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Diversité structurelle et fonctionnelle des peuplements sablo-vaseux de Bretagne sud:
Impact de l'expansion d'*Haploops nirae*

Soutenue le 22 février 2013 devant le jury composé de :

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Dr Stanislas Dubois, Centre Ifremer de Bretagne	(co-directeur de thèse)

Résumé :

Ce travail de thèse a pour objectif, en s'appuyant sur le cas de la baie de Concarneau, de comprendre l'impact du développement de denses populations de l'amphipode tubicole *Haploops nirae* sur la diversité structurelle et fonctionnelle des peuplements sablo-vaseux de Bretagne Sud. L'étude des peuplements à *Haploops* dans ce projet de thèse se décline selon plusieurs niveaux d'organisation du vivant, du rôle spécifique d'*Haploops nirae* jusqu'au rôle fonctionnel du peuplement au sein de l'écosystème en passant par la description de la composition spécifique du peuplement et son rôle sur la biodiversité en général. Nos résultats suggèrent dans un premier temps que le rôle fonctionnel de l'espèce seule (pression de filtration, production secondaire) est potentiellement important. De plus, les modifications physiques de l'habitat par les *Haploops* se sont révélées avoir des conséquences très importantes sur la composition des peuplements et la diversité spécifique. *A contrario*, l'étude de la diversité fonctionnelle abordée par l'analyse des traits biologiques (BTA) et la production secondaire des peuplements révèle que les conséquences fonctionnelles de la présence des *Haploops* dans un écosystème sont dans l'ensemble faibles. De la même façon, l'étude du fonctionnement trophique des peuplements benthiques de la baie de Concarneau (grâce à l'utilisation des isotopes stables) révèle une faible incidence fonctionnelle du développement des *Haploops* sur la structure du réseau trophique benthique. Bien que les peuplements à *Haploops* ne soient pas caractérisés par de profonds changements fonctionnels, les flux trophiques vers les niveaux trophiques supérieurs sont cependant vraisemblablement affectés par la présence des *Haploops*.

Mots-clés: Ampeliscidae – espèce ingénieure – Bretagne Sud – diversité macrofaune benthique – diversité fonctionnelle – réseau trophique

Abstract:

This thesis aims here, based on the case of the Bay of Concarneau, to understand the impact of the development of dense populations of the tubiculous amphipod *Haploops nirae* on the structural and functional diversity of sandy-mud communities of South Brittany. The study of *Haploops* communities was developed on various levels of organization of life, from the specific role of *Haploops nirae* to functional role of *Haploops* community in the ecosystem passing through the description of the community composition and its role on the biodiversity. Our results suggest firstly that the functional role of *Haploops nirae* alone (filtration pressure, secondary production) is potentially important. Moreover, the physical changes induced by *Haploops* were found to have important consequences on the composition of species assemblages and species diversity. In contrast, the study of the functional diversity addressed by biological traits analysis (BTA) and secondary production at the community scale reveals that the functional consequences of *Haploops* occupation in an ecosystem are generally low. In addition, the analysis of the trophic functioning of benthic communities from the Bay of Concarneau (through the use of stable isotopes) showed low incidence of *Haploops* occupation on the functioning of the benthic food web. Although *Haploops* communities are not characterized by profound functional changes, trophic flows to higher trophic levels, however, are likely to be affected by the presence of *Haploops*.

Keywords: Ampeliscidae – engineer species – South Brittany – benthic macrofauna diversity – functional diversity – food web

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Introduction générale

1. Les écosystèmes côtiers

Situées à l’interface entre l’océan et le continent, les zones côtières sont des espaces d’intérêt majeur tant sur le plan écologique que socio-économique. Ces systèmes sont le lieu d’une activité biologique particulièrement importante qui se traduit par l’existence d’espaces de forte biodiversité et d’intense productivité (Gattuso et al., 1998 ; Gazeau et al., 2004). Ainsi, bien que les zones côtières n’occupent que 7% de la surface de l’océan mondial, la production primaire de ces milieux représenterait près de 20% de la production primaire océanique totale (Gattuso et al., 1998 ; Gazeau et al., 2004) et 17 % des flux de CO_2 à l’interface océan-atmosphère (Cai, 2011). Ils fournissent par ailleurs à l’homme de nombreux biens et services écosystémiques de grande valeur (Constanza et al., 1997 ; Beaumont et al., 2008) : l’approvisionnement en nourriture et en matériaux, le cadre de différentes activités récréatives et culturelles mais aussi des services de régulation et de support qui dépendent de différents processus écologiques de première importance (ex : la régulation du cycle des nutriments, la bioremédiation de polluants, la stabilité du sédiment, la création d’habitats et de refuges pour les espèces marines et la constitution de zones de nourriceries pour de nombreuses espèces de poissons).

Plusieurs facteurs se combinent pour expliquer la forte productivité des écosystèmes côtiers. Contrairement à l’océan ouvert où les peuplements benthiques sont basées sur l’utilisation de phytoplancton sédimenté - à l’exception notable de quelques milieux dépendant d’une production chimiosynthétique (ex : sources hydrothermales, suintements froids) - l’origine de la matière organique dans les zones côtières est de nature complexe et d’origine très variable (Mann, 1982). En effet, les apports continentaux détritiques peuvent être importants et se surajoutent aux apports de différents producteurs primaires tels que le phytoplancton, le microphytobenthos, les macroalgues et les phanérogames marines. Il existe ainsi une large diversité de sources potentielles de matière organique susceptible de soutenir l’activité biologique des écosystèmes côtiers (Cloern et al., 2002 ; Vinagre et al., 2012). Cependant, cette diversité des sources de matière organique complexifie le fonctionnement des écosystèmes côtiers, notamment le fonctionnement des réseaux trophiques et complique ainsi fortement la compréhension des liens trophiques existant entre producteurs primaires et consommateurs primaires.

Outre leur caractère fortement productif, une autre caractéristique majeure des systèmes côtiers est qu'ils sont soumis à une grande variabilité naturelle des paramètres environnementaux, à la fois dans le temps et dans l'espace, due aux influences externes telles que, par exemple, les saisons, la marée ou les tempêtes. Cette forte variabilité spatio-temporelle des paramètres physico-chimiques, cyclique ou non, se traduit en premier lieu par de fortes hétérogénéité et diversité des habitats. En corollaire, ces modifications qui influent simultanément sur la nature du milieu et sur la composition qualitative et quantitative des peuplements, se traduisent par des dynamiques spatiotemporelles complexes et très spécifiques aux écosystèmes côtiers dans lesquels s'entremêlent différents processus cycliques ou impulsionnels à diverses échelles.

Par ailleurs, en dépit de leur valeur écologique majeure, les écosystèmes côtiers n'en sont pas moins fortement affectés par les activités humaines et le changement global qui en résulte. En effet, ces écosystèmes particuliers et fragiles à l'interface terre/mer sont souvent situés dans des zones très densément peuplées où ils subissent de nombreuses pressions locales : influence des activités implantées dans les bassins versants (agriculture), urbanisation des côtes et dégradation des habitats, influence des activités de la pêche artisanale et de l'aquaculture (Halpern et al., 2008 ; Lotze et al., 2006 ; Airoldi et Beck, 2007). A titre d'exemple, les zones côtières sont touchées depuis plusieurs années par une eutrophisation croissante qui provoque des phénomènes d'hypoxie, voire d'anoxie, et entraîne la disparition de nombreuses espèces (Diaz et Rosenberg 2008). Ces écosystèmes subissent également les conséquences, à une échelle plus grande, du changement climatique qui provoque différentes modifications de l'environnement des zones côtières : l'accroissement de la température et l'acidification des eaux côtières, l'élévation du niveau de la mer particulièrement prégnant en zones littorales ou le changement des conditions hydrodynamiques (Harley et al. 2006). Les répercussions des modifications récentes et rapides des conditions environnementales dans l'océan mondial sont multiples et touchent différents niveaux d'organisation du vivant, directement ou indirectement. En influençant directement les taux métaboliques des organismes, les modifications des propriétés de l'environnement influent sur les caractéristiques du cycle de vie des organismes (e.g. temps de développement), la dynamique des populations et le fonctionnement des écosystèmes (e.g. productivité). Un des effets les plus spectaculaires de la hausse des températures est la modification de l'aire de répartition des espèces, la disparition de certaines espèces clés et l’introduction de nouvelles espèces (Harley et al, 2006 ; Helmuth et al. 2006). La variabilité du degré de tolérance des différents organismes au changement global conduira ainsi inexorablement à la constitution de nouveaux peuplements qui n’ont pas d’équivalents passés ou contemporains et dont la compréhension de la dynamique constitue un enjeu fort tant pour le scientifique que le gestionnaire. Ainsi, lors de l’évaluation réalisée par le *Millemium Ecosystem Assessment* (MEA, 2005), 60% des écosystèmes côtiers dans le monde étaient considérés comme dégradés.

La structure des écosystèmes côtiers est ainsi impactée par une forte variabilité naturelle et des perturbations anthropiques qui à terme peuvent avoir des conséquences sur le fonctionnement des écosystèmes côtiers. Mieux comprendre la nature des principaux processus physiques, chimiques et biologiques qui interviennent sur la modification de la structure et de la fonctionnalité des écosystèmes côtiers permet d’évaluer les réponses des systèmes côtiers face aux changements de l’habitat marin induits par l’homme et leurs conséquences sur les biens et services écosystémiques.

2. Biodiversité et fonctionnement des écosystèmes

2.1. De la mesure de la richesse spécifique à celle de la diversité fonctionnelle

Dans le contexte actuel où l’intérêt pour la biodiversité est en plein essor, et où se généralise la prise de conscience de la responsabilité humaine dans la crise d’extinction en masse qui frappe la biodiversité à l’échelle de la planète, il apparaît primordial d’étudier les différentes facettes de la biodiversité et de comprendre son rôle dans le fonctionnement des écosystèmes (Purvis et Hector, 2000 ; Hooper et al., 2005). La biodiversité est ainsi devenue le thème central de nombreuses études en écologie allant jusqu’à être considérée comme une mesure de l’état global d’un écosystème. En effet, elle est actuellement considérée comme une variable prédictive du fonctionnement des écosystèmes et l’un des principaux facteurs déterminant la stabilité des écosystèmes et leur résilence (i.e. capacité à se remettre de perturbations). Par définition, la biodiversité correspond à la variabilité existante parmi les organismes vivants et les systèmes écologiques auxquels ils appartiennent (Harper et Hawksworth, 1994). On reconnaît généralement trois grands niveaux d’étude de la biodiversité qui se déclinent selon trois échelles d'organisation du vivant: la diversité génétique (qui correspond à la diversité au sein d'une espèce), la diversité spécifique (qui correspond à la diversité entre les espèces au sein d'un écosystème) et la diversité des écosystèmes (qui correspond à la diversité des peuplements biologiques vivant dans un écosystème).

Les opinions divergent sur la manière de mesurer la biodiversité dans la mesure où il n'existe aucune mesure universelle pour l'estimer (Carney, 2007). Néanmoins, dans de nombreuses études sur la diversité, la richesse spécifique est l'unité de mesure la plus couramment utilisée, à tel point que la biodiversité est souvent confondue avec la notion de richesse spécifique (Gaston, 2000). D'autre part, de très nombreuses études ont utilisé des indices de mesure de la diversité structurelle qui sont basés sur la richesse spécifique et l'abondance relative des espèces tels que l'indice de diversité de Shannon, l'indice de Simpson, les indices de Hill ou l'équitabilité de Pielou (Gray, 2000). La signification fonctionnelle de ces indices est loin d'être évidente puisque deux peuplements composés d'assemblages d'espèces totalement différents assurant des fonctions écologiques différentes peuvent avoir la même diversité structurelle. Ils renseignent par ailleurs très peu sur l'état de santé d'un écosystème (Ghertsos et al., 2000).

Des études relativement récentes se sont attachées à explorer la relation entre le nombre d'espèces et certaines fonctions essentielles des écosystèmes, principalement dans les écosystèmes terrestres (Naeem et al., 1994 ; Tilman et Downing, 1994 ; Hector et al, 1999). Ces travaux ont alors suscité l'émergence d'un nouveau concept en écologie : le concept de diversité fonctionnelle basé sur la relation entre la diversité et le fonctionnement des écosystèmes (Loreau et al., 2001). Dans ce contexte, une attention croissante a été portée sur l'étude de la diversité fonctionnelle des peuplements ces dernières années et sur le développement d'approches pertinentes et adaptées pour la mesurer (Mason et al., 2005 ; Lepš et al., 2006 ; Schleuter et al., 2010 ; Mouillot et al., 2011).

Le concept de diversité fonctionnelle renvoie à la diversité des processus biologiques, des fonctions ou des caractéristiques d'un écosystème particulier. A l'opposé de la diversité structurelle qui se focalise uniquement sur l'identité taxinomique des espèces, l'écologie fonctionnelle présente l'avantage de se focaliser sur la fonction des espèces afin de mieux cerner leurs effets sur les écosystèmes. Ces fonctions exercées par les espèces sont extrêmement variées et englobent tous les processus de transformation de la matière qui se produisent dans un écosystème (Cooper et al., 2008). Elles incluent tous les processus du métabolisme et des processus dynamiques tels que (i) la bioturbation ou la remise en suspension active du sédiment, (ii) la production de matière organique ainsi que (iii) les transferts de nourriture, d'oxygène et de nutriments entre compartiments, et (iv) la résilience des écosystèmes. Récemment, Cooper et al. (2008) ont identifié 12 méthodes différentes pour quantifier la réponse fonctionnelle des écosystèmes marins côtiers (Tableau 1). Parmi celles-ci, l'analyse des traits biologiques des espèces (BTA) s'est très largement développée ces dernières années et s'est avérée être un outil très utile pour identifier les changements fonctionnels dans des assemblages d'espèces préalablement soumis à des perturbations anthropiques variables telles que la pêche, l'extraction de granulats ou l'eutrophisation (Bremner et al., 2006; Tillin et al., 2006; De Juan et al., 2007; Paganelli et al., 2012). Cette méthode considère que les rôles fonctionnels accomplis par les espèces sont déterminés par leurs traits biologiques (Bremner et al., 2006) et utilise donc ces traits (i.e. traits d'histoire de vie, caractéristiques morphologiques et comportementales) pour relier la composition d'un peuplement aux processus écologiques qu'elle assure.

Sur la base de l'utilisation des traits biologiques des espèces, de nombreux indices de diversité fonctionnelle ont été proposés par analogie avec les indices de diversité spécifique depuis une dizaine d'années tels que la divergence fonctionnelle, i.e. FD (Petchey et Gaston, 2002), la variance de la divergence fonctionnelle, i.e. FDvar (Mason et al., 2003), l'équitabilité fonctionnelle, i.e. FE (Mouillot et al., 2005), l'entropie quadratique de Rao, i.e. Q (Botta-Dukat, 2005) ou encore les indices développés par Villéger *et al.* (2008) (i.e. FRich, FEve and FDiv). Toutefois, aucun ne fait actuellement consensus (Petchey et Gaston, 2006). Sur la base de ces indices, la diversité fonctionnelle peut alors être décrite en ne considérant qu'un seul trait biologique (ex : FDvar, FE) (Mason et al., 2003 ; Mouillot et al., 2005) ou avoir une vision plus synthétique en considérant plusieurs traits (FAD, FD, Q, indices de Villéger (Villéger et al. 2008). Au-delà de l'indice retenu, une question centrale à cette approche est de déterminer le nombre et la nature des traits à prendre en considération en fonction des écosystèmes analysés. En particulier, si le degré de connaissance de la biologie des principales espèces d'un peuplement conduit le plus souvent à une situation de compromis, il est essentiel d'évaluer l'influence du nombre et du type de traits considérés sur la robustesse des résultats et donc sur la perception rendue du fonctionnement des écosystèmes, par exemple le degré de redondance ou de compensation fonctionnelle.

Tableau 1: Indices utilisés pour évaluer la fonction des écosystèmes marins. D'après Cooper et al. (2008).

Index	Name	Application Area	Objective	Reference
AZTI	The AZTI Marine Biotic Index	Europe	Response to disturbance	Borja et al. (2000)
BHQ	Benthic Habitat Quality	International	Response to disturbance	Nilsson et Rosenberg (1997)
BRI	Benthic Response Index	California Shelf	Objective index	Smith et al. (2001)
BTA	Biological Trait Analysis	Europe	Ecosystem functioning index	Bremner et al. (2003, 2006)
ITI	Infaunal Trophic Index	California	Response to organic enrichment	Maurer et al. (1999)
IQI	Infaunal Quality Index	Europe	Describe biological status	Borja et al. (2007)
MMI	Macrofauna Monitoring Index	New Zealand	Response to dredge material	Roberts et al. (1998)
Ps	Somatic Production	International		Brey (2001), Cusson et Bourget (2005)
Rao's Q	Quadratic Entropy Coefficient	International	Ecosystem functioning index	Ricotta (2005), Botta-Dukat (2005)
Sensitivity	Sensitivity assessment	North Sea	Management plans	Hiddink et al. (2007)
SES	Sustainable Ecological Succesion	Canada	Biodiversity recovery	Ellis (2003)
TD	Taxonomic Distinctness	Europe	Taxonomic index	Warwick et Clarke (1995)

2.2. La production secondaire et l'architecture des réseaux trophiques:des mesures fondamentales du fonctionnement des ecosystems

D'un point de vue fonctionnel, les écosystèmes peuvent être conceptualisés comme un ensemble de compartiments qui échangent de la matière et de l'énergie. La notion de production est alors fondamentale puisque c'est elle qui synthétise le mieux l'ensemble des données (biomasse, croissance individuelle, reproduction, temps de génération, survie) caractérisant le bon fonctionnement d'un compartiment biologique, d'une population ou d'un écosystème (Medernach et Grémare, 1999). Ainsi, la quantification de la production somatique peut être vue comme une approche d'évaluation du fonctionnement des écosystèmes. La production somatique (Ps) est la quantité de matière (d'énergie) qui est potentiellement disponible comme nourriture pour le niveau trophique supérieur (i.e. pour les prédateurs) (Cusson et Bourget, 2005). La meilleure façon d'évaluer correctement la production somatique des organismes passe par l'utilisation de méthodes basées sur des séries de mesures dans le temps des densités, de la taille individuelle des organismes d'une population et du poids moyen individuel des organismes (sommation des incréments, sommation des pertes). Ces approches nécessitent néanmoins des efforts d'échantillonnage et d'analyse particulièrement importants qui ont conduit au développement de modèles empiriques fondés sur la corrélation observée entre certaines caractéristiques des populations (la durée de vie de l'espèce, le poids maximum des organismes, le poids moyen) et/ou du milieu (la profondeur et la température), et la productivité, i.e. le rapport P/B (Medernach et Grémare, 1999 ; Cusson et Bourget, 2005). Ainsi, la simple connaissance des paramètres intervenant dans chacun des modèles permet d'évaluer la production secondaire d'une population sans avoir besoin de réaliser des échantillonnages importants. Il faut néanmoins souligner que cette méthode est beaucoup plus sujette à caution que les traditionnelles méthodes de suivi de la structure des populations dans le temps. Elle offre *a contrario* l'opportunité de calculer la production à l'échelle d'un peuplement et de décrire son évolution dans le temps en réponse à des modifications des conditions environnementales (Barrio Frojan et al., 2011 ; Dolbeth et al., 2011).

Dans ce contexte de prise en compte des transferts d'énergie au sein d'un écosystème, l'étude des relations trophiques entre espèces joue un rôle central. La compréhension et la quantification des voies de transfert trophiques, essentielles au fonctionnement des écosystèmes, sont alors un moyen supplémentaire de décrire et de quantifier le fonctionnement général des écosystèmes marins. Ainsi, une attention particulière a été portée en écologie sur les liens trophiques entre espèces pour décrire la structure et le fonctionnement général des écosystèmes marins (Paine, 1980). De nombreux concepts ont été ainsi développés en fonction de la nature et de l'intensité de ces liens tels que les contrôles "bottom-up" et "top down" des peuplements (Power, 1992), la notion d'espèce clef de voute au sein des réseaux trophiques (Power et al., 1996) ou les phénomènes de cascade trophique (Estes et Palmisano, 1974).

Originellement, les liens trophiques entre espèces ont souvent été étudiés par l'analyse des contenus stomacaux des consommateurs. Cependant, cette technique présente des difficultés méthodologiques (difficulté d'identification des proies dans le cas d'invertébrés de petite taille ou d'utilisation de matériel détritique, image ponctuelle du régime alimentaire) et présente également l'inconvénient de déduire la composition du régime alimentaire des animaux en se fondant sur l'ingestion plutôt que sur l'assimilation. Le développement de nouveaux outils comme les isotopes stables, en particulier ceux de l'azote et du carbone, s'est avéré être un outil indispensable et très utile pour l'étude des relations trophiques entre espèces (Encadré 1) (Peterson et Fry, 1987 ; Layman et al., 2012). Ces nouveaux traceurs ont grandement amélioré la compréhension de la structure trophique des peuplements et ont également permis d'aborder les réseaux trophiques dans le cadre d'une approche écosystémique (Schindler et Scheuerell, 2002). Une approche plus fonctionnelle de l'utilisation des isotopes stables a été développée dans plusieurs études récentes (Bearhop et al., 2004 ; Cornwell et al., 2006 ; Layman et al., 2007a). Ces dernières ont proposé plusieurs indices basés sur les valeurs isotopiques des organismes, pour quantifier et mesurer les différents aspects de la structure trophique des peuplements (ex : diversité des sources de nourriture, longueur du réseau trophique, diversité trophique, redondance trophique). Une autre approche prometteuse liée à l'utilisation des isotopes stables consiste à quantifier la contribution des différentes sources de nourriture dans le régime alimentaire d'un organisme grâce à l'utilisation de modèles d'équations de mélange (Phillips et Gregg, 2003) .

Encadré 1 : Principe d'utilisation des isotopes stables en écologie trophique

Les isotopes d'un même élément chimique sont caractérisés par un nombre de protons identique et par un nombre de neutrons variable. Ce qui distingue deux isotopes est donc leur nombre de masse : on parle alors d'isotopes « légers » et « lourds ».
De nombreux isotopes sont stables car ils ne subissent pas de désintégration radioactive et n'émettent pas de rayonnement, tandis que d'autres isotopes sont instables. En effet, la proportion de neutrons dans le noyau de certains isotopes leur confèrent une instabilité énergétique et le retour à une forme isotopique stable se fait par l'émission d'une particule, on parle alors d'isotopes radioactifs.

Le rapport entre isotopes stables s'exprime en unité δ (‰) qui compare le rapport isotope lourd / isotope léger à un rapport fixé par un standard international selon l'équation suivante :

$$\delta X = ((R_{\text{échantillon}}/R_{\text{standard}}) - 1) \times 1000\ (‰)$$

où $X = {}^{13}C$ (carbone) ou ${}^{15}N$ (azote) et $R = {}^{13}C/{}^{12}C$ pour le carbone et ${}^{15}N/{}^{14}N$ pour l'azote.
Pour le carbone ($\delta^{13}C$), la composition isotopique du standard est celle de la Pee Dee Belemnite (fossile calcaire, VPDB, $\delta^{13}C=0$ ‰) et pour l'azote ($\delta^{15}N$), la référence est celle de l'azote atmosphérique ($\delta^{15}N=0$‰).

Les propriétés chimiques des isotopes d'un même élément sont identiques car ces isotopes ont le même nombre d'électrons (et de protons). En revanche, la différence de masse entre isotopes d'un même élément (dûe à un nombre de neutrons différents) engendre des propriétés cinétiques et thermodynamiques légèrement différentes. Ainsi, les isotopes d'un même élément participent aux mêmes réactions chimiques mais la vitesse de réaction ou les concentrations à l'équilibre thermodynamique seront plus ou moins grandes selon qu'il sagit des isotopes légers ou lourds. A chaque réaction physique, chimique ou biologique, l'isotope léger (${}^{12}C$,${}^{14}N$) est préférentiellement utilisé par le métabolisme et la matière organique s'enrichit en isotope lourd (${}^{13}C$,${}^{15}N$). Cet enrichissement crée une différence de composition isotopique entre une source et son consommateur appelée fractionnement isotopique. Ainsi, la composition isotopique en carbone et en azote d'un producteur primaire est fonction non seulement des sources de carbone et d'azote minéral utilisées mais aussi des voies métaboliques utilisées lors de l'assimilation de ces éléments. La composition isotopique en carbone et en azote d'un animal dépend de la composition en isotopes stables de sa source de nourriture et du fractionnement isotopique pendant le processus d'assimilation et d'intégration.

Même si le fractionnement dépend de multiples facteurs comme le type de nourriture, les conditions environnementales et le groupe taxonomique considéré (Vander Zanden et Rasmussen, 2001 ; Vanderklift et Ponsard, 2003 ; Mc Cutchan et al., 2003), les rapports isotopiques en carbone et en azote stable (nommés $\delta^{15}N$ et $\delta^{13}C$) sont typiquement enrichis de la proie au consommateur de 3,4‰ pour le $\delta^{15}N$ et de 1‰ pour le $\delta^{13}C$ (DeNiro et Epstein, 1981 ; Minagawa et Wada, 1984).

Classiquement, le carbone et l'azote ont des applications différentes : l'analyse du $\delta^{13}C$ est utilisée pour comprendre l'origine des sources de matière organique dans les réseaux trophiques et la signature en $\delta^{15}N$ des consommateurs et des proies est utilisée comme un indicateur de la position trophique d'un organisme dans le réseau trophique (Post, 2002). Ainsi, l'utilisation couplée des isotopes stables du carbone et de l'azote permet d'étudier les transfert d'énergie dans les écosystèmes tel que identifier et quantifier les sources de matière organique et leur utilisation, reconstruction des chaînes trophiques.

2.3. La notion d'espèce ingénieure

Bien que toutes les espèces jouent un rôle dans les processus écologiques qui structurent les écosystèmes, certaines espèces telles que les espèces clef de voûte ou les espèces ingénieures sont considérées plus importantes que d'autres pour le fonctionnement et la structuration des écosystèmes (Ellison et al., 2005).

Le concept d'espèce clef de voûte est attribué à Paine (Paine, 1966, 1969) qui postule que certaines espèces sont plus importantes que d'autres et jouent un rôle pivot, notamment dans les réseaux trophiques, en dépit de leur niveau d'abondance modéré (Estes et al., 1978). Ces espèces exercent un rôle clé dans la structuration des peuplements, en particulier en limitant la prolifération de certaines espèces compétitrices et en favorisant ainsi d'autres espèces. Le concept d'espèce clef de voûte s'applique à des espèces dont les effets sont plus importants que ne laisse prévoir leur biomasse (Power et al., 1996).

Le concept d'espèce ingénieure a été proposé par Jones et al. (1994) qui définissent les espèces ingénieures comme des organismes qui, par leur activité biologique, entrainent un changement physique de l'habitat. En modifiant les conditions biotiques ou abiotiques de leur environnement, de telles espèces modulent directement ou indirectement la disponibilité de l'habitat et des ressources pour d'autres espèces. Elles ont en particulier la capacité de créer, transformer ou de maintenir des habitats pour d'autres espèces. Par exemple, la complexification de la structure physique de l'environnement due à la présence de terriers, de constructions récifales ou de tapis de tubes formés par les organismes ingénieurs modifie les assemblages d'espèces qui leur sont associées (Gutiérrez et al., 2012). De même, ces espèces influencent les flux biogéochimiques et la composition des sédiments de surface, jouant ainsi un rôle décisif dans plusieurs processus écologiques (Woodin et al., 2012).

Deux types d'espèces ingénieures ont été distingués (Jones et al., 1994, 1997) : les ingénieurs autogéniques qui modifient le milieu du fait de leur propre structure physique (ex: coraux) et les ingénieurs allogéniques qui changent leur environnement en transformant des matériaux vivants ou morts (ex: castors). Dans les milieux marins et essentiellement dans les systèmes côtiers, une large diversité d'organismes ingénieurs tels que les palétuviers formant les mangroves, les coraux, les polychètes tubicoles, les ascidies coloniales, les bancs de moules et les herbiers constitue les exemples parmi les plus étudiés. De nombreux auteurs ont ainsi démontré que ces espèces, qui modifient physiquement les habitats benthiques marins, jouent des rôles fonctionnels majeurs au sein de l'écosystème (Wright et Jones, 2006 ; Voultsiadou et al., 2007 ; Reise et al., 2009). Certaines espèces tubicoles grégaires de crustacés amphipodes sont au contraire beaucoup moins bien connues. C'est notamment le cas des amphipodes de la famille des Ampeliscidae dont certaines espèces peuvent atteindre des densités très élevées excédant plusieurs milliers d'individus par m^{-2}. Ils forment alors de denses tapis de tubes qui colonisent d'importantes surfaces et structurent le paysage à grande échelle (Bellan-Santini et Dauvin, 1988 ; Franz et Tanacredi, 1992 ; Sudo et Azeta, 1996 ; Göransson, 2002). Dans ces conditions, les Ampeliscidés créent un habitat unique en son genre (Fig. 1), beaucoup plus complexe et hétérogène que les fonds sédimentaires voisins et jouent potentiellement un rôle important dans les processus écologiques.

Dans le but de comprendre comment la complexité topographique du substrat induite par la présence de tubes peut avoir des conséquences sur les peuplements benthiques, Eckman (1983) a étudié l'effet de la densité de tubes (sous forme de pailles en plastique) sur le recrutement. Eckman a ainsi mis en évidence que la présence de tubes a une répercussion sur l'hydrodynamisme local, sur les taux de sédimentation mais également sur la fixation et le recrutement benthique des larves. Grâce à cette étude, Eckman montre ainsi comment seule la structure physique des tubes (l'hétérogénéité du substrat), en modifiant les processus hydrodynamiques à petite échelle, peut influencer directement les caratéristiques des peuplements benthiques comme la répartition des espèces, l'abondance et la diversité spécifique.

Figure 1 : Exemple de fond à Ampeliscidés. (Vases consolidées à *Haploops*, Baie de Concarneau). Photo Xavier Caisey.

3. Les peuplements à Ampeliscidés

3.1. Caractéristiques générales

La famille des Ampeliscidae est l'une des familles d'amphipodes les plus diversifiées en milieu marin (Dauvin et Bellan-Santini, 1996). Les Ampeliscidés, qui renferment 4 genres différents (i.e. *Ampelisca*, *Byblisoides*, *Byblis* et *Haploops*), sont distribués dans tous les océans du globe et se répartissent de la zone intertidale jusqu'aux profondeurs abyssales. Le genre *Haploops* Liljeborg, 1855 comprend actuellement 20 espèces valides et comprend moins d'espèces que les deux autres genres principaux de la famille : le genre *Ampelisca* avec plus de 160 espèces et le genre *Byblis* avec environ 60 espèces (Bellan-Santini et Dauvin, 2008). Seul le genre *Byblisoides* ne comporte que 6 espèces reconnues. Contrairement au genre *Ampelisca* qui est caractéristique des eaux chaudes et tempérées peu profondes, le genre *Haploops* est considéré comme étant associé aux eaux profondes et froides, occupant des profondeurs variant de 10 à 3570 m (Dauvin et Bellan-Santini, 1990). Les *Haploops* se distribuent principalement dans les océans Nord Atlantique, Nord Pacifique et Arctique (Fig. 2). Toutefois, certaines espèces ont été décrites dans d'autres régions de l'océan mondial : *Haploops descansa* et *Haploops oonah* en mer de Tasmanie, dans le Sud-Ouest Pacifique, *Haploops meloi* dans l'Atlantique Sud, et *Haploops antarctica* dans l'Océan Austral.

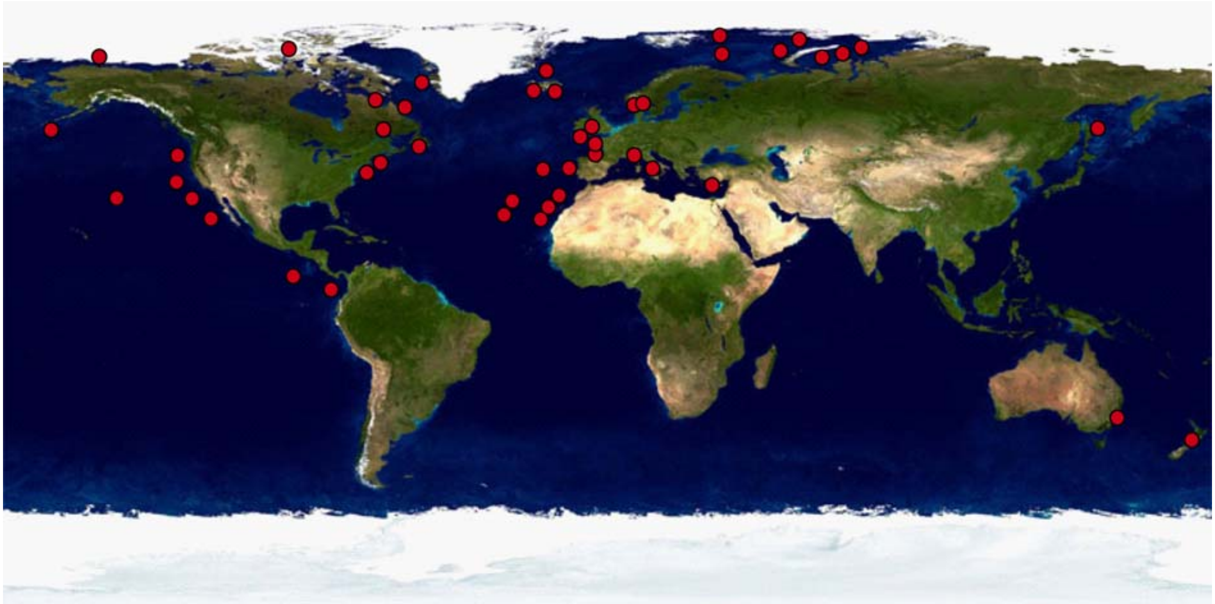

Figure 2: Carte de répartition des espèces du genre *Haploops* à l'échelle mondiale. D'après Bellan-Santini et Dauvin (2008). Les positions de *Haploops meloi* et *Haploops antarctica* ne sont pas représentées.

Les amphipodes Ampeliscidae privilégient les sables fins et les sédiments vaseux, notamment pour leur permettre de construire leur tube. En effet, la plupart des espèces appartenant à la famille des Ampeliscidae sont tubicoles et se tiennent en position dorsale près de l'orifice du tube pour se nourrir à l'aide de leurs antennes (Fig. 3). Le régime alimentaire des Ampeliscidae varie néanmoins en fonction des genres considérés. Les *Haploops* sont définis comme étant des suspensivores stricts qui se nourrissent en filtrant l'eau grâce à leurs deux paires d'antennes (Enequist, 1949). *A contrario*, les Ampelisca auraient plutôt un régime alimentaire mixte, étant capables de s'alimenter de deux manières distinctes (Mills, 1967). La première consiste à utiliser leur deuxième paire d'antennes (A2) pour collecter les grains de sable à la surface du sédiment et les ramener à eux afin d'en retirer la nourriture associée à l'aide de leurs pièces buccales. La deuxième méthode, plus fréquente, consiste à créer un courant avec la deuxième paire d'antennes qui tournoient d'arrière en avant, et les pléopodes. Ce courant circule de la partie postérieure de l'animal vers les gnathopodes et les deux premières paires de périopodes pourvus de nombreuses soies plumeuses. Les particules s'accumulent sur ce filtre créé par les soies et sont ramenées à la bouche par les gnathopodes.

Les différents travaux menés sur la biologie des Ampeliscidae (Dauvin, 1984 ; Klein et al., 1975 ; Hastings, 1981 ; Bellan-Santini et Dauvin, 1988) ont mis en évidence des durées de vie très variables chez les Ampeliscidae: de quelques mois chez une espèce bivoltine comme *Ampelisca tenuicornis* jusqu'à 3 ans chez l'espèce boréale *Ampelisca macrocephala*. La durée du développement varie également chez une même espèce en fonction de la température (Dauvin, 1984). De même, plusieurs études (Klein et al., 1975 ; Hastings, 1981) ont mis en évidence que la durée et l'époque de la reproduction des espèces sont fortement influencées par la latitude. Il a ainsi été mis en évidence qu'*Ampelisca brevicornis* se reproduit toute l'année en Méditerranée, de mars à décembre à Arcachon et seulement de mai à septembre en mer d'Irlande (Bellan-Santini et Dauvin, 1988). Outre les variations observées sur les durées de vie, les Ampeliscidae présentent également des cycles reproducteurs très divers. En effet, les genres *Ampelisca* et *Byblis* présentent des cycles de vie univoltin (1 génération par an), bivoltin (deux générations par an) ou encore trivoltin (trois générations par an). Le cycle de vie biannuel (1 génération tous les deux ans) a également été mis en évidence chez les Ampeliscidae mais ce type de cycle reproducteur semble être rare pour les genres *Ampelisca* et *Byblis* et apparaît en revanche caractéristique du genre *Haploops*. Le mode d'incubation est le même pour tous les Ampeliscidae : les embryons sont incubés et se développent dans le marsupium des femelles qui est formé par les oostégites (expansions lamellaires portées par le coxopodite des péréiopodes). Néanmoins. il semble que certaines espèces d'Ampeliscidae (e.g. *Haploops abyssorum*) soient dépourvues d'oostégites et n'incubent pas leurs embryons dans le marsupium. Le développement chez les Ampeliscidae est direct comme chez tous les amphipodes et résulte en une absence de phase larvaire. La majorité des études portant sur la biologie des Ampeliscidae montre que les femelles meurent après que les embryons aient quitté le marsupium. Les mâles matures, quant à eux, meurent après l'accouplement après une courte vie pélagique (Mills, 1967 ; Sheader, 1977 ; Hastings, 1981).

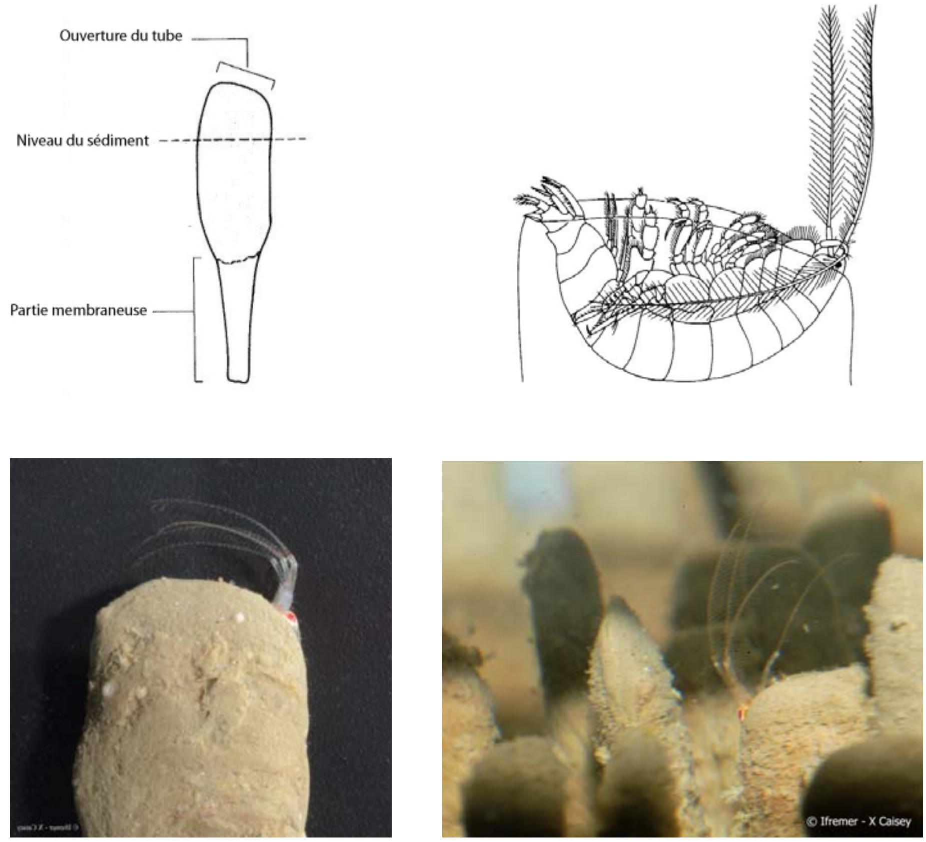

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Figure 3 : Les Ampeliscidae dans leur tube. (A) Tube d'Ampeliscidae ; (B) Schéma d'un individu du genre *Haploops* situé à l'extrémité de son tube en position dorsale ; (C et D) Photos d'un *Haploops* situé à l'ouverture de son tube, en position dorsale.

Bien qu'il soit relativement commun de trouver des Ampeliscidae sur les côtes de l'hémisphère nord, il est néanmoins beaucoup plus rare de trouver des peuplements dominées par les Ampeliscidae dont les densités avoisines ou dépassent le millier d'individus par m^2. Bellan-Santini et Dauvin (1988) ont recensé les peuplements à *Ampelisca* à l'échelle mondiale

(Tableau 2). Ainsi, des populations très denses d'*Ampelisca* ont été rapportées dans l'Atlantique Nord-Est, avec des densités pouvant atteindre 31 000 ind.m^{-2} en baie de Morlaix (*Ampelisca armoricana*), et dans les zones subtidales peu profondes de l'océan Atlantique Nord-Ouest, où des densités de respectivement 73 000 et 95 000 ind.m^{-2} ont été signalées pour *Ampelisca abdita* dans le Barnstable Harbor et dans la Jamaica bay (New York). D'autres peuplements à *Ampelisca* ont également été répertoriées dans le Pacifique avec des densités particulièrement importantes d'*Ampelisca agassizi* qui atteignent 135 000 ind.m^{-2} en Basse Californie (Mexique) et 41 000 ind.m^{-2} dans la Pachenay Bay au Canada.

En ce qui concerne les *Haploops*, ils sont également susceptibles de former des populations denses dans certaines zones subtidales de l'hémisphère Nord, notamment dans l'Øresund et le Kattegat (Suède) avec des densités allant jusqu'à 3000-4000 ind.m^{-2} (Petersen, 1913) (Fig. 4). Des peuplements similaires ont été trouvées dans le golfe de Clyde (Allen, 1953) et dans la partie nord du golfe de Gascogne (Glémarec, 1969; Ménesguen, 1980; Bellan-Santini et Dauvin, 1988). Ménesguen (1980) rapporte des densités moyennes de 3 200 ind.m^{-2} (max = 8 600 ind m^{-2}) en baie de Concarneau. Des populations moins denses ont été observées sur les fonds vaseux de la baie de Fundy (Canada) où les densités d'*Haploops fundiensis* oscillent entre 108 et 923 ind.m^{-2} avec une densité moyenne de 376 ind.m^{-2} (Wildish, 1984) et dans le Northumberland (Buchanan, 1963) où les densités d'*Haploops tubicola* avoisinent 600 individus.m^{-2}. *Haploops laevis* qui est relativement commun dans l'océan Arctique et dans le nord de l'océan Atlantique présente des densités de l'ordre de 400 ind.m^{-2} en mer de Sibérie orientale (Russie) (Gukov, 2011).

Le genre *Byblis* présente également de fortes densités au Japon (Sudo et Azeta, 1996) et dans le nord de la mer de Bering (Highsmith et Coyle, 1992) où les densités atteignent respectivement 4 100 et 1 250 ind.m^{-2}. Plus communément, les autres espèces d'Ampeliscidae sont présents à des densités plus faibles de l'ordre de quelques individus par m^{-2}.

Tableau 2: Données concernant les densités maximales atteintes lors des récoltes d'*Ampelisca* dans le monde. D'après Bellan-Santini et Dauvin (1988).

Espèce	Ind. m^{-2}	Lieu	Auteurs
Atlantique Nord-Est			
A. *armoricana*	31 494	Baie de Morlaix, Manche	Dauvin, 1979
A. *spinipes*	8 360	Yorkshire, Mer du Nord	Atkins, 1983
A. *sarsi*	24 000	Baie de Morlaix, Manche	Poggiale et Dauvin, 2001
A. *tenuicornis*	6 020	Rance Maritime, Manche	Dauvin, 1984
A. *tenuicornis*	20 000	Baie de Morlaix, Manche	Poggiale et Dauvin, 2001
A. *brevicornis*	1 334	Ile de Man, Mer d'Irlande	Hastings, 1981
A. *typica*	737	Baie de Morlaix, Manche	Bellan-Santini et Dauvin, 1988
Atlantique Nord-Ouest			
A. *abdita*	73 000	Barnstable Harbor	Mills, 1967
A. *abdita*	94 600	Jamaica Bay	Franz et Tanacredi, 1992
A. *agassizi*	8 900	Block Island	Steimle, 1982
Pacifique			
A. *agassizi*	135 000	Baja California, San Quintin	Oliver et al., 1983
A. *agassizi*	40 871	Pachenay Bay, Canada	Oliver et al., 1984
A. *macrocephala*	14 500	Mer du Japon	Deryugin et Somova, 1940
A. *araucana*	12 000	Golfe d'Arauca, Chili	Carrasco et Gallardo, 1983
A. *macrocephala*	8 903	Mer de Bering	Oliver et al., 1983

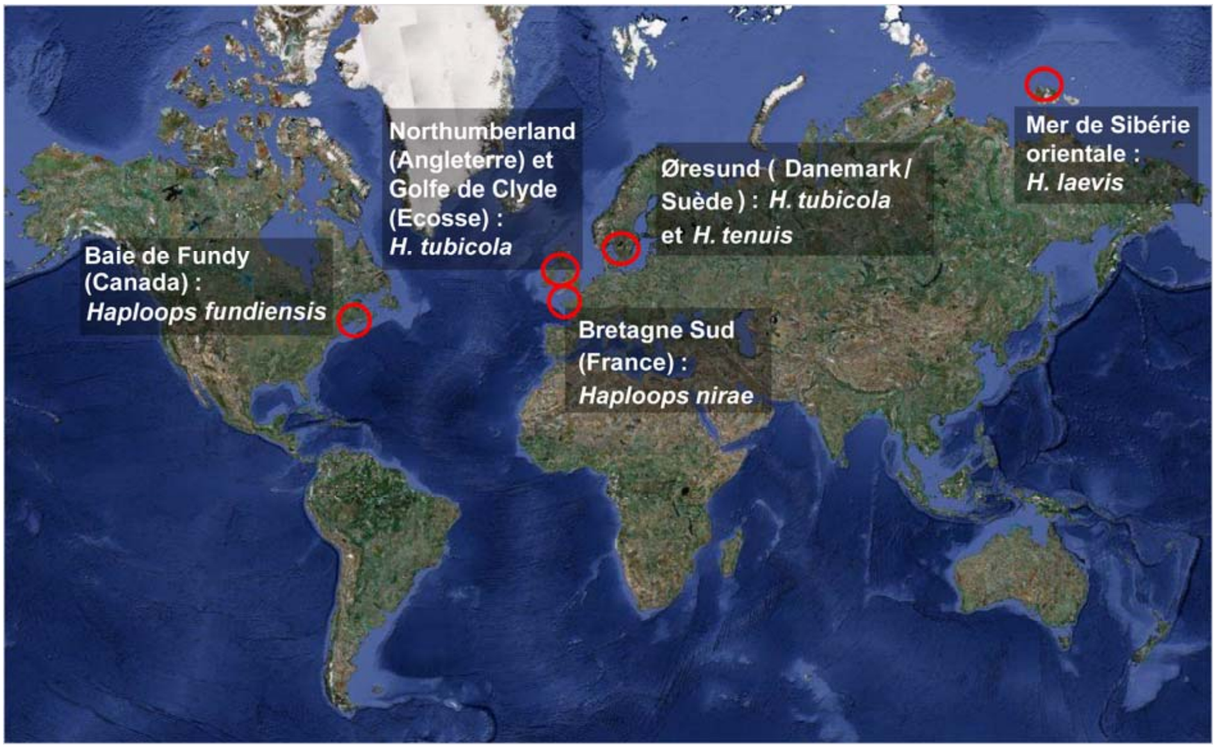

Figure 4 : Répartition des principaux peuplements à *Haploops* connues à l'échelle mondiale.

3.2. Dynamique temporelle

Alors que des peuplements à Ampeliscidés prospèrent dans plusieurs régions du globe, l'analyse de la dynamique temporelle de certaines d'entre elles a permis de montrer que les populations d'Ampeliscidés étaient l'objet de fluctuations d'abondances extrêmement spectaculaires en réponse à des modifications de la qualité du milieu.

Le biologiste Carl Georg Johannes Petersen, qui s'est attaché au début du XXe siècle à l'étude des peuplements benthiques dans le Kattegat, le Skagerrak et la mer du Nord entre 1910 et 1912, décrivit à partir de données quantitatives 7 peuplements benthiques principaux selon leurs espèces caractéristiques. Parmi ces peuplements figurait un peuplement à *Haploops* où cohabitaient deux espèces : *Haploops tubicola* et *Haploops tenuis*. Dans l'Øresund et le Kattegat, les densités d'*Haploops* allaient jusqu'à 3000-4000 ind.m^{-2} (Petersen, 1913, 1924). La revisite dans les années 1980 des stations échantillonnées par Petersen en 1910-1912 dans le Kattegat (Pearson et al., 1985) ainsi que dans l'Oslo Fjord et le Skagerrak (Rosenberg et al.,1987), selon un protocole d'échantillonnage rigoureusement identique à celui suivi par Petersen, a mis en évidence une quasi-disparition des *Haploops* et un remplacement du peuplement dominé par les *Haploops* par un peuplement où l'ophiure

Amphiura filiformis domine. Dans les années 1990, des résultats comparables ont été obtenus à la fois dans le Kattegat et dans l'Øresund comme en atteste l'examen des données obtenues en deux stations : la station P22 dans le Kattegat et la station HA dans l'Øresund (Göransson, 2002). Alors que les *Haploops* étaient le taxon dominant à la station P22 en 1910 avec des densités de 3 500 ind.m^{-2}, Göransson y observa en 1990 une diminution drastique des densités. Parallèlement à la disparition des *Haploops*, il observa une augmentation considérable des densités d'*Amphiura filiformis* de 0 ind.m^{-2} en 1910 à 1 000 ind.m^{-2} en 1990. De même, alors que les *Haploops* représentaient 15 % de la biomasse à la station P22 en 1910, *Amphiura filiformis* constituait 57 % de la biomasse à cette même station en 1990. Selon Göransson (2002), la station P22 que Petersen avait définie comme un peuplement à *Haploops* a été remplacé par un peuplement à *Amphiura filiformis*. Les modifications de la structure du peuplement à cette station sont telles que le pourcentage de similarité de la macrofaune benthique entre 1910-1912 et 1990 n'est que de 15%. A la station HA dans l'Øresund, un même déclin progressif des densités d'*Haploops* a été décrit entre 1910 et 2009 avec des densités proches de 4 000 ind.m^{-2} entre 1910 et 1946, 1500 ind.m^{-2} en 1992 et 100 ind.m^{-2} actuellement (Göransson et al., 2010). Les *Haploops* ont donc disparu sur de vastes superficies depuis plusieurs décennies dans les mers Danoises et ne maintiennent que des populations résiduelles très localisées dans l'Øresund.

Selon Göransson (2002), les changements structurels qui ont affecté la macrofaune benthique des eaux Danoises se sont produits au cours des dernières décennies. Le chalutage n'est probablement pas la cause de ces changements dans la mesure où il est interdit dans l'Øresund depuis 1932. Cependant, l'augmentation des apports en nutriments des eaux côtières et l'eutrophisation qui en a résulté durant ces dernières décennies pourrait être la cause principale de la dégradation des peuplements benthiques dans la région du Skagerrak-Kattegat-Øresund (Pearson et al., 1985 ; Rosenberg et al., 1987). En effet, une augmentation des apports en nutriments entraîne une sédimentation accrue du phytoplancton pouvant conduire à un manque d'oxygène pour la macrofaune benthique et à l'élimination de la faune benthique (Diaz et Rosenberg, 2008). Alors que les concentrations en oxygène dans les eaux de fond de l'Øresund étaient, durant les années 80, régulièrement au-dessus de 2 ml.l^{-1} (Göransson, 2002), un suivi réalisé entre 1998 et 2009 montrent qu'elles tombent régulièrement sous le seuil des 2 ml.l^{-1} à 30 m de profondeur (Fig. 5) (Göransson et al., 2010).

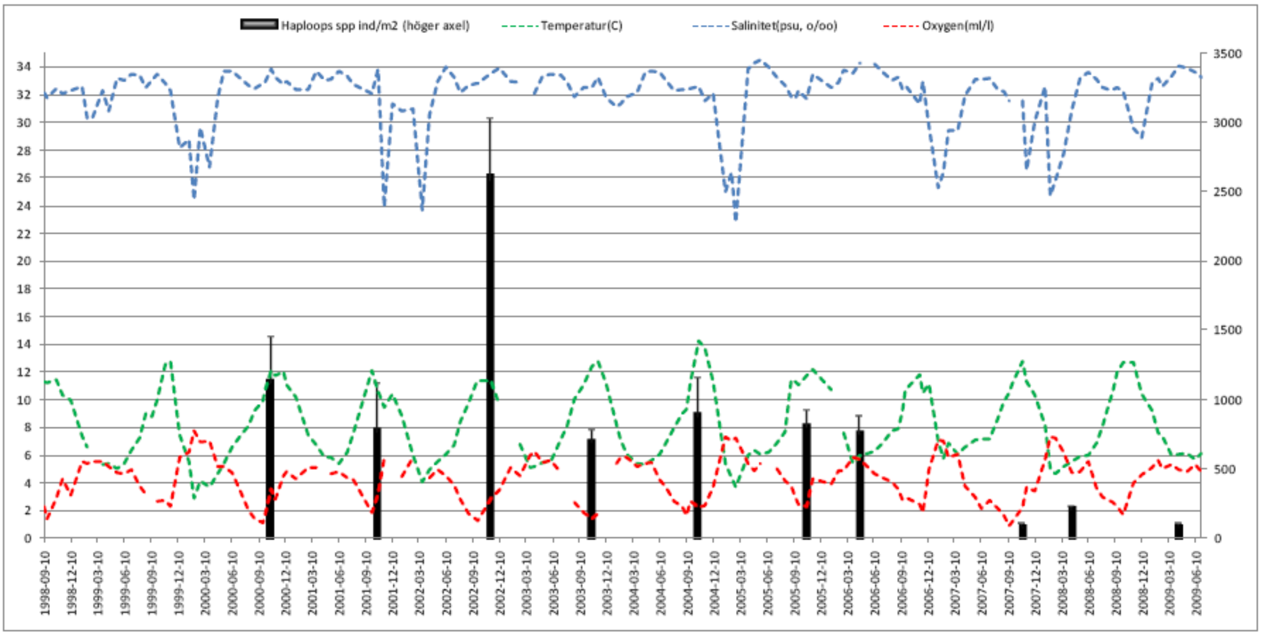

Figure 5 : Evolution entre 1998 et 2009 des densités d'*Haploops* spp. (ind.m^{-2}) et des paramètres physico-chimiques à 30 m de profondeur dans l'Øresund (station HA). D'après Göransson (2010).

Pour des raisons tout autres, les populations de plusieurs espèces d'*Ampelisca* du peuplement des sables fins envasés de la baie de Morlaix ont également vu leurs densités fortement fluctuer. Alors que leurs densités atteignait 40 000 ind.m^{-2} en 1977, la pollution par les hydrocarbures du pétrolier Amoco Cadiz en mars 1978 entraîna la disparition totale de cinq des six espèces du genre *Ampelisca* présentes (i.e. *A. armoricana*, *A. brevicornis*, *A. spinipes*, *A. tenuicornis* et *A. typica*) et la réduction drastique des abondances de la seule espèce survivante (i.e. *A. sarsi*) dont les effectifs ont décru de 99,4 % en avril 1978 (Dauvin, 1979, 1984). Ainsi, alors que la densité annuelle moyenne des *Ampelisca* était de 18 700 ind.m^{-2} en 1977-1978, elle chuta à 36 ind.m^{-2} après la pollution en 1978-1979.

La recolonisation du peuplement par les *Ampelisca* s'est faite de façon graduelle par quelques individus (Fig. 6). Alors qu'*Ampelisca spinipes* a de nouveau été échantillonné dès l'automne 1978, *Ampelisca tenuicornis* n'a été rapporté sur la zone qu'en décembre 1985 soit près de 8 ans après sa disparition. Comme le suggère Dauvin (1987), la réimplantation des *Ampelisca* dans les sables fins de la baie de Morlaix s'est avérée lente et difficile compte tenu des stratégies démographiques des différentes espèces d'*Ampelisca* (i.e. absence de phase larvaire, faible fécondité) et de l'éloignement des populations pouvant servir de base de repeuplement. Des abondances équivalentes à celles observées (i.e. > 40 000 ind.m^{-2}) avant la pollution n'ont été observées qu'à partir du milieu des années 90 (Dauvin et al., 1993 ;

Dauvin, 1998). Les différences inter-spécifiques dans les taux de recolonisation peuvent s'expliquer par des sensibilités différentes des diverses espèces à la pollution et à la température, et par des varaitions interspécifiques du nombre de générations par an (Poggiale et Dauvin, 2001). Pour des raisons encore inexpliquées, si ce n'est une réponse non linéaire des peuplements benthiques à des variations progressives des conditions environnementales, les densités d'*Ampelisca* en baie de Morlaix ont de nouveau brutalement chuté depuis 2005 et se maintiennent depuis à des valeurs maximales de quelques centaines d'individus par m^2.

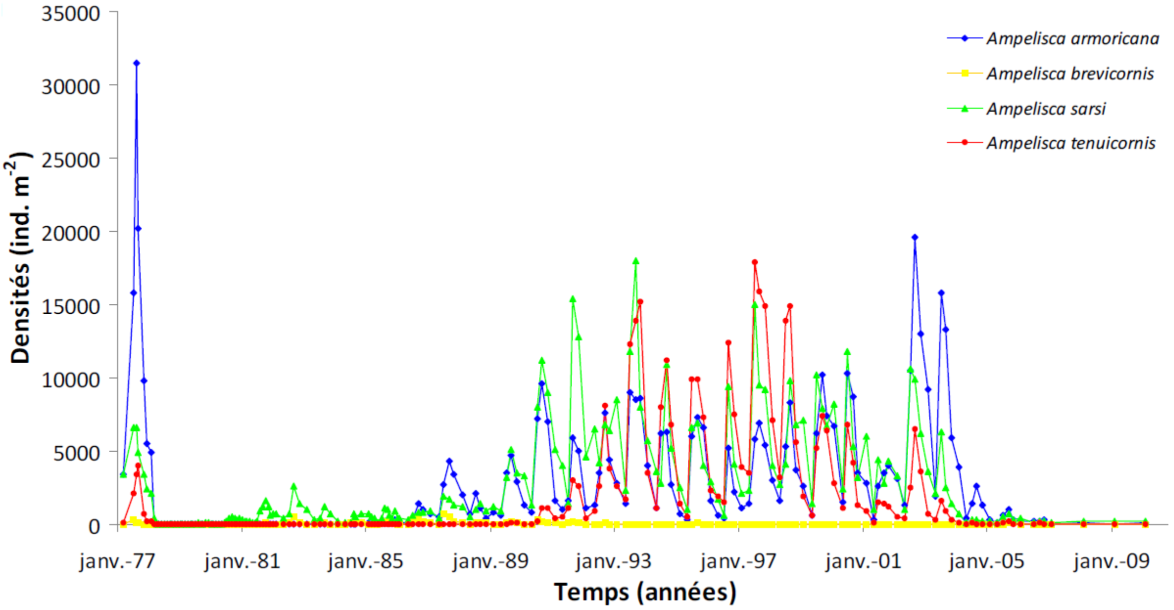

Figure 6 : Evolution temporelle des densités de 4 espèces d'*Ampelisca* dans les sables fins plus ou moins envasés de la baie de Morlaix entre 1977 et 2010. D'après Gaudin (2012).

D'autres exemples moins bien documentés de variations importantes des abondances d'Ampeliscidés ont également été rapportés dans diverses régions côtières en réponse à une dégradation de l'environnement ou à une modification de l'intensité des interactions biotiques. Dans le nord de la mer Adriatique, des variations intra- et inter-annuelles des densités d'*Ampelisca diadema* ont été communément signalées au cours des dernières années en réponse à différentes perturbations environnementales, comme des variations des apports d'eaux douces (Occhipinti-Ambrogi et al., 2005) ou des crises hypoxiques liées à l'eutrophisation et des températures anormalement élevées (Simonini et al., 2004 ; N'Siala et al., 2008). En mer de Béring, la prédation par la baleine *Eschrichtius robustus* contrôlerait la densité de plusieurs populations de crustacés amphipodes des genres *Byblis* et *Ampelisca* (Coyle et al., 2007). L'augmentation des populations de baleine grise d'environ 4 % au cours des dernières décennies serait la cause d'une baisse des biomasses d'Ampeliscidés d'environ

50% sur une période allant de 1986-1988 à 2002-2003. Coyle et al. (2007) ont ainsi estimé que les baleines consommaient 10 à 20 % de la production annuelle des amphipodes arctiques dont les faibles taux de croissance et les longs temps de génération réduisent les capacités de réponses à cette nouvelle pression.

Encadré 2 : Quelques définitions

Assemblage : Groupe d'espèces (populations) vivant dans un lieu ou un environnement déterminé, sans aucune notion d'interrelation entre les espèces (Pérès, 1982).

Communauté : *Sensu stricto*, le terme communauté est un synonyme de biocénose. Néanmoins, ce terme fait souvent référence à une entité de la biocénose comme les communautés macrobenthiques (définies quantitativement, à travers l'abondance, la dominance ou la constance), ou des communautés fonctionnelles (définies selon les groupes trophiques d'espèces benthiques) (Dauvin et al., 2008).

Peuplement : Ensemble des populations d'un même niveau taxonomique qui vivent dans le même biotope et qui crée une entité relativement stable et homogène étendue sur une large aire (par exemple: le peuplement des bivalves des sables fins infralittoraux) (Dauvin et al., 2008).

Habitat : Lieu regroupant l'ensemble des conditions environnementales dans lequel une espèce, une population ou une communauté peut survivre et se maintenir à l'état spontané (Carpentier et al., 2005).

4. Les peuplements à *Haploops* en Bretagne Sud

4.1. Evolution temporelle des peuplements à Haploops depuis les années 60

La première bionomie benthique des baies de Bretagne Sud établie à partir de missions réalisées de 1964 à 1966 a mis en évidence pour la première fois la présence de peuplements à *Haploops* sur les côtes bretonnes, en baie de Concarneau au N-E des Glénan, en baie de Vilaine et dans l'avant fosse du Croisic (Glémarec, 1969) (Fig. 7). L'examen de cartographies plus récentes et un travail de recherche bibliographique ont permis d'inventorier les zones où des peuplements à *Haploops* sont actuellement répertoriés en Bretagne Sud. Bien que des peuplements à *Haploops* aient été essentiellement rapportées en baie de Concarneau et en baie de Vilaine, d'autres sites hébergent également ces amphipodes, tels qu'une large zone autour du plateau du Four (données Natura 2000), l'entrée du chenal de la Loire et la zone entre l'île de Groix et la presqu'île de Quiberon (Barillé, comm. pers.) (Fig. 8). Par ailleurs, lors de son étude des fonds meubles du plateau continental Ouest-armoricain de 1963 à 1968, Toulemont (1972) a rapporté la présence d'un peuplement à *Brissopsis* et *Haploops* au large de la pointe de Penmarc'h. Cette signalisation est néanmoins ancienne et n'a fait l'objet d'aucune vérification depuis. Au regard des données disponibles à ce jour, la distribution des *Haploops* sur la façade Atlantique française s'étendrait actuellement de la pointe de Penmarc'h jusqu'à l'estuaire de la Loire.

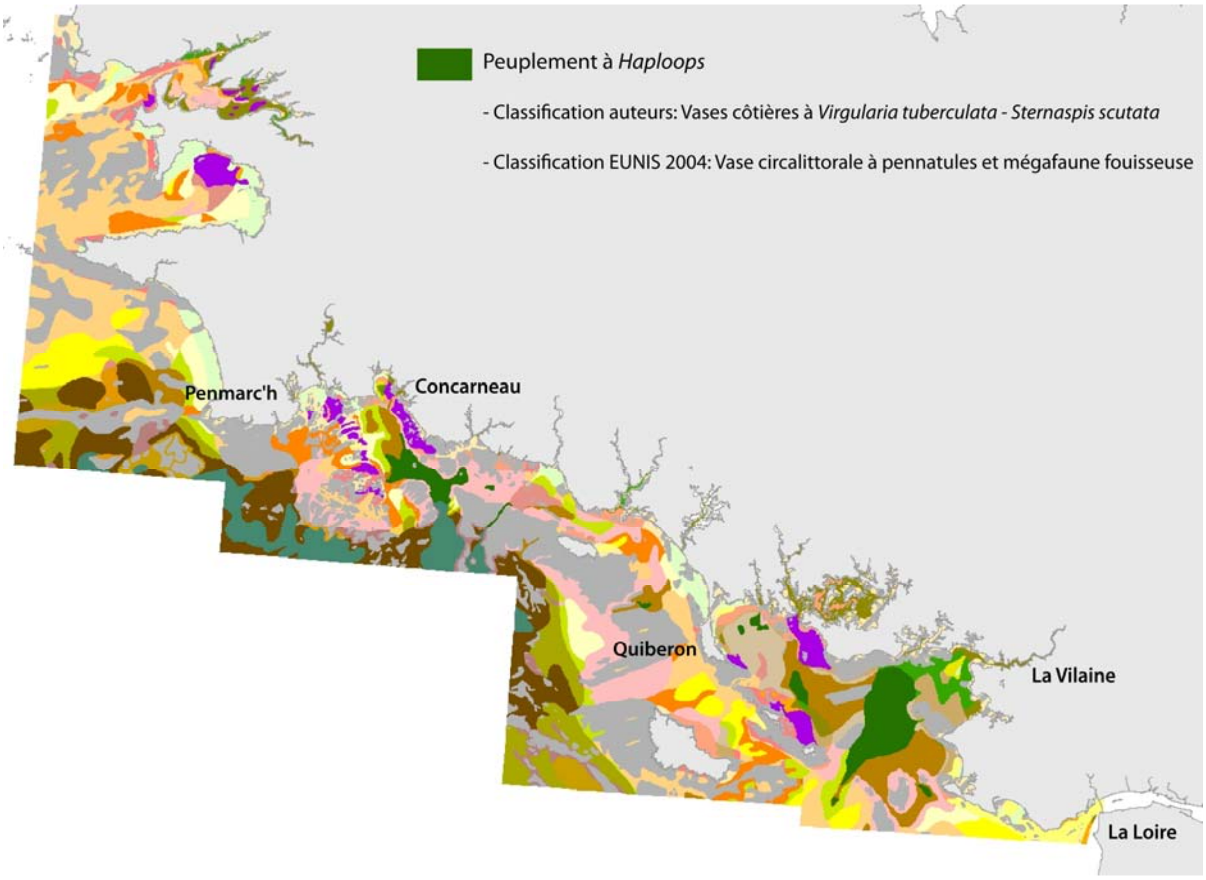

Figure 7 : Carte de distribution des peuplements benthiques du sud Bretagne à la fin des années 1960. D'après la synthèse des cartes de l'atlas de Chassé et Glémarec (1976). Le peuplement à *Haploops* est figuré en vert. D'après Chassé et Glémarec (1976) ce peuplement est nommé Vases côtières à *Virgularia tuberculata –Sternaspis scutata*. D'après la classification EUNIS 2004, cet habitat est nommé Vase circalittorale à pennatules et mégafaune fouisseuese. Pour la légende détaillée : voir site http://www.rebent.org/cartographie/index.php

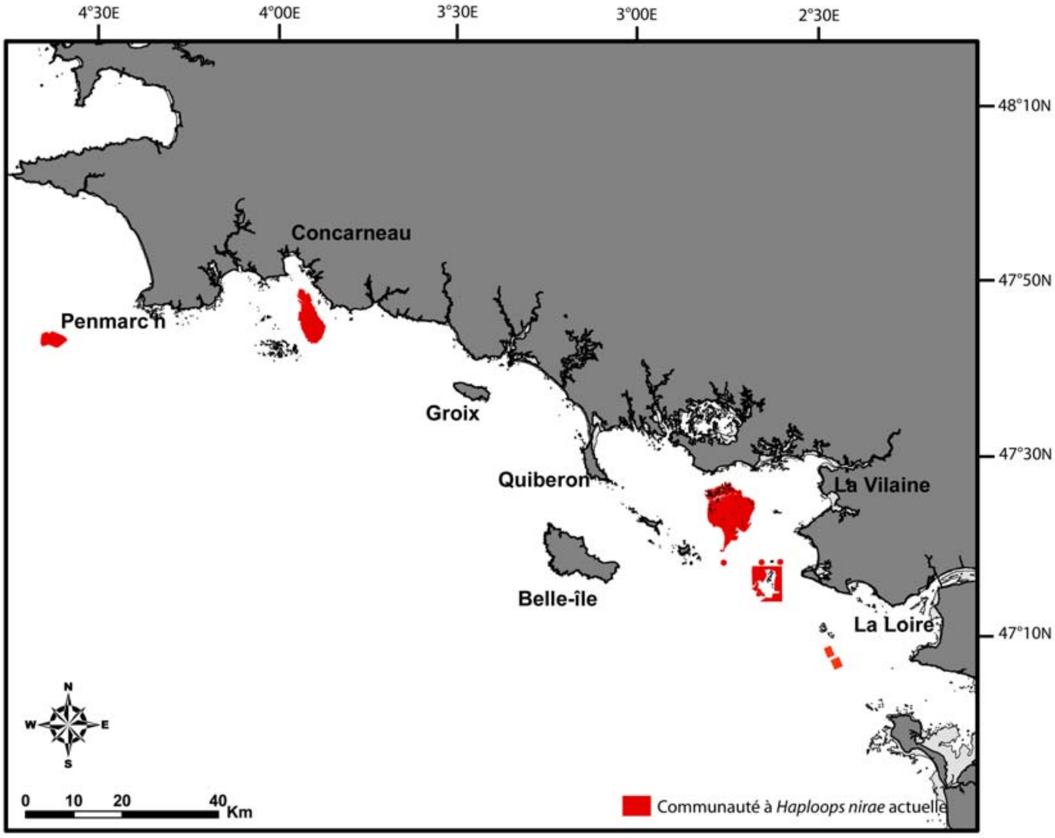

Figure 8 : Zones où ont été signalés des peuplements à *Haploops* à l'échelle du littoral de la Bretagne Sud. D'après les données de Toulemont (1972), Ehrhold et al. (2006), Ehrhold et al. (2007) et données Natura 2000.

La baie de Concarneau constitue l'extrémité occidentale de la dépression prélittorale sud-armoricaine (Delanoë et Pinot, 1977). Son fond est relativement plat et tapissé entre 15 et 35 mètres de profondeur par des vases et des sables envasés à l'abri des houles dominantes d'ouest, formé par l'archipel des Glénan et les Moutons (Fig. 9). En 1964, les peuplements benthiques de la baie se répartissaient d'Ouest en Est suivant le gradient sédimentaire. Faisant suite aux sables fins situés au pied des massifs rocheux, des sables fins envasés hébergeaient un peuplement de sables fins à *Amphiura filiformis* puis un peuplement de vases sableuses à *Maldane glebifex*. Au centre de la vasière, entre la pointe de Trévignon et les Glénan, dans le secteur le plus abrité de la baie, des populations très denses d'*Haploops,* considéré alors comme *Haploops tubicola*, formaient une enclave au sein du peuplement à *Maldane*. Les densités d'*Haploops* étaient alors de 2000 à 5000 ind.m^{-2} (Fig. 10).

Dix années plus tard, en 1974, l'essentiel du peuplement à *Maldane* avait fait place à un peuplement à *Nucula turgida-Abra alba*, caractérisant non plus des vases sableuses mais des vases molles, tandis que les populations d'*Haploops* avaient colonisé vers le nord une grande partie des vases à *Maldane* (Ménesguen, 1980). En 1977, une nouvelle couverture de la zone confirmait les évolutions observées en 1974 avec une migration vers le nord des *Haploops* et un net déclin des populations à *Maldane* (Fig. 10). Entre 1983 et 1997, de nouveaux prélèvements ont montré une relative stagnation de la distribution des *Haploops* et la prédominance d'*Amphiura filiformis* sur les anciennes zones à *Maldane* (Glémarec et Grall, 2003).

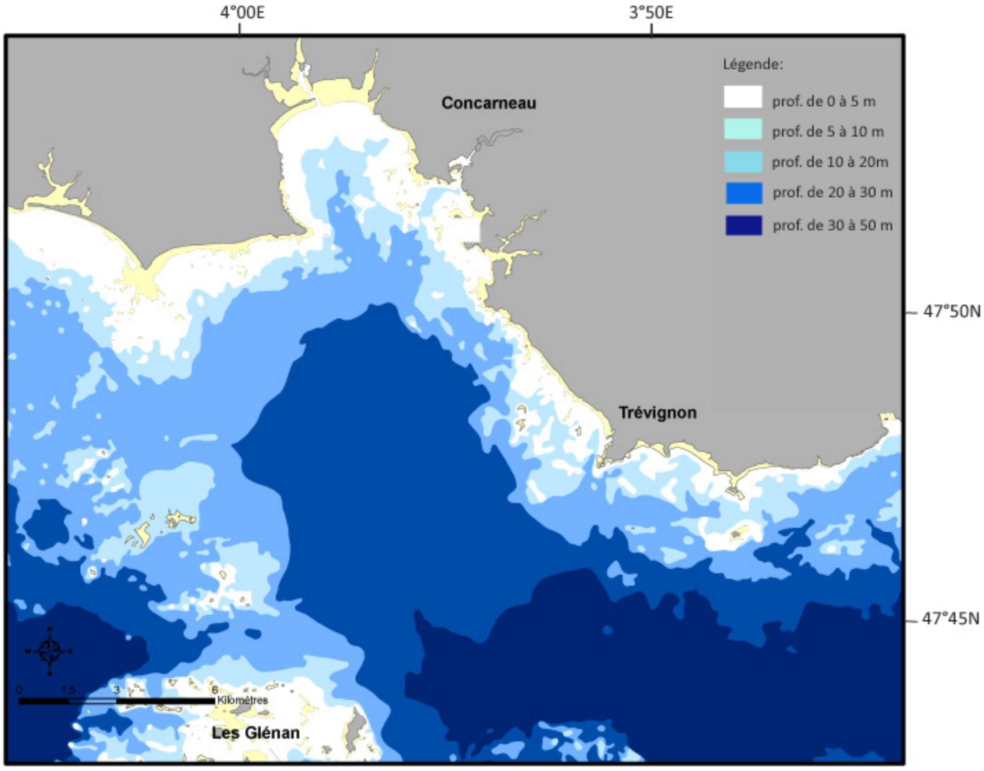

Figure 9 : Carte bathymétrique de la baie de Concarneau

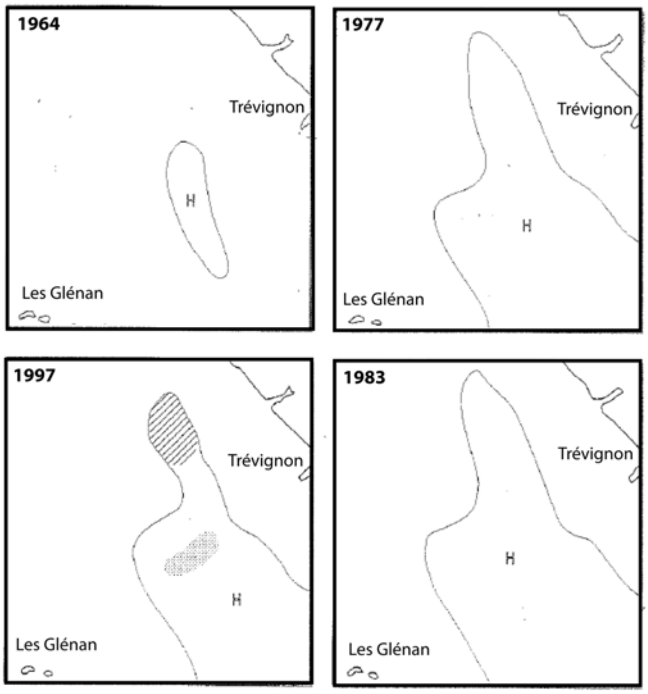

Figure 10 : Distribution des populations d'*Haploops* (H) en 1964, en 1977, en 1983 et en 1997 entre la pointe de Trévignon et l'archipel des Glénan. La zone hachurée en 1997 correspond à la zone de densités maximales d'*Haploops* tandis que la zone en pointillés est dépourvue d'*Haploops*. D'après Glémarec et Grall (2003).

Une cartographie récente des peuplements benthiques de la baie de Concarneau effectuée dans le cadre du REBENT montre que les fonds sablo-vaseux de la baie sont actuellement occupés par 4 peuplements (Ehrhold et al., 2006) : les sables envasés à *Owenia fusiformis* situés à l'ouest de la baie, près des Glénan, les vases sableuses à *Amphiura filiformis* situées plus au nord, les vases molles à *Sternaspis scutata,* et enfin les vases consolidées à *Haploops* (Fig. 11). Les surfaces colonisées par les *Haploops* dépassent désormais 3000 ha. La comparaison avec les cartographies réalisées par Glémarec dans les années 1960 et Ménesguen dans les années 1970 permet de visualiser l'extension des zones à *Haploops* (Fig. 12). Contrairement aux affirmations de Glémarec et Grall (2003) qui notaient une stagnation de l'extension des *Haploops* en baie de Concarneau après 1977, la comparaison de la cartographie récente réalisée par Ehrhold et al. (2006) avec celle de Ménesguen (1980) (Fig. 12) révèle une poursuite de l'extension des peuplements à *Haploops* vers le nord de la baie entre 1980 et 2003. Il est à noter que Ménesguen n'a pas échantillonné le sud de la baie de Concarneau qui hébergeait pourtant déjà en 1964 des peuplements à *Haploops*. La zone occupée par les *Haploops* en 1980 est donc probablement sous-estimée.

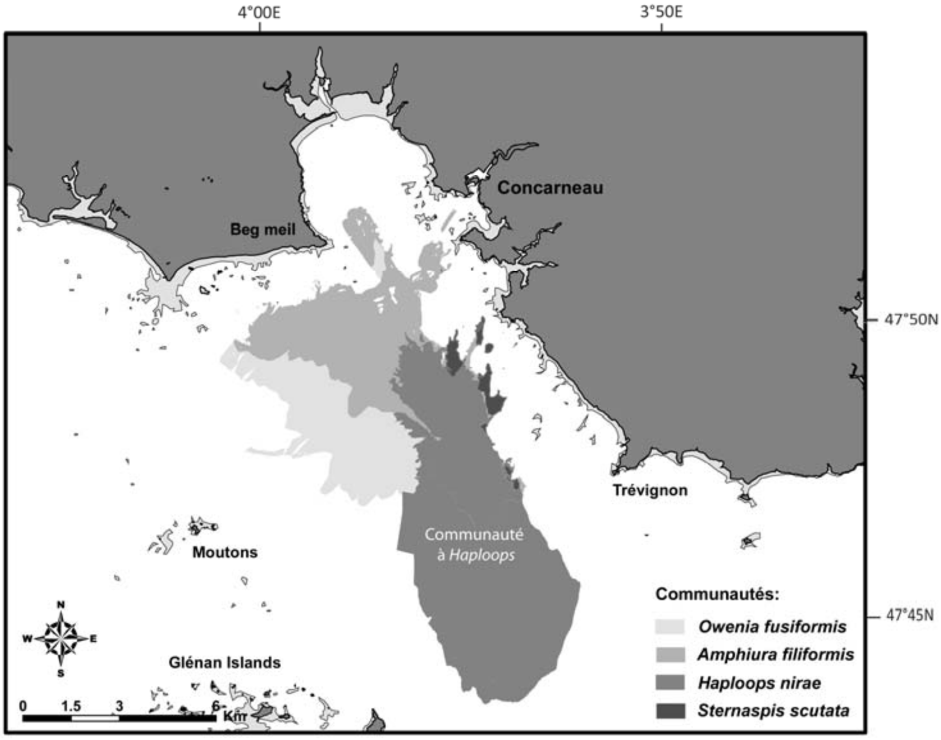

Figure 11 : Cartographie actuelle des peuplements macrobenthiques de la baie de Concarneau. D'après Ehrhold et al. (2006).

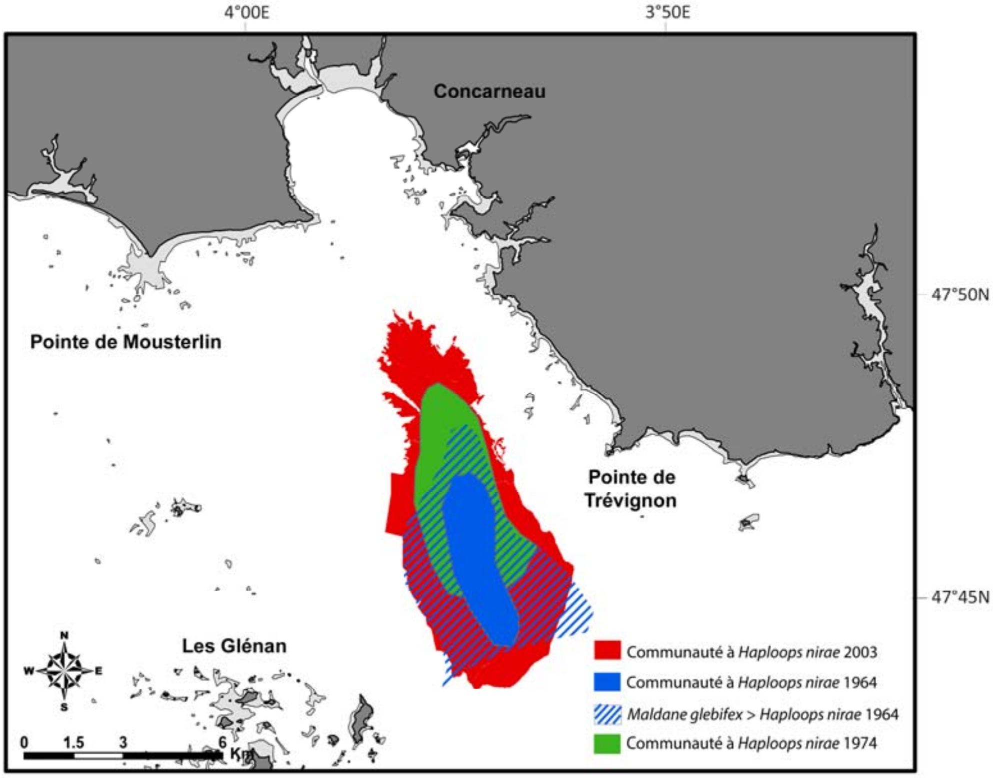

Figure 12 : Comparaison de la répartition actuelle des peuplements à *Haploops* en baie de Concarneau avec la cartographie réalisée par Glémarec en 1964 et par Ménesguen en 1974.

En 1962, la baie de Vilaine était composée d'une vasière très étendue dont une grande partie était habitée par un peuplement à *Sternaspis scutata*, *Virgularia tuberculata* et *Amphiura filiformis* tandis que des vases sableuses situées à l'Ouest et au Sud-Est de la baie, à l'abri des massifs rocheux, hébergaient un peuplement à *Maldane* et *Haploops*. La construction du barrage d'Arzal en 1970 sur la Vilaine a entraîné de profondes modifications de la distribution des peuplements macrobenthiques au niveau du delta de la Vilaine mais également au centre de la baie : les *Haploops* ont colonisé la vasière centrale, précédemment occupée par le peuplement à *Sternaspis* et *Virgularia* et le peuplement à *Maldane* a régressé (Le Bris, 1988). De manière analogue aux observations faites en baie de Concarneau, l'évolution des peuplements benthiques en baie de Vilaine révèlait une augmentation générale de l'aire de répartition des *Haploops* et des modifications importantes de la distribution des peuplements.

Actuellement, les fonds vaseux de la baie de Vilaine sont occupés par trois peuplements benthiques majeures : les vases molles à *Sternaspis scutata* (au centre de la baie), les sables envasés à *Owenia fusiformis* plus à l'est, et les vases consolidées à *Haploops* (Ehrhold et al., 2007) (Fig. 13 et Fig. 14 pour la bathymétrie). La présence du plateau de la recherche et la présence de « langues » de vases au sein de l'aire de répartition des *Haploops* rend cette zone beaucoup moins homogène en termes de densités d'*Haploops* que la baie de Concarneau.

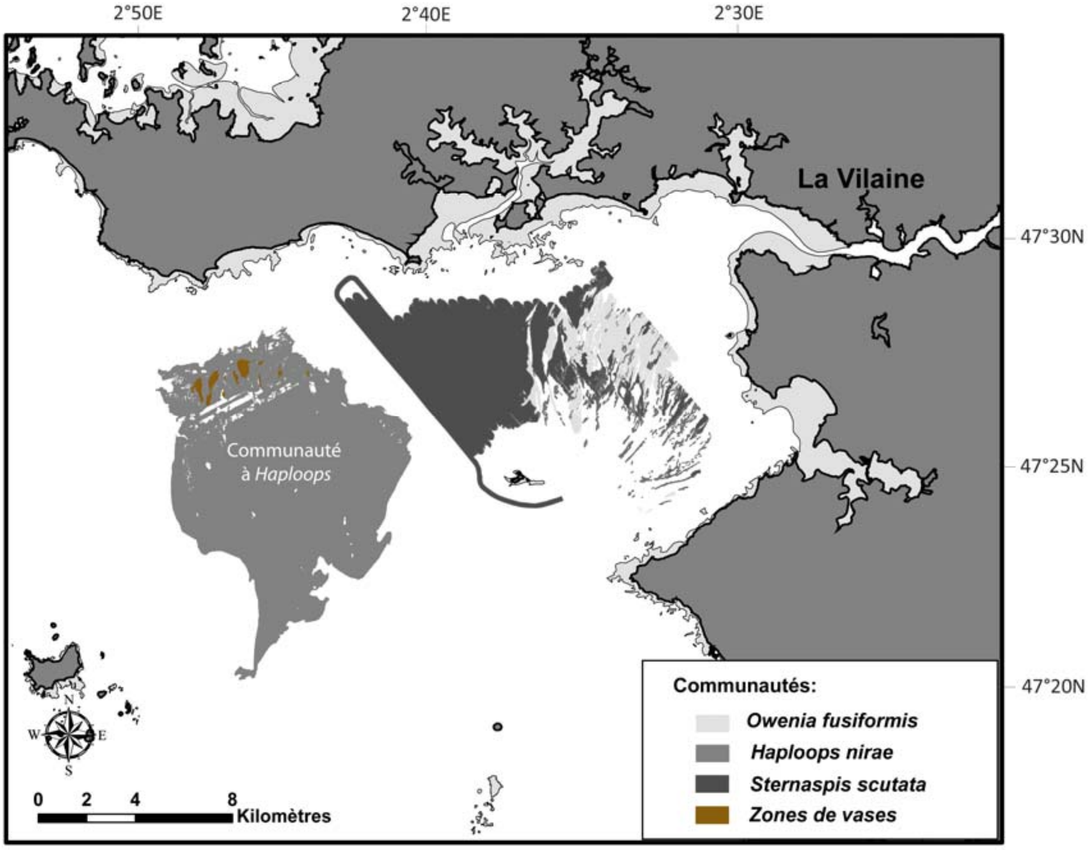

Figure 13 : Cartographie actuelle des peuplements benthiques de la baie de Vilaine. D'après Ehrhold et al. (2007).

En baie de Vilaine, la superposition des cartographies actuelles avec les données historiques révèle que les changements entre 1962 et 2003 ont été très importants (Fig. 15). Cependant, la comparaison avec la carte établie par Le Bris (1988) à partir d'observations réalisées en 1985 montre que les principaux changements dans la répartition des *Haploops* sont antérieurs à cette date. Alors que l'évolution des peuplements à *Haploops* en Bretagne Sud indique une augmentation générale de l'aire de répartition des *Haploops* le long des côtes bretonnes, en particulier entre les années 60 et les années 80, des ouvrages anciens tels que ceux de Bonnier (1887) et ceux de Chevreux (1900) mentionnent la présence assez commune des *Haploops* (i.e. *Haploops tubicola*) en Bretagne sud, plus précisément en baie de Concarneau et au Croisic, à la fin du XIXème siècle.

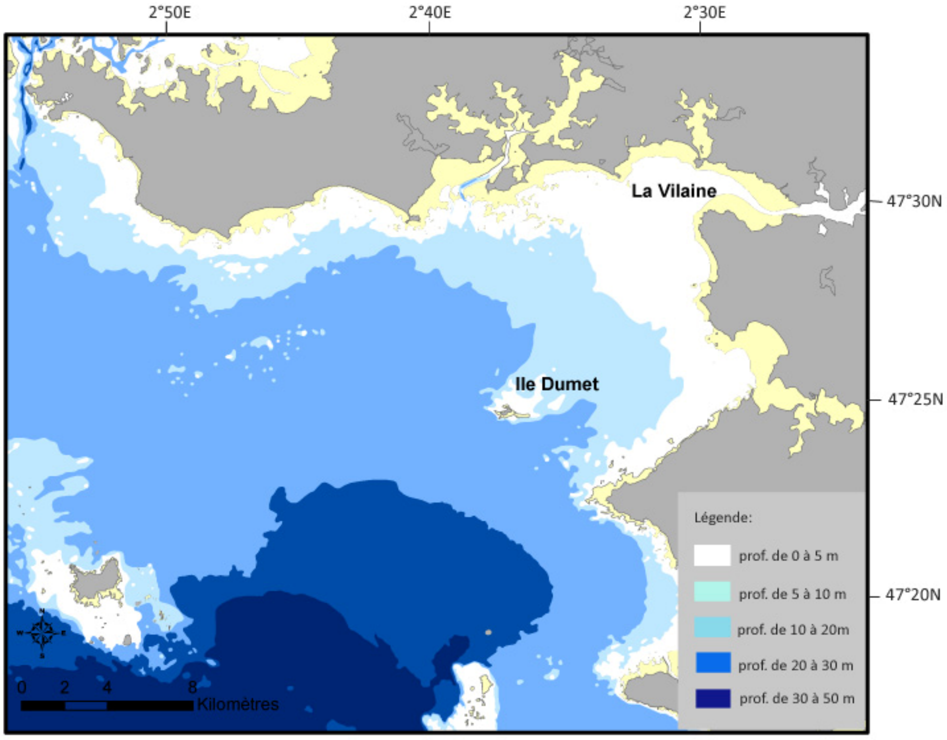

Figure 14 : Carte bathymétrique de la baie de Vilaine.

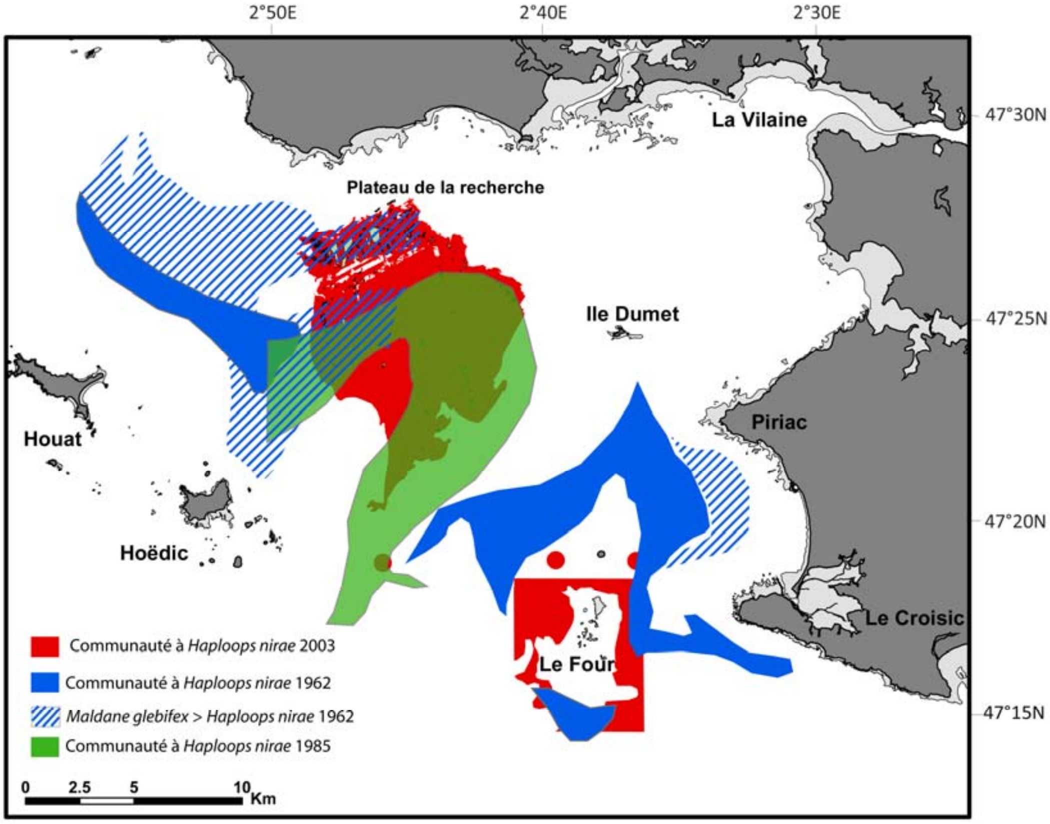

Figure 15 : Comparaison de la répartition actuelle des peuplements à *Haploops* en baie de Vilaine avec la cartographie réalisée par Glémarec en 1962 et Le Bris en 1985.

4.2. Les modèles de successions écologiques en Bretagne Sud

Afin d'expliquer les modifications importantes de la distribution des peuplements benthiques en baie de Concarneau et en baie de Vilaine depuis le début des années 60, Glémarec et collaborateurs portèrent un grand intérêt sur les dynamiques successionnelles des peuplements et proposèrent un scénario d'évolution basé sur les comportements des organismes « constructeurs » et les modifications des conditions environnementales (Glémarec et al., 1986; Glémarec et Grall, 2003).

Pour expliquer la colonisation des zones à *Maldane* par les *Haploops* en baie Concarneau, ces auteurs suggèrent que les *Maldane* qui construisent de larges tubes cylindriques de vase compactée consolident le sédiment. Cette transformation du sédiment favoriserait alors l'implantation des *Haploops* et inhiberait le propre développement de leur population, correspondant ainsi au modèle de facilitation parmi les modèles de succession définis par Connell et Slatyer (1977). D'autre part, Glémarec et al (1986) indiquent que l'installation des *Haploops* favorise à son tour l'installation (1) d'une épifaune vagile composée d'ophiures *Ophiothrix fragilis*, de crabes, de pagures en provenance des terrasses de maërl voisines et, (2) d'une endofaune caractéristique de graviers hétérogènes telle que la palourde rose *Polititapes virgineus* (Fig. 16). Néanmoins, certaines données historiques ont montré que les *Haploops* peuvent envahir des vases molles en l'absence préalable de *Maldane* (i.e. en Baie de Vilaine), suggérant qu'une telle succession ne constitue pas une étape obligatoire au développement des *Haploops* (Glémarec et al., 1986).

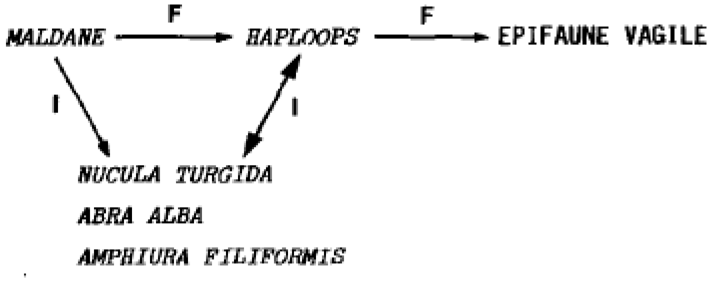

Figure 16 : Séquences possibles de successions écologiques dans les sédiments envasés des baies bretonnes : I modèle d'inhibition, F modèle de facilitation. D'après Glémarec et al. (1986).

En baie de Concarneau, les *Haploops* seraient stoppés dans leur extension géographique vers le nord par la présence de bivalves déposivores tels que *Nucula turgida* et *Abra alba* ou de l'ophiure *Amphiura filiformis* qui maintiennent une certaine fluidité de la surface sédimentaire. Selon, Glémarec et al. (1986), ce schéma correspond au modèle d'inhibition de Connell et Slatyer (1977).

Bien que le modèle de facilitation suggéré par Glémarec et al. (1986) puisse potentiellement expliquer la quasi disparition des *Maldane* au profit des *Haploops*, les populations de *Maldane* ont néanmoins décliné dans des zones qui n'ont pas été colonisées par la suite par les *Haploops* mais où se sont installés des bivalves déposivores et l'ophiuride *Amphiura filiformis*. En plus de l'action des organismes sur les propriétés du sédiment, une cause allogénique pourrait être responsable de ce déclin. *Maldane glebifex* étant une espèce d'affinité méridionale en limite nord de distribution en Bretagne sud, le réchauffement de la fin des années 50 aurait pu favoriser le développement des *Maldane* tandis que le refroidissement intervenu après 1962 serait la cause de leur déclin. Selon cette hypothèse climatique, la hausse très significative des températures observée depuis le milieu des années 1980 aurait dû être propice au développement des *Maldane*.

4.3. Un environnement sédimentaire particulier

Une particularité structurale de l'habitat à *Haploops* dans le sud Bretagne est son association très étroite avec la présence de pockmarks, dépressions sédimentaires en forme de cratères qui correspondent à des figures d'échappement de fluides en surface, vraisemblablement du méthane biogénique (Ehrhold et al. 2007). En baie de Concarneau, le champ de pockmarks semble suivre en surface les paléo-chenaux décrits par Menier (2003) et Delanoë et Pinot (1977). Les densités les plus fortes sont de l'ordre de 90 pockmarks pour 1 hectare, voire exceptionnellement 150 au sein de couloirs en bordure du champ ou dans la partie médiane. Celles-ci sont très supérieures à celles mentionnées dans les travaux de synthèse se rapportant à ce type de figure (Ferrin et al., 2003, Rogers et al., 2006). Si la forme sub-circulaire à elliptique est la plus fréquente, les contours peuvent devenir localement plus complexes par coalescence de pockmarks de tailles intermédiaires. Disposés de façon aléatoire et rarement organisés en chapelets, leur diamètre est variable, de moins d'1 m à 35 m au maximum. Leurs profondeurs sont modestes, de l'ordre de quelques dizaines de cm et dépassent rarement 2 m. Ces champs de pockmarks seraient d'une origine récente comme le suggèrent plusieurs indices (Ehrhold et al. 2007) :

- La forme circulaire de certains d'entre eux avec des contours nets, caractérise une géométrie qui n'a pas encore été effacée ou étirée par les courants ;
- Les profils de sismique réflexion révèlent occasionnellement dans la colonne d'eau sus-jacente, des panaches acoustiques pouvant indiquer localement la présence d'expulsion de gaz ;
- Certains cratères présentent un faciès oeillet qui correspond à la formation de pockmarks de plus petite taille au sein même de pockmarks plus anciens ;
- Des cratères sont scellés par une couche de vase fluide alors qu'à proximité, d'autres présentent des dépressions révélant une mise en place postérieure à l'épisode de dépôt de vase ;
- Des observations en plongée suggèrent que certains cratères sont totalement dépourvus de macrofaune benthique.

Les pockmarks sont des figures observées dans de nombreuses mers (ex : mer du Nord, mer de Béring, mer de Barents) et dans différents contextes géomorphologiques (ex : plateau, talus, fjord) (Hovland et Judd, 1988). Ils sont très variables en taille (de moins de 1 m à plus de 4 km) comme en profondeur (moins de 1 à plus de 200 m). Ces structures instables qui complexifient la topographie du fond créent des conditions environnementales originales susceptibles d'influencer la structure des peuplements benthiques. En mer du Nord, des pockmarks de grande taille (plus de 100 m de diamètre) et peu denses (moins de 30 par km²) possèdent une biodiversité bien supérieure à celle des fonds environnants (Hovland et Judd, 1988) et sont caractérisés par deux espèces possédant des bactéries endosymbiotiques sulfato-oxydantes : le bivalve *Thyasira sarsi* et le nématode *Astomonema sp.* (Dando et al., 1991). En Baie de Fundy où les pockmarks sont plus petits (entre 1 et 100 m de diamètre) et plus denses (plus de 30 par km²), certains pockmarks possèdent une faune à l'équilibre identique à celle du milieu environnant alors que d'autres ont une faune témoignant d'un milieu plus instable et perturbé (Wildish et al., 2008). Dans le fjord d'Oslo, la faune des pockmarks ne se différencie que faiblement de celle de la faune environnante, non pas en terme de composition faunistique mais seulement en termes d'abondances relatives des différents taxons : les espèces les plus abondantes dans les pockmarks (e.g. *Terebellides stroemi*, *Heteromastus filiformis*) sont des espèces moins tolérantes aux perturbations que les espèces dominantes à l'extérieur des pockmarks (e.g. *Diplocirrus glaucus*, *Chaetozone setosa*) (Webb et al., 2009).

En baie de Concarneau, les origines de l'association entre les pockmarks et l'habitat à *Haploops* et les liens de causalité restent à comprendre. En particulier, se posent les questions de l'influence des pockmarks sur l'expansion du peuplement à *Haploops* et sur les caractéristiques à petite échelle des peuplements.

4.4. Quelle espèce d'Haploops en Bretagne Sud?

Comme l'ont souligné Dauvin et Belllan-Santini (1990), la séparation des différentes espèces du genre *Haploops* sur des critères morphologiques est extrêmement difficile en raison de fortes similitudes morphologiques entre espèces. Jusqu'à récemment, les individus présents en Bretagne Sud ont été rapportés comme appartenant à l'espèce *Haploops tubicola* (Glémarec, 1969 ; Ménesguen, 1980 ; Le Bris, 1988 ; Le Bris et Glémarec 1996). Pourtant, dès 1976, Kaim-Malka avait décrit une nouvelle espèce (i.e. *Haploops nirae*) qui se différenciait d'*Haploops tubicola* principalement par la présence d'une deuxième paire de cornées assez difficile à observer (Fig. 17) (Kaim-Malka, 1976). Cette nouvelle description se basait sur des échantillons principalement récoltés dans le Golfe de Marseille (entre -61 et -200 m de profondeur) et dans le Golfe de Fos (entre -100 et -320 m de profondeur), mais aussi sur le ré-examen de matériels provenant de la collection de Chevreux collectés en 1882 sur la côte océanique du Maroc, au Croisic et en baie de Concarneau, et de celle du musée de Vérone concernant les côtes d'Israël. Alors que les organismes provenant de ces deux collections avaient été initialement identifiés comme appartenant à l'espèce *Haploops tubicola*, Kaim-Malka attribua ces organismes à l'espèce *Haploops nirae,* remettant en cause de nombreuses identifications, à commencer par toutes les études précédentes qui signalaient *Haploops tubicola* en Bretagne sud. Dauvin et Bellan-Santini (1986) qui ont également réexaminé la collection de Chevreux du Muséum National d'Histoire Naturelle de Paris, ont confirmé ces observations et indiquaient que tous les individus d'*Haploops tubicola* de cette collection appartennaient à l'espèce *Haploops nirae.*

Si différents auteurs avaient signalé la présence d'*Haploops tubicola* en Méditerranée (Bellan-Santini, 1965 ; Ledoyer, 1970 ; Bellan-Santini et Ledoyer, 1973) ou en mer Adriatique (Pesta, 1920 ; Gurjanova, 1951), le réexamen d'une partie de ce matériel indique qu'il s'agit en fait d'*Haploops nirae* et suggère que la présence d'*Haploops tubicola* en mer Méditerranée est peu probable (Kaim-Malka, 1976). La répartition de cette espèce semble se limiter aux eaux froides de l'hémisphère nord avec une probable limite sud de répartition en mer d'Irlande. Selon toute vraisemblance, la présence de l'espèce *Haploops tubicola* en Bretagne sud et en Méditerranée correspondrait à des signalisations erronées dues à une confusion avec l'espèce *Haploops nirae*. Cet exemple traduit également la difficulté de transfert des travaux des taxonomistes vers l'écologie des peuplements.

Plus récemment, en se basant sur le nombre de cornées et leur position (Fig. 17), Kaim-Malka (2012) a décrit une nouvelle d'espèce d'*Haploops* (*Haploops antennata*) à partir de 5 individus collectés en décembre 1969 dans la baie de Concarneau, plus précisément dans des vases sableuses de la baie de la Forêt (Fig. 18). Cette espèce ne possède qu'une seule paire de cornées supérieures et a les antennes 1 plus longues que les antennes 2. Ces caractéristiques n'ont cependant jamais été observées sur les individus que nous avons échantillonnés en baie de Concarneau et en baie de Vilaine. Cette nouvelle description soulève cependant la question de la présence potentielle de plusieurs espèces d'*Haploops* en Bretagne sud.

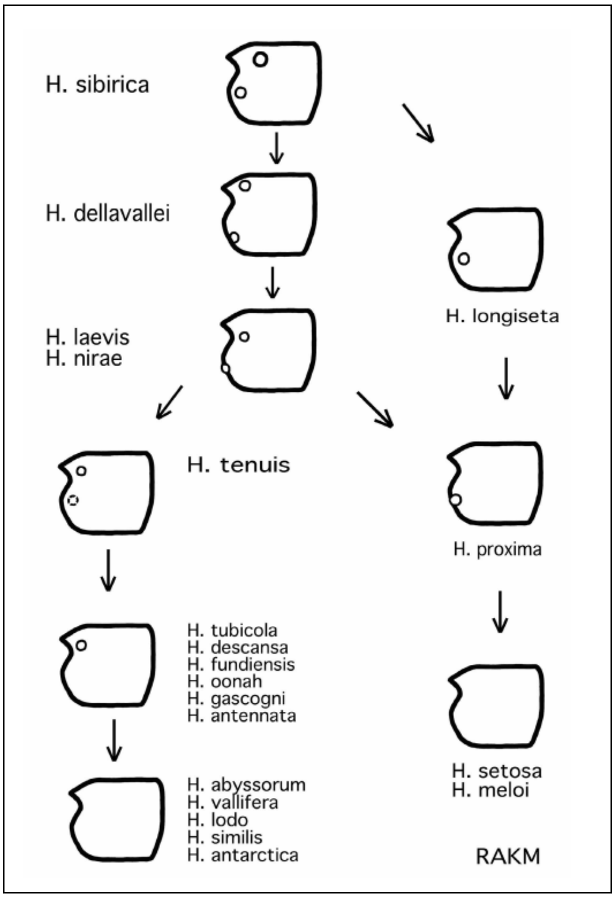

Figure 17 : Clé illustrée synthétique des différentes espèces connues du genre *Haploops* basée sur le nombre et la position relative des cornées. D'après Kaim-Malka (2012).

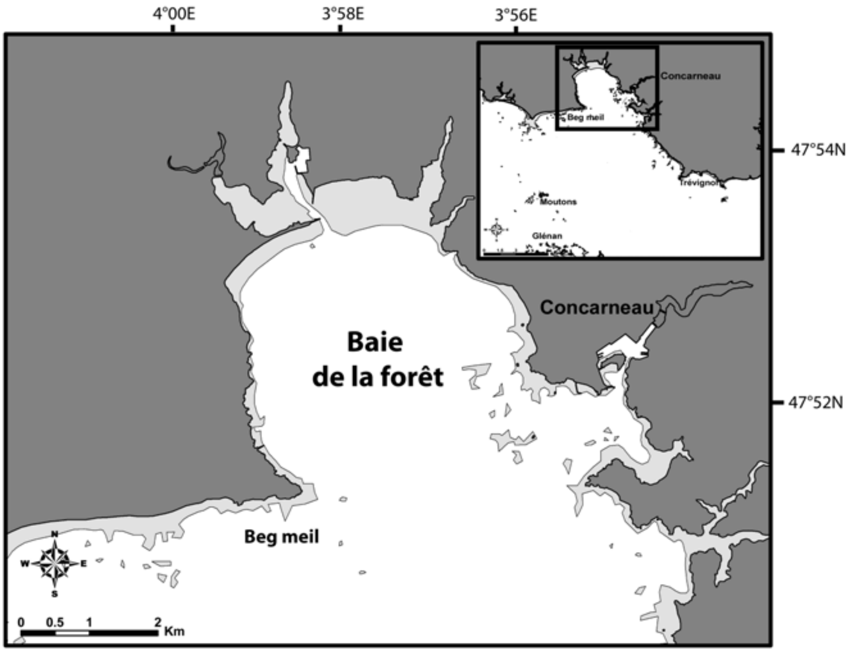

Figure 18 : Positionnement géographique de la baie de la Forêt (où on été collectés les 5 individus d'*Haploops antennata*).

Face aux problèmes d'identifications rencontrés pour le genre *Haploops*, un travail d'identification basé sur une approche de type barcode moléculaire a été entrepris en marge de mon travail de thèse en collaboration avec Claire Daguin-Thiébaut à la Station Biologique de Roscoff. Il constituait une étape préliminaire essentielle et indispensable pour déterminer avec certitude quelle espèce d'*Haploops* était présente dans mes échantillons en Bretagne Sud. Pour ce faire, des individus de 4 espèces différentes d'*Ampelisca* (identifiés par Franck Gentil) provenant du suivi à long terme de la baie de Morlaix (*A. armoricana*, *A. brevicornis*, *A. sarsi* et *A. tenuicornis*), des individus d'une espèce indéterminée d'*Ampelisca* de l'estuaire de la Loire et, d'*Haploops* récoltés en baie de Concarneau, en baie de Vilaine et dans l'estuaire de la Loire ont été analysés. Des individus de référence correspondant à *Haploops tubicola* et *Haploops tenuis* récoltés dans l'Øresund (identifiés par Peter Göransson) ont également été analysés. Enfin, le jeu de données a été complété par les séquences d'autres espèces d'Ampeliscidae (i.e. *Ampelisca eschrichti* et *Byblis gaimardi*) obtenues dans Genbank.

Au cours de cette étude, deux marqueurs moléculaires ont été étudiés :

- Le gène mitochondrial codant pour la sous-unité 1 de la cytochrome oxydase (CO1). Ce gène est universellement utilisé dans les études de barcode moléculaire chez les animaux (Hebert et al., 2003) et recommandé par le consortium ‘Barcode of Life’. Le gène CO1 est supposé peu variable entre les individus d’une même espèce mais suffisamment variable entre individus d’espèces différentes pour les discriminer ;

- Le gène nucléaire codant pour la petite sous-unité de l’ARN ribosomal (ARN 18S). Ce gène est supposé invariable au niveau intraspécifique mais variable entre espèces. Il permet ainsi également d’évaluer si des individus appartiennent ou non à la même espèce.

Après l’extraction de l’ADN des amphipodes, l’amplification des gènes d’intérêt par PCR et leur séquençage, des arbres phylogénétiques ont été construits selon la méthode du Neighbor-Joining à partir de la distance de Kimura à 2 paramètres (Fig. 19 & Fig. 20). Les deux marqueurs utilisés permettent de distinguer les différentes espèces d’*Ampelisca* identifiés sur la base de critères morphologiques et attestent ainsi de la pertinence de notre démarche. Ils différencient également *Haploops tubicola* d’*Haploops tenuis*. Dans les deux cas de figure, les *Haploops* échantillonnés en Bretagne Sud constituent un groupe homogène qui se distingue d’*Haploops tubicola* et d’*Haploops tenuis*. Ces résultats permettent donc d’affirmer que les individus récoltés en Bretagne Sud appartiennent très probablement à une seule espèce d’*Haploops* et que cette espèce n’est pas, comme l’ont affirmé Kaim-Malka (1976) ainsi que Dauvin et Bellan-Santini (1986), *Haploops tubicola*. Au regard des travaux de ces auteurs, nous admettrons dans le reste de ce travail que seule l’espèce *Haploops nirae* est présente sur une zone géographique assez large en Bretagne sud (baie de Concarneau, baie de Vilaine et estuaire de la Loire). Néanmoins, seule la prise en compte d’*Haploops* de référence en provenance de localités méditerranéennes permettrait de conclure avec certitude sur l’appartenance des individus de Bretagne Sud à l’espèce *Haploops nirae.*

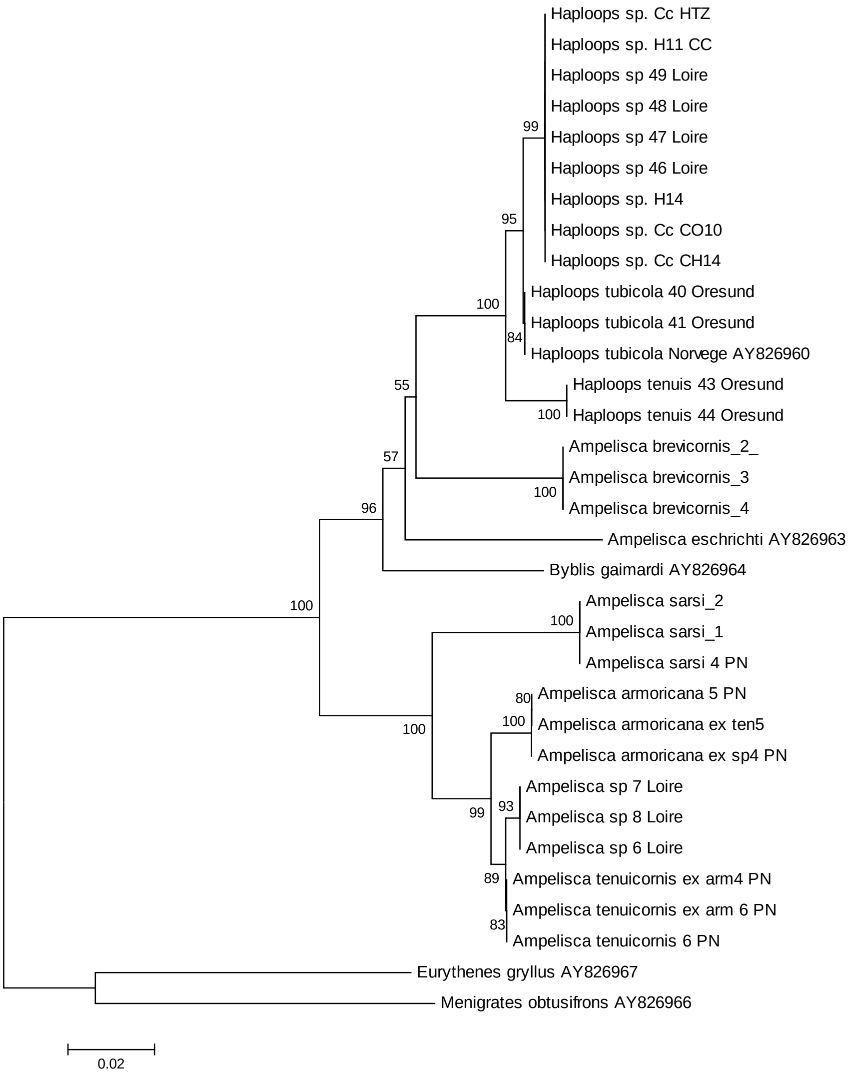

Figure 19 : Arbre phylogénétique de Neighbor-Joining basé sur la distance de Kimura à 2 paramètres à partir des séquences obtenues pour le gène codant pour l'ARN 18S. Deux séquences de la famille des Gammaridae ont été utilisées comme groupe externe pour raciner la topologie. La robustesse des nœuds a été testée par la méthode du boostrap dont les valeurs sont indiquées sur chaque nœud (N=500). Les séquences « AY XXXXXX » proviennent de Genbank. Les individus du sud Bretagne sont notés *Haploops* sp.

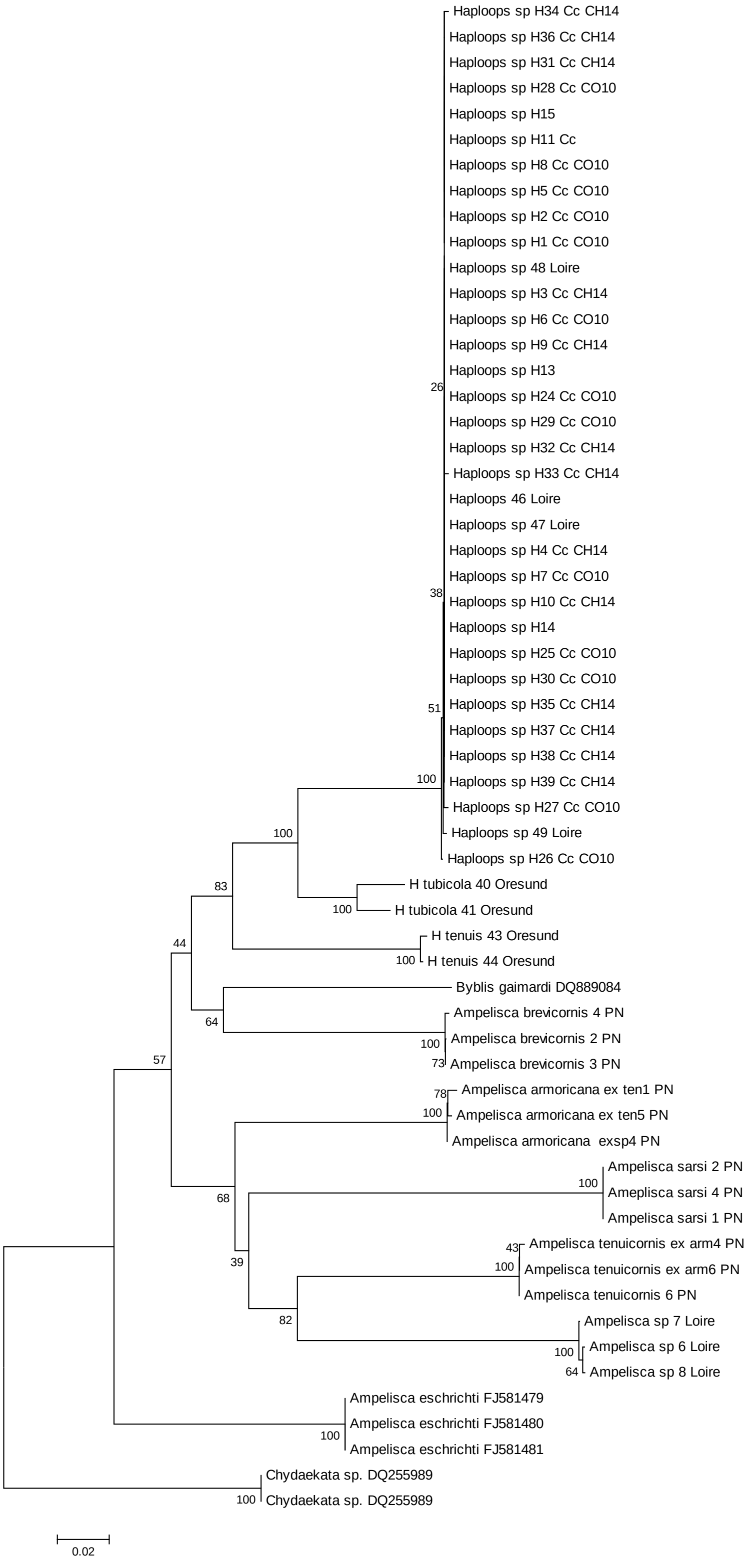

Figure 20 : Arbre phylogénétique de Neighbor-Joining basé sur la distance de Kimura à 2 paramètres à partir des séquences obtenues pour le gène mitochondrial codant pour la cytochrome oxydase 1 (CO1). Deux séquences de la famille des Gammaridae ont été utilisées comme groupe externe pour raciner la topologie. La robustesse des nœuds a été testée par la méthode du boostrap dont les valeurs sont indiquées sur chaque nœud (N=500). Les séquences « FJ XXXXXX » et DQ889084 proviennent de Genbank. Les individus du sud Bretagne sont notés *Haploops* sp.

5. Objectifs de la présente étude

Les peuplements à *Haploops* dont les plus importants sont localisés le long des côtes sud de la Bretagne, en baie de Concarneau et en baie de Vilaine constituent un habitat marin côtier particulièrement original le long des côtes françaises à plusieurs titres : (1) son aire de distribution en Bretagne sud correspond à la présence de champs de pockmarks résultant d'émanations gazeuses, (2) plusieurs observations récentes suggèrent que *Haploops nirae* est devenue une espèce proliférante susceptible d'engendrer des problèmes de gestion de l'espace littoral, et (3) le peuplement joue un rôle clé dans les dynamiques successionnelles au sein des vasières de Bretagne Sud en se développant préférentiellement au détriment des peuplements à *Maldane* et en inhibant le développement de peuplements à *Nucula turgida* ou *Amphiura filiformis* (revue de Glémarec et Grall, 2003). Si les vasières côtières de Bretagne sud on fait l'objet d'inventaires faunistiques au cours desquels la composition des principaux peuplements et la compétition entre eux a été décrite (Ménesguen, 1980 ; Glémarec et al., 1986 ; Le Bris, 1988 ; Le Bris et Glémarec, 1996), le rôle du peuplement à *Haploops* dans l'organisation locale de la biodiversité et dans le fonctionnement général des baies côtières demeure largement méconnu. Alors que la présence de fortes densités de tubes est souvent considérée comme favorable à l'implantation d'une forte richesse spécifique (Bolam et Fernandes, 2003), comment la présence de fortes densités d'*Haploops nirae*, organisme tubicole, influence-t-elle la structure des peuplements ? Quelle place occupent les *Haploops* dans le réseau trophique, à la fois comme organisme suspensivore susceptible de réguler la production primaire, ou comme source de nourriture pour des prédateurs tels que les poissons nectobenthiques ?

L'objectif général de ma thèse est donc d'évaluer et de comprendre l'impact d'*Haploops* sur la biodiversité structurelle et fonctionnelle à travers la modification de la structure physique de son habitat et sur le fonctionnement de l'écosystème qui les abrite. Ce projet se focalise sur la baie de Concarneau, zone colonisée par les *Haploops* pour laquelle des données historiques précises et des données cartographiques récentes acquises dans le cadre du projet REBENT existent (Ehrhold et al., 2007). Trois volets complémentaires qui se déclinent selon trois niveaux d'intégration du vivant que sont la population, le peuplement et le réseau trophique, structurent ce manuscrit.

Le premier volet de la thèse porte sur la biologie et la dynamique de population de l'espèce *Haploops nirae* et a pour objectif d'évaluer le rôle fonctionnel que cette espèce seule tient dans le système. Cette première partie inclut ainsi une étude de l'écophysiologie de l'alimentation de l'espèce dans le but de comprendre son comportement trophique mais également d'estimer son importance en terme de pression de broutage à l'échelle de l'écosystème. Elle comprend aussi une description du cycle de vie de l'espèce et de la dynamique locale de la population en un site de la baie de Concarneau permettant d'évaluer la production secondaire des *Haploops* de ce site. Ce volet s'appuie sur deux articles publiés.

Le second volet s'intéresse à la biodiversité des différents peuplements macrobenthiques à l'échelle de la baie de Concarneau incluant le peuplement à *Haploops*. Cette partie abordera essentiellement la question de l'impact des *Haploops* en tant qu'organismes ingénieurs sur la diversité structurelle du macrobenthos et ses conséquences sur la diversité fonctionnelle. Elle reposera sur des études comparées de la diversité spécifique et fonctionnelle des peuplements benthiques entre les vases à *Haploops* et les peuplements adjacents : le peuplement des vases à *Sternaspis scutata*, le peuplement des sables envasés à *Owenia fusiformis* et celui des vases sableuses à *Amphiura filiformis*. Cette approche comparative sera traitée dans un premier temps dans l'espace seul, à une saison, puis dans un second temps, sur un nombre réduit de stations, dans l'espace et dans le temps. L'étude de la dynamique saisonnière des peuplements benthiques de la baie de Concarneau fournira l'occasion d'estimer leur production secondaire et, par conséquent, d'évaluer l'impact de la prolifération des *Haploops* sur la productivité du macrobenthos de la baie de Concarneau. Ce volet s'articule autour d'un article soumis et d'un article en préparation. Ce travail est réalisé à une échelle spatiale qui ne permet pas d'appréhender explicitement l'influence des pockmarks sur les peuplements macrobenthiques.

Enfin, le troisième volet a pour objectif de replacer les *Haploops* dans le réseau trophique des écosystèmes colonisés. Cette troisième partie passe dans un premier temps par la description des caractéristiques générales des réseaux trophiques des substrats meubles subtidaux de la baie et de leur architecture. Elle inclut dans un second temps une réflexion sur la définition d'indicateurs trophiques renseignant sur le degré de complexité et le fonctionnement du réseau trophique. Cette dernière partie repose sur un article en préparation et un article prêt à être soumis.

PARTIE I

Propriétés biologiques et fonctionnelles d'*Haploops nirae*

- **CHAPITRE 1 : Ecophysiologie de l'alimentation d'*Haploops nirae***

Article n°1 : Group sweeping: feeding activity and filtration rate in the tubiculous amphipod *Haploops nirae* (Kaim-Malka, 1976)

- **CHAPITRE 2 : Dynamique de population et production secondaire d'*Haploops nirae* en baie de Concarneau**

Article n°2 : Life history and secondary production of the amphipod *Haploops nirae* (Kaim-Malka, 1976) in the Bay of Concarneau (South Brittany)

La première partie de ce manuscrit traite des caractéristiques biologiques et fonctionnelles d'*Haploops nirae*. Elle comprend deux chapitres qui ont été publiés respectivement en 2011 dans Journal of Experimental Marine Biology and Ecology et en 2012 dans Estuarine, Coastal and Shelf Science.

Le premier chapitre de cette partie (article 1) s'intéresse à l'écophysiologie de l'alimentation d'*Haploops nirae*. Cette étude offre dans un premier temps une description de la structure et de la fonction des organes de filtration (i.e. les antennes) et les méchanismes impliqués dans la capture des particules alimentaires. Dans un second temps, cette étude aborde l'effet des paramètres environnementaux (i.e. la vitesse du courant, la concentration en nourriture et la turbidité) sur l'activité de filtration d'*Haploops nirae*. Enfin, l'efficacité de rétention et le taux de filtration d'*H.nirae* sont évalués et ces résultats sont extrapolés au milieu naturel.

Le second chapitre (article 2) porte sur l'étude de la dynamique de population d'*Haploops nirae* qui a été entreprise de Janvier 2010 à Mars 2011 à une station de la baie de Concarneau située à 29 m de profondeur et échantillonnée toutes les 3 semaines. L'analyse modale de la distribution des fréquences de taille à chaque date d'échantillonnage a permis de décrire le cycle de vie mais également de fournir une évaluation de la production secondaire annuelle d'*Haploops nirae* en baie de Concarneau. Les résultats renseignent également sur la croissance, la longévité et la mortalité de l'espèce. Les résulats obtenus lors de cette étude sont comparés aux valeurs disponibles dans la littérature pour d'autres d'espèces d'Ampeliscidae.

ARTICLE N°1

Group sweeping: feeding activity and filtration rate in the tubiculous amphipod *Haploops nirae* (Kaim-Malka, 1976)

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Marine Biology and Ecology**

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Abstract.

Haploops nirae is a gregarious tubiculous amphipod that uses its two pairs of antennae to filter particles from the water column. Recent sonar mappings of *Haploops* seabeds revealed that thousands of hectares of soft-bottom muddy sediments in South Brittany coastal ecosystems are now colonized by this amphipod. The present study investigates (1) the structure of the feeding organs and the mechanisms involved in particle capture, (2) the effect of environmental parameters (current velocity, turbidity and food concentration) on the feeding activity of *H. nirae*, quantified by the percentage of active individuals, the frequency of antennae beats and the number and duration of feeding events and (3) the retention efficiency and clearance rate of *H. nirae* individuals, so extrapolation to colonized areas and grazing impact of this species can be estimated. Staining techniques and scanning electron microscopy revealed that *Haploops* antennae have a more complex structure than congeneric *Ampelisca* species, involving long setae bearing short setules and that mucus is involved in particle capture. An increase in current velocity seemed to have very little effect on feeding activity but unexpectedly slightly increased the frequency of antennae beats. However, an increase in both organic and inorganic matter both exponentially increased the number of filtering individuals and showed that *Haploops* are well adapted to feed in turbid conditions: the total time individuals spent filtering remained constant while inorganic particulate matter increased from 10.7 to 85.6 $mg.L^{-1}$. Using a flow-through system, evaluation of retention efficiency showed that only particles larger than 20 µm equivalent spherical diameter were 100% retained by feeding structures, which corresponds to the mean distance between two setules. Clearance rate was estimated at 14.6 ± 0.4 $mL.h^{-1}.ind^{-1}$ or standardized to 25.2 ± 0.7 $L.h^{-1}.g^{-1}$ dry weight. Those values are discussed in light of values obtained in other suspension-feeding species and also extrapolated to the whole *Haploops* community. We estimated that *Haploops* have the capacity to filter the entire water column in 4–5 days and a volume of water equivalent to the whole bay in 29–30 days. This study provides evidence that changes in the spatial extent of *Haploops* communities may have serious impacts within coastal ecosystem they have colonized.

1. Introduction

The tube-building amphipod *Haploops nirae* (Kaim-Malka) is a gregarious species that inhabits shallow coastal waters and belongs to one of the largest amphipod families Ampeliscidae. Ampeliscids are classified as suspension-feeders but differences occurred between genera even if all species share a common feature of lying in a Ushaped bend in their silty tube with the ventral side uppermost and collect particles from the surrounding water by sweeping their antennae (2 pairs) in the water column (Enequist, 1949). *Ampelisca* species are known to leave their tube and migrate in the water column (Dauvin and Zouhiri, 1996) and also forage in the sediment by scraping freshly sedimented organic matter. *Haploops* species are all strictly tubiculous and unlike congeneric *Ampelisca* species, individuals only leave their tube in exceptional cases. They are hence most likely strictly suspension-feeders (Enequist, 1949). However, most of the knowledge on ampeliscid feeding ecology is based on qualitative observations and to our knowledge, very little is known about the filtration rate and the filter-feeding activity of *Haploops* species.

Ampeliscidae in general and *Haploops* species in particular comprise several gregarious species capable of colonizing large areas with densities over a thousand individuals per square meter (Bellan-Santini and Dauvin, 1989). In specific environmental conditions, *Haploops* or *Ampelisca* species similarly carpet the seabed with silty-tubes protruding several centimeters above the sediments. When colonizing extensive surfaces, dense tubiculous mats can deeply modify biological and physical processes at sediment-water interface. Diaz et al. (2008) showed that dense tube mats formed by *Ampelisca* spp. improve benthic habitat quality by processing large amounts of particulate organic matter, and reworking the sediment thereby promoting increased oxygenation of interstitial space. It has also been suggested (Mackenzie et al., 2006) that dense tubiculous amphipod colonies of *Ampelisca* cover and stabilize sediments, thereby minimizing the transport of silt, and facilitating the colonization and the development of suspension-feeding species. *Haploops* species have been reported to cover extensive areas in subtidal shallow muddy areas in the Bay of Fundy, Canada (Wildish and Dickinson, 1982), in Øresund, Sweden (Göransson, 2002) and in several bays of South Brittany, France (LeBris and Glémarec, 1995). A recent mapping survey revealed that *Haploops* communities from South Brittany extended more that 12 000 hectares (Ehrhold et al., 2006), with densities exceeding 10 000 individuals.m^{-2} (Rigolet, Unpublished results). As part of a larger project designed to understand the functioning of *Haploops* habitats in coastal ecosystems, the ecological role of *Haploops* communities as a biological filter must first be addressed. The aim of this study was hence (1) to describe the filtering structures of *Haploops* species, (2) to evaluate the clearance rate and retention efficiency of *Haploops* individuals, and (3) to quantify the feeding activity of *Haploops* and to determine how environmental parameters (current velocity, concentration of food particles, turbidity) affect the feeding behavior of this species.

Complementary approaches using unique mesocosm flowthrough systems were deployed to address those questions and extrapolate filtration rate to ecosystem level. This investigation provides a first estimate of ecosystem-level grazing impact of *Haploops* individuals to determine if the filtering activity of this tubiculous amphipod species, currently spreading in South Brittany, may be of significant importance.

2. Materials and methods

2.1. Amphipod collection, maintenance and experimental setup

H. nirae (Kaim-Malka) were collected in the bay of Concarneau (South Brittany, France, 47°47’632N; 3°54’369E) in February 2009 by divers at ca. 30 meters depth using 30 cm deep cylindrical plastic cores. Care was taken to ensure that core surfaces (113 cm^2) were undisturbed while sampling. Time from core extraction and removal to temperature-controlled laboratory conditions was less than an hour. A new system was created to avoid disturbing the sediment while manipulating *Haploops* tubes (Fig. 21): individual cores were placed on an adjustable piston pin and pushed up, so that the sediment surface reached the top of the core. Once in optimal position, the core was placed in a 6 liter tank and a partition plate inserted at the top of the plastic core, creating a 1.5 liter flow-through chamber (i.e. the volume used for filtration measurements) that was disconnected from the rest of the tank, while keeping the whole core under water. Prerequisites for using flow-through chambers (influence of chamber geometry, recirculation etc.) were tested according to recommendations by Riisgård (2001). The whole experimental setup was similar to previous work with tubiculous worms (Dubois et al., 2009) and consisted of 3 experimental troughs and 1 trough containing a sedimentation control connected in parallel to a continuous supply of filtered and sterilized seawater (temperature 12 °C, salinity 34.5). A mixture of

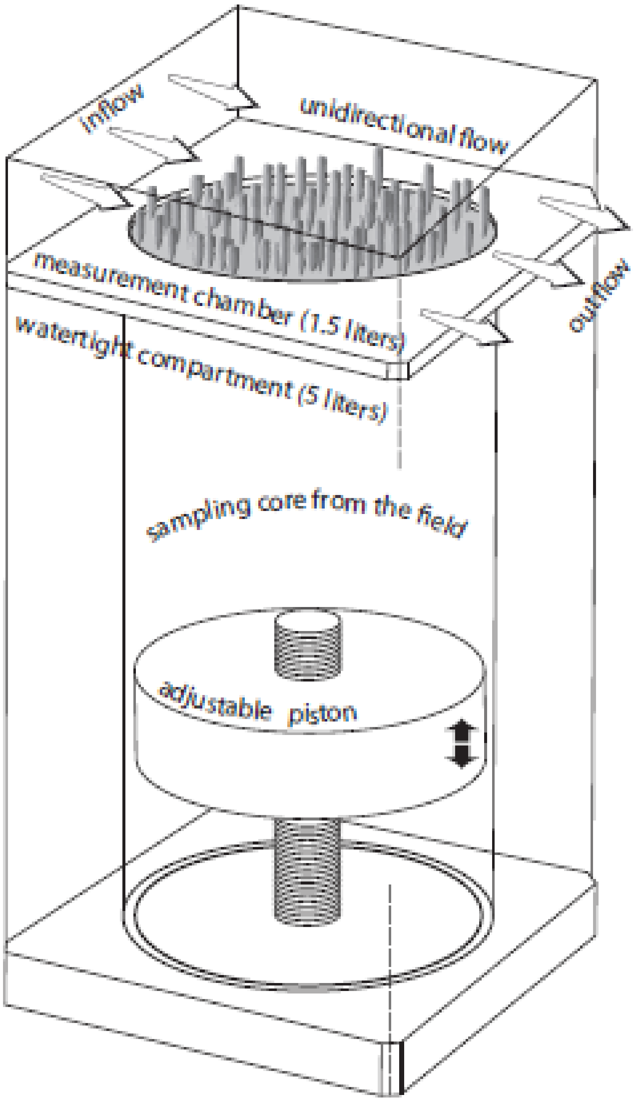

Figure 21 : Details of an experimental trough designed to contain a core of sediment colonized by *Haploops nirae*. An adjustable bottom mounted on a screw allows pushing up the sediment core, so that the surface reaches a plate used as the bottom of the measurement chamber. The flow in the measurement chamber is unidirectional and there is no connection between the two compartments hence created by the plate.

several microalgal species were used, so that a broad range of particle sizes was covered (Table 3). The flow rate was adjusted with Gilmont© flow-meters with a precision of 2 mL.min^{-1} (under 1 atm at 20 °C). *Haploops* individuals were acclimated 48 h before beginning an experiment. During the acclimation period, attention was paid to remove associated burrowing species (e.g. small bivalves, polychaetes, nemerteans or other crustaceans) found in the sediment between tubes, to avoid physical disturbances and to assure that the measured filtration was only due to *Haploops* individuals.

Table 3 : Composition of the experimental diet. Microalgae were cultivated separately at the Experimental Marine Station of Argenton (IFREMER) and mixed before supplied to *Haploops nirae* individuals. Sizes (in ESD) were determined from pure culture algae using the particle counter.

Species	Family	Class	Min-Max Size (µm)	Mode (µm)
Isochrysis galbana (Parke)	Isochrysidaceae	Prymnesiophyceae	3-6	4
Skeletonema costatum (Greville)	Skeletonemaceae	Mediophyceae	4-10	6
Thalassiosira weissflogii (Grunow)	Thalassiosiraceae	Mediophyceae	9-17	12
Scrippsiella trochoidea (Stein)	Peridiniaceae	Dinophyceae	20-40	27

2.2. Description of filtering structures

Along with core samples, some individuals were collected and extracted from their tube, then washed in filtered seawater to remove mud particles. They were narcotised with increasing concentrations of 7.5% $MgCl_2$ in filtered seawater (63 µm) and placed in a solution of 2.5% glutaraldehyde in a slightly hyperosmotic, 0.1 M sodium cacodylate buffer (Beninger et al., 1995). An alternative method to the critical point drying (CPD) technique (Boyde and Wood, 1969) was used for SEM preparation, consisting of airdrying of specimens by the evaporation of hexamethyldisilazane (HMDS). HMDS has been evaluated as better than CPD for SEM observations of many biological samples (e.g. Hochberg and Litvaitis, 2000). Photographs were obtained with the FEI Quanta™ 200 of the Brittany IFREMER Research Center. Additional measurements were performed on freshly narcotized specimens, using a microscope with a calibrated optical scale, in order to assess artefactual shrinkage due to this technique. All measurements made on SEM preparations have been corrected in this manner.

To determine if mucus is involved in particle capture in *Haploops*, narcotized specimens were placed in aqueous Bouin's fixative (Martoja and Martoja, 1967). Whole bodies were embedded in paraffin and processed histologically as developed for mucocyte secretions (mucopolysaccharides, MPS) in bivalves (Beninger and Dufour, 1996) or polychaete worms (Dubois et al., 2005). Thick transverse and longitudinal sections (6 µm) were stained in periodic acid-Schiff–Alcian blue (PAS–AB). Entire antennae and body portions sectioned under a dissecting microscope were placed in staining capsules as well. According to their degree of acidity, acid MPS are PASnegative and AB-positive, and present high viscosity, whereas neutral MPS are PAS-positive and AB-negative, and present low viscosity.

2.3. Determination of the retention efficiencies and clearance rate

To assess retention efficiencies, particle size distributions were determined using a Multisizer 3 particle counter (Beckman Coulter Electronics) fitted with 100 µm apertures, with coefficients of coincidence <5%. All particle sizes were expressed as equivalent spherical diameter (ESD). Particle concentrations were estimated for a size range of 1.8 to 40 µmESD and also represented as particle volume (in $mm^3.mL^{-1}$), as volume provides a better proxy of food quantity. Retention efficiencies (Er) were computed for this entire size range as: Er (%) = 100 × [(inflow – outflow) × $inflow^{-1}$], where inflow represents particle concentration in the control and outflow is particle concentration in the troughs containing the animals. Details of Er calculations are given in Barillé et al. (1993). Er data were used to take into account possible underestimation of clearance rate (CR), due to small particles passing through the filtering structures without being retained and hence released into the chambers with the outflow (Barillé et al., 2006; Dubois et al., 2009). Thus, given the mean flow in an individual trough, CR ($l.h^{-1}$) was calculated as [(inflow – outflow) × $inflow^{-1}$] × flow rate, using particles above a threshold that ensured all cleared with 100% efficiency (Jorgensen et al., 1984). During all CR experiments, flow was kept constant at 2.7 $L.h^{-1}$ (or 0.95 $cm.s^{-1}$). After completion, all individuals were sacrificed in 4.5% formalized seawater. All tubes were opened and individuals collected, counted and weighed after drying for 48 h at 60 °C.

2.4. Determination of feeding activity

As a proxy to estimate the feeding activity of *Haploops*, the number of individuals actively filtering, i.e. with antennae in the water column, was determined by monitoring the core surface with a high resolution CCD camera (6.106 pixels) mounted on a frame to record the entire core surface. The experimental room was completely isolated from noises and possible vibrations, and kept at a constant temperature (12 °C) with a low luminosity, approximating the luminosity measured at 30 meters depth where the *Haploops* individuals were collected. The camera was connected to a laptop and was remotely controlled with Nikon Camera Control Pro^{TM}. Each experiment was conducted over 6 h while high resolution pictures were taken every 3 min (120 pictures total for each experiment). *Haploops* tubes were mapped on the first picture and then each picture was analyzed using Adobe Photoshop CS3™ to count and map open tubes (i.e. filtering activity) and closed tubes (i.e. no filtering activity).

Besides the total number of filtering individuals, 15 tubes were randomly selected and monitored over the course of each experiment, assuming that the feeding activity status (filtering or non-filtering) of individuals for one snapshot remains the same until the following snapshot (3 minutes). Several individual parameters were then determined, as (1) the mean time of filtering activity, (2) the number of feeding events (a feeding event began when an individual deployed its antennae and ended when it withdrew into its tube), (3) the mean time of a filtering event and (4) the frequency of the antennae beats per minute, recorded visually with hand-counters.

All the experiments designed to test environmental factors are listed in Table 4. Food (e.g. microalgae) was provided using peristaltic pumps with a pure culture of the diatom *Thalassiosira weissflogii*. The cell concentration was determined using a Malassez cell counting chamber and the relationship between Chl *a* (µg.L^{-1}) and cell concentration (C_c 10^3 cell.mL^{-1}) was Chl *a* = 2.7 x Cc (Møller and Riisgård, 2006). To mimic an increasing range of particulate inorganic matter (hereafter PIM), silt (Kaolinite BS1, AGS Montguyon, France) was added to the diet. Water samples were collected and filtered on pre-weighed GF/F filters dried at 60 °C for 24 h, so that the amount of PIM in the diet was obtained.

Several preliminary runs were carried out to verify that no significant differences existed in feeding activity between 12 hour and 6 hour experiments or between full day light and low light intensity. Because of light penetration issues in the water, only the experimental conditions with particulate inorganic matter (PIM) ≤ 85.5 mg.L^{-1} enabled a reliable detection of filtering individuals. The counting of beat frequency was not possible for PIM > 23.3 $mg.L^{-1}$. After each experiment, all *Haploops* tubes were collected, counted and opened to determine the total number of *Haploops* individuals.

Table 4 : Environmental parameters and conditions used to test for the feeding activity of *Haploops nirae.*

Parameters	Conditions	Comments
Current velocity ($cm.s^{-1}$)	0.8 / 4.4 / 8.2 / 13.1	Concentration in *T.weissflogii* = 10^4 $cell.mL^{-1}$
Food concentration (Chl.*a* in $\mu g.L^{-1}$)	0 / 1.3 / 2.1 / 13.5 / 27.0 / 121.5	Flow rate = 3.5 $L.h^{-1}$ (1.23 $cm.s^{-1}$)
Concentration in inorganic matter (PIM) ($mg.L^{-1}$)	2.3 / 7.3 / 11.0 / 23.3 / 40.5 / 85.5	Concentration in *T.weissflogii* = 10^4 $cell.mL^{-1}$ and flow rate = 3.5 $L.h^{-1}$

2.5. Statistical analysis

One-way repeated measures ANOVA were used to test for differences in clearance rate (CR) values and feeding activity measurements between experimental conditions. Data were accordingly checked for normality and homogeneity of variance. When normality tests failed, non-parametric Friedman repeated measures analyses of variance were used. A significance level of $p \leq 0.05$ was used in all tests. When significant, pairwise post-hoc comparisons were performed using the Tukey HSD tests for parametric tests and Holm–Sidak method for non-parametric tests. Changes in feeding activity (FA) parameters were fitted against tested environmental conditions (EC) using an exponential decay curve $FA = FA_0 + a \times \exp^{(-\lambda\ EC)}$, where FA_0 is the asymptotic value of the measured FA parameter, a is the intercept, and λ is the slope. Estimation of FA_0, a and λ was achieved with Sigmastat™ 2.0 by using the downhill simplex method. All curve fittings between observations and the asymptotic model were tested by analyses of variance ($p \leq 0.05$).

3. Results

3.1. Description of feeding structures

When feeding, *H. nirae* used its 2 pairs of antennae (A1 and A2) independently from each other. Antennae A1 was in the middle upright position and used a backwards–forward motion, while the antennae A2 either moved synchronously with A1 or independently sweep sideward. The four antennae of *H. nirae* are about as long as the amphipod body and are slightly bent when extended in the water column. Two rows of long setae are attached to each antenna and form an angle of 90° in the water. Scanning electron micrographs as well as microscope measurements revealed that setae are between 1 and 2 mm long and irregularly inserted proximally every 150 µm and distally every 110 µm onto the antenna (Fig. 22A). When extended in the water column, there is very little overlap in the setae and the four antennae form a semi-circular basket. On each setae, two singlerowed pairs of 10 µm spine-like setules are inserted. Two setules are positioned at an angle of 90° and the distance between 2 pairs of setules range from 25 µm to 10 µm (mean 19.35 ± 0.34 µm, n=25) in the proximal and in the distal part of the setae, respectively (Fig. 22B and C). In addition, a non-rigid filamentous structure (about 200 µm long) is located at each insertion point of setae along the antennae (see details in Fig. 22C). Both pairs of antennae are similarly structured. Examinations of co-occurring species *H. nirae* and *H. tubicola* did not reveal any structural difference, except the total length of antennae, 50% shorter in *H. tubicola*.

Whole-mounts of antennae and longitudinal sections of *Haploops* individuals stained with periodic acid-Schiff–Alcian blue (PAS–AB) revealed the occurrence of a large acid mucous gland in the propodus of the gnathopod (Fig. 22D). No mucocytes were detected in transversal or longitudinal sections of antennae but large portions of whole mounts antennae were stained in blue, indicating the presence of acid mucus at the surface (Fig. 22E).

Additional scanning electron micrographs of several species of *Ampelisca* (e.g. *A. spinipes*, *A. brevicornis* and *A. spooneri*) showed that while the general organization and distribution of setae seemed similar to the *Haploops* genus, the setae in *Ampelisca* species appeared smooth and did not bear setules (see *A. spinipes* in Fig. 22F).

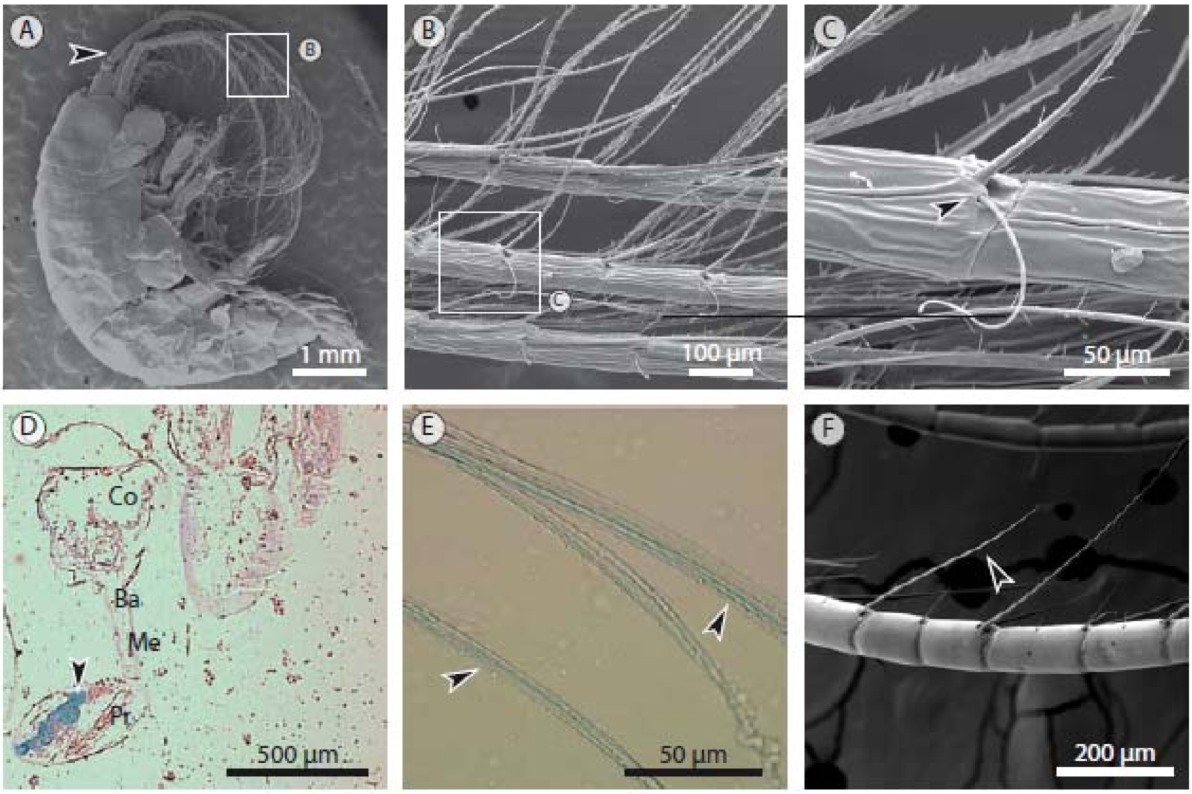

Figure 22 : Scanning electron micrographs (A-C) and microscope photographs (D-E) of *Haploops nirae*. (A) Whole individual (adult) showing the two long pairs of antennae (arrow). (B) Close-up of the median portion of antennae showing groups of setae bearing small setules. (C) Close-up of the insertion area of setae on antennae. Note the presence of a non-rigid sensory filament (arrow) at each insertion point of setae. (D) Longitudinal section of the thoracic region showing the propodus (Pr), the merus (Me), the basis (Ba) and the coxal plate (Co) of the gnathopod 2. Note the large acid mucous gland revealed by Alcian-Blue (arrow). (E) Whole-mount of antennae stained with Alcian-Blue revealing acid mucous on the antennae surface. (F) Close-up of the median portion of *Ampelisca spinipes* antennae showing setae. Note the absence of setule on the setae (arrow).

3.2. Retention efficiency and clearance rate

Size spectra obtained with the particle counter—and expressed in ESD showed 4 modes at the inflow and outflow of the experimental troughs (Fig. 23). The first, at around 4 µm ESD, was due to *Isochrysis galbana* (linear length of cells= 5–6 µm), the second, more dispersed and centered around 9–10 µm ESD, was due to *Skeletonema costatum* which usually form two-cell chains of in batch culture, the third was centered around 13–14 and due to *Thalassiosira weissflogii* and the fourth was centered around 24–25 and due to *Scrippsiella trochoidea*. In some cases (as the example showed in Fig. 23), particle peaks recorded at the outflow was higher (and broader) than peaks at the inflow (control outflow). This phenomenon is traditionally explained by animal activities which resuspend particles previously deposited and prevent any deposition in the measurement chambers. This phenomenon made the use of a sedimentation control irrelevant in those cases. Each size distribution at the outflow of the troughs was therefore carefully examined prior to retention efficiency calculations and samples with abnormal peaks were discarded. Regardless, inflow of experimental troughs was used instead of outflow of control trough for the calculations.

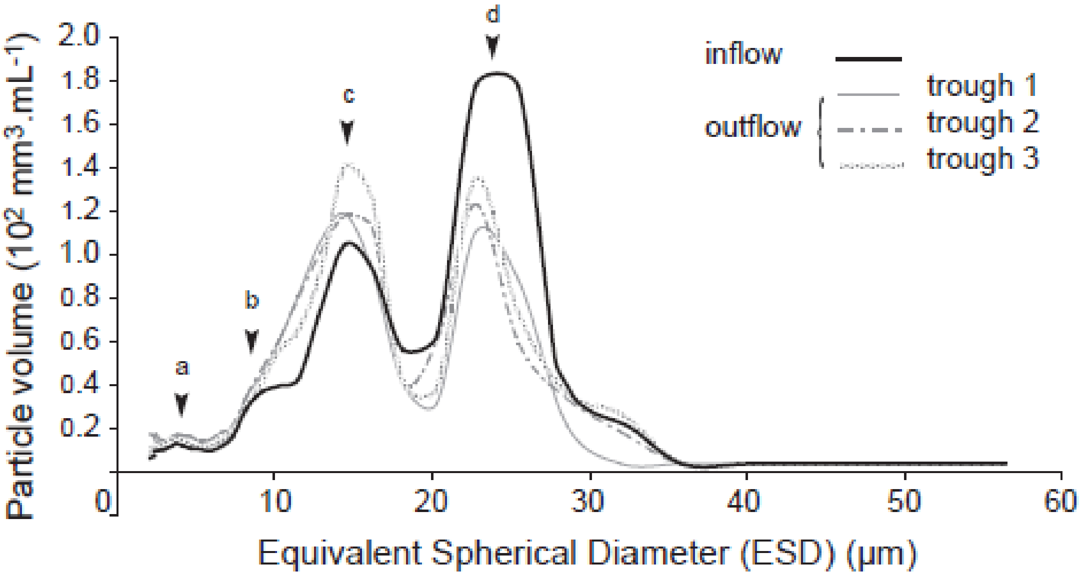

Figure 23 : Example of particle size spectra (expressed as particle volume) of the experimental diet at the inflow and the outflow of the experimental troughs. (a) *Isochrysis galbana* peak, (b) *Skeletonema costatum* peak, (c) *Thalassiosira weissflogii* peak and (d) *Scrippsiella trochoidea* peak. Note that outflow particle volumes are larger than inflow in this example, because of *Haploops* individual resuspension activity.

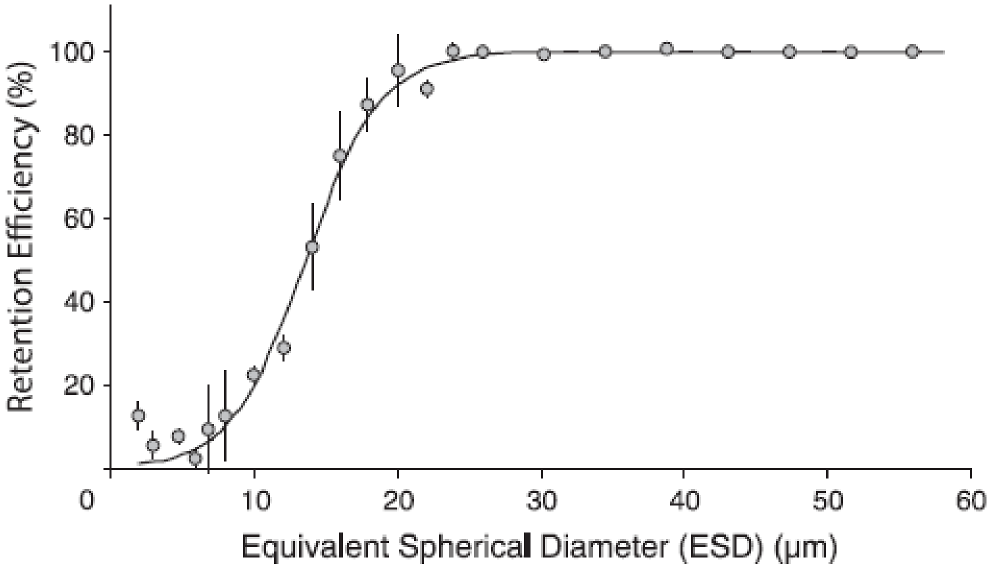

Figure 24 : Retention efficiency (mean ± SE) of *Haploops nirae* for the tested experimental diet.

The retention efficiency curve showed an inflection at around 20 µm ESD (Fig. 24): all particles larger than 20 µm ESD were cleared with 100% efficiency. Below this size, retention efficiencies decrease rapidly: 80% of 17 µm ESD particles were retained, 50% of 14 µm ESD particles, but *Haploops* individuals are unable to retain particles smaller than 8 µm ESD. The clearance rate calculation was therefore based on particles above 20 µm ESD, as determined by the particle counter, which corresponded mainly to the microalgae *S. trochoidea* and a few *T. weissflogii* along with long chains of *S. costatum* cells.

Comparison of the mean clearance rate (CR) calculated at 3 different times after the beginning of the experiment (60, 90 and 180 min) did not reveal any significant statistical differences (Fig. 25, ANOVA, P = 0.887). A mean clearance rate of 1.06 ± 0.14 L.h^{-1} was calculated for all data. The mean number of filtering individualswas counted at 78 ± 9 individuals. Post-experiment, individual dry weights were measured at 0.578 ± 0.076 mg. Assuming that all the filtering individuals were filtering equally, and that there were no significant differences in individual sizes and weights, the mean clearance rate of an individual was hence estimated at 14.6 ± 0.4 mL.h^{-1}. This hypothesis is supported by the low individual dry weight variability and the post-experiment counts showing that only adults occurred at this time of the year (early winter). The standardized clearance rate for *H. nirae* was hence estimated to be 25.2 ± 0.7 L.h^{-1}.g^{-1} dry weight.

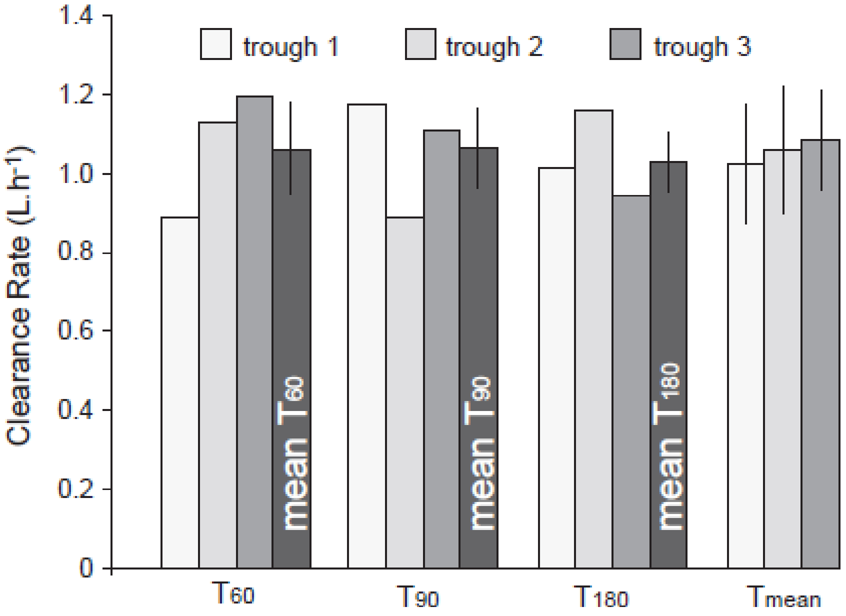

Figure 25 : Variations in clearance rates calculated for the three troughs and the mean of the three troughs (black bars) ± SE after 60, 90 and 180 minutes. No significant differences were shown in mean clearance rates according to time and between the troughs.

3.3. Feeding activity

3.3.1. Effect of current velocity

The mean percentage of filtering individuals varied from 10.6% (SE=0.3) for a 13.1 cm.s^{-1} flow speed to 21.0 % (SE=0.4) for a 0.8 cm.s^{-1} flow speed. For each flow speed, no significant variations occurred in the mean percentage of filtering individuals during the 6 hour experiments. However, significant differences were detected between the different flow speed conditions (ANOVA, p = 0.003). The highest number of filtering individual occurred for the lowest velocity but no clear pattern can be determined and no fitted model can be satisfactorily applied (Fig. 26). The examination of 15 randomly selected individuals revealed that the mean time *Haploops* individuals were filtering was 13.6 % (SE = 2.9) of 6 hours (or about 50 min), without significant differences according to flow speed (Table 5). Significant differences were also detected in the mean number of filtration events and the time of each filtration event. Overall, the number of filtration events decreased and the mean time of a filtration event increased as flow speed increased. Antennae beat frequencies showed a large difference: A1 frequency was much slower (between 3 and 7 beats.min^{-1}) than A2 (between 18 and 30 beats.min^{-1}) (Table 5). Statistically, the frequencies of A1 and A2 are significantly different for the lowest flow speed and remained slightly higher and constant from 4.4 to 13.4 cm.s^{-1}.

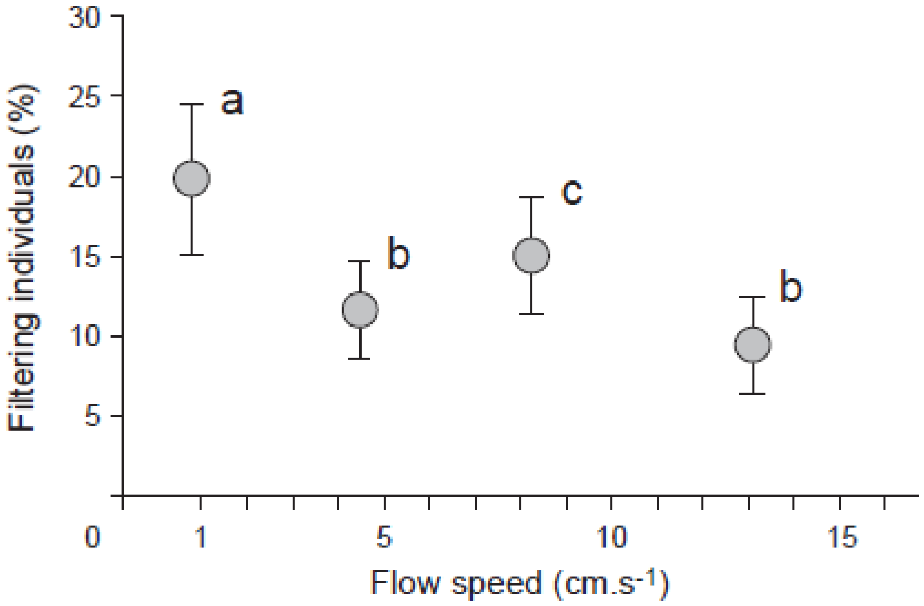

Figure 26 : Effect of current velocity (cm.s^{-1}) on the number of filtering individual (%) (mean ± SE). No non-linear regression model was statistically valid.

Table 5 : Effect of current velocity (cm.s^{-1}) on feeding activity parameters of *Haploops nirae* individuals. Results are mean ± SE. n = 15 individuals randomly selected. When significant, global p-level are mentioned as * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Results of post-hoc comparisons are reprented by superscript letters, two similar letters indicating non-significant variation.

Current velocity (cm.s^{-1})	**0.8**	**4.4**	**8.2**	**13.1**	**p-level**
Mean individual time spent filtering (%)	20.9 ± 4.3	9.0 ± 2.7	13.6 ± 3.2	11.1 ± 1.8	P = 0.111
Mean individual number of filtration events	23.7 ± 2.8^{a}	12.1 ± 3.0^{b}	10.1 ± 2.1^{b}	10.2 ± 1.3^{b}	**
Mean time of filtration events (min)	5.7 ± 0.7^{ab}	4.7 ± 0.4^{b}	9.6 ± 0.7^{c}	7.8 ± 1.2^{bc}	**
A1 antennae beat frequency (min^{-1})	2.7 ± 0.7^{a}	4.7 ± 1.3^{ab}	7.7 ± 1.3^{b}	7.1 ± 1.1^{b}	*
A2 antennae beat frequency (min^{-1})	18.5 ± 0.7^{a}	27.1 ± 1.8^{b}	30.3 ± 2.6^{b}	27.8 ± 2.3^{b}	**

3.3.2. Effect of food concentration

For each condition, no significant variations occurred in the mean percentage of filtering individuals during the 6 hour experiments. The total number of filtering *Haploops* showed highly significant variations according to changes in food concentrations (Chl *a*) (Fig. 27). The model showed a sharp increase in the percentage of filtering individuals from 2.16 to 13.5 µg.L^{-1} (or 8.10^{2} to 5.10^{3} cells.mL^{-1}) where the percentage reached a plateau (ca. 75% of individuals were filtering). The percentage P of filtering individuals varied according to Chl *a* concentrations as $P(\text{Chl } a) = 10.31 - 64.20 \exp(-3.10^{4} \text{ Chl } a)$ (adjusted $r^{2} = 0.925$) (Fig. 27). Overall, all individual parameters of feeding activity followed the same pattern (Table 6). The total time *Haploops* individuals spent filtering did not significantly vary between 0 and 2.2 µg.L^{-1} Chl *a* (mean = 16.3 ± 5.3 % or ca. 60 min) and sharply increased and plateaued at 83.0 ± 7.3% (or 300 min) as Chl *a* concentrations reached 13.5 µg.L^{-1}. All other measured parameters followed a similar but less pronounced pattern. The mean number and time of filtration events showed an increase in feeding activity, with high inter-individual variability in filtration time when Chl *a* concentration reached 13.5 µg.L^{-1}. The mean time of each filtration event started from 5.2 min up to ca. 30 min at the plateau (for Chl *a* concentration=13.5 µg.L^{-1}). The antennae (A1 and A2) beat pattern also followed the same increase with a relative sharper increase (4 times, from 2 to 8 beats.min^{-1}) for A1 than for A2 (2.5 times, from 15 to 40 beats.min^{-1}) when Chl *a* reached 13.5 µg.L^{-1}. The beat frequency ratio A2/A1 consistently decreased from 9 to 4 for the highest Chl *a* concentrations.

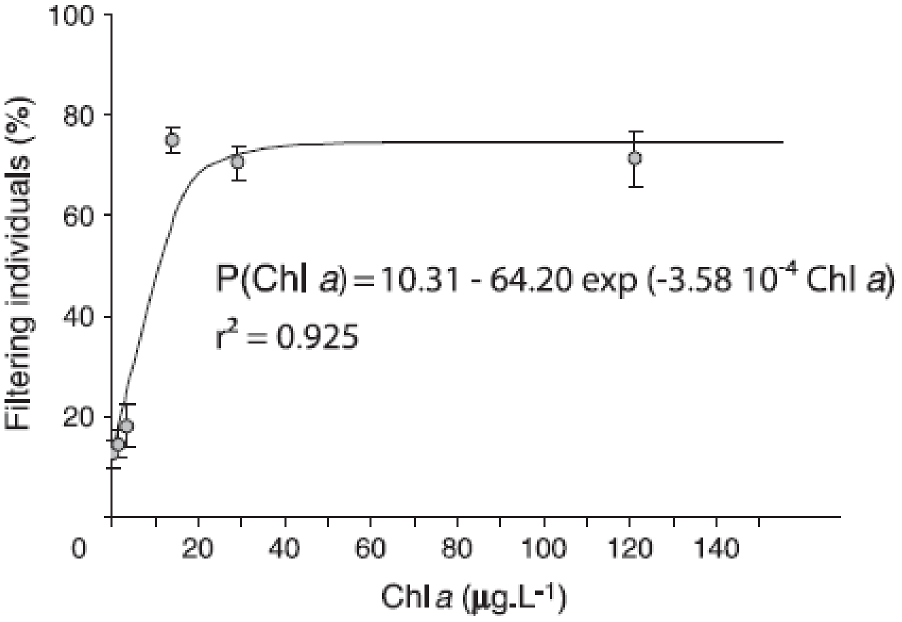

Figure 27 : Effect of food concentration (µg Chl *a*.L^{-1}) on the number of filtering individual (%). A non-linear model was fitted to the experimental values. Adjusted r^2 = 0.925.

Table 6 : Effect of particulate organic matter, measured as concentration in Chl. *a* (µg.L^{-1}) on feeding activity parameters of *Haploops nirae* individuals. Results are mean ± SE. n = 15 individuals randomly selected. When significant, global p-level are mentioned as * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Results of post-hoc comparisons are reprented by superscript letters, two similar letters indicating non-significant variation.

Food concentration – Chl *a* (µg.L^{-1})	**0**	**1.3**	**2.2**	**13.5**	**27.0**	**121.5**	**p-level**
Mean individual time spent filtering (%)	10.3 ± 1.5^{a}	18.6 ± 5.3^{a}	20.1 ± 1.7^{a}	91.2 ± 3.4^{b}	80.7 ± 3.4^{b}	77.2 ± 4.8^{b}	***
Mean individual number of filtration events	7.3 ± 0.9^{a}	8.9 ± 1.5^{a}	9.6 ± 1.3^{ab}	6.1 ± 1.4^{ab}	12.5 ± 1.4^{ab}	14.0 ± 1.3^{b}	**
Mean time of filtration events (min)	5.2 ± 0.4^{a}	9.9 ± 3.8^{ab}	8.9 ± 1.3^{a}	144.4 ± 36.4^{b}	29.2 ± 3.9^{b}	24.3 ± 3.7^{b}	***
A1 antennae beat frequency (min^{-1})	2.1 ± 0.5^{ab}	1.2 ± 0.3^{a}	2.3 ± 0.5^{ab}	9.0 ± 0.8^{b}	3.7 ± 0.8^{b}	8.5 ± 0.8^{b}	***
A2 antennae beat frequency (min^{-1})	19.4 ± 1.1^{a}	9.7 ± 1.6^{b}	14.6 ± 2.6^{ab}	41.9 ± 2.3^{c}	29.5 ± 2.6^{d}	40.3 ± 1.8^{c}	***

3.3.3. Effect of concentration in inorganic matter (PIM)

Silt (Kaolinite) was added in the water until tubes were not easily counted (85.6 mg.L^{-1}). Due to the relative transparency of antennae, counting of their beat frequency was not possible with silt content over 11.0 mg.L^{-1}. For each tested condition from 2.3 to 85.6 mg.L^{-1}, no significant variations occurred in the mean percentage of filtering individuals over the 6 hours experiments. The model (adjusted r^2 = 0.945) showed that the number of filtering *Haploops* increased exponentially and closely approximates a 0–1 response model (Fig. 28). The number of filtering individuals shifted and plateaued from 17% (2.3 mg.L^{-1}) to 69% for a silt concentration of 7.3 mg.L^{-1}. From 11.0 to 85.6 mg.L^{-1}, the number of filtering individual remained at the plateau. The total time *Haploops* individuals spent filtering and the number of feeding events followed the same pattern but the mean time of each feeding event first increased (from ca. 9 to 30 min) from 2.3 mg.L^{-1} to 7.3 and 11.0 mg.L^{-1} but then significantly decreased to ca. 15 min up to 85.6 mg.L^{-1} (Table 7). The frequency of A1 and A2 beat frequency did not show large variations (even though only 3 PIM conditions were available) except for a decrease in A1 frequency for 7.3 mg.L^{-1}. A2 beat frequency remained much higher than A1.

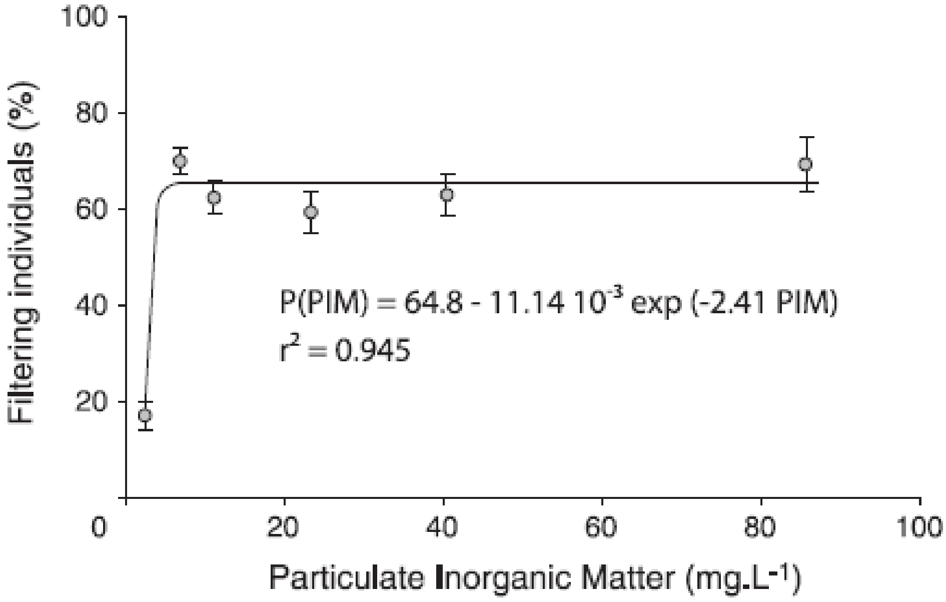

Figure 28 : Effect of particulate inorganic matter (mg kaolinite.L^{-1}) on the number of filtering individual (%). A non-linear model was fitted to the experimental values. Adjusted $r^2 = 0.945$.

Table 7 : Effect of particulate inorganic matter (mg.L^{-1}) on feeding activity parameters of *Haploops nirae* individuals. Results are mean ± SE. n = 15 individuals randomly selected. When significant, global p-level are mentioned as * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Results of post-hoc comparisons are reprented by superscript letters, two similar letters indicating non-significant variation. NA = no results.

Particulate inorganic matter (mg.L^{-1})	**2.3**	**7.3**	**11.0**	**23.3**	**40.5**	**85.6**	**p-level**
Mean individual time spent filtering (%)	13.1 ± 3.4^{a}	80.7 ± 3.4^{b}	76.8 ± 3.6^{b}	58.1 ± 5.0^{c}	64.3 ± 7.2^{bc}	74.6 ± 2.9^{bc}	***
Mean individual number of filtration events	5.1 ± 1.3^{a}	12.5 ± 1.4^{bc}	11.5 ± 0.9^{b}	19.5 ± 1.4^{c}	17.9 ± 2.2^{c}	16.9 ± 1.1^{c}	***
Mean time of filtration events (min)	9.2 ± 0.8^{a}	29.2 ± 3.9^{b}	31.1 ± 3.4^{b}	11.9 ± 1.7^{a}	13.8 ± 1.2^{a}	17.2 ± 1.5^{a}	***
A1 antennae beat frequency (min^{-1})	7.7 ± 1.2^{a}	3.7 ± 0.6^{b}	7.9 ± 0.9^{a}	NA	NA	NA	**
A2 antennae beat frequency (min^{-1})	30.3 ± 2.7	29.5 ± 2.5	36.4 ± 2.1	NA	NA	NA	P = 0.108

4. Discussion

Ampeliscid species – one of the largest amphipod families (Dauvin and Bellan Santini, 1996) – are known to be both suspension- and deposit-feeders, collecting food particles by scrapping the sediment surface but also by sweeping their two pairs of antennae in the water column (Enequist, 1949). Within this family, while *Ampelisca* genus exhibits a mix between suspension- and deposit-feeding species with often contradictory statements (Kanneworff, 1966), *Haploops* species are apparently all suspension-feeders. However, most of the understanding of ampeliscid feeding behavior came from qualitative aquaria experiments and very little detailed information is available. As a model for suspension-feeding ampeliscids, we provided here a better understanding of the filtering structure and feeding behavior of *H. nirae*, as well as an estimate of its clearance rate.

4.1. Filtering structures and particle capture in **Haploops nirae**

A close examination of *H. nirae* filtering structures using complementary approaches (e.g. scanning electron micrographs, histological mucocyte mapping and traditional microscope photographs) revealed that *Haploops* – both *H. nirae* and *H. tubicola* – antennae bear long setae and that those setae had short spine-like setules. Plumose setae are a common feature in amphipods, and are traditionally found on coxal plates and appendages such as mouthparts, gnathopods, pereopods or pleopods but it has been disregarded in the description of *Haploops* species (Dauvin and Bellan Santini, 1990; Lincoln, 1979). No such setules were observed in the 3 *Ampelisca* species we scanned, and along with the low number of setae on the antennae, this feature could serve as a quick and easy morphological trait in ampeliscid to possibly separate *Ampelisca* from *Haploops* species. Similar observations have to be extended to additional species, including the genus *Byblis* (the third genus belonging to the Ampelicidae family). These differences also have functional consequences for the Ampeliscidae feeding ecology. A 3-dimensional filtering structure offers a much more complex and extended surface to collect particles and is commonly observed in obligatory suspension-feeders (Levinton, 1995). The observed antennae structures provide evidence that *Haploops* species are strictly suspension-feeders while *Ampelisca* species exhibit mixed feeding behaviors. These observations also bring new insight into the general behavior of these two genera. Most *Ampelisca* species are tubiculous species but are known to easily leave their tube and even migrate in the water column (Dauvin and Zouhiri, 1996), hence having access to a large variety of food sources. *Haploops* rarely leave their tube (Enequist, 1949) and consequently suspended particles are the only food source accessible. The longer and the more setose the antennae, the more area they can subtend and therefore the more water they can potentially filter. *Haploops* species seemed hence to be more specialized in suspension-feeding than *Ampelisca* species.

For suspension-feeders, mucus plays a primary role in the collection and the transport of food particles, as evidenced in bivalves (e.g. Beninger and St-Jean, 1997) or polychaetes (e.g. Dubois et al., 2005). Using staining techniques (PAS-AB techniques), we have demonstrated here that the mucus is also used in suspension-feeding amphipods. To our knowledge, this is the first evidence of crustaceans using mucus in particle capture (see review of Riisgård and Larsen, 2010). Acid (i.e. stained in blue) mucus secretions were detected on *Haploops* antennae and evidence of a large acid mucus gland was found in the distal region of the gnathopods. Mucus glands have been described in several amphipod species but are mainly associated with the mouthparts and alimentary canal (Shyamasundari and Rao, 1977) and used in tube building (Shillaker and Moore, 1978). We hypothesized here that antennae do not have mucocytes (as shown by transversal and longitudinal sections) but are coated in mucus by the gnathopods when the antennae are flexed down and then brushed out with the first coxal plates and the gnathopods, before the antennae are redeployed in the water. With this mechanism, particles are stuck with high viscosity, acid mucus to the antennae. Viscous acid or acid-dominant mucopolysaccharides are used on exposed surfaces of feeding structures by other species, such as in the ordinary filament crest of the gill in the scallop *Placopecten magellanicus* (Beninger et al., 1993), or the frontal filament of the gill in the blue mussel *Mytilus edulis* (Beninger et al., 1993) exposed to siphonal currents. Polychaetes such as *Sabellaria alveolata* also use mucus in the frontal surface of tentacles and grooves of that are directly exposed to currents in the water column (Dubois et al., 2005). Particles stuck on *Haploops* antennae would therefore require a high-viscosity mucus to avoid resuspension.

When antennae are spread out in the water column, the setae and the bristles form a net that collect particles larger than 20 µm, as shown by calculation of retention efficiencies. This calculation is supported by the mean distance between two bristles along the setae (mean 19.35 ± 0.34 µm, n=25). Because *Haploops* species only live in muddy habitat, where turbidity is often high (LeBris and Glémarec, 1996), not being able to retain smaller particles seems well adapted to this amphipod's ecological constraints. Antennae structures are hence less rapidly saturated by small inorganic particle (2–5 µm ESD).

4.2. Effects of environmental parameters on feeding activity in **Haploops nirae**

Environmental parameters seemed to be of unequal importance in affecting *Haploops* feeding behavior. We chose to test three ecologically important parameters that are classically integrated in numerical models designed to estimate grazing impact of filter-feeders (see for example Cugier et al., 2010): the current velocity, the food concentration (Chl *a*) and the turbidity (PIM). Numerical models of South Brittany (e.g. see Teissier, 2006 for flow speed and turbidity, and Gohin et al., 2003 for Chl *a* values) showed that the tested experimental conditions approximated those from the field. However, the maximal turbidity value (e.g. 85.6 mg.L^{-1}) corresponds classically to very estuarine conditions and occurred in rare cases during winter storm and the maximum Chl *a* value (e.g. 121.5 µg.L^{-1}) corresponds to unexpected values in South Brittany where spring phytoplanktonic blooms only result in Chl *a* values between 10 and 20 µg.L^{-1}. Parameters were tested separately, so that the importance of each parameter on the feeding ecology of *Haploops* can be distinguished, despite obvious possible co-variations in natural environments (e.g. turbidity and flow speed).

The experiments revealed that the current velocity did not have a strong effect on *Haploops* feeding behavior (Fig. 26). Based on literature, it was expected that flow speed could trigger some changes in feeding behavior, as reported for spionid polychaetes (Hentschel and Larson, 2005; Taghon et al., 1980) or other crustaceans such as porcelain crabs *Porcellana longicornis* (Achituv and Pedrotti, 1999) or barnacles *Semibalanus balanoides* (Trager et al., 1990), which actively beat their cirri at low current speeds (active suspension-feeding) but hold them passively extended at high current speed (passive suspension-feeding). This behavior allows organisms not to waste energy in actively collecting particles when the flow is passively bringing food particles to the collecting organs. *Haploops* however seemed to not obey this general behavior for crustacean suspension-feeders (Riisgård and Larsen, 2010) since their beat frequency for A1 and A2 increased with flow speed. It is worth noticing the large difference between A1 and A2 beat frequency: A2 was generally 4 to 9 times faster than A1 and responded more rapidly to changes in environmental parameters (Tables 5 to 7). In contrast to other crustacean suspension-feeders, *Haploops* seemed to exhibit an active (A2) and a passive (A1) feeding behavior at the same time. The current speed did not have an effect on the time individuals spent filtering either:

while the number of feeding events decreased, the time of each feeding event increased. A large inter-individual variability was also reported for this experiment, supporting the idea that flow speed is not of primary importance in stimulating foraging behavior in *Haploops*.

The concentration of organic (POM) or inorganic (PIM) particles seemed to have similar effects on *Haploops* feeding behavior. Both PIM and POM increases lead to an exponential increase in the total number of filtering individuals (Fig. 27 and Fig. 28). As for POM, the threshold to reach the plateau is very rapid (Chl *a* = 13.5 µg.L^{-1}) but actually corresponds to Chl *a* values of a late planktonic bloom on the South Brittany coast (Gohin et al., 2003). Below this value, only 20% of *Haploops* individuals were actively filtering in a Chl *a* range indicative of the South Brittany coast for most of the year. This leads to the conclusion that *Haploops* are not very sensitive to variations in low food concentration but rapidly respond to phytoplankton blooms. *Haploops* individuals respond to an increase in food concentration by spending more time filtering and greatly increasing the mean time of filtration events. The beat frequency also increased.

As for PIM, the maximum percent of filtering individuals is reached for PIM = 7.3 mg.L^{-1}, which is a common value for muddy habitats colonized by *H. nirae*. Effects of inorganic matter on suspension-feeding activity are relatively well documented for bivalves (e.g. Barillé et al., 1997; Sobral and Widdows, 2000) and gastropods (Barillé et al., 2006) or for polychaetes (e.g. Dubois et al., 2009; Hentschel and Larson, 2005) but there is no equivalent literature on crustaceans in general and amphipods in particular. Studies in other taxonomic groups have revealed a complex set of physiological and morphological adaptations to seston variability. Small inorganic particles are known to clog filters (cnenidial filters or tentacles), hence drastically reducing the clearance rate and affecting retention efficiencies (see references above). *Haploops* individuals seemed to be highly stimulated even at low PIM concentrations. Also, the mean time individuals spent filtering increased along with the number of individual filtration events, but not the mean time of a filtration event (except one significant difference between 7.3 and 11.0 mg.L^{-1}). This behavior of numerous withdrawings in the tube is probably an adaptation to turbid environments, allowing the amphipod to increase the time filtering and to fully clear the antennae with its pereopods (and to reject pseudofeces pellets, as observed with videos). *Haploops* individuals are hence able to feed in turbid conditions, even if the food is diluted by inorganic matter, and to collect enough organic matter to cover their needs. We also suggest that the presence of a non-rigid sensory filament close to each seta is a mechanism that triggers the withdrawal of an individual into its tube when several filaments are being clogged by particles. The clogging is also limited by the distance between two bristles (ca. 20 µm) corresponding to the particles efficiently retained by *Haploops* antennae. For the amphipod *Corophium volutator*, Møller and Riisgård (2006) showed that the distance between two bristles on the gnathopods (filter organs) corresponds to the particle diameter retained with 100% efficiency (i.e. 6–7 µm). But even if *C. volutator* colonizes intertidal mudflats, this species lives in a burrow and uses its pleopods to create a current. *Haploops* antennae are directly out in the water column without any other protection, except withdrawing in its tubes. One can easily imagine that longer and closer bristles on setae would increase the antennae clogging speed.

4.3. Clearance rate in **Haploops nirae** *and grazing impact at ecosystem level*

The calculation of clearance rate (CR) can be biased by particles not retained by feeding organs and this bias increases with seston concentration (see details on CR calculations in Barillé et al., 1993). CRs were systematically lower with a high standard deviation when taking into account the entire ESD range, in comparison when using the 20–40 µm size range, corresponding to the particles retained with 100% efficiency. A mean CR of 1.06 ± 0.14 $L.h^{-1}$ was then calculated for each *Haploops* core, corresponding to a mean individual CR of 14.6 ± 0.4 $mL.h^{-1}$ (for a 7.2 ± 0.78 mm individual) and a standardized CR of 25.2 ± 0.7 $L.h^{-1}.g^{-1}$ dry meat weight. To our knowledge, the only study dealing with filtration in amphipods showed that mean individual filtration rate in C. volutator was 64 ± 5.9 $mL.h^{-1}$ for 6.3 ± 0.21 mm individuals (Møller and Riisgård, 2006). This value, while slightly above our results, falls within the same range of CRs even if clearance experiments were conducted in closed systems using exponential decrease in algal concentration. When using standardized dry weights (DW), *H. nirae* CR is 25.2 ± 0.7 $L.h^{-1}.g^{-1}$DW, while *C. volutator* is 47.2 $L.h^{-1}.g^{-1}$DW. One of the main differences between those two amphipod models was the actual feeding mode, since *H. nirae* is an obligatory suspension-feeder and *C. volutator* is able to switch between deposit- and suspension-feeding (Riisgård and Schotge, 2007). Another difference is that the ratio of the totalweight to the weight of the feeding organs is smaller in *H. nirae* – which utilizes two large setose antennae (Fig. 22A) – than in *C. volutator* which uses only collecting fans formed by setae on the second gnathopod. This probably means that if expressed as a function of feeding organs alone, the *C. volutator* suspension-feeding mode is more efficient (i.e. capable of straining a larger volume of water per unit time) than *H. nirae*.

Weight-standardized CRs of amphipods are much higher than those reported for suspension-feeders in other taxonomic groups such as bivalves (CR of *Crassostrea gigas*=4.2 L.h^{-1}.g^{-1}; Ropert and Goulletquer, 2000), gastropods (CR of *Crepidula fornicata*=0.76 L.h^{-1}.g^{-1}; Barillé et al., 2006) or polychaetes (CR of *Sabellaria alveolata*=0.35 L.h^{-1}.g^{-1}; Dubois et al., 2009). In numerous ecosystems where ampeliscid amphipods colonize large areas, dense tube mats and 'lawns' of feeding appendages can potentially have significant grazing impact on phytoplankton and on food web functioning (Sheader, 1998). However, while studies have demonstrated effects of *Ampelisca* mats on sediment remodeling and subsequent sediment stabilization and geochemical process (Diaz et al., 2008) or enhancement of associated species (Mackenzie et al., 2006), there is no quantitative evaluation of suspension-feeding pressure of amphipod mats. In a modeling approach designed to evaluated grazing impact by most dominant filter-feeding species in Odense Fjord, Riisgård et al. (2007) estimated that dense (18000 ind·m−2) population of the burrowing amphipod *C. volutator* is able to filter a volume of water equivalent to the entire column of about 25 times per day. In South Brittany (France), shallow coastal ecosystems are mainly composed of soft-bottom communities ranging from slightly muddy sandy communities to muddy communities and recent mappings involving acoustic side-scan sonar approach, Ehrhold et al. (2006) revealed that *H. nirae* was spreading over large areas in the bay of Concarneau (over ca. 3000 hectares) and in the bay of Vilaine (over ca. 7500 hectares). Using core samples, mean densities were estimated at 9950 ind.m^{-2} in the bay of Concarneau (min=3160; max=22 050 ind.m^{-2}) and 9820 ind.m^{-2} in the bay of Vilaine (min=1300; max=18 000 ind.m^{-2}) (Rigolet, Unpublished results). CRs values obtained for *Haploops* cores were considered representative of the entire habitat and were then extrapolated to each colonized area. Grazing impact of *H. nirae* is estimated to be 189.3 L.h^{-1}.m^{-2} and hence 136 10^{6} m^{3}.day^{-1} in the bay of Concarneau and 340 10^{6} m^{3}.day^{-1} in the bay of Vilaine. By using the numerical model MARS-3D (Lazure and Dumas, 2008), we estimated the timeneeded for the *Haploops* to filter a volume ofwater equivalent to the entire column is 4–5 days (assuming efficient verticalmixing andawater column height calculated for a mean tide) and the time needed to filter a volume of water equivalent to the whole bay of Concarneau or Vilaine is 29–30 days. Even if the grazing impact of *H. nirae* is less pronounced than that of *C. volutator* on intertidal communities (Riisgård et al., 2007), this study provides here evidences that tubiculous amphipod communities play a significant role in the food web within the ecosystem they colonize. Further regression or extension in *Haploops* communities are hence likely to adversely affect the balance of the coastal trophic web.

ARTICLE N°2

Life history and secondary production of the amphipod *Haploops nirae* (Kaim-Malka, 1976) in the Bay of Concarneau (South Brittany)

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Abstract

Haploops nirae is a gregarious tubiculous amphipod that creates dense tube mats in two ecosystems of South Brittany (i.e. the Bay of Vilaine and the Bay of Concarneau). To assess the ecological consequences of its recent expansion, the pattern of population dynamics of *H. nirae* was determined from January 2010 to March 2011 at a 29 m deep station in the Bay of Concarneau with a sampling interval of ca. 3 weeks (23 sampling dates). Modal analysis of size-frequency distribution at each date was used to describe the life cycle and the population dynamics of *H. nirae*, and to estimate the annual secondary production using the increment summation method. We showed that *H. nirae* is a semelparous species exhibiting a biannual life cycle with a lifespan ranging from 24 to 28 months. The recruitment was extremely high in 2010 and occurred between January and April but most recruits arrived at the end of March. Recruits are produced by two year old individuals, which die shortly after hatching. Female densities were low in winter. Females produced only one brood during their lifetime with an average brood size of 29. *H. nirae* secondary production was estimated at 9.66 gDW $m^{-2}y^{-1}$ and the production to biomass ratio (P/B) was 2.26 y^{-1}. Results are compared with previous published data on other Ampeliscid amphipods. The biannual life cycle appears unusual for most of Ampeliscidae except for the genus *Haploops* where a biannual life cycle appears characteristic of this genus. The secondary production calculated for *H. nirae* was high compared to other biannual Ampeliscidae species and constituted one of the highest production values calculated for an Ampeliscid.

1. Introduction

Ampeliscidae are common tubicolous amphipods, play important roles in ecosystem processes and are the dominant species in many soft-bottom communities inhabiting temperate and subarctic waters of the Atlantic and Pacific Oceans. However, very dense populations occur only in rare instances regardless of depth. Such populations occur in the Bay of Morlaix (English Channel) (Dauvin, 1988a, 1988b) and Jamaica Bay (New York) (Franz and Tanacredi, 1992) for the genus *Ampelisca*, the Shijiki Bay (Japan) (Sudo and Azeta, 1996) for the genus *Byblis*, or the Øresund (Sweden) (Göransson, 2002) and South Brittany (France) (Ménesguen, 1980; Bellan-Santini and Dauvin, 1988) for the genus *Haploops*. In each of these examples, amphipods represent a major component of the secondary production in coastal ecosystems, and production levels are among the highest observed for benthic invertebrate communities (e.g. Carrasco and Arcos, 1984; Highsmith and Coyle, 1990; Franz and Tanacredi, 1992). Moreover, several Ampeliscid species play significant ecological roles. Feeding primarily on phytodetritus, they require a high flux of phytoplankton to the bottom and greatly influence the pelagic-benthic coupling (Grebmeier and McRoy, 1989). They also constitute a major food source for higher-level consumers such as finfishes and marine mammals (Gallardo, 1962; Franz and Tanacredi, 1992; Highsmith and Coyle, 1992). Finally, the presence of dense tube mats of ampeliscid amphipods alters the biogeochemical fluxes and the composition of the surface sediments (MacKenzie et al., 2006). As underlined for many tubiculous, gregarious species, tube occurrences increase engineered habitat complexity and affect the local biodiversity but also modify the availability of resources and ultimately biological and sedimentary patterns (Berkenbusch and Rowden, 2007 and references therein).

The species *Haploops nirae* has been recorded from the Mediterranean Sea (e.g. south of France, Israel, Italy) and the Atlantic Ocean from the coast of Morocco to South Brittany, where it reaches its northern limit, at depths from 15 to 320 m (Dauvin and Bellan-Santini, 1990). In shallow waters of south Brittany, two coastal embayments (i.e. the Bay of Concarneau and the Bay of Vilaine) support very abundant and widespread populations of this species (initially misidentified as *Haploops tubicola* (Glémarec, 1969) as revised in Bellan-Santini and Dauvin (1988), with average densities around 10 000 to 15 000 ind.m^{-2} (unpublished data). The presence of high densities of *Haploops* creates an unusual macrobenthic community of thick and consolidated muds in contrast to the surrounding muddy and sandy benthic communities (Glémarec et al., 1986; Le Bris and Glémarec, 1996). In the Bay of Concarneau, surveys of the benthos revealed that *Haploops* habitat had expanded from 650 ha in 1963 to 3680 ha in 2003 (Glémarec, 1969; Ehrhold et al., 2006). As a consequence of this expansion, *H. nirae* is today the most abundant species in this bay.

The expansion of *Haploops nirae* in the Bay of Concarneau raises several issues regarding major changes in community structure and regional diversity, and probably in the functioning of the ecosystem. Nevertheless, the biology and ecology of *H. nirae* has been little studied and this species remains poorly known. As a suspension-feeder, it collects microalgae from the surrounding water by sweeping its antennae in the water column (Enequist, 1949; Rigolet et al., 2011). The weight-standardized filtration rate is 25.2±0.7 $L{\cdot}h^{-1}{\cdot}g^{-1}$DW which is much higher than those reported for many suspension-feeders, including bivalves, gastropods or polychaetes (Rigolet et al., 2011). While this gregarious species reaches densities of several thousand individuals m^{-2}, only fragmentary data are available on *H. nirae* population dynamics, despite a preliminary unpublished temporal survey of the macrobenthic communities in the Bay of Concarneau between November 1974 and March 1976 (Ménesguen, 1980).

To evaluate the potential ecological consequences associated with the expansion of *Haploops nirae* for the functioning of the marine ecosystem of the Bay of Concarneau, it is necessary to understand the life cycle, population dynamics, and rate of secondary production of *H. nirae*, which are the focus of this study. Results are analyzed in the light of previous data obtained for other Ampeliscid amphipods which form dense populations and are discussed according to the ecological importance of *H. nirae* in the Bay of Concarneau.

2. Materials and Methods

2.1. Study area and sampling protocol

Sampling was performed at one station (47°47.632’ N, 3°54.368’ W) in the eastern part of the Bay of Concarneau (Bay of Biscay) within the *Haploops* community from January 2010 to August 2011 (Fig. 29). The study site was located on muddy bottoms at ca. 29 m depth. Environmental data (i.e. surface water temperatures and chlorophyll *a* concentrations) were retrieved from the REPHY network (Phytoplankton and Phycotoxin monitoring network; IFREMER Quadridge Data base). This network was designed to monitor phytoplankton (diversity and total chlorophyll *a*) every two weeks over a total of 123 marine areas along the French coast. We selected the closest survey site available in the Bay of Concarneau (47°49.939’ N, 3°57.083’ W) during the temporal sampling period, January 2010 to August 2011; it was located about 2 nm from the population sampling site (Fig. 29). During the period of the study, sea surface temperatures ranged from 7°C in winter to 18°C in summer (Fig. 30a). In 2010, the phytoplankton bloom (proxied by water chlorophyll *a* concentration) consisted of one major peak with a maximum of 6.53 $\mu g.L^{-1}$ in May 2010 followed by a weaker bloom in autumn at 2.4 $\mu g.L^{-1}$ (Fig. 30b). In 2011 the spring phytoplankton bloom was much lower than in 2010, with chlorophyll *a* concentration not exceeding 2.7 $\mu g.L^{-1}$. Minimum chlorophyll *a* concentrations occurred in winter with values ranging from 0.29 to 2.02 $\mu g.L^{-1}$.

Benthic cores (inner diameter 12 cm; depth 25 cm; surface 113 cm^2) were collected by scuba divers at the study site. The sampling period lasted from January 2010 to March 2011 (15 months) with an approximately 3-week frequency (23 sampling dates). At each sampling date, 3 replicates were randomly extracted within a total surface of ca. 400 m^2. As a follow-up to the survey, one sampling date was added in August 2011 in order to compare with the results from August 2010. Cores were brought undisturbed to the laboratory, sieved on a 500 mm screen and preserved in 5% buffered seawater-formalin solution. Depending on *Haploops* densities, benthic cores were sub-sampled so that a sufficient number of individuals (minimum of 141 individuals, maximum of 459 individuals) could be obtained at each sampling time. This protocol allowed us to sort 25% of *Haploops* tubes for the densest (i.e. recruitment) periods up to 100% of *Haploops* tubes in most cases. *Haploops* were extracted from their tubes and densities of individuals were recorded for each sampling date.

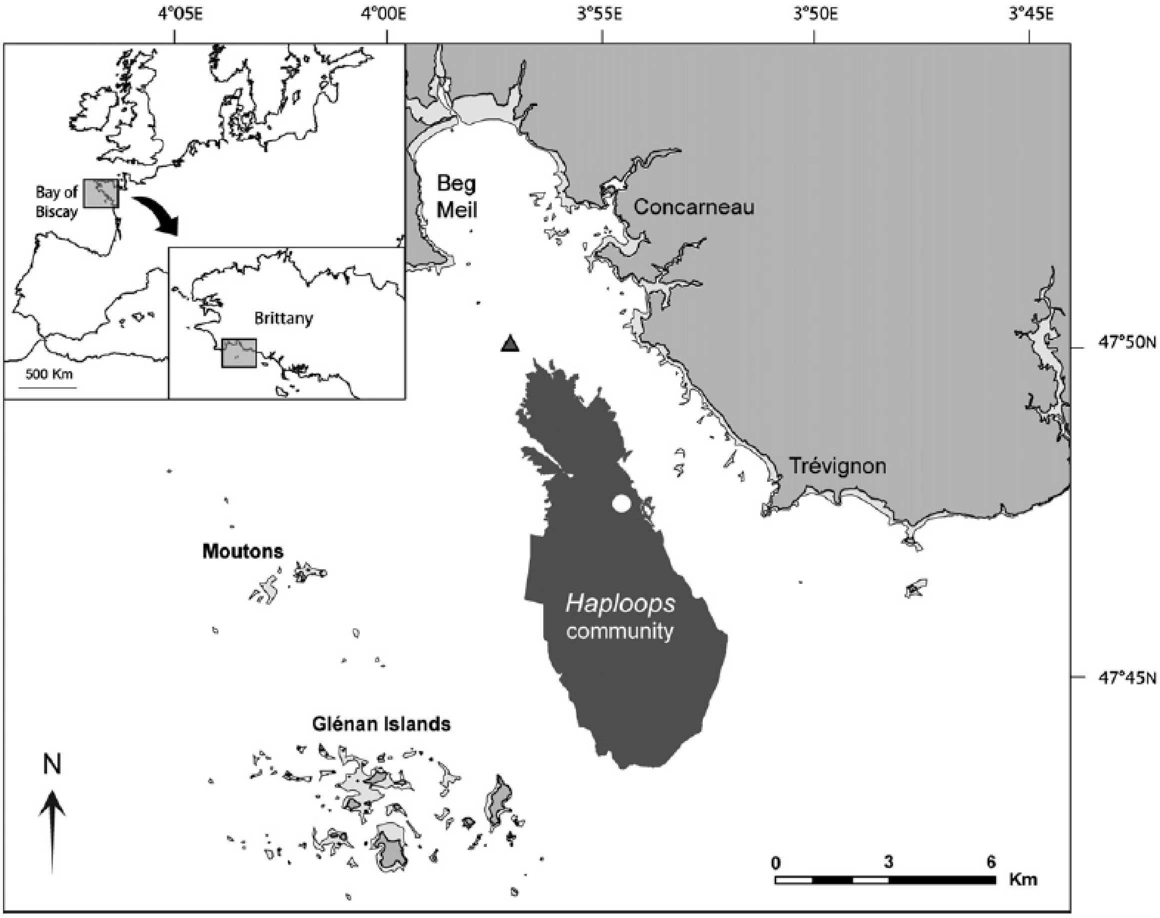

Figure 29 : Location of the study site in the Bay of Concarneau (Bay of Biscay). *Haploops* community is represented in dark grey, the study site is indicated by a white circle. Environmental parameters were retrieved from a monitoring station (triangle).

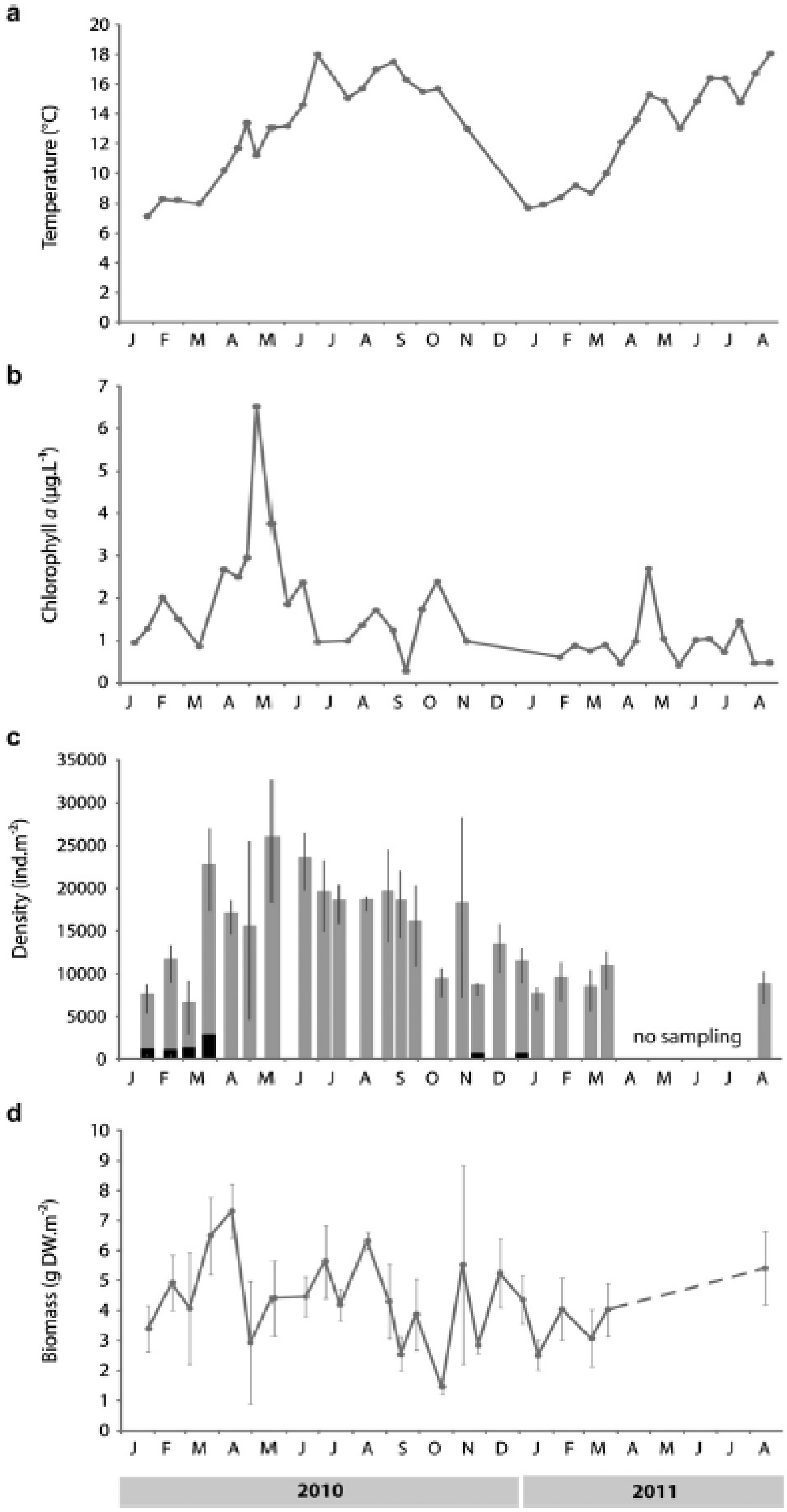

Figure 30 : Temporal variations in (a) sea surface temperature, (b) water chlorophyll *a* concentration of the study site, and (c) mean density ± SE with black areas corresponding to ovigerous females and (d) mean biomass ± SE of *Haploops nirae* by month during the study period.

2.2 Morphometrics

Previous studies dealing with Ampeliscid population dynamics revealed that several morphometrics can be used. Total body length (i.e. from the tip of the rostrum to the tip of the telson) was the most commonly measured parameter for different species of *Ampelisca* and *Byblis* (Carrasco and Arcos, 1984; Collie, 1985; Highsmith and Coyle, 1992). Cephalic length was used by Dauvin (1988a,b,c,d, 1989) to calculate production of 5 *Ampelisca* species of the western English Channel, and by Sudo and Azeta (1996) for *Byblis japonicus*. Others lengths such as the length of the antenna 2 peduncle and the length of the second segment of the antenna 1 peduncle were also selected to determine population dynamics of *Haploops fundiensis* (Wildish, 1984) and *Haploops nirae* (Ménesguen, 1980) respectively. Consequently, in order to use the most relevant biometric parameter, we tested the relationship among four morphometric measurements (i.e. body length, cephalic length, length of the first segment of the antenna 1 peduncle and length of the second segment of the antenna 1 peduncle) and the dry weight of *H. nirae*. For this purpose, 192 amphipods were measured using a proprietary image analysis system (Analysis® 3.1, Soft Imaging System GmbH) coupled to a binocular microscope (precision 0.01 mm), then dried at 60°C for 24 h, and weighted individually to the nearest 0.001 mg using an electronic microscale. Linear regression analyses were then carried out on log-transformed data to assess the length-weight relationships (Table 8). All morphometric parameters are strongly correlated to dry weight (DW), especially body length ($r^2 = 0.95$) and cephalic length ($r^2 = 0.93$). Because of the time necessary to properly estimate the body length of individuals due to curvature from preservation artifacts, and the similarity of the r^2 values, cephalic length (LC) was used as the morphometric parameter.

To describe the reproductive cycle of *Haploops nirae*, individuals were classified into 3 categories: (1) immature individuals, i.e. lacking distinctive morphological characteristics; (2) ovigerous females, i.e. with a marsupium, and (3) mature males, i.e. with numerous tufts of setae on antennae. In order to estimate female fecundity, the number of embryos carried by each brooding female was recorded. The relationship between the number of embryos and the cephalic length of females was determined. Since some embryos could have been lost during the sieving, only ovigerous females inhabiting undamaged tubes were selected for this estimation.

Table 8 : Linear regression coefficients between morphometric parameters and dry weight of *Haploops nirae*. DW = dry weight; LC = cephalic length; L1A1 = length of the first segment antenna 1 peduncle; L2A1 = length of the second segment antenna 1 peduncle; LT = body length.

	R²	Slope	Intercept	P value
Log (DW) vs Log (LC)	0.928	4.349	-0.146	<0.001
Log (DW) vs Log (L1A1)	0.827	4.022	0.772	<0.001
Log (DW) vs Log (L2A1)	0.828	4.103	-0.127	<0.001
Log (DW) vs Log (LT)	0.946	2.992	-3.174	<0.001

2.3. Data analyses

Temporal variations of *Haploops* density and biomass were assessed using a Kruskal-Wallis one-way analysis of variance test (Kruskal and Wallis, 1952). To quantify the sampling error on *Haploops* densities, we used the formula given by Elliott (1971) to estimate the number of samples necessary to a certain precision, according to the mean and the variance of the studied variable, such as:

$$n = \frac{s^2}{D^2 \times \bar{x}^2}$$

where n is the number of samples to collect (i.e. $n = 3$ in the present case), s^2 is the variance, $\bar{x}$ is the mean and D is the sampling error.

Modal analysis of size-frequency distribution at each date was performed according to the method of Bhattacharya (Bhattacharya, 1967) using the FiSAT II software (Gayanilo et al., 2005). For a dataset with multiple peaks the peaks are assumed to represent different cohorts each with an underlying normal distribution. This method provided the mean length, the standard deviation and the number of individuals per cohort. Temporal changes in the number of individuals and the mean cephalic length of each cohort from January 2010 to March 2011 were used to describe the survival curve and the mean individual growth curve of *Haploops nirae*, respectively. Mortality rate (Z) is calculated assuming an exponential decay model, expressing the decrease of a group of individuals born at the same time (i.e. a cohort) through time:

$$N_t = N_0 \times e^{-Z\,t}$$

where N_0 is the initial number of individuals at time zero, N_t is the number of remaining individuals at the end of time t and Z is the instantaneous rate of total mortality.

Secondary production for each cohort was calculated by the Increment Summation Method using the following equation (Crisp, 1984):

$$P_{0-T,i} = \sum_{t=0}^{t=T} \left(\left(N_{t,i} + N_{t+\Delta t,i} \right) \div 2 \right) \times \left(W_{t+\Delta t,i} - W_{t,i} \right)$$

where $P_{0-T,i}$ is the secondary production of the i^{th} cohort between time t = 0 and time t = T, $N_{t,i}$ is the number of individuals belonging to the cohort i at the time t, and $W_{t,i}$ is the average dry weight of the individuals belonging to the i^{th} cohort at time t.

The total annual production (i.e. secondary production) was then calculated as the summation of the production of each cohort. Productivity was assessed by the production to biomass ratio (P/B ratio), which relates production P to the average biomass B from the period of the study.

3. Results

3.1. Abundance and biomass of Haploops nirae

Temporal variations in *Haploops* density and biomass from January 2010 to March 2011 are represented in Fig. 30c and d, respectively. The abundances varied significantly throughout the year with a mean density (3 core samples) ranging from 6 800 ind. m^{-2} in March 2010 to 25 500 ind. m^{-2} in May 2010 ($p < 0.001$, Kruskal-Wallis test). The mean sampling error for 3 replicates in the estimates of *Haploops* densities remained low (i.e. 16.8%). *Haploops* density showed seasonal variations with the lowest values during winter, from January 2010 to early March 2010, followed by a rapid increase up to 25 000 ind. m^{-2} in spring, from March to June 2010. The period of high *Haploops* densities from March to June is characterized by strong variations in densities between successive sampling dates, related to the high spatial heterogeneity in *Haploops* distribution at a local scale. A gradual decrease occurred then from July to October 2010 followed by a new period at low densities from October 2010 to March 2011. In August 2011, mean densities were estimated at 8 300 ind. m^{-2} and were less than half those observed in August 2010 (i.e. 18 000 ind. m^{-2}). *Haploops* biomass also varied significantly over time from 1.47 g DW m^{-2} in October 2010 to 7.31 g DW m^{-2} in April 2010 ($p < 0.001$, Kruskal-Wallis test). As the total biomass is a function of the density but also the mean size of individuals, it fluctuated widely during the study period and exhibited a less obvious seasonal pattern despite a major peak in March-April 2010 and low values during winter. Secondary peaks were also observed in August 2010 and November 2010 (Fig. 30d).

Temporal variations in densities and biomass exhibited the same pattern as seasonal variations in environmental factors with the peaks in density and biomass reported during the spring warming, in phase with the phytoplankton bloom (Fig. 30).

3.2. Reproduction of Haploops nirae

Ovigerous females occurred in winter, from January 2010 to the end of March 2010 and from November 2010 to January 2011, suggesting a release of juveniles from the end of winter to the early spring corresponding with the density peak. The percentage of ovigerous females in the population was highly variable during the two winters. While it ranged between 4.5% and 12% in 2010, fewer brooding females representing 0.5 to 0.64% of the population were recorded in 2011. No mature male was observed during the study period. Sizes of ovigerous females analyzed during the study (71 individuals) spanned from 0.81 to 1.56 mm cephalic length (7.6 to 19.6 mm body length) with a mean size of 1.08 mm cephalic length (11.5 mm body length).

Females found in undamaged tubes (41 females) carried between 12 and 71 eggs with a mean number of 29 embryos per female. There was a significant linear relationship between brood size (N) and female cephalic length (LC), as $N = 117.7\ Lc - 98.72$ ($r^2 = 0.373$, $N = 41$, $p < 0.001$) (Fig. 31).

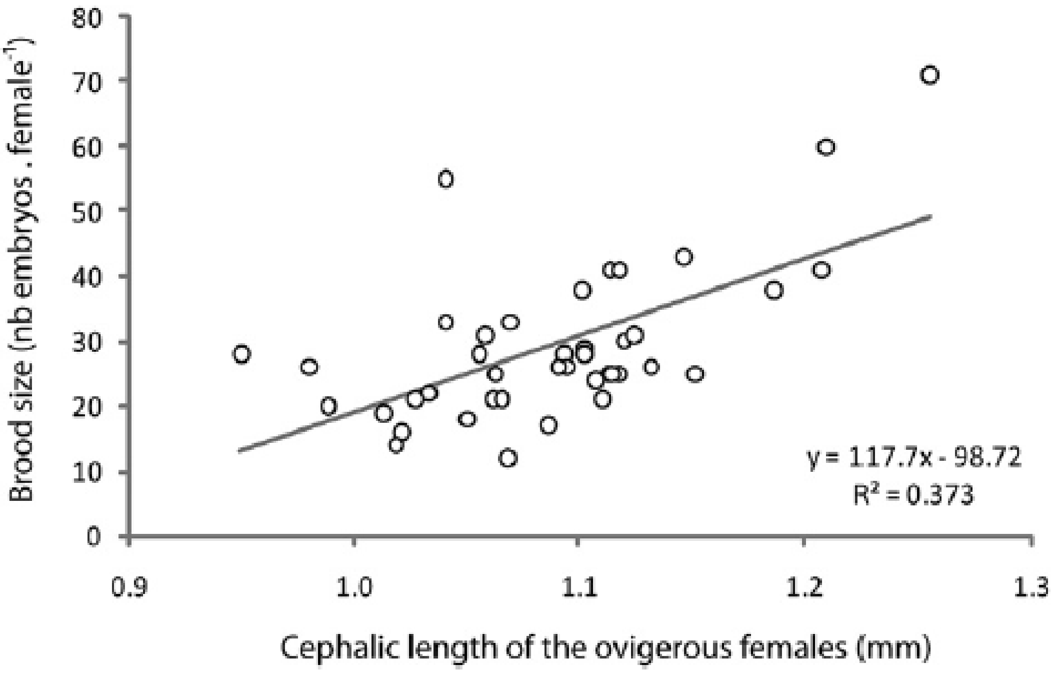

Figure 31 : Relationship between the brood size and the cephalic length of ovigerous females in *Haploops nirae*.

3.3. Modal analysis

Size-frequency distributions revealed a polymodal structure of the population with two or three cohorts (hereafter Classes 2008 to 2011) identifiable at all sampling times (Fig. 32). Only one recruitment event was observed in 2010. This cohort, Class 2010, recruited between the end of January 2010, or even earlier and April 2010 but the appearance of recruits in the population retained on a 500 mm screen occurred mainly at the end of March (Fig. 32). In late March, the Class 2010 accounted for 55% of the total population versus 14-22 % in January to early March. During months following March, the Class 2010 constituted the major part of the population forming between 45 and 97% of the population. This cohort was produced by the Class 2008 which was sexually active between January and March 2010 as indicated by the presence of ovigerous females. The Class 2008 disappeared after reproduction by the end of March 2010. The Class 2009 was probably recruited in winter-early spring 2009, grew during 2010 and matured during the winter 2010-2011. It produced the Class 2011 which recruited at the beginning of 2011 (January-March 2011, Fig. 32). In agreement with the previous observation where the Class 2008 died by March 2010, the Class 2009 disappeared by March 2011. However, while the Class 2008 constituted 32 to 52% of the population in early 2010, the Class 2009 accounted for only 2 to 4 % of the population at the same period of the year 2011. In the same way, recruits accounted for only 0 to 8 % of the total population in early 2011 (i.e. January to March) while they accounted for 18-53 % of the total population in early 2010. Consequently, the low recruitment event observed in 2011 was related to the low proportion in mature adults observed between the end of 2010 and March 2011. The beginning of the year 2011 was thus characterized by the scarcity of mature adults (Class, 2009), low densities of recruits (Class, 2011) and by the high proportion of one-year-old individuals (Class, 2010) compared to the situation described one year earlier. The additional sample from August 2011 indicated that juveniles were present at a very low density compared to the situation in August 2010 (Fig. 32). This sample confirmed the low recruitment in early 2011 and that no additional recruitment occurred in 2011 beyond the sampling period.

According to size-frequency data, the lifespan of *Haploops nirae* was estimated to be 24 and 28 months. *H. nirae* was hence considered as a biannual semelparous species, with 2 year-old females producing one brood during their life and dying after hatching. Presumably the males similarly die post-reproduction but no mature males were seen in the samples.

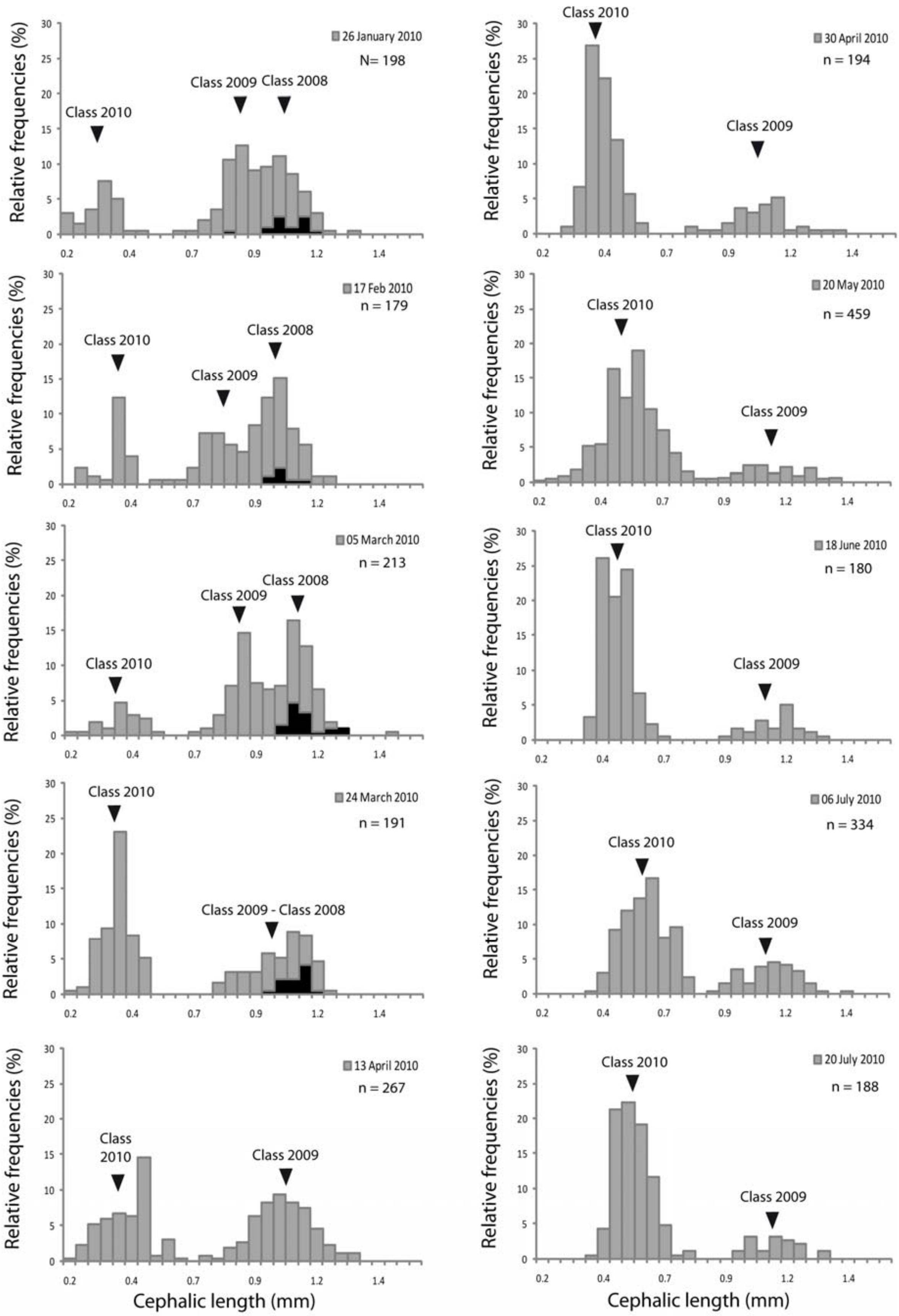

Figure 32 : Length-frequency distribution of *Haploops nirae*. Sampling dates are indicated. n = number of individuals measured. Triangles indicate average cephalic length of each Class. Black bars correspond to ovigerous females.

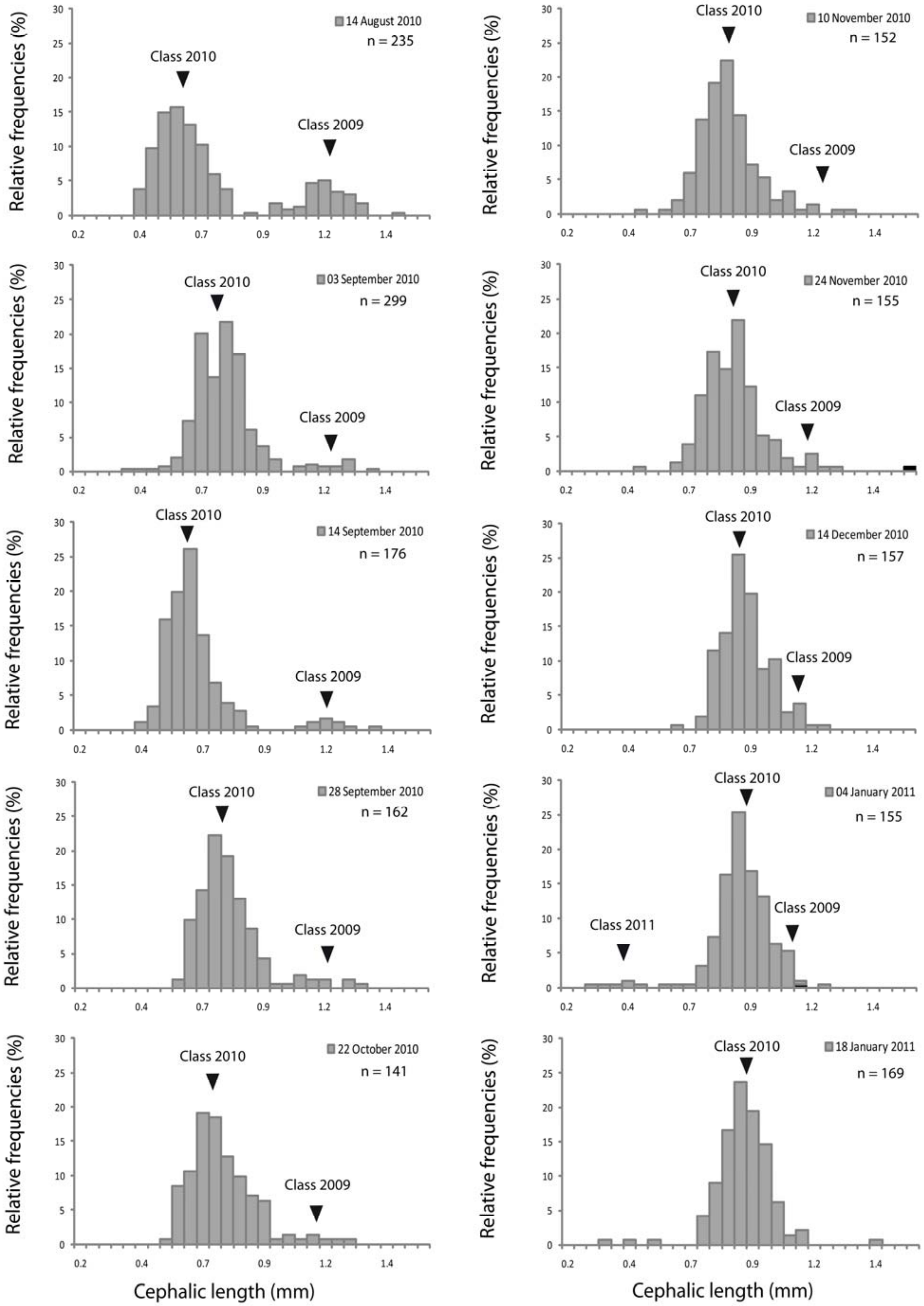

Figure 32 *(continued)*

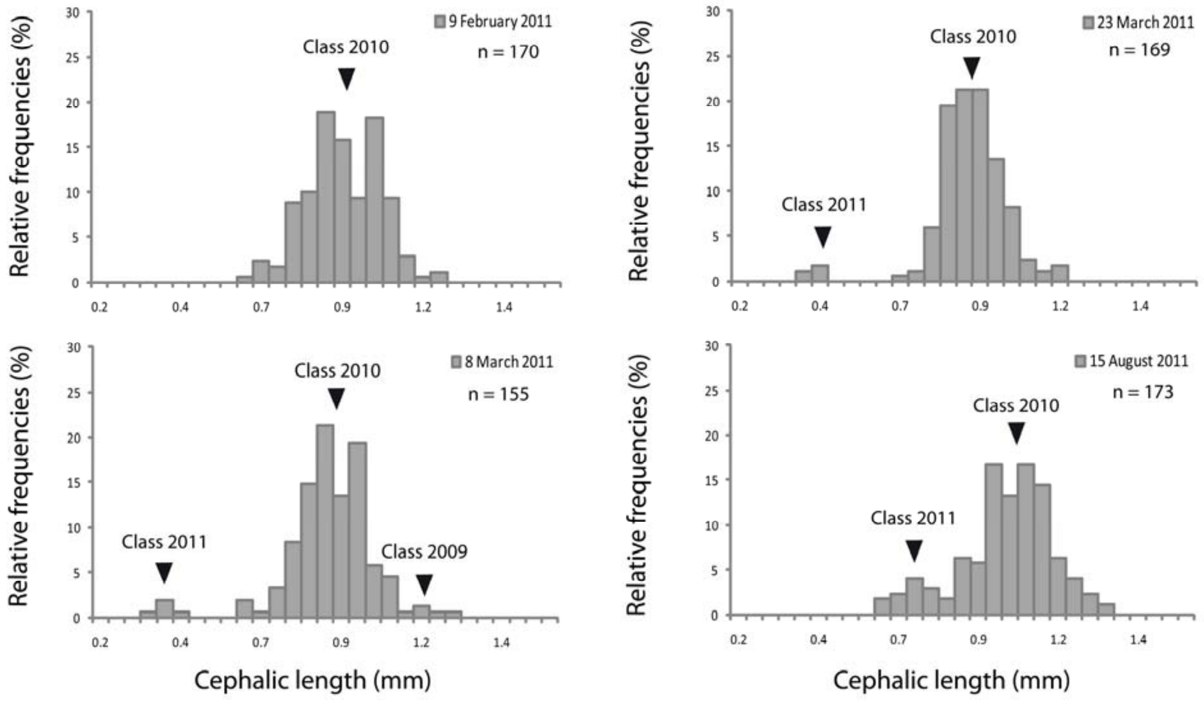

Figure 32 *(continued)*

3.4. Growth and survival curves

Although growth appeared continuous throughout the life cycle of *Haploops*, it exhibited both seasonal and age-specific variation (Fig. 33). Following hatching of juveniles at a mean cephalic length of around 0.3 mm (2.81 mm body length), growth of *Haploops* during their first year of their life was split into two phases as observed for the Class 2010: a phase of rapid growth from April to November which corresponded to the period of high water temperatures and a less rapid phase of growth in winter when water temperatures were the lowest. At the end of the first year, *Haploops* reached a cephalic length of 0.80 - 0.85 mm (7.9 mm body length). During the second year of an individual's life span (i.e. Class, 2009), growth showed a slightly different pattern compared to one year-old individuals. Growth of overwintered individuals resumed only from February to July and ceased in summer when they reached a cephalic length of 1-1.2 mm (11.2 mm body length). Mean cephalic length of two year-old individuals remained largely unchanged during the last 8 months of their life span (Fig. 33). The maximal cephalic length observed was 1.18 mm for some individuals collected in August 2010.

Mortality of *Haploops nirae* was estimated for the Class 2010 from the decrease in the number of individuals throughout the time of the study (Fig. 34). The number of individuals in the cohort was the highest in May 2010; so we used this as the initial point on the survivorship curve. Assuming an exponential decay curve, the mortality rate of *H. nirae* was estimated at $2.8.10^{-3}$ day^{-1} ($r^2 = 0.723$, $n = 18$, $p < 0.01$). At the end of the first year (i.e. December 2010), around 11 000 $ind.m^{-2}$ (52% of the Class 2010) were still present. In August 2011, more than 6 000 $ind.m^{-2}$ (29% of the Class 2010) were present having survived more than one year.

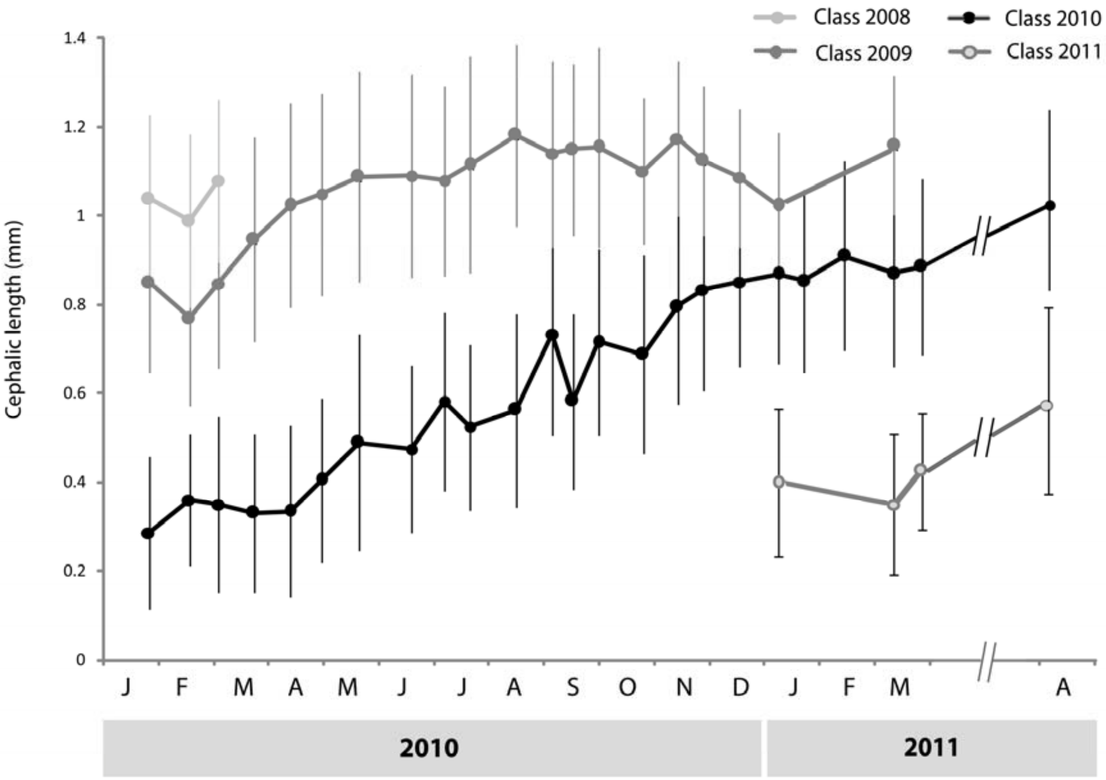

Figure 33: Growth curves of *Haploops nirae* at the study site for cohorts born in 2008 (Class, 2008), 2009 (Class, 2009), 2010 (Class, 2010) and 2011 (Class, 2011). Bars represent standard deviation.

3.5. Estimation of secondary production

Annual secondary production was calculated from temporal changes in the densities and mean weight of each Class during the period from March 2010 to March 2011. The annual production of each Class was estimated at 4.33 gDW m^{-2} y^{-1}, 5.33 $gDWm^{-2}y^{-1}$and 0.004 gDW m^{-2} y^{-1} for Classes 2009, 2010 and 2011, respectively. The total annual production was therefore estimated at 9.66 gDW m^{-2} y^{-1}. With an annual mean biomass equal to 4.3 gDW m^{-2}, the annual P/B ratio was calculated at 2.26 y^{-1}.

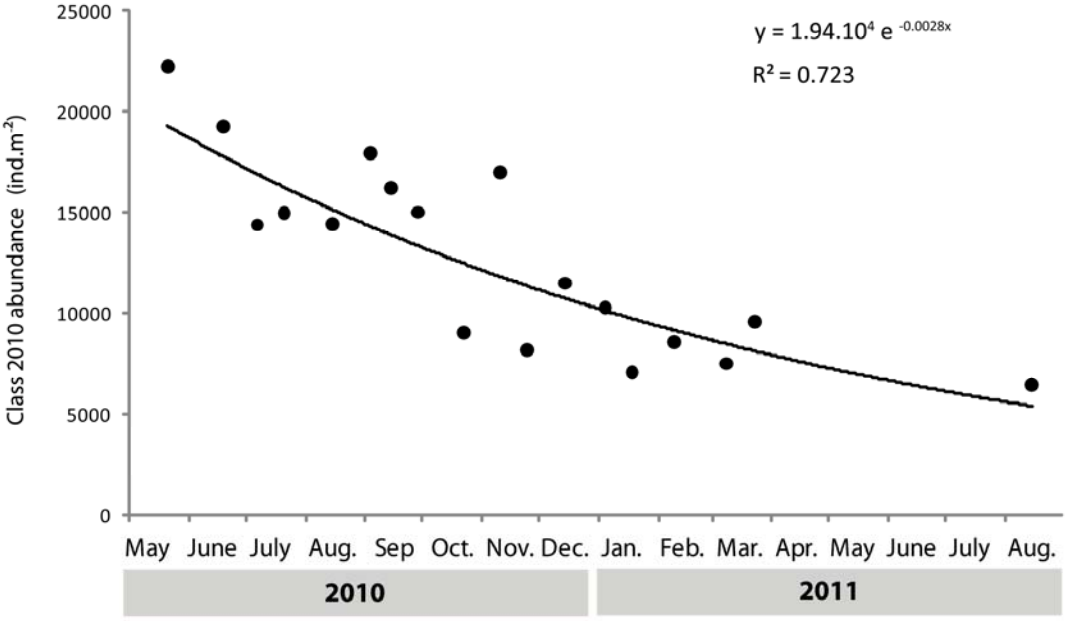

Figure 34 : Survival curve showing the number of individuals in the Class 2010 over the study period.

4. Discussion

4.1. Densities in **Haploops** *habitat*

Mean densities of *Haploops nirae* recorded in this study, ranging from 6 800 to 25 500 ind.m^{-2} over the sampling period, are the highest reported for the genus *Haploops* (Table 9). Other investigations of the genus *Haploops* have reported lower densities of *Haploops fundiensis* (Bay of Fundy, Canada) around 376 ind.m^{-2} (Wildish, 1984) or *Haploops laevis* in the East Siberian Sea (Russia) ca. 400 ind.m^{-2} (Gukov, 2011). As for *Haploops tenuis* and *Haploops tubicola*, their densities dramatically declined during the last 100 years in the Øresund (Sweden) where they were first reported, decreasing from 3 500 in 1912 to 100 ind.m^{-2} today (Göransson, 2002; Göransson et al., 2010). Ménesguen (1980) reported mean densities of *H. tubicola* (revised as *H. nirae*) of 3 200 ind.m^{-2} (max 8 600 ind.m^{-2}) in the Bay of Concarneau (France). Our results indicate higher densities of *Haploops* in this area (up to 35 000 ind.m^{-2} for one core sample), hence emphasizing the importance of this species in this benthic habitat and its likely important ecological role. Densities exceeding 10 000 ind.m^{-2}

have been observed elsewhere in temperate waters for different species from the genus *Ampelisca*: *Ampelisca abdita* in Barnstable Harbor (Massachusetts): 146 200 ind.m^{-2} (Mills, 1967); *Ampelisca araucana* off the central coast of Chile: 11 280 ind.m^{-2} (Carrasco and Arcos, 1984); *Ampelisca agassizi* off British Columbia: 150 007 ind.m^{-2} (Oliver et al., 1984); *Ampelisca armoricana* in the Bay of Morlaix (English Channel): 31 494 ind.m^{-2} (Dauvin, 1988d) (Table 9).

4.2. Life cycle of **Haploops nirae**

A life span of 24 to 28 months was estimated for *Haploops nirae* consistent with a study on a similar species *Haploops fundiensis* (24 to 30 months) in the Bay of Fundy (Wildish, 1984). These values are higher than those reported for the genus *Ampelisca* (Table 9). For most *Ampelisca*, lifespan does not exceed one year for temperate species. Only the cold temperate species *Ampelisca agassizi* and the subarctic species *Ampelisca macrocephala* have a maximum life span of 2 and 3 years respectively. This broad latitudinal variation in lifespan among species is in good agreement with the metabolic theory of ecology which predicts that life span decreases with temperature and body mass: lifespan is longer for species living in boreal areas at low temperatures as already reported for amphipods (Gillooly et al., 2001; Wildish et al., 2011). The relatively long lifespan of *H. nirae* which inhabits temperate waters could be related to among species differences in biological rates (Gillooly et al., 2001) and to local factors such as food availability, local adaptation and population density (Munch and Salinas, 2009). For example, for a species from a genus associated with cold waters, phylogenetic constraints may influence the lifespan.

For *Haploops nirae*, a single recruitment event occurred annually in winter and early spring (Fig. 32). This is also the time when ovigerous females were recorded (November to March); their densities were low, never exceeding 12% of the population. Modal analysis and growth curves indicated that recruits are produced by two year old individuals which achieve sexual maturity and die shortly after hatching of the juveniles (Fig. 32). Growth of the juveniles was rapid from May to November during their first year and then slowed down during the winter months (Fig. 33). Growth resumed in the next spring, from February to July before stopping probably when gametogenesis was initiated. Growth rate was higher during the first year than during the second. *H. nirae* is a semelparous species exhibiting a biannual

	Brood size (min-max)	Adult size (mm)	Mesh size (mm)	Life span (months)	Mean density (no.m^{-2}) (year of sampling)	Maximum density (no.m^{-2})	Number of generation/year	Production (P) (g. DW.m^{-2}.y^{-1})	P/B (y^{-1})	Area	Reference
Ampelisca abdita	-	6.5	1	10 - 12	25400 - 38300 (1988 - 1989)	73800 - 94600	2	25.3 - 47.1	3.53 - 4.16	Jamaica Bay	Franz and Tanacredi, 1992
Ampelisca agassizi	-	10	0.3	15 - 24	2660 (1981 - 1983)	6200	0.5	2.2	1.4 - 1.6	Georges Bank	Collie, 1985
Ampelisca araucana	-	7.2	0.5	7	4500 (1976 - 1977)	11800	2	8.03 - 9.79	3.65 - 4.45	Bay of Conception	Carrasco and Arcos, 1984
Ampelisca armoricana	40 - 55	13.2	0.5	12	142 (1985 - 1986)	315	1	9.65	2.57	English Channel	Dauvin, 1988d
Ampelisca birulai	12	12	1	-	790 (1986 - 1988)	930	0.5	6.73	0.9	Northern Bering Sea	Highsmith and Coyle, 1992
Ampelisca brevicornis	12 - 43	15.4	-	13	-	380	1	1.0	4.0	North Sea	Klein et al., 1975
Ampelisca brevicornis	22 - 70	15.8	0.5	14	284 (1978 – 1979)	1314	1	1.31 - 1.68	2.49 - 3.21	Isle of Man	Hastings, 1981
Ampelisca brevicornis	19 - 48	16	0.5	4 - 12	-	403 - 501	1.5	0.04 - 0.3	2.15 - 2.80	English Channel	Dauvin, 1988b
Ampelisca macrocephala	40 - 80	30	1	36	2400 (1986 - 1988)	2520	0.5	31.2	0.87	Northern Bering Sea	Highsmith and Coyle, 1992
Ampelisca sarsi	8 - 21	6.5 – 7.3	0.5	12	613 (1985 - 1986)	1130	1	0.02 - 1.0	1.93 - 2.99	English Channel	Dauvin, 1989
Ampelisca spinipes	-	-	-	24	-	-	1	0.2	2.4	South Brittany	Glemarec and Menesguen, 1980
Ampelisca tenuicornis	13 - 45	10.5	-	12 - 15	-	400	1.5	0.2	3.4	Northeastern England	Sheader, 1977
Ampelisca tenuicornis	18 - 56	9.8 – 10.5	1	4 - 12	- (1977 - 1978)	4000 - 6000	2	0.7 - 1.7	3.12 - 4.2	English Channel	Dauvin, 1988a
Ampelisca typica	20 - 50	10.5	0.5	4 - 12	235 (1985 - 1986)	1020	2	0.07 - 0.16	4.06 - 4.36	English Channel	Dauvin, 1988c
Byblis japonicus	9 - 55	11.4 - 13.2	0.5	3 - 8	1924 (1982 - 1983)	4100	3	7.53	10.83	Japan	Sudo and Azeta, 1996
Byblis spp.	25	-	1	-	993 (1986 - 1988)	1250	-	3.73	1.33	Northern Bering Sea	Highsmith and Coyle, 1992
Haploops fundiensis	2 - 13	7 - 8	0.5	24 - 30	376 (1978 - 1980)	923	0.5	0.2 - 1.8	1.29 - 2.04	Bay of Fundy	Wildish, 1984
Haploops tenuis	30 - 40	8 - 9	-	24 - 36	-	-	0.5	-	-	Oresund	Kanneworff, 1966
Haploops nirae	-	-	-	30	8200	-	0.5	-	-	South Brittany	Menesguen, 1980
Haploops nirae	12 - 71	11.5	0.5	24 - 28	14400 (2010 - 2011)	25500	0.5	9.66	2.26	South Brittany	This study
Haploops tubicola	40 - 50	10 - 11	-	36	-	-	-	-	-	Oresund	Kanneworff, 1966

Table 9 : Literature data review on life cycle, production and productivity for common ampeliscids amphipods.

life cycle, which seems to be typical of members of the *Haploops* genus but unusual for other Ampeliscids (Table 9). Except for *Ampelisca agassizi* which is also a biannual species, all other Ampeliscids from the genera *Ampelisca* and *Byblis* are either univoltine, bivoltine or trivoltine.

It is of note that no males were recorded during this survey. The scarcity of mature males in the *Ampelisca* genus has been reported by many authors. Hastings (1981) indicated that only mature males were active in the water column, presumably searching out sexually receptive females which remain in the sediment. Other author (e.g. Kanneworff, 1966) indicated that the mature male is a fleeting stage where males copulated with females in the water column and then died. According to Sheader (1977), Hastings (1981) and Dauvin (1989), mature males of *Ampelisca* are generally found in the water column and are consequently absent from grab samples. This is likely to be the case for *Haploops nirae*, since no mature males were identified in this study and only a few (2 individuals) were found during a macroinfauna survey in November 2010 (unpublished data).

Females of *Haploops nirae* have a brood size ranging from 12 to 71 embryos; the average brood size was 29 embryos per female. This mean reproductive effort is close to the brood size estimated by Kanneworff (1966) for *Haploops tenuis* (30-40 eggs) in the Øresund but much higher than that reported for *Haploops fundiensis* (2-13 eggs) in the Bay of Fundy (Wildish and Dickinson, 1982). A small brood size is probably related to the slow growth and the small size of *H. fundiensis*. Previous authors (Hastings,1981; Dauvin, 1988a; Sainte-Marie, 1991) found a significant linear relationship between the brood size and the female body length in Ampeliscids. Our investigation supports this relationship: the largest females of *H. nirae* can produce up to 70 embryos which is slightly lower than the maximal fecundity observed for some large Ampeliscid species (i.e. *Ampelisca macrocephala*: 40-80 embryos) (Table 9). *H. nirae* do not appear to exhibit higher fecundity than other amphipods with the same body size in general or than ampeliscidae in particular (Sainte-Marie, 1991); so, there is no evidence for an increase in fecundity with age beyond the relationship with size. According to Wildish (1979, 1982), the reproductive potential of an amphipod population is related to the number of embryos per brood but also to the number of broods per female and the proportion of reproductive females in the population. Despite a moderate to high fecundity, the reproductive strategy of *H. nirae* does not solely explain the success of this species in the Bay of Concarneau, as the percentage of ovigerous females in the population is low and females reproduce only once in their lifetime. From the calculation of the reproductive potential (R) for *H. fundiensis*, *H. tenuis* and *Haploops tubicola*, Wildish (1982) pointed out that R values for these biannual species as expected was considerably lower than those of annual and semiannual amphipods with more reproductive events per year.

Our study suggested that abundances of *Haploops nirae* followed a seasonal pattern and co-varied with water temperatures, with a maximum abundance in early spring and a minimum in winter. Recruitment of juveniles into the population is synchronous with the peak of chlorophyll *a* concentration (Fig. 30). *Haploops* are suspension-feeders and the arrival of recruits coincides with an increase in food availability and thus favorable conditions for growth and survival of juveniles. According to several investigations (e.g. Klein et al., 1975; Ménesguen, 1980; Hastings, 1981), reproduction of ampeliscid species living in the northern part of their distribution is strongly influenced by water temperatures. Klein et al. (1975) noticed that reproduction of *Ampelisca brevicornis* began when water temperature exceeded 10 C°, hence explaining the occurrence of only one recruitment event per year in the North Sea, while reproduction of the same species occurred throughout the year in the warmer waters of the Mediterranean Sea. For the same species, Dauvin (1988b) reported an intermediate reproductive cycle between univoltism and bivoltism in a study site located in the middle of its biogeographic distribution (i.e. English Channel). The *Haploops* genus is typically associated with deep and cold waters (Dauvin and Bellan-Santini, 1990). However, *H. nirae* occurs from south Brittany to the Mediterranean coast, (including North Africa) and therefore exhibits a Lusitanian-like distribution. In the northernmost part of its distribution, *H. nirae* exhibits reproductive traits similar to species typically found in boreal waters (e.g. reproduction during the second year of life, reproduction in winter, relatively low fecundity, long lifespan).

The composition of the population was not similar in 2011 to 2010. While in both years, recruits first appeared in January, densities of new recruits were an order of magnitude lower in early 2011 compared to the previous year at the sampling site (Fig. 32). The additional samples collected in August 2011 confirmed that recruitment was actually low in 2011 and not merely delayed. Low recruitment in 2011 is the consequence of low recruitment in 2009 (i.e. Class, 2009) and a low survivorship of these individuals during the second year of their lifespan yielding few reproductive adults (Fig. 32). In contrast, the high recruitment in 2010 was driven by the abundance of reproductive individuals, Class 2008. Our investigation suggested that a strong heterogeneity in recruitment occurred between years, implying that population dynamics of *Haploops nirae* - and subsequently the extension of the population - can be adversely affected by large inter-annual variabilities. These strong fluctuations in recruitment between two successive years can ultimately lead to stronger intraspecific competition between juveniles issued from a successful recruitment (Class, 2010) and far less abundant adults (Class, 2008 and Class, 2009). Competition for both space and food is strongly size-dependent and could probably explain why most individuals from the Class 2009 were lost before they reached sexual maturity.

According to Ménesguen (1980), many of the structuring species of benthic assemblages from the Bay of Concarneau (e.g. *Ampelisca spinipes* and *Ampelisca brevicornis*, *Owenia fusiformis*, *Maldane glebifex*, *Amphiura filiformis*, *Nucula turgida*) exhibited two recruitment events per year, spring and fall. The timing of recruitment of *Haploops nirae*, winter-early spring, and the potential of very large numbers of recruits of *H. nirae* due to direct development could then partly explain the success of this species within the bay by allowing the settlement of new recruits of *Haploops* before the recruitment of other competitors. The modification of the habitat engineered by *Haploops* tube-building activity (sediment features, sediment-water interface fluxes, changes in spatial niche) could inhibit the settlement of other species or reduce their survivorship. Global changes in environmental parameters could also partly explain the spreading of the *Haploops* community in South Brittany. Le Bris and Glémarec (1995) suggested that eutrophication occurring in South Brittany coastal waters could favor small suspension-feeders, such as *Haploops*. Also, increases in human fishing activities (dredging and trawling) off south Brittany coasts (Grande Vasière) ultimately resulted in increases in sediment resuspension and coastal turbidity and were suspected to facilitate populations of tubiculous species (Hily et al., 2008).

4.3. Production and ecological role of **Haploops** *habitat*

The annual secondary production of *Haploops nirae* during the period March 2010 to March 2011 was estimated at 9.66 gDW m^{-2} y^{-1} with a P/B ratio of 2.26 y^{-1}. Published production values for Ampeliscid species span a broad range, from 0.02 to 47.1 gDW m^{-2} y^{-1} with most values between 0.1 and 1 gDW. $m^{-2}.y^{-1}$ (Table 9). For *Haploops fundiensis*, which is the only production value for the genus *Haploops*, Wildish (1984) reported an annual production of 0.2 gDW. $m^{-2}.y^{-1}$. The production calculated for *H. nirae* in south Brittany falls within the highest values calculated for an Ampeliscid, close to those measured for *Ampelisca armoricana* and *Ampelisca araucana* (Table 9).

For marine amphipods, Dauvin (1989) found a positive significant relationship between the number of generations per year (G) and the values of the P/B ratio such as: $\log (P/B) = 0.18\ G + 0.24$. This relationship predicts a mean P/B of 2.64 y^{-1} for species with one generation per year, a P/B of 3.97 y^{-1} for species with two generations per year and a P/B of 13.55 y^{-1} for species with five generations per year. Following this relationship, the P/B ratio predicted for a biannual species is estimated at 2.14 y^{-1} and is in good agreement with the P/B calculated for *Haploops nirae* (i.e. 2.26 y^{-1}). According to the same author, seawater temperature is also a major factor affecting benthic amphipod populations: organisms inhabiting warmer regions exhibit faster growth, shorter lifespans and higher metabolic rates, increasing their productivity. Consequently, a reduction of the P/B ratio was also related to the geographic position, the populations from the cold water having a smaller P/B ratio. As an example, the biannual species *Ampelisca agassizi* with a low P/B ratio (i.e. 1.4-1.6 y^{-1}) lives in the Georges Bank area where the bottom seawater temperature ranges from 2 to 8°C over one year. In contrast, the trivoltine *Byblis japonicus* with an unusually high P/B ratio (i.e. 10.83 y^{-1}) lives in the Shijiki Bay (Japan) where the bottom seawater temperature ranges from 12 to 26°C. In this context, *H. nirae* exhibited a higher productivity than other biannual species like *A. agassizi* in the Georges Bank or *Ampelisca birulai* and *Ampelisca macrocephala* in the northern Bering Sea (Table 9). Despite its biannual life cycle, *H. nirae* exhibits a P/B value close to the values recorded for univoltine Ampeliscidae species living in temperate waters in the English Channel, the Irish Sea or south Brittany (e.g. *Ampelisca sarsi*, *Ampelisca spinipes*, *Ampelisca armoricana*) (Table 9).

Wildish (1984) calculated the P/B ratio for *Haploops fundiensis* using two different approaches. The size-frequency method yielded a P/B value of 2.04 y^{-1}, which is close to the present estimation for *Haploops nirae* of 2.26 y^{-1}. The summation of losses method yielded a P/B value of 1.29 y^{-1}, which is closest to the productivity of ampeliscid species of cold waters (e.g. *Ampelisca agassizi* in Georges bank or *Ampelisca birulai* in the Bering Sea), but half of the value estimated here for *H. nirae*.

The *Haploops* community occupies a large area in the Bay of Concarneau (ca. 3600 ha) which has increased by 400% over the last 2 decades. If we assume that productivity is homogeneous over the whole *Haploops* community, the ecological significance of the temporal changes in the macrobenthic communities of the Bay of Concarneau over the last decades can be evaluated by comparing our production estimation with previous results obtained by Glémarec and Ménesguen (1980) and Ménesguen (1980). Three benthic communities (*Amphiura filiformis*, *Nucula turgida* and *Haploops* communities) were investigated in 1974-1975, and secondary production of the dominant species in each community were estimated (Table 10). At that time, the *Amphiura* community was dominated by *A. filiformis*, *Abra alba*, *Cirolana borealis* and *N. turgida* which produced 15.7, 1.7, 3.5

and 10.2 gDW $m^{-2}y^{-1}$ respectively. The *N. turgida* community was dominated by *A. alba*, *C. borealis*, *Maldane glebifex* and *N. turgida* which produced in this area 3.2, 3.7, 2.2 and 3.7 gDW $m^{-2}y^{-1}$ respectively. The *Haploops* community was also investigated but the authors failed to calculate the *Haploops* secondary production. These data (Table 10) indicate that the structuring species from the *A. filiformis* community produced around 31 gDW $m^{-2}y^{-1}$, while 12.9 gDW $m^{-2}y^{-1}$ was produced by the structuring species from the *N. turgida* community. *Haploops* is by far the dominant species in its community. Secondary production of the *Haploops* community can therefore be estimated from the data presented here as 9.66 gDW $m^{-2}y^{-1}$, close to the value calculated for the *N. turgida* community in 1974 (i.e. 12.9 gDW $m^{-2}y^{-1}$) but much less than the estimate of production for the *Amphiura* community (i.e. 31 gDW $m^{-2}y^{-1}$). As a result, the extension of the *Haploops* community probably leads to an overall loss in benthic production when replacing the *Amphiura* community. While previous investigations showed that large *Ampelisca* spp. communities are amongst the most productive benthic communities (Highsmith and Coyle, 1990; Franz and Tanacredi, 1992), we show here that an ampeliscid community can take over more productive areas and does not necessarily result in an increase in secondary production.

Table 10 : Comparisons in estimates of secondary production (g dry weight.m^{-2}. y^{-1}) in *Haploops* community (this study) and the two surrounding muddy communities of the bay of Concarneau, after Glémarec and Menesguen (1980) and Menesguen (1980).

Period studied	**1974-1975**	**1974-1975**	**2010-2011**
Community	Muddy sands of *Amphiura filiformis*	Sandy muds of *Nucula turgida*	Consolidated muds of *Haploops nirae*
Dominant species	*Abra alba* : P = 1.67 g m^{-2}. y^{-1} (P/B = 3.3)	*Abra alba* : P = 3.18g m^{-2}. y^{-1} (P/B = 4.0)	*Haploops nirae*: P = 9.66 g m^{-2}. y^{-1} (P/B = 2.3)
	Cirolana borealis : P = 3.51 g m^{-2}. y^{-1} (P/B = 2.2)	*Cirolana borealis* : P = 3.72 g m^{-2}. y^{-1} (P/B = 2.3)	
	Nucula turgida: P = 10.20 g m^{-2}. y^{-1} (P/B = 2.4)	*Nucula turgida*: P = 3.74 g m^{-2}. y^{-1} (P/B = 3.7)	
	Amphiura filiformis : P = 15.70 g m^{-2}. y^{-1} (P/B = 2.9)	*Maldane glebifex*: P = 2.21 g m^{-2}. y^{-1} (P/B = 4.31)	

5. Conclusions

Haploops nirae is a biannual species which appears unique to the *Haploops* genus within the family Ampeliscidae, contrasting with the known life cycles of the vast majority of *Ampelisca* and *Byblis* species (Table 9). Moreover, while the *Haploops* reproductive potential is moderate, its strategy of reproduction (massive and recruitment in late winter/early spring) in the Bay of Concarneau plus its capacity to strongly modify its habitat can probably explain the success of this species within the bay, along with environmental changes generated by human activities. Among biannual amphipod species, *Haploops* exhibits a relatively high secondary production but a change from an *Amphiura* to a *Haploops* community results in a loss of benthic production. The question of whether the observed expansion of the *Haploops* community in the Bay of Concarneau will ultimately adversely affect the functioning of the food web needs to be further investigated.

PARTIE II

Impact des *Haploops* sur la diversité structurelle et fonctionnelle

- CHAPITRE 1 : **Changements structurels et fonctionnels induits par les peuplements à *Haploops***

  Article n°3 : Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the structural and functional diversity of benthic communities

- CHAPITRE 2 : **Dynamique saisonnière des peuplements benthiques de la baie de Concarneau**

  Article n°4 : Seasonal dynamics and secondary production of benthic communities in the bay of Concarneau (South Brittany, France): the functional consequences of changes induced by the tubiculous amphipod *Haploops nirae*

La seconde partie de ce manuscrit aborde l'impact des populations d'*Haploops* sur la diversité structurelle et fonctionnelle des peuplements de la baie de Concarneau. Cette partie comprend deux chapitres qui s'organisent chacun sous forme d'un article : le premier article a été soumis à Journal of Sea Research tandis que le second est en préparation.

Le premier chapitre de cette seconde partie (article 3) présente une comparaison des quatre principaux peuplements benthiques de la baie de Concarneau. Cette étude passe dans un premier temps par une comparaison de la diversité structurelle de ces peuplements (abordée par l'utilisation d'indices de diversité structurelle et par l'analyse de la composition spécifique des peuplements) et dans un second temps par une comparaison de la diversité fonctionnelle (abordée par l'analyse des traits biologiques des espèces). Cette étude démontre le caractère ingénieure d'*Haploops nirae* et montre comment la présence de cette espèce influence son environnement et les organismes qui lui sont associés.

Le second chapitre (article 4) poursuit la démarche du chapitre précédent en visant à préciser les conséquences de la présence des populations d'*Haploops nirae* par un suivi de la dynamique saisonnière des peuplements benthiques de la baie de Concarneau. Un échantillonnnage pratiqué aux quatre saisons de l'année 2010 sur deux transects côte-large permet d'appréhender non seulement la dynamique temporelle de la structure des peuplements, mais également d'estimer le stock de biomasse benthique et la production secondaire annuelle des peuplements benthiques de la baie de Concarneau. Cette étude permet notamment d'évaluer l'impact de l'expansion des *Haploops* sur la productivité du macrobenthos de la baie de Concarneau.

ARTICLE N°3

Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the structural and functional diversity of benthic communities

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Abstract

Haploops nirae is a gregarious tubiculous amphipod which extended its habitat over thousands of hectares in shallow waters of South Brittany bays (Bay of Biscay, Atlantic) over the last decades and created uniquely large and dense tube mats. In the bay of Concarneau, we investigated the structural (i.e. species richness and species composition) and functional (i.e. biological traits) diversity of the macrofauna associated with this *Haploops* community as a comparison with several surrounding soft-sediment communities to determine the effect of this engineer species on ecosystem functions.

We showed that the occurrence of *Haploops* tubes and individuals significantly modify sediment features (e.g. change in sediment grain size, increase in C and N organic content) but also largely affect species diversity and benthic composition. The species richness is significantly higher but most importantly the species assemblage associated with *Haploops* habitat is very homogeneous and unique with 33% of all species exclusively found in this community. We also tested the effect of tube density on species diversity and abundances and the intermediate disturbance hypothesis but we showed surprisingly no significant changes. Multivariate analysis (dbRDA) revealed that *Haploops* density was by far the factor explaining most of the variation in species composition of benthic communities. A biological trait analysis performed on selected traits revealed that the functional structure of the *Haploops* community was characterized by a greatly reduced proportion of small to medium long lived, sensitive to disturbance, free living or burrowing/tube-building filter-feeding species. *Haploops nirae* appears to be a bioengineer and a foundation species that largely modifies its hydro-sedimentary features, controlling diversity and abundances of associated species, and creating a complex set of positive and negative interactions so that a unique benthic assemblage is found in sediments they colonized.

1. Introduction

Ecosystem engineering is a concept introduced by Jones et al. (1994) who described ecosystem engineers as organisms that cause a major biologically mediated habitat modification. By altering biotic or abiotic materials that compose a habitat, these organisms directly or indirectly influence resource availability to other organisms. Ecosystem engineers therefore have the capacity to modify, maintain and/or create habitats for other organisms (Jones et al., 1994; 1997). Many studies have shown that ecosystem engineers affect neighboring organisms and local biodiversity, thus having significant impacts throughout the biological community and the entire ecosystem (Stachowicz, 2001; Crooks, 2002).

A large diversity of marine organisms physically engineers marine ecosystems and play key functional roles. Examples include salt marsh plants (e.g. mangroves), seagrasses, reef-forming coral species, mussel beds, burrowing crustaceans, colonial ascidians and burrowing or tubiculous polychaetes (Wright and Jones, 2006; Voultsiadou et al., 2007; Reise et al., 2009). Not only do they physically modify the structure of their habitat (e.g. burrow nets, reef-like bioconstructions, tube mats, rock boring), but they also modify hydro-sedimentary features and ultimately impact ecological processes (nutrient cycling, erosion and sediment stability for example) and associated species (Gutiérrez et al, 2012). In this context, special attention has been given to several tubiculous gregarious polychaete species that increase habitat complexity, modify the sediment dynamics and strongly influence micro- and macro-invertebrate diversity and composition (e.g. Woodin, 1978; 1981; Dubois, 2002; Callaway, 2006). Less is known about other taxonomic groups, especially small tube-building crustaceans (but see Mills, 1967).

Ampeliscids are tubiculous amphipods commonly found in shallow environments in temperate and subarctic waters, where they can reach high densities and form dense tube mats (Bellan-Santini and Dauvin, 1988; Dauvin, 1988; Franz and Tanacredi, 1992; Sudo and Azeta, 1996; Göransson, 2002). In those cases, they create a very unique habitat, considerably more complex and heterogeneous than the adjacent homogeneous soft-bottom areas and potentially play significant roles in different ecosystem processes. Many authors revealed that Ampeliscids constitute a major food source for higher-level consumers (Franz and Tanacredi, 1992; Highsmith and Coyle, 1992; Stoner, 2001) and are in some cases major contributors to the highest production levels observed for benthic invertebrate communities (Carrasco and Arcos, 1984; Franz and Tanacredi, 1992). By feeding primarily on phytodetritus, they also greatly influence the pelagic-benthic coupling (Grebmeier and McRoy, 1989). On the other hand, through the tube building and the bioturbation activity, Ampeliscids could be seen as infaunal hydraulic ecosystem engineers that physically modify their habitat by altering the biogeochemistry fluxes and the composition of the surface sediments (Woodin et al., 2010). How large tube mats affect the composition of benthic communities is less investigated.

The ampeliscid *Haploops nirae* was first recorded in 1884 in the shallow waters of South Brittany (France) (Bonnier, 1887). Recent acoustic surveys revealed that this species is spreading and proliferate over large areas of the entire South Brittany coast. For example, the mapping of the bay of Concarneau revealed a 5-fold increase in *Haploops nirae* habitat surface between 1963 (650 ha in Glémarec, 1969) and 2003 (3680 ha in Ehrhold et al., 2006). Similar patterns were observed for the bay of Vilaine (ca. 7000 ha in 2010) and other muddy coastal environments (unpublished reports). As many gregarious species, *Haploops nirae* exhibits dense populations, spanning from 6 800 to 25 500 ind. m^{-2} (Rigolet et al., 2012). In comparison, densities did not exceeded 5 000 ind. m^{-2} 25 years ago (Glémarec et al., 1986). Although the environmental causes of these recent changes remain unknown, the increase in density and the spreading of this engineer species provides a backdrop to investigate the effects of large tubiculous species mats on ecosystems, and especially regarding major changes in communities' structure, on local and regional diversity, and ultimately on the functioning of the ecosystem. While the link between species richness and diversity, and ecosystem functions is still debated in marine ecology (Stachowicz et al., 2007), increasing attention has been paid to investigate the functional diversity in communities (Mouillot et al., 2011) and to develop relevant approaches to assess marine ecosystem functioning. Biological Traits Analysis (BTA) has proven to be a very useful tool for identifying changes in functioning of benthic assemblages exposed to disturbance such as bottom trawling (e.g. Tillin et al., 2006; De Juan et al., 2007) and marine aggregate dredging (e.g. Barrio Frojan et al., 2011). Based on the assumption that functional roles performed by species are determined by the species biological traits (Bremner et al., 2006), BTA utilizes species traits (e.g. life history, morphological and behavioral characteristics) as a proxy for functional roles to determine the occurrence of these traits over assemblages (Bremner, 2008). However, Lepš et al. (2006) pointed out that the functional diversity of a community is dependent on the context of the study because the number of traits selected and their identity depends on the question asked and on which processes being investigated in the study. As a result, ecological functions of structuring species (bioengineers) may be overlooked if irrelevant combinations of traits are used, providing therefore erroneous information about the ecological functioning of the ecosystem studied.

The present study addresses the question of the effects of a widely dispersed tubiculous gregarious species – namely the Ampeliscid amphipod *Haploops nirae* – on the structural and functional diversity of soft-bottom muddy communities. We use complementary estimates of diversity and species composition to test whether tube mats enhance or adversely affect local and regional diversity. Amphipod species are sensitive to human activity and the former largest European *Haploops* habitat has largely decreased in the

Øresund area (Baltic Sea), likely because of human developments and resulting eutrophication (Göransson et al., 2002). We discuss here potential consequences of the loss (or conversely further spreading) of dense tubiculous bioturbators on species richness and ecosystem functions.

2. Materials and methods

2.1. Study area

This study was conducted in the bay of Concarneau, situated in the Northern part of the Bay of Biscay (France) (Fig. 35). This area reflects many coastal embayments in Brittany as it is sheltered by a succession of rocky islets and is characterized by soft-bottom substrates, spanning from muddy to muddy-sand, with a depth ranging from 15 to 35 m (Ménesguen, 1980). The westernmost part (north Mouton islets and Glénan Islands) is composed of muddy sands and sandy muds. The central part of the bay, where currents are strongly reduced, is composed of pure muds supporting a dense population of the tubiculous amphipod *Haploops nirae*. The western edges of the *Haploops* habitat are surrounded by patchy muddy sediments (Ehrhold et al., 2006).

2.2 Sampling strategy and laboratory analyses

To investigate the effects of *Haploops* on benthic diversity and species assemblages, we compared the macrofauna associated with *Haploops* with the adjacent benthic communities. A mapping survey of the seabed using geoacoustic approaches and complementary benthic biological grab samples was conducted in the bay of Concarneau (Ehrhold et al., 2006). Preliminary macrofauna analysis reported 4 benthic communities in the bay: the *Sternaspis scutata* muddy community, the *Amphiura filiformis* sandy-mud community, the *Owenia fusiformis* muddy-sand community and the *Haploops* muddy community (Fig. 35). Using this map contours, 18 stations were randomly distributed in each of the 4 communities. To investigate the effects of changes in *Haploops* density on diversity and benthic assemblages, the sampling effort was increased in the *Haploops* community and 9 stations (among 18 stations) were sampled in this community. Three stations were then distributed in each of the other communities (i.e. the *Sternaspis* community, the *Amphiura* community and the *Owenia* community) (Fig. 35). The 18 stations (3 replicates per station) were sampled during summer time (July 2009) using a 0.1 m^2 Van Veen grab. Samples were sieved on a 1 mm circular mesh-size screen and fixed with a 5% buffered formalin solution. In the laboratory, samples were rinsed, sorted and the macrofauna was identified to the lowest taxonomic level (i.e. generally the species level) and counted.

To characterize each community, environmental parameters from the sediment were sampled at each station using a Reineck box-corer (2 replicates) to collect undisturbed samples. Chlorophyll *a*, phaeopigments, organic matter concentration (C and N) and sediment grain size were analyzed from the first 5 cm layer of sediment. Sediment samples were first frozen at -20°C and then freeze-dried to perform analyses, except for granulometry for which samples were kept at 4°C to prevent bias in measurements of silt and clay proportion. Grain size distribution was analyzed using a laser particle analyzer (Malvern Mastersizer 2000). Granulometric parameters (i.e. mean grain size in µm, % of mud, % of sand, sorting index, clay:silt ratio) were estimated using the GRADISTAT software (Blott and Pye, 2001). Nitrogen and carbon organic content in sediment were measured with an elemental analyser after acidification with 1M HCl to remove inorganic calcium carbonates. Primary producer pigments (i.e. chlorophyll *a* and phaeopigments) were estimated using the monochromatic technique (Lorenzen, 1967) as described in Aminot and Kérouel (2004).

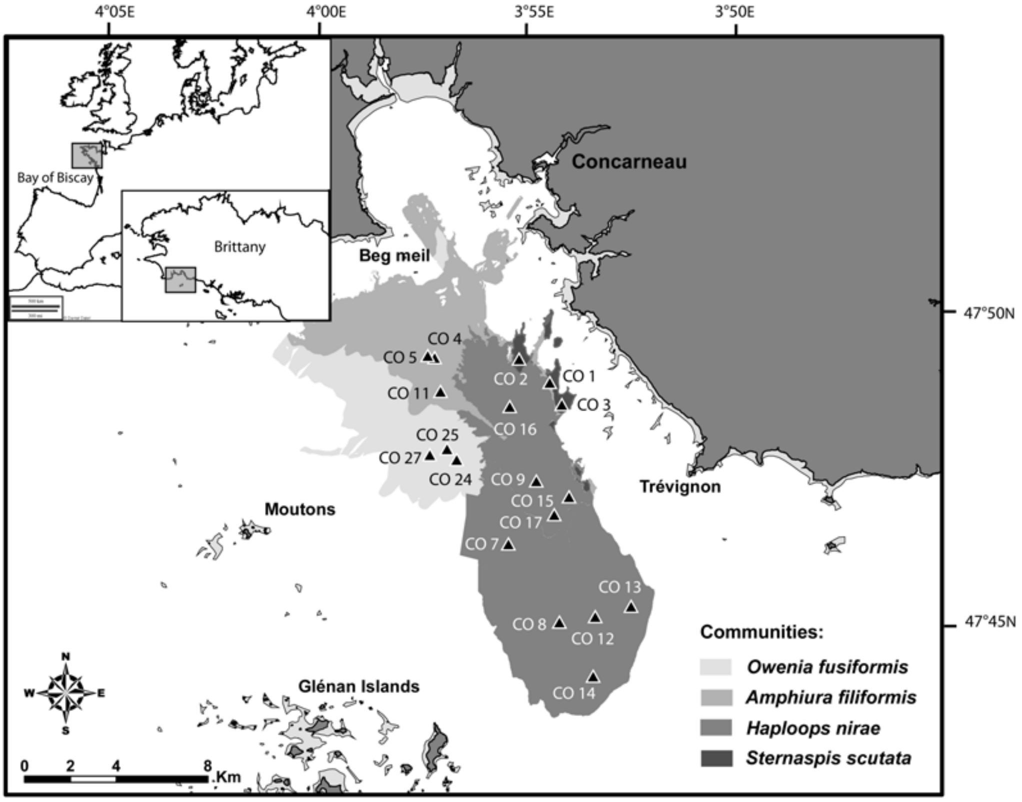

Figure 35 : Spatial distribution of the four sampled benthic communities (i.e. *Owenia fusiformis*, *Amphiura filiformis*, *Sternaspis scutata* and *Haploops nirae* communities) in the bay of Concarneau (South Brittany, Bay of Biscay). Sampling stations (3 reps per stations) are indicated by a black triangle. The map was issued from a benthic survey conducted in 2003 (Ehrhold et al., 2006).

2.3. Data analysis

Community structure. To check for the validity of the *a priori* grouping stations for each community, a non-metric multi dimensional scaling (nMDS) combined with a cluster analysis was first used. Analyses were conducted on a Bray-Curtis similarity matrix calculated from log-transformed abundances to downweigh the influence of abundant species. Species that appeared once in the dataset (i.e. occurring in less than 2% of the samples) were removed from multivariate analyses. According to the role of *Haploops* as an ecosystem engineer, we assume that *Haploops* densities correspond primarily to an environmental parameter. Consequently, *Haploops* individuals were removed from multivariate analyses so that only the associated species were considered. Cluster analyses were performed using the group average linkage method. A similarity profile test was performed to test the null hypothesis that a single set of samples, which are not *a priori* divided into groups do not differ from each other in the multivariate structure using the SIMPROF routine of the

PRIMER 6 software package (Clarke and Gorley, 2006). To conduct this test, an “observed” similarity profile was firstly generated in which all Bray-Curtis similarities between the samples were plotted against their rank. A permutation procedure (based on 1000 permutations) was then used to produce the “mean” similarity profile in which all resemblances in the subset of samples were equally plotted against their rank. The statistical test corresponds to the sum of the absolute distance (π) between the “observed” similarity profile and the simulated mean profile. A further 999 simulated profiles were then generated and π was computed between each of these and the mean simulated profile, defining therefore the range of likely values under the null hypothesis.

In addition, taxa that contributed the most to the observed differences between communities (expressed as %) were determined from the Bray-Curtis similarity matrix using the SIMPER procedure of the PRIMER 6 software package (Clarke and Gorley, 2006).

Macrofauna diversity. The macrofauna diversity of the sampled communities as defined from the multivariate analyses, was assessed using indices recommended by Gray (2000) for characterizing local diversity, namely Hill’s indices (N0, N1 and N2) (Hill, 1973). As described in Hill (1973), N0 corresponds to the species richness (number of species), N1 = exp (H’) where H’ is Shannon-Wiener diversity (loge) and N2 = 1/SI, where SI is the Simpson’s dominance Index. The N1 index is affected by species situated in the middle of the rank sequence, while the Simpson index used in the calculation of N2 addresses the degree of dominance of one or a few very abundant species (Whittaker, 1972). The N1 and N2 indices are two measures of heterogeneity diversity. *Haploops* individuals were also removed from the dataset so that only the associated fauna was considered. A one-way ANOVA was used to test for significant differences between benthic communities in diversity indices and macrofauna abundances. Normality of data was assessed using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. When significant differences occurred between communities, a pairwise multiple comparison procedure (Holm-Sidak Test) was used. All statistical analyses were performed using the Sigmastat 3.5 software (Systat Software, Inc., CA, USA).

As suggested by Gray (2000), diversity indices can meaningfully be estimated at a larger level than at the sample scale. We therefore also calculated the diversity indices at the whole community scale. Since the number of sampled stations differed between communities, diversity measures such as N0, N1 and N2 were assessed using a bootstrap procedure. This method estimates diversity indices for each community through the use of accumulation curves for randomised samples. Bootstrap calculations (50 randomisations) were performed using the EstimateS Win 8.20 software (Colwell, 2009).

Furthermore, as a measure of beta diversity, the taxonomic similarity between the communities was assessed. According to Whittaker (1960), beta diversity is the extent of change in species composition from one location to another. The Jaccard index of similarity which is commonly used in beta diversity analyses (Nekola and White, 1999; Qian, 2009; Condit et al., 2002) was used as a measure of macrofaunal similarity between the benthic communities sampled. The Jaccard's index (coefficient of community CC) is defined as CC= Ss / (Sj + Sk -Ss), where Ss is the number of species shared by two samples, Sj the number in the first sample and Sk the number in the second sample (Jaccard, 1912; Whittaker, 1972). This index ranges from 0 (no species shared) to 1 meaning that all species are shared by two samples. A low number of shared species between two communities corresponds to a high turnover in species composition between the two communities, reflecting high beta diversity. To overcome the problem related to a non-homogeneous sampling effort, we calculated the number of species common to two stations for all pairwise permutations of stations.

Linking assemblage species to environmental parameters. A one-way ANOVA was used to determine whether environmental parameters (Chl *a*, phaeopigments concentration, organic C and N concentrations and grain size descriptors) differed between the benthic communities. Normality of data was assessed using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. To fulfil conditions of normality and homogeneity of variances, the environmental parameter Mean grain size was log transformed. When significant differences occurred between communities, a pairwise multiple comparison procedure (Holm-Sidak Test) was used. To determine the relationships between environmental variables and macrofauna assemblages, a distance-based redundancy analysis (dbRDA) was performed using the PERMANOVA + software (Anderson et al., 2008). The dbRDA is a method of constrained ordination, which displays the relationships among samples points from a fitted model (Legendre and Anderson, 1999). The DISTLM (distance-based linear modeling) routine of the software was therefore used first to analyze and model the linear relationships between multivariate data (community composition) and predictor variables (environmental variables) (Anderson et al., 2008). The parsimonious model built by the DISTLM routine provides a reduced number of environmental variables that best correlate with macrofauna data. The "Akaike Information Criterion" (AIC) which is a measure of the relative goodness of fit of a statistical model was used to determine this model. The selection procedure used calculates the AIC criterion for all possible models (i.e. combinations of predictor variables) and provides the overall 10 best models that were found using the AIC criterion. The model that achieved the lowest AIC value can be considered as the best of the candidate models. The dbRDA routine was then used to perform an ordination of fitted values from the given model built by the DISTLM routine. Before doing the DISTLM and dbRDA routines, preliminary diagnostics have to be made to avoid multi-collinearity (strong inter-correlations) among predictor (environmental) variables. Thus, when two environmental variables showed strong correlation (i.e. R>0.95), one of these two variables was removed from the analysis, since they contain redundant information. Moreover, environmental variables that show a great deal of skewness (identified by the use of Draftman Plots) were transformed to approach normality. In this way, from the 12 environmental variables submitted to the dbRDA analysis (i.e. Chl *a*, phaeopigments, %C, %N, C:N ratio, mean grain size, % Mud, % Sand, sorting index, clay:silt ratio, water depth and *Haploops* tube density), only 7 (Chl *a*, phaeopigments, %C, C:N ratio, mean grain size (log transformed), water depth and *Haploops* tube density (fourth root transformed)) were selected to be processed by the DISTLM routine for the dbRDA analysis. It is worth noting that *Haploops* tubes physically modify their habitat and could be considered a source of disturbance in bare sediment, therefore we chose to consider the density of tubes as an environmental variable.

Table 11 : Biological traits and modalities of species selected for the biological traits analysis.

No.	Traits	No.	Modalities
1	Trophic group	1	Filter feeder
		2	Carnivore-omnivore
		3	Surface deposit feeder
		4	Sub-surface deposit
2	Type of movement	1	Swimmer
		2	Burrower
		3	Crawler
		4	Walker
		5	None
3	Habit	1	Tube dwelling
		2	Burrow dwelling
		3	Free living
4	Bioturbation	1	Diffusive mixing
		2	Surface deposition
		3	Conveyer belt transport
		4	No bioturbation
		5	Buldozing
5	Life span	1	Short (<2 years)
		2	Medium (2-5 years)
		3	Long (>5 years)
6	Ecological group	1	Sensitive (I)
		2	Indifferent (II)
		3	Tolerant (III)
		4	Second-order
		5	First order
7	Individual size	1	Very small (<1 cm)
		2	Small (1-2 cm)
		3	Small-medium (3-10
		4	Medium (11-20 cm)
		5	Medium-large (21-50

Biological Traits Analysis (BTA). As suggested by Bremner (2008), the initial stage of traits analysis involves the identification of key aspects of functioning in the ecosystem under consideration and the selection of suitable indicator traits. In this perspective, traits that are functionally important have to be selected to provide a relevant picture of the ecosystem functioning. While morphological characteristics of species are commonly used in BTA analyses (Bremner et al., 2006; Paganelli et al., 2012), such characteristics are strongly related to the taxonomic classification of species and could potentially hamper the functional approach: for example, the body form “laterally compressed” or “vermiform” is usually very close to the composition in amphipods and polychaetes, respectively. To assess the functional diversity associated with each community, we selected 7 biological and ecological traits that reflect ecological processes that we consider functionally important to understand how an ecosystem engineering, bioturbating amphipod may induce changes in the functional characteristics of the ecosystem. We choose to gather information concerning (1) the feeding strategy of the taxa (i.e. trophic group) to provide important information about resource utilisation in each community as well as its availability, (2) the life cycle (i.e. lifespan and adult individual size) because those traits are directly related to the secondary production (Brey, 1990; Cusson and Bourget, 2005) and provide information related to the amount of organic matter and energy produced by the community and (3) the behavior (i.e. type of movement, life mode, bioadvective activity) to provide details on overall activity such as the mode of movement of species and how species occupy their area and contribute to sediment reworking and biogeochemical fluxes at the water-sediment interface. Biological traits are listed in Table 11. As suggested by Paganelli et al. (2012), we also included the AMBI Index (AZTI's Marine Biotic Index) as a biological trait, as it classifies the species according to their tolerance to disturbance (Borja and Muxika, 2005). Each trait was then sub-divided into modalities and a fuzzy coding procedure (Chevenet et al., 1994) was used to assign a score to each modality of a trait. The species traits were fuzzy coded on a 0 to 3 scale with "0" indicating "no affinity" to "3" indicating "high affinity" of the taxon for the modality. This approach avoids the assignment of a taxon to a single category, allows taxa to exhibit modalities to different degrees and incorporates information on intraspecific variability in trait expression. In this way, the fuzzy coding procedure leads to a more precise description of species traits. Biological and ecological information on species were gathered from a variety of literature sources, from general handbooks to specialized papers (i.e. taxonomic guides with descriptions of species). We used the Biological Traits Information Catalogue developed by the Marine Life Information Network (www.marlin.ac.uk/biotic/) as well as the AZTI list for the AMBI Index (Borja and Muxika, 2005 and see also www.azti.es) for complementary information, as well as expert input. In rare cases, no information was found. Similarly to the analysis of benthic assemblages, the *Haploops* species was removed from the dataset and taxa that were found only once in the samples were not retained for the biological traits analysis; we thus constitute an array of 211 taxa by biological traits with 7 variables (traits) and 30 modalities. This "species by traits" array was ordinated using a Fuzzy coded multiple Correspondence Analysis (FCA) which is well adapted for fuzzy coded table (Chevenet et al., 1994). Before FCA calculation, a fuzzy coded file is processed and computes the frequency of use of each modality per trait so that the sum of values by group of modalities is equal to 1. If the affinity of a species for a variable (trait) is unknown, it is coded "0" for all the modalities. The missing values (2% of cases) were thus replaced by the average profile for the corresponding variable during the computation of the fuzzy coded file. In this way, a species with such a score is not taken into account in the calculation of the column weight (Chevenet et al., 1994). We then constituted clusters of species with similar associations of traits using the output of the Fuzzy Correspondence Analysis (i.e. the scores of taxa on the first four axes of the FCA) using Ward's linkage method (Ward, 1963) on Euclidean distances (Usseglio-Polatera et al., 2000). The two first axes of the FCA explained 27.1% of the variance, in order to take into account a larger amount of explained variance to constitute the clusters we decided to use the first four axes explaining 43 % of the variance. Functional groups of species with similar associations of traits were identified and plotted on the two first axes of the Fuzzy Correspondence Analysis at the weighted average of their taxa and constituted the reference typology of functional groups (Usseglio-Polatera et al., 2000). For each functional group identified, we generated a biological profile which indicates for each trait the proportion of trait modalities exhibited by the group.

To compare the functional diversity among the benthic communities studied, we calculated (from the log-transformed abundances of species per sampling station) the relative frequency of each functional group in the four communities (i.e. *Sternaspis*, *Amphiura*, *Owenia* and *Haploops)*. To test for significant differences in the relative frequency of functional group between benthic communities, a one-way ANOVA was performed. Normality of data was assessed using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. When the conditions of normality and homogeneity of variances were not fulfilled even after data transformation, we used the nonparametric test Kruskal-Wallis Analysis of Variance on Ranks. When significant differences occurred between communities, a pairwise multiple comparison procedure (Holm-Sidak Test) was used. Finally, the relative frequency distribution of functional groups in sampling stations was used to plot stations on the reference typology of functional groups, so that the stations are located at the center of the relative frequency distribution of functional groups (Usseglio-Polatera et al., 2000).

Calculations were performed using the statistical software R 2.11.1 (R Development Core Team, 2008 – www.R-project.org) with the ade4 package (Thioulouse et al., 1997).

3. Results

3.1. Community structure

Hierarchical cluster analysis and SIMPROF test revealed that 4 main clusters, i.e. species assemblages that correspond to communities are grouped at a similarity level of 60%. In agreement with the mapping of the bay of Concarneau, the four communities described *a priori* (i.e. *Sternaspis*, *Amphiura*, *Owenia* and *Haploops*) are well separated on the nMDS plot (Fig. 36). Except for the *Sternaspis* community, each benthic community constituted a separate cluster. One station (CO3) sampled in the *Sternaspis* community exhibited a species assemblage that shared strong similarity to the species assemblage associated with the *Haploops* stations. Data revealed that this station actually had a relatively low density of *Haploops* (2 000 ± 930 ind.m^{-2}). In the following diversity analyses, we will therefore consider the *Sternaspis* community as a group of 2 stations (instead of 3) and exclude station CO3. The nMDS plot also showed that *Haploops* stations are well discriminated, even though a larger sampling effort was made. Species assemblages associated with *Haploop*s community are very different from surrounded benthic assemblages but also very homogeneous.

Species that contributed the most to the Bray-Curtis dissimilarity between communities are listed in Table 12. In all cases between 7 and 9 species represented ca. 20 % of the dissimilarity between the communities, each species contributing approximately the same to the dissimilarity. Polychaetes *Terebellides stroemi*, *Schistomeringos rudolphii* and *Mediomastus fragilis* typified the fauna associated with *Haploops* community. Overall, amphipods other than *Haploops* contributed largely to dissimilarity between communities: *Ampelisca* species (Ampeliscids tubiculous amphipods) are in part responsible for differences between the *Owenia* community (where they were abundant) and the surrounding communities (where *Ampelisca* were relatively scarce). Commensal organisms such as the small bivalve *Kurtiella bidentata* and the brittle star *Amphiura filiformis* were found in all communities except in the *Haploops* community. Moreover, the highest density of the polychaete *Maldane glebifex* (that lives in a consolidated mud tube) in the *Amphiura* community is in part responsible for the differences with the *Sternaspis* and *Owenia* communities. Finally, the presence of the bivalve *Abra alba* and the small cirratulid *Chaetozone gibber* contributed to distinguish the *Owenia* community from the *Sternaspis* communtiy.

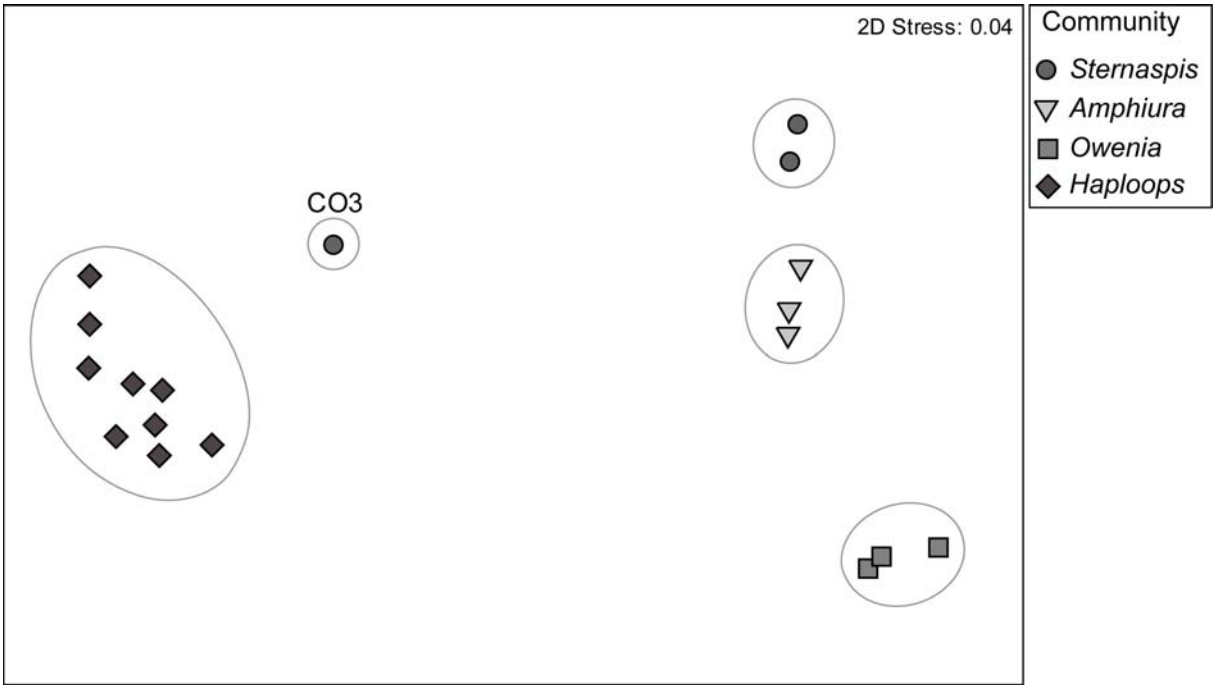

Figure 36 : Non-metric multidimensional scaling (nMDS) plot of the benthic macrofauna of the *Sternaspis*, *Amphiura*, *Owenia* and *Haploops* communities. The groupings (grey circles) resulted from the SIMPROF test and significantly differs from each other. The community symbols are related to benthic communities defined *a priori* on the basis of the study investigated in 2003 by Ehrhold et al. (2006). Note that the station CO3 *a priori* belonging to the *Sternaspis* community significantly differs.

Table 12 : Main species contributing to the dissimilarity between sampled communities (cut-off 20%):

Community pairwise comparisons		Species	Average abundance in 1st community (ind/0.1m²)	Average abundance in 2nd community (ind/0.1m²)	Cumulative contribution (%)
Sternaspis	*Amphiura*	*Maxmuelleria lankesteri*	0	4	3.34
		Maldane glebifex	4	22	6.67
		Labidoplax digitata	4	0	9.93
		Ampelisca typica	0	3	13.04
		Abra alba	1	6	15.86
		Ampelisca tenuicornis	0	2	18.25
		Phoronis spp.	0	3	20.42
Sternaspis	*Owenia*	*Abra alba*	1	22	3.10
		Chaetozone gibber	0	11	6.00
		Ampelisca spinifer	0	8	8.78
		Ampelisca brevicornis	0	9	11.47
		Labioleanira yhleni	7	0	14.07
		Ampelisca tenuicornis	0	7	16.59
		Spio decoratus	0	6	19.07
		Ampelisca spinipes	1	11	21.37
Amphiura	*Owenia*	*Maldane glebifex*	22	0	4.45
		Ampelisca brevicornis	0	9	7.41
		Kurtiella bidentata	218	31	10.26
		Spio decoratus	0	6	12.91
		Ampelisca spinifer	1	8	15.43
		Maxmuelleria lankesteri	4	0	17.78
		Photis longicaudata	6	1	20.00
Sternaspis	*Haploops*	*Kurtiella bidentata*	97	0	4.86
		Amphiura filiformis	26	0	8.60
		Nucula nitidosa	20	0	12.01
		Terebellides stroemi	0	12	14.94
		Mediomastus fragilis	0	7	17.23
		Labioleanira yhleni	7	0	19.51
		Schistomeringos rudolphii	0	8	21.78
Amphiura	*Haploops*	*Kurtiella bidentata*	218	0	5.23
		Amphiura filiformis	46	0	9.16
		Terebellides stroemi	0	12	11.52
		Nucula nitidosa	8	0	13.77
		Schistomeringos rudolphii	0	8	15.97
		Pholoe inornata	8	0	17.98
		Mediomastus fragilis	0	7	19.96
Owenia	*Haploops*	*Amphiura filiformis*	26	0	2.75
		Kurtiella bidentata	31	0	5.38
		Abra alba	22	0	7.96
		Terebellides stroemi	0	12	10.14
		Pholoe inornata	15	0	12.24
		Chaetozone gibber	11	0	14.19
		Ampelisca brevicornis	9	0	16.10
		Ampelisca spinifer	8	0	17.96
		Schistomeringos rudolphii	0	8	19.77

3.2. Structural diversity

Mean values of macrofauna diversity measures and abundances within each community are reported in Table 13. For all tested parameters, overall significant differences between communities were observed (ANOVA, $p<0.05$). Total abundance of individuals was the highest in the *Amphiura* community and was significantly different from the low abundances reported from the *Haploops* community (*Haploops* being excluded). Indeed, the macrofauna abundance associated with *Haploops* community was estimated at 157±37 ind.0.1m^{-2} and was 1.5 to 3 times lower than those reported in the adjacent areas. *Owenia* and *Sternaspis* communities exhibited intermediate densities which did not significantly differ from *Amphiura* and *Haploops* communities. When the *Haploops* individuals are included, the abundances in this community are far higher than those from adjacent areas ($p<0.001$, ANOVA) with a mean density of 1 208 ± 317 ind. 0.1m^{-2}. While the number of stations sampled in the *Haploops* community was the highest (9 stations), a very low standard error in abundances was observed, revealing that the *Haploops* community is characterized by a high homogeneity in the abundances of associated fauna.

Mean species richness (N0) was higher in the *Owenia* and *Haploops* communities compared to the *Sternaspis* community and the *Amphiura* community. N1 and N2 indices exhibited the same pattern and indicated significantly lower diversity in *Sternaspis* and *Amphiura* than in the two others communities. *Haploops* community showed the highest value for N1 but no significant differences were reported between the high values of N2 in *Owenia* and *Haploops* communities.

At a larger scale (i.e. community scale), cumulated values of N0, N1 and N2 based on 50 randomisation bootstraps revealed that for the same sampling effort, highest species richness and diversity values distinguished the *Haploops* community from all adjacent areas.

The mean proportion of shared species between two communities assessed with the Jaccard's index spanned from 0.16 ± 0.03 to 0.41 ± 0.04 (Table 14). *Owenia* and *Haploops* communities had a mean of 16% species in common, while *Sternaspis* shared 41% of species with the *Amphiura* community. With a slight turnover of species from one community to another (Jaccard's index ranging from 0.26 to 0.41), *Sternaspis*, *Amphiura* and *Owenia* communities showed a relatively high similarity in species composition. In contrast, lowest values of the Jaccard's index (ranging from 0.16 to 0.21) were recorded when the *Haploops* community was compared with the adjacent areas, implying a high turnover of species and very few species shared. Moreover, on the 274 species recorded in the four benthic communities of the bay of Concarneau during this study, 90 species (i.e. 33 % of the total number of species) were exclusively found in the *Haploops* community. Among these species, some are consistently found in all samples collected in the *Haploops* community such as the predatory polychaetes of the family *Eunicidae* (i.e. *Eunice vittata* and *Nematonereis hebes*), Terebellidomorph polychaetes (i.e. *Lysippe labiata*, *Amaeana trilobata*, *Axionice maculata*, *Pista cristata* and *Trichobranchus glacialis*), the Maldanid polychaete *Praxillella gracilis*, the Paraonid polychaete *Aricidea sp.*, some amphipod species such as *Leptocheirus pectinatus*, *Lysianassa insperata* and *Photis inornatus* but also the small brittle star *Amphipholis squamata* and the large bivalve *Polititapes virgineus*.

Table 13 : Mean values (± standard errors) of abundance, N0 (species richness), N1 (exp (H')), N2 (1/SI) (at station and community scales) within the 4 communities studied (*Sternaspis*, *Amphiura*, *Owenia* and *Haploops*). Note that because of different number of stations, diversity indices at the community scale were assessed using a bootstrap approach. Significant differences ($p<0.05$) are in bold and *post-hoc* results of ANOVA are reported as superscript letters. *Haploops* were removed from the macrofauna data set of all benthic communities to achieve calculations of diversity indices.

	STATION Diversity					**COMMUNITY diversity**			
	Number of stations	Abundances (0.1 m^{-2})	N0	N1	N2	Total species richness	N0	N1	N2
Sternaspis	2	235±108^{ab}	59±9^{a}	11.5±6.0^{a}	4.8±2.2^{a}	84	80±9^{a}	10.4±2.4^{a}	4.2±1.2^{a}
Amphiura	3	466±272^{a}	74±3^{ab}	9.6±5.4^{a}	3.7±1.9^{a}	113	95±13^{b}	7.2±2.3^{a}	2.8±0.8^{a}
Owenia	3	279±102^{ab}	80±7^{b}	31.9±7.1^{b}	19.4±7.2^{b}	119	103±10^{b}	31.7±3.2^{b}	18.1±2.9^{b}
Haploops	9	157±37^{b}	85±9^{b}	43.2±6.0^{c}	26.4±3.8^{b}	183	130±9^{c}	51.1±4.0^{c}	32.0±3.4^{c}
p-value		**p=0.016**	**p=0.006**	**p<0.001**	**p<0.001**		**p<0.001**	**p<0.001**	**p<0.001**

Table 14 : Jaccard's index (mean values ± standard error) of the four communities pairwise comparisons (i.e. *Sternaspis*, *Amphiura*, *Owenia* and *Haploops*).

Community pairwise comparisons		Number of	Mean Jaccard's index
Sternaspis	*Amphiura*	6	0.410 ± 0.038
Sternaspis	*Owenia*	6	0.260 ± 0.015
Amphiura	*Owenia*	9	0.352 ± 0.033
Sternaspis	*Haploops*	18	0.182 ± 0.022
Amphiura	*Haploops*	27	0.209 ± 0.025
Owenia	*Haploops*	27	0.159 ± 0.027

3.3. Linking species assemblages to environmental parameters

The comparison of sedimentary features revealed that strong differences occurred between the four studied communities (Table 15). The mud content was overall important but was the lowest in the *Owenia* community (19%), and significantly increasing from *Sternaspis* and *Amphiura* communities (58% and 49% respectively) to the *Haploops* community (72%). In good agreement with the mud content, the mean grain size followed the same pattern, with significantly lower values in *Haploops* stations. All communities significantly differed in organic N% and C% in sediment. Values were significantly higher in the *Haploops* area (N% = 0.30 and C% = 1.85) and lower in the *Owenia* community (N% = 0.07 and C% = 0.47) suggesting that organic loads were the highest in the *Haploops* community. The *Haploops* area was moreover characterized by the lowest C:N ratio, which is a proxy for higher organic matter quality. Finally, while no significant differences in chlorophyll *a* were evidenced between communities, the highest content of phaeopigments in sediment was reported in the *Haploops* area.

Table 15 : Mean values (± standard errors) for sediment characteristics between the benthic communities of the bay of Concarneau (*Sternaspis*, *Amphiura*, *Owenia* and *Haploops*). Significant differences ($p<0.05$) are in bold and *post-hoc* results of one-way ANOVA are reported with superscript letters.

	Sternaspis	*Amphiura*	*Owenia*	*Haploops*	p-value
Mud %	58.3 ± 1.2^{b}	49.3 ± 4.7^{b}	18.6 ± 0.9^{a}	72.4 ± 5.8^{c}	**P<0.001**
Mean grain size (µm)	34 ± 1^{b}	39 ± 5^{b}	152 ± 17^{a}	23 ± 4^{c}	**P<0.001**
N %	0.22 ± 0.03^{c}	0.13 ± 0.02^{b}	0.07 ± 0.01^{a}	0.30 ± 0.03^{d}	**P<0.001**
C %	1.48 ± 0.14^{c}	0.92 ± 0.02^{b}	0.47 ± 0.04^{a}	1.85 ± 0.16^{d}	**P<0.001**
C:N ratio	6.9 ± 0.2^{a}	7.1 ± 0.8^{a}	7.2 ± 1.2^{a}	6.1 ± 0.2^{b}	**P=0.010**
Chlorophyll *a* (µg/g sediment)	0.72±0.41	0.46±0.23	0.13±0.22	1.35±0.81	P=0.061
Pheopigments *a* (µg/g sediment)	18.19 ± 0.76^{a}	13.07 ± 1.91^{a}	10.82 ± 1.14^{a}	27.51 ± 4.29^{b}	**P<0.001**

Environmental variables that best explained the relationships between environmental parameters and macrofauna assemblages were as followed: (1) *Haploops* density (fourth root transformed), (2) mean grain size (log transformed) and (3) water depth. These three variables composed the parsimonious model which explained a very large part (70.3 %) of the total variation in species assemblages. The distance-based redundancy analysis (dbRDA) plot is illustrated in Fig. 37. The first two axes explained 95.3 % of the fitted variation and 67 % of the total variation. On the dbRDA plot, macrofauna samples modelled by the 3 predictor variables exhibited a "V" shape, hence suggesting that macrofauna assemblages are divided up according to two gradients. The first gradient was largely driven by *Haploops* density and to a lesser extent by water depth, which kept *Haploops* stations separated from *Sternaspis*, *Amphiura* and *Owenia* stations. The second gradient was mainly driven by mean grain size and water depth and discriminated *Sternaspis* and *Amphiura* stations from the *Owenia* stations. Although faunal differences between communities were associated with mean grain size and water depth, the greatest proportion of differences in macrofauna assemblages was explained by the density of *Haploops*. This variable alone explained 54.1 % of the total variation in macrofauna assemblages, far beyond the % variation explained by the mean grain size (11.5%) and the water depth (4.8%). Considering that *Haploops* individuals were removed from the species matrix and that only associated species were processed, this approach revealed that *Haploops* density is the parameter that best explained variations in species assemblages.

Variations in species richness and abundance of macrofauna (*Haploops* individuals excluded) as a function of *Haploops* density are plotted in Fig. 38. With a density of *Haploops* ranging from 920 ind.m^{-2} to 22 000 ind.m^{-2}, the species richness (N0) did not show significant differences (Pearson correlation coefficient, p=0.234). Moreover, no significant relationship was found between the abundance of associated macrofauna and *Haploops* density (Pearson correlation coefficient, p=0.232). Similarly, N1 and N2 diversity indices were not affected by an increase in *Haploops* density (Pearson correlation coefficient, p=0.678 and p=0.725 respectively).

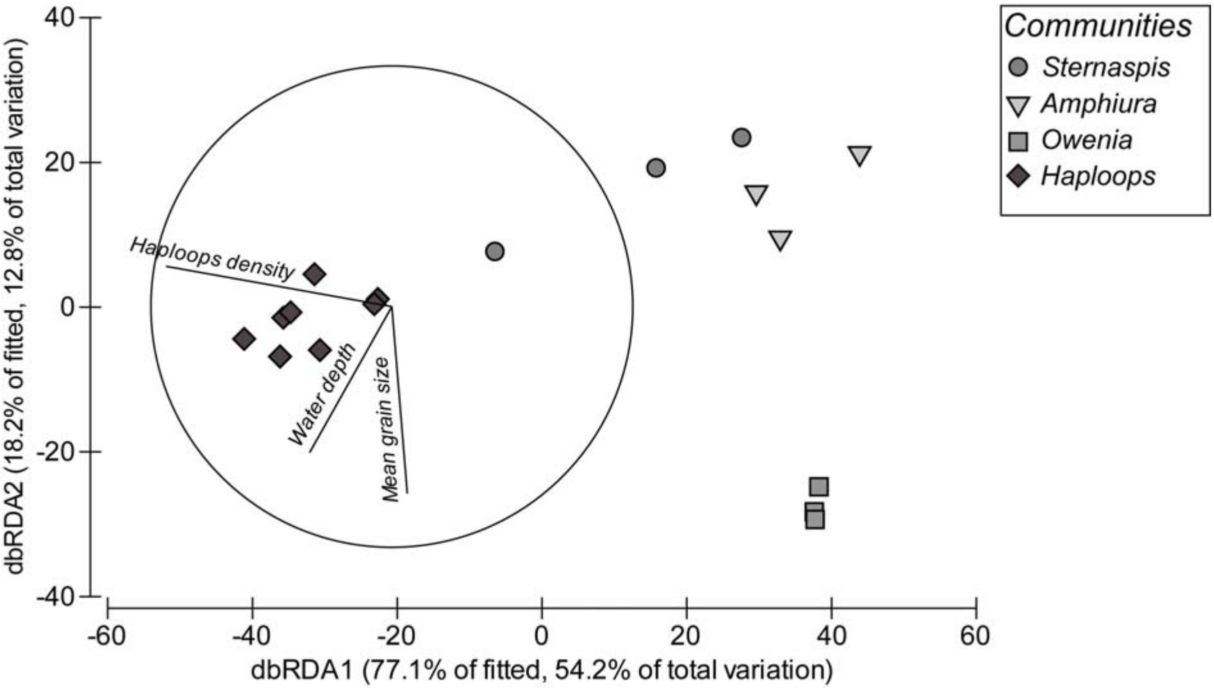

Figure 37 : dbRDA ordination of macrofauna community composition as predicted by the DISTLM model. It shows the relationship between environmental predictors that best explain the variation in macrofauna composition in the four communities studied. Note that *Haploops* individuals were removed from the species matrix and that *Haploops* density was used as a factor (see data analyses section). Symbols represent macrofauna samples and vectors represent environmental variables included in the parsimonious model. The length of the vector is related to the effect induced by the environmental variable on species assemblages. Note that symbols are related to benthic communities *a priori* defined on the basis of the study investigated in 2003 by Ehrhold et al. (2006).

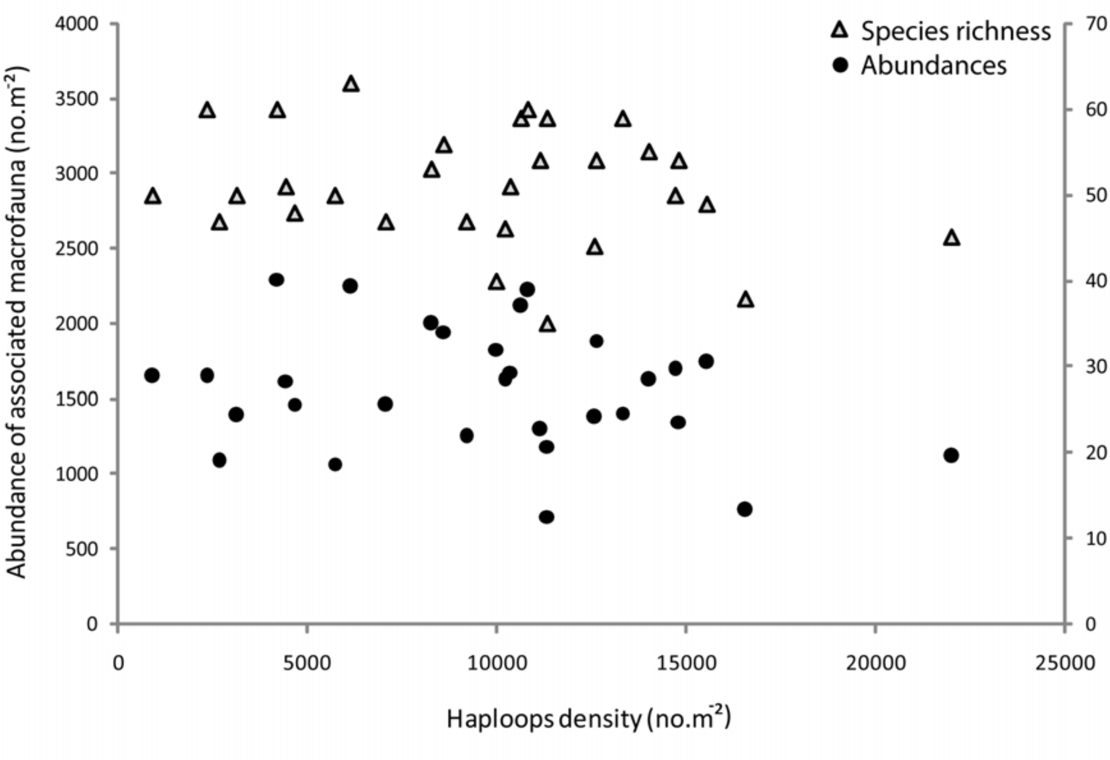

Figure 38 : Relationship between species richness (N0) or macrofauna abundances (*Haploops* individuals excluded) and *Haploops* density (ranging from 920 to 22 000 ind.m^{-2}) in the bay of Concarneau. Note that the same pattern applied for other diversity indices (N1 and N2).

3.4. Functional diversity

The first two factorial axes of the fuzzy correspondence analysis (FCA) explained respectively 15.8 and 11.3% of the total variability in species biological traits (Fig. 39). The correlation ratios issued from this analysis revealed which variables (traits) were best explained by the first two axes of the analysis (Table 16). On the F1 axis of the FCA, the modalities of the variables 'trophic group', 'type of movement', 'habit', 'bioturbation' and 'ecological group (AMBI)' are well separated with 41 to 80% of the variance explained. On the F2 axis, the modalities of the variable 'bioturbation' are well separated with a percentage of explained variance of 48%. The modalities of variables 'life span', 'ecological group (AMBI)' and 'individual size' are less well separated on this axis, but better explained on the F3 and F4 axes.

Overall, the F1 axis of the FCA separated carnivore-omnivore free living organisms from sessile tube or burrow-dwellers organisms (Fig. 39). Positive F1 scores are associated with free living carnivorous species that move by crawling and walking, which create diffusive mixing and bulldozing at the sediment surface. Negative F1 scores were associated with sessile deposit- or filter-feeders, which are tube-dwellers and burrowers. The F2 axis separated crawler and/or burrower species with medium life spans, which are disturbance tolerant and of relatively large size to fixed, swimmer and/or walker species, which are of small size and sensitive to disturbance.

Table 16 : Correlation ratios of each biological trait with axes F1 and F2 of the FCA.

	F 1	F 2
Trophic group	**0.804**	0.319
Type of movement	**0.407**	0.236
Habit	**0.629**	0.009
Bioturbation	**0.473**	**0.484**
Life span	0.001	0.316
Ecological group (AMBI)	**0.464**	0.298
Individual size	0.038	0.351

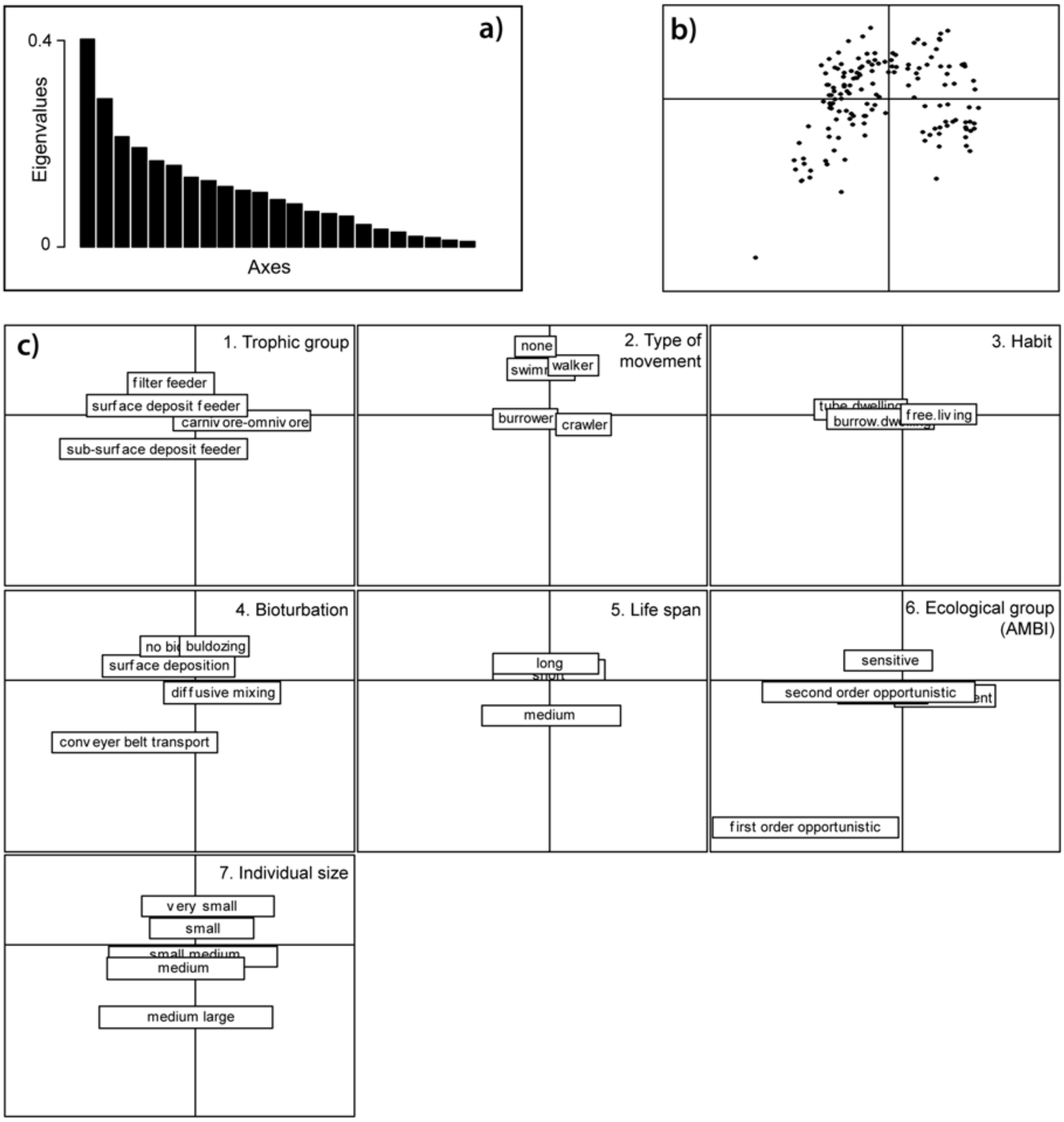

Figure 39 : Ordination of taxa and biological traits by Fuzzy Correspondence Analysis. a) Histogram of eigenvalues. b) Distribution of taxa (solid circles) on the 2 first factorial plane of the Fuzzy Correspondence Analysis. c) Distribution of the modalities of the 7 biological traits on the 2 first factorial plane of the analysis. Each modality was located at the weighted average of taxa positions that are presenting this modality.

From FCA results, the cluster revealed five groups of taxa that each exhibit similar associations of biological traits (Fig. 40). These five groups are relatively well separated on the F1-F2 factorial plane and each of these groups presents a unique set of biological traits (Fig. 41). The group 1 is composed exclusively of sub-surface deposit-feeders which are mainly burrowers (burrow-dwellers or tube–dwellers) and create almost exclusively a translocation of sediment from lower layers to the surface and *vice versa* (conveyer belt transport). They exhibit short to medium life span, are mainly sensitive or tolerant to disturbance and of a medium to large size. Species that are most representative of the functional group 1 are Maldanid polychaetes such as *Maldane glebifex* and *Euclymene oerstedii* but also Orbiniid species such as *Orbinia cuvieri* and Capitellid species (i.e. *Notomastus latericeus* and *Heteromastus filiformis*). The group 2 is composed of burrowing organisms that are mainly deposit-feeders and/or filters-feeders in a lesser extent. Organisms from this group live in tube or burrow and create a deposition of particles and a diffusive mixing at the sediment surface. Most species of this group are short-lived species and are of small to medium size; their sensitivity to disturbance varied from sensitive to opportunistic. Species that are most representative of this functional group are small burrowing suspension- and deposit-feeding bivalves (such as *Kurtiella bidentata* and *Abra alba*) but also polychaetes such as *Ampharete finmarchica* and *Chaetozone gibber* for example. The group 3 is mainly composed of burrowing filter–feeders, living in tubes, burrows or free living. They induced no bioturbation nor create a surface deposition or bulldoze the sediment. The species from this group have long lifespan, are of medium size and are mainly sensitive to disturbance. Species typifying this group are the brittle star *Amphiura filiformis*, large bivalves such as *Dosinia lupinus* and *Polititapes virgineus* and sabellid polychaetes. The group 4 is composed of species with diverse trophic guilds, type of movement, habit and mode of bioturbation. All species in this group have a short lifespan, are sensitive to disturbance and of very small size. Its representative species are almost exclusively crustaceans such as amphipods and isopods. Finally, the group 5 is composed exclusively of carnivorous-omnivorous, free living species that mainly move by crawling and create a diffusive mixing at the sediment surface. They are mainly indifferent to disturbance and of small size. Predatory-omnivorous polychaetes constitute almost exclusively this functional group; some scavenger gastropods such as *Nassarius incrassatus* and *Euspira pulchella* are also included in this group.

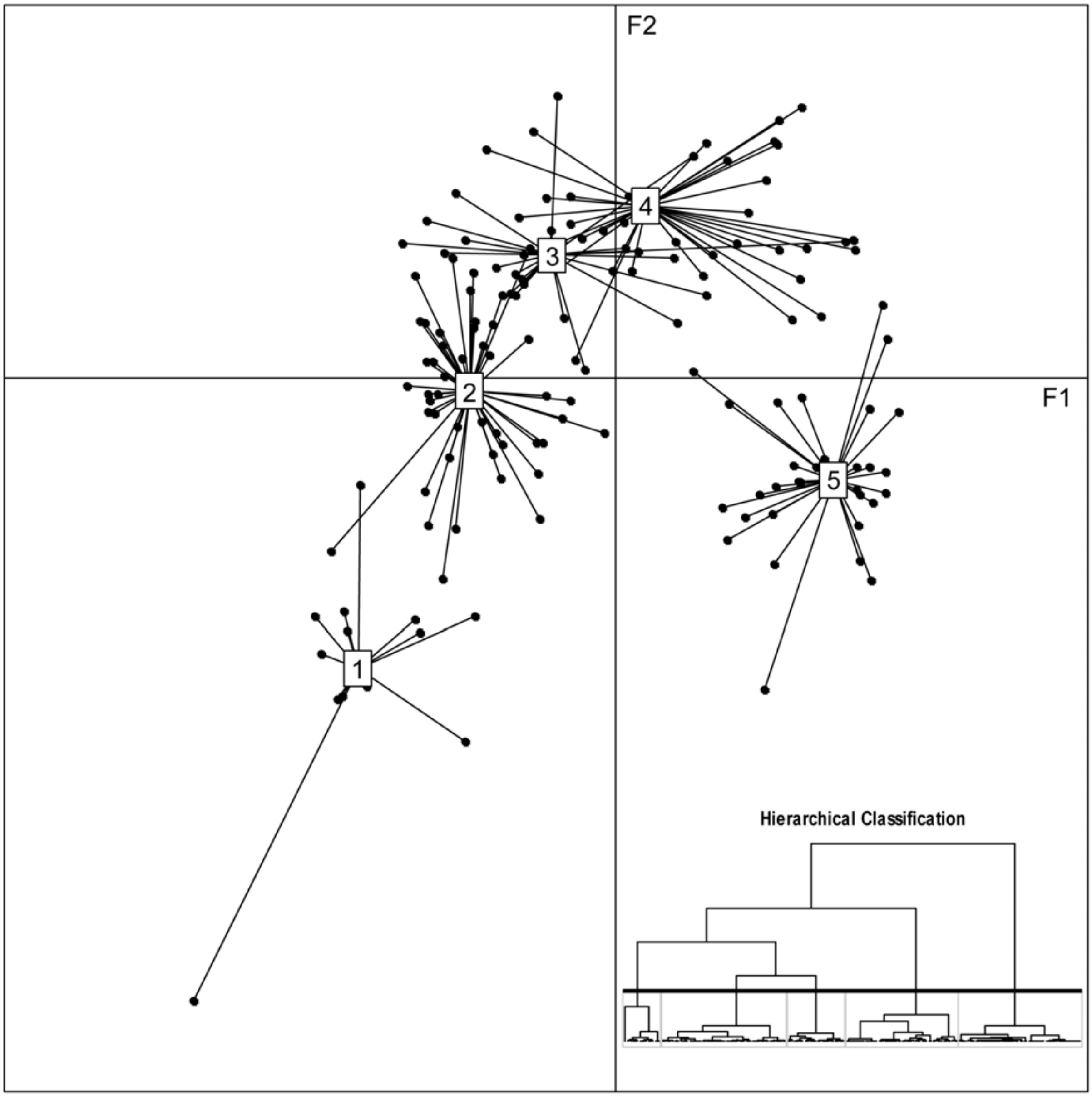

Figure 40 : Reference typology of groups of similar traits on the F1-F2 factorial plane of Figure 39. Functional groups (open squares) were positioned at the weighted average of their taxa (solid circles). Lines correspond to the link of the mean location of each group to its taxa (solid circles). Dendrogram which results from the clustering analysis processed on the FCA results. The vertical line indicated the partitioning level selected to define groups of similar association of biological traits.

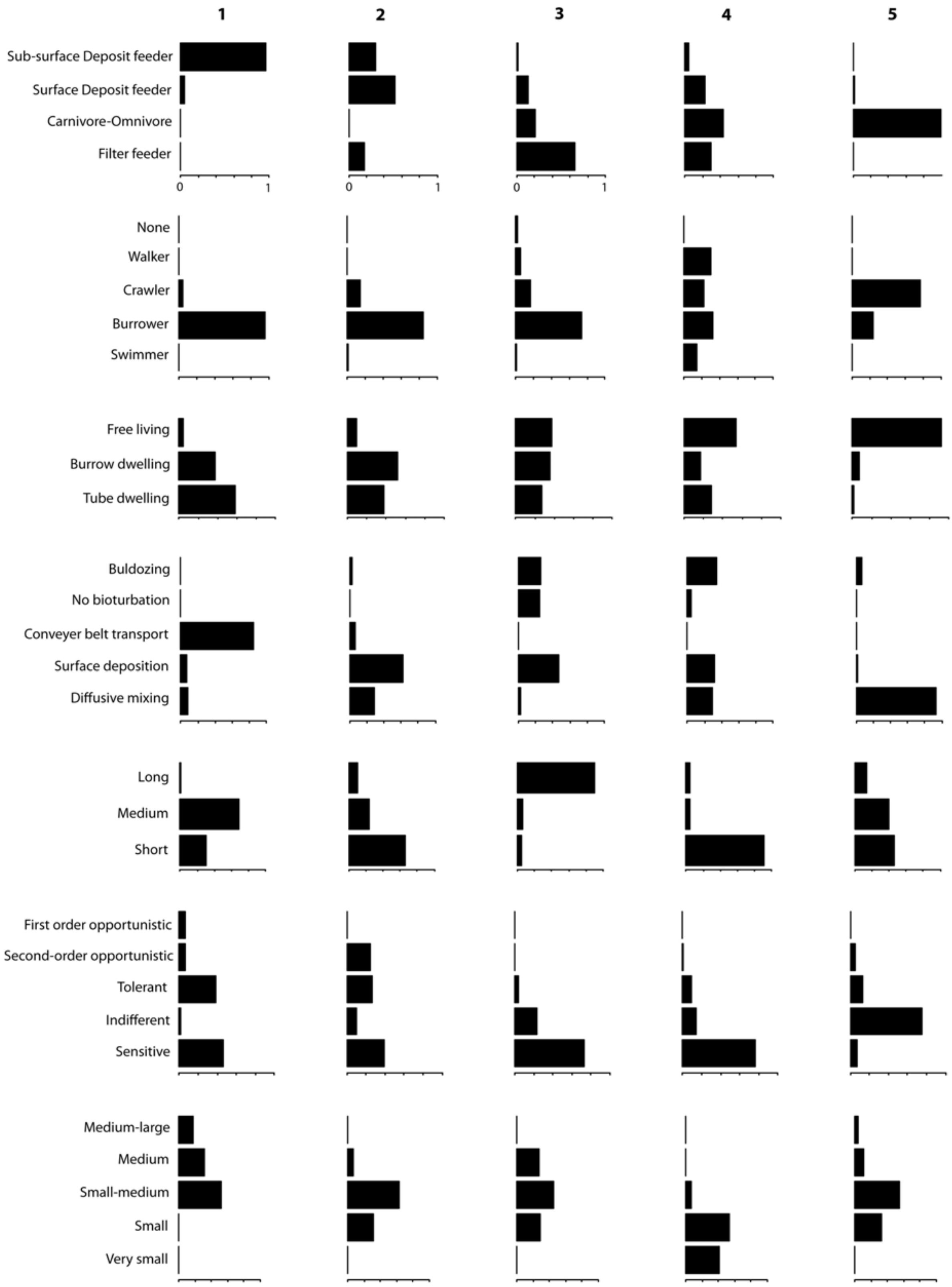

Figure 41 : Mean biological profiles of the 5 groups of similar traits showing for the 7 traits the proportion of trait modalities exhibited by each group. Numbers at the top of the graphic corresponded to the labels of the functional groups.

Significant differences between communities were observed in the proportions of the 5 functional groups (Fig. 42): the proportion of the group 1 was significantly lower in the *Owenia* community compared to the *Amphiura* and *Haploops* communities ($p<0.001$, ANOVA). Functional group 2 was significantly greater in the *Owenia* community, with a higher proportion of short-lived burrowing species ($p<0.001$, ANOVA). Also, the relative proportion of the functional group 3 significantly differed for all communities ($p<0.001$, ANOVA) except between the *Amphiura* and the *Owenia* communities. The *Sternaspis* community showed the highest relative proportion of group 3. The *Haploops* community is only composed of a small proportion of species from this group. No significant differences in the proportion of the functional group 4 were observed between communities. Finally, group 5 is better represented in the *Haploops* community as compared to the *Amphiura* and *Owenia* communities ($p<0.001$, ANOVA on ranks) but did not significantly differ from the *Sternaspis* community.

Based on the relative frequencies of the 5 functional groups in each sampling station, samples are plotted along with the reference typology of groups on the F1-F2 factorial plane (Fig. 43). The relative positions of stations in this space provide information about the functional structure of the benthic macrofauna communities and the functional resemblance between communities. While the relative grouping of all the stations revealed functional redundancy between the four communities, it is worth noting that stations from the *Haploops* community slightly differed from the others, mainly because of its large proportions of species from groups 1 and 5, and small proportion of species from group 3.

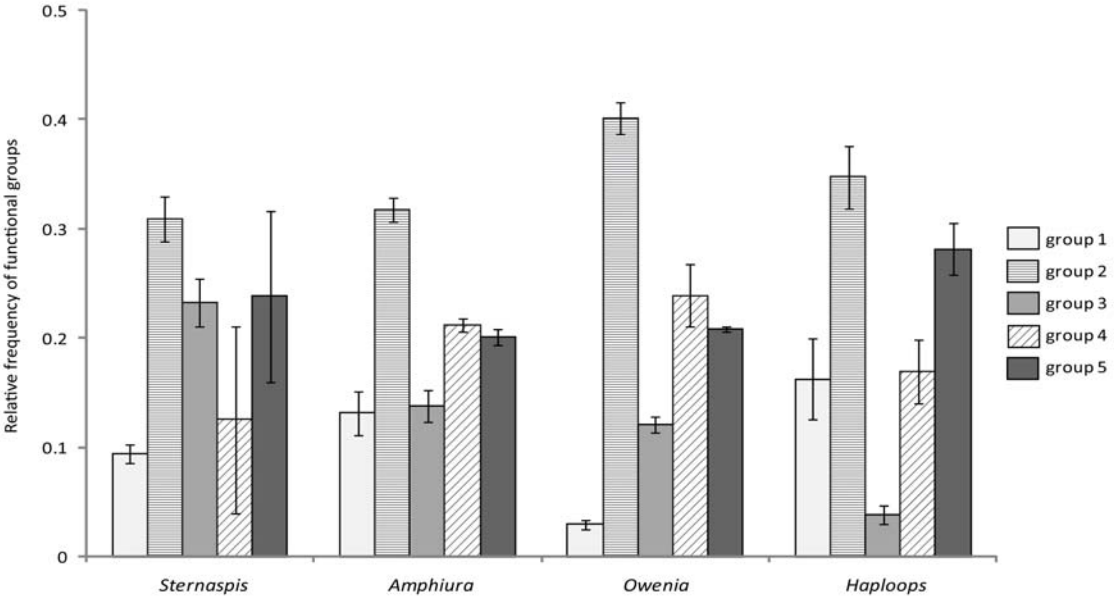

Figure 42 : Relative frequency distribution of the five groups of similar traits in the four benthic communities (i.e. *Sternaspis*, *Amphiura*, *Owenia* and *Haploops*) of the Bay of Concarneau.

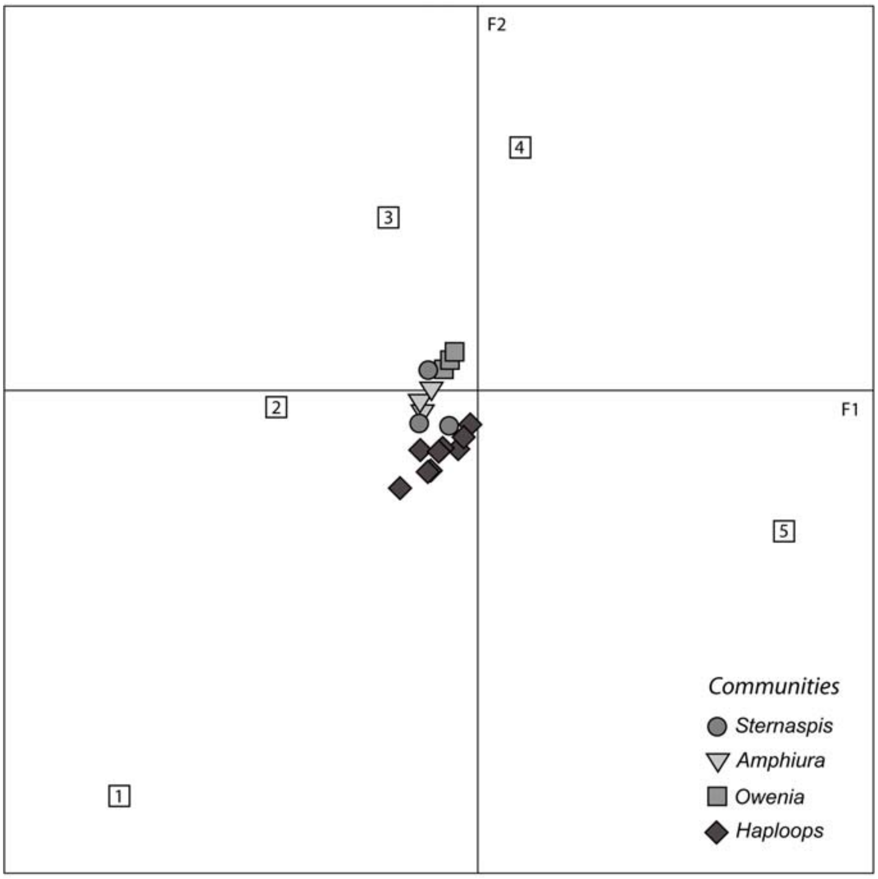

Figure 43 : Relative positions of sampling stations in relation to the reference typology of groups with similar traits. Functional groups are represented by open squares with numbers inside the open squares corresponding to the labels of the functional groups. Stations are located at the weighted average of its group frequency distribution.

4. Discussion

Dense and extensive tube mats created by the tubiculous ampeliscid *Haploops nirae* in the bay of Concarneau (South Brittany) were investigated here to determine the effects of a dense bioengineer species on benthic assemblages, from both a structural and a functional perspective. This species is a good candidate because (1) Ampeliscidae is one of the largest amphipod families which may form dense populations (Dauvin and Bellan-Santini, 1996) and is commonly considered to be composed of important bioengineers due to their ability to construct dense tubes mats (MacKenzie et al., 2006), and (2) this species is reportedly spreading over large geographical scales in South Brittany raising questions on the consequences of the proliferation of a native species in coastal embayments.

4.1. Impact of Haploops nirae on benthic macrofauna community

Using an extensive spatial sampling approach, this study demonstrated that species assemblages associated with *Haploops nirae* strongly differed from those in adjacent communities even when removing *Haploops nirae* individuals from the species matrix. The distance based redundancy analysis (dbRDA) revealed that the environmental parameter mainly responsible for macrofauna differences between the *Haploops* community and the surrounding communities is actually the density of *Haploops*: 54 % of the total variation in species assemblages is explained by this variable, well above the percentage of variance explained by factors commonly reported to primarily influence macrofauna distribution, i.e. the mean grain size and the water depth (Ellingsen, 2002). This result highlights that the abundance of *Haploops* individuals is not the prime reason for the uniqueness of species assemblages in *Haploops* habitat, but that this engineer species strongly affects and controls the species colonizing this habitat. Through the construction of dense tube mats (around 10 000 ind.m^{-2}) *Haploops* individuals actively build a physically complex and heterogeneous environment comparatively very different from the adjacent, less heterogeneous substrates. These tube aggregations also affect environmental parameters, by increasing the quantity and quality (low CN ratio) of the organic matter or by modifying the granulometry of this muddy habitat (see Table 15 for example). Ultimately, *Haploops nirae* seems to facilitate the settlement and further development of a peculiar macrofauna species assemblage. The consequences of the sole occurrence of *Haploops nirae* on the structure of benthic communities are well illustrated from the data for the station CO3. This station originally reported as a *Sternaspis* community-station from an exhaustive mapping of the area (Ehrhold et al., 2006) exhibited small but significant *Haploops* densities (ca 200 ind. 0.1 m^{-2}) which cause sharp changes in associated fauna. It harbored then a species assemblage which is intermediate between both communities even though *Haploops* individuals were removed from the analyses.

Other dense Ampeliscid habitats shared similarities with *Haploops* community, especially large *Ampelisca abdita* community from the North-American coast (Franz and Harris, 1988, Larsen and Gilfillan, 2004). Benthic surveys revealed that the *Ampelisca abdita*-dominated community in Jamaica bay (New York, USA) was clearly different from the adjacent uncolonized communities (Franz and Harris, 1988). Mills (1967) also showed that colonization of dense aggregations of *Ampelisca abdita* in the Barnstable Harbor (Massachusetts, USA) was followed by marked changes in the macrofauna. Similarly, engineer species *de facto* strongly influence associated fauna, as reported for reef-building bivalves aggregating into beds and hardening soft sedimentary systems (Tsuchiya and Nishihira, 1985; Gutiérrez et al, 2012) or seagrass beds stabilizing soft sediment and preventing erosion (Edgar, 1990). A large body of literature also reported that tubiculous polychaete species such as *Lanice conchilega* and *Owenia fusiformis* profoundly change associated species assemblages (Somaschini, 1993; Zühlke, 2001; Callaway et al., 2010).

Not only did we demonstrate the uniqueness of species assemblages when the sediment is colonized by *Haploops* but we also showed that the *Haploop*s community is characterized by a strong homogeneity in species assemblages, as evidenced by the very low variability in spatial changes and the high similarity indices in macrobenthic comparison. Similar results were observed by Castilla et al. (2004) for the mounts formed by the ascidia *Pyura praeputialis*, which exhibit highly similar species assemblages. We can therefore assume that engineered habitat promotes the stability and the constancy of the community structure. Jones et al. (1997) indicated that in the absence of severe abiotic environmental disturbance, many engineers create very stable conditions for those species that are dependent upon them for habitat. In that perspective, the physical constraints created by tubes likely provides a stable environment for a particular combination of species.

4.2. Impact of **Haploops nirae** *on species diversity and abundances*

Our results demonstrated a larger cumulated species richness in the *Haploops* community (i.e. 130 species) compared to adjacent communities where the total species richness was estimated at 80, 95 and 103 species respectively for the same sampling effort. Diversity indices (N1 and N2) equally showed that the *Haploops* community was more diversified than the adjacent communities when *Haploops* densities are not included. Similar results were found in literature: Larsen and Gilfillan (2004) who used the species richness as indicator of diversity, showed that among 11 benthic stations sampled in the Cobscook bay (Maine, USA), the highest species richness occurred in stations colonized by ampeliscids. Sanders (1958) also reported the greatest species richness in stations dominated by three ampeliscid species in the Buzzards bay (Massachusetts, USA). The vast majority of studies have reported positive effects of biogenic habitat structures on diversity indices, species richness and abundances (Crooks, 2002; Godet et al., 2011). This study is thus in agreement with the general idea that tubes of any taxonomic group increase both the sediment stability and the spatial complexity of the bottom and ultimately promote the diversity and the abundances of the associated species (Young and Rhoads, 1971). But interestingly, we also demonstrated that within the *Haploops* community, both species richness and diversity indices are not affected by an increase in *Haploops* tube density. Even at very high tubes densities (i.e. 22 000 tubes.m^{-2}), species diversity levels remain high. Assuming that the occurrence of tube-building species can be considered as a disturbance, this result is not in agreement with the intermediate disturbance hypothesis model which states that species richness is maximized when ecological disturbance is neither too rare nor too frequent. For example, even small densities of tubiculous Terebellids increase local species richness up to a certain point, but that richness decreases past an apparent tube density threshold (e.g. Trueblood, 1991; Zühlke, 2001). Similarly, Dubois et al. (2006) evidenced that only an intermediate covering of the *Sabellaria* reefs by epibionts (oysters) is correlated with the greatest reef species richness and heterogeneity of diversity index values. Unexpectedly, this investigation showed that the density of *Haploops* (i.e. the level of disturbance) did not matter, because species richness and other diversity measurements remain unchanged, while consistently supporting unique and homogeneous species assemblages. We are confident that the range of *Haploops* density (i.e. 920 to 22 000 ind.m^{-2}) is large enough to encompass areas with a lot of available space and scarce tubes as well as densely colonized areas where bare sediment is no longer visible and where *Haploops* tubes attach to each other. As pointed out by Stachowicz (2001) in a review of positive interactions in ecological communities, *Haploops* could be seen as a foundation species offering refuges from predation and a larger trophic niche by creating a new habitat on which numerous species depend, and ultimately increasing species richness compared to the surrounding bare sediment. Positive interactions may then modify the intermediate disturbance hypothesis by broadening the conditions under which higher diversity is maintained. However, we hypothesized here that the modification of the environment (e.g. sediment features, processes at the sediment water interface etc.) with only a very low density of *Haploops* would generate new stresses so that only a few species could settle and develop in a newly colonized area. *Haploops nirae* can have then antagonistic effects on local diversity: a stressor at low densities and a foundation species at moderate to very high densities.

The beta diversity is not specifically tied to a spatial scale but refers to the turnover of species between different habitats composing the ecosystem (Colwell, 2009). The analysis of the turnover of species between the four studied communities showed that the community that shared the lowest number of species with the adjacent areas was the *Haploops* community. While this community adjoined the surrounding communities, very few species are held in common, reflecting high beta diversity and low connectivity. The presence of the *Haploops* community in the bay of Concarneau seems therefore to bring new species to the ecosystem that would otherwise remain excluded from the bay: a third of all species recorded were exclusively found in the *Haploops* community. A newly discovered species of amphipod (*Photis inornatus sp. nov.*) was for example consistently found in the *Haploops* community but not in surrounding muddy environments (Myers et al., 2012). This engineer species contributes to increase the turnover of species in the bay at a previously unseen level and appears to play a crucial role in term of regional biodiversity.

4.3. Impact of **Haploops nirae** *on habitat characteristics*

The diversity of organisms and uniqueness of species assemblages recorded within the *Haploops* habitat can be related to the resources (food or space) available for the macrofauna. The large set of environmental parameters analyzed here showed significant differences between all sampled communities for almost all parameters. The *Haploops* habitat is characterized by an enriched sediment, as the amount of organic carbon and nitrogen are significantly higher, with the lowest C:N ratio, and the highest chlorophyll *a* and phaeopigment concentrations. As a result, the organic matter is more abundant and of better quality (higher digestibility correlates with lower C:N ratio) when the sediment is colonized by *Haploops*. Tubes commonly alter flow patterns at the sediment-water interface and ultimately affect the flux of sedimented particles (Friedrichs et al., 2009). Reducing interface currents and increasing sedimentation processes both contribute to trap suspended organic matter (phytoplankton and marine snow) but the biological activity of *Haploops* individuals also need to be considered. By actively filtering the water column with their antennae and producing large quantity of pseudofeces (and feces) (Rigolet et al., 2011), *Haploops* contribute to enrich the sediment they colonized. In Raritan Bay (New Jersey, USA) where a dense population of *Ampelisca abdita* was observed (about 24 000 ind. m^{-2}), McKenzie et al. (2006) reported that the sediment surface of the mud was mostly composed of fecal pellets of *A. abdita* mixed with a relatively small mixture of silt and clay. Likewise, while investigating *Ampelisca abdita* community in Jamaica bay (New York, USA), Franz and Harris (1988) also showed that %C in sediment spanning from 0.9 to 4.4% (i.e. higher than for *Haploops* community) were greater than in the adjacent uncolonized areas.

Haploops habitat offers hence potentially rich sediment for an abundant macrofauna. Paradoxically, abundances of associated fauna in *Haploops* habitat are the lowest. This is not in accordance with a common result for similar sediment features where the quantity and quality of organic matter largely affect the diversity (Wieking and Kroncke, 2005). For example, Grebmeier et al. (1989) found positive correlations between diversity and sediment total organic carbon, silt and clay content and concluded that low food supply is related to low faunal diversity. However, the space available is probably inversely linked with the quantity of organic matter trapped by tube mats. This factor is then a likely explanation for the limited abundance in associated fauna. Numerous inhabitants of engineered habitats are dependent upon the physical conditions modulated by engineer species, and upon resource flows which they influence but do not directly provide; without the engineers, most of these other organisms would disappear (Jones et al. 1994). *Haploops* tubes and *Haploops* biological activity engineer a unique habitat that is suitable for a unique set of species to settle, but the competition for space with this engineer species controls the development of other populations and probably limits their abundances.

4.4. Impact of* Haploops nirae *on functional diversity

Changes in species assemblages are not necessarily linked with changes in ecological functions played by organisms and assessing functional diversity has become of primary importance to fully understand the consequence of changes in benthic assemblages (see for example Bremner, 2008). We investigated whether a complete shift in species assemblages following a colonization of sediment by the amphipod *Haploops nirae* is ultimately also associated with a change in functional diversity. Analyses of ecosystem functions through biological traits and ecosystem functions revealed that the change in the species richness and benthic composition is much deeper than the change in the functional diversity. Of course, the massive colonization of the sediment by a gregarious suspension-feeder such as *Haploops nirae* has led to a massive increase in suspension-feeding organisms but as for the associated fauna, we showed that contrary to the adjacent sandy and muddy communities (i.e. *Sternaspis*, *Amphiura* and *Owenia*), the functional structure of the *Haploops* community was characterized by a greatly reduced proportion of organisms from the functional group 3. Long-lived, burrower, filter-feeders are therefore proportionally less represented in the *Haploops* community compared to the adjacent areas. The establishment of *Haploops* communities thus controls and prevents other suspension-feeders – burrowers or other tubiculous species – from colonizing. While competition for food and space is often mentioned as a driving factor to explain variations in sessile suspension-feeding invertebrate assemblages (e.g. Buss, 1979; Lesser, 1992), it has been shown that one suspension-feeding species may completely exclude another species by competition for feeding space. Sanders et al. (1962) indicated that the suspension-feeding bivalve *Gemma gemma* is taking over the dominant suspension-feeders (such as *Mya arenaria*) in some stations of Barnstable Harbor (Massachusetts) making up more than 94% of the individuals of that feeding type, hence explaining why other suspension-feeders are not commonly represented in areas where *G. gemma* is represented in large numbers. Similarly, one should consider that *Haploops* could exclude or limit other suspension–feeding species. By contrast, there was a greater proportion of small mobile predators (i.e. functional group 5) in the *Haploops* community which may directly predate *Haploops* or other small organisms associated to this habitat.

A marked reduction in the proportion of long-lived burrowing suspension–feeders may have major consequences in benthic functioning as it is well known that such organisms represent an important link in the food chain, contributing to the benthic-pelagic coupling and providing food sources for demersal finfishes (Sköld et al., 1994). Moreover, large and long-lived organisms are commonly considered to be productive organisms since the size and the lifespan are directly related to the secondary production of species (Brey, 1990). They represent therefore an important biomass and provide significant energy transfer to higher trophic levels. This could in turn explain why the secondary production of this *Haploops* community negatively compares with the production of surrounding muddy communities (i.e. *Amphiura* and *Owenia* communities), as estimated in a previous study from the same area (Rigolet et al., 2012).

4.5. Consequences of further **Haploops** *expansion*

Haploops communities have been reported in a few locations all over the world: the bay of Fundy (Canada) (Wildish and Dickinson, 1982), the East Siberian Sea (Russia) (Gukov, 2011), the Øresund and Kattegat (Sweden) (Göransson, 2002) and the Northumberland coast (Scotland) (Buchanan, 1963). Densities of *Haploops* recorded in South Brittany are the highest reported for the genus *Haploops* (Rigolet et al, 2012). Unlike the dramatic decline in *Haploops* densities that occurred in the Øresund during the last 100 years (decreasing from 3500 to 100 ind. m^{-2} today), along with a drastic shrinking of their distribution area (Göransson, 2002) in response to the alteration of environmental conditions (e.g. eutrophication), it is likely that the *Haploops* community will continue to expand in the whole Bay of Biscay (Atlantic). The *Haploops* community occupies a wide area in the Bay of Concarneau (ca. 3600 hectares) which has increased by 400 % since the 1960s (Glémarec, 1969). Complementary acoustic mapping surveys conducted in the EU Marine Strategy Framework Directive revealed that *Haploops* communities are spreading over larger areas in South Brittany. This investigation addresses a crucial issue related to the spreading of an ecosystem engineer species: *Haploops* habitat contributes to the seascape diversity and to the overall regional increase in species diversity. If the importance of an ecosystem habitat is linked to the uniqueness of its associated fauna, then *Haploops* are of primary importance in the seascape of the shallow water of South Brittany in the fight against the loss of biodiversity. However, the strong spatial stability and homogeneity in macrofauna assemblages associated with *Haploops* habitats could adversely affect the total species diversity in the ecosystem as the connectivity between adjacent habitats and *Haploops* habitat is low. The expansion of *Haploops* habitat could then ultimately increase the homogenization in benthic habitats at large scale. Similar results have been reported in different coastal embayments of the Atlantic coasts following the introduction and the proliferation of the invasive slipper limpet *Crepidula fornicata*. By increasing the sediment heterogeneity, the presence of *C. fornicata* stimulates zoobenthic community diversity and abundance in muddy sediments while its expansion promoted the habitat homogenization (de Montaudoin and Sauriau, 1999). Models of habitat-dependant species-area relationships predict biodiversity losses when biogenic habitats in soft-sediments are homogenized or conversely when they are colonizing an entire ecosystem (Thrush et al., 2006). Franz and Harris (1988) suggested that the permanent loss of one or more superdominants such as *Ampelisca abdita* in Jamaica bay (New York) coupled with a further reduction in species richness could lead to more unstable benthic associations, in which short-term and random species invasions might dominate the benthic community structure. Our results provide evidence that small densities of *Haploops* would cause a complete change in species assemblages, hence suggesting that *Haploops* is highly controlling species assemblages and ultimately forcing a one-way succession in its benthic habitat, as many abundant species structuring other adjacent communities (such as *Amphiura filiformis* and *Kurtiella bidentata, or Nucula nitidosa*) were not even found in *Haploops* samples. In that case, even a decrease in *Haploops* density would not allow other species to take over and somehow balance benthic successional stages.

ARTICLE N°4

Seasonal dynamics and secondary production of benthic communities in the bay of Concarneau (South Brittany, France): the functional consequences of changes induced by the tubiculous amphipod *Haploops nirae*

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Article en préparation

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Abstract

Seasonal taxonomic composition, biomass and annual production were measured for macroinvertebrate communities in two inshore-offshore transects in the bay of Concarneau. Data revealed that *Haploops* induced strong structural changes in species composition compared to adjacent bare sediments but had no effects on the species richness. Biomass values were mainly influenced by standing crops of filter feeders *Amphiura filiformis* in bare sediments and *Haploops nirae* in the *Haploops* community. While season had no effects on the benthic biomass, biomass appeared significantly affected by the *Haploops* occurrence. The mean annual biomass in the *Haploops* community was 12.37 ± 4.71 g AFDW.m^{-2} and was on average 1.6 times lower than in bare sediments (19.91 ± 3.65 g AFDW.m^{-2}). Secondary production of the entire community was estimated using the empirical model developed by Brey (1990). In bare sediments, the mean annual secondary production was estimated at 24.58 ± 2.15 g AFDW.m^{-2}.y^{-1} and did not significantly differ from values reported in *Haploops* stations (22.40 ± 5.56 g AFDW.m^{-2}.y^{-1}). The bulk of the total secondary production estimated at the community scale was attributable to the same species that dominate the benthic biomass (i.e. *Amphiura filiformis* in bare sediments and *Haploops nirae* in *Haploops* stations). Whereas the *Haploops* community was as productive as the *Amphuira filiformis* community, evidences from fish communities led to the hypothesis that trophic flows to higher levels differ among habitats and are probably altered by the presence of dense tube mats

1. Introduction

Secondary production defined as the assimilation of organic matter into body tissue mass by consumers (Tagliapietra et al., 2007) is an ecological fundamental measure as it reflects many aspects of ecosystem functioning. First, secondary production can be viewed as the most comprehensive representation of success for any population in its environment, being of great importance for understanding populations' dynamics (Benke, 1993). Second, because secondary production corresponds to the rates at which organic matter is made available to higher trophic levels, it also reflects the relative importance of organisms as consumers and nutrient recyclers, and is of key importance to understand energy flows through ecosystems and food web interactions (Taylor, 1998; Ricciardi and Bourget, 1999). It ultimately provides a measure of food provision delivered by an ecosystem. Finally, as it summarizes all of the information relative to the health of a biological system (i.e. biomass, individual growth and community growth, reproduction, generation time and survival) (Medernach and Grémare, 1999), secondary production can also be considered as one of the most comprehensive assessments of ecosystems integrity (Buffagni and Comin, 2000) and can be viewed as a valuable quantitative measure of changes in ecosystem processes. It may reveal greater insights into ecosystem change than static parameters such as density, biomass or diversity.

Methods based on time series measurements of population densities and body size or biomass (e.g. cohort and size frequency methods) are the best way to correctly assess the somatic production of benthic animals and are widely used in ecological studies, particularly for single species or a few species studied simultaneously (Cusson and Bourget, 2005; Benke and Huryn, 2010). In contrast, few studies have been carried out on entire invertebrate assemblages mainly because such methods require long and time-consuming studies supported by adequate sampling designs and strategies. On the other hand, most species are present at low densities which prevent the application of direct methods to measure secondary production. Yet, many ecological studies required estimates of secondary production, not only for a single abundant species but also for the whole communities. In this perspective, different empirical models were proposed for estimating benthic secondary production at the community-wide level and were developed on the basis of correlations between measured secondary production and population features (e.g. life span, average biomass, individual weight at sexual maturity, etc..), often in combination with some key environmental variables (e.g. temperature, depth) (e.g. Brey, 1999; Medernach and Grémare, 1999; Tagliapietra et al., 2007).

Ampeliscidae are common tubicolous amphipods inhabiting temperate and subarctic waters of the Atlantic and Pacific Oceans. They can reach high densities and form very dense tube mats in shallow subtidal zones (Bellan-Santini and Dauvin, 1988; Franz and Tanacredi, 1992; Sudo and Azeta, 1996; Göransson, 2002). In such cases, ampeliscids can play significant ecological roles in different ecosystem processes. As underlined for many tubiculous gregarious species, tube occurrences create a very unique habitat, considerably more complex and heterogeneous than the adjacent homogeneous soft-bottom areas and affect the local biodiversity (Reise et al. 2009). They modify the availability of resources and ultimately biological and sedimentary patterns (Berkenbusch and Rowden, 2007). They can also represent a major component of the secondary production in coastal ecosystems with production levels among the highest in benthic invertebrate communities (e.g. Carrasco and Arcos, 1984; Highsmith and Coyle, 1990; Franz and Tanacredi, 1992). By feeding primarily on phytodetritus, they greatly influence the pelagic-benthic coupling (Grebmeier and McRoy, 1989). Several studies also demonstrated that ampeliscids can constitute a major component in the diet of higher-level consumers such as finfishes and marine mammals (Gallardo, 1962; Franz and Tanacredi, 1992; Highsmith and Coyle, 1992) and likely play an important role in transferring matter and energy from the benthic compartment to higher trophic levels.

In shallow South Brittany coast, two coastal embayments (i.e. the bay of Concarneau and the bay of Vilaine) support very abundant and widespread populations of the ampeliscid *Haploops nirae* (initially misidentified as *H. tubicola* ; Glémarec, 1969), with average densities around 10 000 ind.m^{-2} (Rigolet et al., 2012). Acoustic surveys (Ehrhold et al., 2006) revealed that this species is spreading and proliferate over large areas of the entire South Brittany coast. For example, the mapping of the bay of Concarneau revealed a 5-fold increase in the surface of the *Haploops nirae* habitat between 1963 (650 ha in Glémarec, 1969) and 2003 (3680 ha in Ehrhold et al., 2006). In those systems, *Haploops nirae* dominates the fauna and represents numerically over 90 % of the benthic macrofauna. The recent extent of this engineer species raises several issues regarding major changes in the structure of benthic communities and the local diversity, and ultimately on the functioning of the ecosystem. In this context, Rigolet et al. (submitted) compared the structural and functional diversity of the macrofauna associated with *Haploops* community with several surrounding soft-sediment communities. They highlighted that the occurrence of *Haploops nirae* significantly modifies sediment features (e.g. decrease in sediment grain size, increase in C and N organic content) but also largely affect species diversity and macrofauna composition. The *Haploops* community is characterised by higher species richness, and a large portion invertebrates inhabiting the sandy and muddy habitats of the bay of Concarneau is endemic to the *Haploops* community. Changes in macrofauna composition are however much deeper than changes in the functional diversity assessed with biological traits analyses. Nevertheless, such physical and subsequent community changes induced by *Haploops* could greatly influence the ecosystem functional properties, including the macrofauna secondary production.

From an annual survey in 2010, the annual secondary production of *Haploops nirae* at a single site in the bay of Concarneau has been estimated at 9.66 gDW m^{-2} y^{-1} using the increment summation method (Rigolet et al., 2012). Although this value constituted one of the highest production values calculated for an Ampeliscid, it was close but lower to values reported for the dominant species of the other communities during the 70s (Ménesguen, 1980). How the extent of dense *Haploops* tube mats affects the whole secondary production of benthic communities in the bay of Concarneau is still to be investigated. In this perspective, the objectives of the present study are to 1) assess the seasonal variability of community structure of the *Haploops* community and other surrounding communities and 2) determine how the expansion of dense tubiculous amphipods alter standing stock biomass and secondary production at the ecosystem scale. As secondary production is a direct reflection of resource availability, habitat-specific resource consumption and processing rates, potential consequences of *Haploops* expansion on energy flows will be discussed, more particularly relative to the amount of energy made available to higher trophic levels.

2. Materials and methods

2.1. Study area

This study was conducted in the bay of Concarneau, situated in the Northern part of the Bay of Biscay (France) (Fig. 44). This area typifies many coastal embayments in South Brittany as it is sheltered by a succession of rocky islets and is characterized by soft-bottom substrates, spanning from muddy to muddy-sand, with a depth ranging from 15 to 35 m (Ménesguen, 1980). The westernmost part of the bay (north Mouton islets and Glénan Islands) is composed of muddy sands and sandy muds. The central part of the bay, where currents are strongly reduced, is composed of pure muds supporting a dense population of the tubiculous amphipod *Haploops nirae*. The western edges of the *Haploops* habitat are surrounded by patchy muddy sediments. A recent mapping survey of the seabed using geoacoustic approaches and complementary benthic biological grab samples reported 4 distinct benthic communities in the bay: the *Sternaspis scutata* muddy community, the *Amphiura filiformis* sandy-mud community, the *Owenia fusiformis* muddy-sand community and the *Haploops* muddy community (Ehrhold et al., 2006) (Fig. 44).

2.2. *Sampling strategy and laboratory analyses*

To investigate the effects of *Haploops nirae* on species assemblage structure, standing stock biomass and secondary production of benthic communities, we compared the macrofauna associated with *Haploops* to the one associated with the adjacent benthic communities. Following the mapping of benthic communities in the bay of Concarneau (Ehrhold et al., 2006), 6 stations distributed along two north-south transects reflecting an inshore-offshore gradient were sampled (Fig. 44). Stations CO 9, CO 14 and CO 16 formed one transect located in the *Haploops* community. Stations CO 4, CO 24 and CO 28 constituted the second transect and were located in muddy sands overall dominated by the ophiurid *Amphiura filiformis* (station CO 4) or the polychaete *Owenia fusiformis* (station CO 24). Although the station CO 28 belongs to an unspecified area, *Amphiura filiformis* was previously reported as one of the dominant species in this part of the bay (Glémarec et al., 1986).

At each station, the benthic macrofauna was sampled once per season (winter, spring, summer and autumn) from February 2010 to November 2010 using a 0.1 m^2 Van Veen grab. Three replicates per station were collected at each season. Samples were sieved on a 1 mm circular mesh-size screen and fixed with a 5% buffered formalin solution. In the laboratory, samples were rinced, and the macrofauna was sorted, identified to the lowest taxonomic level (i.e. generally at the species level) and counted. The biomass of the species for which density is greater than 20 individuals.m^{-2} as well as the biomass of larger and more dispersed species (e.g. *Aphrodita aculeata* and *Thyone fusus*) were estimated. Biomass of each taxon was measured by weight loss after combustion at 450°C for 6 hours (ash-free dry weight) and by pooling the three replicates subsets. Since organisms were preserved in formalin, a correction factor of 1.2 was applied as suggested by Brey (1986) to compensate the weight loss caused by the preservative.

In addition, a sediment sample was collected at each station using a Reineck box-corer to determine the grain size of the first 5 cm of the sediment layer. Grain size distribution was analysed using a laser particle analyser (Malvern Mastersizer 2000) in equivalent spherical diameter.

2.3. Data analysis

Community structure. To check for the validity of the *a priori* grouping of stations for each community, a non-metric multi dimensional scaling (nMDS) combined with a cluster analysis was first used. Analyses were conducted on a Bray-Curtis similarity matrix calculated from log-transformed abundances to downweight the influence of abundant species. Species that appeared only once in the dataset (i.e. occurring in less than 2% of the samples) were removed from multivariate analyses. As ecosystem tube-building engineer species, *Haploops nirae* has strong effect on environment. We hence considered here *Haploops* tube densities as an environmental parameter. Consequently, *Haploops* individuals were removed from multivariate analyses so that only the associated species only were considered. Cluster analyses were performed using the group average linkage method. These different analyses were performed using the PRIMER 6 software package (Clarke and Gorley, 2006).

Macrofauna diversity. The macrofauna diversity of the sampled communities - as identified from the multivariate analyses - was assessed using indices recommended by Gray (2000) for characterizing local diversity namely Hill's indices (N0, N1 and N2) (Hill, 1973). As described in Hill (1973), N0 corresponds to the species richness (number of species), N1 = exp (H') where H' is the Shannon-Wiener diversity index (loge) and N2 = 1/SI, where SI is the Simpson's dominance Index. The N1 index is affected by species situated in the middle of the rank sequence, while the Simpson index used in the calculation of N2 addresses the degree of dominance of one or a few very abundant species (Whittaker, 1972). The N1 and N2 indices are two measures of the heterogeneity diversity. *Haploops* individuals were also removed from the dataset so that only the associated fauna was considered.

Two-way ANOVAs were performed to evaluate simultaneously the effects of *Haploops* occurrence and season on species richness, heterogeneity diversity, and abundances. Normality of data was assessed using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. Following the 2-way ANOVAs, post hoc comparison tests were made using the Holm-Sidak multiple comparison test. All statistical analyses were performed using the Sigmastat 3.5 software (Systat Software, Inc., CA, USA).

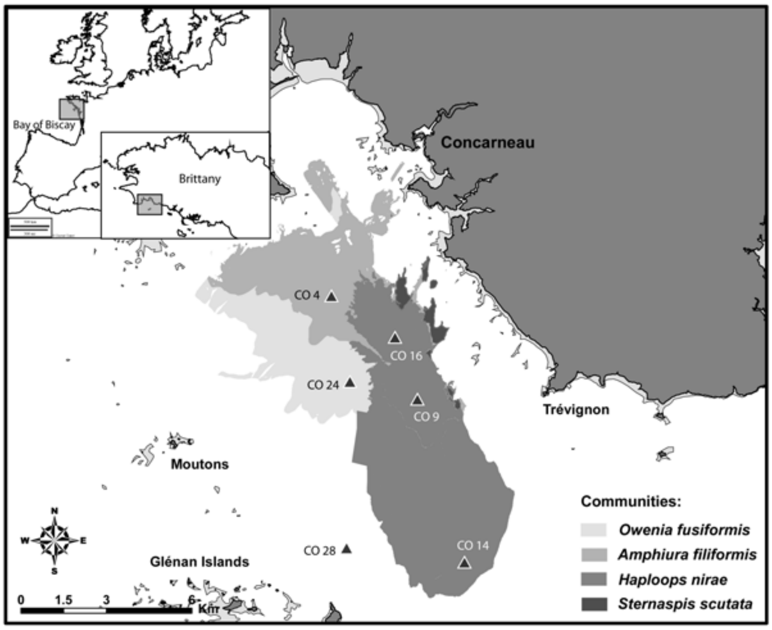

Figure 44 : Geographical distribution of the subtidal benthic communities of the bay of Concarneau and location of the six stations sampled at each season along two transects studied (i.e. within the *Haploops* community: CO16, CO9, CO14 and within the surrounding communities": CO4, CO24 and CO28). Sampling stations coded with a triangle.

Biomass and secondary production. To estimate the secondary production at the six sampling sites, we used one of the several empirical models proposed in the literature. As some models required the measurement of some environmental parameters and biological traits not available for this investigation (such as the individual weight at first maturity and the maximum individual weight), models proposed by Plante and Downing (1989), Benke (1993) and Tumbiolo and Downing (1994) were considered not suitable to be used with our dataset. Based on such limitations, the annual secondary production was estimated using the empirical model developed by Brey (1990) using the following equation:

$$\text{Log } P = -0.473 + 1.007 \log B - 0.274 \log W_{mean}$$

where P is the annual secondary production (g AFDW.m^{-2}.y^{-1}), B is the mean annual biomass (g AFDW.m^{-2}) and W_{mean} is the mean individual body weight (g AFDW) of the marine benthic invertebrates.

This empirical model has been recently used by different authors to estimate changes in the secondary production in response to environmental changes or human disturbances (Cooper et al., 2008; Dolbeth et al., 2011).

To test for the effects of *Haploops* and season on the benthic macrofauna standing stock biomass, two-way ANOVAs were performed. Normality of data was assessed using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. A Student's t-test was applied to compare the annual secondary production between the two different communities.

3. Results

3.1. Seasonal changes of species assemblages and structural diversity

The hierarchical cluster analysis as well as the nMDS revealed that, whatever the season, 2 main clusters, i.e. species assemblages that correspond to two different communities, are discriminated at a similarity level close to 40 % (Fig. 45). In agreement with the previous mapping of the bay of Concarneau (Fig. 44), all *Haploops* stations were discriminated from bare sediment stations, suggesting that the species assemblage associated with *Haploop*s community was different from surrounded benthic assemblages for all seasons. Only the station CO 14 slightly differed from the others *Haploops* stations (i.e. CO 9 and CO 16). For the surrounding sediment environment, the station from the *Amphiura* sandy mud community (i.e. CO 4) was separated on the nMDS plot from the two other stations located in the *Owenia* muddy sand community (i.e. CO 24 and CO 28). These differences were linked to a inshore-offshore gradient of sediment grain size due to a decrease in mud content (Table 17). Whatever the season, replicates from a given station consistently belonged to the same cluster, suggesting that seasonal variations have little effect on the structure of species assemblages compared to the existing spatial differences between stations and communities.

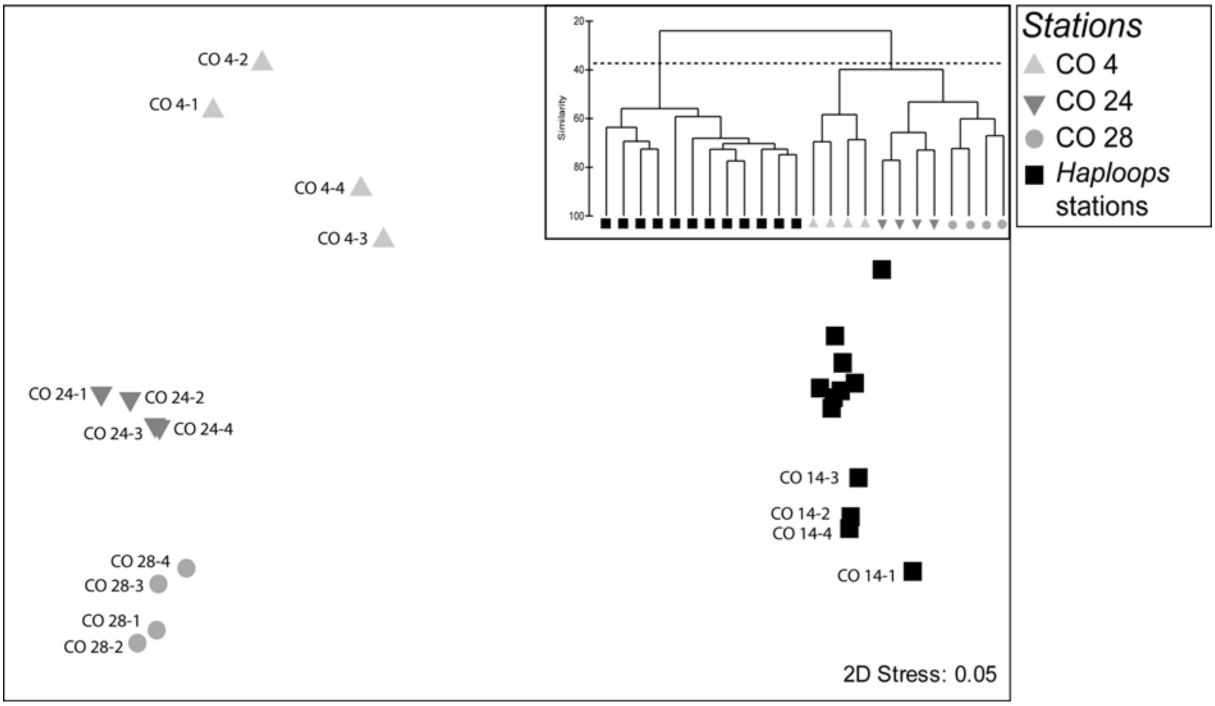

Figure 45 : Non-metric multidimensional scaling ordination plot for log-transformed abundance data based on the Bray-Curtis similarities for the 6 stations sampled seasonally. Samples code indicates first the number of the station and then the season: for example CO 4-1 and CO 4-2 corresponded to station CO 4 sampled in winter (1) and spring (2) respectively). The hierarchical clustering of log-transformed abundance data using group-average linking on Bray-Curtis similarities is added.

Table 17 : Proportion of mud (grain size < 63 µm) at the 6 stations investigated during the present study.

	Adjacent communities			***Haploops* community**		
	CO4	**CO24**	**CO28**	**CO9**	**CO14**	**CO16**
Winter 2010	0.43	0.22	0.09	0.73	0.77	0.74
Spring 2010	0.50	0.20	0.29	0.72	0.82	0.72
Summer 2010	0.48	0.22	0.12	0.77	0.83	0.76
Autumn 2010	0.47	0.25	0.21	0.75	0.78	0.72

Mean values of macrofauna abundances and diversity measure within each community at all seasons are reported in Table 18. Except for the species richness (N0), heterogeneity diversity (N1 and N2) and abundances significantly differed between the *Haploops* community and the adjacent communities. When *Haploops* are removed from the dataset, significant effects of season, *Haploops* occurrence and interaction were showed for macrofauna abundances (Table 19). While no difference in abundances was reported between *Haploops* and adjacent stations in winter and spring, significant differences between the two transects occurred in summer and autumn with lower abundances in the *Haploops* community (pairwise multiple comparison: Holm-Sidak Test, $p<0.05$). Indeed, a significant increase in abundances occurred in adjacent stations between the first part of the year (winter-spring) and the second one (summer-autumn). Seasonal effects on abundances in *Haploops* stations were in contrast much less pronounced and significant differences were observed only between winter and the second part of the year 2010 (summer-autumn). Species richness was significantly affected by seasons but not by the *Haploops* occurrence (Table 19). However, the interaction between the two factors was significant. Species richness did not significantly differ between the two transects except in spring where the species richness in *Haploops* stations was significantly higher (Holm-Sidak Test, $p<0.05$). In bare sediment stations, species richness showed significant seasonal changes: species richness in summer and autumn was significantly higher than in spring (Holm-Sidak Test, $p<0.05$). Conversely, season had no significant effect on species richness in *Haploops* stations (Holm-Sidak Test, $p>0.05$). Contrary to species richness, N1 and N2 were significantly affected by the *Haploops* occurrence but not by the season and the interaction between the two factors. These two indices did not significantly differ between the two transects in winter and summer but were significantly higher in *Haploops* stations in spring and autumn (Holm-Sidak Test, $p<0.05$).

Table 18 : Abundances, N0 (species richness), N1 (exp (H')), N2 (1/SI) within the 2 transects (bare sediments and *Haploops* community). *Haploops* species was removed from the macrofauna dataset prior calculations of diversity indices and abundances.

Season	**Diversity indices**	**Adjacent communities**			***Haploops* community**		
		CO4	**CO24**	**CO28**	**CO16**	**CO9**	**CO14**
Winter 2010	N0	75	80	86	66	94	62
	N1	23.7	28.6	27.5	34.9	42.4	28.6
	N2	11.2	15.9	13.2	23.6	26.1	18.7
	Abundances (no.0.1 m-²)	189	231	211	107	202	135
Spring 2010	N0	69	82	64	96	98	91
	N1	18.4	30.9	13.7	43.4	41.7	36.3
	N2	8.8	17.1	5.2	28.2	25.0	21.0
	Abundances (no.0.1 m-²)	209	224	208	223	227	234
Summer 2010	N0	99	98	97	87	93	95
	N1	30.4	42.3	20.9	35.3	39.1	33.5
	N2	13.8	28.5	10.2	22.0	24.3	19.2
	Abundances (no.0.1 m-²)	393	387	417	280	261	269
Autumn 2010	N0	89	105	104	90	104	84
	N1	18.7	38.3	23.9	40.0	44.0	35.7
	N2	7.2	24.1	12.6	26.0	28.0	21.4
	Abundances (no.0.1 m-²)	375	394	438	290	289	171

Table 19 : Summary of two-way ANOVA results for factors season and *Haploops* occurrence on macrofauna abundances (*Haploops* removed), species richness (N0), heterogeneity diversity (N1 and N2), and biomass. Significant differences ($p<0.05$) are in bold.

Variable	Factor	P value
N0	*Haploops* occurrence	NS
	Season	**0.005**
	Haploops × Season	**0.023**
N1	*Haploops* occurrence	**<0.001**
	Season	NS
	Haploops × Season	NS
N2	*Haploops* occurrence	**<0.001**
	Season	NS
	Haploops × Season	NS
Abundances (*Haploops* removed)	*Haploops* occurrence	**<0.001**
	Season	**<0.001**
	Haploops × Season	**<0.001**
Biomass	*Haploops* occurrence	**<0.001**
	Season	NS
	Haploops × Season	NS

3.2. *Benthic biomass*

The mean benthic biomass varied with the seasons and ranged from 6.22 to 19.79 g AFDW.m^{-2} in the *Haploops* transect and from 15.62 to 30.94 g AFDW.m^{-2} in bare sediments (Fig. 46). Benthic biomass is significantly affected by the *Haploops* occurrence while the season and the interaction between the two factors were not significant (Table 19). The benthic biomass was significantly lower in *Haploops* stations in winter (Holm-Sidak Test, $p<0.05$) while no significant differences were reported during the remainder of the year. Overall, the mean annual biomass in the *Haploops* community was 12.37 ± 4.71 g AFDW.m^{-2} and was on average 1.6 times lower than in bare sediments (19.91 ± 3.65 g AFDW.m^{-2}). Data also revealed a higher variability within bare sediment stations. While the stations CO 24 and CO 28 followed the same trend across the year with an increase in spring, the station CO 4 exhibited a sharp decrease of biomass values from winter to spring followed by a slight increase from spring to autumn. In summer and autumn, biomass estimated at the station CO 4 were similar to values exhibited by other bare sediment stations. Similarly, the southern station of the *Haploops* transect (i.e. CO 14) showed biomass values consistently higher than the two other *Haploops* stations, especially in spring and autumn. As already reported for abundances, seasonal variations in biomass in the *Haploops* community are smaller than those reported for the surrounding communities.

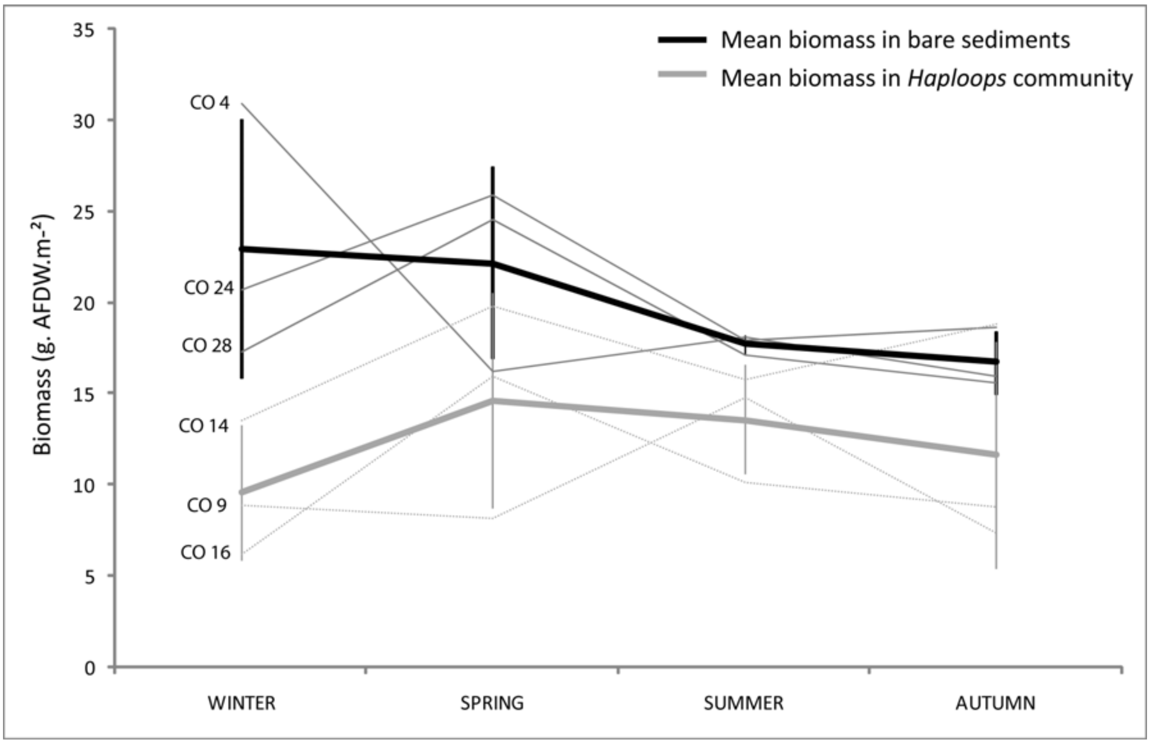

Figure 46 : Seasonal changes in benthic biomass (g.AFDW.m^{-2}) in *Haploops* and bare sediment stations. Mean values (± SD) are represented.

Among the 122 and 97 taxa for which the biomass was estimated in *Haploops* and adjacent communities respectively, only 3 to 6 species accounted for 50% of the benthic biomass in both transects (Table 20). In adjacent communities, echinoderms contributed most to the benthic biomass (from 24.4 to 61.2 % of the total biomass) mainly due to the ophiurid *Amphiura filiformis* (Table 21). As expected, *A. filiformis* formed an essential part of the benthic biomass at all bare sediment stations (from 12.5 % to 27 % of the benthic biomass in the stations CO 4 and CO 28 respectively). On the other hand, the sea cucumber *Thyone fusus* accounted also for a large part of the biomass at all bare sediment stations, constituting from 19 to 49 % of the total biomass. Molluscs accounted for between 8.4 and 24.3 % of the benthic biomass due to the high contribution of the large bivalve *Dosinia lupinus* and the gastropod *Turritella communis.* The relative contributions of the different taxonomic groups varied widely from one station to another. For example, echinoderms that accounted for 61.2 % of the benthic biomass in the station CO 28, constituted only 24.4% of the biomass in the station CO 4. Conversely, the station CO 4 differed from the stations CO 24 and CO 28 by the occurrence of maldanid species (i.e. *Maldane glebifex* and *Macroclymene santandarensis*) that accounted for the largest part of the biomass at this station.

At *Haploops* stations, arthropods and annelids are the main contributors of the benthic biomass with a mean contribution of 34.3 and 33.0 % respectively mainly due to *Haploops nirae* for arthropods, and Glycerid polychaetes such as *Glycera unicornis* or *Glycera alba* and the maldanid polychaete *Maldane glebifex* for annelids. *Haploops nirae* was the first contributor to the benthic biomass at all stations of the *Haploops* transect and accounted for between 22.2 and 29.3 % of the total biomass depending on the station. Among Molluscs, the large bivalve *Polititapes virgineus* consistently contributed for a large proportion of the biomass (on average 10 %) excepted at station CO 14. While echinoderms are responsible for the bulk of the biomass in adjacent communties, they accounted for a small part of the benthic standing stock biomass in the *Haploops* community.

While the most abundant species in terms of biomass belong to suspension-feeders and in a lesser extent to subsurface deposit-feeders at the station CO 4 in the bare sediments, a large proportion of the biomass in the *Haploops* community was due to suspension-feeders and carnivorous.

Table 20 : Main species contributing to the benthic biomass (average over the year) at the six stations investigated. The trophic group of each species is given. C: Carnivorous; DF: Surface deposit-feeder; S: suspension-feeder; SDF: Subsurface deposit-feeder.

Station	Species	Trophic group	Contribution to the benthic biomass (%)	Cumulated biomass (%)
CO 4	*Maldane glebifex*	SDF	14.2	14.2
	Amphiura filiformis	S	12.5	26.7
	Macroclymumene santandarensis	SDF	6.3	33.0
	Thyone fusus	S	6.2	39.2
	Notomastus latericeus	SDF	5.9	45.1
	Turritella communis	S	5.0	50.1
CO 24	*Amphiura filiformis*	S	15.0	15.0
	Aphrodita aculeata	C	14.2	29.2
	Aspidosiphon (Aspidosiphon) muelleri muelleri	DF	9.5	38.7
	Thyone fusus	S	8.7	47.4
	Leptopentacta elongata	S	7.6	55.0
CO 28	*Amphiura filiformis*	S	27.0	27.0
	Thyone fusus	S	19.6	48.6
	Dosinia lupinus	S	7.3	55.9
CO 9	*Haploops nirae*	S	22.2	22.2
	Polititapes virgineus	S	10.7	32.9
	Glycera unicornis	C	10.5	43.3
	Aspidosiphon (Aspidosiphon) muelleri muelleri	DF	7.5	50.8
CO 14	*Haploops nirae*	S	25.5	25.5
	Ophiura albida	C	15.2	40.7
	Aspidosiphon (Aspidosiphon) muelleri muelleri	DF	7.8	48.6
	Glycera alba	C	6.5	55.1
CO 16	*Haploops nirae*	S	29.3	29.3
	Polititapes virgineus	S	9.7	39.0
	Glycera unicornis	C	8.6	47.6
	Maldane glebifex	SDF	5.4	53.0

Table 21 : Mean values (± SD) of benthic biomass and corresponding percentage for the different taxonomic groups in *Haploops* (stations CO9, CO14 and CO16 averaged) and adjacent communities (stations CO4, CO24 and CO28).

	CO4		**CO24**		**CO28**		***Haploops* transect**	
	Mean ± SD	%	Mean ± SD	%	Mean ± SD	%	Mean ± SD	%
Annelids	10.15 ± 6.09	47.5 ± 10.5	6.07 ± 3.97	27.7 ± 12.7	2.33 ± 0.38	12.6 ± 1.1	3.76 ± 1.23	33.0 ± 13.2
Arthropods	1.05 ± 0.80	6.0 ± 5.2	0.46 ± 0.25	2.3 ± 1.5	0.29 ± 0.34	1.8 ± 2.2	4.48 ± 2.09	34.3 ± 10.6
Others	2.52 ± 0.37	13.6 ± 4.6	2.84 ± 0.94	13.6 ± 3.9	0.02 ± 0.03	0.1 ± 0.1	1.40 ± 1.11	12.8 ± 9.9
Echinoderms	4.76 ± 1.24	24.4 ± 6.8	7.85 ± 2.48	38.9 ± 14.5	11.45 ± 3.16	61.2 ± 11.1	1.17 ± 1.91	6.5 ± 9.7
Mollusques	1.81 ± 1.33	8.4 ± 4.4	3.58 ± 1.23	17.5 ± 6.8	4.56 ± 1.95	24.3 ± 9.1	1.55 ± 0.98	13.4 ± 8.5
TOTAL	20.30 ± 7.16		20.80 ± 3.60		18.64 ± 4.00		12.37 ± 4.71	

3.3. Annual secondary production

The empirical model developed by Brey (1990) resulted in an annual secondary production in adjacent communties ranging from 21.8 g AFDW.m^{-2}.y^{-1} at the station CO 28 to 27.1 g AFDW.m^{-2}.y^{-1} at the station CO 4 with a mean secondary production of 24.58 ± 2.15 g AFDW.m^{-2}.y^{-1} (Fig. 47). In *Haploops* stations, secondary production ranged from 19.1 g AFDW.m^{-2}.y^{-1} at the station CO 9 to 28.8 g AFDW.m^{-2}.y^{-1} at station the CO 14 with a mean secondary production of 22.40 ± 5.56 g AFDW.m^{-2}.y^{-1}. Values of secondary production recorded in the two transects did not significantly differ (Student's t-test, p = 0.573). Secondary production varied among stations depending on the location of the stations along the inshore-offshore gradient. In the adjacent communities, annual secondary production was the highest at the northernmost station (i.e. CO 4) and the lowest at the southernmost station (i.e. CO 28). Interestingly, an opposite pattern occurred in *Haploops* stations where the lowest production occurred at the two northernmost stations (i.e. CO 16 and CO 9) and the highest value at the southernmost station of the transect (i.e. CO 14). Whatever the habitat, secondary production was maximal at stations exhibiting the maximum mean annual biomass.

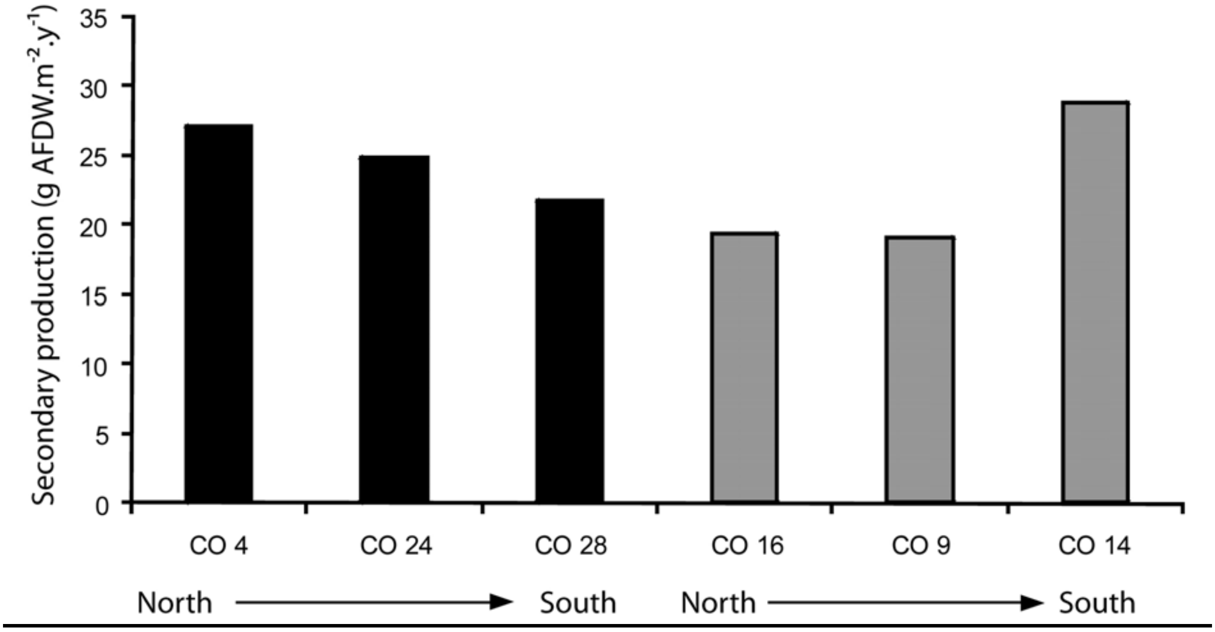

Figure 47 : Annual secondary production at the six stations investigated in bare sediments (CO 4, CO 24 and CO 28) and in the *Haploops* community (CO 16, CO 9 and CO 14) in 2010.

As expected, species accounting for the greatest part of the benthic biomass also largely contributed to the benthic secondary production (Table 22). In this way, *Amphiura filiformis* constituted the largest part of the secondary production in bare sediment stations accounting for up to 36% of the production at station CO 28. In the *Haploops* community, the tubicolous amphipod *Haploops nirae* was by far the largest contributor to the benthic secondary production at all stations with a strong contribution ranging from 43.2 % to 56.0 %. While *Haploops nirae* accounted on average for 25 % of the biomass of the community, it represented almost 50 % of the secondary production in the *Haploops* community.

From 1 to 6 species account for more than 50 % of the benthic production depending on the station investigated. In the *Haploops* community, a strongly reduced number of species consistently constituted the largest part of the secondary production (i.e. 1 to 3 species) while a greater number of species (i.e. 6 species for stations CO 4 and CO 24) - excepted for the station CO 28 - accounted for the half of the secondary production in bare sediments. Although carnivorous were important in terms of biomass in this community, their contribution to the secondary production was lower.

Table 22 : Main species contributing to the annual benthic secondary production (on average over the year) at the six stations investigated. The trophic group of each species is given. C: Carnivorous; DF: Surface deposit-feeder; S: suspension-feeder; SDF: Subsurface deposit-feeder.

Station	Species	Trophic group	% of secondary production	Cumulated % of secondary production
CO4	*Maldane glebifex*	SDF	16.8	16.8
	Amphiura filiformis	S	16.1	32.9
	Notomastus latericeus	SDF	5.7	38.5
	Macroclymene santandarensis	SDF	5.3	43.9
	Turritella communis	S	5.0	48.8
	Owenia fusiformis	S/DF	3.9	52.8
CO24	*Amphiura filiformis*	S	20.8	20.8
	Aspidosiphon (Aspidosiphon) muelleri muelleri	DF	10.2	31.0
	Aphrodita aculeata	C	5.6	36.6
	Leptopentacta elongata	S	5.6	42.2
	Notomastus latericeus	SDF	5.1	47.3
	Thyone fusus	S	4.6	51.9
CO28	*Amphiura filiformis*	S	36.2	36.2
	Thyone fusus	S	12.3	48.5
	Dosinia lupinus	S	12.2	60.7
CO9	*Haploops nirae*	S	43.8	43.8
	Aspidosiphon (Aspidosiphon) muelleri muelleri	DF	4.9	48.7
	Polititapes virgineus	S	4.5	53.2
CO 14	*Haploops nirae*	S	43.2	43.2
	Ophiura albida	C	12.1	55.4
CO16	*Haploops nirae*	S	56.0	56.0

4. Discussion

The *Haploops* community occupies a large area in the bay of Concarneau (ca. 3600 ha) which has increased by 400% over the last 2 decades (Rigolet et al., 2012). To determine ecological impacts of this expansion, we quantified in this study how the ecosystem engineer *Haploops nirae* altered the benthic community structure (i.e. species richness, heterogeneity diversity, species composition) over the seasons and the ecosystem functioning (macrofauna standing stock biomass and secondary production).

Haploops nirae, as ecosystem engineer species, heavily modifies the structure of the benthic communities and creates an original species assemblage compared to adjacent communities. If such modifications in terms of species composition do not result in significant changes in the macrofauna species richness, a significant increase in the diversity heterogeneity indices (N1 and N2) was observed in the *Haploops* community, suggesting a higher evenness. These results confirm in part our previous findings on the uniqueness of the composition of the *Haploops* community in comparison with adjacent homogeneous areas from a sampling carried out at only in summer time (Rigolet et al., submitted). By contrast, in contradiction with our previous study the *Haploops* community is not characterized by higher mean annual species richness than adjacent communities. The species richness varied from 74 to 95 in the *Haploops* community while it ranged from 72 to 99 in the bare sediments. This result leads to counterbalance our previous conclusion which was mainly explained by the very low species richness in the *Sternaspis* muddy community – not sampled in the present study – and by a different sampling effort which may have affected the species richness.

Marked changes induced by the expansion of *Haploops nirae* on the structure of the benthic community have only moderate effects on the standing stock biomass which was 1.6 times lower in the *Haploops* community than in the surrounding bare sediments and do not alter the macrofauna secondary production measured as a proxy of the ecosystem functioning. Rigolet et al. (submitted) already stated that changes in the community structure are much deeper than changes in the functional diversity assessed by a biological traits analysis. However, a major difference between the two communities is the relative importance of different species to the overall production. In the *Amphiura*/*Owenia* community, the secondary production is more evenly distributed among the dominant species which exhibit different biological traits (trophic group, habitat, availability for higher trophic levels). Conversely, in the *Haploops* community, *Haploops nirae* constitutes by far the major contributor to the macrofauna secondary production (up to half of the secondary production), suggesting a high contribution to the flux of organic matter in this community. This major contribution can be viewed as a weakness of the *Haploops* community for which spatial and temporal variations in *Haploops* densities can lead to drastic changes in the secondary production and ultimately affect upper trophic levels. The dominance of *H. nirae* could compromise its resilience to disturbance assuming that higher functional diversity would increase resilience (Peterson et al., 1998).

Secondary production changes from bare sediments to *Haploops* communities were estimated using an indirect approach suggested in Brey (1990). The best way to accurately assess the somatic production is however to use direct methods based on time series of the size frequency distribution (increment summation or loss summation). Since assessment of production in macrobenthic populations and communities is extremely time-consuming, empirical models have been developed to estimate secondary production without the requirement of intense sampling programs. Empirical models have the advantage to allow comparisons between communities from different sites or habitats and may help to assess community production with limited data, including rare species or species with unknown dynamics (Cusson and Bourget, 2005). These models have nevertheless some limitations and may never be as reliable as direct production estimations. For example, Cusson and Bourget (2005) examined the reliability of four empirical equations proposed by Robertson (1979), Brey (1990), Tumbiolo and Downing (1994) and Brey (2004) by comparing observed production values with results of these models. They suggested that overall all models successfully predicted the observed production values with a R^2 ranging from 0.78 to 0.89. But, they also showed that some models better predict their production dataset compared to others, the less efficient model being the one proposed by Tumbiolo and Downing (1994) to improve the predictions of the Brey's (1990) model. In addition, they indicated that Brey's (1990) model slightly underestimates the production while the others have a tendency to overestimate the production. Medernach and Grémare (1999) compared 3 direct methods and 8 indirect methods to estimate the secondary production of a population of the polychaete *Ditrupa arietina* and highlighted the inability of indirect methods (i.e. empirical models) to describe the production of *Ditrupa arietina*. To get an idea of the reliability of empirical models, we compared the annual secondary production value of *Haploops nirae* estimated by Brey's method with the actual production (i.e. 9.66 gDW m^{-2} y^{-1}) calculated from an annual survey during the same year (i.e. 2010) using the increment summation method at one site close to the station CO 9 in the bay of Concarneau (Rigolet et al., 2012). Using a weight to weight conversion factor (AFDW/WW) for amphipoda (Ricciardi and Bourget, 1999), the secondary production of *Haploops nirae* calculated using the increment summation method was estimated at 7.72 gAFDW.m^{-2}.y^{-1}. This value is very close to the secondary production value reported for *Haploops nirae* at station CO 9 in the present study (i.e. 8.37 gAFDW.m^{-2}.y^{-1}), hence revealing the accuracy and the relevance of Brey's empirical model for our investigation.

Although it is rather difficult to make comparison among different studies and locations because of differences in sampling procedures, mesh sizes and calculation methods, our production estimates (a mean of 24.58 ± 2.15 g AFDW.m^{-2}.y^{-1} for bare sediments and 22.40 ± 5.56 g AFDW.m^{-2}.y^{-1} for the *Haploops* communities) are within the wide range of secondary production found for subtidal environments (from 1.7 to 47 gAFDW.m^{-2}.y^{-1} (Buchanan and Warwick, 1974; Maurer et al., 1992)) (Table 23). However, production estimates for the whole *Haploops* community and bare sediments are slightly lower than estimates for estuaries (from 13.3 to 119.9 gAFDW.m^{-2}.y^{-1} (McLusky, 1989)) and quite low compared to high production values previously reported for intertidal areas (from 13 to 468 gAFDW.m^{-2}.y^{-1} (Warwick and Price, 1975; Asmus, 1987)).

Based on a comparison between the actual secondary production of *Haploops nirae* and measures of the secondary production of the dominant species in the *Amphiura filiformis* community in the 70s, we previously suggested that a change from an *Amphiura* community to a *Haploops* community could result in a loss of benthic production (Rigolet et al., 2012). Our new estimates of secondary production at the community scale do not support this hypothesis. They showed that a shift from a benthic community dominated by *Amphiura filiformis* to a benthic community dominated by *Haploops nirae* would leave the secondary production grossly unchaged at the scale of the entire Bay of Concarneau, that is around 20-25 g AFDW.m^{-2}.y^{-1}. While secondary production remains unchanged between the two environments, the transfers of this benthic production to higher trophic levels are likely to varied from one community to another and are fundamental to ecosystem functioning. As the two communities investigated here contained the same number of species, are equally productive (i.e. the same amount of food is made available to higher trophic levels) and are both dominated by suspension feeders, we can assume that trophic flows in the benthic system do not differ greatly between the *Haploops* community and bare sediments. Yet, Desaunay et al. (2006b) showed that many finfishes tend to avoid the *Haploops* habitat and predominantly occurred in adjacent homogeneous bare sediments, such as several flatfishes (e.g. the Dover sole *Solea solea* , the plaice *Pleuronectes platessa* and the wedge sole *Dicoglossa cuneata*), the European hake *Merluccius merluccius* and the whiting *Merlangius merlangus* and reported that *Haploops* communities constituted a preferential habitat for only a few commercial fish species such as the nursehound *Scyliorhinus stellaris*, the pouting *Trisopterus luscus* and the black seabream *Spondyliosoma cantharus*. Accordingly, these authors indicated that *Haploops* habitat is of less importance for fishing and nursery grounds compared to adjacent areas. On the other hand, analyses of fish stomach contents in two coastal embayments colonized by *Haploops nirae* (i.e. the bay of Concarneau and Vilaine) revealed a reduce variety of preys within the stomach content of fish sampled on the *Haploops* habitat compared to those sampled in the *Amphiura* community (Weppe, 2011). Examinations of fish stomachs have also shown that some species such as the dragonet *Callionymus lyra*, the pouting *Trisopterus luscus* and the black goby *Gobius niger* feed almost exclusively on *Haploops nirae* when they are sampled within the *Haploops* habitat. Such observations corroborate results on the dominance of *Haploops* on the secondary production and suggest a dominant contribution of *Haploops nirae* to the flux of organic matter in its community. In the Bay of Morlaix, Dauvin (1988e) also reported that some demersal fishes like the dragonet *Callionymus lyra* and the pouting *Trisopterus luscus* feed preferentially on *Ampelisca* spp. As only a small proportion of fish predate on *Haploops nirae*, one can assume that only a reduced portion of its production is exported to the water column by fish. Polychaetes, decapods and others benthic species are probably other important predators. For example, McDermott (1993) suggested that suctorial Hoplonemerteans (e.g. *Nipponnemertes pulcher*) can be instrumental in the regulation of the dominant *Haploops* species (*Haploops tubicola* and *Haploops tenuis*) in soft bottom community in the Northern Øresund.

Analyses of fish stomachs content from the bay of Concarneau and the bay of Vilaine did not reported the presence of *Amphiura filiformis* within fish stomachs, but Duineveld and Noort (1986) indicated that *A. filiformis* forms an important food item for flatfish, crabs and seastars. They showed for example that *Amphiura* arms is part of the diet of the dab *Limanda limanda* in the Oyster Ground (Southern north sea). Because *Haploops* community compared equally with the production of adjacent benthic communities, evidences from fish communities led to the hypothesis that trophic flows to higher levels differ among habitats and are probably altered by the presence of dense tube mats. A further expansion of *Haploops* tube mats will hence have potential implications for fish feeding patterns and fish populations.

Table 23: Literature data review on secondary production of benthic assemblages (g.AFDW.m^{-2}.y^{-1}).

	Location	Secondary production (g.AFDW.m^{-2}.y^{-1})	Habitat	Reference
Estuarine	Grevelingen, Netherlands	14.4 - 26.2	Very fine sands	McLusky, 1989
Estuarine	Grevelingen, Netherlands	73.3	Very fine sands with mud	McLusky, 1989
Estuarine	Grevelingen, Netherlands	119.9	Fine sand	McLusky, 1989
Estuarine	Lyner estuary, UK	13.3	Fine sand and clay	McLusky, 1989
Estuarine	Forth Estuary, UK	22.7	Mud	McLusky, 1989
Estuarine	Sacca di Goro, Italy	49.8 - 75.0	Mud	Mistri et al., 2001
Estuarine	Königshafen, Germany	19.9	Mud	Reise, 1985
Estuarine	Königshafen, Germany	56.9	Sand	Reise, 1985
Estuarine	Königshafen, Germany	54.8	Seagrass bed	Reise, 1985
Estuarine	Berg River estuary, South Africa	87.6	Seagrass bed	Kalejta and Hockey, 1991
Intertidal	Wadden Sea	468	Mussel bed	Asmus, 1987
Intertidal	California	53 - 100	Mud flat	Nichols, 1977
Intertidal	Portugal	72	Mud flat	Sprung, 1994
Intertidal	Portugal	34	Sand flat	Sprung, 1994
Subtidal	New Zealand	30	Urchin barrens	Taylor, 1998
Subtidal	Wales	26	Fine sand	Warwick et al., 1978
Subtidal	Delaware	4 - 47		Maurer et al., 1992
Intertidal	England	13	Mud flat	Warwick and Price, 1975
Subtidal	Northumberland, England	1.7	Mud	Buchanan and Warwick, 1974
Deep ecosystems	Norwegian fjord (230 m depth)	0.4 - 41.5		Kutti et al., 2008

PARTIE III

Les réseaux trophiques des peuplements sablo-vaseux - Rôle d'*Haploops nirae*

- **CHAPITRE 1 : Impact des *Haploops* sur la structure des réseaux trophiques benthiques de la baie de Concarneau**

  Article n°5: Food web structure on muddy habitats colonized by a tubiculous gregarious species: insight from stable C and N isotopic composition

- **CHAPITRE 2 : Effet des *Haploops* sur le fonctionnement du réseau trophique, developpement de nouveaux indicateurs**

  Article n°6: Using isotopic functional indices to reveal changes in the structure of marine benthic communities

La troisième partie de ce manuscrit se focalise sur la structure et le fonctionnement des réseaux trophiques des peuplements sablo-vaseux de la baie de Concarneau. Cette partie se structure en deux chapitres qui s'articulent chacun autour d'un article en préparation.

Le premier chapitre de cette partie (article 5) décrit les caractéristiques générales et l'architecture des réseaux trophiques des substrats meubles subtidaux de la baie de Concarneau par la technique des isotopes stables en comparant le réseau trophique associé au peuplement à *H. nirae* avec celui des peuplements adjacents. Cette étude a pour objectif de replacer les *Haploops* dans le réseau trophique des systèmes colonisés mais également d'évaluer les conséquences d'*Haploops nirae* sur la structure générale des réseaux trophiques.

Le dernier chapitre (article 6) utilise de nouveaux indicateurs trophiques pour appréhender le fonctionnement des réseaux trophiques de la baie de Concarneau. Le principe de ces indices repose sur une utilisation couplée des biomasses des espèces et de leurs signatures isotopiques. Trois indices de diversité fonctionnelle isotopique sont ainsi proposés : la richesse fonctionnelle isotopique (IFR), la régularité fonctionnelle isotopique (IFE) et la divergence fonctionnelle isotopique (IFD). Dans le but de préciser l'influence fonctionnelle des populations d'*Haploops nirae* en baie de Concarneau, ces indices sont appliqués sur les peuplements de la baie de Concarneau à quatre saisons de l'année 2010.

ARTICLE N°5

Food web structure on muddy habitats colonized by a tubiculous gregarious species: insight from stable C and N isotopic composition

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Article en préparation

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Abstract

We used stable C and N isotopic composition of benthic organisms to understand the effects of a gregarious tubiculous amphipod species (*Haploops nirae*) on benthic food web structures. The habitat engineered by this species was sampled along with the adjacent uncolonized habitat. The isotopic signature of all the macro- and mega-fauna species associated to each habitat were analysed along with potential food sources, for winter and summer seasons. We showed similar food web structures for each habitat (and each season), with high δ^{15}N ranges, spanning over 3 trophic levels. The amphipod *Haploops nirae* appears to play a baseline role with the lowest δ^{15}N value and δ^{13}C value indicates that it primarily feed on phytoplankton. Using Bayesian mixing models, we estimated the contributions of potential food sources to the diet of the species accounting for most of the biomass in each habitat. We revealed that the epiphytes covering tube mats (mainly benthic diatoms) are a key contribution to both of the habitats food webs and minimize food competition with other large suspension-feeders such as *Polititapes virgineus* on *Haploops* habitats. This is a first evidence that microphytobenthic producers contribute to subtidal (25-35 m deep) muddy habitats food webs. We conclude that *Haploops* mats offer a suitable support for benthic primary producer to develop and to sustain all immediate surrounding habitats.

1. Introduction

Coastal zones are considered among the most productive marine systems in the world with both high ecological and economic values. They offer a wide variety of ecosystem services for humans but also sustain ecological processes of primary importance for marine wildlife such as nutrient regulation, carbon sequestration and detoxification of polluted waters (Constanza *et al.* 1997; Gattuso et al., 1998). Coastal ecosystems are also known to support particularly species rich and abundant benthic communities, resulting in areas of high benthic secondary production which are of major importance for supporting nursery grounds and feeding areas for most coastal and many oceanic species. The importance of coastal systems in sustaining the marine wildlife had consequently required a much better knowledge of biological and ecological processes in coastal systems. Flows of organic matter within systems constitute a crucial aspect of ecosystem functioning, yet the understanding of trophic dynamics and pathways in coastal systems need further investigations. Indeed, while the primary production in the open-ocean is only dominated by phytoplankton, a large variety of primary producers (e.g. macrophytes, salt marshes plants, mangroves leaves, seagrass beds and microphytobenthos) contribute to the organic matter pool in coastal ecosystems. Such a large number of sources, while creating a high benthic productivity, also greatly increases the complexity of coastal food webs (Peterson, 1999).

Stable carbon and nitrogen isotope ratios have proven to be a powerful tool in evaluating feeding relationships and organic matter flows through marine food webs. As stable isotopes are frequently used to understand feeding behavior and trophic relationships between species (Peterson and Fry, 1987), they can also be used at the community scale to describe the overall structure of a food web such as food web length or niche space (Bearhop et al., 2004; Cornwell et al., 2006; Layman et al., 2007a), providing for example valuable information on the health of the system (Layman et al., 2007b; Zambrano et al., 2010a). But stable isotopes (mostly C and N) have been more specifically used to disentangle trophic pathways in coastal systems by ranking the organic matter sources supporting food webs, and to provide estimates of food sources contributions to consumers' diet. When wisely used, the development of mixing models has greatly enhance the power in isotopic tools (Phillips and Greg, 2003; Parnell et al., 2010).

Among all benthic coastal systems, some are commonly considered as of particularly high ecological value (Wright and Jones, 2006; Voultsiadou et al., 2007), and above all, systems which are physically modified by engineer species (Jones et al., 1994). Mangroves, seagrasses or coral reefs habitats have been shown not only to enhance the local biodiversity of benthic and pelagic species but also to modify the availability of resources for others species (Berkenbusch and Rowden, 2007). Ecosystems engineers act often as key species in ecosystem functioning. While their effects on the structural biodiversity of benthic communities have been widely investigated (e.g. Reise et al., 2009), only few studies have paid attention to the consequences of ecosystem engineers on the structure of the marine food webs. Yet, ecosystem engineers can induce changes in the intensity of biological interactions (mainly predation-prey interactions) (Irlandi and Peterson, 1991) or can alter the food supply to other organisms (Allen and Williams, 2003) having thus major consequences on flows of organic pathways in benthic coastal systems.

In South Brittany (France), an original benthic community dominated by the gregarious tubicolous Ampeliscid *Haploops nirae* forms dense tube mats in two main coastal ecosystems (i.e. the bay of Concarneau and the bay of Vilaine). As for many gregarious species, *Haploops nirae* exhibits there dense populations, with average densities between 10 000 and 15 000 ind.m^{-2} (Rigolet et al., 2012) constituting the most abundant species. This species was first recorded in 1884 in shallow waters of South Brittany (Bonnier, 1887) but recent acoustic surveys showed a significant spreading (Ehrhold et al., 2006). For example, the mapping of the bay of Concarneau revealed a 5-fold increase in *Haploops nirae* habitat surface between 1963 (650 ha in Glémarec, 1969) and 2003 (3680 ha in Ehrhold et al., 2006). Rigolet et al. (2012) investigated the structural and functional diversity of the macrofauna associated with *Haploops* community as a comparison with several surrounding soft-sediment communities. They showed that *Haploops* significantly modify sediment features (e.g. change in granulometry, increase in C and N organic content) and therefore deeply affect species diversity and benthic composition by creating unique macrofauna assemblage. Analysis of species composition revealed that *Haploops* community shared very few species with surrounding communities. However, very little is known about the effect of this engineer species on food web functioning and whether changes in species composition also goes with changes in trophic pathways and food web structure. Several studies provided evidence that dense populations of Ampeliscids could play major role in energy transfer in some marine systems, not only because they can affect benthic-pelagic coupling and have a major grazing impact on phytoplankton production (Grebmeier and Mc Roy, 1989 ; Rigolet et al., 2011) but also because they export a high production towards higher trophic levels (Franz and Tanacredi, 1992 ; Highsmith and Coyle, 1992). We used here stable C and N isotopes to investigate the benthic food web structure associated with the *Haploops* community in comparison with adjacent soft-bottom communities and to identify the main trophic pathways and main food souces that support the macrofauna assemblages in this system.

2. Material and Methods

2. 1. Study area and sampling stations

This study was conducted in the bay of Concarneau, situated in the Northern part of the Bay of Biscay (France) (Fig. 48). This area is sheltered by a succession of rocky islets and is characterized by soft-bottom substrates, spanning from muddy to muddy-sand, with a depth ranging from 15 to 35 m (Menesguen, 1980). The westernmost part of the bay (North Mouton islets and Glénan Islands) is composed of muddy sands and sandy muds. The central part of the bay - where currents are strongly reduced - is composed of pure muds supporting a dense population of the tubiculous amphipod *Haploops nirae*. The western edges of the *Haploops* habitat are surrounded by patchy muddy habitats (Ehrhold et al., 2006).

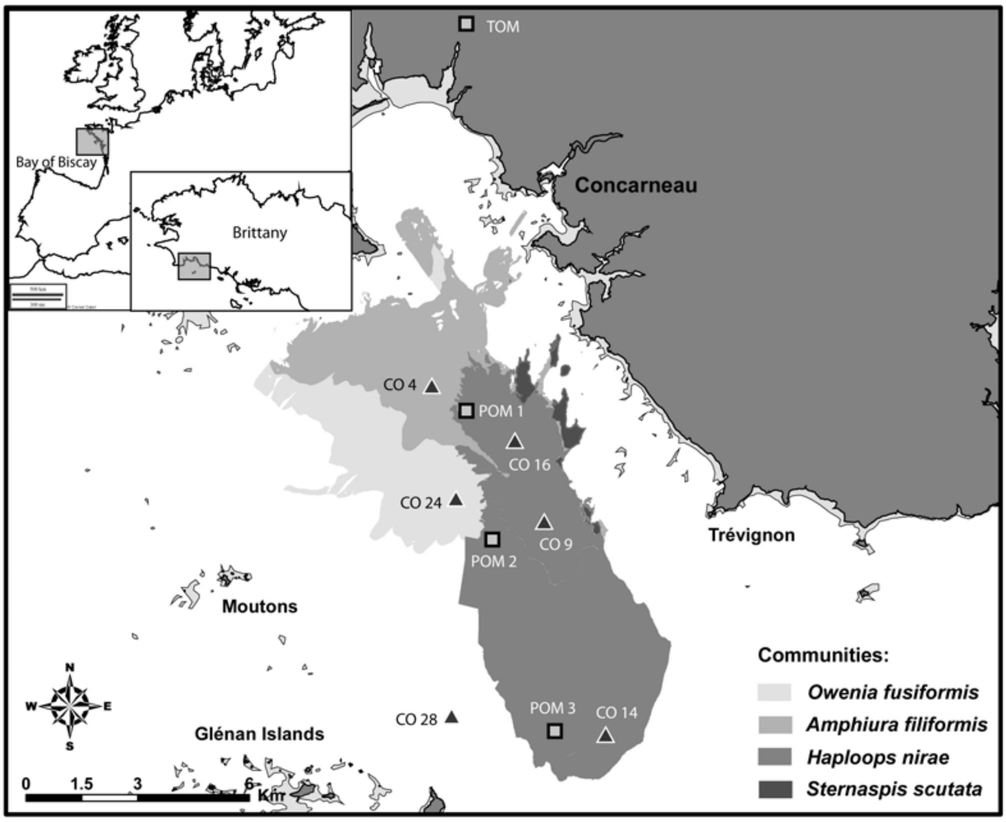

Figure 48 : Geographical distribution of the subtidal benthic communities of the bay of Concarneau and the six stations seasonally sampled along two transects (i.e. the *Haploops* community: CO16, CO9, CO14 and the adjacent *Amphiura-Owenia* community: CO4, CO24, CO28). Sampling stations for the benthic fauna are indicated by a triangle and sampling station for POM and TOM are represented by squares. Benthic communities identified from previous acoustic and benthic survey mappings (Ehrhold et al., 2006) are color-coded using grey scale.

To investigate the effects of *Haploops* tube mats on benthic trophic structure, we compared the structure of the food web associated with *Haploops* with the adjacent benthic communities. A mapping survey of the seabed using geoacoustic approaches and complementary benthic biological grab samples was conducted in the bay of Concarneau (Ehrhold et al., 2006). This preliminary macrofauna analysis reported 4 benthic communities in the bay: the *Sternaspis scutata* muddy community, the *Amphiura filiformis* sandy-mud community, the *Owenia fusiformis* muddy-sand community and the *Haploops* muddy community (Fig. 48). Using this map contours, 6 stations were distributed along two north-south transects reflecting an inshore-offshore gradient (Fig. 48). Stations CO 9, CO 14 and CO 16 were located within the *Haploops* community. Stations CO 4, CO 24 and CO 28 were located within the adjacent sandy mud community dominated by the ophiurid *Amphiura filiformis* (hereafter called bare sediment as opposed to the sediment colonized by *Haploops nirae*). Six stations were sampled during two contrasting seasons: in winter (February 2010) when food inputs are particularly low and when the benthic fauna has a biological activity markedly reduced, and in summer (August 2010) at the end of a period characterized by high supply of pelagic production in this area.

2. 2. Samples collection

To investigate the trophic structure within each community (i.e. *Haploops* and *Amphiura* communities), we collected the largest possible variety of macrofaunal and megafaunal organisms for isotopic analyses at all stations of each community-transect and for the two seasons. Macrofauna (individual mean size: 1-10 mm) was sampled using a 0.1 m² Van Veen grab (at least 2 replicates per station) and megafauna species (individual mean size > 10 mm) using a modified beam trawl (width = 2 m , sampled area = ca. 2300 m²) (Desaunay et al., 2006a) with one trawl at each station.

All collected benthic organisms were carefully sorted on board and keep frozen. In the laboratory, organisms were identified to the lowest taxonomic level (i.e. generally at the species level). Isotopic analyses were then performed on muscle tissue samples for megafauna and large macrofauna. The whole body (gut-dissected) was used for smaller species. In rare instances, several individuals were pooled to match the minimum weight requested for stable isotope analyses. All samples were rinsed with Milli-Q water and freeze-dried. Three replicates were analyzed. For calcified organisms (crustaceans and echinoderms), a sub-sample was acidified (10% HCl) to remove any inorganic carbonates, then rinsed with distilled water and freeze-dried again for ^{13}C values (a sub-sample was left untreated for ^{15}N value). Even though we kept track of the station for each the organisms, we used the mean isotopic value of organisms for each community by pooling organisms found in 3 stations of the transect. The mean isotopic value was then representative of the community and integrate a potential spatial variability.

All the potential sources of organic matter available for the benthic fauna were collected for isotopic analyses. Because of a reduced light input, subtidal soft-bottom systems are commonly assumed to host very low benthic primary production, especially in muddy turbid waters (Le Loc'h et al., 2008). Consequently, most of the organic mater (OM) available for benthic primary consumers originates from the particulate organic matter (POM) (composed mainly of phytoplankton) sedimenting from upper water layers. Yet, close observations of *Haploops* tubes revealed that the surface of tubes is covered with epiphytes (EPI) in general and mostly with benthic diatoms mats that belong to the genus *Navicula*, especially during spring blooms (identification Siano R., unpubl.). It is hypothesized here that benthic diatoms could be considered as a potential food source. Moreover, because sampled stations are below the photic limit required by attached macroalgae to grow (between 25 and 35m deep), the ability of macroalgae to develop in such soft-bottom habitats is strongly reduced. However, macroalgae fragments and detritus originating from adjacent islets (i.e. Glenan and Moutons) could also be considered as a source for benthic organisms. Terrestrial inputs of organic matter (TOM) are very limited in this bay that receives freshwaters inputs from small rivers only.

Practically, surface water was collected using Niskin bottles for TOM and 3 POM stations along an inshore-offshore transect (Fig. 48). Water samples were prefiltered on a 100 µm mesh to remove small animals such as zooplankton and then filtered on pre-combusted GFF filters (4h, 550°C). Half of GFF filters were acidified with 10N HCl fumes to remove traces of inorganic carbonates. The organic matter from the sediment (SOM) was sampled at each of the 6 stations using a Reineck corer to extract undisturbed sediment core. For the 3 *Haploops* stations (CO 16, CO 9, CO 14)), the surface of several tubes were gently scrapped with a razor blade under a dissecting scope and collected with distilled water. For both SOM and EPI samples, a sub-sample was acidified (10% HCl) to remove inorganic carbonates (^{13}C) and the rest was left untreated (^{15}N). Finally, brown, red and green macroalgae detritus were collected in trawls in summer as very little macroalgae was noticed during winter.

2. 3. Isotopic analyses

After freeze-drying, each sample was ground to a homogeneous powder and 1 mg was weighed in tin capsules for isotopic analyses. The isotopic composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were then measured with a stable isotope ratio mass spectrometer Finnigan MAT Delta Plus, operating in continuous-flow method coupled to an elemental analyser Carlo Erba NC2500 (Cornell University, Stable Isotope Laboratory, New York). Isotopic ratios for carbon and nitrogen were expressed using the standard δ notation according to the following equation:

$$\delta X = ((R_{sample}/R_{reference}) - 1) \times 1000\ (‰)$$

where X= ^{13}C (carbon) or ^{15}N (nitrogen) and R= $^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for nitrogen. The reference for carbon was Vienna Pee Dee Belemnite (VPDB, $\delta^{13}C=0$ ‰) and for nitrogen was atmospheric nitrogen ($\delta^{15}N=0$‰). The analytical precision was 0.2 ‰ for both nitrogen and carbon.

2. 4. Data analysis

To provide a detailed description of the structure of the food web associated with both communities, macrofaunal and megafaunal species were classified into five trophic groups: suspension-feeders (SF), surface deposit-feeders (SDF), subsurface deposit-feeders (SSDF), omnivores-carnivores (C-O) and grazers (G). Trophic information on species were gathered from several scientific publications and from the Biological Traits Information Catalogue developed by the Marine Life Information Network (www.marlin.ac.uk/biotic/).

Since organisms tend to fractionate nitrogen positively by 3-4 ‰ (Minagawa and Wada, 1984; Post, 2002), the nitrogen isotope ratio is commonly used to estimate the trophic position of aquatic consumers (Cabana and Rasmussen, 1996; Vander Zanden et al., 1997; Post, 2002). In this context, Vander Zanden and Rasmussen (2001) showed that the $\delta^{15}N$ baseline used to determine the trophic level of consumers is of primary importance. Indeed, the error variance in consumer trophic position was threefold greater when using primary producers rather than primary consumers as baseline indicator organisms. In this way and by considering that primary consumers are time integrators of the primary producer isotopic variability, the primary consumer *Haploops nirae* that feeds on phytoplankton (Rigolet et al., 2011) was used as isotopic baseline. As a result, consumer trophic position can be calculated using the following formula:

$$\text{Trophic Level} = (\delta^{15}N_{consumer} - \delta^{15}N_{mean\ \textit{Haploops}})/3.4 + 2$$

where 3.4 ‰ is the assumed ^{15}N trophic-enrichment factor according to Minagawa and Wada (1984). Primary, secondary and tertiary consumers were thus designated as the second, third and fourth trophic levels respectively.

Mixing models are frequently used to quantify the relative contributions of primary producers to species diets (Phillips and Gregg, 2003; Parnell et al., 2010; Phillips, 2012).

Such models require an *a priori* estimate of the enrichment in $\delta^{15}N$ and $\delta^{13}C$ values between prey and predator. In this context, Vander Zanden and Rasmussen (2001) also showed that the variation in fractionation values contributed to the major part of the error variance in mixing model outputs, implying thus the necessity to use appropriate $\delta^{15}N$ and $\delta^{13}C$ fractionation values. It is commonly assumed that the $\delta^{15}N$ and the $\delta^{13}C$ values of a consumer are typically enriched by 3.4 ‰ and 1 ‰ respectively (Minagawa and Wada, 1984), and fractionation values implemented into mixing models consequently use these values. However recent reviews indicated that fractionation values are affected by multiple factors, such as food quality, tissues turnover, environmental conditions and even taxonomic group (Vander Zanden and Rasmussen, 2001; Vanderklift and Ponsard, 2003; Mc Cutchan et al., 2003). Caut et al. (2009) reviewed carbon and nitrogen isotopic discrimination factors from the literature and suggested linear models for different taxonomic groups, to obtain discrimination factors according to each potential food source.

We ran a Bayesian mixing models with the package SIAR (Stable Isotope Analysis in R) of the free software R, version 2.11.1 (R Development Core Team 2008) using default parameters (iterations = 500,000, burnin = 50,000, thinby = 15). For a more comprehensive output, the model was performed on species that account for the greatest part of the benthic biomass (i.e. 80 %): we retrieved biomass data from a complementary benthic survey conducted during the same time and not presented here. The model was run in summer only as it has been showed that mixing models results from winter period in temperate regions were irrelevant since turnover in organisms' tissues was close to zero (Leal et al., 2008) and food assimilation ultimately negligible. Two variables ($\delta^{13}C$ and $\delta^{15}N$) were used and three sources (POM, SOM and EPI) were considered for the computation of the model. Preliminary $\delta^{13}C$ – $\delta^{15}N$ biplot showed that macroalgae and TOM sources contributions were likely too low to be integrated in the mixing model (Phillips and Gregg, 2003). To obtain the most appropriate enrichment factor and standard deviation, we calculated a trophic enrichment factor (TEF) for each source following the equations provided by Caut et al. (2009) for invertebrates. We therefore used source-specific TEF for the POM (4.04 ± 0.20 ‰ for $\delta^{15}N$ and 2.18 ± 0.11‰ for $\delta^{13}C$), for the SOM (3.32 ± 0.12 ‰ for $\delta^{15}N$ and 1.68 ± 0.02 ‰ for $\delta^{13}C$) and for the EPI (3.03 ± 0.05 ‰ for $\delta^{15}N$ and 0.05 ± 0.07 ‰ for $\delta^{13}C$). For secondary consumers, trophic enrichment factors were multiplied by the number of trophic levels between the basal resources and the consumer (Phillips, 2012).

3. Results

3. 1. Food sources

Isotopic ratios of potential organic matter sources for the two transects and the two seasons are listed in Table 24. The $\delta^{13}C$ of potential food sources were well discriminated and varied from -34.29 ‰ (*Dasya corymbifera*, a red macroalgae) to -17.42 ‰ (*Ulva ulva*) in winter, and from -34.29 ‰ (*Dasya corymbifera*) to -13.19 ‰ (EPI on *Haploops* tubes) in summer. Potential food sources displayed thus a $\delta^{13}C$ range of 16.9 ‰ in winter which strongly increased to 21.1‰ in summer mainly due to the ^{13}C-enrichment of benthic diatoms that grow on *Haploops* tubes (Table 24). TOM $\delta^{13}C$ values strongly differ between the two seasons: -28.58 ‰ in winter and -22.80 ‰ in summer. As for the POM, $\delta^{13}C$ values recorded in winter (-24.06 ‰) and summer (-23.73 ‰) did not significantly differ (Student's t-test, p=0.626). The isotopic signature of macroalgae displayed group-specific isotopic ratios ($\delta^{13}C$) with strongly ^{13}C-depleted red algae (*Palmaria palmaria*, *Hypoglossum hypoglossoides*, *Dasya corymbifera*) and more ^{13}C-enriched brown (*Laminaria* sp., *Dichyota dichotoma*) and green (*Ulva ulva*) algae. Isotopic ratios of SOM exhibited the same values between bare sediments stations (sandy muds) and *Haploops* stations (muds) (Student's t-test, p=0.508 in winter and p=0.060 in summer) for both seasons. Therefore, all isotopic values for SOM were averaged into one isotopic value for the sedimented organic matter. The $\delta^{15}N$ values of potential food sources were relatively homogeneous, spanning from 3.06 ‰ to 7.67 ‰ in winter and from 4.14 ‰ to 7.21 ‰ in summer.

Table 24 : Stable nitrogen and stable carbon isotope values (mean and standard deviation) of the potential food sources in the bay of Concarneau in winter and summer 2010.

	WINTER			**SUMMER**		
Potential Sources for Primary Consumers	**δ^{15}N (SD)**	**δ^{13}C (SD)**	**n**	**δ^{15}N (SD)**	**δ^{13}C (SD)**	**n**
Terrestrial Organic Matter	4.05 (0)	-28.58 (0)	3	5.56 (0)	-22.80 (0)	3
Sub-surface Particulate Organic Matter	3.06 (1.20)	-24.06 (0.34)	3	4.14 (1.04)	-23.73 (1.08)	3
Sedimented Organic Matter (*Haploops* habitat)	6.70 (0.03)	-21.14 (0.04)	3	6.60 (0.14)	-21.35 (0.04)	3
Sedimented Organic Matter (bare sediment habitat)	6.17 (0.40)	-21.23 (0.21)	3	6.08 (0.30)	-21.18 (0.10)	3
Epiphytes on *Haploops* tubes	7.67 (0.82)	-21.43 (0.36)	3	7.21 (0.15)	-13.19 (0.34)	3
Laminaria sp. (brown macroalgae)	5.07 (0.78)	-18.77 (2.26)	3	5.07 (0.78)	-18.77 (2.26)	3
Dichyota dichotoma (brown macroalgae)	NA	NA	-	5.80 (0)	-21.13 (0)	3
Palmaria palmaria (red macroalgae)	NA	NA	-	6.09 (0)	-33.94 (0)	3
Hypoglossum hypoglossoides (red macroalgae)	NA	NA	-	5.49 (0)	-33.35 (0)	3
Dasya corymbifera (red macroalgae)	NA	NA	-	6.85 (0)	-34.29 (0)	3
Ulva ulva (green macroalgae)	NA	NA	-	4.18 (0)	-17.42 (0)	3

3. 2. Food webs structure

The δ^{13}C and δ^{15}N values displayed by the benthic fauna for the two habitats in winter and summer are represented in Fig. 49 and 50 respectively. Graphically, three potential food sources (i.e. SOM, POM and EPI) are likely to support the primary consumers in the two communities. Yet, the particular isotopic signatures exhibited by a few species indicate particular diet: in winter the sea slug *Aplysia punctata* (Fig. 49) displayed ^{13}C-depleted values (-29.41 ‰ and –30.81 ‰ in bare sediment and *Haploops* transects respectively) and appeared to feed on ^{13}C-depleted red macroalgae (such as *Palmaria palmaria*, *Hypoglossum hypoglossoides* and *Dasya corymbifera*). The polychaete *Nereis* sp. (δ^{13}C = -24.71 ‰), seemed to partly feed on ^{13}C-depleted red macroalgae too. The Nudibranch *Geitodoris planata* displayed ^{13}C-enriched values (Fig. 50) in both communities in summer (δ^{13}C = -11.83 ‰ and –11.64 ‰ in bare sediment and *Haploops* communities respectively). The bivalve *Thyasira flexuosa* displayed strongly depleted δ^{13}C (-26.40 ‰) and δ^{15}N values (-0.3 ‰) (see Appendices).

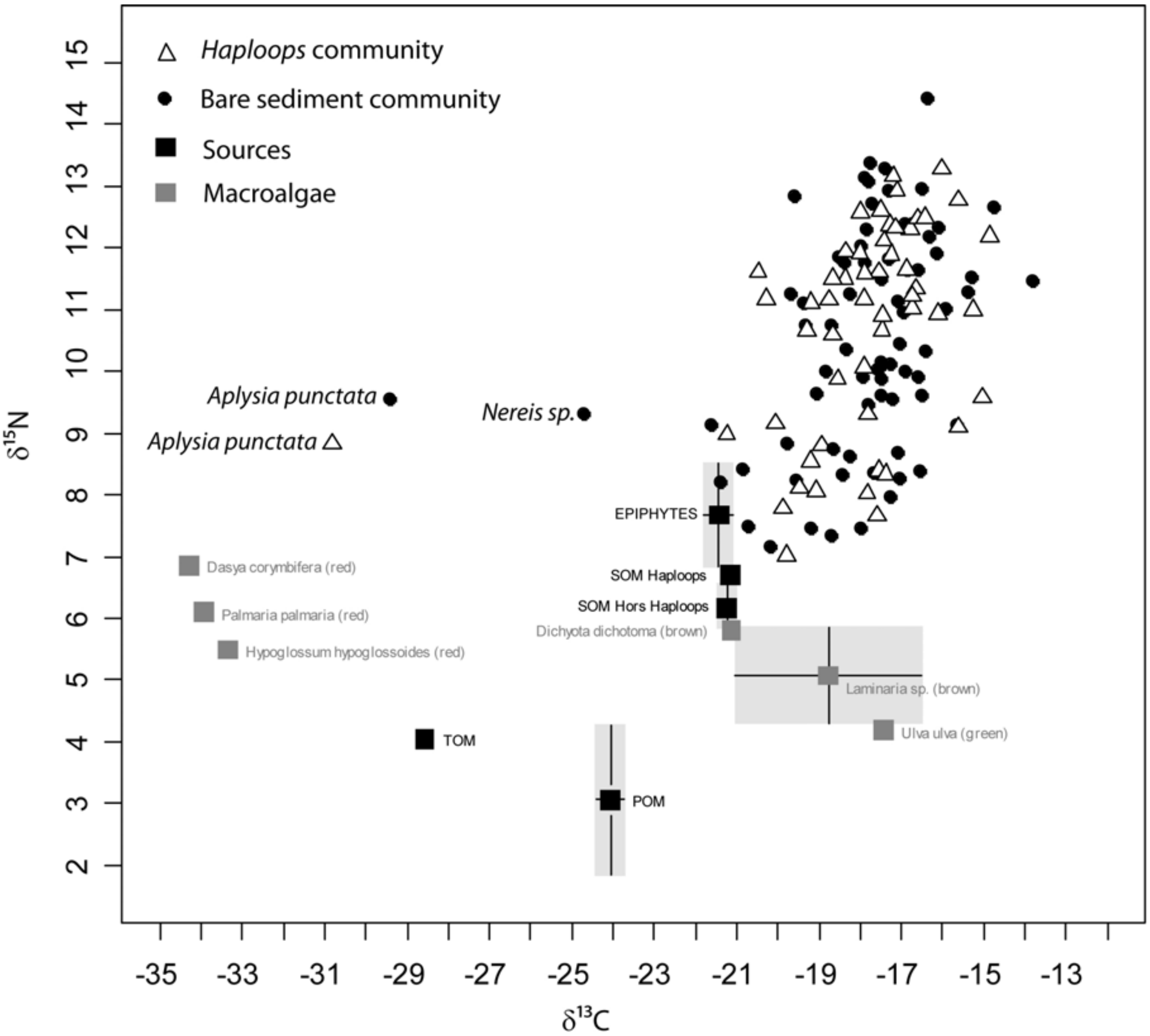

Figure 49 : Stable isotope $\delta^{13}C$ – $\delta^{15}N$ bi-plots for all food web compartments (potential food sources and benthic consumers) in bare sediment (black dots) and *Haploops* (white triangles) communities in winter. Sources are represented with squares. For benthic consumers values, mean $\delta^{13}C$ and $\delta^{15}N$ values are represented without error bars for clarity. The isotopic signature of *Thyasira flexuosa* ($\delta^{15}N$ =-0.30 ± 0.46; $\delta^{13}C$ = -26.40 ± 0.29) was not represented on this graphic.

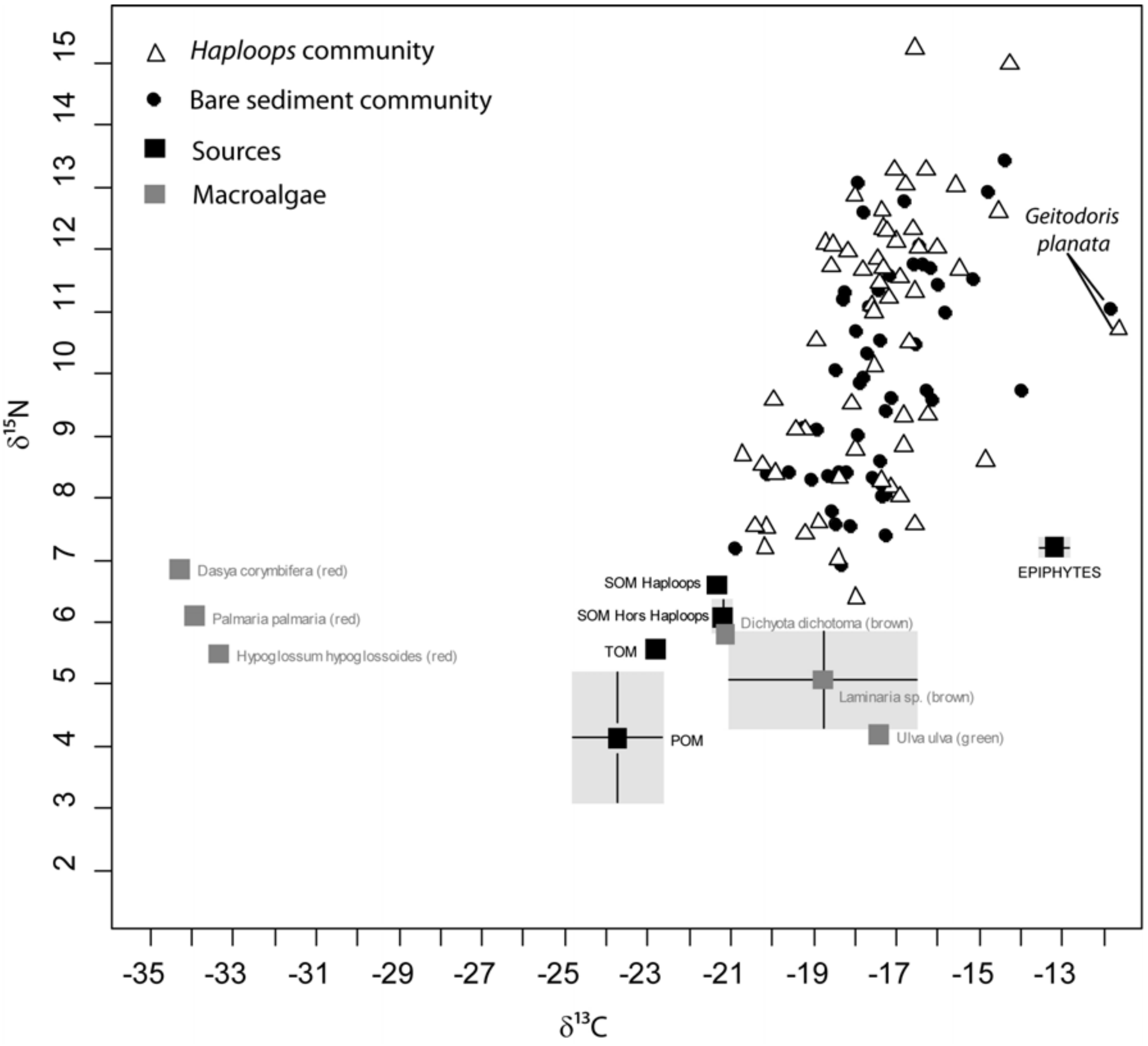

Figure 50 : Stable isotope $\delta^{13}C$ – $\delta^{15}N$ bi-plots for all food web compartments (potential food sources and benthic consumers) in bare sediment (black dots) and *Haploops* (white triangles) habitats in summer. Sources are represented with squares. For benthic consumers values, mean $\delta^{13}C$ and $\delta^{15}N$ values are represented without error bars for clarity.

The $\delta^{13}C$ and $\delta^{15}N$ values displayed by all sampled species in the two communities in winter and summer are listed in Appendix 1 and 2, respectively. Once species with particular isotopic values (*Aplysia punctata*, *Nereis* sp., *Thyasira flexuosa* and *Geitodoris planata*) are removed, the two transects exhibited a similar range in $\delta^{13}C$ values, with winter values spanning from -21.63 ‰ (*Psammechinus miliaris*) to -14.75 ‰ (*Aphrodita aculeata*) in bare sediments and from –21.24 ‰ (*Nereidae* sp. in *Haploops* tube) to –14.86 ‰ (*Buccinum undatum*) in the *Haploops* community. In summer, $\delta^{13}C$ isotopic values displayed the same pattern with values ranging from -20.91 ‰ (*Ampelisca spinipes*) to -13.98 ‰ (*Philine aperta*) in bare sediments and from –20.43 ‰ (*Ampelisca typica*) to –14.26 ‰ (*Luidia ciliaris*) in the

Haploops community. Similarly, $\delta^{15}N$ values exhibited close variations in the two communities, ranging from 7.17 ‰ (*Ampharete finmarchica*) to 14.43 ‰ (*Glycera unicornis*) in winter in the bare sediment transect and from 7.02 ‰ (*Haploops nirae*) to 13.28 ‰ (*Maja squinado*) in the *Haploops* community. In summer, $\delta^{15}N$ values showed almost identical variations with $\delta^{15}N$ values ranging from 6.93 ‰ (*Cultellus pellucidus*) to 13.45 ‰ (*Luidia ciliaris*) in bare sediments and from 6.40 ‰ (*Timoclea ovata*) to 15.24 ‰ (*Glycera unicornis*) in the *Haploops* community.

When pooled into trophic groups, organisms' isotopic signatures revealed that the two communities have very similar trophic structure (Fig. 51 and 52 for winter and summer, respectively). Indeed, the average values of both $\delta^{13}C$ and $\delta^{15}N$ for each trophic groups did not show significant differences between the two communities (ANOSIM, $p>0.05$), whatever the season. Moreover, except for the *Haploops* community in winter, there is a linear trend in both communities with increasing $\delta^{13}C$ and $\delta^{15}N$ values in feeding groups from suspension-feeders, surface deposit feeders and sub-surface deposit feeders, up to carnivore-omnivores The stable isotope values of surface deposit-feeders were in between those of suspension-feeders and sub surface deposit feeders while sub-surface deposit feeders consistently exhibited isotopic values overlapping those of carnivores-omnivores species (ANOSIM, $p>0.05$).

Figures 51 and 52 also suggested that trophic groups are characterized by large within-group variations in $\delta^{13}C$ values. Suspension - feeders (SF) spanned consistently over the same ranges in $\delta^{13}C$ values (i.e. mean $\delta^{13}C$ range = 4.62 ‰), not only between the two seasons but also between the two communities (Table 25). For the two seasons and the two communities, carnivores-omnivores had the same mean $\delta^{13}C$ range (i.e. 4.62 ‰), except in the *Haploops* community in winter where carnivores-omnivores spread on a larger $\delta^{13}C$ range (6.38 ‰). Unlike others, surface deposit feeders (SDF) had no clear pattern in $\delta^{13}C$ ranges and varied from 1.82 ‰ up to 4.51 ‰. Finally, the *Haploops* community is characterized for both seasons by a narrower $\delta^{13}C$ range in subsurface deposit feeders (SSDF) (mean 1.25 ‰) as compared to bare sediment community (mean 3.64 ‰). Variations in $\delta^{15}N$ among trophic groups showed that subsurface deposit feeders values are consistently above TL = 3 and largely overlapping with carnivores-omnivores. The largest community variation is due to surface deposit feeders in winter, exhibiting higher $\delta^{15}N$ value in *Haploops* community (TL>3) than in bar sediment community (TL<3)

Table 25 : Range in $\delta^{13}C$ values for trophic groups for the two communities (i.e. bare sediment and *Haploops*) for the two seasons (i.e. winter and summer).

	WINTER		**SUMMER**	
Range $\delta^{13}C$	Bare sediment	*Haploops*	Bare sediment	*Haploops*
C-O	4.87	6.38	4.51	4.47
SSDF	4.11	1.63	3.16	0.87
SDF	4.51	3.64	1.82	3.28
SF	4.85	4.44	4.74	4.46

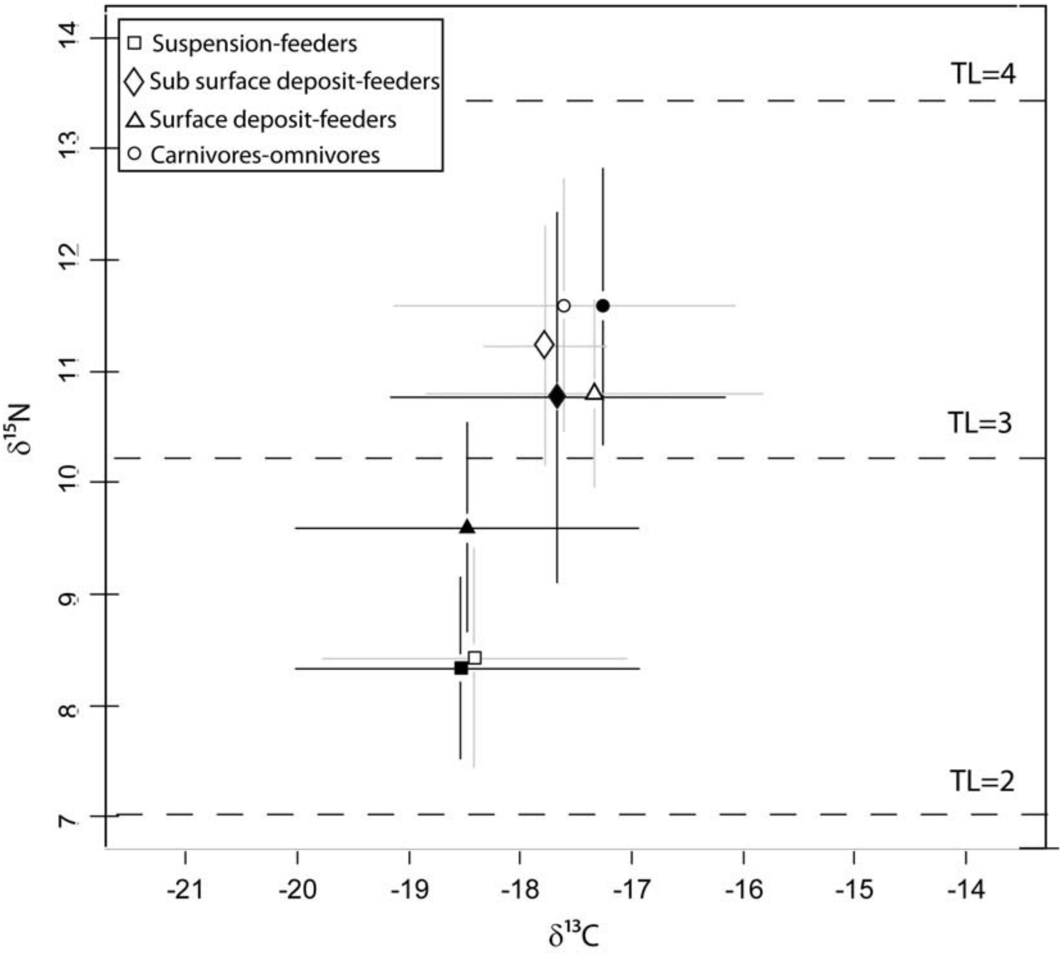

Figure 51 : Dual isotopic plot of mean $\delta^{13}C$ and $\delta^{15}N$ values for species pooled into trophic groups (see Appendix 1 for details) for the two communities (i.e. bare sediment and *Haploops*) in winter. Grazers are omited. White symbols correspond to the *Haploops* community and black symbols correspond to bare sediment community.

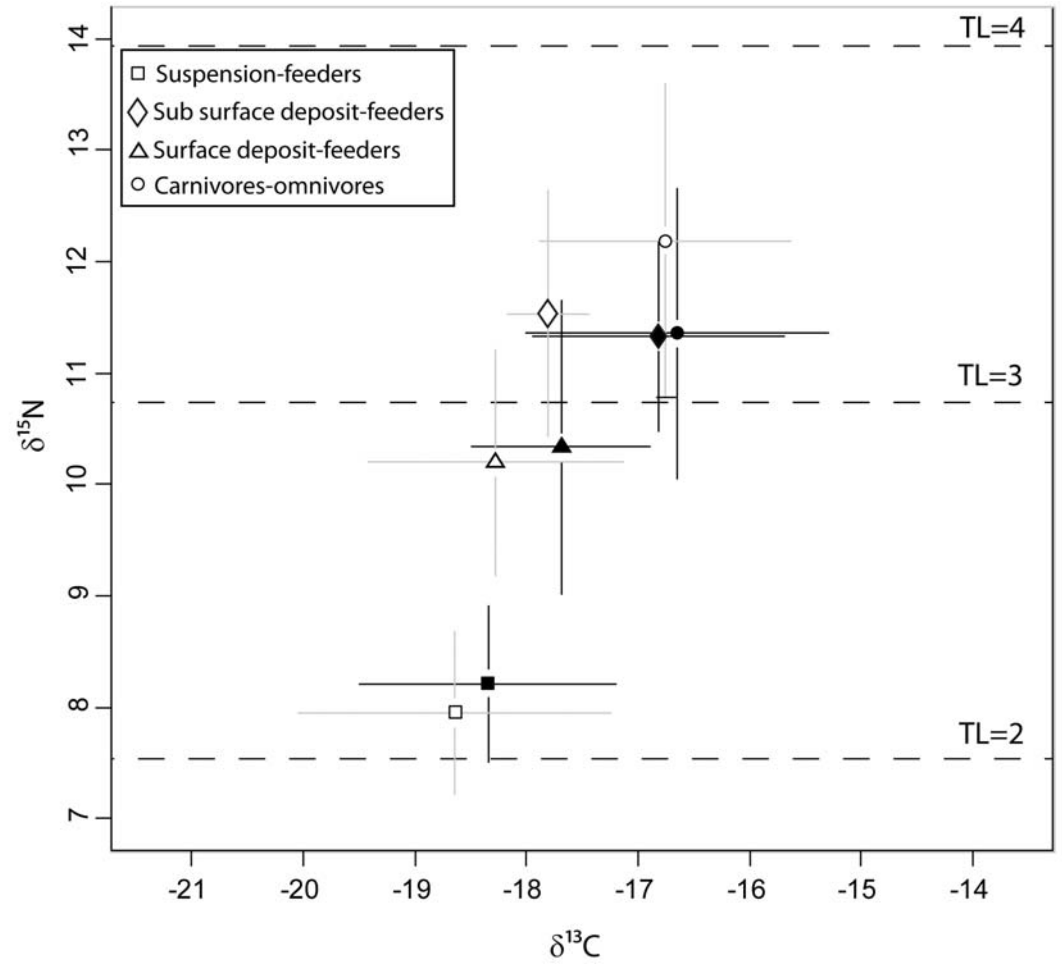

Figure 52 : Dual isotopic plot of mean δ^{13}C and δ^{15}N values for species pooled into trophic groups (see Appendix 2 for details) for the two communities (i.e. bare sediment and *Haploops*) in summer. Grazers are omited. White symbols correspond to the *Haploops* community and black symbols correspond to bare sediment community.

3. 3. Comparison of isotopic values of species shared by the two communities

Twenty-eight and seventeen species where found to belong to both communities in winter and summer, respectively. Stable isotopes ratios measured for the 2 communities are represented in the same biplots (Fig. 53 and 54): species close to the line 1:1 (bold dotted line) indicate no significant differences whatever the community (with the 95% confidence interval represented with a regular dotted lines). Overall, the majority of species falls within the range of the 1:1 ratio, for the two seasons. However, some species exhibited isotopic significantly different in the two communities. For example, in winter the δ^{15}N value of the predators *Eunice vittata* and *Liocarcinus pusillus* and the suspension-feeder *Pecten maximus* were lower in the *Haploops* community than in bare sediments. Conversely, the predator *Inachus dorsettensis* and the surface deposit-feeder *Terebellides stroemi* exhibited higher δ^{15}N values in *Haploops* community compared to bare sediments. As for winter δ^{13}C values, common species tend to be ^{13}C enriched in the *Haploops* community, as evidenced for the two suspension-feeders *Pecten maximus* and *Anapagurus hyndmanni* as well as the deposit-feeder *Labidoplax digitata* and the predators *Eunice vittata* and *Natatolana neglecta*. The same pattern is observed in summer. Several species showed enriched δ^{15}N values in the *Haploops* community (*Lumbrineris fragilis* and *Sabellaria spinulosa*) while others are ^{15}N depleted (*Sabellidae* sp.). As for summer δ^{13}C values, subsurface deposit-feeders (*Aricia cuvieri* and *Maldane glebifex*) were ^{13}C depleted in the *Haploops* transect while the suspension-feeder *Crepidula fornicata* displayed slightly enriched δ^{13}C values in the *Haploops* community.

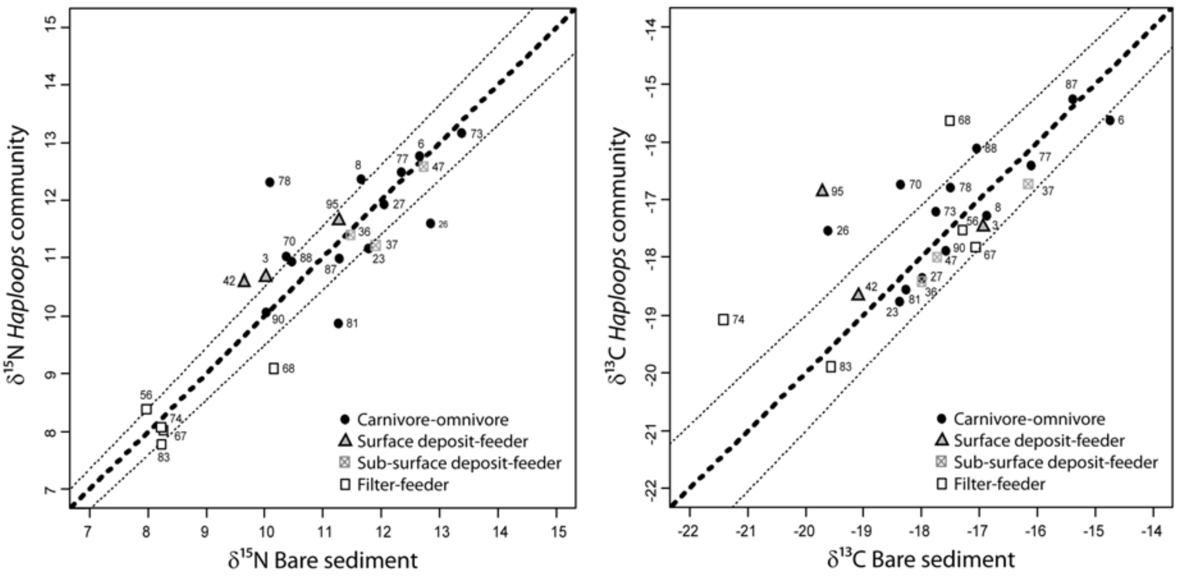

Figure 53 : Comparison of nitrogen (left panel) and carbon (right panel) isotope ratios for species collected in the the two communities (bare sediment and *Haploops*) in winter. The bold dotted line indicated a 1:1 correlation (95% interval confidence in light dotted line). Labels correspond to a code given at each species (see Appendix 1 for corresponding species names).

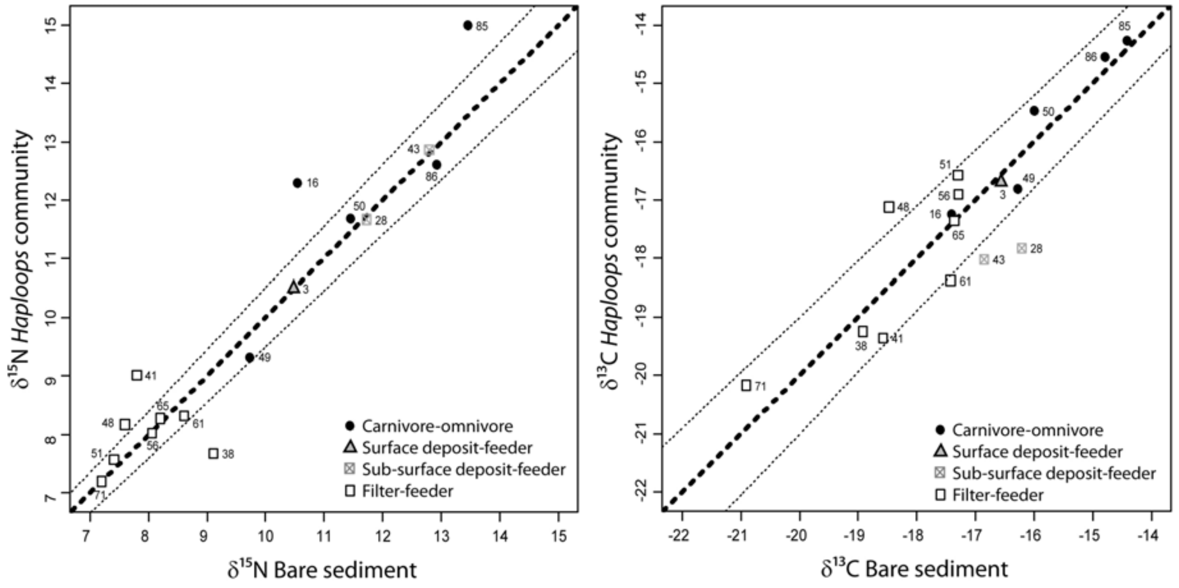

Figure 54 : Comparison of nitrogen (left panel) and carbon (right panel) isotope ratios for species collected in the the two communities (bare sediment and *Haploops*) in summer. The bold dotted line indicated a 1:1 correlation (95% interval confidence in light dotted line). Labels correspond to a code given at each species (see Appendix 2 for corresponding species names).

3. 4. Contribution of food sources to benthic food webs

According to biomass data retrieved from a previous benthic survey, 5 and 6 species accounted for 80 % of the benthic fauna biomass in summer in the *Haploops* community and bare sediment community, respectively (Fig. 55). In bare sediments, the suspension-feeders *Amphiura filiformis*, *Thyone fusus*, *Dosinia lupinus* and *Chamelea striatula* made up for the bulk of the benthic biomass (Fig. 55). The subsurface deposit-feeder *Maldane glebifex* and the surface deposit-feeder *Aspidosiphon (Aspidosiphon) muelleri muelleri* accounted in a lesser extent for the biomass in this habitat. In the *Haploops* habitat, the large bivalve *Polititapes virgineus* alone accounted for 44.5% of the biomass of the benthic fauna (Fig. 55). The two other main suspension-feeders of this transect (*Haploops nirae* and *Turritella communis*) as well as the surface deposit-feeder *Aspidosiphon (Aspidosiphon) muelleri muelleri* and the predator *Sthenelais boa* accounted for the remaining benthic biomass in the *Haploops* transect.

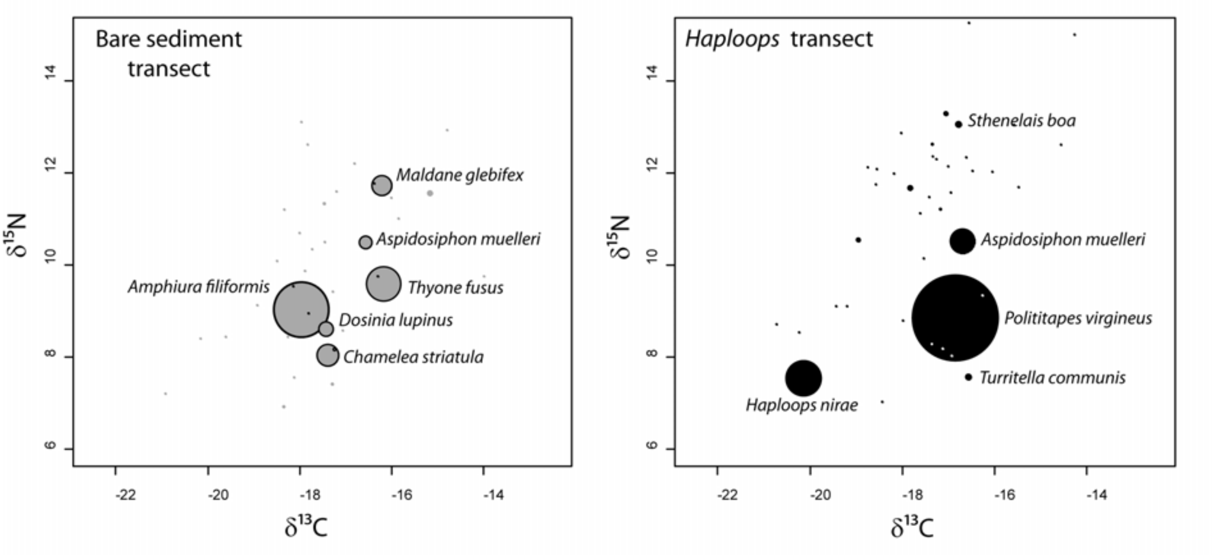

Figure 55 : Dual isotopic $\delta^{13}C$ - $\delta^{15}N$ biplot of species collected in the two habitat in summer. Bubble values represent relative contribution of each species to the total biomass for each community.

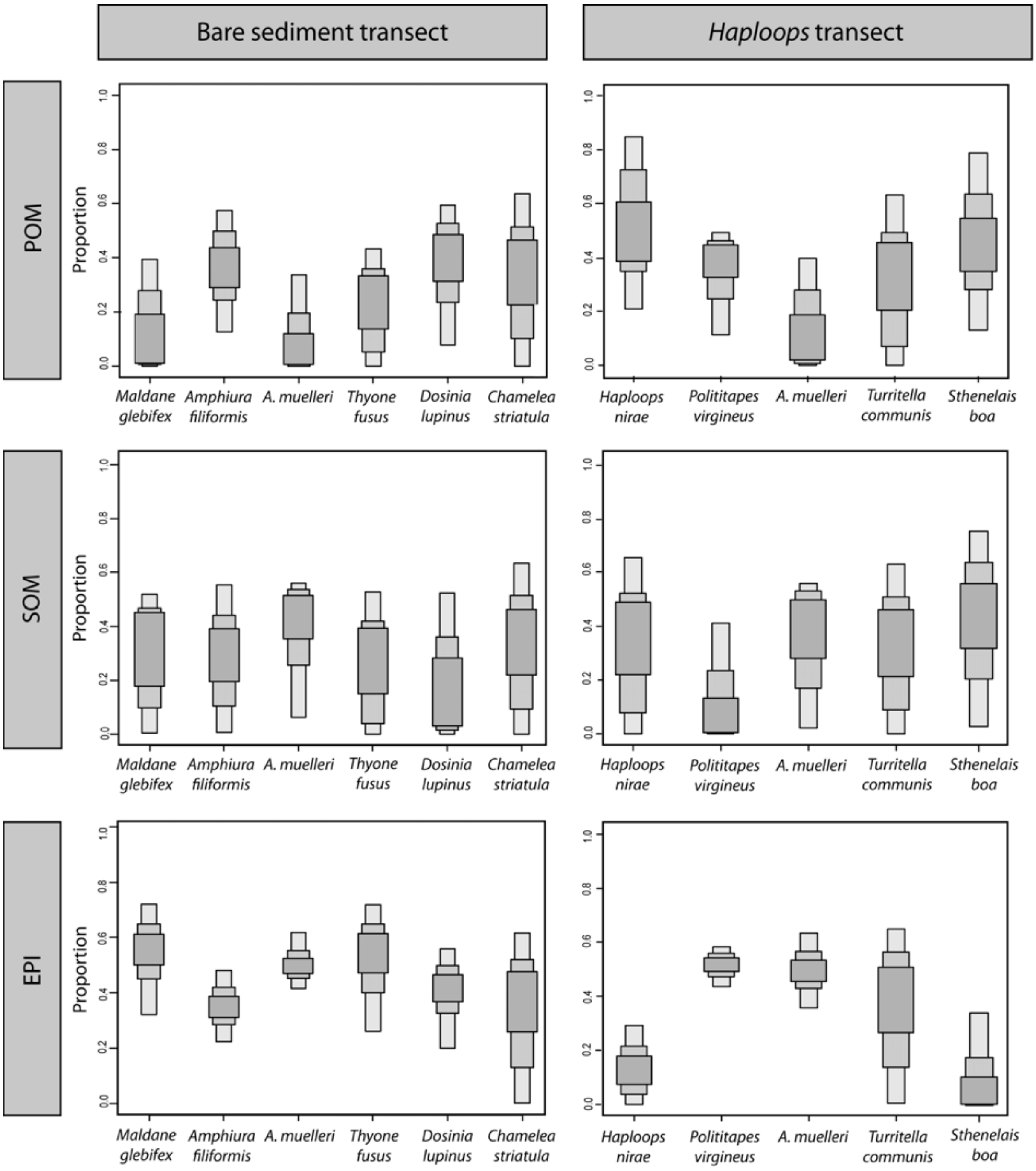

Figure 56 : Estimated contributions of the 3 main food sources (particulate organic matter, sedimented organic matter and epiphytes) in the two communities (i.e. bare sediment on the left panels and *Haploops* community on the right panels) in summer from SIAR mixing model. Boxplots indicate 50%, 75% and 95% confidence intervals for species that account for 80% of the biomass in each community.

Results of the bayesian mixing model computed on species that account for 80% of the biomass in summer are shown in Fig. 56. Overall, the 2 communities exhibited similar patterns in food sources contributions. Even though large uncertainties hampered accurate quantifications, epiphytes (mainly represented by benthic diatoms) seemed to be the largest contributors, along with particulate organic matter (POM). The phytoplankton contribution is however associated with large 95% confidence intervals but significantly contributes to suspension-feeders diets *Polititapes virgineus* and *Haploops nirae* in *Haploops* community or *Dosinia lupinus* and *Chamelea striatula* in bare sediments. The predator *Sthenelais boa* seemed to feed primarily on organisms which feed themselves primarily on POM. The contribution of organic matter from the sediment seemed to be less obvious from SIAR outputs, as it is also associated with large uncertainties.

SIAR outputs (mean contributions) were plotted in a ternary plot to provide an estimate of the trophic niche occupied by the species representing most of the biomass in the two habitats. The Fig. 57 showed a larger trophic niche width on *Haploops* community, with a large overlap of bare sediments.

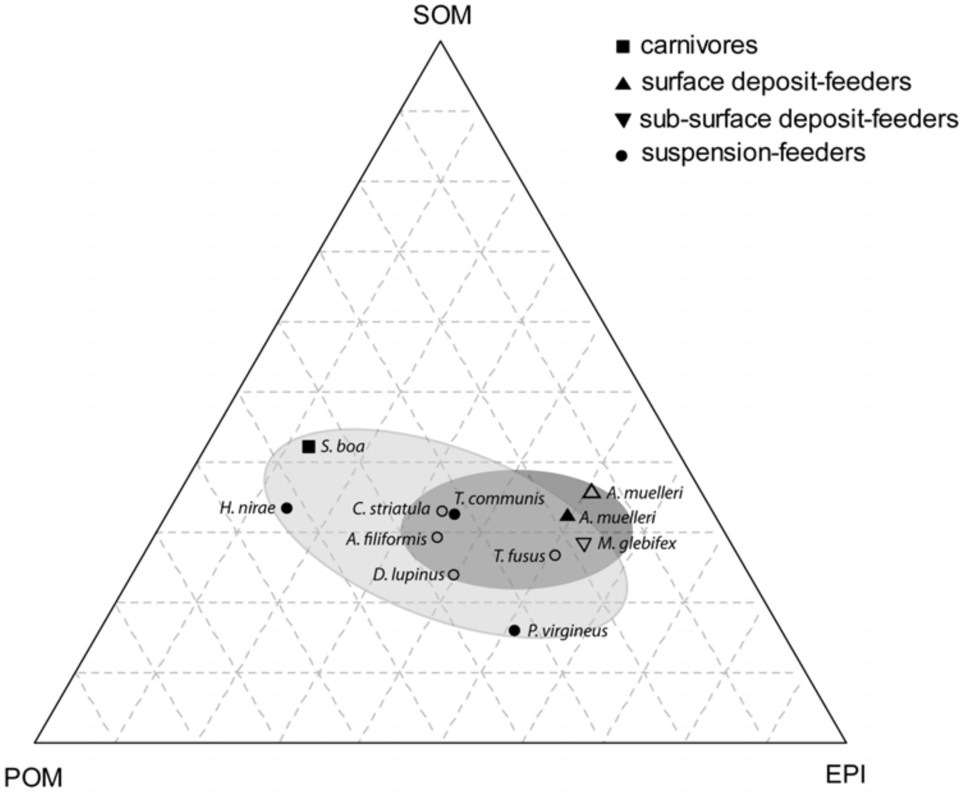

Figure 57 : Ternary plot for mean source contributions of species diet accounting for 80 % of the total benthic biomass in the two habitats (i.e. bare sediment and *Haploops*) in summer. Species are represented with full labels for *Haploops* community and empty labels for bare sediment. Ellipses are used to represent the trophic niche width of the species in *Haploops* community (light grey) and in bare sediment (dark grey).

4. Discussion

In shallow subtidal zones, ampelicids populations are common and can generate in some instances extensive tube mats that considerably increase local habitat complexity (Bellan-Santini and Dauvin, 1988; Franz and Tanacredi, 1992; Sudo and Azeta, 1996; Göransson, 2002). We investigated here dense tube mats created by the common ampeliscid *Haploops nirae* in the bay of Concarneau (South Brittany) to determine the effects of a gregarious engineer species on food web structure, using stable C and N isotopes.

Effect of tube mats on food web structure

Engineer species in general and tubiculous species in particular are known to affect species composition of soft-bottom communities (Reise et al., 2008). Rigolet et al. (unpubl.) showed that the presence of *Haploops nirae* in the bay of Concarneau (South Brittany) affects the local biodiversity, species assemblages. By affecting local sedimentary features, *Haploops* individuals create conditions for a unique species assemblage to settle and develop, with species only found within *Haploops* community (Myers et al., 2012). To investigate whether drastic changes in species composition comes with changes in food web structure, we sampled a large diversity of benthic organisms associated to the *Haploops* community and to the adjacent sandy-mud community, for 2 contrasted seasons. Our results first showed that the overall isotopic food web structure was similar between the two communities, since the isotopic spaces occupied by the species in the $\delta^{13}C$-$\delta^{15}N$ biplots largely overlap. Moreover, the length of the benthic food web in *Haploops* community did not differ from the one in adjacent sediment and extent over a continuum of almost three different trophic levels defined according to an isotopic baseline (Post, 2002). It is well known that food web length in aquatic systems influences ecosystem functioning and food-web stability (Long et al., 2011) but is also recognized that longer food webs are predicted in more productive systems because more energy can be transferred between trophic levels (Morin and Lawler, 1995). Isotope results from the benthic species showed strong differences between the two sampled communities. However, the mean trophic position for a random benthic organism is higher in *Haploops* community and the comparison of summer $\delta^{15}N$ values of common species found in the two communities also revealed a higher trophic position for species occurring in *Haploops* community (Fig. 54). Estimates of biomass and secondary production are not significantly different in *Haploops* communities in comparison with surrounding communities

(Rigolet et al., 2012; Rigolet, unpubl.) but the $\delta^{15}N$ results could suggest a higher stability of trophic web associated with *Haploops* community. This stability correlates with the very strong homogeneity in species assemblages associated with Haploops (Rigolet, unpubl.). As for many tubiculous species, *Haploops* tubes can be considered as sediment disturbances (Grant, 1983) and *Haploops* colonization can ultimately be considered as a perturbation. Available evidences in stream ecology showed that food chain length can be affected by ecosystem size but also by environmental or physical disturbances (Mc Hugh et al., 2010). In that perspective, we conclude here that *Haploops* tube mats do not adversely affect the overall trophic functioning of community they colonize.

The distribution of species over a continuum of three trophic levels appears to be a common feature in temperate subtidal benthic ecosystems. Indeed, Le Loc'h et al. (2008) for the muddy *Nephrops* communities in the bay of Biscay, Grall et al. (2006) for the north-eastern Atlantic maerl beds maerl community or Carlier et al. (2007) for the north-western Mediterranean bay of Banyuls also reported food web structure of macrofauna with three trophic levels. We also showed that isotopic values for both primary and secondary consumers spread on a large range of $\delta^{13}C$ values. A large range of $\delta^{13}C$ values within primary consumers is also consider a common feature of continental shelf communities (Hobson et al., 2002, Le Loc'h et al., 2008), where a larger number of food sources are available. And yet, the $\delta^{13}C$ ranges for subtidal shallow benthic communities seem to remain stable between -14‰ and -22‰ for the whole macrofauna community (Grall et al., 2006 ; Carlier et al., 2007 ; Le Loc'h et al., 2008), if we exclude a few 'outlining' species exhibiting special isotopic signatures from special diets (e.g. specialists of very ^{13}C-depleted red macroalgae or species with endosymbiotic bacteria). One should consider that between-communities variations are constrained within variations at the ecosystem level.

Several studies reported that ampeliscids can constitute the major prey for some top-predators marine mammals and finfishes (Franz and Tanacredi, 1992; Highsmith and Coyle, 1992; Cui et al, 2012). But to our knowledge, no study have paid special attention to the position of the amphipods in a food web, especially using stable isotopes. *Haploops* occupied the lowest $\delta^{13}C$ – $\delta^{15}N$ position in the isotopic biplot. Interestingly, ampeliscid always exhibit the lowest $\delta^{15}N$ value in food web structures determined with stable isotopes, as showed from the muddy bottoms of the southern Tyrrhenian Sea (western Mediterranean) for *Ampelisca* spp. (Fanelli et al., 2009) to the South Orkneys island (Antarctic Peninsula) for *A. richardsoni* (Nyssen et al., 2005). We suggest here that Ampeliscid in general, despite observations reporting strong trophic plasticity and changes in foraging behavior, can be used as isotopic trophic baseline for coastal marine and estuarine systems.

Despite the strong bioturbating tube-building activity (over 10 000 tubes.m^{-2}; Rigolet et al., 2012) and the active grazing activity (Rigolet et al., 2011), *Haploops* individuals do not seem to affect the higher trophic levels. As suggested by Mills et al. (1993), the feeding activities of dense species greatly affect community features (such as sediment characteristics) but do not necessarily have direct trophic effects on other species. Similarly, Jones et al. (1997) reviewed that many engineer species physically affect their environment in numerous ways but that not all of the changes have important (positive or negative) ecological consequences. Studies that compared food webs of engineered community with adjacent homogeneous bare sediment using stable isotopes are very scarce. Yet, Baeta et al. (2009) investigated whether the occurrence of the eelgrass *Zostera marina* changed the benthic and pelagic food web structures in comparison with uncolonized sediment. They showed – in line with our global finding – no major difference in the structure of the benthic food web. This result has strong implications in terms of trophic niche partitioning: as species assemblages with *Haploops* community drastically differ from those in adjacent sediments, it means that each species or each group of species from the *Haploops* community has its trophic-equivalent species or group of species in the adjacent uncolonized sediments. As a result, with deep changes in diversity and species composition do no always come changes in food web structure, even though the physical environment is remarkably affected by an engineer tubiculous species.

Effects of dense tube mats on food sources contributions and main trophic pathways

Food web structure can be very different whether one considers all the species or only the species that play a functional role, i.e. the species accounting for most of the biomass (Villeger et al., 2007). In coastal shallow systems, the biomass and the secondary production of benthic consumers originate from a diversity of sources (Peterson, 1999). In the bay of Concarneau, many sources are potentially available for the benthic fauna, particulate organic matter (POM) and sedimented organic matter (SOM), terrestrial inputs of organic matter (TOM) as well as macroalgae detritus from surroundings. It is commonly assumed that the subsurface POM (as a proxy for phytoplankton) directly or indirectly after sedimentation and resuspension is the major contribution to the benthic primary consumers (Grall et al., 2006 ; Le Loc'h et al., 2008). Unlike shores and estuaries where benthic primary production (microphytopbenthos) play a key role in benthic food webs (Dubois et al. 2007 ; Lefebvre et al., 2009), benthic primary producers are disregarded in subtidal benthic food webs, despite isotopic evidences that a food source is missing to explain usually δ^{13}C-enriched signature of suspension- and deposit-feeders (e.g. Grall et al., 2006). However Grippo et al. (2011) investigated the microphytobenthos as potential support of benthic food web in Louisiana shoals (Gulf of Mexico) and revealed that subtidal sandy dunes are supporting a benthic production during spring and summer times. In temperate subtidal sedimentary systems, evidences of microphytobenthos contributions are still very rare (but see Evrard et al., 2010; 2012). From preliminary visual observations, we showed here that *Haploops* tube can be a physical support for epiphytes in general and benthic diatoms mats in particular (*Navicula* sp.). The δ^{13}C value from the tube epiphytes falls within the expected value of microphytobenthos in summer (ca. –13%, Fig. 50) (Riera and Richard, 1996 ; Leal et al., 2008 ; Grippo et al., 2011). However in winter (reduced luminosity and higher turbidity), tube scrapings revealed a δ^{13}C value similar to the sedimented organic matter (Fig. 49), hence supporting the absence of growing primary producers on *Haploops* tubes. *Haploops* tubes are made of mud, pseudofeces and mucus secreted by individuals (Rigolet et al. 2011) and offer a quality support of polysaccharides for benthic diatom to grow (Barillé and Cognie, 2000), providing light is not limiting (summer time). This study bring hence new input in the contribution of food sources to subtidal soft-bottom muddy systems, evidencing that microphytobenthic production can significantly be integrated in subtidal food web, even below 25 m deep in muddy environments.

While SIAR Bayesian mixing models incorporate isotope and fractionation uncertainty in the development of posterior probability distributions of sources contributions, we need to be clear that such results are approximate and include a margin of error that can be high. Since SOM and POM are not well isotopically discriminated, results of the mixing model can thus be hindered by these close values. Yet, epiphytes (benthic diatoms mostly) exhibited very significantly enriched δ^{13}C value and their contribution to the diet to the species with the most eriched δ^{13}C values is undoubted. From the species contributing the most to the total biomass in each community, bayesian mixing models revealed that epiphytes can contribute to 50% to the diet of suspension-feeders such as *Polititapes virgineus* or *Amphiura filiformis*, while other suspension-feeders rely mainly on phytoplankton (*Haploops nirae*) (Fig. 56). The bivalve *P. virgineus* is only found on *Haploops* community and represents one of the largest biomass. Mackenzie et al. (2006) similarly reported high biomass of bivalves *Mercenaria mercenaria* in *Ampelisca* mats of the southeastern Raritan Bay (New

Jersey). We hypothesized here that *Haploops* community offers a broader diversity and quantity in food sources, which is supported by a larger trophic niche width (Fig. 57). Benthic organisms from adjacent communities benefit from benthic production on *Haploops* community, as the overall isotopic space is similar between the two community (Figs. 49 and 50) and the isotopic $\delta^{13}C$ signature of the SOM in adjacent sediments did not show enriched values indicative of primary production. *Haploops* community – and potentially all large tube mats from muddy coastal systems – appears as a food exporter to adjacent communities. While engineer species are defined as species with the capacity to directly or indirectly control resources for others species(Allen and Williams, 2003), we showed in this study that (1) *Haploops nirae* diet is mainly constituted of phytoplankton which limits trophic competition with the main suspension-feeder *P. virgineus* but also that (2) *Haploops* tubes provide a physical support to export benthic production which does not support Allen and William (2003) definition of engineer species.

The contribution of potential food sources have been calculated for summer only as turnover in tissues are close to zero in winter and timelag between food uptake and food assimilation between 6 and 12 months (Lefebvre et al., 2009). This explains why the overall isotopic space did not change between summer and winter seasons, while the food sources signatures did.

Conclusion

Macroinvertebrate communities of the bay of Concarneau showed deep changes in their structure due to the subsequent success of the tubiculous ampeliscid *Haploops nirae* (Rigolet et al., unpubl.). Despite those changes, the overall structure of the food web associated with the *Haploops* habitat remains similar to adjacent muddy or sandy mud habitats. Our findings revealed that benthic diatoms constitute one of the main input of energy source for the benthic fauna, while it is generally assume that no primary production occurred in subtidal areas. The contribution of this unexpected source as well as the biomass represented by *Haploops* grazing primarily on phytoplankton to higher trophic levels (finfishes) is still to be investigated. It is well recognized that densely packed ampeliscid tube mats provide important feeding grounds for bottom-feeding marine mammals (e.g. gray whales and walrus) and benthic fish (e.g. Arctic cod, Bering flounder, winter flounder and snailfish) (Cui et al., 2012), constituting therefore an essential link in the food web (Cui et al., 2009). *Haploops nirae* could thus provide an important link to the food web in South Brittany by converting planktonic matter into useable energy for fish.

Appendices

Appendix 1: Stable-nitrogen and stable-carbon isotope ratio values (mean ± SD) and corresponding trophic level (TP) and feeding group (TG) for the two communitie (i.e. bare sediment and *Haploops*) in winter. The underlined species names corresponds to species collected in the two transects.

			Bare sediment transect					***Haploops* transect**				
Species	**TG**	**Code**	**n**	**TP**	**C/N**	**$\delta^{15}N$**	**$\delta^{13}C$**	**n**	**TP**	**C/N**	**$\delta^{15}N$**	**$\delta^{13}C$**
Cnidarians												
Cerianthus lloydii	C-O	1						1	3.50	3.97	12.13	-17.43
Alcyonium digitatum	C-O	2	1	2.85	6.61	9.92	-16.62					
Sipunculids												
Aspidosipho (Aspidosiphon) muelleri muelleri	SDF	3	3	2.88	3.59	10.02 ± 0.04	-16.93 ± 0.13	2	3.07	3.86	10.67 ± 0.13	-17.48 ± 0.28
Nemertina												
Nemertina indet. found in *Haploops* tubes	C-O	4						2	3.20	4.56	11.12 ± 0.01	-19.19 ± 0.55
Nemertina indet.	C-O	5						3	3.07	4.86	10.67 ± 0.39	-19.28 ± 0.59
Polychaetes												
Aphrodita aculeata	C-O	6	3	3.66	3.10	12.66 ± 0.19	-14.75 ± 0.27	1	3.69	3.16	12.77	-15.62
Alentia gelatinosa	C-O	7						1	3.64	3.66	12.61	-17.51
Harmothoe antilopes	C-O	8	3	3.36	3.55	11.66 ± 0.90	-16.88 ± 0.83	1	3.57	3.50	12.37	-17.28
Malmgreniella andreapolis	C-O	9						1	3.73	3.66	12.92	-17.12
Malmgreniella sp.A	C-O	10	3	3.75	3.82	12.97 ± 0.37	-16.52 ± 0.04					
Malmgreniella sp.B	C-O	11	1	3.40	4.17	11.78	-17.90					
Glycera alba	C-O	12	1	3.85	4.44	13.30	-17.42					
Glycera unicornis	C-O	13	1	4.18	3.76	14.43	-16.38					
Goniada maculata	C-O	14	3	3.80	4.78	13.14 ± 0.91	-17.92 ± 0.20					
Phyllodoce lineata	C-O	15						1	3.56	4.29	12.32	-17.14
Labioleanira yhleni	C-O	16	3	3.58	3.82	12.41 ± 0.20	-16.94 ± 0.46					
Sthenelais boa	C-O	17						1	3.44	3.62	11.92	-18.01
Sthenelais sp.	C-O	18	2	3.42	3.49	11.84 ± 0.21	-17.34 ± 0.58					
Pholoe inornata	C-O	19	2	3.36	3.63	11.64 ± 0.10	-16.62 ± 0.62					
Nephtys hombergii	C-O	20	3	3.52	3.69	12.18 ± 0.44						
Nereidae sp. found in *Haploops* tube	C-O	21						1	2.58	5.54	8.98	-21.24
Nereis sp. station CO24	C-O	22	2	2.67	4.40	9.31 ± 0.50	-24.71 ± 1.31					
Nereis sp.	C-O	22	1	3.56	4.51	12.31	-17.86	2	3.22	4.99	11.17 ± 1.88	-20.27 ± 3.37
Lumbrineris gracilis	C-O	23	2	3.40	4.03	11.78 ± 0.65	-18.39 ± 0.27	3	3.22	4.14	11.16 ± 0.87	-18.75 ± 0.85
Lumbrineris sp. A	C-O	24	1	3.22	3.61	11.16	-17.08					
Schistomeringos rudolphii	C-O	25						1	3.35	7.47	11.61	-20.48
Eunice vittata	C-O	26	1	3.71	3.73	12.84	-19.62	2	3.35	4.17	11.60 ± 1.00	-17.54 ± 0.13
Nematonereis unicornis	C-O	27	1	3.48	4.14	12.05	-17.98	3	3.45	4.62	11.94 ± 0.72	-18.36 ± 0.52
Arabella iricolor	C-O	28	2	3.79	3.87	13.10 ± 0.05	-17.81 ± 0.21					
Hyalinoecia bilineata	C-O	29	3	3.09	3.93	10.74 ± 0.15	-18.69 ± 0.41					
Sternaspis scutata	SDF	30	1	2.62	2.50	9.14	-15.67					
Notomastus latericeus	SSDF	31	3	3.32	3.57	11.50 ± 0.19	-17.52 ± 0.07					
Dasybranchus caducus	SSDF	32						2	2.67	3.70	9.30 ± 0.26	-17.81 ± 0.30
Euclymene oerstedi	SSDF	33	2	2.88	4.09	10.01 ± 0.34	-18.87 ± 0.03					
Euclymene robusta	SSDF	34	1	3.74	3.62	12.95	-17.33					
Praxillura longissima	SSDF	35	1	3.20	4.45	11.12	-19.39					
Macroclymene santandarensis	SSDF	36	4	3.31	4.05	11.48 ± 0.82	-17.99 ± 1.07	2	3.29	3.92	11.40 ± 0.07	-18.42 ± 0.14
Maldane glebifex	SSDF	37	3	3.44	4.79	11.90 ± 0.44	-16.15 ± 1.38	6	3.23	3.75	11.22 ± 0.14	-16.74 ± 0.42
Metasychis gotoi	SSDF	38						1	3.22	3.97	11.17	-17.89
Piromis eruca	SDF	39						3	2.75	4.72	9.57 ± 0.21	-15.03 ± 0.46
Pherusa plumosa	SDF	40	1	2.85	4.07	9.91	-17.96					
Ampharete finmarchica	SDF	41	1	2.04	4.36	7.17	-20.18					
Terebellides stroemii	SDF	42	3	2.77	4.09	9.65 ± 0.32	-19.09 ± 0.86	3	3.05	4.43	10.59 ± 0.38	-18.65 ± 0.06
Pista cristata	SDF	43						2	3.32	4.45	11.50 ± 0.32	-18.67 ± 0.89
Pectinaria (Amphictene) aricoma	SSDF	44	3	2.72	3.97	9.48±0.50	-17.82±0.57					

Sabellidae sp.	SF	45	1	2.41	4.90	8.41	-20.87					
Euchone rubrocincta	SF	46						1	2.63	4.35	9.15	-20.07
Orbinia cuvierii	SSDF	47	1	3.68	3.90	12.73	-17.73	2	3.64	3.82	12.58 ± 0.25	-18.00 ± 0.13
Owenia fusiformis	SDF	48	3	2.76	4.18	9.61 ± 0.46	-17.50 ± 0.17					
Gastropods												
Scaphander lignarius	SSDF	49	1	3.32	3.40	11.52	-15.28					
Crepidula fornicata	SF	50						3	2.19	3.54	7.66 ± 0.21	-17.59 ± 1.01
Nassarius reticulatus	C-O	51	4	3.18	3.52	11.04 ± 2.64	-15.91 ± 0.67					
Buccinum undatum	C-O	52						3	3.52	3.39	12.20 ± 0.28	-14.86 ± 0.14
Gibbula cineraria	G	53	3	2.75	3.67	9.56 ± 0.10	-17.25 ± 1.52					
Philine aperta	C-O	54	3	2.76	3.60	9.61 ± 0.07	-16.53 ± 0.31					
Aplysia punctata	G	55	3	2.75	4.01	9.57 ± 0.16	-29.41 ± 1.62	1	2.53	4.20	8.83	-30.81
Bivalves												
Nucula nitidosa	SF	56	3	2.28	3.73	7.97 ± 0.22	-17.29 ± 0.43	2	2.40	3.89	8.39 ± 0.02	-17.54 ± 0.08
Thyasira flexuosa	SF	57	3	-	4.63	-0.30 ± 0.46	-26.40 ± 0.29					
Kurtiella bidentata	SF	58	1	2.40	26.92	8.37	-17.69					
Polititapes virgineus	SF	59						9	2.39	3.82	8.34 ± 0.77	-17.38 ± 0.97
Chamelea striatula	SF	60	2	2.38	4.25	8.32 ± 0.05	-18.46 ± 0.83					
Dosinia lupinus	SF	61	3	2.49	5.35	8.69 ± 0.12	-17.09 ± 0.22					
Spisula subtruncata	SF	62	1	2.10	3.60	7.35	-18.69					
Gari fervensis	SF	63	2	2.09	3.72	7.33 ± 0.07	-18.71 ± 0.40					
Solecurtus scopula	SF	64						1	3.14	3.49	10.91	-17.45
Abra alba	SF	65	3	2.51	3.87	8.74 ± 0.25	-18.65 ± 0.22					
Phaxas pellucidus	SF	66	3	2.13	4.07	7.46 ± 0.04	-19.21 ± 0.47					
Aequipecten opercularis	SF	67	3	2.37	3.03	8.27 ± 0.26	-17.06 ± 0.17	2	2.29	3.11	8.02 ± 0.20	-17.83 ± 0.86
Pecten maximus	SF	68	1	2.92	3.19	10.16	-17.51	7	2.61	3.03	9.09 ± 0.24	-15.63 ± 0.43
Palliolum tigerinum	SF	69						1	2.32	3.37	8.12	-19.47
Crustaceans												
Natatolana neglecta	C-O	70	1	2.98	9.04	10.37	-18.36	1	3.18	7.31	11.02	-16.73
Ampelisca spinipes	SF	71	1	2.14	8.74	7.50	-20.74					
Haploops nirae	SF	72						3	2.00	8.31	7.02 ± 0.29	-19.79 ± 0.24
Palaemon serratus	C-O	73	3	3.87	3.24	13.38 ± 0.71	-17.76 ± 0.99	3	3.80	3.21	13.16 ± 0.32	-17.21 ± 0.18
Anapagurus hyndmanni	SF	74	2	2.35	7.42	8.22 ± 0.51	-21.42 ± 0.34	1	2.31	3.70	8.07	-19.07
Pagurus bernhardus	C-O	75						3	3.43	3.66	11.90 ± 0.19	-17.25 ± 0.51
Pagurus cuanensis	SF	76						2	2.52	4.10	8.80 ± 0.01	-18.93 ± 0.72
Pagurus prideaux	C-O	77	3	3.57	3.20	12.35 ± 0.40	-16.11 ± 0.28	3	3.61	3.36	12.49 ± 0.14	-16.42 ± 0.64
Inachus dorsettensis	C-O	78	3	2.90	8.53	10.09 ± 1.08	-17.50 ± 0.73	3	3.55	3.28	12.31 ± 0.73	-16.79 ± 0.24
Macropodia rostrata	C-O	79	1	3.10	6.71	10.76	-19.34					
Maja squinado	C-O	80						1	3.84	3.39	13.28	-16.04
Liocarcinus pusillus	C-O	81	3	3.25	8.03	11.26 ± 0.62	-18.27 ± 1.07	1	2.84	9.33	9.88	-18.55
Liocarcinus depurator	C-O	82						3	3.60	3.27	12.48 ± 0.66	-16.62 ± 0.14
Pisidia longicornis	SF	83	1	2.36	10.64	8.23	-19.56	1	2.22	11.14	7.78	-19.89
Xantho pilipes	C-O	84						2	3.27	3.22	11.33 ± 0.05	-16.66 ± 0.01
Upogebia deltaura	SF	85	1	2.54	4.50	8.85	-19.78					
Echinoderms												
Astropecten irregularis	C-O	86	3	3.16	19.35	10.96 ± 0.30	-16.94 ± 0.62					
Asterias rubens	C-O	87	3	3.25	13.75	11.28 ± 0.16	-15.39 ± 0.95	3	3.17	14.20	11.00 ± 0.10	-15.25 ± 0.02
Marthasterias glacialis	C-O	88	1	3.01	8.82	10.46	-17.05	2	3.15	10.85	10.94 ± 0.37	-16.11 ± 0.11
Ophiura ophiura	C-O	89	2	3.31	15.19	11.24 ± 1.36	-16.49 ± 1.56					
Ophiura albida	C-O	90	1	2.88	67.12	10.03	-17.58	3	2.90	38.09	10.07 ± 0.55	-17.89 ± 0.15
Amphiura filiformis	SF	91	3	2.87	16.99	10.00 ± 0.17	-17.40 ± 0.40					
Ophiothrix fragilis	SF	92	3	2.47	19.08	8.63 ± 0.49	-18.28 ± 0.29					
Psammechinus miliaris	G	93	3	2.62	22.68	9.13 ± 0.89	-21.63 ± 0.87					
Thyone fusus	SF	94	3	2.40	3.08	8.40 ± 0.88	-16.57 ± 0.26					
Oestergrenia digitata	SDF	95	1	3.25	4.48	11.27	-19.71	1	3.36	3.16	11.65	-16.86

Appendix 2: Stable-nitrogen and stable-carbon isotope ratio values (mean ± SD) and corresponding trophic level (TP) and feeding group (TG) for the two communities (i.e. bare sediment and *Haploops*) in summer. The underlined species names corresponds to species collected in the two transects.

			Bare sediment transect					***Haploops* transect**				
Species	**TG**	**Code**	**n**	**TP**	**C/N**	**$\delta^{15}N$**	**$\delta^{13}C$**	**n**	**TP**	**C/N**	**$\delta^{15}N$**	**$\delta^{13}C$**
Cnidarians												
Adamsia carciniopados	C-O	1						2	3.27	3.61	11.84 ± 0.41	-17.45 ± 0.42
Epizoanthus incrustatus	C-O	2	1	2.61	1.99	9.60	-17.14					
Sipunculids												
Aspidosiphon (Aspidosiphon) muelleri	SDF	3	3	2.87	3.76	10.48 ± 0.50	-16.56 ± 0.20	3	2.87	3.55	10.50 ± 0.73	-16.69 ± 0.41
Golfingia (Golfingia) vulgaris vulgaris	SDF	4						2	3.08	3.13	11.22 ± 0.59	-17.18 ± 0.44
Nemertina												
Nemertina indet.	C-O	5						2	3.02	4.12	11.00 ± 0.34	-17.54 ± 0.18
Polychaetes												
Aphrodita aculeata	C-O	6						1		3.09	13.03	-15.56
Glycera alba	C-O	7	3	3.49	3.78	12.60 ± 0.45	-17.82 ± 0.40					
Glycera unicornis	C-O	8						1	4.27	3.76	15.24	-16.54
Glycinde nordmanni	C-O	9	1	3.64	4.31	13.10	-17.95					
Labioleanira yhleni	C-O	10	1	3.12	3.52	11.34	-17.46					
Sthenelais boa	C-O	11						3	3.62	3.48	13.05 ± 0.43	-16.77 ± 0.16
Sthenelais limicola	C-O	12	1	2.82	3.75	10.33	-17.72					
Nephtys assimilis	C-O	13	1	3.33	3.66	12.06	-16.46					
Nephtys hombergii	C-O	14	3	3.25	3.58	11.78 ± 0.43	-16.60 ± 0.26					
Lumbrineris gracilis	C-O	15	1	3.19	4.03	11.59	-17.20					
Lumbrineris fragilis	C-O	16	3	2.89	3.80	10.54 ± 0.36	-17.41 ± 0.05	1	3.40	4.14	12.30	-17.24
Schistomeringos rudolphii	C-O	17						1	3.35	5.12	12.11	-18.73
Eunice vittata	C-O	18						3	3.05	3.66	11.11 ± 0.10	-17.61 ± 0.06
Nematonereis unicornis	C-O	19						3	3.50	3.82	12.62 ± 0.35	-17.35 ± 0.55
Arabella iricolor	C-O	20						3	3.69	3.72	13.29 ± 0.64	-17.05 ± 0.22
Sternaspis scutata	SDF	21						1	2.46	3.78	9.09	-19.43
Notomastus latericeus	SSDF	22	2	3.24	3.57	11.76 ± 0.31	-16.37 ± 0.13					
Dasybranchus caducus	SSDF	23						1	2.58	3.76	9.51	-18.08
Euclymene oerstedi	SSDF	24	1	2.93	3.97	10.69	-18.00					
Euclymene lombricoides	SSDF	25						1	3.15	4.25	11.46	-17.40
Praxillura longissima	SSDF	26	1	3.08	3.97	11.19	-18.33					
Macroclymene santandarensis	SSDF	27						3	3.31	3.92	11.97 ± 0.18	-18.18 ± 0.18
Maldane glebifex	SSDF	28	3	3.23	4.05	11.72 ± 0.19	-16.21 ± 0.64	3	3.22	4.63	11.67 ± 0.71	-17.82 ± 0.12
Metasychis gotoi	SSDF	29						1	3.23	4.06	11.70	-17.31
Piromis eruca	SDF	30						2	2.76	3.74	10.13 ± 0.56	-17.53 ± 0.14
Pherusa plumosa	SDF	31						1	2.37	3.49	8.79	-17.98
Lysippe labiata	SDF	32						1	2.60	5.87	9.57	-19.97
Terebellides stroemii	SDF	33						3	2.88	5.01	10.54 ± 0.19	-18.95 ± 0.27
Lanice conchilega	SF	34	1	2.24	5.11	8.36	-18.67					
Pista cristata	SDF	35						2	3.24	4.67	11.74 ± 0.06	-18.56 ± 0.20
Amaeana trilobata	SDF	36	1	3.12	4.17	11.33	-18.28					
Lagis koreni	SSDF	37	2	2.71	4.24	9.94 ± 0.21	-17.81 ± 0.83					
Sabellidae sp.	SF	38	1	2.46	4.13	9.11	-18.92	1	2.04	4.75	7.67	-19.25
Euchone rubrocincta	SF	39	1	2.47	4.63	9.14	-19.25					
Demonax brachychona	SF	40	1	2.25	5.08	8.40	-20.14					
Sabellaria spinulosa	SF	41	1	2.08	4.47	7.80	-18.58	2	2.44	4.05	9.02	-19.36
Hydroides elegans	SF	42	1	2.23	4.04	8.31	-19.07					
Orbinia cuvierii	SSDF	43	1	3.55	4.02	12.80	-16.85	3	3.57	3.71	12.86 ± 0.81	-18.01 ± 0.29
Owenia fusiformis	SDF	44	3	2.27	4.64	8.44 ± 1.04	-18.38 ± 0.59					
Aricidea (Aricidea) pseudoarticulata	SDF	45						1	3.34	4.07	12.08	-18.55
Scalibregma inflatum	SDF	46	2	2.26	4.22	8.43 ± 0.60	-18.24 ± 0.24					
Gastropods												
Scaphander lignarius	SSDF	47	1	3.02	4.17	10.99	-15.83					
Crepidula fornicata	SF	48	3	2.02	3.62	7.60 ± 0.08	-18.48 ± 0.07	3	2.19	3.83	8.17 ± 0.14	-17.12 ± 0.48
Euspira pulchella	C-O	49	2	2.65	3.69	9.74 ± 0.29	-16.28 ± 0.07	1	2.53	3.77	9.32	-16.81
Buccinum undatum	C-O	50	1	3.15	3.26	11.45	-16.00	2	3.22	3.47	11.68 ± 1.02	-15.47 ± 0.96

Turritella communis	SF	51	2	1.96	4.07	7.41 ± 0.70	-17.30 ± 0.47	1	2.01	3.42	7.57	-16.57
Gibbula sp.	G	52	3	2.55	3.58	9.40 ± 0.98	-17.27 ± 0.68					
Trivia monacha	C-O	53	1	2.75	4.07	10.08	-18.49					
Philine aperta	C-O	54	1	2.65	4.00	9.74	-13.98					
Geitodoris planata	G	55	2	3.04	4.82	11.06 ± 0.33	-11.83 ± 0.90	1	2.93	5.02	10.71	-11.64
Bivalves												
Nucula nitidosa	SF	56	4	2.16	3.64	8.06 ± 0.35	-17.29 ± 0.12	2	2.14	3.49	8.02 ± 0.04	-16.91 ± 0.05
Corbula gibba	SF	57						1	1.97	4.85	7.43	-19.19
Polititapes virgineus	SF	58						6	2.38	3.83	8.84 ± 0.26	-16.83 ± 0.33
Timoclea ovata	SF	59						1	1.67	3.62	6.40	-17.98
Chamelea striatula	SF	60	1	2.15	3.69	8.03	-17.38					
Dosinia lupinus	SF	61	3	2.32	4.59	8.60 ± 0.46	-17.43 ± 0.62	1	2.23	4.61	8.32	-18.38
Abra alba	SF	62	3	2.23	3.94	8.33 ± 0.62	-17.61 ± 0.20					
Phaxas pellucidus	SF	63	2	1.82	4.05	6.93 ± 0.54	-18.35 ± 0.01					
Lyonsia norwegica	SF	64						1	2.02	3.92	7.60	-18.87
Aequipecten opercularis	SF	65	9	2.20	3.44	8.20 ± 0.36	-17.36 ± 0.46	9	2.22	3.30	8.27 ± 0.58	-17.36 ± 0.30
Pecten maximus	SF	66						7	2.53	3.44	9.33 ± 0.37	-16.26 ± 0.30
Anomia ephippium	SF	67						1	1.85	4.07	7.02	-18.42
Antalis novemcostata	SDF	68	1	3.04	3.81	11.08	-17.69					
Crustaceans												
Ampelisca brevicornis	SF	69	1	2.00	4.84	7.54	-18.11					
Ampelisca spinifer	SF	70	1	2.27	5.56	8.44	-19.61					
Ampelisca spinipes	SF	71	2	1.90	7.94	7.19 ± 0.64	-20.91 ± 0.66	3	1.90	8.36	7.20 ± 1.33	-20.17 ± 0.45
Ampelisca typica	SF	72						1	2.01	5.60	7.55	-20.43
Haploops nirae	SF	73						3	2.00	6.83	7.53 ± 0.15	-19.74 ± 0.67
Pandalina brevirostris	C-O	74						3	3.41	3.23	12.34 ± 0.59	-17.33 ± 0.19
Pontophilus spinosus	C-O	75						2	3.69	3.12	13.29 ± 0.20	-16.28 ± 0.57
Paguroidea spp.	SF	76						1	2.29	7.75	8.53	-20.22
Pagurus prideaux	C-O	77						3	3.32	3.31	12.02 ± 0.25	-16.03 ± 0.11
Galathea intermedia	SF	78						1	2.34	6.39	8.70	-20.71
Inachus dorsettensis	C-O	79						3	3.32	3.14	12.03 ± 0.45	-16.47 ± 0.12
Macropodia rostrata	C-O	80						1	2.46	8.64	9.09	-19.19
Atelecyclus rotundatus	C-O	81						1	3.12	3.26	11.33	-16.55
Liocarcinus navigator	C-O	82						1	3.41	3.31	12.33	-16.59
Liocarcinus pusillus	C-O	83						3	3.35	3.24	12.13 ± 0.09	-17.00 ± 0.20
Xantho pilipes	C-O	84						3	3.18	3.46	11.56 ± 0.19	-16.93 ± 0.26
Echinoderms												
Luidia ciliaris	C-O	85	1	3.74	3.93	13.45	-14.41	1	4.19	3.74	14.99	-14.26
Marthasterias glacialis	C-O	86	2	3.59	3.97	12.92 ± 0.65	-14.79 ± 0.31	3	3.49	3.48	12.61 ± 0.35	-14.54 ± 0.03
Amphiura filiformis	SF	87	3	2.44	11.93	9.01 ± 0.54	-17.95 ± 0.33					
Psammechinus miliaris	G	88	1	2.68	17.67	9.86	-17.88					
Thyone fusus	SF	89	3	2.60	3.94	9.58 ± 0.75	-16.17 ± 0.86					
Leptopentacta elongata	SSDF	90	2	3.18	3.80	11.54 ± 0.26	-15.16 ± 0.29					
Sponges												
Sycon ciliatum	SF	91						1	1.97	16.96	7.43	-19.21
Suberites suberia	SF	92						1	2.25	5.04	8.39	-19.91

ARTICLE N°6

Using isotopic functional indices to reveal changes in the structure of marine benthic communities

Short title: **Isotopic Functional Indices for marine benthic communities**

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Abstract

Stable isotope ratio can generate isotopic space to be used as a proxy to represent an organism's or a community's trophic niche. Isotopic spaces (often $\delta^{13}C$ vs $\delta^{15}N$) have been used to quantitatively characterize community-wide trophic structures by investigating metrics describing the position of species with each other. However the relative contribution of species to the total biomass (or abundance) has never been considered. We suggest here several indices, drawing on similar approaches from biological and functional trait analyses, that can be used to describe community or habitat trophic structure providing abundances or biomass data are available. In the mean time, we applied those Isotopic Diversity Indices (IDI) to the comparison of two marine coastal benthic habitat with different structure, using an original and extensive set of data (the *Owenia fusiformis* muddy sand community and the *Haploops nirae* muddy community). In a 2D $\delta^{13}C$ - $\delta^{15}N$ isotopic space, we calculated 3 IFI and discussed (1) the Isotopic Functional Richness (IFR) as the convex-hull area of all the species above a certain density of biomass threshold composing the isotopic to quantify the biomass distribution relative to the food sources, (2) the Isotopic Functional Eveness (IFE) as a measure of the species and biomass packing and as a proxy of the redundancy and inter-individual competition and (3) the Isotopic Functional Divergence (IFD) as a measure of the spreading of the species representing most of the biomass and as an average degree of trophic diversity. From the knowledge we have of the functioning of the two habitat models, we showed that those metrics are relevant to accurately describe seasonal changes within a single community or differences between two community.

1. Introduction

Stables isotopes have become a common and often powerful tool to investigate trophic pathways in ecosystems as well as animal foraging behaviour or inter and intra-specific trophic competition (Fry, 2006). Beyond this original and now traditional use of stable isotopic tools, they have recently been suggested to be used as a proxy to help define the Hutchinson's ecological niche concept. Newsome et al. (2007) noticed that the stable isotope values of each organism interestingly gathered information relative to the use of the physical habitat and to the use of its resources, i.e. two crucial factors to define the ecological niche. In the mean time, Layman et al. (2007) noticed that stable isotopes have not been applied to quantitatively characterize the food web structure at a community-wide scale and suggested using metrics such as the convex-hull area occupied by species in a $\delta^{13}C$ - $\delta^{15}N$ biplot or the distance of centroid and the nearest neighbor distance to reflect the relative position of species to each other within the space – called the isotopic space – defined by the species isotopic signatures (e.g. in a $\delta^{13}C$ - $\delta^{15}N$ biplot). Those metrics were proven successful to detect for example effects of top-predator on food web structure in fragmented habitats (e.g. Layman et al., 2007b) and were interestingly suggested to be used a variable response to experiment testing the effect of biodiversity on ecosystem functions. However, all species have been considered as equals in isotopic spaces, while numerous investigations (for terrestrial or aquatic systems) showed that the biomass is unequally distributed among species and that species with the largest biomass are likely to have the largest impact on ecosystem functioning (Grime, 1998; Diaz and Cabido, 2001). Ultimately, one can easily imagine two very similar isotopic spaces representing the trophic web of two communities with the same number of species, but with drastic differences in biomass distribution: one with most of the biomass represented by the primary consumer and a decreasing contribution to higher trophic levels and one – for example polluted (e.g. in Woodward and Hildrew 2002) – with bottleneck effect and a larger biomass in top levels versus intermediate levels, and an increased turnover to compensate. As a result, all field-investigation using metrics solely based on isotope data – as metrics suggested by Bearhop et al., 2004, Cornwell et al., 2006 or Layman et al., 2007 – somehow disregarded energy flow and relative forces in species' trophic interactions (see for example Zambrano et al., 2010b).

To depict and quantify structural and ultimately functional characteristics of complex food webs, we suggest coupling metrics designed to assess functional diversity in ecosystem through biological trait analysis with isotopic spaces defined by organisms isotopic signatures in a δ-space. Indeed, abundances and more specifically biomasses (which are directly linked to the amount of energy assimilated by a species) have been used to provide relevant functional indices: several indices used in multivariate analyses such as FD var (Mason et al., 2005), FRO (Mouillot et al., 2005), the quadratic entropy (Botta-Dukát, 2005) and several indices proposed by Villéger et al. (2008) take into account the relative abundance (or biomass) of species. Those indices use organisms' biological traits as multiple spaces to define functional niches. In the mean time, efforts were made to use isotopic niche defined in an isotopic space as a proxy to quantify trophic niche (Newsome et al., 2007). The coupling between isotopic ratio and functional indices appears to be a promising challenge, leading functional ecology to new tools and indices to better assess ecosystem functioning.

In this study, we hence described new indices combining functional indices based on single biological trait (Masson et al. 2005) or transposed to multiple-traits approaches (Villeger et al., 2008) and community-wide isotopic indices suggested by Layman et al. (2007). We tested here those indices on a marine benthic ecosystem partly colonized by a gregarious tubiculous Ampeliscid engineer species, namely *Haploops nirae*, which forms dense tube mats in coastal ecosystems they colonized. The largest habitats engineered by this species are off South Brittany coast (e.g. the bay of Concarneau and the bay of Vilaine). Sonar mappings revealed a 5-fold increase in *Haploops nirae* habitat surface between 1963 (650 ha; Glémarec, 1969) and 2003 (3680 ha; Ehrhold et al., 2006) for the sole bay of Concarneau. *Haploops nirae* exhibits there dense populations, with average densities around 10 000 to 15 000 ind.m^{-2} (Rigolet et al., 2012) and appears today as the most abundant species of this bay. This extend of *Haploops nirae* in the bay of Concarneau – and in the whole South Brittany – raised several issues regarding major changes in food web structure and trophic functioning in the *Haploops* community. Effects of dense gregarious tubiculous populations on food webs structure are of primary importance in coastal humanly-driven systems. Yet, functional and easy-to-use indices are still lacking. Several studies have shown that dense populations of Ampeliscids constitute a major food source for higher-level consumers such as finfishes and marine mammals (Gallardo, 1962; Franz and Tanacredi, 1992; Highsmith and Coyle, 1992) and represent a major component of the secondary production in coastal ecosystems with production levels among the highest observed for benthic invertebrate communities (e.g. Carrasco and Arcos, 1984; Highsmith and Coyle, 1990; Franz and Tanacredi,1992). First investigations of *Haploops* population dynamics already reported a possible loss in benthic secondary production in colonized habitat as opposed to uncolonized surrounding soft-bottom habitats (Rigolet et al., 2012). Moreover, as evidenced for many tubicolous gregarious species, tube occurrences increase engineered habitat complexity, affect the local biodiversity but also modify the availability of resources for others species (Berkenbusch and Rowden, 2007). It is hence likely that dense Ampeliscids populations significantly affect trophic interactions and main trophic pathways in a food web, inducing changes in structural and functional characteristics of the food web of the ecosystems they have colonized. Building community-wide metrics that take into account both diversity and biomass could then be a promising facet to understand ecosystem functioning.

This investigation aims here at assessing seasonal changes in the trophic structure and trophic functioning associated with the *Haploops* community, as compared to an immediate surrounding soft-bottom community. We developed an original community-wide approach that combines stable isotopes ratio and species biomasses to quantify food webs structural characteristics.

2. Material and Methods

2. 1. Study Site

The Bay of Concarneau is situated in the northern part of the Bay of Biscay (South Brittany, France). This area is characterized by soft-bottom muddy substrates, spanning from muddy to muddy-sand bottoms, with a depth ranging from 15 to 35 m (Delanoë and Pinot, 1977). The bay is sheltered by a succession of rocky islets, and tidal currents are relatively weak (10 – 80 cm.s^{-1}), with a water circulation mainly influenced by winds (Tessier, 2006). Moreover, freshwater inflow and sediment supply are very low (Glémarec et al., 1986). The central part of the bay is composed of muddy sands and sandy muds distributed along an inshore-offshore gradient. These sediments are colonized and structured by the echinoderm *Owenia fusiformis* (hereafter the *Owenia* community) with associated species such as *Amphiura filiformis* or *Ampelisca spp.* which abundances vary with sand/mud ratio. A large portion of the bay (Fig. 58) is colonized by *Haploops nirae* (hereafter *Haploops* commuity), forming a discrete and habitat with dense a tube mat (ca. 10 000 tubes.m^{-2}) and a unique species assemblage (Rigolet et al., unpublished data).

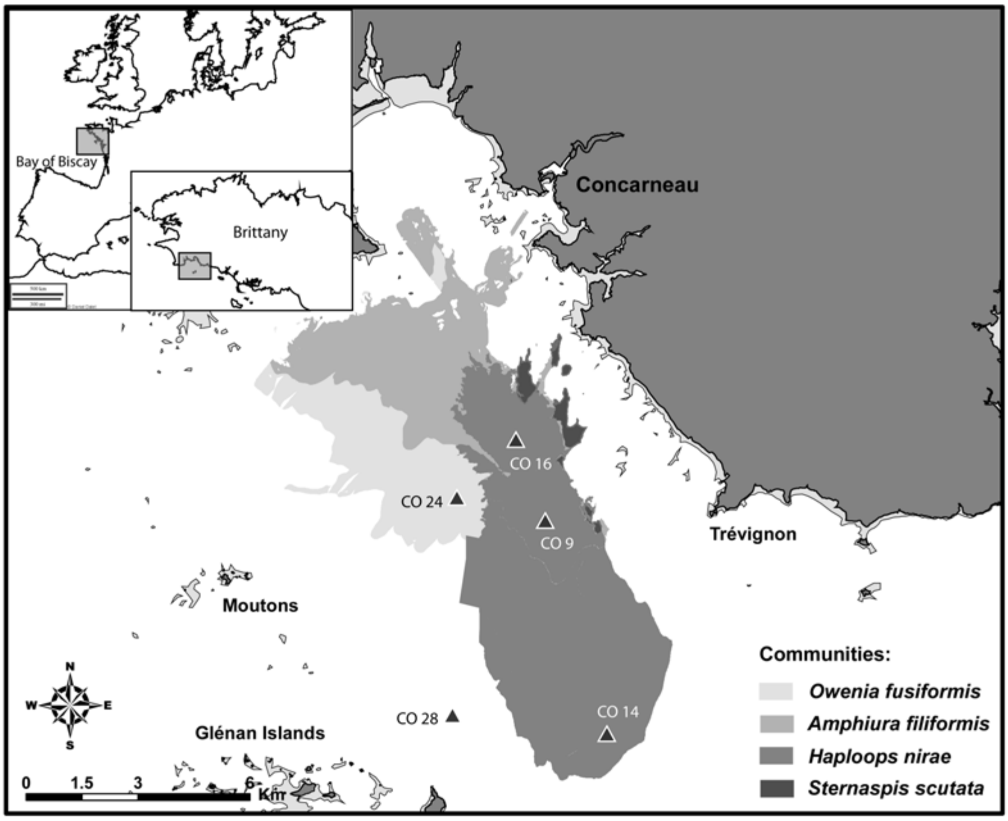

Figure 58 : Geographical distribution of the five stations seasonally sampled along the two transects studied (i.e. *Haploops* transect: CO16, CO9, CO14 and "*Owenia* transect": CO24, CO28) in the bay of Concarneau. Sampling stations are indicated by a triangle.

2. 2. Data Collection

From February 2010 to November 2010, 2 inshore-offshore transects with three stations each were sampled during each season (winter, spring, summer and autumn): stations CO16, CO9 and CO14 were sampled in the *Haploops* community, and stations CO24 and CO 28 were sampled in the *Owenia* community. The distance between the stations ranged from 2.5 km to 5.8 km (Fig. 58).

Faunal samples. To assess the composition of the macrofauna (between 1 and 10 mm in size), the five stations were sampled at each season using a 0.1 m² Van Veen grab (3 replicates per station). Samples were sieved on a 1 mm circular mesh-size screen and fixed with a 5% buffered formalin solution. In the laboratory, samples were rinced, sorted and the macrofauna was identified to the lowest taxonomic level (i.e. generally at the species level) and counted. The biomass of each macrofauna species with a density greater than 20 individuals.m-^{2} was estimated (i.e. more than 2 individuals per grab samples). The biomass of the large species (disregarding their abundances) (e.g. *Aphrodita aculeata* and *Thyone fusus*) was also estimated. Biomass of each taxa was measured by weight loss after combustion at 450°C for 6 hours (ash-free dry weight). Since organisms were preserved in formalin, a correction factor of 1.2 was applied as suggested by Brey (1986) to compensate the weight loss caused by the preservative. Quantitative estimates of over-dispersed megafauna species densities were made with a modified benthic trawl (called 'string', width = 3 meters) over a 1150 m transect (sampled area = ca. 3400 m^2) (Desaunay et al., 2006a). Megafaunal organisms were sorted on board, identified to species level, counted and weighted (wet weight).

Specific weight-to-weight conversion factors were used to compare megafauna wet-weight and macrofauna dry-weigths (Ricciardi and Bourget, 1998) and all biomasses were then converted to wet-weight. To homogenize the data, abundances and biomasses of macrofauna and megafauna species were converted to units per m^2.

Isotopic analysis. To investigate the trophic structure associated with each community, macrofaunal and megafaunal organisms were collected for all seasons. The organisms collected from grab and trawl samples were carefully sorted on board and immediately kept frozen (-24°C on board and -80°C afterwards). In the laboratory, organisms were identified and prepared for isotopic analyses. At least three organisms were analyzed for each species on each habitat and each season. Juveniles or damaged individuals were excluded and 3 adult individuals were randomly selected. For very small species, several individuals were pooled to reach the minimum dry weight requested for stable isotope analyses. Isotopic analyses were performed on muscle tissue samples for megafauna or large macrofauna organisms but the whole-body was used for small macrofauna species (i.e. crustaceans and polychaetes). In that case, a special care was paid to empty the digestive tractus. All samples were rinsed with Milli-Q water and freeze-dried. Samples of species containing calcium carbonates (i.e. crustaceans and echinoderms) were spit and a subsample was acidified (10% HCl) to remove any inorganic carbonates. Nitrogen signatures were obtained from untreated subsamples, as effect of acid on ^{15}N content is uncertain . Each dried sample was ground to a homogeneous powder and 1 mg was weighed in tin capsules for isotopic analyses. The isotopic composition of carbon (δ^{13}C) and nitrogen (δ^{15}N) were then measured with a stable isotope ratio mass spectrometer Finnigan MAT Delta Plus, operating in continuous-flow method coupled to an elemental analyser Carlo Erba NC2500 (Cornell University, Stable Isotope Laboratory, New York). Isotopic ratios for carbon and nitrogen were expressed using the standard δ notation according to the following equation:

$$\delta X = ((R_{sample}/R_{reference}) - 1) \times 1000 \text{ (‰)}$$

where X= ^{13}C (carbon) or ^{15}N (nitrogen) and R= $^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for nitrogen. The reference for carbon was Vienna Pee Dee Belemnite (VPDB, $\delta^{13}C$=0 ‰) and for nitrogen was atmospheric nitrogen ($\delta^{15}N$=0‰). The analytical precision was 0.2 ‰ for both nitrogen and carbon.

2. 3. Data Analysis

Food web structures and trophic diversity. To quantitatively characterize the trophic structure associated with the two communities sampled, we first used the 5 quantitative metrics suggested by Layman et al. (2007). Based on stable isotope biplots ($\delta^{13}C$ *vs* $\delta^{15}N$), Layman et al. (2007) indices provided community-wide metrics to quantify important aspects of the trophic structure, such as:

(1) the $\delta^{15}N$ range (NR), which is the distance between the two species with the most enriched and the most depleted $\delta^{15}N$ values. The NR gives information on the length of the food chain and on the diversity of trophic levels;

(2) $\delta^{13}C$ range (CR), which is the distance between the two species with the most enriched and the most depleted $\delta^{13}C$ values. The CR gives information on the diversity in food sources at the base of the food web;

(3) the Total Area (TA), which corresponds to the convex-hull area encompassed by all species in $\delta^{13}C$ *vs* $\delta^{15}N$ biplot space (Cornwell et al., 2006). It is a representation of the total extent of trophic diversity within a food web (Layman et al., 2007);

(4) the mean Distance of each species isotopic signature to Centroid (CD), where the centroid the mean $\delta^{13}C$ and $\delta^{15}N$ value for all species in the food web. It provides a measure of the degree of feeding behaviour and strategy (diet diversity);

(5) the mean Nearest Neighbor Distance (NND), which is the mean distance of each species to each species' nearest neighbour in the $\delta^{13}C$ - $\delta^{15}N$ bi-plot space. It provides a measure of the species packing and illustrates trophic redundancy.

While Layman et al. (2007) indices are very useful to quantify the structure of a food web, they consider each species of the community as similar contributors and do not take into account the biomass of the species, yet an essential component of the trophic functioning. We therefore used 3 functional diversity indices described by Villéger et al. (2008) to incorporate the biomass component in the characterization of communities' trophic structure. These indices were created to measure several facets of the functional diversity of a community defined by Mason et al. (2005): the functional richness, the functional evenness and the functional divergence. In this study, we applied these multidimensional functional diversity indices to isotopic data, re-scaled in a two-dimensional isotopic δ-space (^{13}C and ^{15}N in δ-space). We thus consider here all the isotopic signatures of species from a community plotted in the δ-space as a proxy of the trophic niche in a 2D space (Newsome et al., 2007). The position of a species in a δ-space is the result from its inter- and intra-specific trophic relationships as well as its foraging behaviour and morphological characteristic. The relative importance of each species in the food web was quantified using the biomass rather than number of individuals, since biomass is directly related to metabolism and secondary production, and thus more relevant to proxy the functional impact of an individual species within an ecosystem (Grime 1998). Three new isotopic functional indices (IFI) were then calculated in this study. IFI are graphically represented in Fig. 59 and described as follow:

(1) The Isotopic Functional Richness (IFR) index corresponds to the amount of the functional space occupied by the community (Fig. 59). This index corresponds to the TA index in Layman et al. (2007) in that it uses the existing convex hull area index (Cornwell et al., 2006) but only consider species with a significant biomass threshold. It does not however weight each species' contribution with its biomass or abundance. In that perspective, it is similar to the functional richness index (FRic) described in Villeger et al. (2008), but in a δ-space. As a result IFR describes the extend of the isotopic (i.e. trophic) niche as used by species which actually significantly contributes to the production of the system;

(2) The Isotopic Functional Evenness (IFE) index is a proxy of the regularity in biomass (or abundance) in the δ-space. IFE is close to the functional evenness index in a biological trait functional space (FEve) (Mason et al., 2003; 2005). It is based on the minimum spanning tree which links all the species in the functional space with the minimum of branch lengths (Villéger et al., 2008). It takes into account both the regularity of space between species and the evenness in the distribution of abundances (or biomasses) of species. This index ranges from 0 to 1 (1 = species regularly distributed), indicating a level of fullness of the δ-space by biomasses (or abundances). IFE provides information whether

some parts of the trophic niche space are underutilized and quantifies if the biomass is evenly distributed in the isotopic space or if most of the biomass is packed in a portion of the δ-space.

(3) The Isotopic Functional Divergence (IFD) quantifies how species biomasses (or abundances) diverge from the center of gravity of the δ-space. Apart from the change in space, IFD is similar to FDiv index (Villéger et al., 2008). This index ranges from 0 to 1. A low value of FDiv means that the species with the largest biomass (or the most abundant species) are close to the center of gravity relative to species with a small biomass (or with little abundances). And conversely for IFD = 1. A high value of IFD reflects therefore a trophic specialisation of species with high biomass (or abundant species), hence corresponding to a smaller level of trophic redundancy in the whole community. In that perspective, IFD is close to the distance of centroid index (CD) suggested by Layman et al. (2007).

Comparisons of Layman et al. (2008) and IFI indices were performed using the statistical software R 2.11.1 (R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org).

As pointed out in a comment of the community-wide metrics suggested by Layman et al. (2007), Hoeinghaus and Zeug (2008) showed that these indices are very sensitive to the number of species sampled in the community. To compare the two communities (e.g. *Owenia* vs. *Haploops* community), all metrics were calculated using a bootstrap procedure. This method provides an estimate of each index for each community by randomising 1000 times an increasing number of species (from 3 to the total number of species). This method interestingly provides a mean and a standard deviation for each index computed and therefore not only allows index comparisons for a similar number of species but also allows statistical testing. Bootstrap calculations were performed using the statistical software R (http://www.R-project.org).

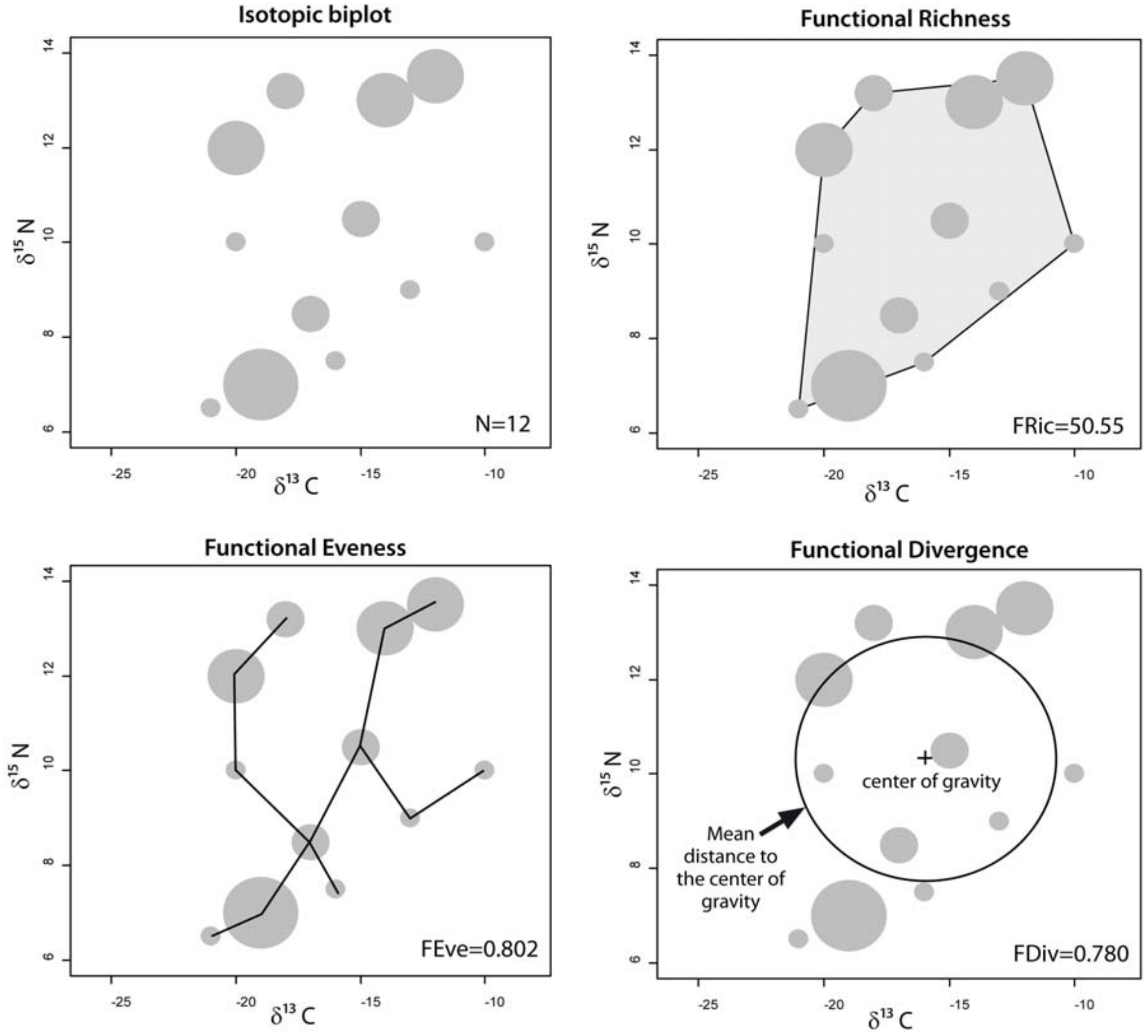

Figure 59 : Geometrical representation of functional indices proposed by Villéger et al. (2008) in a two-dimensional isotopic space ($\delta^{13}C$-$\delta^{15}N$). A theoretical food web of 12 species is considered here where species are plotted according to their isotopic signatures with circle areas of species proportional to their abundances or biomasses. The Functional Richness (FRich) corresponds to the extent of the isotopic space occupied by the community. The Functional Evenness (FEve) corresponds to the regularity in the distribution of species abundances or biomasses in the isotopic space and Functional Divergence (FDiv) quantifies how species abundances (or biomasses) diverge from the center of gravity of the isotopic space. Note that the Functional Richness as well as the coordinates of the center of gravity are calculated without taking into account the relative abundance or biomass of species.

3. Results

Calculations of Isotopic Functional Indices. The δ-space ($\delta^{13}C$ *vs* $\delta^{15}N$ biplots) for the two community are represented for winter (Fig. 60), as well as spring, summer and autumn (Fig. 61) samplings. The Fig. 60 shows that the δ-space provided by the isotopic signatures of all the species sampled in each community can be overlapped to visually detect differences in the isotopic niche defined by the two communities. In winter, the extent of the two communities clearly overlaps, revealing a strong similarity in the way the trophic niche is used by the *Owenia* and *Haploops* communities. The Fig. 61 shows only minor changes between spring, summer and autumn, but a significant change in community overlap with the winter samples (Fig. 60). While the *Owenia* community seemed to exhibit a larger isotopic niche in winter, the δ-space revealed a smaller convex hull area for the other season compared to *Haploops* community. However, the number of species sampled in the *Owenia* community is smaller for summer and autumn, making comparisons difficult.

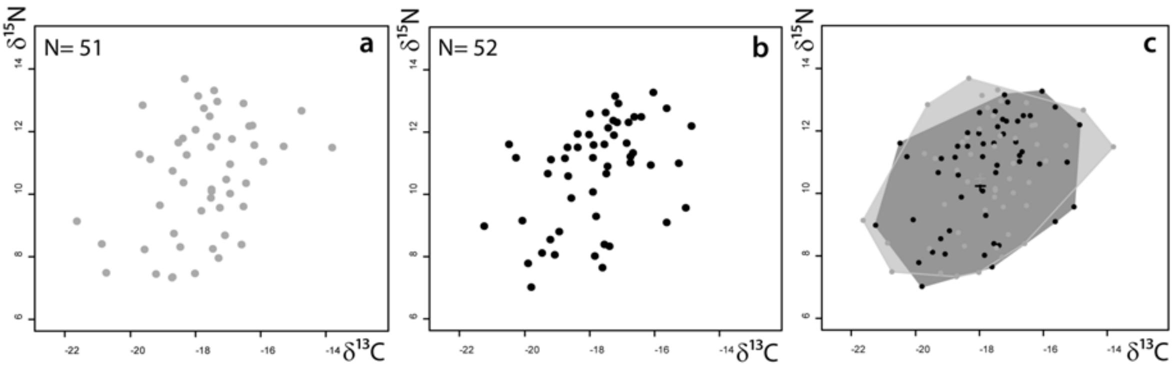

Figure 60 : Stable isotope bi-plots based on species collected in *Owenia* (a) and *Haploops* (b) communities in winter 2010. Overlap of the total extents of the two communities is represented in c where convex hull volumes are filled respectively in light grey and dark grey for *Owenia* and *Haploops* communities. Each point of the graphic represents the mean value of 1 to 3 species and error bars around the mean were removed for better clarity. N corresponds to the number of species isotopically analysed.

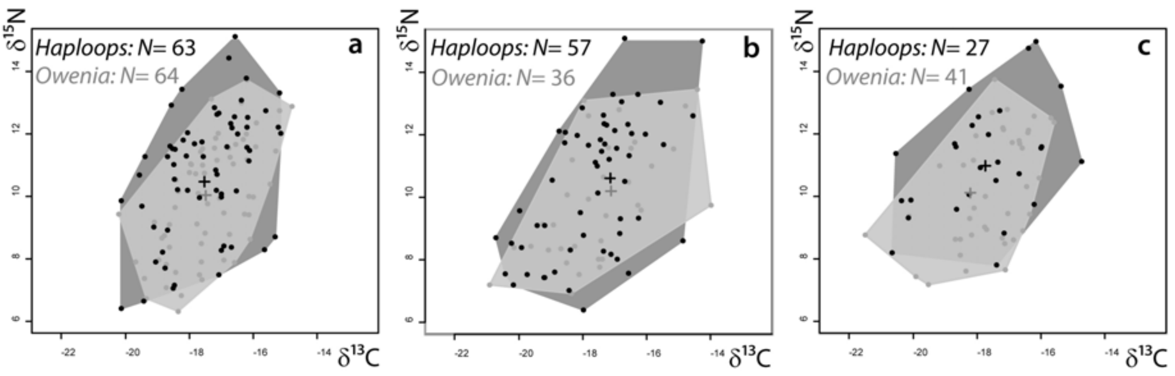

Figure 61 : Overlaps of the total extents of the two communities (*Owenia* and *Haploops*) in spring (a), summer (b) and autumn 2010 (c). Isotopic signatures of species are plotted respectively in grey and black in *Owenia* and *Haploops* communities. Convex hull volumes are filled respectively in light grey and dark grey for *Owenia* and *Haploops* communities. Each point of the graphic represents the mean value of 1 to 3 species and error bars around the mean were removed for better clarity. N corresponds to the number of species isotopically analysed.

Bootstrap results (Fig. 62) showed that for the same sampling effort (i.e. the same number of species sampled) in the two communities, significant differences in community-wide metrics occurred between *Owenia* and *Haploops* communities. Except for winter, the δ^{15}N range (NR) is higher for the food web associated with the *Haploops* community, supporting the graphic observations from the isotopic biplots (Fig. 61). As for the δ^{13}C range (CR), bootstraps results showed overall higher values for the food web associated with the *Owenia* community, except in summer (not significantly different). Finally, the Total Area (TA) showed no consistent pattern across the year. While TA was higher for the *Haploops* community in spring and summer, it was not significantly different in autumn and lower than TA for the *Owenia* community in winter.

The Fig. 63 graphically illustrates changes induced by the consideration of the species biomass in the food web representation. Unlike traditional isotopic biplots, the biomass data immediately highlights major components of the food web and of the isotopic space. From 4 to 5 species accounted for 78.3 to 85.0 % of the total biomass in the *Owenia* community (Fig. 63 and 64): the brittle star *Amphiura filiformis*, the large bivalve *Dosinia lupinus* as well as the holothurian *Thyone fusus* and the sipunculid *Aspidosiphon muelleri* constituted the major part of the biomass in this community for all seasons. *Aphrodita aculeata*, *Chamelea striatula* and *Leptopentacta elongata* represented a significant proportion of the biomass of the community only for some season. As for the *Haploops* community, 3 species (the tubiculous amphipod *Haploops nirae*, the bivalve *Polititapes virgineus* and *Aspidosiphon muelleri*) consistently accounted for a large part of the biomass of the community (between 59.3 and 76.0 % of the total biomass). The predator polychaete *Glycera* sp. and the brittle star *Ophiura albida* accounted for a large part of the biomass in the *Haploops* community for some season (spring and autumn). The Fig. 64 visually provides qualitative information relative to the distribution of the biomass along the food chain. For example, it shows that the major components of the biomass are more scattered in the δ-space for the *Haploops* community, with species at the top (high $\delta^{15}N$) or at the bottom (low $\delta^{15}N$) of the food chain, or that species representing the largest part of the biomass in the *Owenia* community exhibit low and close isotopic values (suspension-feeders), particularly in winter, summer and autumn.

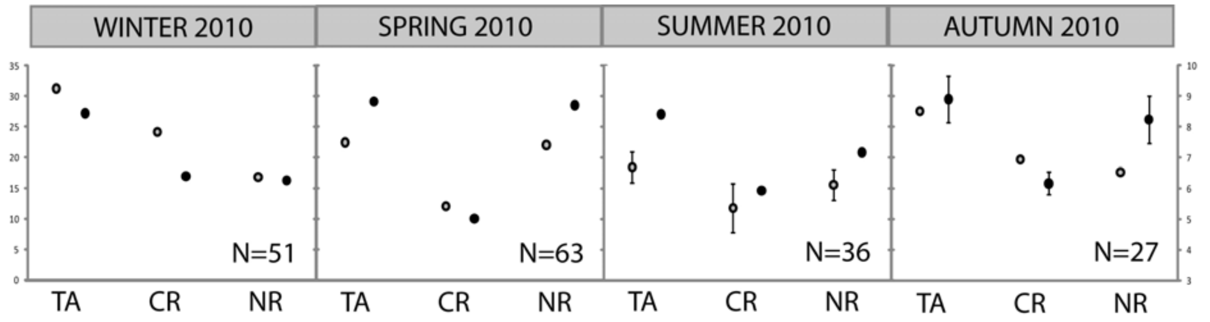

Figure 62 : Results of bootstrap calculations (100 randomizations) made on Layman indices (TA, CR and NR). Results are indicated for the same number of species (N) sampled in the two communities. Values for the *Owenia* community are represented by grey dots and with black dots for the *Haploops* community.

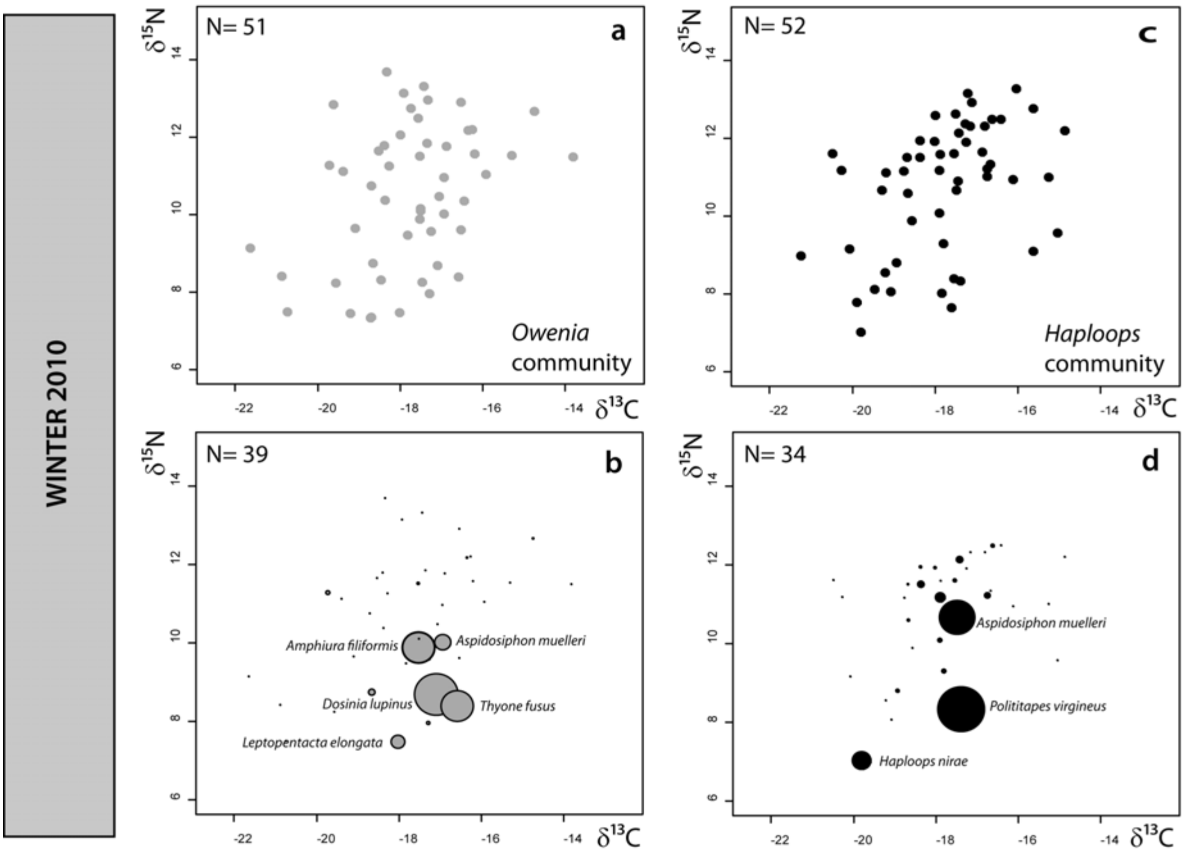

Figure 63 : Stable isotope bi-plots based on species collected in *Owenia* (a) and *Haploops* (c) communities in winter 2010. Isotopic signatures of species are respectively represented by grey dots and black dots in *Owenia* and *Haploops* communities. Graphics b and d correspond to the two graphics illustrated above (a and c) with circle areas of species plot proportionally to their biomasses. N corresponds to the number of species isotopically analysed.

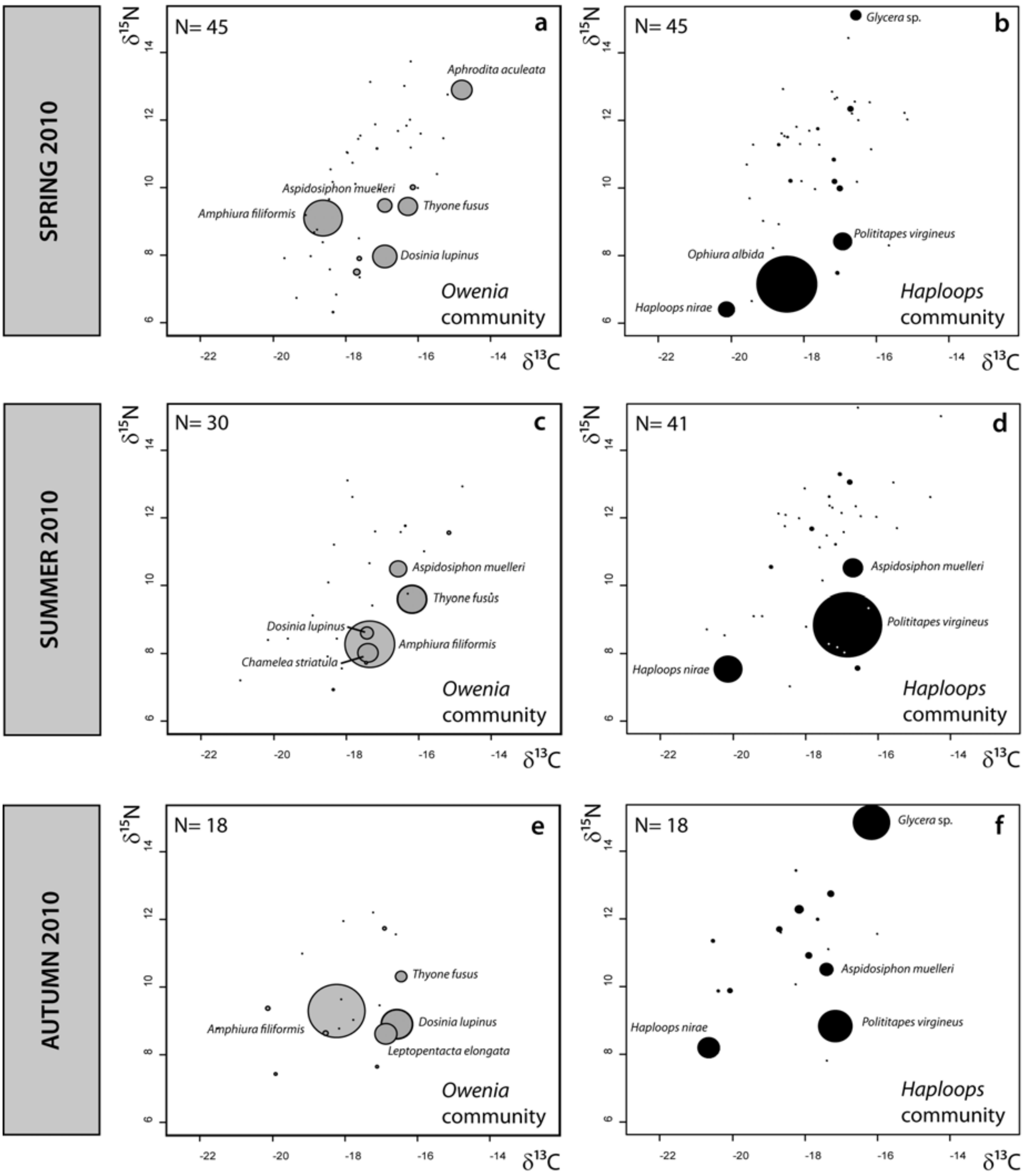

Figure 64 : Stable isotope bi-plots based on species collected in *Owenia* (a) and *Haploops* (c) communities in spring, summer and autumn 2010. Isotopic signatures of species are respectively represented by grey and black circles in *Owenia* and *Haploops* communities where circle areas of species are proportional to their biomasses. N corresponds to the number of species isotopically analysed.

Isotopic Functional Indices (IFI) were then calculated incorporating species with a significant contribution to the total biomass (see the method section). Modelled accumulation curves from bootstrap results for IFI (i.e. IFR, IFE and IFD indices) for the winter season are plotted in Fig. 65. For the same number of species (i.e. N = 34 species), the Isotopic Functional Richness (IFR) was significantly higher in the Owenia community but Isotopic Functional Eveness (IFE) and Isotopic Functional Divergence (IFD) did not significantly differ. Bootstrap results of IFI for all seasons are summarized in Fig. 66: IFR was significantly higher for the *Haploops* community food web in spring and autumn but in contrast higher for the *Owenia* community food web in winter. No significant difference was detected in summer. The Isotopic Functional Eveness (IFE) showed very low values in winter and spring for both communities but remained higher for *Owenia* community for summer and autumn, indicating that biomasses are more regularly distributed in the isotopic space in the *Owenia* community. Finally, the Isotopic Functional Divergence (IFD) was significantly higher for the *Haploops* community food web, except in winter were values did not significantly differ. High values of IFD (up to 0.85) in the *Haploops* community suggested that species that accounted for the largest part of the biomass in the *Haploops* community exhibited isotopic signatures more distant from the center of gravity of the food web than in the *Owenia* community.

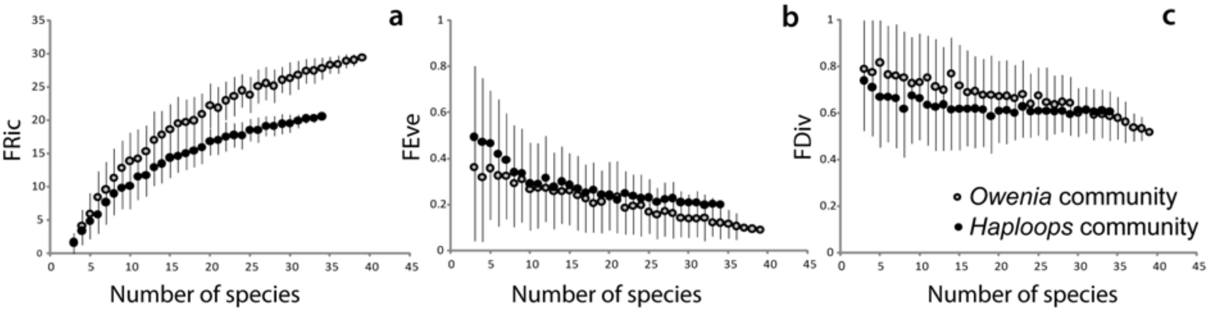

Figure 65 : Results of bootstrap calculations (100 randomizations) made on functional indices proposed by Villéger et al. (2008) (FRich, FEve and FDiv) for the *Owenia* (grey dots) and the *Haploops* (black dots) communities.

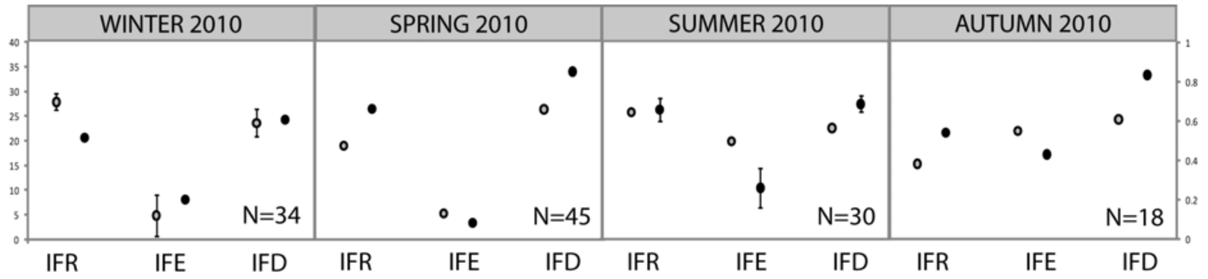

Figure 66 : Results of bootstrap calculations (100 randomizations) made on functional indices proposed by Villéger et al. (2008) (IFR, IFE and IFD) for the *Owenia* (grey dots) and the *Haploops* (black dots) communities. Results are indicated for the same number of species (N) sampled in the two communities.

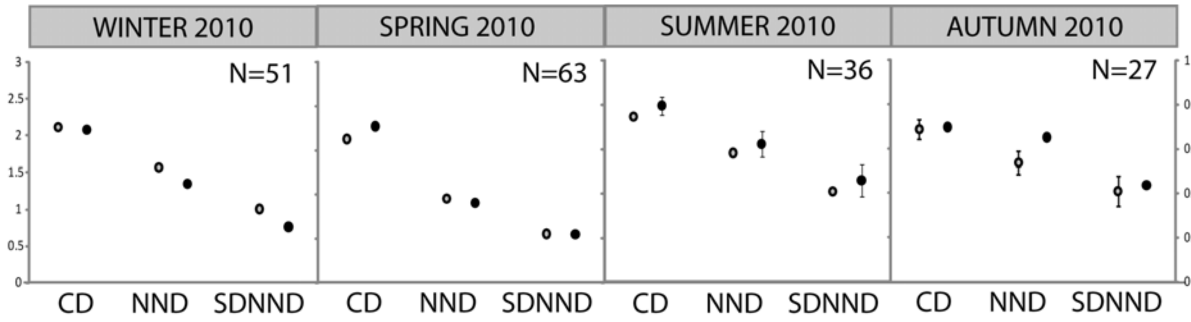

Figure 67 : Results of bootstrap calculations (100 randomizations) made on Layman indices (CD, NND and SDNND). Results are indicated for the same number of species (N) sampled in the two communities. Values for the *Owenia* community are represented by grey dots and with black dots for the *Haploops* community.

4. Discussion

We suggest here a similar approach where all species are weighted by its biomass we calculated new functional indices, called Isotopic Functional Indices. Such indices are often very sentitive to the sampling effort and ultimately to a difference in species number (Hoeinghaus and Zeug, 2008). We therefore used a bootstrap approach to model our results and compare our two habitats for the same number of species. This allowed us to provide a mean value and an error estimate to test for differences between the two habitat models.

Effect of an Engineer Species on Isotopic Functional Richness (IFR)

We reviewed functional indices designed to explore functional diversity in ecosystem, using a morphological and biological traits approach but considering species biomass (Villeger et al., 2008). As suggested by Layman et al. (2007), the convex-hull area TA (called functional richness in Villeger et al., 2008) provides an overall estimate of the isotopic space encompassed by all species in the $\delta^{13}C – \delta^{15}N$ biplot space for a specific habitat but also provides a proxy of the trophic niche occupied by the whole community colonizing this same habitat. Even though the isotopic functional richness (IFR) does not specifically account for species biomass, we calculated IFR for the whole community and for the species representing 80% of the total biomass.

Our habitat model revealed that TA and IFR did not showed exact similar pattern, whether we consider all the species (TA) or all the species above a density threshold (20 ind.m^{-2}) and hence a minimum contribution to the community total biomass (IFR). We showed that over the year, the habitat colonized by the tubiculous amphipod engineer species *Haploops nirae* had a larger trophic niche than for the surrounding *Owenia fusiformis* habitat, except in winter. This is due to more diverse potential food sources associated with *Haploops* habitats, especially epibionts colonizing the amphipod tubes themselves and contributing to the diet of micro- and macro-grazers (Rigolet et al. in prep) but also to an intense bioturbating and filtering activity of this engineer species (Rigolet et al., 2011) allowing increased microphytobenthic production. This does not explain the TA and IFR results for the winter period. When considering the species contributing to 80% of the total biomass (Fig. 68), IFR revealed a much higher discrepancy between the *Haploops* and the *Owenia* habitats, even for the winter season. We found this result more relevant as it actually represent the extend of the core of the food web structure and revealed differences that may have been smothered by a pool of diverse associated species with minimal role in terms of organic matter fluxes. This result highlights a higher contribution of macrofauna predator (large polychaete species *Glycera* sp.) associated with *Haploops* habitat but also larger differences in diet between suspension- and deposit-feeding species in *Haploops* habitats. Conversely, in *Owenia* habitat, 80% of the biomass is distributed between suspension-feeders competing for the same food sources and showing similar isotopic signatures (Fig. 64). As a result this approach revealed that the biomass is more evenly distributed on the $\delta^{13}C$ axis (supported by a more diverse pool of food sources) but also more evenly distributed on the $\delta^{15}N$ axis with a higher contribution of top macrofauna predators. It was showed that high density of amphipods host larger abundances (and biomass) of macrofauna predators such as polychaetes or large nemerteans (e.g. McDermott, 1993).

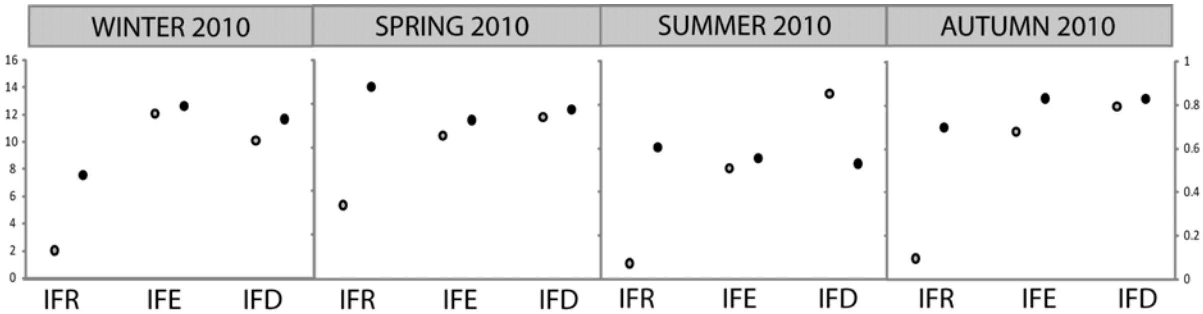

Figure 68 : Results of bootstrap calculations (100 randomizations) made on functional indices proposed by Villéger et al. (2008) (IFR, IFE and IFD) when only species that account for 80% of the total biomass in the *Owenia* (grey dots) and the *Haploops* (black dots) communities were considered

Effect of an Engineer Species on Isotopic Functional Eveness (IFE) and Divergence (IFD)

Isotopic Functional Eveness (IFE) and Isotopic Functional Divergence (IFD) are two metrics where species isotopic signatures are weighted by their biomass, as recommended by Grime (1998) but since then evidenced as of primary importance for functional metrics in general (Mason et al., 2005; Villeger et al., 2008). Mason et al. (2005) developed the idea that the functional diversity can be investigated using three complementary components, i.e. the functional richness (as described above), the functional eveness and the functional divergence. Those metrics are calculated in a functional-trait space (Rosenfeld, 2002) where all the traits are representing one axis. Using a $\delta^{13}C – \delta^{15}N$ isotopic biplot space as a unique 2-dimentionnal space aims at combining several biological traits all related to the trophic niche, such as the foraging behaviour and feeding movements, the morphological characteristics of the feeding apparatus and the inter-species relationships relating to food competition such as the prey-predator relationships. The isotopic space can then be seen as a multi-dimensional space that contains what ecologists refer to as the trophic niche (Newsome et al., 2007).

The Layman et al. (2007) metrics CD (mean Centroid Distance) and NND (mean Nearest Neighbour Distance) shared the same philosophy and the same goals with the FDiv (Functional Divergence) and FEve (Functional Eveness) suggested by Masson et al. (2005) or Villeger et al. (2007), respectively. IFE (Isotopic Functional Eveness) and IFD (Isotopic Functional Divergence) are FEve and FDiv calculated in an isotopic space.

The metrics CD and IFD are measurements of species spacing in relation to the whole total space and are classically interpreted with the measurement of the evenness of species packing in an isotopic space or a multidimensional trait-space. From our habitat models, we showed that CD and IFD are telling relatively similar stories (fig. 67): CD is significantly higher for the *Haploops* habitat in Spring only but when considering also the biomass, IFD is significantly higher from spring to autumn. This revealed that the biomass is actually more distant from the center of gravity of the food web for the *Haploops* habitat than for the *Owenia* habitat and this is also true when considering the species representing 80% of the biomass. It means that a larger number of species and a higher proportion of the total biomass is produced outside the isotopic range of the main food source (i.e. food derived from open-sea phytoplankton). The results obtained for the species representing 80% of the biomass are supporting a larger utilisation of additional food sources other than phytoplankton-derived food, which primarily contributes to the suspension-feeders’ diet representing most of the biomass in *Owenia* habitat.

The metrics NND and IFE are measuring how regularly and evenly species or biological traits distributed are between each other. Low values indicate that species (at least some of them) are packed and/or that there is isotopic or functional redundancy between species. Estimates of NND and IFE from *Haploops* and *Owenia* habitats showed opposite and contradictory patterns: the overall density of species packing (NND) is slightly higher in winter for the *Owenia* habitat but the differences vanished in spring and summer but in autumn, the *Haploops* habitat had significantly higher NND value (and thus a lower density of species packing). IFE showed no significant differences in winter but revealed that when the nearest neighbour distance is weighted by the biomass, there was more biomass packing and trophic redundancy in the *Haploops* habitat. This result highlight how crucial are biomass data to describe food web functioning. Interestingly, when considering only the species representing 80% of the biomass, IFE metrics were lower for the *Owenia* habitat revealing that most of the biomass is actually occupying the same isotopic niche. This was due to a small group of species (i.e. the bivalves *Dosinia lupinus* and *Chamelea striatula* and the echinoderms *Amphiura filiformis*, *Thyone fusus* and *Leptopentacta elongata*) clearly feeding on sedimented organic matter and competing for the same food source.

Relevance of Isotopic Functional Indices

Incorporating biomass data into δ-spaces drastically affect how one can picture and quantify the food web structure. The biomass threshold above which species should be considered is still to be discussed as it deeply changes the results. Abundances data are common in benthic ecology investigations but biomass data are much scarce, mostly because they are very time consuming. We have chosen here two common habitat models to apply IFI: as in most coastal benthic habitat, most of the biomass is represented by a limited number of species and this investigation showed that if almost all the species are used to calculate IFI, the results would not necessarily differ from their equivalent metrics in an unweighted δ-space. We therefore recommend being selective in the abundance or biomass threshold and the use of abundances-biomass comparison (ABC) curves (Clarke, 1990) could be of significant help to draw a relevant threshold.

Those new Isotopic Diversity Indices (IFI: IFR, IFE and IFD) are derived from metrics which all meet the criteria and properties of sensitivity and independency for community wide metrics (Mason et al., 2003 ; Ricotta, 2005 ; Villeger et al., 2007) and are fully operational, providing abundances or biomass data are available to be explained in an isotopic space.

Unlike the biological-trait approach which needs (1) a relevant *a priori* selection of traits and (2) a decent number of measures traits (Petchey and Gaston, 2002), the $\delta^{13}C$ – $\delta^{15}N$ isotopic space integrates all biological traits related to food capture, foraging behaviour and inter-species / inter-individual relationships in a single 2D-space. However, this approach still suffer from two pitfalls. Hoeinghaus and Zeug (2008) cristism of Layman et al. (2007) still partly apply to IFI, as those metrics are sensible to the number of species (hence the boostrap procedures to cope with different number of species) and sensitive to the changes in potential food sources supporting the habitat models. The two investigated habitats are nearby habitats sharing the same potential autochthonous and allochtonous food sources. This is a prerequisite to compare IFI ranges. To cope with this issue, hampering comparisons of two isotopic δ-spaces, Newsome et al. (2007) suggested to use a p-space, with all organisms' isotopic signatures transformed into a space combining the contributions of all potential food sources to each consumer's diet. While this idea offers broader comparison between different systems, output results of mixing models are often associated with too many uncertainties to allow such transformations.

Conclusions

Our Isotopic Functional Indices enables investigators to build relevant community-wide metrics from extensive applications of stable isotope ratios by ecologists. They offer new perspectives for the use of δ-spaces, by focusing on the distribution of the biomass within the food web, and hence the main organic matter fluxes. We showed that IFI can be used to detect the effects of a colonization of an engineer species on benthic habitat trophic structure and we can easily imagine to apply such metrics to detect changes in food web structure in impacted or polluted habitats, or after introduction of an invasive species.

Conclusion générale et perspectives

Les vasières à *Haploops,* dont les plus importantes sur le littoral français sont localisées en baie de Concarneau et en baie de Vilaine, constituent un habitat marin côtier particulièrement original. Depuis leur description et leur cartographie par Glémarec (1969), les études ciblées sur la structure et la dynamique du peuplement à *Haploops* ont été rares ; seuls Ménesguen (1980) en baie de Concarneau et Le Bris (1988) en baie de Vilaine ont étudié plus en détail ce peuplement particulier en termes de composition spécifique. Le rôle du peuplement à *Haploops* sur l'organisation de la biodiversité dans toute sa complexité et le fonctionnement écologique des baies côtières demeurait jusqu'alors largement méconnu. Ce projet de thèse avait pour objectif de déterminer le rôle fonctionnel des peuplements à *Haploops* de Bretagne Sud et leur valeur écologique, et de comprendre les conséquences qu'aurait une extension ou une disparition de l'espèce structurante *Haploops nirae* dans l'écosystème. Les résultats obtenus sur le site atelier de la baie de Concarneau couvrait plusieurs niveaux d'organisation du vivant, de la biologie de l'espèce jusqu'au rôle fonctionnel du peuplement au sein de l'écosystème qui l'abrite. Comprendre le rôle structurel et fonctionnel du peuplement à *Haploops* au sein des écosystèmes côtiers de Bretagne Sud est d'autant plus important que ce peuplement est en expansion dans cette région, soulevant le problème de l'incidence de la prolifération d'une espèce sur les fonctionnalités des milieux affectés.

Du rôle spécifique d'*Haploops nirae* au rôle fonctionnel du peuplement à *Haploops*

Au cours de la première partie de ma thèse, les principales caractéristiques biologiques d'*Haploops nirae* ont été appréhendées avec le souci de définir le potentiel de colonisation de l'espèce et de comprendre son rôle dans les flux de matière et d'énergie dans l'écosystème : la filtration du phytoplancton et la production secondaire. *Haploops nirae* est une espèce biannuelle, ce qui apparaît comme un caractère commun aux espèces du genre *Haploops* qui les différencie de celles du genre *Ampelisca*, et possède une fécondité moyenne comparable à celles des autres Ampeliscidés. D'autre part, son recrutement est sujet à d'importantes fluctuations interannuelles à une échelle locale. De telles caractéristiques du cycle de vie ne permettent vraisemblablement pas d'expliquer le succès récent de cette espèce sur les côtes de Bretagne Sud. A titre d'exemple, *Ampelisca abdita* qui forme des populations denses semblables à celles des *Haploops* en Bretagne Sud et qui est communément considérée comme une espèce opportuniste de par sa capacité à coloniser des sédiments récemment perturbés (comme après un dragage, e.g. Grassle and Grassle 1974), est une espèce bivoltine :

les recrutements dans la population se produisent plusieurs fois dans l'année et lui assurent *de facto* la capacité de coloniser de nouvelles zones.

Si l'analyse écophysiologique de l'alimentation de l'espèce a permis de confirmer le comportement suspensivore des *Haploops* (excepté Enequist, 1949), elle a surtout permis de quantifier le taux de filtration de l'espèce à 14,6 ± 0,4 $mL{\cdot}h^{-1}.ind^{-1}$ soit 25,2 ± 0,7 $L{\cdot}h^{-1}{\cdot}g^{-1}$. Bien que le comportement trophique des *Haploops* varie en fonction des conditions du milieu (i.e. concentration en nourriture, vitesse du courant, turbidité), un tel résultat soulève des questions quant à l'importance des *Haploops* au sein du réseau trophique et leur capacité potentielle à réguler la production primaire pélagique. Ainsi, alors qu'il est communément admis que les mollusques suspensivores sont en mesure de contrôler la biomasse phytoplanctonique de zones côtières (Cloern, 1982 ; Chauvaud et al., 2000), les taux de filtration normalisés calculés (25.2 ± 0.7 $L.h^{-1}.g^{-1}$ poids sec) pour *Haploops nirae* excèdent les valeurs rapportées dans la littérature pour l'huître creuse *Crassostrea gigas* (4.2 $L.h^{-1}.g^{-1}$) ou la crépidule *Crepidula fornicata* (0.76 $L.h^{-1}.g^{-1}$). La production secondaire d'*Haploops nirae*, estimée localement à 9,66 gPS m^{-2} y^{-1} s'est avérée être élevée pour une espèce biannuelle même si elle demeure en deçà des valeurs mesurées chez d'autres espèces d'Ampeliscidae telles que *Ampelisca macrocephala* et *Ampelisca abdita*. Par ailleurs, une comparaison de la valeur obtenue avec des estimations plus anciennes des espèces dominantes des principaux peuplements sablo-vaseux adjacents au peuplement à *Haploops* suggère que l'expansion des *Haploops* a eu un rôle neutre, voire négatif sur la production benthique de la baie de Concarneau.

Ainsi, si les caractéristiques biologiques de l'espèce (e.g. taux de filtration, production secondaire) en lien avec des densités et des biomasses très importantes suggèrent un rôle fonctionnel potentiellement important de l'espèce, seule une étude menée à l'échelle du peuplement peut permettre d'affiner cette impression.

Un autre rôle important des *Haploops* dans le fonctionnement des peuplements réside dans leur capacité, en tant qu'espèce ingénieure, à modifier physiquement leur habitat avec des conséquences sur la diversité structurelle et fonctionnelle de la macrofaune benthique. Les études comparées de la diversité des différents peuplements benthiques de la baie de Concarneau qui ont fait l'objet de la deuxième partie de mon travail révèlent le caractère unique et très original des fonds à *Haploops*. La modification des écoulements en couche limite benthique due à la présence des tubes (Friedrichs et al., 2000) se traduit dans un premier temps par un changement de la granulométrie du sédiment. Les tubes fonctionnent alors comme un piège à particules qui favorise la sédimentation de particules fines (i.e. forte augmentation de la teneur en vase) et un enrichissement du sédiment en matière organique de bonne qualité (faible C:N ratio) disponible pour la macrofaune benthique. Par ailleurs, la forte production de pelotes fécales par les *Haploops* contribue également à l'enrichissement du milieu.

Les modifications physiques induites par la création de champs denses de tubes se traduisent dans un premier temps par un profond changement des assemblages d'espèces de sorte qu'une biocénose très particulière se développe en lien avec les tubes d'*Haploops*. Le cortège d'espèces répertoriées au sein du peuplement à *Haploops* est très spécifique à cet habitat : en 2009 près d'un tiers des 250 espèces recensées dans les sédiments sablo-vaseux de la baie était présent uniquement sur les fonds à *Haploops*. Ceci tend à augmenter fortement le taux de renouvellement des espèces entre peuplements et donc la diversité béta. De plus, comme cela a été rapporté auparavant pour de nombreuses espèces ingénieures, la présence d'*Haploops* peut induire une augmentation de la richesse spécifique locale, principalement par l'augmentation de la complexité topographique de l'habitat et dans une moindre mesure par une augmentation des ressources disponibles pour la macrofaune associée. Outre le développement d'une faune diversifiée qui a bénéficié d'un environnement favorable au sein des vases à *Haploops*, des interactions négatives de type compétition sont susceptibles de se produire. Les densités extrêmement élevées de tubes exerçent alors un contrôle de l'abondance des autres espèces au sein du peuplement. Ainsi, les abondances de la macrofaune sont significativement plus faibles sur les fonds à *Haploops*.

Le cortège d'espèces associées au peuplement à *Haploops* en baie de Concarneau présente également la particularité d'être très homogène dans l'espace. Cette caractéristique est très certainement liée à la forte contrainte physique et structurante qu'exercent les tubes d'*Haploops* à des densités très élevées. Une telle homogénéité, bien qu'indicatrice d'une stabilité du peuplement, n'est pas nécessairement un signe de bonne santé des écosystèmes dans le cas de l'extension des vases à *Haploops* (passée et peut-être future). Si le développement du peuplement à *Haploops* a pu représenter un bénéfice en terme de diversité en augmentant la richesse spécifique à l'échelle de la baie de Concarneau, son expansion pourrait néanmoins se traduire dans le futur par une diminution de la diversité béta et une homogénéisation des fonds.

Alors que les modifications physiques de l'habitat par les *Haploops* ont des effets particulièrement importants sur la diversité spécifique et la composition des peuplements, l'originalité du peuplement d'un point de vue fonctionnel apparaît moins évidente, que celle-ci ait été abordée par l'analyse des traits biologiques des espèces (BTA) ou par l'estimation de la production secondaire des peuplements. Dans ce contexte, la production secondaire est vue comme un indicateur fonctionnel multi-facettes qui traduit tout à la fois le succès d'une espèce dans son environnement, la disponibilité des ressources pour les niveaux trophiques supérieurs et l'état écologique du peuplement. Bien que les différences dans la structuration des peuplements soient très marquées en présence ou non d'*Haploops*, leurs conséquences fonctionnelles sont dans l'ensemble faibles. L'analyse des traits biologiques des espèces (BTA) révèle uniquement au sein du peuplement à *Haploops* une légère diminution de la proportion des suspensivores de grande taille et une augmentation des carnivores mobiles de petite taille. Ces changements marginaux de la diversité fonctionnelle des traits biologiques ne peuvent être assimilés à un profond bouleversement du fonctionnement des habitats benthiques créé par la présence des *Haploops*. L'estimation de la production secondaire à l'échelle des principaux peuplements benthiques de la baie de Concarneau corrobore les résultats précédents. Le peuplement à *Haploops* apparaît être ni plus ni moins productif que les peuplements benthiques voisins de la baie de Concarneau ou que d'autres peuplements benthiques subtidaux en zone tempérée. Une spécificité du peuplement à *Haploops* tient néanmoins au fait qu'une large part de sa production secondaire (i.e. 50%) est due à l'unique espèce *Haploops nirae*. Ce résultat est en phase avec de précédentes observations qui indiquaient que les Ampeliscidae pouvaient représenter une partie essentielle de la production secondaire dans les écosystèmes côtiers (Highsmith and Coyle, 1990).

La dernière partie de ce projet s'inscrivait dans une démarche de compréhension du fonctionnement trophique des peuplements macrobenthiques de la baie de Concarneau grâce à l'utilisation des isotopes stables. Comme attendu suite aux résultats obtenus sur le comportement trophique des *Haploops*, ces derniers en tant que suspensivores occupent une place trophique importante à la base du réseau trophique des consommateurs et jouent un rôle essentiel dans le couplage benthos-pélagos et le transfert de la matière organique vers les niveaux trophiques supérieurs. La description de l'architecture des réseaux trophiques des substrats meubles subtidaux de la baie révèle de manière surprenante une forte similarité entre le réseau trophique associé au peuplement à *Haploops* et celui des fonds adjacents. Ce résultat constitue, s'il en était besoin, un indice supplémentaire de la faible incidence fonctionnelle du développement du peuplement à *Haploop*s en baie de Concarneau. Toutefois, dans ce contexte, la définition de nouveaux indicateurs trophiques (IFI) a indéniablement représenté une avancée dans l'analyse fonctionnelle des réseaux trophiques par rapport aux indices précédents (Layman et al., 2007a) en couplant les biomasses des espèces à leurs signatures isotopiques en azote et en carbone. Ainsi, les 3 composantes de la diversité fonctionnelle trophique (i.e. richesse fonctionnelle, régularité fonctionnelle et divergence fonctionnelle) sont significativement plus élevées dans le réseau trophique associé au peuplement à *Haploops* dans le cas où seules les espèces les plus représentatives des peuplements étudiés (i.e. celles qui représentent 80 % de la biomasse benthique) sont prises en compte. Ceci indique donc une plus grande diversité fonctionnelle trophique : une plus grande niche trophique globale, moins de compétition inter spécifique pour la même ressource, une plus forte spécialisation trophique des espèces dominantes du peuplement et en corollaire une moindre redondance trophique. A titre d'exemple, les deux principaux consommateurs primaires du peuplement à *Haploops* (i.e. *Haploops nirae* et *Polititapes virgineus*) possèdent des signatures isotopiques nettement différenciées suggérant que ces espèces se nourrissent sur deux fractions distinctes du pool de producteurs primaires et limitent ainsi la compétition inter-spécifique directe. Un autre élément pouvant expliquer les relatives similitudes dans l'organisation des réseaux trophiques des habitats tels qu'ils peuvent être décrits au moyen des isotopes stables est l'existence d'une connectivité trophique entre les habitats. Cette connectivité pourrait être assurée par les cellules microphytobenthiques qui se développent sur les tubes d'*Haploops* et sont remises en suspension par les courants.

Le peuplement à *Haploops* et les ressources halieutiques

Bien que la structure des réseaux trophiques benthiques et la productivité à l'échelle de la baie de Concarneau n'aient été que faiblement affectées par les modifications de structure induites par les *Haploops*, les flux trophiques vers les niveaux trophiques supérieures (i.e. mégafaune et poissons) sont vraisemblablement différents selon les peuplements. En baie de Vilaine, Desaunay et al. (2006b) ont mis en évidence que certaines espèces de poissons qui constituent pourtant la part essentielle des captures des chalutiers côtiers de la région semblent éviter l'habitat à *Haploops*. Il s'agit notamment des poissons plats tels que la sole, la plie ou le céteau dont le comportement fouisseur est perturbé par la présence des tubes mais également du merlu, du merlan et du bar. Seules certaines espèces de moindre valeur commerciale semblent préférer les fonds à *Haploops* : les roussettes, le tacaud et la dorade grise. Outre les poissons, les *Haploops* peuvent néanmoins constituer un support alimentaire important pour différents invertébrés (décapodes, polychètes prédateurs, némertes). Bien que ces résultats ne ressortent pas des analyses présentées au cours de mon travail de thèse, l'habitat à *Haploops* abrite en effet une mégafaune vagile abondante. Des données complémentaires obtenues à partir d'expérience en mésocosmes par exemple seraient nécessaires dans le but de pouvoir affirmer si ce sont les *Haploops* ou non qui soutiennent le réseau trophique de cette mégafaune vagile.

En termes d'interactions avec les ressources halieutiques, d'autres fonctions non abordées au cours de mon travail peuvent être influencées par la présence ou non d'*Haploops*. En ce qui concerne le rôle de nourriceries des habitats benthiques côtiers, les juvéniles de merlu, merlan, bar, plie, sole et céteau sont mieux représentés à l'extérieur de l'habitat à *Haploops* (Desaunay et al., 2006b). La fonction de nourricerie des fonds à *Haploops* de la baie de Vilaine est limitée à quelques espèces que sont la petite roussette, la dorade grise et le Saint Pierre. *A contrario*, les vases à *Haploops* sont moins chalutées que les habitats benthiques adjacents pour au moins deux raisons : la faible valeur économique de la ressource et la possibilité réduite de chalutage sur ces fonds en raison du colmatage très rapide du chalut par les tubes (Desaunay et al., 2006b). Bien que la zone à *Haploops* soit de moindre intérêt pour la pêche, on ne peut exclure un potentiel rôle de récif joué par ces fonds structurellement complexes qui constitueraient une zone de refuge pour certaines espèces vis-à-vis d'une pression d'exploitation. Certaines observations pourraient soutenir cette hypothèse. En effet, les plus grands individus de bar et de sole ont été capturés sur les fonds à *Haploops* en baie de Vilaine (Désaunay et al., 2006b). De tels fonds pourraient aussi être favorables à des espèces prédatrices de grande taille comme les roussettes, la baudroie et le bar (Desaunay et al., 2006b). Dans le cadre de nos propres observations, nous avons pu noter la concentration de certaines espèces d'invertébrés à forte valeur marchande dans le peuplement à *Haploops* telles que la palourde rose *Polititapes virgineus* et la coquille Saint-Jacques *Pecten maximus*.

Différentes études ont montré que, à l'inverse des fonds à *Haploops* de Bretagne Sud, les zones à Ampeliscidae pouvaient constituer des zones importantes de pêche. En effet, depuis le milieu des années 1990, le sud de la baie de Raritan (New Jersey) est le lieu d'une pêche commerciale à l'année pour *Mercenaria mercenaria* qui est capturé presque exclusivement sur la partie vaseuse de la baie qui est colonisée par *Ampelisca abdita*

(Mackenzie et al., 2006). Si des analyses de contenus stomacaux suggèrent que les *Haploops* de Bretagne Sud sont peu consommés par les poissons de forte valeur commerciale mais le sont plutôt par certaines espèces comme le tacaud, le dragonet ou le Gobie noir (Weppe, 2011), ces observations vont à l'encontre de nombreuses autres qui rapportent une prédation accrue sur les fonds à Ampeliscidae (Cui et al., 2012; Coyle and Highsmith, 1994).

Quelles conséquences à l'expansion du peuplement à *Haploops* ?

Dans le but de comprendre les conséquences qu'aurait une extension ou une régression des vases à *Haploops* en Bretagne Sud, il apparaît nécessaire, voire essentiel, d'évaluer de manière globale les retombées d'une telle dynamique sur le fonctionnement des écosystèmes côtiers. Evitant toute vision manichéenne qui consisterait à voir la présence des *Haploops* dans un système donné comme néfaste ou bénéfique, il convient de garder un propos nuancé et de proposer une grille de lecture qui amène à déterminer l'intérêt du peuplement au regard de la fonction mise en avant. Dans ce cadre, la perception du gestionnaire peut être amenée à évoluer selon les objectifs de gestion fixés. Ainsi, les principaux avantages qui ont pu être mis en avant au cours de mon travail sont les suivants :

- Une profonde modification de l'environnement sédimentaire qui se traduit par un peuplement très original en termes de composition faunistique et de niveau d'endémisme ;
- Une tendance à l'augmentation de la richesse spécifique à l'échelle locale comme à celle de la baie ;
- Une augmentation de la diversité béta et création d'un habitat qui se traduit par une augmentation de la diversité gamma (à l'échelle régionale) : déterminant pour lutter contre la perte de la biodiversité ;
- Une source de nourriture potentielle pour certaines espèces de la mégafaune ou pour certaines espèces de poissons à faible valeur marchande ;
- Une zone de refuge potentielle contre l'exploitation pour différentes espèces pêchées de poissons (sole, baudroie) ou de mollusques (palourde rose, coquille Saint-Jacques).

A l'inverse, une expansion du peuplement à *Haploops* est susceptible d'engendrer différents inconvénients :

- Des abondances de la macrofaune plus faibles d'un facteur 2 environ à l'origine d'une baisse significative de la biomasse, vraisemblablement en réponse à des processus de compétition interspécifique ;
- Un risque d'homogénéisation des fonds dans le cas d'une extension future avec une possible diminution de la diversité gamma et béta ;
- Des retombées négatives de plusieurs natures sur les ressources halieutiques dans la mesure où les *Haploops* ne constituent pas une proie privilégiée pour de nombreux poissons commerciaux ; le peuplement à *Haploops* n'est donc pas une zone de nourricerie ou d'alimentation privilégiée pour de nombreuses espèces.

A côté de ces effets positifs ou négatifs sur le fonctionnement des écosystèmes et les activités humaines qui lui sont associées, le développement du peuplement à *Haploops* a un effet très limité sur la diversité fonctionnelle, l'organisation du réseau trophique benthique et *in fine* la productivité du macrobenthos en baie de Concarneau.

Perspectives.

Si mon travail a contribué à évaluer les conséquences de l'expansion récente d'*Haploops nirae* dans les vasières de Bretagne sud, il ne permet pas d'expliquer les causes de cette dernière. Il est communément admis que le peuplement à *Haploops* joue un rôle clé dans les dynamiques successionnelles au sein des vasières en se développant préférentiellement au détriment du peuplement à *Maldane* et en inhibant le développement de peuplements à *Nucula turgida* ou *Amphiura filiformis* (revue de Glémarec et Grall, 2003). La théorie de l'amensalisme a ainsi été évoquée dans un premier temps par Glémarec et al. (1986) pour tenter d'expliquer l'expansion des vases à *Haploop*s. Bien qu'il semble plausible, au regard de nos propres observations, que les tubes de *Maldane* favorisent l'installation des *Haploops* en s'en servant comme support pour la construction de leur propre tube, il apparaît difficile d'attribuer cette expansion à la seule relation de facilitation *Maldane-Haploops*.

Selon Le Bris et Glémarec (1996), les vases à *Haploops* se seraient étendues en baie de Vilaine sous l'action de l'envasement et de l'eutrophisation côtière, entraînant une augmentation des apports en sels minéraux et des hypoxies périodiques. L'envasement de la baie de Vilaine engendré par la construction du barrage d'Arzal est certainement un facteur déterminant dans l'extension des vases à *Haploops* pour ce secteur. Nos résultats ayant montré que les *Haploops* sont associés à un sédiment composé en moyenne à 70 % de vase, le pourcentage de particules fines dans le sédiment semble donc être un paramètre qui détermine la distribution des *Haploops*. Néanmoins, le pourcentage de vase à la station CO 3 de la baie de Concarneau qui était en cours de colonisation par les *Haploops* au cours de mon travail était plus faible (i.e. 55%) que dans toutes les autres stations à *Haploops* (i.e. 70%). Ce résultat tendrait donc plutôt à suggérer que si les *Haploops* ont besoin d'un environnement vaseux pour s'installer, les fortes teneurs en pélites dans les milieux colonisés sont le fruit de l'activité des organismes et une conséquence de la présence des tubes.

Une autre explication possible pour l'envasement des zones côtières du sud Bretagne concerne la remise en suspension de la vase sous l'effet du chalutage. Dans la Grande Vasière, une diminution de la proportion de vase semble avoir eu lieu depuis 40 ans. Selon Hily et al. (2008) et Lorance et al. (2011), la cause de ce changement n'est pas certaine mais pourrait être une conséquence de la remise en suspension de la vase par les chaluts. La remise en suspension favorise l'augmentation de la turbidité et le transport des particules au-delà du plateau ou plus à la côte par les courants de marées.

L'hypothèse de l'eutrophisation comme un facteur explicatif de l'extension des *Haploops* n'est pas triviale. Si une augmentation de la production primaire et de la biomasse phytoplanctonique disponible peut être bénéfique pour les *Haploops*, suspensivores, les épisodes hypoxiques voire anoxiques liées à l'eutrophisation ont en revanche des conséquences dramatiques sur les peuplements à Ampeliscidae. Ainsi, dans l'Øresund, la cause principale du déclin dramatique des *Haploops* serait l'eutrophisation qui entraine des anoxies régulières du milieu (Göransson et al., 2010). De même, dans Hillsborough Bay (Tampa, Floride), Santos and Simon (1980) ont montré qu'*Ampelisca abdita* qui était l'espèce dominante de la zone étudiée n'était réapparu qu'à de très faibles densités après deux cycles de perturbations dues à des anoxies du milieu.

Une rétroanalyse des conditions environnementales, en particulier hydrologiques, en baie de Concarneau, pourrait apporter de premiers éléments de réponses sur les principaux bouleversements qui ont affecté la baie au cours des 40 dernières années. En revanche, l'absence de séries temporelles régulières limite notre potentiel explicatif. Face aux enjeux que pourraient représenter la prolifération d'*Haploops*, la pertinence d'un suivi à long terme des peuplements benthiques à une échelle spatiale adaptée se pose.

Il a été montré qu’une particularité des fonds à *Haploops* réside également dans la présence de champs de pockmarks dont les contours se superposent (Souron, 2009). Les origines de l’association entre les pockmarks et l’habitat à *Haploops* à la fois en baie de Concarneau et en baie de Vilaine et les effets de cette association particulière restent à comprendre. En particulier, se pose la question des processus responsables de l’émanation de gaz en surface dans les baies colonisées par les *Haploops*. Quelle est la fréquence de ces émanations ? Quel degré d’instabilité du peuplement les pockmarks génèrent-ils ? Quelles sont leurs conséquences sur la structure des peuplements benthiques à petite échelle ? Quelle est l’influence des pockmarks sur l’expansion ou la régression du peuplement à *Haploops* sur des échelles de temps plus longues ? Des carottages réalisés à l’intérieur des pockmarks en plongée ont révélé la présence de méthane à des concentrations significatives ce qui suggère que certains pockmarks sont actifs. Or, le méthane relâché au sien des pockmarks a une signature isotopique théorique en carbone caractéristique (< -70 ‰). Une entrée même modeste de méthane dans le réseau trophique macrobien aurait été facilement décelée lors des analyses isotopiques que nous avons réalisées. L’influence de ce méthane sur la géochimie du sédiment et son éventuel incorporation par des organismes microbiens restent des questions en suspens. La relation pockmark-*Haploops* devrait donc faire l’objet d’études approfondies à l’avenir en privilégiant un travail conjoint entre écologues, géologues et géochimistes. Plusieurs échantillons récoltés lors des campagnes qui ont servi de support à ce travail de thèse pourraient néanmoins apporter de premiers éléments de réponse à court terme (e.g. effet des pockmarks à petite échelle). Par ailleurs, certains auteurs ont suggèré que les pockmarks constitueraient des zones de refuges pour la mégafaune mais également pour les poissons (Dando, 2001; Webb et al., 2009), ce que des prélèvements en plongé ont permis de vérifier en baie de Concarneau. La présence des pockmarks au sein des peuplements à *Haploops* de Bretagne sud serait donc un élément supplémentaire pour envisager les habitats à *Haploops* comme des zones de refuges pour la mégafaune benthique et les poissons. Ainsi, quelques observations en plongée ont montré la présence de terriers de langoustine *Nephrops norvegicus* sur les flancs des pockmarks non échantillonnés avec les moyens traditionnels de récolte (i.e. carottier, benne, chalut à perche). Des campagnes d’observations à l’aide d’un ROV pourraient s’avérer fort utile.

Comprendre la dynamique de la biodiversité n’est pas seulement comprendre les variations du nombre d’espèces présentes ou leur identité mais également comprendre comment les écosystèmes fonctionnent et répondent aux multiples pressions anthropiques qu'ils subissent. Une attention accrue a ainsi été portée au fonctionnement des écosystèmes au cours des dernières années dans un souci de compréhension des conséquences possibles de l'érosion de la biodiversité sur les biens et services que procurent les écosystèmes aux sociétés humaines. Cependant décrire ou mesurer le fonctionnement des écosystèmes marins est extrêmement difficile pour de multiples raisons : (1) la notion même de fonctionnement d'un écosystème est l'objet de différentes définitions incluant aussi bien des processus écologiques (ex : production primaire) que des propriétés des systèmes (ex : résilience), (2) le fonctionnement global des écosystèmes est complexe et implique de nombreux facteurs physiques, chimiques et biologiques qu'il est difficile de reconduire expérimentalement au laboratoire ou d'appréhender à travers un simple indicateur. Le parti pris au cours de ma thèse a été d'appréhender le fonctionnement de l'écosystème de manière intégrée à travers le calcul de la production secondaire ou l'analyse des traits biologiques. Une alternative possible est de se focaliser sur l'étude détaillée de certaines fonctions importantes à travers l'étude du métabolisme benthique (i.e. respiration et production primaire) et les flux de sels nutritifs à l'interface eau-sédiment à l'aide de cloches expérimentales (Migné et al., 2005 ; Martin et al., 2007) ou d'incubations de carottes sédimentaires (Rauch & Denis, 2008).

Enfin, l'analyse des traits biologiques pour estimer la diversité fonctionnelle demeure balbutiante dans le domaine marin et a fait l'objet d'un nombre encore réduit de travaux. Il conviendrait donc, au-delà du cas d'étude présent, d'approfondir la pertinence de cette approche en écologie benthique par des études comparatives en privilégiant deux axes : comment les perturbations environnementales se répercutent sur la diversité fonctionnelle ? Comment s'exprime le lien entre diversité spécifique et diversité fonctionnelle ? Au-delà de l'intérêt scientifique fondamental que représente l'étude du lien entre la diversité spécifique et la diversité fonctionnelle, elle ouvre également la voie à une réflexion sur la définition d'indicateurs pertinents du bon état écologique des peuplements tels que demandés par la Directive Cadre européenne 'Stratégie pour le Milieu Marin'.

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Annexes

A new species of amphipod, *Photis inornatus* sp. nov. (Corophiidea, Photidae) from a '*Haploops* community'in Brittany, (Myers et al., 2012)

Systematic section

Superfamily Photoidea

Family Photidae

Diagnosis. Body laterally compressed, rostrum short, lateral cephalic lobe weakly or strongly extended, eye, if present, situated proximal to lobe or completely of partially enclosed in extended lobe; anteroventral margin moderately to strongly recessed and moderately excavate. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterior margin or subsymmetrical with setae mostly distal. Gnathopod 2 in male larger than gnathopod 1, merus not enlarged. Pereopods 5–7 not subchelate. Pereopod 7 slightly longer than pereopod 6; urosomites free. Uropod 3 peduncle short with sides expanded or long, parallel-sided or narrowing distally; telson without hooks or denticles.

Photis Krøyer, 1842

Diagnosis. Head with eye lobes produced forward; antenna 1 with accessory flagellum absent; coxae long, weakly overlapping; gnathopods subchelate, gnathopod 2 slightly to greatly larger than gnathopod 1; pereopod 5 with large robust seta on palm and accessory spine on dactylus; uropod 3 peduncle long, equal to or longer than outer ramus, inner ramus reduced to vestigial.

Photis inornatus sp. nov.

(Figs 1–3)

Type material. HOLOTYPE, Holotype female, 3.2 mm (MNHN-IU-2009-585), Paratypes: 4 males, 12 females, same data as holotype (MNHN-IU-2009-586).

Type locality. Bay of Concarneau (47°44'16.3"N ; 3°53'34.7"W and 47°48'32.1"N ; 3°55'31.8"W)

Etymology. Latin *inornata*, meaning unornamented, referring to the uniform palms of the gnathopods in both sexes.

Description. Based on Paratype male MNHN-IU-2009-586, 3.4 mm.

Head. *Head* with strongly forward produced, rounded eye lobe. Eye, black, composed of many ommatidea, situated fully in eye lobe. *Antenna 1* almost equal to body length; peduncular article 3 longer than 2; flagellum longer than peduncle, composed of about 13 flagellar articles. *Antenna 2* longer than 1; peduncular articles 4 and 5 subequal in length; flagellum longer than peduncle, with about 20 articles. *Labrum* anterior margin weakly setiferous. *Mandible* with strong molar, palp 3-articulate, article 1 very short, article 2 much longer than 3, article 3 subsymmetrical, spatulate, with long distal setae. *Maxilla 1* inner plate small, subtriangular, asetiferous, palp 2-articulate, article 2 extending well beyond outer plate. *Maxilla 2* inner plate with oblique setal row. *Labium* mandibular processes rounded. *Maxilliped* outer plate posterior margin scalloped, palp very long, article 2 elongate, extending well beyond distal margin of outer plate.

Pereon. *Gnathopod 1* coxa unproduced, rounded; basis moderately stout, about two and a half times as long as broad, with 6–8 long setae on the posterior margin; carpus and propodus subequal; propodus palm evenly rounded delineated by stout robust seta, but evenly continuous with posterior margin; dactylus strong, overlapping position of robust seta. *Gnathopod 2* similar to gnathopod 1, basis stout, length less than twice breadth; carpus a little shorter than propodus; propodus subovoid, palm scarcely delineated, delimited by robust seta; dactylus strong, overlapping position of robust seta. *Pereopods 3–4* stout, coxa deeper than broad: basis strongly setiferous; dactylus elongate, shorter than propodus. *Pereopod 5* basis broad, less than one and one half times as long as broad, posterior margin with long setae; propodus palm with long robust seta; dactylus short, recurved with accessory spine on anterior margin. *Pereopod 6* dactylus with small accessory spine on anterior margin. *Pereopod 7* basis anterior margin sinuous; dactylus lacking accessory spine.

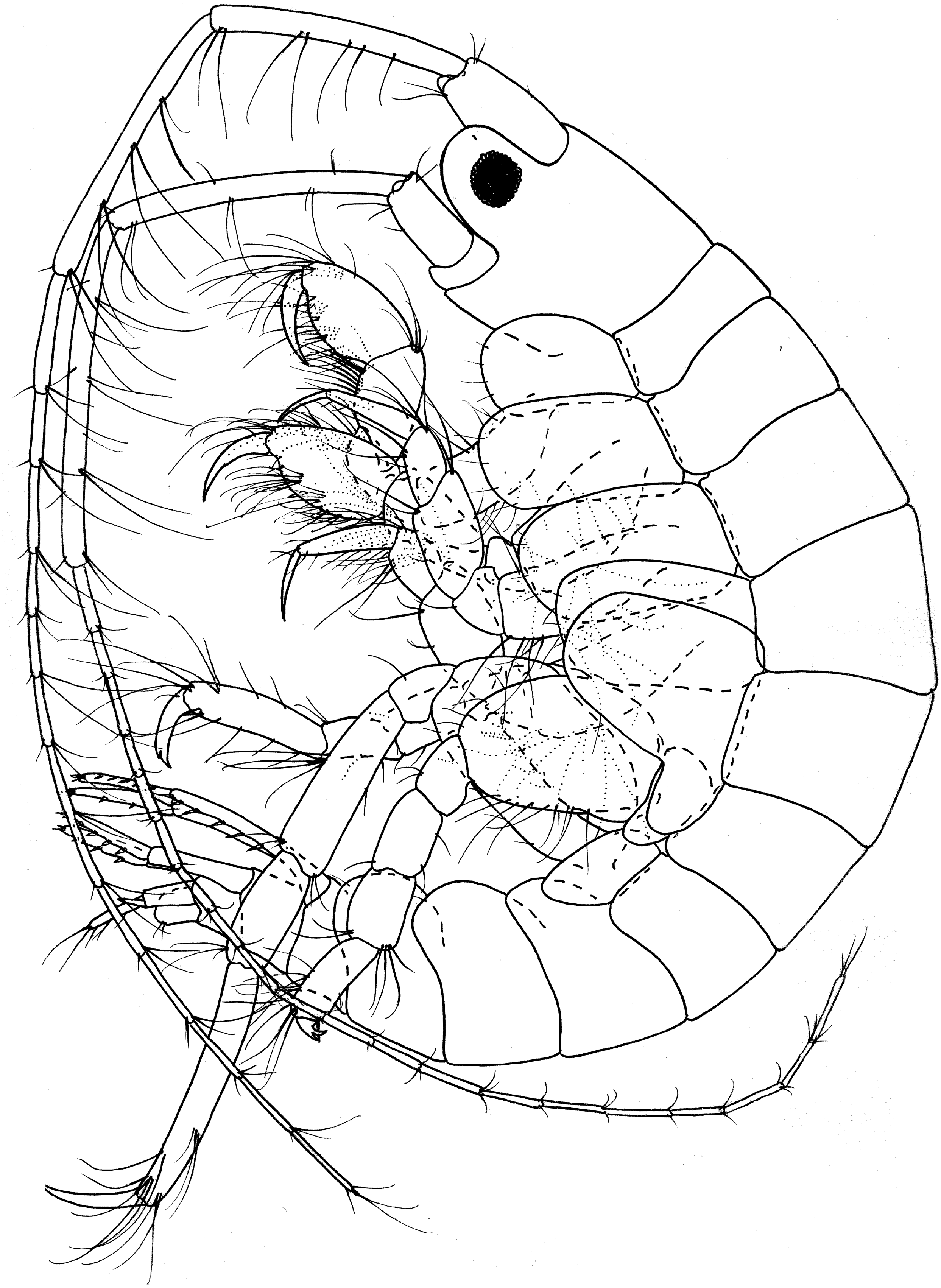

FIGURE 1. *Photis inornatus* **sp. nov.**, male paratype, 3.4 mm. Bay of Concarneau

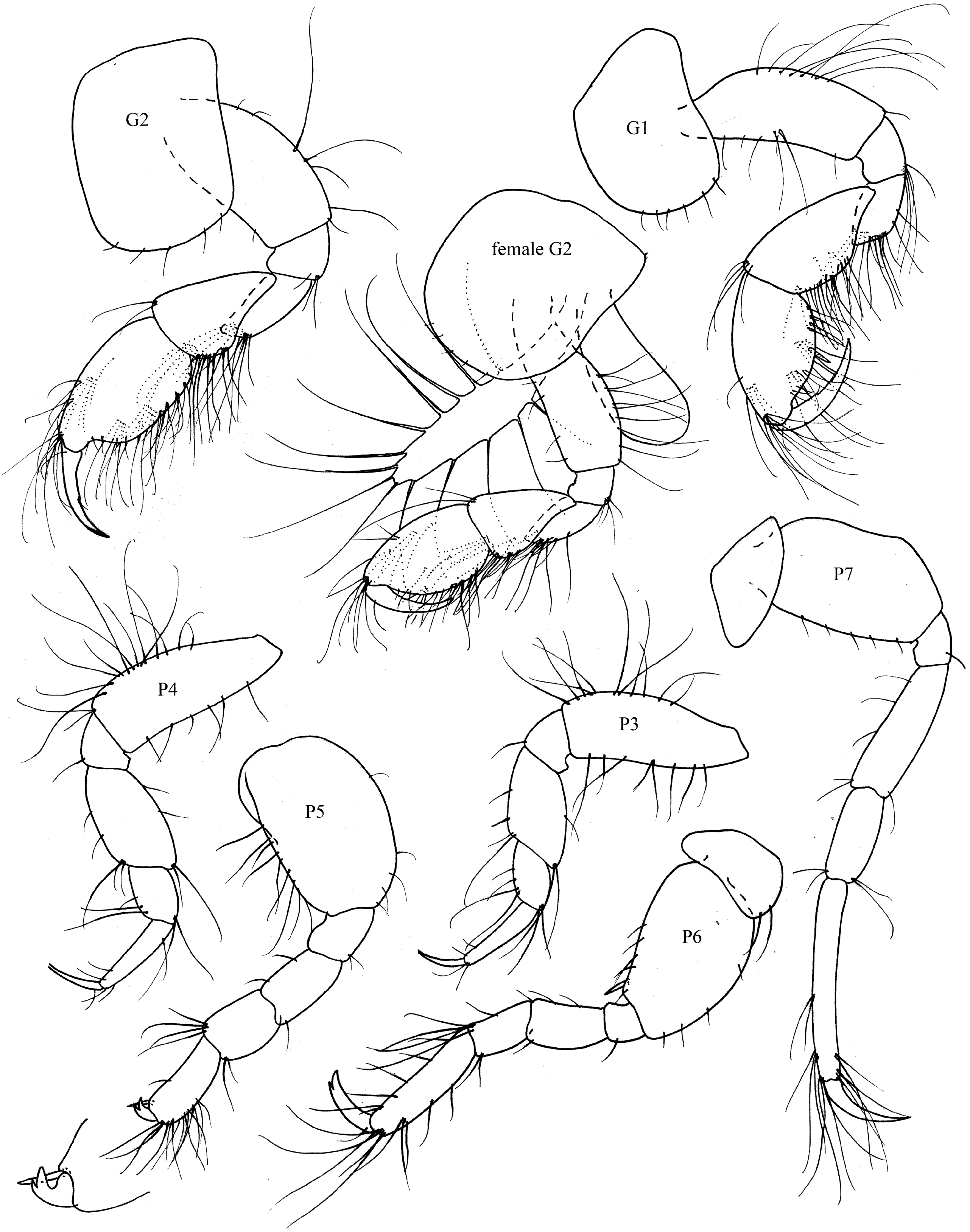

FIGURE 2. *Photis inornatus* **sp. nov.**, male paratype, 3.5 mm, female holotype 3.3 mm. Bay of Concarneau

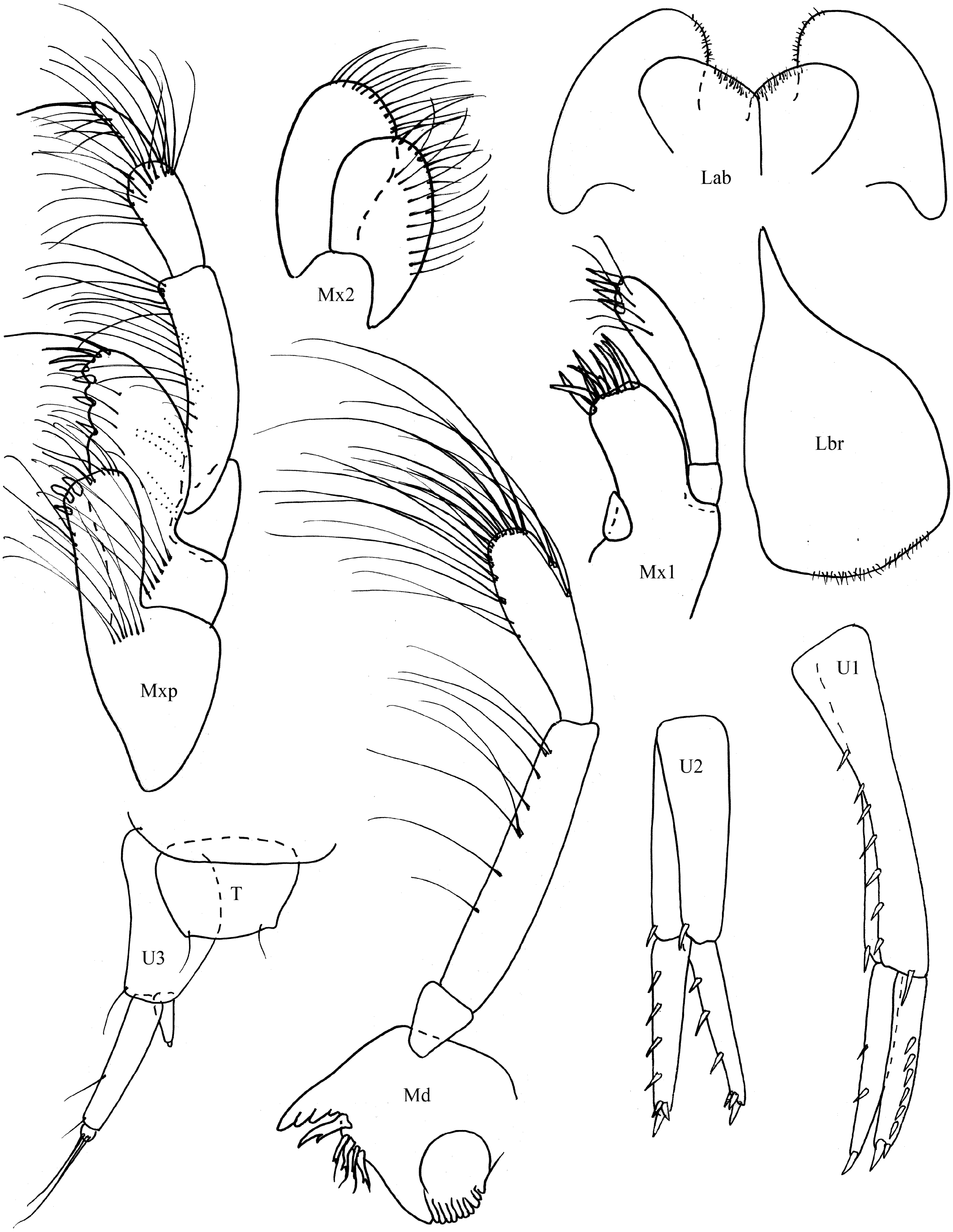

FIGURE 3. *Photis inornatus* **sp. nov.**, male paratype, 3.5 mm, Bay of Concarneau.

Pleon. *Epimera 1–3* rounded. Uropod 1 elongate, peduncle much longer than rami; inner ramus a little longer than outer, outer margin with few robust setae; outer ramus, outer margin with numerous robust setae. *Uropod 2* peduncle a little longer than rami, rami subequal with robust setae. *Uropod 3* peduncle subequal in length with outer ramus; inner ramus scarcely one third length of outer ramus, with small second article and lacking setae, outer ramus slender, with small second article bearing two long distal setae. *Telson* dorsoventrally thickened, distal margin weakly convex, with a single fine seta on either side.

Female. Based on Holotype female MNHN-IU-2009-585, 3.2 mm, Scarcely differing from male. Gnathopod 2 basis a little less stout.

Habitat. Individuals were found between 20 and 35 m depth in muddy sediments (mud percent ranging from 56% to 82%) within the *Haploops* community. This species was absent from surrounding sampled benthic communities, i.e. *Owenia fusiformis* fine sand community (% mud = 17–19% ; depth ~ 30 m), *Amphiura filiformis* muddy sand community (% mud = 46–55% ; depth ~ 25 m), and *Sternaspis scutata* muddy community (% mud = 58–60% ; depth ~ 20 m).

Distribution. Currently known only from the type locality.

Discussion. ***Photis inornatus* sp.nov.** is unique amongst world *Photis* species in having unornamented palms on gnathopods 1–2 in both sexes. It also differs from other North Atlantic species in having antennae equal in length to the body

Photis inornatus was found to be restricted to the *Haploops* muddy habitat, while other similar sedimentary environments were prospected (Table 1). Within this former habitat, it was present in most sampled stations at densities ranging between 0 and 125 ind.m^{-2}. Over the year, it was only absent during winter samples (February 2010). Conversely, *P. longicaudata* was reported in all habitats investigated in the bay of Concarneau, indicated that both species may live in sympatry. It is also hypothesized here a close relationship between *Haploops nirae* and *P. inornatus*, either directly due to inter-specific relationships or indirectly due to the special features created by *Haploops* tube mats.

A key to the European Atlantic species of *Photis* is provided below.

TABLE 1. Mean and min-max densities (ind.m^{-2}) and occurrence frequency of *Photis inornatus* **sp. nov.** and *Photis longicaudata* in the Bay of Concarneau, France, in 2009–2010.

	Mean density (± SD) (ind.m^{-2}) min-max values		Frequency of occurrence	
Community sampled	Haploops	Others	Haploops	Others
Number of stations	22	20	22	20
Photis inornatus **sp. nov.**	33.1 ± 36.5	0	86.36%	0.00%
	0–124	-		
Photis longicaudata	27.5 ± 30.1	23.9 ± 34.6	90.91%	60.00%
	0–100	0–124		

Key to the species of *Photis* species of the European Atlantic and Mediterranean.

1. Antenna 1 longer than half body length 2
- Antenna 1 half or less than half body length. 3
2. Male gnathopod 2 propodus palm complexly excavate . . . . *P. longicaudata* Bate & Westwood1863
- Male gnathopod 2 propodus palm evenly rounded indistinct from posterior margin . . . . *P. inornatus* **sp. nov.**
3. Male coxa 1 narrowing distally, coxa 2 distinctly shorter than coxa 3.. . . . . *P. pollex* Walker, 1895
- Male coxa 1 not narrowing distally, coxa 2 not distinctly shorter than coxa 3 3
3. Uropod 3 peduncle longer than rami. . . . . *P. reinhardi* Krøyer, 1842
- Uropod 3 peduncle shorter than or subequal with rami . . . . *P. tenuicornis* Sars, 1883

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Résumé :

Ce travail de thèse a pour objectif, en s'appuyant sur le cas de la baie de Concarneau, de comprendre l'impact du développement de denses populations de l'amphipode tubicole *Haploops nirae* sur la diversité structurelle et fonctionnelle des peuplements sablo-vaseux de Bretagne Sud. L'étude des peuplements à *Haploops* dans ce projet de thèse se décline selon plusieurs niveaux d'organisation du vivant, du rôle spécifique d'*Haploops nirae* jusqu'au rôle fonctionnel du peuplement au sein de l'écosystème en passant par la description de la composition spécifique du peuplement et son rôle sur la biodiversité en général. Nos résultats suggèrent dans un premier temps que le rôle fonctionnel de l'espèce seule (pression de filtration, production secondaire) est potentiellement important. De plus, les modifications physiques de l'habitat par les *Haploops* se sont révélées avoir des conséquences très importantes sur la composition des peuplements et la diversité spécifique. *A contrario*, l'étude de la diversité fonctionnelle abordée par l'analyse des traits biologiques (BTA) et la production secondaire des peuplements révèle que les conséquences fonctionnelles de la présence des *Haploops* dans un écosystème sont dans l'ensemble faibles. De la même façon, l'étude du fonctionnement trophique des peuplements benthiques de la baie de Concarneau (grâce à l'utilisation des isotopes stables) révèle une faible incidence fonctionnelle du développement des *Haploops* sur la structure du réseau trophique benthique. Bien que les peuplements à *Haploops* ne soient pas caractérisés par de profonds changements fonctionnels, les flux trophiques vers les niveaux trophiques supérieurs sont cependant vraisemblablement affectés par la présence des *Haploops*.

Mots-clés: Ampeliscidae – espèce ingénieure – Bretagne Sud – diversité macrofaune benthique – diversité fonctionnelle – réseau trophique