports fluviaux (taux de dépôt des sédiments, teneurs en carbone organique et en sédiments plus grossiers) indiquée par l'apparition de *Nonionella turgida*, *Ammonia beccarii* f. *beccarii* et *Q. lata* (Fig. 5c). La contribution croissante de ces espèces jusqu'à environ 60 cm de profondeur indique une hausse continue des apports fluviaux (matériel terrigène et organique) jusqu'au milieu du 20^{ème} siècle. Par la suite, l'apparition de *Nonion fabum* dans les derniers 60 cm de la carotte, semblant remplacer *V. bradyana*, témoignerait d'une baisse de la qualité des apports de matière organique au cours des dernières décennies.

En résumé, les assemblages fossiles de foraminifères benthiques enregistrés dans le lobe de Roustan ont mis en évidence la hausse graduelle de l'influence du Rhône à ce site au cours des 400 dernières années, conséquence des changements successifs de chenal et d'exutoire. La calibration des assemblages morts récents de foraminifères benthiques a donc permis de mettre au point un outil valide de reconstruction paléo-environnementale au sein du système prodeltaïque du Rhône.

CONCLUSION GÉNÉRALE

Ce travail avait pour but premier de définir les paramètres environnementaux influençant les assemblages de foraminifères benthiques peuplant actuellement les sédiments de la plate-forme continentale sous l'influence directe du fleuve Rhône. En effet, même si l'impact du Rhône semblait évident, il était nécessaire de préciser la nature et l'intensité de cette influence, ainsi que l'existence potentielle d'autres facteurs forçant la variabilité spatio-temporelle des faunes benthiques. Aux vues des résultats obtenus, le prodelta du Rhône apparaît comme un environnement extrêmement complexe. Les apports du Rhône, et notamment de sédiment lors d'épisodes de crue, constituent un stress majeur pour les faunes benthiques essentiellement au débouché du fleuve. En dehors de ces conditions définies comme instables, la nature et la quantité de matière organique contenue dans les sédiments, ainsi que l'ensemble des processus liés à sa dégradation (i.e., conditions redox dans les sédiments), influencent significativement les communautés de foraminifères benthiques dans l'ensemble de la zone et au cours des saisons. Ainsi, des faunes spécialisées se succèdent dans l'espace et dans le temps. Près de l'embouchure et/ou suite à un événement de crue, les faunes bénéficient d'une matière organique fortement continentale. Au contraire, en s'éloignant de l'embouchure et/ou en période de bloom (printemps), les apports de matière organique sont liés à la production phytoplanctonique dans les eaux de surface. Néanmoins, un couplage pélagos-benthos n'a pu clairement être identifié lors de ces périodes de forte production primaire. En effet, la couche néphéloïde de fond jouerait un rôle prépondérant dans les transferts de matière organique dans la zone d'étude. Ainsi, cette couche constituerait un vecteur de transport notable du matériel rhodanien (organique et inorganique) depuis le fleuve jusqu'au domaine marin (i.e., apports latéraux). En revanche, celle-ci agirait aussi comme une zone « tampon » entre les eaux de surface et les sédiments marins, réduisant ainsi fortement les transferts de matériel organique issus de la production de surface (i.e., apports verticaux). Par ailleurs, les assemblages de foraminifères benthiques se révélant être d'excellents bio-indicateurs des caractéristiques environnementales actuelles, il a été possible de les utiliser en tant qu'indicateurs des conditions passées au sein du prodelta du Rhône. Ainsi, les assemblages fossiles préservés au cours des 400 dernières années reflètent parfaitement les conditions environnementales prévalant dans la zone d'étude, enregistrant l'évolution liée aux forçages naturels (conditions climatiques extrêmes) mais aussi anthropiques (aménagement du fleuve) de l'influence du Rhône en termes d'apports fluviaux terrigènes mais aussi organiques.

PERSPECTIVES

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A l'issue de ce travail de thèse, de nombreuses interrogations restent en suspens quant à l'écologie des foraminifères benthiques dans le prodelta du Rhône. Afin de répondre à ces questionnements, des travaux complémentaires pourraient être entrepris en prolongement de cette étude :

- L'influence de la matière organique sur la structure des faunes de foraminifères benthiques semble évidente. Néanmoins, il reste toujours une part d'ombre quant à la nature de cette influence, i.e., directe ou indirecte. Une influence directe serait liée à la nature (fraîche ou dégradée), l'origine (continentale, marine), la composition (e.g., acides aminés, lipides) mais aussi aux quantités de matière organique disponibles dans les sédiments, influençant les faunes de foraminifères benthiques d'un point de vue trophique. En revanche, une influence indirecte engloberait l'ensemble des processus liés à la dégradation de cette matière organique, modifiant les conditions physico-chimiques (i.e., conditions redox) dans les sédiments. Dans ce cas, la composition faunistique serait déterminée selon la tolérance des espèces au degré d'oxygénation du sédiment, et donc potentiellement à leur capacité de survie en l'absence d'oxygène (i.e., respiration des nitrates). Seules des analyses expérimentales en laboratoires testant chacun de ces paramètres sur différentes espèces permettraient de répondre en partie à ces interrogations.
- La variabilité temporelle des faunes de foraminifères benthiques s'est basée sur deux sites échantillonnés près de l'embouchure et en bordure externe du prodelta au cours de quatre périodes. Il serait intéressant de poursuivre ce travail aussi bien dans l'espace, en étudiant d'autres sites couvrant l'ensemble des environnements définis au sein du site d'étude (i.e., partie distale du panache, plate-forme externe), mais aussi dans le temps en adoptant une stratégie d'échantillonnage plus serrée dans le temps (tous les mois).
- De même, l'étude de la variabilité spatiale à petite échelle (décimétrique) a été effectuée à deux stations au cours d'une seule période d'échantillonnage. Cependant, les faunes de foraminifères démontrent une certaine variabilité dans l'espace mais aussi dans le temps en réponse aux variations des conditions environnementales. Ainsi, poursuivre cette étude à d'autres sites mais aussi au cours d'autres périodes

d'échantillonnage révélerait peut-être une variabilité spatiale à petite échelle plus ou moins importante et/ou fluctuante au cours du temps.

– D'un point de vue plus analytique, l'utilisation du Rose Bengal afin de mettre en évidence les individus vivants peut montrer quelques failles, notamment en colorant les spécimens morts récemment ou colonisés par des consortia bactériens. Une étude comparative de la technique du Rose Bengal avec plusieurs autres méthodes de « coloration » des spécimens vivants permettrait d'éprouver la validité de cet outil. Depuis quelques années, de telles études ont été effectuées entre le Rose Bengal et une nouvelle méthode utilisant le Cell-Tracker Green (CTG), une molécule intégrée par les cellules uniquement de façon active, et donc théoriquement uniquement par les individus vivants.

– Les archives fossiles de foraminifères benthiques ont été étudiées dans une carotte prélevée au droit de l'embouchure. Malgré la longueur significative de la carotte (~8 m), les forts taux de sédimentation caractérisant cette zone n'ont pas permis de retracer l'évolution de l'environnement prodeltaïque du Rhône au-delà des 400 dernières années. Pourtant, il serait des plus intéressant de pouvoir remonter bien plus loin dans l'histoire du Rhône, notamment au cours de l'Holocène depuis la dernière déglaciation (i.e., Terminaison I, ~18000 ans BP) lorsque les variations du niveau marin ont initié une série de modifications significatives dans l'architecture du système deltaïque. Compte-tenu de la situation géographique actuelle et passée du système deltaïque du Rhône, le prélèvement de plusieurs longues carottes à la limite du prodelta et du plateau externe (~80 à 100 m de profondeur), depuis le Petit Rhône jusqu'au débouché actuel du Grand Rhône, permettrait de retracer cette évolution. Une telle étude est actuellement en cours dans le cadre d'une thèse poursuivie à l'Université de Perpignan par Anne-Sophie Fanget.

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ANNEXES

ANNEXES

ANNEXE 1

Planches photos de quelques unes des espèces majeures identifiées dans le prodelta du Rhône.
L'échelle représente 100 μm .

ANNEXE 2

Communications et publications

ANNEXE 1 : PLANCHE 1

Photo 1 : *Ammonia beccarii* forma *beccarii*

Photo 2 : *Ammonia tepida*

Photo 3 : *Nonionella turgida*

Photo 4 : *Nonion fabum*

Photo 5 : *Cassidulina carinata*

Photo 6 : *Bolivina alata*

Photo 7 : *Bulimina aculeata*

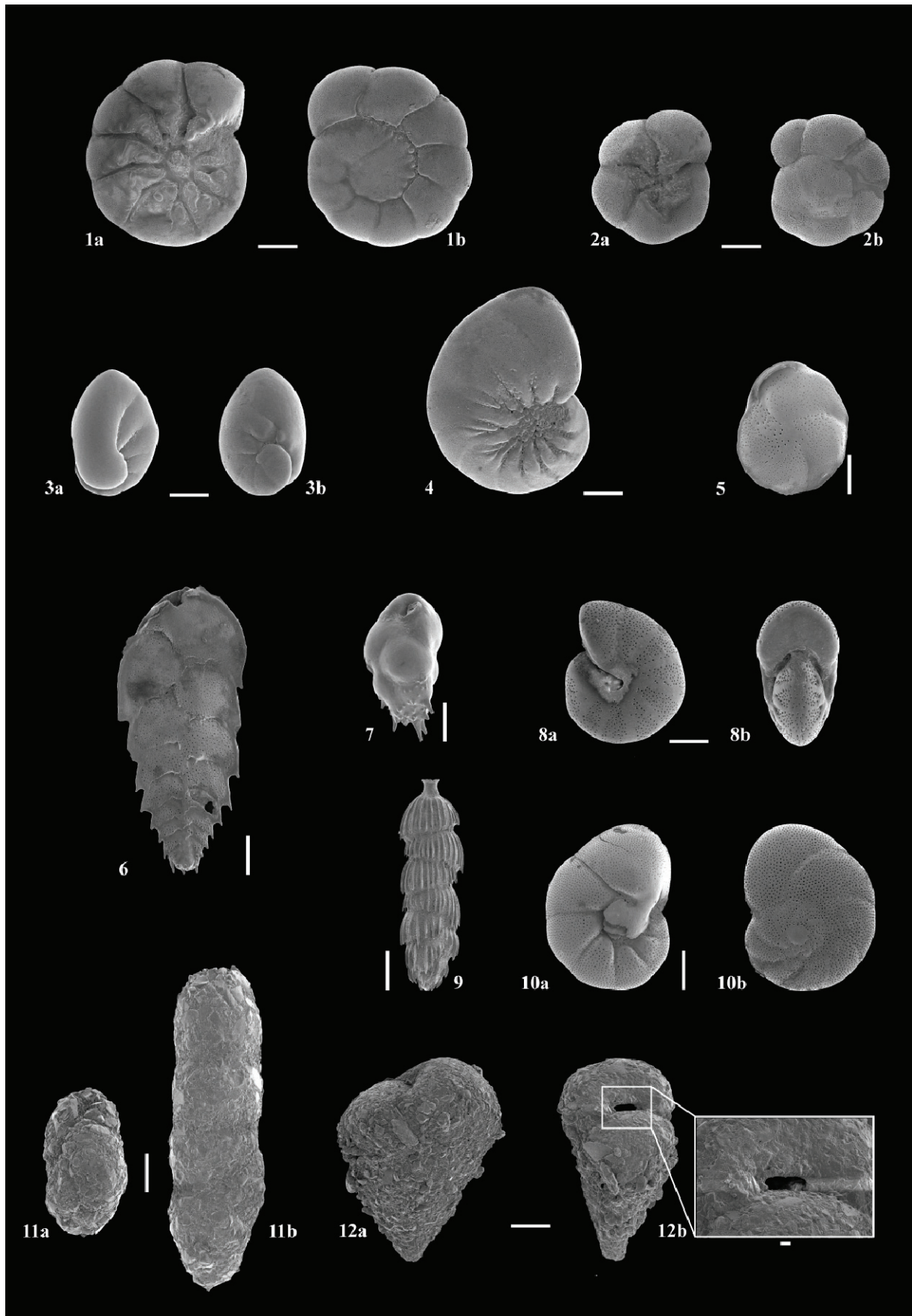
Photo 8 : *Nonion fabum*

Photo 9 : *Rectuvigerina phlegeri*

Photo 10 : *Valvulineria bradyana*

Photo 11 : *Clavulina cylindrica* formes juvénile (a) et adulte (b)

Photo 12 : *Textularia agglutinans*



ANNEXE 1 : PLANCHE 2

Photo 13 : *Quinqueloculina lata*

Photo 14 : *Quinqueloculina seminula*

Photo 15 : *Triloculina trigonula*

Photo 16 : *Quinqueloculina tenuicollis*

Photo 17 : *Trochammina globigeriniformis*

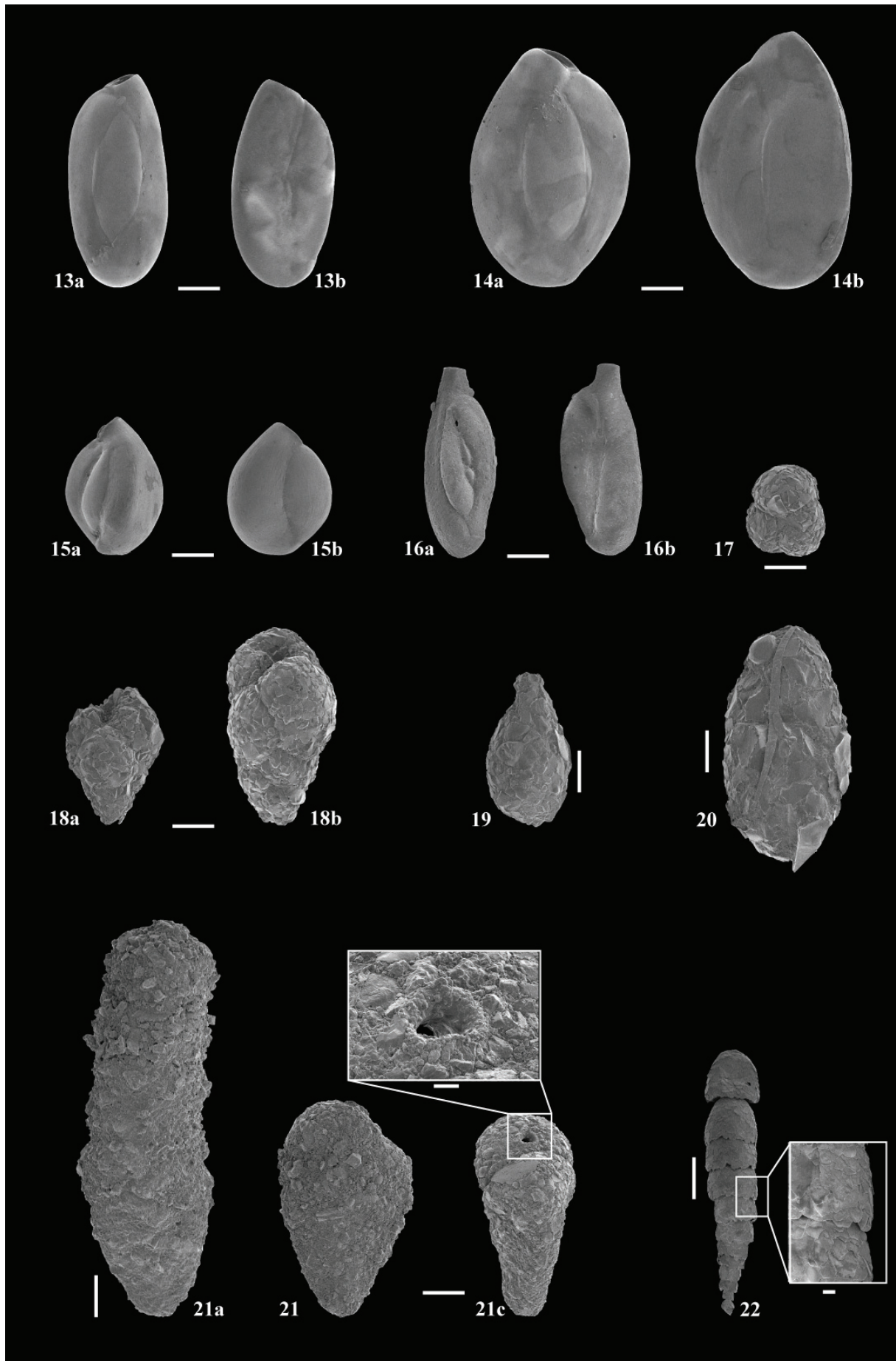
Photo 18 : *Eggerella scabra*

Photo 19 : *Lagenammina difflugiformis*

Photo 20 : *Nouria polymorphinoides*

Photo 21 : *Bigenerina nodosaria*

Photo 22 : *Leptohalysis scottii*



ANNEXE 2 : PUBLICATIONS ET COMMUNICATIONS**Publications**

Goineau, A., Fontanier, C., Jorissen, F.J., Buscail, R., Kerhervé, P., Raimbault P., Pruski, A., Cathalot, C., Pastor, L., Deflandre, B., Metzger, E., Rabouille, C. Temporal dynamics of live (stained) benthic foraminiferal faunas in a river-dominated shelf: assessing the impact of the Rhône River in the prodelta (Gulf of Lions, NW Mediterranean). A soumettre en Janvier 2011 dans *Biogeosciences*.

Goineau, A., Fontanier, C., Jorissen, F.J., Buscail, R., Kerhervé, P., Hunault, G., Cathalot, C., Pastor, L., Deflandre, B., Metzger, E., Rabouille, C. Spatial variability (decimetric-scale) of live (stained) benthic foraminifera from a river-dominated shelf (Gulf of Lions): applications for foraminiferal studies. Soumis à *Journal of Foraminiferal Research*.

Goineau A., Fontanier C., Jorissen F.J., Lansard B., Buscail R., Mouret A., Kerhervé P., Zaragosi S., Ernoult E., Artéro C., Rabouille C., Anschutz P., Metzger E, In press. Live (stained) benthic foraminifera from the Rhône prodelta (Gulf of Lion, NW Mediterranean): environmental controls on a river-dominated shelf. *Journal of Sea Research*.

Communications orales

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Fanget A.-S., Bassetti M.-A., Berné S., **Goineau A.**, Fontanier C., Jouet G., Cossa D., Arnaud M., Buscail R., Maillet G. Histoire sédimentaire récente du prodelta du Rhône révélée par une approche multi-proxy (Golfe du Lion, NW Méditerranée). 23^e Réunion des Sciences de la Terre à Bordeaux, France, Octobre 2010.

Goineau A., Fontanier C., Jorissen F., Buscail R., Kerhervé P., Pruski A., Cathalot C., Rabouille C. Temporal dynamics of live (stained) benthic foraminiferal faunas in a river-dominated shelf: assessing the impact of the Rhône River dynamic in the prodelta (Gulf of Lions, NW Mediterranean). FORAMS 2010 – International Symposium on Foraminifera à Bonn, Allemagne, Septembre 2010.

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Goineau A., Fontanier C., Ernoult E., Lansard B., Buscail R., Mojtahid M., Kerhevé P., Zaragosi S., Metzger E., Mouret A., Artéro C., Rabouille C. Live (stained) benthic foraminifera from the Rhône prodelta: environmental controls and temporal variability. The Micropaleontological Society's Foraminifera and Nannofossil Groups Joint Spring Meeting: Bioindicators of past and present environments à Tübingen, Allemagne, Mai 2008.

Goineau A., Zaragosi S., Eynaud F., Malaizé B., Toucanne S., Turon J.-L., Bourillet J.-F., Dennielou B., Trentesaux A., Fontanier C., Etcheber H., Kissel C. Etude très haute résolution des évènements de Heinrich par analyse d'images et géochimie élémentaire. 11^o Congrès de l'Association des Sédimentologistes Français (ASF) à Caen, France, Octobre 2007.

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Goineau A., Fontanier C., Fanget A.S., Bassetti M.A., Berné S., Jouet G., Cossa D., Arnaud M., Buscail R., Maillet G., Dennielou B., Jorissen F. Evolutions naturelle et anthropique récentes du Rhône enregistrées par les faunes de foraminifères benthiques (Golfe du Lion, Mer Méditerranée). 23^{ème} Réunion des Sciences de la Terre à Bordeaux, France, Octobre 2010.

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Vulgarisation scientifique

Goineau A., Fontanier C., Jorissen F.J. La fabuleuse aventure des foraminifères... ou comment retracer l'histoire du Rhône ! Poster présenté lors du 10^o Forum des Doctorants de l'Université d'Angers, France, Mai 2010.

➤ **2^o Prix du meilleur poster de vulgarisation scientifique.**

Goineau A., Fontanier C., Jorissen F.J. Ecologie des foraminifères benthiques à l'embouchure du Rhône–Du terrain au laboratoire. Poster présenté lors du 9^o Forum des Doctorants de l'Université d'Angers, France, Mai 2009.

23ème Réunion des Sciences de la Terre à Bordeaux, France, Octobre 2010.



Evolution historique du Rhône enregistrée par les faunes de foraminifères benthiques (Golfe du Lion, Mer Méditerranée)

Aurélie Goineau¹,

Christophe Fontanier¹, Anne-Sophie Fanget², Maria-Angela Bassetti², Serge Berné^{2,3}, Gwenaél Jouet³, Daniel Cossa⁴, Mireille Arnaud⁵, Roselyne Buscaill⁶, Grégoire Maillet⁷, Bernard Dennielou³, Frans Jorissen¹

¹ Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), Université d'Angers – ² Institut de Modélisation et d'Analyse en Géo-Environnement et Santé (IMAGES), Université de Perpignan
³ Ifremer, Géosciences Marines, Laboratoire de Géochimie et de Métallogénie (GM-LÉS), Centre de Brest, Plouzané – ⁴ Ifremer, Laboratoire Biogéochimie des contaminants métalliques (LBCM), Centre de Nantes
⁵ Institut de Radioprotection et de Sûreté Nucléaire (IRSN), La Seyne-sur-Mer – ⁶ Centre de Formation et de Recherche sur l'Environnement Marin (CEFREM), Université de Perpignan
⁷ Laboratoire d'Etudes Environnementales des Systèmes Anthropisés (LEESA), Université d'Angers

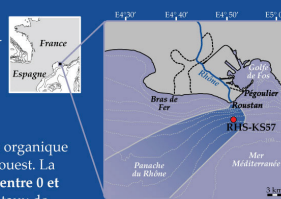
Coordonnées de l'auteur : aurelie.goineau@univ-angers.fr, Téléphone: (33) 2 41 73 54 08, Fax: (33) 2 41 73 53 52

Les assemblages fossiles de foraminifères benthiques ont été étudiés dans une carotte sédimentaire échantillonnée dans le prodelta du Rhône (Golfe du Lion, Nord-ouest de la Mer Méditerranée) lors de la mission RHOSOS (Septembre 2008, N/O Le Suroit). Grâce à ces faunes, l'évolution du système prodeltaïque du Rhône au cours des 400 dernières années a pu être retracée en termes d'apports sédimentaires et de matière organique.

Cadre de l'étude

La carotte RHS-KS57 a été prélevée dans le lobe deltaïque de Roustan à environ 3,8 km de l'embouchure (79 m de profondeur). Le calage chronostratigraphique de la carotte a été effectué à partir d'une datation $\Delta^{14}C$ sur un spécimen de *Turritella* sp. (700 cm de profondeur) ainsi que d'analyses du plomb anthropique ($^{210}Pb/^{210}Pb$) et du ^{137}Cs .

La zone d'étude est alimentée par le fleuve en matériel terrigène et matière organique (MO) par le panache du Rhône, dévié en moyenne sur une année vers le sud-ouest. La plus grande partie de ces apports sédimentaire près de l'embouchure du Rhône entre 0 et 60 m de profondeur et jusqu'à 6 km de l'embouchure, générant de très forts taux de dépôt des sédiments (jusqu'à 50 cm.an⁻¹).



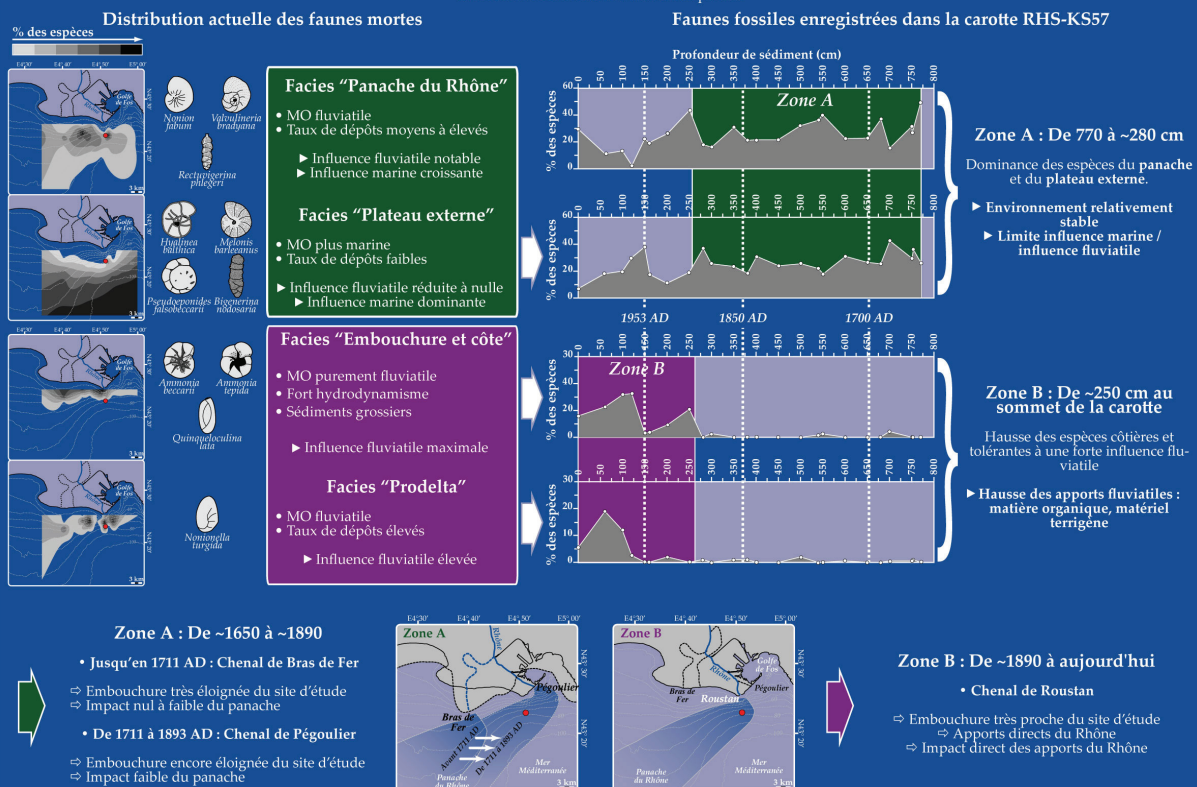
Depuis 4000 ans, le Rhône a changé de cours à plusieurs reprises au gré des migrations de ses chenaux.

Après la migration naturelle du chenal de Bras de Fer vers le chenal de Pégoulie en 1711 AD (239 ans BP), la fixation de l'embouchure et des chenaux par des travaux d'ingénierie (stabilisation des berges, construction de barrages hydro-électriques, travaux de dragage des fonds) ont stoppé l'évolution naturelle du Rhône.

L'exutoire actuel de Roustan est actif depuis 1893 AD (57 ans BP).

Résultats & Discussion

Les faunes vivantes de foraminifères benthiques ont été étudiées dans l'ensemble du prodelta du Rhône au cours de travaux antérieurs, apportant des connaissances majeures concernant leurs préférences écologiques actuelles (Goineau et al., *Sous presse*; Goineau et al., *Soumis*). A partir de ces connaissances, les faunes subfossiles (i.e., mortes récemment) ont pu être calibrées en tant qu'outil indicateur des conditions environnementales passées.



Les assemblages fossiles de foraminifères benthiques échantillonnés dans le lobe de Roustan ont enregistré la hausse graduelle de l'influence du Rhône à ce site au cours des 400 dernières années, conséquence des changements successifs de chenal et d'exutoire.

Bibliographie

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 Goineau A et al. *Soumis*. Spatial variability (decimetric scale) of live (stained) benthic foraminifera from a river-dominated shelf (Rhône prodelta, Gulf of Lions): applications for foraminiferal studies. *Journal of Foraminiferal Research*.
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 Cette étude a été financée par l'ANR/UMC - EXTREMA/Vulnérabilité, Milieux et Climat - Episodes météo-climatiques extrêmes et redistribution des masses sédimentaires et des polluants associés au sein d'un système côtier.

ASLO Aquatic Science Meeting à Nice, France, Janvier 2009



Decimetric scale spatial variability of live (stained) benthic foraminifera from the Rhône prodelta (Northwestern Mediterranean)

Aurélien Goineau^{a*}, Christophe Fontanier^b, Frans Jorissen^c, Roselyne Buscaill^b, Bruno Lansard^b, Philippe Kerhervé^b, Céline Artéro^b, Gilles Hunault^d, Christophe Rabouille^e, Elodie Ernault^b, Edouard Metzger^b

^aLaboratory of Recent and Fossil Bio-Indicators (BIAF), UPRES EA 2644, University of Angers, 2 boulevard Lavoisier, 49045 Angers, and Laboratory for the study of Marine Bio-Indicators (LEBIM), 85350 Ile d'Yeu, France
^bCentre de Formation et de Recherche sur l'Environnement Marin (CEFREM), University of Perpignan, UMR 5110 CNRS, 52 Avenue Paul Alduy, 66860 Perpignan Cedex, France
^cLaboratoire des Sciences du Climat et de l'Environnement (LSE), UMR 1572 CEA-CNRS-UVSQ, F-91198 Gif-sur-Yvette Cedex, France
^dHémodynamique Interaction Fibrose et Invasivité Tumorales Hépatiques (IHETH), University of Angers, UPRES 3859, IFR 132, Pavillon Ollivier, Rue Haute de Reculée, 49045 Angers Cedex, France

*Corresponding author: aurelien.goineau@univ-angers.fr, Telephone: (33) 2 41 73 54 08, Fax: (33) 2 41 73 53 52

The RIOTECH cruise (September 2007, R/V Téthys II, CNRS-INSU) permitted us to investigate live (stained) benthic foraminiferal faunas of the >150 µm size fraction from the Rhône prodelta. The aim of this study is to determine small scale spatial variability (patchiness) of benthic foraminiferal distribution in a river-dominated ocean margin (RIOMar) system.



Study area and Material & Methods

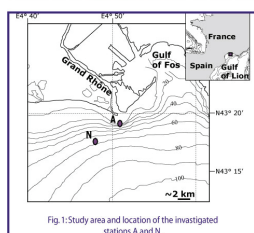


Fig. 1: Study area and location of the investigated stations A and N.

2 stations, A and N, located at 19 and 68 m depth in the Rhône prodelta (Fig.1) were sampled with a Barnett multicorer. This multicorer allows a sampling of 8 cores with a relatively undisturbed sediment-water interface (Photos). At each station, 4 cores (~72 cm² surface area) were investigated on the same multicorer

deployment. Each core was sliced every 0.5 cm down to 2 cm depth. Living foraminiferal faunas were stained with Rose Bengal, a commonly used stain.

This study allowed the collection of an important data set of environmental parameters (organic matter quantity, quality; geochemistry,...).

Environmental settings



Organic matter

The study area is enriched in Organic Carbon (OC), with sediment content > 1.2 % d.w. The most labile organic compounds (Lipids; Sugars; Amino acids; nd) constitute more than ~14 % of the OC. C:N atomic ratio values > 10 in both stations indicate the contribution of degraded continental organic matter and/or a mixture of organic material from continental and marine origins.

Bottom water characteristics

Bottom water temperatures range between 14.5 and 18.2 °C, with highest values in the vicinity of the Rhône river mouth (Station A). Bottom water oxygen concentration is high (>200 µmol.l⁻¹) on the whole area. However, values decrease with distance from the river mouth.

Decimetric scale spatial variability: results

The 4 cores recovered at each station integrate a decimetric scale spatial variability ranging from ~16 to 48 cm (Fig. 2a and 3b).

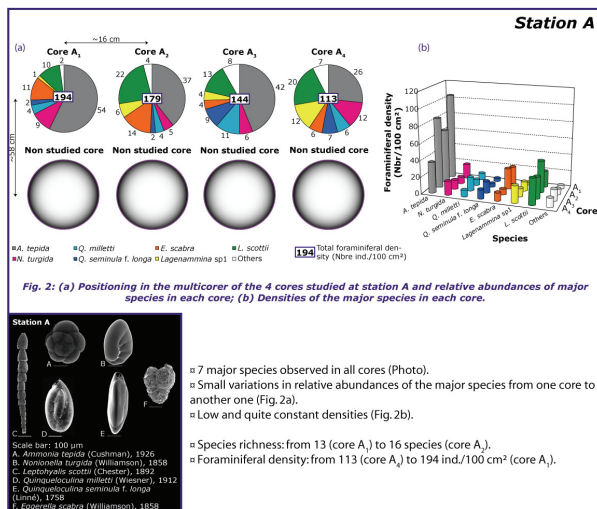


Fig. 2: (a) Positioning in the multicorer of the 4 cores studied at station A and relative abundances of major species in each core; (b) Densities of the major species in each core.

7 major species observed in all cores (Photo).
 Small variations in relative abundances of the major species from one core to another one (Fig. 2a).
 Low and quite constant densities (Fig. 2b).
 Species richness: from 13 (core A₁) to 16 species (core A₄).
 Foraminiferal density: from 113 (core A₁) to 194 ind./100 cm² (core A₄).

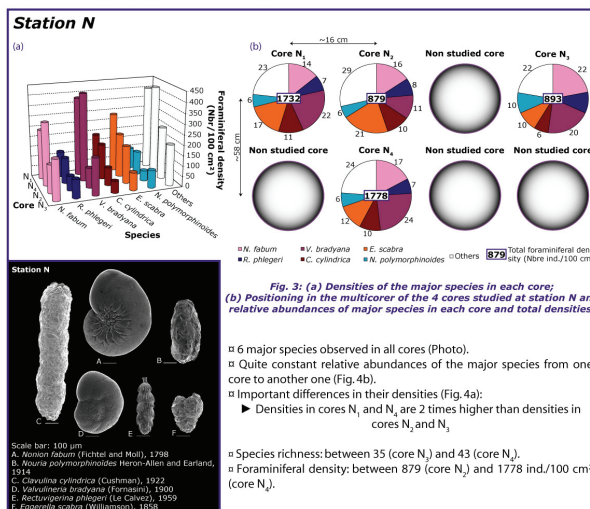


Fig. 3: (a) Densities of the major species in each core; (b) Positioning in the multicorer of the 4 cores studied at station N and relative abundances of major species in each core and total densities.

6 major species observed in all cores (Photo).
 Quite constant relative abundances of the major species from one core to another one (Fig. 4b).
 Important differences in their densities (Fig. 4a):
 Densities in cores N₁ and N₂ are 2 times higher than densities in cores N₃ and N₄.
 Species richness: between 35 (core N₁) and 43 (core N₂).
 Foraminiferal density: between 879 (core N₁) and 1778 ind./100 cm² (core N₂).

Discussion & Conclusions

Station A

- Species living in environments under fluvial influence with important organic matter supplies (deposit feeders).
- Stressed conditions so close to the river mouth (hydrosedimentary processes, oxygen penetration depth in the sediment,...).
- Non equilibrium faunas and very low densities despite the high lability of the organic matter.

Core	A ₁	A ₂	A ₃	A ₄	N ₁	N ₂	N ₃	N ₄
A ₁	1,000							
A ₂	0,926	1,000						
A ₃	0,958	0,919	1,000					
A ₄	0,825	0,917	0,880	1,000				
N ₁	0,046	0,084	0,007	0,016	1,000			
N ₂	0,093	0,144	0,038	0,057	0,923	1,000		
N ₃	0,017	0,025	0,019	0,000	0,921	0,855	1,000	
N ₄	0,019	0,037	0,006	-0,011	0,981	0,873	0,959	1,000

Table: Correlation matrix based on relative abundances.

Station N

- Species living in environments with poorly oxygenated sediment, high amounts of organic matter of more or less bad quality (degraded).
- Less stressed environmental conditions than at Station A, but with still a strong influence of the Rhône river.
- Eutrophicated faunas with high densities and specific richness thanks to the high lability of the organic matter.

- Strong positive correlation (r > 0.825; Table) based on relative abundances between duplicates of both stations.
 - Within each station, significantly similar assemblages are found in terms of relative abundances.
- High variability of the densities at Station N, may be due to organic matter patches related to topography.
 - Within Station N, different assemblages are found in terms of densities.

►► Necessity to use relative abundances in seasonal surveys to compare the assemblages.

Perspectives

- Analysis of the size fraction 63-150 µm on the same cores.
- Study integrated in a seasonal survey of benthic foraminiferal faunas (September 2006, April 2007, September 2007, May 2008 and December 2008).
- Paper in preparation: Goineau A. et al. (in prep) Live (stained) benthic foraminifera from the Rhône prodelta (Gulf of Lion, NW Mediterranean): environmental controls on a river-dominated shelf.

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10° Forum des Doctorants de l'Université d'Angers, France, Mai 2010 (2° Prix du meilleur poster de vulgarisation scientifique)

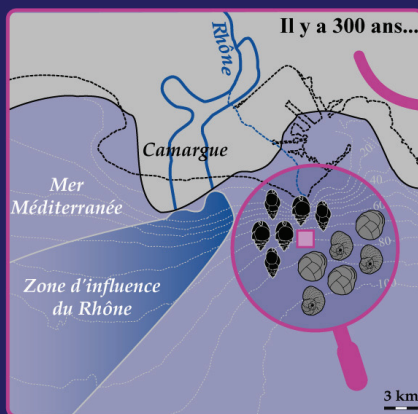
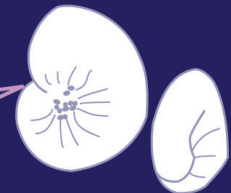


La fabuleuse aventure des foraminifères... ... ou comment retracer l'histoire du Rhône !

Aurélie Goineau

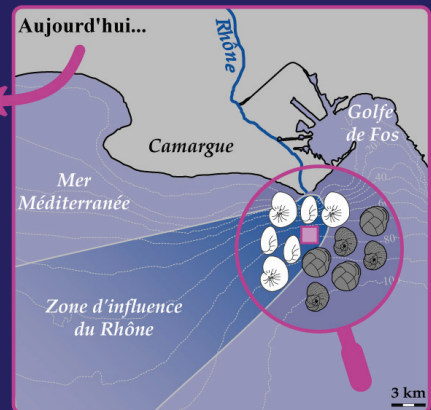
Dr de thèse : Frans Jorissen & Christophe Fontanier
Laboratoire des Bio-Indicateurs Actuels et Fossiles (BIAF), UPRES EA 2644, Angers

Bonjour ! Je me présente, *Nonion fabum*, mais appelez-moi *Nonion* ! Je suis un foraminifère, un minuscule organisme vivant dans les sédiments des océans. Avec ma petite cousine *Nonionella*, nous allons vous raconter comment, grâce à nous et nos consœurs, Aurélie a pu retracer l'histoire du Rhône !

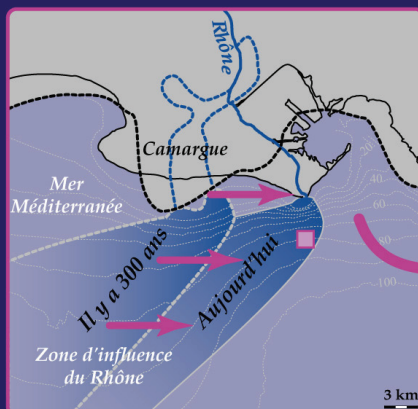


En étudiant de vieux sédiments prélevés près de l'embouchure actuelle du Rhône ■, Aurélie a constaté qu'il y a plus de 300 ans les soeurs *Bulimina* et *Cassidulina* cohabitaient ici avec *Valoulineria*.

Pourtant, aujourd'hui, ce ne sont plus les soeurs *Bulimina* mais moi et *Nonionella* qui vivons là !



Pourquoi...?



Nonionella et moi apprécions particulièrement le tumulte du fleuve. Au contraire, les soeurs *Bulimina* préfèrent les environnements beaucoup plus calmes... Or, il y a plus de 300 ans, le Rhône se déversait dans la Méditerranée plus à l'Ouest, à la place de l'actuelle Camargue. Les soeurs *Bulimina* se plaisaient donc là où nous vivons aujourd'hui car le Rhône ne les importunait pas !

Grâce à nos ancêtres, Aurélie a pu retracer l'histoire récente du Rhône... mais elle aurait pu remonter bien plus loin ! 1 000 ans, 10 000 ans, même 100 000 ans en arrière ! Les chercheurs nous aiment donc beaucoup car nous sommes très utiles pour étudier les environnements et les climats du passé.

aurelie.goineau@univ-angers.fr

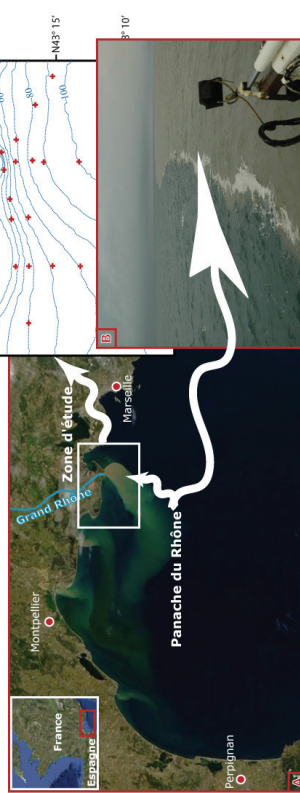
**Ecologie des foraminifères benthiques à l'embouchure du Rhône
Du terrain au laboratoire**

Aurélie GOINEAU
Directeurs de thèse : Christophe FONTANIER, Frans JORISSEN



Pourquoi étudier l'embouchure du Rhône ?

Le milieu côtier est un milieu vulnérable, soumis à une pression humaine grandissante (augmentation de la population, développement de l'agriculture et des apports associés d'engrais, mise en place de barrages hydroélectriques...). Aujourd'hui, il est admis que cet environnement agit comme une pompe à CO₂ grâce aux apports nutritifs des fleuves. Or, le changement climatique couplé à la pression humaine grandissante vont influencer largement les zones côtières : ces évolutions risquent de fragiliser fortement les écosystèmes et ce rôle de pompe.



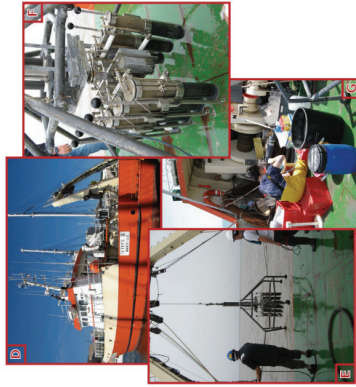
L'objectif du projet ANR "CHACCRA", dans lequel s'intègre cette thèse, est de simuler le changement de ce rôle de pompe à CO₂ au débouché du Rhône, fleuve majeur de la Méditerranée occidentale, lors des modifications futures du climat.

Pourquoi étudier les foraminifères benthiques ?

Les foraminifères sont des organismes unicellulaires de quelques dixièmes de millimètre (photos C au microscope électronique), "benthique" signifiant qu'ils vivent au fond des mers. L'intérêt d'étudier ces organismes réside dans :

- ✕ Leurs milieux de vie variés, des côtes aux plaines abyssales ;
- ✕ Le nombre d'espèces vivantes actuellement : plus de 5 000 ;
- ✕ Leur conservation dans le sédiment pendant plusieurs millions d'années après leur mort grâce à la coquille qu'ils fabriquent autour de leur cellule ;
- ✕ Leur sensibilité à l'environnement qui les entoure ;
- ✕ Leur durée de vie relativement courte (quelques mois).

Ces organismes sont de très bons indicateurs de leur milieu de vie.



Le travail sur le terrain : la mission en mer

La récolte du matériel de recherche s'est effectuée lors de plusieurs missions en mer à bord du navire océanographique le Téthys II (photo D). Au départ de Port St Louis du Rhône, l'embouchure du Rhône a été sillonnée, jusqu'à 20 km vers le large, afin de prélever des carottes de sédiment (photos E et F).

Une fois les carottes sur le pont du bateau intervient un travail d'échantillonnage (photo G) : les cinq premiers centimètres de sédiment sont prélevés et conservés dans des facons auxquels nous rajoutons un colorant teintant en rose les foraminifères vivants.

Le travail de laboratoire

De retour au laboratoire, l'analyse de chaque prélèvement de sédiment s'effectue en plusieurs étapes :

- ✕ Prélèvement de chaque foraminifère coloré en rose (= vivant lors de l'échantillonnage) à l'aide d'une loupe binoculaire et d'un pinceau (photos H et I) ;
- ✕ Reconnaissance puis cartographie de toutes les espèces importantes afin de visualiser leur répartition dans la zone d'étude (photos J et figure K).

Grâce à de nombreuses autres données environnementales acquises lors de la même mission, l'écologie moderne (conditions de vie actuelles dans leur environnement) de chaque espèce peut être définie afin d'être appliquée à l'étude des conditions passées de la même zone, mais aussi à la prévision de l'évolution future de cet environnement (modélisation).

