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Thèse
Présentée en vue de l'obtention du diplôme de DOCTEUR en Sciences de la Mer

Influence de l'environnement sur la structure et la dynamique du peuplement ichtyologique de la zone intertidale de la plage sableuse Sainte Cécile (Baie de Canche - Manche Orientale).

Option : Bioressources Marines

Soutenue le 23 mai 2015
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«On ne va pas sauver la planète en tenant des meetings ou en multipliant les discussions, ni en signant des pétitions (…) La forme la plus importante d'intelligence, c'est l'intelligence écologique, la capacité à vivre dans un écosystème sans le détruire. Et dans ce domaine, on est vraiment en queue de liste...».

Paul Watson- Sea Shepherd

Résumé :

Les zones intertidales jouent un rôle essentiel dans le renouvellement des ressources halieutiques. De nombreuses espèces marines, poissons comme macrocrustacés ont un cycle de vie qui leur impose de passer au cours de leur période juvénile par ces écosystèmes. De par sa position à l'interface terre-mer, la zone intertidale est soumise à d'importantes fluctuations des facteurs environnementaux. Cependant, la façon dont cet écosystème répond aux forçages environnementaux, notamment en ce qui concerne la composition et la structure des peuplements, leurs dynamiques et persistances saisonnières et interannuelles sont encore mal connues.

En Manche Orientale, l'estran sableux représente plus de 70 % du littoral et constitue d'importantes zones de nourriceries pour les juvéniles de poissons. Dans ce contexte scientifique et régional, l'objectif global de cette thèse a été de décrire les assemblages des peuplements de poissons et de macrocrustacés de la zone intertidale et d'analyser l'influence de l'environnement sur les assemblages et la dynamique des espèces. Une telle étude a pour but de mieux comprendre le fonctionnement de cet écosystème et de préciser son importance dans le cycle biologique des espèces marines, notamment des espèces d’intérêt halieutique.

Une première partie de ce travail a permis de déterminer la composition et la variabilité des assemblages de poissons et de macrocrustacés en relation avec les fluctuations environnementales et climatiques. A partir d'un suivi à long terme (11 années) mais aussi saisonnier, nous avons mis en évidence une stabilité des assemblages des peuplements de la macrofaune (poissons et crustacés). À l'inverse, les abondances présentent des fluctuations interannuelles et saisonnières en relation avec des facteurs comme la NAO, la température, la salinité ou encore la turbidité.

Dans la deuxième partie de la thèse, nous avons analysé si les variations des conditions environnementales de la zone intertidale pendant la période printanière sont d'ordre à affecter les performances physiologiques et la survie des juvéniles qui colonisent cet écosystème. Nous avons focalisé notre étude sur l'espèce de poisson dominante de la zone intertidale, la plie *Pleuronectes platessa*. Différents indices qui reflètent les performances physiologiques des juvéniles (croissance et indices de conditions) ont été mesurés sur les juvéniles de plie tout au long de la période de colonisation. Les résultats montrent que la croissance récente, la condition K et l'état nutritionnel (ARN/ADN) des juvéniles de poissons sont élevés tout au long de la période de colonisation des juvéniles et présentent peu de variations intra- et interannuelles, indiquant que l'estran offre des conditions favorables au développement et à la survie des juvéniles de poisson et par conséquent à leur recrutement. Malgré l'importance du bloom de *Phaeocystis globosa* dans la région et de ses fortes variations interannuelles, nous n'avons pas constaté d'effets de ce bloom sur les assemblages, les abondances ou encore les performances physiologiques des poissons.

Mots clés : Zone intertidale, estran, nourricerie, assemblage, poissons, macrocrustacés, variations environnementales, colonisation, période printanière, performances physiologiques, poissons plats, Manche orientale.

Abstract:

Intertidal areas provide an essential habitat to fish and macrocrustaceans. These systems are particularly used by juveniles of many fish and macrocrustacean species as nurseries because of the potential advantages they provide for the growth and survival of young fish, namely high prey availability, refuge from predators and good environmental conditions. These habitats are in permanence subject to strong environmental and human fluctuations.
Therefore, the comprehension of the functioning and the conservation of the sandy beaches are necessary to maintain the biodiversity and to guarantee the renewal of the fisheries.

It is in this framework that our study oriented us to determine the importance of the environmental factors on one hand on the dynamic of the ichtyofauna and on the other hand on physiological performances of the juveniles of fish on the intertidal zones of the English Channel.

First, this work allowed us to determine the composition and variability of the fish and macrocrustaceans assemblages in relationship with the environmental and climatic fluctuations. According to our results, the importance of the role of the intertidal habitats of the English Channel in the renewal of the fisheries was proved.

Standard qualitative community ecology metrics (species composition, richness, diversity, evenness and similarity) indicated notable inter-annual stability over the study period.
Afterward, a 2nd part of this study was consecrated to the seasonal study of the assemblages and the impact of the environmental changes.
Our results allowed us to demonstrate that abiotic and climatic factors (mainly temperature, salinity, suspended matter and the winter NAO) have a great influence on the structure of fish and macrocrustacean assemblages but also the impact of *Phaeocystis globosa* blooms on the population structure.
To better understand the nursery functions, the study of physiological performances of juvenile common plaice *Pleuronectes platessa* during the spring period on the intertidal zone was discussed in order to understand if changes in the environment have an impact on their healthy development.

For this, we analyzed various indices that reflect the physiological performance of juvenile common plaice (growth and condition indeces). The results show that the recent growth, the Fulton’s K and nutritional ratio RNA/DNA juvenile fish are high throughout the juvenile period of colonization, indicating that nurseries are favorable to the development and survival of fish and therefore their recruitment.

Finally, all the work presented shows that the environment of the intertidal areas of the Eastern English Channel is favorable to good life cycle course of marine fish fauna.

Keywords: intertidal zone, nurseries, assemblage, fish, macrocrustacean, environmental variations, colonization, spring period, physiological performance, flatfish, Eastern English Channel.

خلاصة:

المناطق البحرية المدية تلعب دوراً أساسياً في تجديد الموارد السمكية. العديد من أصناف الأسماك و القشريات الماكروسكوبية لها دورة حياة تجبره على المرور خلال فترتهم الشبابية، على أنظمة بيئة تلعب دوراً في تغذيتها. هذه الأنظمة البيئة الساحلية القليلة العمق تعرف تقلبات بيئة قوية (طبيعية كانت أو بشرية المنشأ). من هذا المنطلق فإن فهم سير و المحافظة على مناطق المد و الجزر ظرورية لصيانة التنوع البيولوجي و المحافظة على تجديد المخزون البحري. إن إشكالية هذا البحث ادى بنا إلى تعيين مدى أهمية العوامل البيئية من جهة على ديناميكية الأسماك في النظم الايكولوجية و الفعاليات الفيزيولجية على صغار الأسماك من جهة اخرى في المناطق البحرية المدية في بحر المانش الشرقي.

الجزء الاول من هذا العمل سمح لنا بتحديد تركيبة و قابلية تغيير تجميع الأسماك و القشريات الكبيرة التي لها علاقة بالتقلبات البيئة و المناخية. و حسب النتائج التي حصلنا عليها فإن أهمية دور مناطق المد و الجزر لبحر المانش الشرقي في تجديد المخزونات التي تشمل الأسماك الصغيرة في هذه الأنظمة البيئة قد تم إثباته و تأكيده. في هذه المناطق نجد الأسماك التي تتخذ منها موطنا تظهر تغيرات في التنوع و الوفرةو التجمع و كذلك يمس هذا التغيير حتى احجامها. و يظهر هذا بشكل واضح في سلم ما بين السنوات وداخل السنة الواحدة. وهذا خلال مدة دراستنا التي دامت 11 سنة في جمع العينات.بعد ذلك خصص الجزء الثاني لدراسة موسمية للتركيبات و تأثير التغيرات البيئة عليه. إن هذا العمل وضح أن الصلة بين التقلبات البيئة (الحرارة، درجة الملوحة، المواد المعلقة)لها تأثير على تركيبة الأسماك و القشريات الماكروسكوبية و أيضا تأثير على تزهر *phaeocystis globosa* على بنية المستعمرة الحيوانية.

و لكي نفهم بشكل افضل سير الحظن و دراسة الأداء الفزيولوجي للأسماك الصغيرة (pli)خلال فترة استقطاب المستعمرات الحيوانية في مناطق المد والجزر قد تم تناولها بالتفصيل، لهذا قمنا بتحليل المؤشرات المختلفة التي تعكس الأداء الفزيولوجي للسمك الصغير (نمو و مؤشرات الظروف) و تظهر النتائج أن النمو الحالي و الضرف k و العوامل الغذائية(ARN/ADN)للأسماك الصغيرة مرتفعة خلال كل فترة استقطاب المستعمرات السمكية و هذا مؤشر بأن مناطق الحضانة قابلة و مساعدة للتطور وإبقاء الاسماك على قيد الحياة و تجديدها .

وأخيرا فإن مجموع هذه الأشغال المقدمة تبين أن بيئة المناطق المديه للقناة الشرقية قابلة و مساعدة للسير الحسن في دورة حياة السلسلة الحيوانية للأسماك البحرية.

كلمات البحث: منطقة المد و الجزر، الشواطئ الأمامية، الحضانة،التجمع ,الاسماك (macrocrustace) الاختلافات، التسوية، فصل الربيع، الأداء البيئي الفزيولوجي.

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AFMULT	Analyse Factorielle Multiple
AHC	Acendant Hierarchical Classification
AIC	Akaike's Information Criterion
ANOVA	Analysis of Variance
BET	Bromure d'Ethidium
BMMEm	Basse Mer de Morte-Eau moyenne
BMVEm	Basse Mer de Vive-Eau moyenne
CCorA	Canonical CorrelationAnalysis
CIEM	Conseil International pour l'exploration de la Mer
Cr	Croissance Récente
DAM	Direction des Affaires Maritimes
DCSMM	Directive Cadre Stratégie pour le Milieu Marin
DSF	Documents Stratégiques de Façade
EDTA	Ethylene Diamine TetraAcetic
GIP Seine-Aval	Groupement d'Intérêt Publique Seine-Aval
GLM	Generalized Linear Model
H'	Indice Shannon-Weaver
J'	Indice d'équitabilité de Piélou
K	Indice de condition de Fulton
MES	Matières En Suspension
NA	Nucléi accessoires
NAO	North Atlantic Ocillation
PCA	Principal Component Analysis
PMVEe	Pleine Mer de Vive-Eau exceptionnelle
PMVEm	Pleine Mer de Vive-Eau moyenne
PMMEm	Pleine Mer de Morte Eau moyenne
POC	Particulate Organic Carbon
RV	Real Value
S	La richesse spécifique
SNML	Stratégie nationale intégrée pour la mer et le littoral
SOMLIT	Service d'Observation en Milieu LITtoral
SPM	Suspended Particulate Matter
SST	Sea Surface Temperature
TEB	Tris EDTA Buffer
TNPC	Traitement Numérique des Pièces Calcifiées

CHAPITRE 1

Introduction générale

1. Introduction

1.1. Importance des zones côtières

Les zones côtières ont longtemps joué un rôle important pour l'humanité. Du fait de leur situation à l'interface entre terre et mer, elles constituent des territoires à forts enjeux stratégiques pour les économies et pour l'environnement. Elles fournissent un large éventail de biens et services. D'un point de vue socio-économique, elles constituent des espaces privilégiés pour le développement de nombreuses activités, sources d'emplois : activités portuaires et industrielles ; agglomérations urbaines et touristiques (Allain *et al.,* 2006, Amara, 2011). Au plan environnemental, ces écosystèmes sont parmi les plus riches et les plus productifs de la planète. On y trouve de nombreux habitats littoraux remarquables (mangroves, marais salés, lagunes, côtes rocheuses), des habitats subtidaux benthiques complexes (récifs coralliens, herbiers marins …) ainsi qu'une multitude d'environnements sédimentaires (Christian & Mazzilli, 2007). Ces derniers assurent de nombreuses fonctions biologiques et écologiques : habitats essentiels pour divers organismes (flore, ichtyofaune, avifaune), zones d'épuration et de stockage et de transformation des apports terrigènes.

Néanmoins, elles sont aussi, de par leurs propriétés, très attractives pour l'homme. Les zones côtières se trouvent ainsi soumises à de fortes pressions anthropiques qui menacent leur équilibre et leur intégrité. Depuis longtemps, les civilisations ont cherché à exploiter au mieux les zones littorales afin d'étendre leur pouvoir, leur commerce et leur culture. Depuis la seconde moitié du XXème siècle, le littoral voit sa démographie augmenter. Aujourd'hui, plus de 60% de la population mondiale habite dans les zones côtières (qui représente 12% de la surface terrestre) soit environ 4 milliards d'habitants et on prévoit que dans 25 ans, ce sera plus de 75%. Avec ce développement économique et cette croissance démographique en expansion, de fortes répercussions sont observées sur les écosystèmes notamment la destruction des habitats naturels (aménagements et activités portuaires, chenalisation, activités industrielles, pollutions, dragage, extraction de granulats, activités agricoles, marées noires, développement intensif du tourisme…) et la surexploitation des ressources (surexploitation des mers et des mangroves ainsi que le blanchissement corallien ayant des causes diverses, dont notamment le changement climatique…).

Malgré leur importance socio-économique et environnementale, **les zones côtières et les milieux marins** n'ont reçu une attention particulière de la part des politiques que dans des périodes récentes – l'homme étant (hors période estivale….) plutôt terrien que marin. A l'échelle européenne, les **enjeux de protection de ces écosystèmes** particuliers sont notamment appréhendés par la Recommandation européenne relative à la Gestion Intégrée des Zones Côtières (2002), et plus récemment par la Directive Cadre Stratégie pour le Milieu Marin (DCSMM) adoptée en 2008. Cette dernière demande en particulier aux États membres d'**évaluer les enjeux et besoins de protection** des zones marines qui sont de leur ressort, puis d'élaborer et mettre en œuvre d'une manière concertée **des plans de gestion** assurant le développement durable de ces zones. A l'échelle française, le Grenelle de la Mer a prévu la mise en œuvre d'une **stratégie nationale intégrée** pour la mer et le littoral (SNML) qui se déclinera en documents stratégiques de façade (DSF) pour chacune des quatre façades maritimes métropolitaines.

1.2. La zone intertidale, un environnement peu hospitalier

L'interface dynamique entre terre et mer représente l'écosystème intertidal ou l'estran. C'est la zone de balancement des marées, correspondant à l'étage médiolittoral et au supralittoral (figure 1). Lorsqu'on parle de la pente d'une plage en fait c'est celle de l'estran dont il s'agit. Le profil de l'estran considéré dans son ensemble est légèrement convexe, mais avec de nombreuses irrégularités. Néanmoins, ce profil évolue constamment car il dépend des aléas climatiques tels que les marées, la force des vagues et des flux sédimentaires (importance de la dérive littorale).

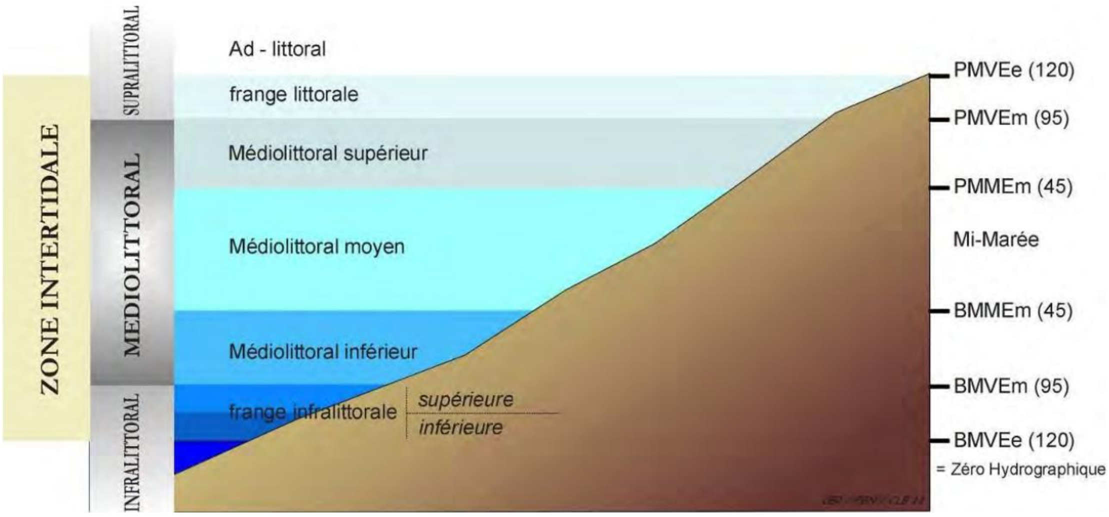

Figure 1. Etagement de la zone intertidale (Loarer & Rollet, 2011 ; IFREMER).
PMVEe: Pleine Mer de Vive-Eau exceptionnelle ; PMVEm: Pleine Mer de Vive-Eau moyenne ; PMMEm: Pleine Mer de Morte Eau moyenne ; BMMEm: Basse Mer de Morte-Eau moyenne ; BMVEm: Basse Mer de Vive-Eau moyenne ; BMVEe: Basse Mer de Vive-Eau exceptionnelle.

La durée de l'immersion, liée à l'amplitude des marées, est le facteur majeur agissant sur la vie dans ce milieu ; elle y provoque dessiccation et déshydratation des organismes et en détermine la température et la lumière. Dans cet écosystème, les variations de température, de salinité, d'oxygène, de turbidité, etc., sont marquées et imposent diverses pressions aux organismes (Denny, 1988; Raffaelli & Hawkins, 1996). Les conditions de vie dans cet écosystème dépendent aussi de la nature du substrat, différant sensiblement selon que celui-ci soit meuble (graviers, sables, vases) ou dur (roches). De ce fait, les conditions écologiques, liées aux marées, sont plus contraignantes pour les organismes des zones à substrats durs.

Les organismes peuplant les estrans rocheux sont soumis à des conditions écologiques qu'aucune protection ne peut atténuer : ils supportent avec rigueur les conséquences de l'alternance émersion-immersion, les problèmes liés à l'amplitude des variations thermiques pendant la marée basse quand la température de l'eau de mer est remarquablement stable sur de longues durées et enfin les problèmes liés aux variations de la salinité (pluie, évaporation...).

Les substrats durs étant favorables à la fixation d'organismes littoraux, les côtes rocheuses présentent un revêtement animal et végétal important les distinguant des plages sableuses. La répartition des organismes sur les estrans rocheux est dépendante de l'action de la mer: ses oscillations régulières déterminent l'étagement des peuplements et l'hydrodynamisme modifie leur composition. Sur l'estran sableux, seuls les organismes capables de s'enfouir dans le sédiment (ex. divers vers marins, bivalves ...) peuvent occuper l'estran à marée basse. Ainsi, la faune et la flore de l'estran obéissent aux conditions d'émersion/immersion se répartissant selon la qualité des mécanismes leur permettant de résister à l'émersion.

1.3. La zone intertidale, une zone de nourricerie pour de nombreuses espèces marines

Au cours de leur vie et en fonction de leur stade de développement (larves, juvéniles, adultes) les poissons occupent des habitats différents : aires de reproduction, de nourricerie, de nutrition, de migration. Ce sont des milieux que l'on qualifie d'habitats essentiels puisqu'ils sont nécessaires au maintien et au renouvellement des ressources. Dans tous les cas, ces changements d'habitats ont pour but d'optimiser la croissance, la survie et le potentiel reproducteur de l'individu (Gibson, 1997). Les changements majeurs d'habitats qui ont lieu durant la vie des poissons sont communs à de nombreuses espèces. Les larves concentrées sur les frayères sont transportées passivement ou activement selon les espèces vers les zones de nourriceries où les juvéniles se développent jusqu'à maturité sexuelle (Harden Jones, 1968) (Figure 2).

Malgré les conditions environnementales dures et fortement variables, la zone intertidale est caractérisée par la diversité et l'hétérogénéité de sa faune ainsi que sa productivité. C'est un habitat provisoire important pour le cycle de vie ou une partie de ce cycle de beaucoup de juvénile d'organismes marins (Potter *et al.*, 1986 ; Elliott *et al.*, 1990 ; Amara & Paul, 2003) tels que la plie commune *Pleuronectes platessa*, le bar *Dicentrarchus labrax*, le sprat *Sprattus sprattus*, le gobie *Pomatoschistus microps*, le syngnathe *Syngnatus accus* ou encore la crevette grise *crangon crangon* pour ne citer que quelques espèces.

De ce fait, les juvéniles de poissons et de macrocrustacés optent de façon temporaire pour la zone intertidale (Day *et al.*, 1989 ; Elliott & Hemingway, 2002), jouant ainsi le rôle de nourricerie, étape importante pour le renouvellement des stocks de pêche. Les nourriceries sont des aires géographiques limitées où se concentrent les juvéniles pour s'y nourrir et grandir durant leurs premières années d'existence (Beck *et al.*, 2001). Selon Miller *et al.* (1984), les nourriceries servent de refuge contre la prédation tout en offrant d'importantes quantités de nourriture. Ces conditions favorisent ainsi la croissance des juvéniles avant qu'ils ne soient recrutés dans la population adulte.

L'utilisation de ces zones de nourricerie est souvent fonction de la saison à laquelle se situe la reproduction (Ross & Epperly, 1985) en association avec les opportunités saisonnières du transport larvaire des frayères qui se trouvent au large vers les zones intertidales (Miller *et al.,* 1984). Ainsi, les rythmes d'arrivée peuvent avoir une importance au niveau du succès du recrutement (Fortier *et al.,* 1987 ; Sinclair et Iles, 1988).

De nombreux auteurs ont souligné qu'une large partie des débarquements dans le monde était constituée d'espèces occupant durant leur cycle de vie les eaux estuariennes et/ou intertidales (Pauly, 1988; Beck *et al.,* 2001; Gillanders *et al.,* 2003; Lamberth & Turpie, 2003). En effet, une étude récente a montré que ces habitats ont un intérêt économique majeur, car 44% des espèces halieutiques évaluées par le Conseil International pour l'exploration de la Mer (CIEM) en dépendent ; ces espèces, dites nourriceries dépendantes, représentent par ailleurs 77% des volumes de débarquements (Seitz, 2014).

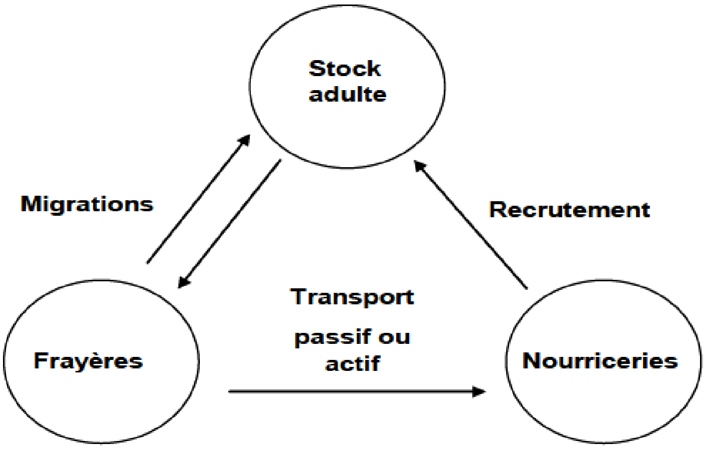

Figure 2. Le « triangle de migration ». Harden Jones, 1968.

1.4. Influence de l'environnement sur les communautés intertidales et leurs dynamiques

De par sa position à l'interface terre-mer, la zone intertidale est influencée par de nombreux facteurs environnementaux (biotiques et abiotiques). Cependant, la façon dont cet écosystème répond aux forçages environnementaux, notamment en ce qui concerne la composition et la structure des peuplements, leurs dynamiques et persistances saisonnières et interannuelles sont encore mal connues, en particulier pour les poissons et les macrocrustacés.

Les organismes utilisant la zone intertidale sont exposés à différents stress environnementaux tels que les fluctuations rapides et importantes de salinité, de température et des radiations solaires (Berghahn, 2000) (Figure 3). Sur les nourriceries, ces facteurs environnementaux peuvent agir sur la composition et la structuration des peuplements et aussi au niveau individuel sur la croissance, la condition et la survie des espèces et par conséquent sur le recrutement.

En général, les ressources disponibles de la zone intertidale conviennent au régime alimentaire des juvéniles et sont suffisamment abondantes pour limiter les compétitions au sein d'un même niveau trophique. Les conditions du milieu, et en particulier les conditions abiotiques sont favorables à l'installation de ces organismes au niveau de l'estran. D'autre part, la faible pression de prédation, qui relève soit de la turbidité (Cyrus et Blaber, 1987a, 1987b), soit de la présence de végétation (Livingstone, 1985), ou de la faible profondeur, permet aux juvéniles de coloniser cet écosystème.

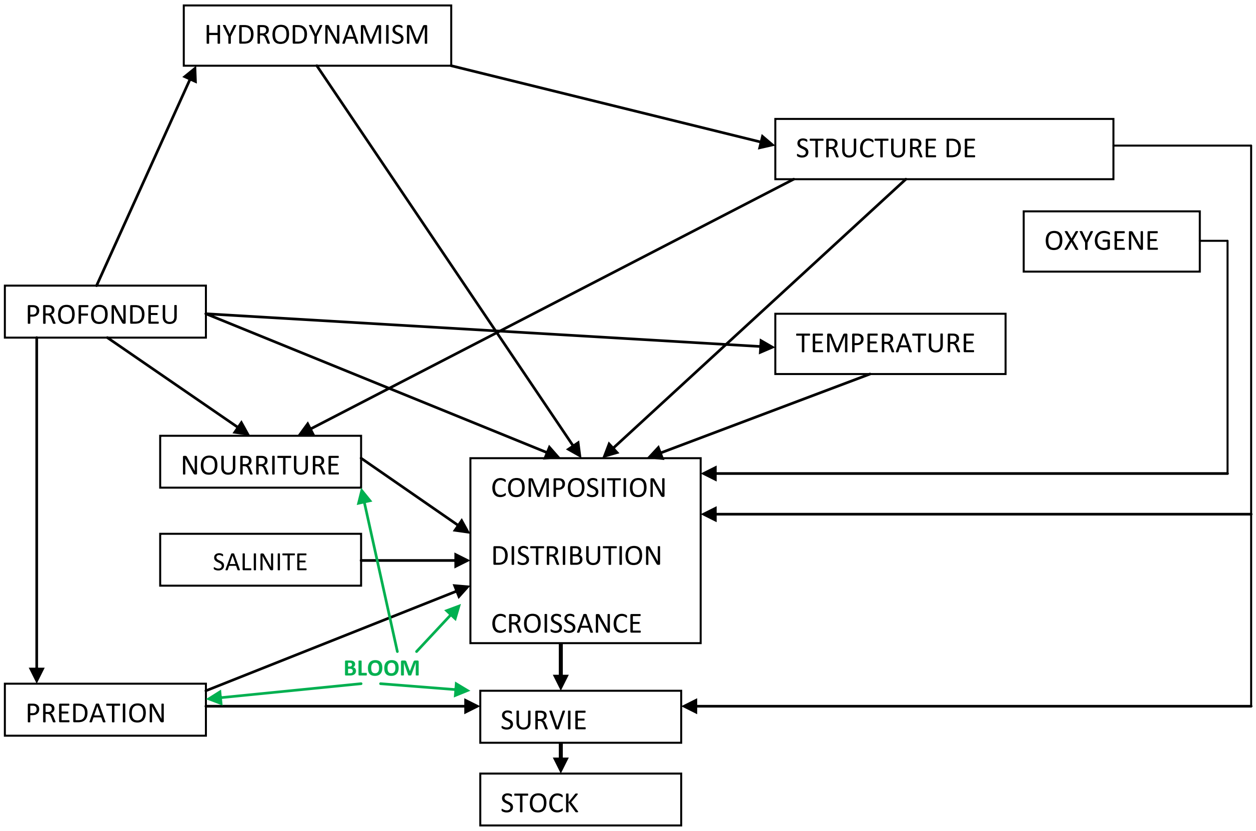

Figure 3. Diagramme (modifié et adapté de Gibson, 1994) illustrant les interactions entre les facteurs contribuant à la qualité de l'habitat qui influencent la composition du peuplement, la croissance et la survie des espèces et donc le recrutement et le renouvellement des stocks.

Par définition, les zones de nourriceries sont considérées comme des milieux où les ressources nutritives sont abondantes et non limitantes (Blaber & Blaber, 1980), des zones où la survie est optimale et où la prédation est limitée (Gibson & Yoshiyama, 1999) et des zones où la croissance des individus est optimale. La fonction de nourricerie jouée par ces écosystèmes apparaît donc capitale pour le développement et la survie des juvéniles et, par conséquent, le renouvellement des stocks (Gibson, 1994). Toutefois, un certain nombre d'études ont souligné l'existence de fortes mortalités durant la période juvénile. En effet, pour certaines espèces, notamment les poissons bentho - démersaux, le renouvellement des stocks halieutiques (recrutement[1]) semble dépendre en partie des événements subis durant la période de croissance juvénile sur ces nourriceries (Bradford, 1992; Rijnsdorp *et al.*, 1992). Les conditions biotiques et abiotiques rencontrées par les juvéniles durant leur séjour sur la

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[1] Le recrutement est le processus qui assure le renouvellement des stocks des espèces marines. Pour la plupart des espèces, le nombre de recrues correspond à la fraction la plus jeune de la population qui s'intègre pour la première fois à l'ensemble des poissons accessibles à la pêche (Laurec & Le Guen, 1981).

nourricerie sont autant de facteurs qui agiront sur le niveau de recrutement et donc sur les capacités de renouvellement des stocks des espèces exploitées. Par exemple, la survie des juvéniles est influencée directement par la prédation mais aussi indirectement par la disponibilité alimentaire qui affecte avant tout leur croissance. Un manque de nourriture altère à court terme la condition du poisson, et à moyen terme, freine sa croissance, voir entraine sa mort si la privation persiste (Gibson, 1994).

Les variations saisonnières et interannuelles des conditions environnementales de la zone intertidale peuvent affecter les juvéniles qui la colonisent. C'est le cas par exemple sur littoral Nord-Pas-de Calais de certaines efflorescences phytoplanctoniques comme le bloom printanier de *Phaeocystis globosa* qui perturbe l'écosystème côtier de la Manche orientale (Spilmont *et al.*, 2009; Desroy & Denis, 2004). Cette espèce coloniale renferme de grandes quantités de mucus qui se déversent dans l'eau lors de la rupture des colonies. Sous des conditions spécifiques de vent, une mousse épaisse et malodorante peut alors recouvrir les plages (Figure 4). En outre, la prolifération de cette espèce modifie complètement le fonctionnement de l'écosystème (Lancelot, 1995).

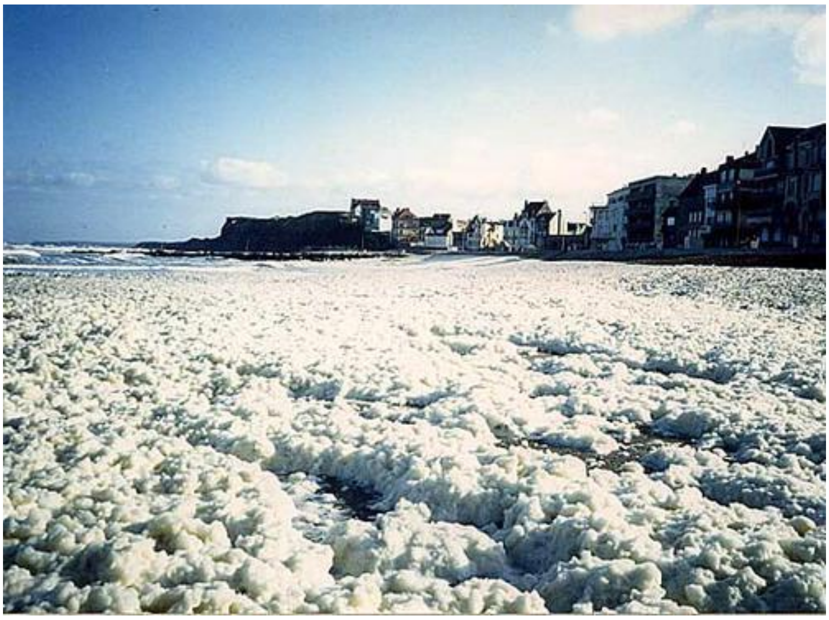

Figure 4. Écume de Phaeocystis sur la côte d'opale (Photo Hubert Grossel).

De bonnes performances physiologiques (croissance rapide et bonne condition) des juvéniles au niveau des nourriceries augmentent leurs chances de survie en diminuant leur vulnérabilité à la prédation (Sogard, 1997; Able *et al.*, 1999), phénomène qui est principalement dépendant de la taille des poissons et des prédateurs (Van der Veer & Bergman, 1987; Van der Veer *et al.,* 1990; Wennhage, 2000). Cela leur permet aussi d'exploiter plus rapidement une plus large gamme de proie. Les conditions environnementales rencontrées par les juvéniles au niveau des nourriceries vont influencer les performances physiologiques des juvéniles de poissons qui sont très sensibles aux changements environnementaux (Adams, 2002).

Si l'on considère que la qualité de l'habitat est une fonction positive de la croissance et/ou de la condition, les performances physiologiques d'une espèce dans son milieu, témoignent de la qualité de ce dernier (Van der Veer *et al.,* 2001; Amara, 2003 ; Amara *et al.,* 2007). L’estimation de la croissance chez les juvéniles de poisson est particulièrement intéressante et est fréquemment utilisée dans le cadre de l’évaluation de la qualité des nourriceries puisqu’elle est déterminée principalement par des processus et/ou facteurs locaux caractéristiques de l’habitat (Scharf, 2000, Sogard *et al.,* 2001; Amara *et al.,* 2007). Outre l’estimation de la croissance, il existe de nombreux indices dits « de condition » qui ont été développés sur les poissons et notamment sur les juvéniles afin d’estimer la croissance, l’état nutritionnel ou l’état de santé des individus (voir la revue dans Ferron & Legget, 1994 et dans Suthers, 1998) : les indices de type biochimique (quantification des acides nucléiques, des composés lipidiques, des protéines) et de type morphométrique (mensurations des poissons) (Blackwell *et al.* 2000; Buckley, 1984 ; Clemmesen, 1994 ; Gilliers *et al.,* 2004 ; 2006 ; Amara *et al.,* 2007 ; Amara *et al.,* 2009).

De nombreuses études ont été effectuées sur les estrans rocheux : leur composition en faune et flore, leurs structures, la diversité des conditions environnementales, les facteurs climatiques et les cycles de marée qui déterminent la distribution des espèces habitant ces zones (Lewis, 1964 ; Connell, 1972 ; Vermeij, 1972 ; McQuaid & Branch, 1984 ; Chelazzi *et al.,* 1988 ; Truchot, 1990 ; Warman *et al.,* 1993 ; Anderson, 1995 ; Little & Kitching, 1996 ; Gibson, 2003 ; Alyakrinskaya, 2004 ; Grube & Blaha, 2005 ; Harley *et al.,* 2009 ; Little *et al.,* 2009).

En opposition, peu d’études sur l’estran sableux ont été faites. Parmi les systèmes intertidaux dans le monde, les plages sableuses sont l'un des plus vaste, dominant la plupart des côtes tempérées (Short, 1999). C'est le cas en Manche Orientale où les plages sableuses représentent 74% du littoral, et constituent d'importantes zones de nourriceries pour les juvéniles de poissons (Amara, 2003 ; Selleslagh & Amara, 2008).

Les études réalisées sur les communautés de poissons et de macrocrustacés de l'estran sableux ont principalement été entreprises sur une courte échelle de temps, pas plus de 5 ans (par exemple, Gibson *et al.,* 1993). Des études à long terme ont porté uniquement sur la dynamique des populations de l'une des espèces dominantes (Van der Veer *et al.,* 1991; Campos *et al.,* 2010).

Dans ce contexte scientifique et régional, l'objectif global de ce travail est de décrire les assemblages des peuplements de poissons et de macrocrustacés de la zone intertidale et d'analyser l'influence de l'environnement sur les espèces. Une telle étude a pour but de mieux comprendre le fonctionnement de cet écosystème et de préciser son importance dans le cycle biologique des espèces marines, notamment des espèces d'intérêt halieutique.

Nous tenterons de répondre aux questions suivantes:

1- Quelle est l'importance et la fonction de la zone intertidale pour les poissons et les macrocrustacés ?

2- Comment évoluent les communautés de poissons et de macrocrustacés fréquentant la zone intertidale sous l'effet des changements environnementaux ? Cette analyse sera réalisée à l'échelle interannuelle sur une série à long terme (11 années) et à l'échelle saisonnière.

3- Les variations des conditions environnementales de la zone intertidale pendant la période printanière sont-elles d'ordre à affecter les performances physiologiques et la survie des juvéniles qui colonisent cet écosystème? Nous avons focalisé notre étude sur l'espèce de poisson dominante de la zone intertidale, la plie commune *Pleuronectes platessa*.

La thèse est structurée en une introduction générale, matériel et méthodes, 3 chapitres représentant les principaux résultats, une conclusion générale, des perspectives d'avenir et des références bibliographiques.

Le 1er chapitre intitulé **Impact des paramètres environnementaux sur la composition des poissons et macrocrustacés de la zone intertidale en période printanière,** nous a permis de comprendre l'utilisation de la zone intertidale de la plage Sainte Cécile plateforme nourricière pour les juvéniles de poissons et de macrocrustacés en période printanière. Les résultats obtenus nous ont permis de définir:

- La composition des assemblages et leur variabilité inter annuelle,
- Les principaux facteurs biotiques et abiotiques les affectant et
- L'impact des blooms de *Phaeocystis globosa* sur la structure du peuplement.

Le chapitre 2 intitulé **Persistance saisonnière et annuelle et stabilité de la structure des communautés de poissons et macrocrustacés en zone intertidale,** aborde l'évolution des assemblages de poissons et de macrocrustacés au fil des saisons et détermine aussi bien les différences qu'il peut y avoir entre les saisons que celles qui existent entre les années. Les espèces et les paramètres environnementaux qui contribuent à ces différences sont ainsi mis en évidence.

Enfin, le chapitre 3 intitulé **Variation des performances biologiques des juvéniles de la plie commune (*Pleuronectes platessa*) en zone intertidale.** Dans ce chapitre, nous avons analysé les performances physiologiques des juvéniles de plie commune *Pleuronectes platessa* à partir d'indices mesurés sur ces individus. Pour déterminer l'état de santé de notre site d'étude, nous avons également évalué les paramètres environnementaux.

CHAPITRE 2

Matériel et méthodes

2. Matériel et méthodes :

2.1. Zone d’étude :

2.1.1. La Manche Orientale :

La Manche, mer épicontinentale, est un carrefour biogéographique et un carrefour économique important de l’Europe du Nord Ouest bordée au Nord par l’Angleterre et au Sud par la France. C’est une zone ouverte à l’Ouest aux influences de l’Océan Atlantique et elle communique avec la mer du Nord par le détroit du Pas de Calais (35 km de large) formant ainsi un corridor long de 500 km et large à son maximum de 250 km. Sa superficie est de près de 77000 km² avec une profondeur maximale dans la fosse centrale au Nord Ouest de la presqu’ile du Cotentin de 174 m. D’un point de vue géographique et océanographique, Cabioch (1968) distingue deux bassins: le bassin occidental, situé à l’Ouest de la ligne des roches des Casquets (Ouest du cap de la Hague) jusqu' à la pointe Bill of Portland en Grande-Bretagne, plus profond et largement influencé par les eaux atlantiques, et à l'Est le bassin oriental qui est limité par une ligne entre Calais et Douvres, moins profond, plus continental et largement influencé par le seul grand fleuve se déversant en Manche, le long des côtes françaises, la Seine.

La partie orientale, sur laquelle l’étude s’est faite, d’une superficie de près de 40000 km², s’étend de la Baie de Seine jusqu’au détroit du Pas de Calais (49°62N-1°E – 51°N-1°90E). La profondeur moyenne de la Manche orientale est de 50 m avec un maximum de 70 m et le fond est essentiellement constitué de substrat sableux et de graviers (figure 5).

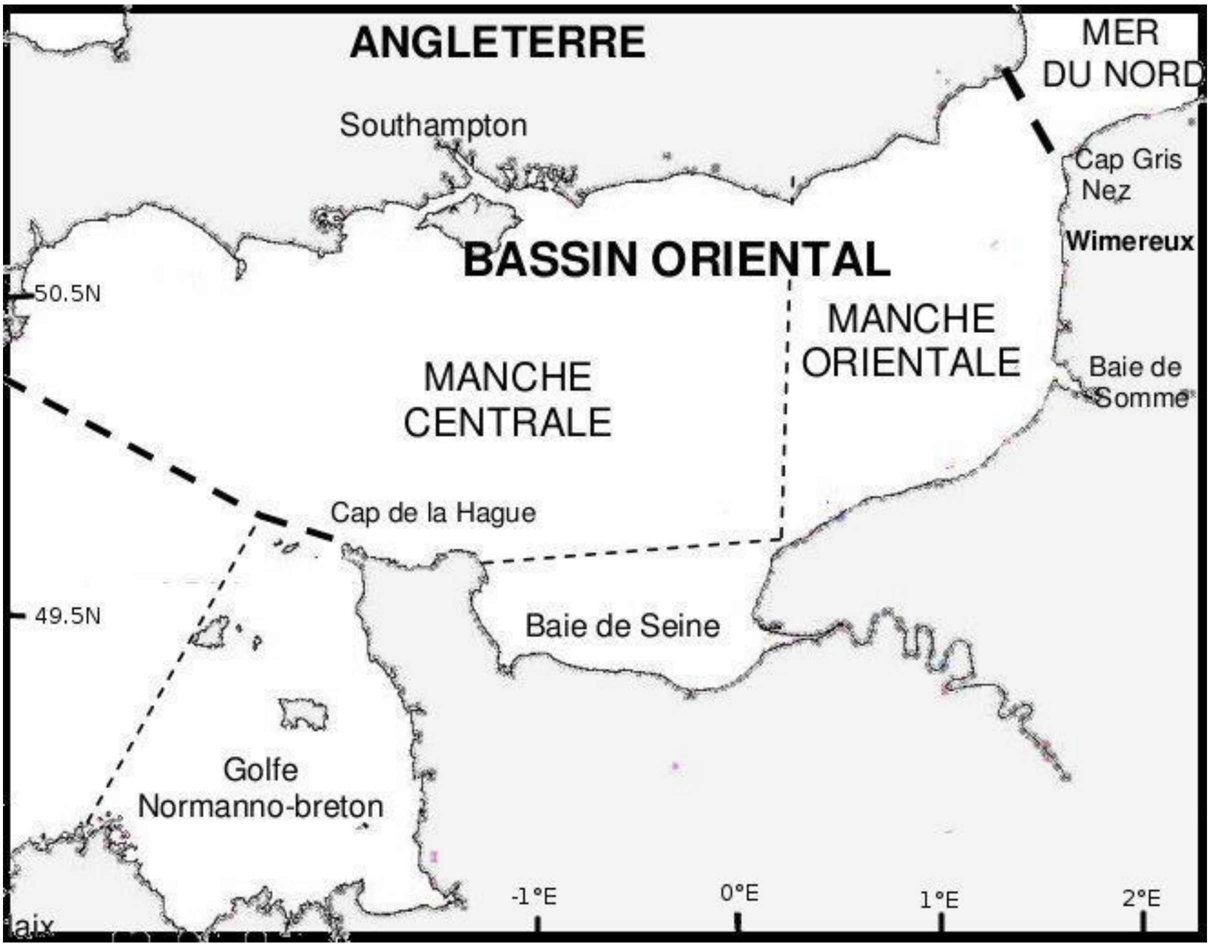

Figure 5. Localisation géographique de la zone d'étude : La Manche orientale (thèse Jouanneau, 2012)

- **Caractéristiques physiques**

Régime marégraphique, circulation des masses d'eau et conditions hydroclimatiques en Manche Orientale

Le régime marégraphique de la Manche Orientale est de type mégatidal (forte marée) (Anonyme, 1988), avec un marnage (différence de hauteur entre haute et basse mer) d'environ 9 m en vives eaux. La Manche orientale est par ailleurs soumise à un important hydrodynamisme lié à de forts courants de marée, qui structure fortement ses écosystèmes et qui est à l'origine d'un classement très marqué du sédiment. Le goulot d'étranglement créé au niveau du détroit du Pas de Calais par sa forme d'entonnoir (d'une largeur de plus de 100 km sur sa limite ouest jusqu'à 35 km au niveau du détroit) engendre une accélération des masses d’eau provenant de l’Océan Atlantique vers la mer du Nord. Les courants instantanés inférés par la marée sont alternatifs (courant de flot portant vers le Nord Est et courant de jusant vers le Sud Ouest) et parallèles à la côte (Brylinski, 1993) et peuvent atteindre jusqu’à 1,5 m/s en vives eaux. Il en résulte une dérive résiduelle de vitesse 2,7 milles par jour (Salomon et Breton, 1993). Le régime tidal en Manche orientale est de type semi-diurne, caractérisé par deux basses mers et deux pleines mers par jour selon une fréquence moyenne de 12h et 24min. Concrètement, il faut 2 à 4 mois à une masse d’eau passant au centre de la Manche pour arriver dans le détroit du Pas de Calais (Guéguéniat *et al.*, 1993).

Ce contexte marégraphique favorise la création d’une masse d’eau côtière permanente bien individualisée, appelée « le fleuve côtier » (Brylinski *et al.*, 1991). Cette masse d’eau est sans cesse alimentée par les apports de plusieurs fleuves et cours d’eau depuis la Baie de Seine jusqu’au détroit du Pas de Calais. La dispersion de ses apports vers le large est freinée par un front les maintenant ainsi en zone côtière (Brylinski *et al.*, 1991). La circulation du fleuve côtier est influencée par le courant résiduel de marée dirigé vers la Mer du Nord et qui est également soumise au forçage du vent orienté préférentiellement du Sud vers l’Ouest (Salomon et Breton, 1991) (figure 6).

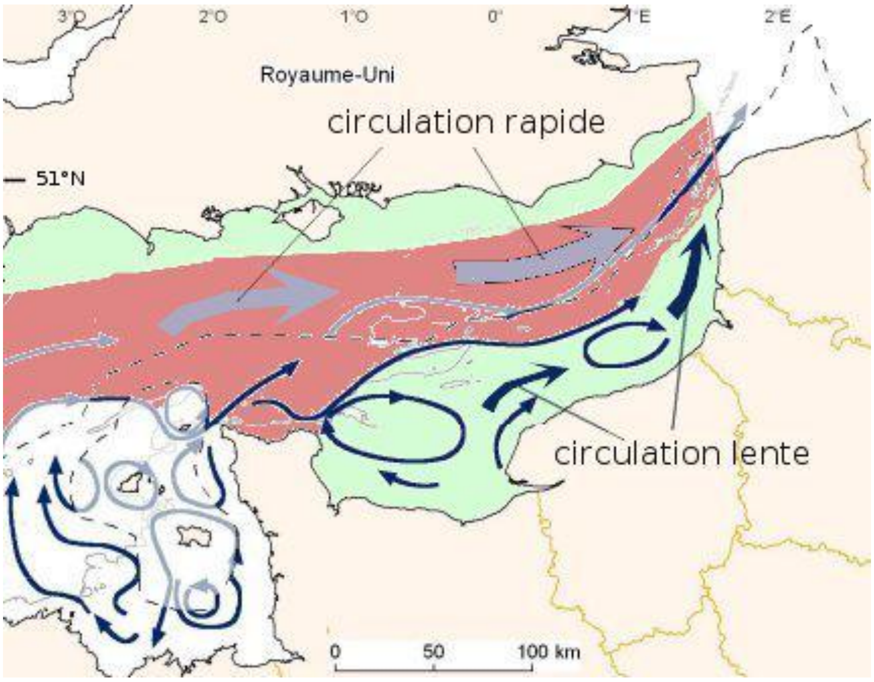

Figure 6. Structuration de la Manche Orientale. Circulation lente observée sur la bande littoral à cause des phénomènes de friction, et circulation rapide de l'eau atlantique dans la zone centrale du détroit (Salomon, et Breton, 1993).

Les forts débits de la Seine (une moyenne de 435 m^3/s) font d'elle la source principale des apports d'éléments transportés (Matières En Suspension : MES, Guéguéniat *et al.,* 1995 ; Lafite *et al.,* 2000 ; cellules algales, Huault *et al.,* 1994 ; sels nutritifs, surtout les nitrates et les phosphates, Bentley *et al.,* 1993) du fleuve côtier et contribuant ainsi à plus de 90% des apports totaux (Prygiel *et al.,* 2000). La Somme représente la seconde source d'apports continentaux en phosphore (380 t), en silicium (5400 t), en azote (9000 t) et en MES (67800 t; Loquet *et al.,* 2000). La baie de Somme serait l'initiatrice d'une production phytoplanctonique qui dérive progressivement vers le nord jusqu'au détroit du Pas de Calais (Brylinski *et al.,* 1996 ; Hoch et Garreau, 1998 ; Breton *et al.,* 2000 ; Vantrepotte, 2003). La Manche orientale constitue ainsi une zone de transfert d'apports non négligeables vers la Mer du Nord (Velegrakis *et al.,* 1999), et plus globalement, comme une zone de transfert entre les eaux atlantiques et celles de la Mer du Nord (Salomon et Breton, 1993).

Les conditions hydroclimatiques en Manche sont très contrastées, depuis les eaux océaniques Atlantiques, dont la température varie peu (10 °C en hiver, 15 °C en été), jusqu'aux eaux peu profondes au niveau du Pas de Calais variant de 6 à 17°C. Les changements de salinité quant à eux sont faibles et ponctuels, ce qui conduit à conclure que la température et les courants sont les principaux facteurs écologiques de la Manche.

Le climat de la région est un climat océanique tempéré avec des températures de l'air variant de façon sinusoïdale avec un maximum en été compris entre 20 et 25 °C (juillet/août) et un minimum en période hivernale entre -5 et 5°C. Le total annuel des précipitations est assez fort et les moyennes annuelles sont entre 800 et 1000 mm d'eau. Les précipitations présentent généralement un maximum saisonnier en automne (précipitations totales moyennes de 80 mm par mois), et des niveaux à peu près équivalents en hiver et en été (entre 40 et 50 mm de précipitations totales par mois). Ces précipitations, réparties tout au long de l'année, influencent fortement les apports fluviatiles. Le régime océanique engendre des vents dominants de secteur Ouest à Sud Ouest, avec la présence marquée au printemps de vents de Nord Est. Les vents sont donc continentaux et leur régime est constant à l'échelle pluriannuelle.

Un seul types d'habitats localisés le long des côtes françaises de la partie Est de la Manche Orientale a été étudié dans le cadre de ce travail : la plage sableuse de Sainte Cécile située à quelques kilomètres au nord de l'estuaire de la Canche, zone que l'on qualifiera de « zone intertidale».

2.1.2. Plage sableuse de Sainte Cécile :

La plage sableuse de Sainte Cécile a constitué le site principal de cette étude (figure 7). Elle est située en rive nord de l'estuaire de la Canche sur les côtes françaises de la Manche Orientale, plus précisément entre Hardelot au nord et Étaples au sud (50°33'N, 1°35'E). La plage est caractérisée par la présence de barres sableuses et de bâches parallèles à la côte constituées de sables moyens et fins. Le régime des marées est semi diurne et la largeur de la zone intertidale étudiée est d'environ 700 m durant les marées de mortes eaux et d'environ 1500 m en marées de vives eaux et un marnage de 3 à 7 m lors des marées de mortes eaux et vives eaux (Amara and Paul, 2003). La plage de Sainte Cécile est soumise à l'action conjuguée de la houle et des courants de marée. Bien qu'elle soit située à proximité de l'estuaire de la Canche, la plage de Sainte Cécile n'est pas influencée par les apports estuariens d'eau douce; la salinité est typiquement marine.

2.2. Mesures des paramètres environnementaux et climatiques :

2.2.1. Données environnementales :

Les données environnementales de : Température de l'eau (T, °C), Salinité (S), Matière Particulaire en Suspension (SPM), Chlorophylle a (Chla), Carbone Particulaire Organique (POC) et la vitesse du vent sont obtenues soit à partir des mesures réalisées lors de nos échantillonnages, soit à partir des données du réseau national de monitoring et de surveillance SOMLIT (Service d'Observation en Milieu LITtoral) (http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). Les données SOMLIT sont obtenues au niveau de la station côtière permanant C (50°40'75 N; 1°31'17 E) (figure 7) localisée près de la plage Sainte Cécile. Les mesures et prélèvements d'eau ont été réalisé à bord du bateau océanographique Sepia II, de façon bimensuelle à marée haute et en subsurface (-2 m, point S) et près du fond de la colonne d'eau (approximativement -20 m, point F)

- **Abondance de *Phaeocystis globosa***

L'abondance des cellules de *Phaeocystis globosa* (Scherffel, 1899) a été déterminée sous microscope inversé selon la méthode Utermöhl à partir d'échantillons préservés dans une solution de Lugol à concentration finale de 2% jusqu'en 2006 et une solution de Lugol glutaraldehyde à concentration finale de 1% après 2006. Le nombre de cellules de

Phaeocystis en forme de colonie a été compté séparément des cellules libres un mois après l'échantillonnage (Schoemann *et al.,* 2005) excepté pour les échantillons de 2000 à 2005 où les comptages ont été faits plusieurs mois voir plusieurs années après l'échantillonnage. A cause de la destruction de la matrice de colonie plusieurs mois après la fixation à la solution de Lugol, seules les cellules libres de *P.globosa* ont été comptées (Chang, 1984). La biomasse de *Phaeocystis* a été estimée à l'aide d'un facteur moyen de conversion du carbone de 89.5 pg.C.cell^{-1} (Schoemann *et al.*, 2005).

- **Débit des estuaires de la Seine et de la Somme:**

Les débits de l'estuaire de la Seine à Poses (m^{3}.s^{-1}) ont été obtenu au près du Groupement d'Intérêt Publique Seine-Ava (GIP Seine-Aval) (http://seine-aval.crihan.fr/web/). Les débits de la Somme à partir du site eaufrance.

2.2.2. Données climatiques :

- **L'indice NAO**

L'oscillation nord-atlantique, en anglais North Atlantic Ocillation (NAO), est un phénomène océanique et atmosphérique qui influence le climat (température et précipitations) sur le pourtour de l'Atlantique nord et régit les hivers d'Europe du Nord. Il fait référence aux mouvements de va-et-vient, selon un axe nord-sud, de masses d'air situées au-dessus de l'Arctique et de l'Islande en direction des Açores et de la péninsule Ibérique. Ce phénomène est plus important en hiver et a deux phases : une phase positive et une phase négative. Chaque phase est responsable de conditions atmosphériques distinctes autour de l'Atlantique nord. L'indice de l'oscillation nord-atlantique est calculé chaque année à partir de la différence de pression entre les Açores à 38°N et l'Islande à 65°N en tenant en compte de la variation de l'écart de pression entre ces deux points par rapport à la moyenne. Ce calcul s'effectue sur les données de Décembre à Mars dont on fait la moyenne et qu'on normalise, c'est-à-dire qu'on divise par l'écart-type de la pression calculé sur une longue période.

Les indices de NAO ont été obtenus à partir du site web du Centre National de la Recherche Atmosphérique (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

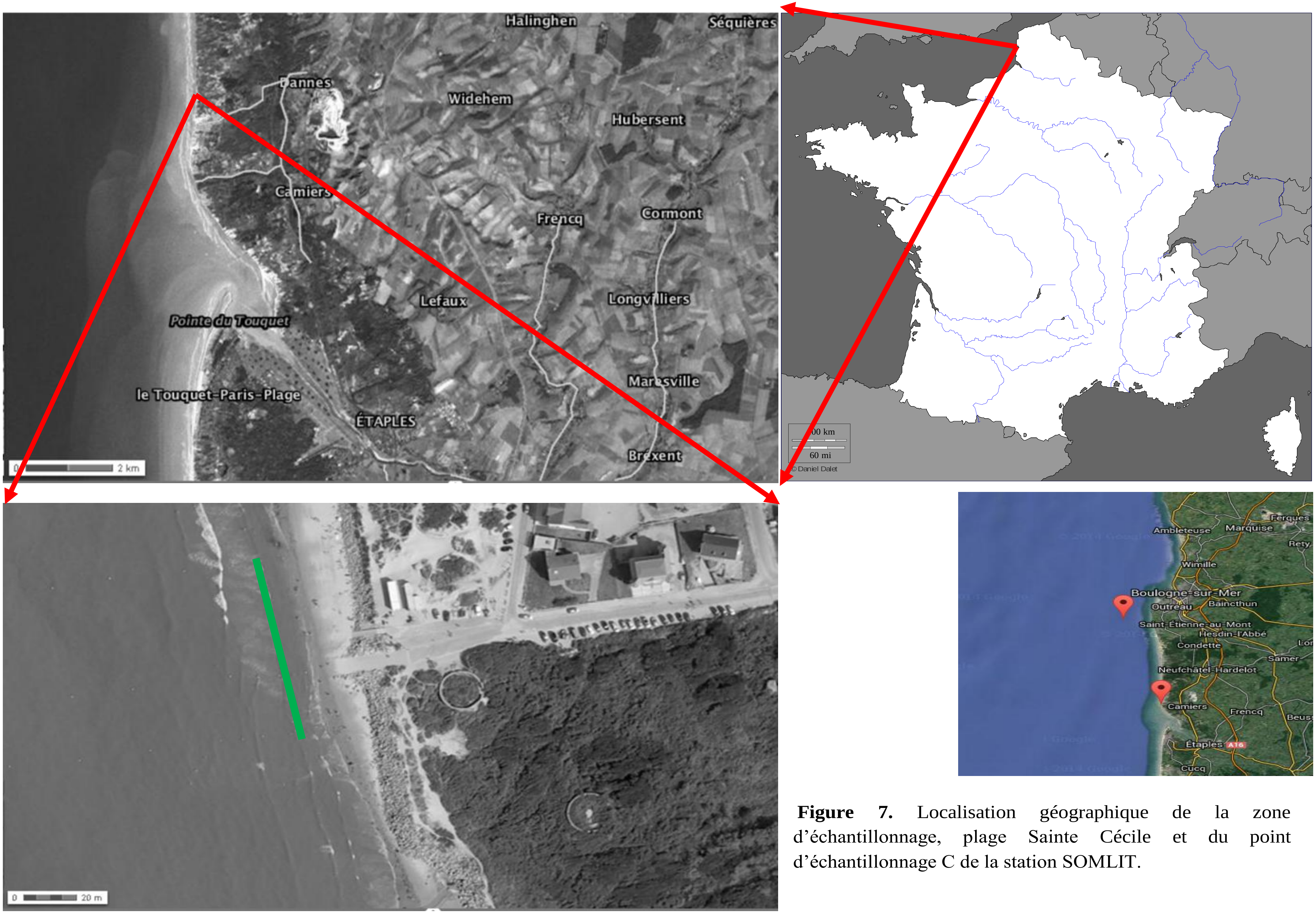

Figure 7. Localisation géographique de la zone d'échantillonnage, plage Sainte Cécile et du point d'échantillonnage C de la station SOMLIT.

2.3. Stratégie d'échantillonnage de la macrofaune :

2.3.1. Engin de pêche en zone intertidale :

En zone intertidale, c'est-à-dire au niveau de la plage de Sainte Cécile, l'échantillonnage a été effectué à l'aide d'un chalut à perche de 1.5 m d'ouverture horizontale, de 5.5 m de profondeur de poche au maillage de 8x8 mm à son entrée et de 5x5 mm au cul et est équipé d'une chaîne qui permet de racler le fond pour une meilleure capture de la faune après remise en suspension (figure 8).

Les pêches ont été réalisées de jour durant la marée descendante lorsque la hauteur d'eau de la bâche est d'environ 1 mètre, soit 2 à 3 heures après la marée haute. Selon les recommandations de Riley et Corlett (1966), la vitesse de traction du filet de pêche doit être maintenue aussi constante que possible pendant l'échantillonnage et est estimée à 38 m/min. le filet est tracté par deux personnes parallèles au trait de côte, à une profondeur inférieur à 1 m durant le jusant sur une distance de 250 m en général et couvrant ainsi une surface de 400 m² (figure 9). Cette distance est mesurée à l'aide d'une corde marquée tous les 50 m, qui est tendue parallèlement à la côte. Toutefois, lorsque les conditions sont défavorables (par exemple colmatage du filet entraînant un refoulement), la distance de chalutage est écourtée afin de ne pas sous-estimer les effectifs.

Figure 8. Chalut à perche utilisé en zone intertidale de la plage Sainte Cécile.

Les campagnes de pêches ont été réalisées durant 11 années (de 2000 à 2013) de façon hebdomadaire en période printanière (de mars à juin), bimensuelle de juillet à septembre et mensuelle de octobre à février (Tableau 1). L'échantillonnage resserré au printemps a été réalisé afin d'étudier la colonisation de la zone intertidale au cours de cette période. Le reste de l'échantillonnage a été réalisé pour étudier les variations saisonnières. Les données de 2000 et 2010 sont issues de campagnes réalisées avant mon arrivée au laboratoire. J'ai pu bénéficier de ces données.

Figure 9. Pêche au chalut à perche en zone intertidale. Le chalut est trainé par deux personnes.

2.3.2. Analyse des captures :

2.3.2.1. Identification et analyse biométrique :

Après chaque pêche, les espèces sont stockées dans des sacs plastiques afin de les transporter rapidement au laboratoire pour le trie. Au laboratoire, tous les individus sont triés, dénombrés puis identifiés au niveau spécifique (tableau 2). Pour les poissons, des mesures de poids (en mg), de la longueur totale (mm) et de la longueur standard (mm) sont effectuées respectivement grâce à une balance électronique (Scout pro OHAUS) et à l'aide d'un ichtyomètre électronique (Mitutoyo CD 15 CP) sur tous les poissons.

Tableau 1 : récapitulatif des campagnes de pêche effectuées entre 2000 et 2013.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
2000														X	X	X	X	X	X	X	X	X		2	X	X	X		X		2				X				X													
2001																																																				
2002																																																				
2003											X	X	X	X	X	X	X	X	X	X																																
2004											X	X	X	X	X	X	X	X		2	X		X																													
2005								X	2		X	X	2	X	X	X	X	X	X	X	X				X			X										X				X					X				X	
2006			X				X		X		X		2	X		X	2		2		X	X	X		X			X								X		X					X									
2007														X	X	X	X	X		X																																
2008																																																				
2009													X	X	X	X	X	2	X	X		X	X		X																											
2010													X	X	X	X	X	X	X	X		2	X	X	X	X																										
2011										X	X	X	X	X	X	X		X	X	2	X	2		X	X																											
2012														X	X	X	X	X	X	2	X	X	X	X	X	X		X		X							X			X			X			X				X		
2013		X				X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X									X					X								X		

Tableau 2. Liste des espèces capturées durant les 11 années d'échantillonnage.

Famille	Espèce	Nom commun
	Poissons	
Pleuronectidae	*Pleuronectes platessa*	Plie
	Platichtys flesus	Flet
Soleidae	*Solea solea*	Sole
Scophtalmidae	*Psetta maxima*	Turbot
	Scophthalmus rhombus	Barbue
Gadidae	*Merlangius merlangus*	Merlan
	Trisopterus luscus	Tacaud
Triglidae	*Trigla lucerna*	Grondin perlon
Clupeidae	*Sprattus sprattus*	Sprat
	Clupea harengus	Hareng
Osmeridae	*Mallotus villosus*	Capelan
Moronidae	*Dicentrarchus labrax*	Bar
Trachinidae	*Echiichthys vipera*	Vive
Cottidae	*ind species (chabot)*	Chabot
Ammodytidae	*Ammodytes tobianus*	Lançon
Gobiidae	*Pomatoschistus microps*	Gobie
Atherinidae	*Atherina presbyter*	Prêtre
Syngnathidae	*Syngnathus acus*	Syngnathe
Agonidae	*Agonus cataphractus*	Souris de mer
Gasterosteidae	*Gasterosteus aculeatus*	Epinoche
	Pungitius pungitius	Epinochette
mugilidae	*Lisa ramada*	Mulet
Lotidae	*Ciliata mustela*	Motelle à 5 barbillons
	Crustacés	
Crangonidae	*Crangon crangon*	Crevette grise
Palaemonidae	*Palaemon longirostris*	Bouquet
	Palaemon serratus	Crevette rose
Portunidae	*Carcinus maenas*	Crabe vert
	Liocarcinus holsatus	Crabe nageur
	Portumnus latipes	Crabe des sables
Porcellanidae	*Pisidia longicornis*	Crabe porcelaine
Majiidae	*Macropodia longirostris*	Araignée de mer
Grapsidae	*Hemigrapsus sanguineus*	Crabe japonais
Varunidae	*Eriocheir sinensis*	Crabe chinois

Une partie de ce travail s'intéresse à l'étude de la plie commune (*Pleuronectes platessa*). Pour cela, les juvéniles de cette espèce dont les tailles sont comprises entre 15 et 30 mm sont conservés à -20 °C pour d'ultérieures analyses.

2.3.2.2. Densité :

Les captures d'une espèce sont exprimées en densité (ind.1000 m^{-2} : Eq. 1), permettant ainsi de comparer différents échantillons en standardisant les données. On la calcule selon l'équation suivante :

$$Di = \frac{Qi}{A} \times 1000 \quad \text{(Eq. 1)}$$

Où Di est la densité et représente le nombre d'individus de l'espèce i par 1000 m^2, Qi, le nombre d'individus pour une espèce i et, A, la surface échantillonnée (en m^2).

Le taux d'occurrence (% ; Eq 2) d'une espèce permet de caractériser l'étendue de la répartition de cette espèce dans un écosystème donné, en particulier de définir si cette espèce est plutôt rare ou commune.

$$Oc = \frac{Ci}{Ct} \quad \text{(Eq. 2)}$$

Où Oc représentent le taux d'occurrence (%), Ci, le nombre de campagnes où l'espèce i est présente et Ct, le nombre total de campagnes.

Les espèces ont été classées dans des catégories selon leur occurrence en suivant les critères définis par Guérault *et al.*, (1995) :

- Rare, (<13%) ;
- 13%<Occasionnelle<25% ;
- 25%<Commune<50% ;
- Constante, (>50%).

2.3.2.3. Indices de diversité :

Les différents indices de diversité permettent d'étudier la structure des peuplements en faisant référence ou non à un contexte spatio-temporel concret et permettent d'avoir une évaluation de la biodiversité du peuplement. Durant toute la période de l'échantillonnage, différents niveaux de diversité ont été mesurés à l'aide de trois indices : la richesse spécifique, l'indice de Shannon-Weaver (H') et l'indice d'équitabilité de Piélou (J').

2.3.2.4. La richesse spécifique S :

La richesse spécifique S est représentée par le nombre total d'espèces capturées par unité de surface.

S= nombre d'espèce de la zone d'étude

Cet indice peut être utilisé pour analyser la structure taxonomique du peuplement et permet de distinguer les variations spatiales (richesse ou pauvreté de la zone en espèces) et les variations temporelles (les minima et maxima en fonction des saisons et des zones).

2.3.2.5. L'indice de Shannon-Weaver H':

Cet indice est le plus couramment utilisé et est recommandé par différents auteurs (Gray *et al.,* 1992). Il permet d'exprimer la diversité en prenant en compte le nombre d'espèces et l'abondance des individus au sein de chacun de ces espèces. Il est exprimé par la formule suivante :

$$H^{'} = -\sum_{i=1}^{s} p_i \log p_i$$

Avec :

p_i = abondance proportionnelle ou pourcentage d'importance de l'espèce : $p_i = n_i/N$.

S= nombre total d'espèces.

n_i= nombre d'individus d'une espèce donnée dans l'échantillon, i allant de 1 à S (nombre total d'espèces).

N= nombre total d'individus de toutes les espèces dans l'échantillon.

Ainsi, une communauté dominée par une seule espèce aura un coefficient moindre qu’une communauté dont toutes les espèces sont codominantes. La valeur de l’indice varie de 0 (si tous les individus du peuplement appartiennent à une seule et même espèce, si dans un peuplement chaque espèce est représentée par un seul individu ou bien une espèce dominant très largement toutes les autres) à log S (lorsque toutes les espèces ont une même abondance et répartis d’une façon égale sur toutes les espèces) (Frontier, 1983). D’après Peet (1974), l’indice Shannon-Weaver H’ est un indice de type I, sensible aux variations d’importance des espèces les plus rares. Cet indice, déterminé à partir des échantillons, dépend non seulement du nombre d’espèces mais aussi du nombre d’individus représentant chaque espèce (la fréquence relative).

2.3.2.6. L’indice d’équitabilité de Piélou J :

L’indice de Shannon est souvent accompagné de l’indice d’équitabilité de Piélou (1975), appelé également indice d’équirépartition (Blondel, 1979) car il prend en compte l’équirépartition des individus par taxon. Il consiste à établir le rapport entre la diversité mesurée et la diversité théorique maximum pour une taille d’échantillon et un nombre d’espèces données. Il est exprimé par la formule suivante :

$$J' = \frac{H'}{H'_{max}} = \frac{H'}{\log_2 (N)}$$

Il varie de 0 (un seul taxon) à 1 (même nombre d’individus dans chaque taxon).

2.4. Indicateurs de performances physiologiques :

2.4.1. Espèces cibles : la plie commune :

La plie commune *Pleuronectes platessa* (Linnaeus, 1758) a été retenue dans ce travail pour étudier les variations des performances physiologiques des poissons fréquentant la zone intertidale. C'est l'espèce de poisson la plus abondante qui fréquente la zone intertidale, particulièrement au printemps. Cette espèce se reproduit au large entre décembre et février (Rijnsdorp *et al.,* 1992), les larves sont transportées par les courants et les marées au niveau des plages sableuses le long du littoral Nord pas de Calais. Tout juste métamorphosés, les juvéniles y restent environ trois mois, de mars à début juin, avant de regagner la zone subtidale et les eaux côtières.

Figure 10. Juvénile de plie commune *Pleuronectes platessa* (Linnaeus, 1758) au moment de la colonisation de la zone intertidale (thèse Selleslagh, 2008).

Pour analyser les performances physiologiques des juvéniles de plie, trois types d'indices ont été retenus et mesurés. Ces indices ont été identifiés comme étant pertinents à l'évaluation de la qualité du milieu aquatique dans d'autres études menées en Manche (Amara, 2003 ; Gilliers *et al.*, 2004,2006 ; Amara *et al.*, 2007). Le temps de réponse étant différent pour chaque indice, cela donne une signification écologique différente. De plus l'utilisation conjointe de plusieurs indices est recommandée afin d'intégrer les réponses des organismes aux différentes échelles de temps et de permettre une estimation fiable des conditions des organismes et d'apprécier l'effet des modifications environnementales (Suthers, 1998 ; Fukuda *et al.*, 2001 ; Adams, 2002).

2.4.2. Indice de condition morphométrique :

L'indice de condition utilisé dans le cadre de ce travail est l'indice de condition K de Fulton K (1911). Il s'obtient à partir des mensurations (taille et poids du poisson) et est donc rapide et facile à calculer et peu coûteux. L'indice K caractérise l'embonpoint d'un poisson et suppose que plus un individu est gros à une taille donnée, meilleure est sa condition. Il est considéré comme représentatif de l'état nutritionnel et de l'état des réserves énergétiques d'un individu (Lambert & Dutil, 1997; Sutton *et al.,* 2000). L'indice K de Fulton se calcule de la façon suivante:

$$\mathbf{K\ (mg.mm^{-3}) = (W/L_t^{3})*100}$$

Où W est le poids du poisson en mg et L_t sa longueur totale en mm.

2.4.3. Indice de croissance :

L'indice de croissance est employé pour décrire la réponse d'un individu aux modifications de son habitat (Jager *et al.,* 1995 ; Karakiri *et al.,* 1989 ; Able *et al.,* 1999).

L'analyse de la microstructure des otolithes, concrétions calcaires situées dans l'oreille interne des poissons qui jouent un rôle d'organe des sens, est utilisée afin de déterminer l'âge, les dates de colonisation de la zone intertidale mais aussi pour déterminer l'indice de croissance récente Cr. Il existe trois paires d'otolithes : les sagittae, les asteriscie et les lapilli. Grace à l'existence d'accroissements journaliers sur les otolithes des poissons, présentés sous forme de stries, la croissance des juvéniles peut être estimée. Cette méthode a été validée pour de nombreuses espèces de poissons (Panella, 1971; Campana & Neilson, 1985 ; Karakiri & Von Westernhagen, 1989 ; Molony & Choat, 1990 ; Reichert *et al.,* 2000). Cet indice est basé sur l'estimation de la distance inter accroissements des stries journaliers (Panella, 1980). Un accroissement correspond à une zone riche en matière protéique (zone discontinue) et une zone de carbonate de calcium (contiguë à la discontinue). La distance entre ces deux zones reflète la croissance du poisson lorsqu'une relation linéaire existe entre la taille du poisson et la taille de son otolithe (Campana et Neilson, 1985). Après la métamorphose (passage de la vie pélagique à la vie benthique chez les poissons plats), les otolithes de la plie se caractérisent par la formation de nucléi accessoires qui bordent l'otolithe (Modin *et al.,* 1996) (figure 9). Cette méthode permet de différencier les événements pré et post métamorphique (Amara & Paul, 2003).

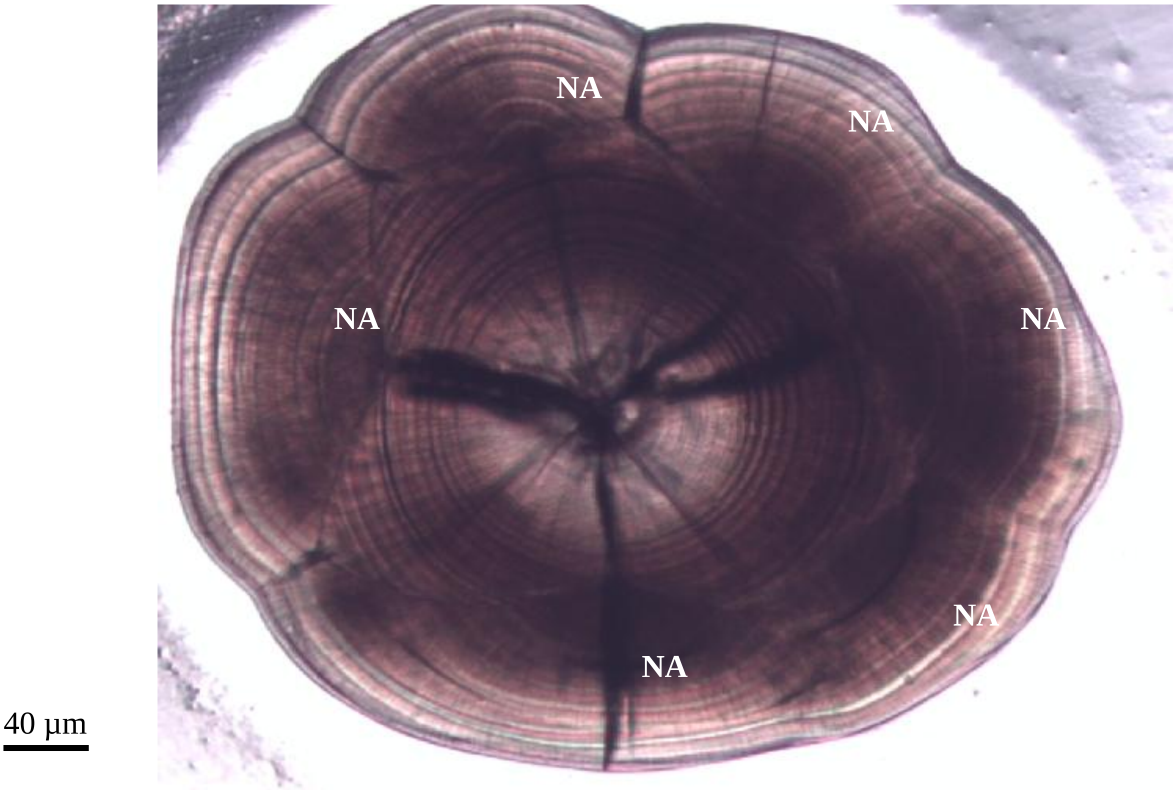

Figure 11. Otolithe (Sagitta) d’une plie de 21.5 mm au grossissement 40X. Six nucléi accessoires (NA) sont observés.

Pour ce faire, la sagitta est extraite du fait de sa grande taille et donc de ses stries journalières bien visibles, nettoyée, déposée face concave sur une lame puis collée avec de la cyanoacrylate. Un polissage est nécessaire afin de réduire la profondeur du champ et rendre les accroissements journaliers bien visibles sous loupe binoculaire qui est équipée d’un polariseur et/ou microscope optique (sous lumière transmise au grossissement 40) équipé d’une caméra. Le polissage est fait manuellement avec un disque de ponçage afin de réduire la profondeur du champ et d’améliorer la définition des stries. Le ponçage se fait jusqu'à l’obtention d’un plan régulier contenant les nucléi accessoires et les accroissements journaliers. Ces derniers vont donc nous donner des indications sur la croissance récente des poissons. Une faible croissance du poisson se traduit par une diminution de croissance de son otolithe et par conséquent un rétrécissement de la largeur des accroissements journaliers. La largeur des accroissements reflète les réponses d’un individu face à un stress tel que la disponibilité en nourriture (Molony et Shaeves, 1998) une pollution (Burke *et al.*, 1993) ou un quelconque stress. Toutes les mesures ont été réalisées le long d'un même axe (figure 10) afin de standardiser les mesures et de ne pas biaiser les lectures.

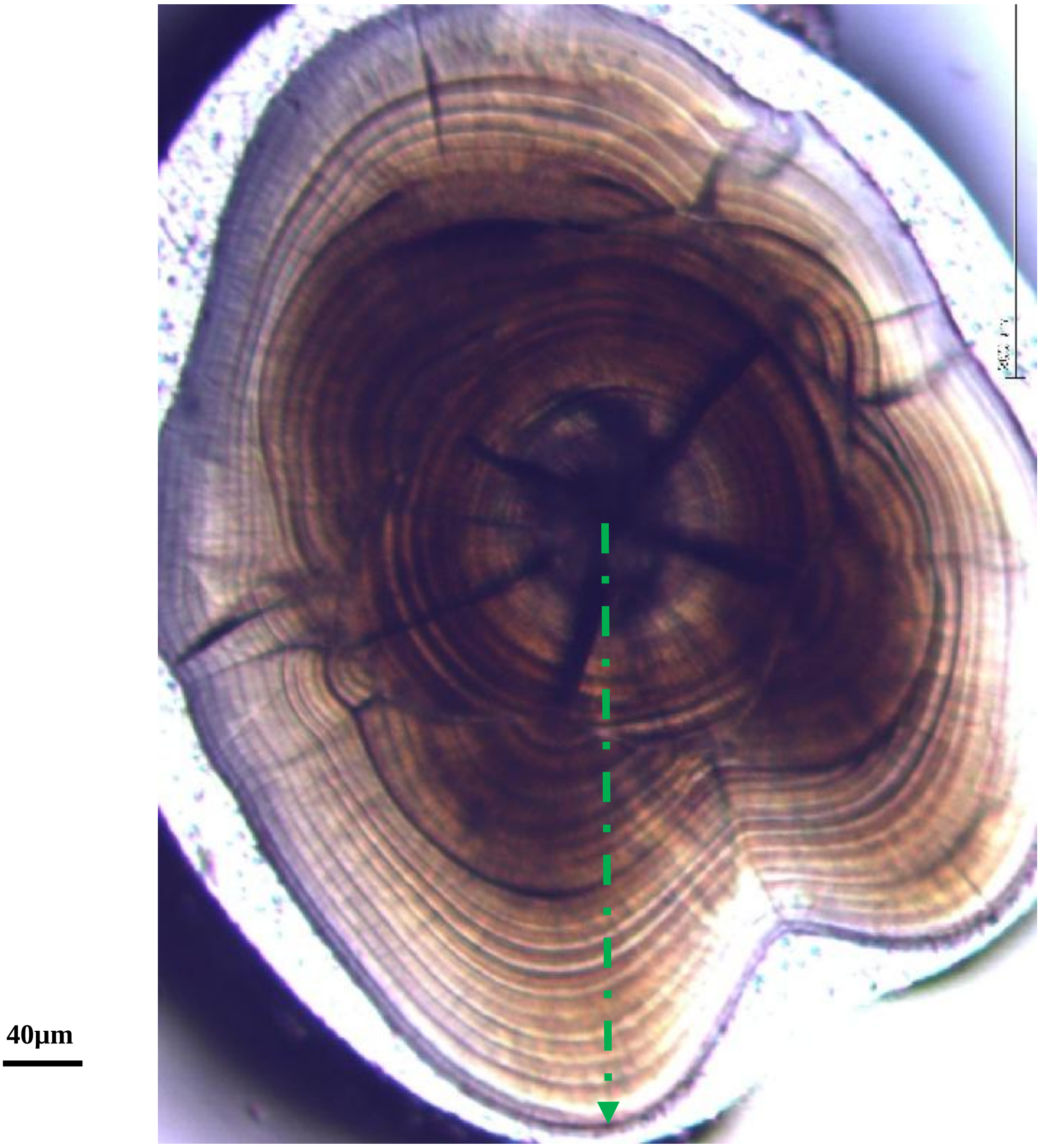

Figure 12. Orientation de l'axe de mesure d'une sagitta de juvénile de plie.

L'indice (Cr, µm) a été déterminé en mesurant la largeur des 7 (ou 5, selon la visibilité) derniers accroissements journaliers situés au bord de l'otolithe (figure 11). Les mensurations sont réalisées le long d'un même axe antéropostérieur afin de standardiser les mesures. Les mesures sont faites à l'aide du logiciel TNPC.

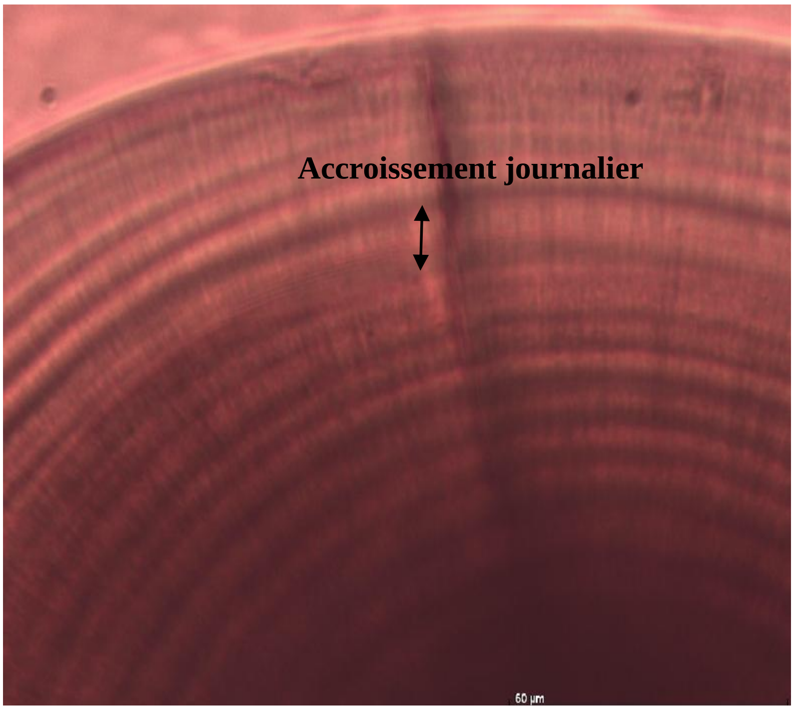

Figure 13. Partie périphérique d'une sagitta de plie observée au microscope optique grossissement x60 après polissage.

2.4.4. Indice nutritionnel : rapport d'acides nucléiques ARN/ADN :

Le rapport d'acide nucléique ARN/ADN a été identifié comme étant un indicateur fiable de la croissance récente et de la condition nutritionnelle des larves et juvéniles des organismes marins (Bullow, 1970; Ferron and Laggett; 1994; Folkvord *et al.*, 1996; Rooker and Holt; 1996; Clemmesen *et al.*, 1997; Chicharo, 1998; Buckley *et al.*, 1999; Heyer *et al.*, 2001; Peck *et al.*, 2003; Buckley *et al.*, 2004; Caldarone *et al.*, 2006; De Raedemaecker *et al.*, 2012). Le but de l'utilisation de cet indice est que la quantité d'acide ribonucléique (ARN) varie avec le taux de synthèse protéique, affecté en cas de stress, alors que la quantité d'acide désoxyribonucléique (ADN) est constante dans les cellules somatiques normales et les tissus même lors d'une longue période sans nourriture (Buckley and Bullow, 1987; Caldarone *et al.*, 2006; Chicharo and Chicharo, 2008; De Raedemaecker *et al.*, 2012).

Afin de déterminer le rapport ARN/ADN individuel, la méthode de fluorométrie utilisée est basée sur le protocole décrit par Clemmesen (1993) et Caldarone (2001). La tête et les nageoires du poisson ont été coupées et 25 gr de muscle ont été utilisés et extraits dans 300 µl N-lauroylsarcosine à 1% de concentration finale (200mg de Sarcosil dans 20 ml de TEB : 0.2M Tris, 0.1N HCl, 1M EDTA, pH= 7.5). Après une sonication de 1min et un passage dans le vortex d'une heure, 450 µl de TEB sont rajoutées avant une centrifugation de 15min à 4°C. 75 µl de surnageant, contenant les acides nucléiques, sont utilisés afin de remplir les puits de la microplaque, et auxquels on a rajouté 75 µl de bromure d'éthidium (BET), marqueur fluorescent spécifique des acides nucléiques (Karsten & Wollenberger, 1977). L'intensité de fluorescence du BET varie linéairement avec la concentration d'acides nucléiques. La fluorescence des acides nucléiques totaux (ARN+ADN) est alors mesurée au spectrofluorimètre, sous longueur d'onde d'excitation 525 nm et une longueur d'onde d'émission de 600 nm. Une deuxième lecture est faite avec 7.5 µl de ribonucléase à 20mg.ml^{-1} dans chaque puits afin de déterminer la fluorescence due à l'ADN uniquement. La concentration en ARN est calculée à partir de la différence de fluorescence entre la 1ere et la 2nd lecture (fluorescence totale-fluorescence ADN) (Caldarone *et al.*, 2001; Caldarone *et al.*, 2006). Les fluorescences sont ensuite converties en concentration (ng/µl) à l'aide de droites d'étalonnages préalablement établies à partir d'ADN standard de thymus de veau (SIGMA D4764) et d'ARN de levure (10206938001 de chez Roche) (figure 12). Le calcul du rapport ARN/ADN est alors possible.

Plus le rapport ARN/ADN est fort, mieux est la condition nutritionnelle (Clemmesen, 1994; Selleslagh and Amara, 2012).

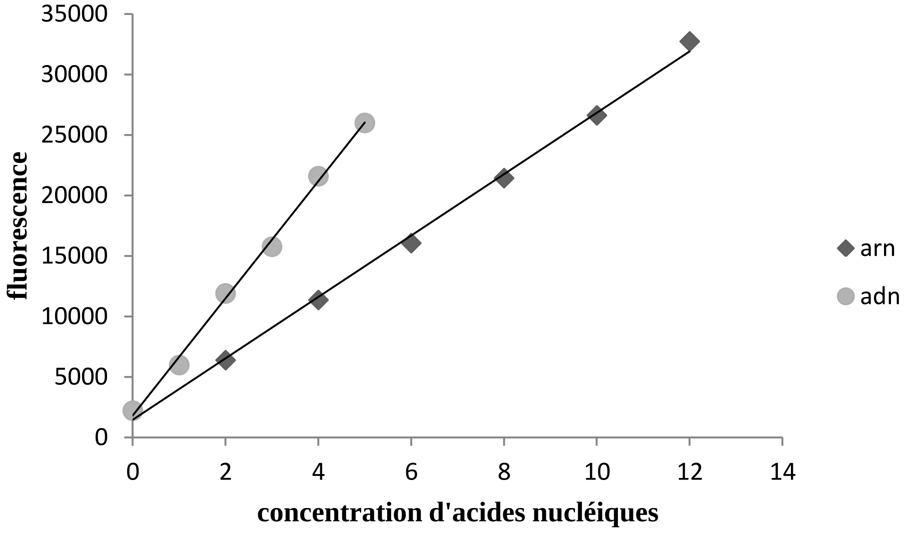

Figure 14. Droites d'étalonnages des concentrations en ARN et en ADN.

ARN : y=2539x+1436,7 ; R²= 0,997

ADN : y=4845,5x+1782,3 ; R²= 0,996

2.4.5. L'indice de Vacuité :

La vacuité (proportion du nombre d'estomacs vides sur le nombre total d'individus examinés) a été calculée. L'activité alimentaire a été exprimée en occurrence (%FO) comme suit :

$$\%FO = FOt/FOi \times 100$$

où FOi est le nombre d'estomac dans lequel la proie i est présente et FOt le nombre total d'estomacs utilisés.

2.5. Analyses statistiques :

Les données environnementales, climatiques et biologiques, après une transformation logarithmique afin de normaliser les distributions et de stabiliser les variances (Sokal & Rohlf, 1995), ont fait l'objet d'analyses statistiques afin de déterminer s'il y avait des différences annuelles et/ou saisonnières durant toute la période de l'échantillonnage. Pour cela, des tests de normalité ont permis de déterminer si une ANOVA ou des analyses Kruskal-Wallis sont nécessaires pour les analyses. Lorsqu'un des tests (ANOVA ou Kruskal-Wallis) montre des différences significatives des tests AdHoc (Tukey ou Dunn) sont effectués par la suite. En mettant toutes les données biologiques, climatiques, environnementales et temporelles dans un seul tableau, on pourrait aboutir à un mélange confus d'effets (Gaertner *et al.,* 1998). Afin de remédier à ça, des analyses multitableaux ont permis de faire des rapprochements et des relations entre les données environnementales, biologiques et temporelles. Le principe de ce type de méthode est de trouver et d'analyser la structure commune entre les séries de données partageant les mêmes lignes et/ou les mêmes colonnes et d'étudier la variabilité de chaque tableau en comparaison avec les structures communes. Les analyses multitableaux ont été utilisées en écologie aquatique par de nombreux auteurs (Amanieu *et al.,* 1981; Dolédec, 1988; Aliaume *et al.,* 1993; Haury, 1996; Blanc and Beaudou, 1998; Cillauren *et al.,* 1998; Gaertner *et al.,* 1999; Licandro and Ibanez, 2000; Anneville, 2002; Lekve *et al.,* 2002).

Dans cette étude, nous nous intéresserons essentiellement à la méthode STATIS (Structuration des Tableaux à Trois Indices de la Statistique, Lavit, 1988 ; Lavit *et al.,* 1994) introduite par Y. Escoufier (1973 ; 1987). Cette dernière est en effet considérée avec l'Analyse Factorielle Multiple (AFMULT, Escofier et Pagès, 1986, 1989, 1990, 1994) comme une des principales méthodes d'ordination simultanée de plusieurs tableaux dont l'essence est euclidienne (Bove et Di Ciaccio, 1994 ; Rizzi & Vichi, 1995). Ces méthodes ont été présentées dans un ouvrage portant sur l'analyse des données évolutives dans le domaine socio économique par Dazy et Le Barzic (1996). Parmi les méthodes d'analyses multitableaux et couplage, nous nous sommes également intéressés à la méthode STATICO. Les abondances de poissons et de macrocrustacés ont-elles aussi fait l'objet d'une analyse des correspondances (STATIS-CoA) proposée par Gaertner et al. (1998).

2.5.1. La méthode STATIS :

Lorsque les données se présentent sous forme de plusieurs tableaux de mesures recueillies sur les mêmes individus dans des situations différentes, la méthode STATIS, basée sur le principe de l'analyse en composantes principales, permet de déceler quels sont les tableaux qui se ressemblent, de fournir un tableau résumé de l'ensemble et enfin de décrire les différences entre tableaux par rapport à ce tableau résumé (les différences sont dues aux individus ou aux variables).

2.5.2. La méthode STATICO :

La méthode STATICO (pour STATIS et Co-Inertie), est une analyse triadique partielle sur les tableaux croisés dans les analyses de co-inertie. On combine alors la logique de STATIS (trouver ce qui constitue le fond typologique commun, fond commun qui peut exister derrière de fortes particularités propres à chaque tableau) et la logique des couplages de co-inertie (trouver ce qui dans deux groupes de descripteurs engendre une typologie commune des objets décrits dans chacun des tableaux).

CHAPITRE 3

Utilisation des nourriceries intertidales: influence des paramètres environnementaux

3.1 Introduction :

L'utilisation des zones intertidales comme des zones de nourriceries est une étape importante pour de nombreux organismes marins: La forte production biologique de cette zone est favorable au développement des poissons et crustacés ainsi que les juvéniles des espèces commerciales (Claridge et al., 1986 ; Day et al., 1989 ; Gibson et al., 1993 ; McLachlan et Brown, 2006). De ce fait, l'étude de l'utilisation de ces habitats a longtemps été un sujet majeur en écologie.

La structure temporelle des communautés dans ces zones est souvent le fruit de vagues de migration consécutives de larves et juvéniles ou de tassements saisonniers. La majorité de ces espèces fraye en eaux profondes au niveau du large, les larves et juvéniles vont ensuite migrer vers la côte au printemps et en été, lorsque les eaux seront relativement chaudes et riches en nourriture.

Si certaines espèces restent en zone subtidale, les stades juvéniles de certains poissons ont développés la possibilité de rester dans la zone intertidale lors de la marée haute. Ces organismes intertidaux seront ainsi exposés aux stress environnementaux tels que la variation de la salinité, les températures extrêmes ou encore les radiations solaires mais aussi aux impacts des activités humaines.

Par conséquent, comprendre le fonctionnement et la dynamique des plages sableuses en tant qu'habitats intertidaux est une étape primordiale pour la conservation et la gestion de ces écosystèmes dont la position de transition, entre les milieux marins et terrestres, les rend vulnérables aux pressions anthropiques et climato-environnementales. La principale source de variation naturelle des assemblages de poissons et macrocrustacés dans les habitats aquatiques est liée à la variabilité environnementale.

La plupart des études menées dans ce cadre, se sont concentrées sur la méiofaune et le macrobenthos et plus récemment sur les oiseaux. De plus, la majorité des études sur les poissons ont été menées sur les écosystèmes intertidaux rocheux. Cela est particulièrement le cas pour les côtes européennes, où seules quelques études ont été menées sur les poissons et macrocrustacés des plages de sable. Ces études ont principalement été prises sur une courte échelle de temps, pas plus de 5 ans. Les études faites à long terme ont été faites principalement sur la dynamique des populations de l'une des espèces dominantes, particulièrement les poissons plats, ou les groupes de macrocrustacés les plus abondants.

Dans ce contexte, la présente étude nous a permis d’analyser la composition du peuplement de la zone intertidale, la persistance et la stabilité de cette composition d’un point de vue saisonnier mais aussi interannuel et enfin explorer leur relation avec les variables environnementales. La zone intertidale étudiée (la plage sableuse Sainte Cécile) est loin de la pression anthropique et est considérée comme une zone à faible perturbation.

La première étude, basée sur les variables environnementales, les poissons et macrocrustacés recueillies en période printanière (de Mars à Juin) sur une période de 11 années intermittentes (2000-2013), cette étude a exploré (i) les changements dans la composition des espèces et la structure de la communauté d'une plage de sable fin intertidale, et (ii) les facteurs environnementaux sous-jacents générant variabilité interannuelle dans les poissons et les communautés macrocrustacean, notamment l'impact négatif potentiel de Phaeocystis floraison printanière.

Les objectifs de ce chapitre sont de trois ordres: à savoir (1) établir une base qualitative et quantitative de la composition des communautés peuplant la zone intertidale, (2) décrire leurs variations temporelles et (3) les relier aux changements des paramètres environnementaux et climatiques (NAO). Ce travail permettra, à plus long terme, l’identification des populations au niveau des nourriceries intertidales et leur évolution en fonction des paramètres environnementaux et les impacts anthropiques. Cette caractéristique permettra d’établir l’état de ces écosystèmes particuliers.

La première étude décrit les variations annuelles des assemblages de poissons et de macrocrustacés en période printanière (de mars à juin) sur une période de 11 années intermittentes (2000-2013), analyse le processus de la colonisation de la zone intertidale par les poissons et les macrocrustacés, et l’impact non seulement des paramètres climato-environnementaux sur les communautés mais aussi l’impact des blooms de *Phaeocystis globosa*.

La deuxième étude se focalise sur les variations interannuelles et saisonnières des assemblages de poissons et macrocrustacés issues de quatre années d’échantillonnage (2005,2006, 2012 et 2013) sont analysées en relation avec les variables environnementales.

3.2. Environmental control on fish and macrocrustacean spring community structure, on an intertidal sandy beach.

Abstract

The inter-annual variability of the fish and macrocrustacean spring community on an intertidal sandy beach near the Canche estuary (North of France) was studied from 2000 to 2013 based on weekly spring sampling over an 11-year period. **Twenty eight** species, representing 21 families were collected during the course of the study. The community was dominated by a few abundant species accounting for > 99% of the total species densities. Most individuals caught were young-of-the-year indicating the importance of this ecosystem for juvenile fishes and macrocrustaceans. Although standard qualitative community ecology metrics (species composition, richness, diversity, evenness and similarity) indicated notable stability over the study period, community structure showed a clear change since 2009. Densities of *P. platessa*, *P. microps* and *A. tobianus* decreased significantly since 2009, whereas over the period 2010-2013, the contribution of *S. sprattus* to total species density increased 4-fold. Co-inertia and generalized linear model analyses identified winter NAO index, water temperature, salinity and suspended particular matter as the major environmental factors explaining these changes. Although the recurrent and dense spring blooms of the Prymnesiophyte *Phaeocystis globosa* is one of the main potential threats in shallow waters of the eastern English Channel, no negative impact of its temporal change was detected on the fish and macrocrustacean spring community structure.

KEY WORDS: Intertidal. Fish. Macrocrustaceans. Spring community-structure. Long-term. Eastern English Channel.

Résumé :

La variabilité interannuelle des communautés printanières de poissons et macrocrustacés au niveau de la zone intertidale de la plage Sainte Cécile (près de l'estuaire de la Canche, Nord de la France) a été étudiée. L'échantillonnage a été effectué de façon hebdomadaire en période printanière sur une période de 11 années allant de 2000 à 2013. Vingt-huit espèces de poissons et de macrocrustacés appartenant à 21 familles ont été recueillies au cours de l'étude. La communauté est dominée par quelques espèces abondantes représentant> 99% du total des densités d'espèces. La plupart des individus capturés étaient des jeunes de l'année : ceci indique l'importance de cet écosystème pour les juvéniles de poissons et macrocrustacés. Malgré que les mesures écologiques qualitatives standards des communautés (composition des espèces, la richesse spécifique, la diversité, l'équitabilité et l'indice de similarité) indiquent une nette stabilité au cours de la période d'étude, la structure des communautés a montré un net changement depuis 2009. Les densités de *P.platessa*, *P.microps* et *A.tobianus* ont diminué de façon significative depuis 2009, alors que sur la période 2010-2013, la contribution de *S. sprattus* à la densité totale des espèces a quadruplé. Grâce à la coinertie et les GLM, il a été identifié que la NAO, la température de l'eau, la salinité et les matières en suspension sont les principaux facteurs environnementaux expliquant ces changements. Bien que les blooms printaniers de *Phaeocystis globosa* soient récurrents et denses, devenant par conséquent l'une des principales menaces potentielles pour l'écosystème de la Manche orientale, aucun impact négatif de son évolution temporelle n'a été détecté sur la structure des communautés printanières de poissons et macrocrustacés.

MOTS CLEF : Intertidal. Poissons. Macrocrustacés. Structure printanière des communautés. Long terme. Manche Orientale.

3.2.1. Introduction

Intertidal ecosystems are dynamic interfaces between the land and the sea. Although these particular environments display harsh and highly variable hydrodynamic conditions, they support a diverse and heterogeneous fauna, and are thought to be highly productive (McLachlan et al.,1996; Beyst *et al.,* 2001). Among intertidal systems worldwide, sandy shorelines are one of the most extensive, dominating most of the temperate coastlines (Short, 1999). These ecosystems are important temporary habitats for the life cycle of many marine organisms such as juvenile fish, and consequently, are considered to play an important role for coastal fisheries (Brown & McLachlan, 1990). Many authors have reported that intertidal areas provide a refuge from predators; abundant food resources and favorable environmental conditions, which promote growth and survival (see Gibson & Yoshiyama, 1999).

However, how such unique and vulnerable ecosystems respond to environmental forcing, notably in regards to inter-annual community structure, dynamics and persistence is still poorly understood, particularly for fish and macrocrustacean communities. Indeed, while many marine fish and macrocrustacean species have the ability to use the intertidal zone during high tide, most studies have concentrated on meiofauna and macrobenthos and more recently on birds (e.g. Cornelius *et al.,* 2001). In addition, the majority of the studies on fish have been conducted on rocky intertidal ecosystems (e.g. Hawkins *et al.,* 2009; Faria & Almada, 1999). This is especially the case for European coasts, where only a few studies have been conducted on exposed sandy beach fish and macrocrustacean communities (Beyst *et al.,* 2001; Gibson *et al.,* 1993; Santos & Nash, 1995; Gibson *et al.,* 1996; Selleslagh & Amara, 2008a). Furthermore, these studies have mainly been undertaken over a short timescale, no more than 5 years (e.g. Gibson *et al.,* 1993). Long-term studies have focused either on population dynamics of one of the dominant species, typically flatfishes (Van der Veer *et al.,* 1991), or the most abundant motile macrocrustacean groups, in particular crabs and shrimps (Campos *et al.,* 2010).

Long-term studies are essential to assess the effect of environmental changes and human activities on intertidal fauna communities. Several recent studies revealed changes in coastal sandy shore macrofaunal communities which were directly or indirectly related to long-term climate variability (e.g. Schückel & Kröncke, 2013; Kröncke *et al.,* 2013). Because of its relatively sessile habit, benthic macrofauna is regarded to be a good indicator for environmental changes and disturbances in the marine environment (Defeo & McLachlan, 2013) and references therein). However, knowledge on how such environmental changes affect intertidal sandy beach motile fauna, such as fish and macrocrustaceans, is still limited. In the subtidal, many studies have observed and described during the past decade the effects of disturbance and environmental changes on fish, macrocrustacean community structure, and diversity in the English Channel and North Sea (e.g. Philippart *et al.*, 1996; Henderson *et al.*, 2011; Tulp *et al.*, 2012). Variations have been related mainly to those of: climate (i.e. the North Atlantic Oscillation (NAO) index), hydrological conditions (temperature and salinity), food, and/or predator abundances. For example, in the eastern English Channel (EEC) hydrological conditions have dramatically changed since the beginning of the 2000s, being influenced by the reduction of freshwater discharge by the main river (the Seine river) (Dauvin & Pezy, 2013). These environmental conditions changes (i.e. lower river discharge and increase of the salinity) have been suggested as the major cause of the suprabenthic faunal changes in the Seine estuary (Dauvin & Pezy, 2013).

Exposed sandy beaches are important habitats along the EEC and southern bight of the North Sea, representing 74% of the mainland coast, and providing important nursery habitat for juvenile fish and macrocrustaceans (Beyst *et al.*, 2001; Selleslagh & Amara, 2008a; Amara, 2004). One of the main threats affecting shallow waters of the EEC is the recurrent and dense algal spring bloom of the Prymnesiophyte *Phaeocystis globosa*, which induce foam accumulation on the surface of the sea and beaches by the release of mucilaginous polysaccharides. Colony proliferation affects the penetration of light in the water column, thus seriously impacting on the abundance, metabolism, growth, feeding and behaviour of marine organisms (Spilmont *et al.*, 2009). Both macrobenthic species richness (potential prey for fish and crustaceans) and densities have been simultaneously reduced during a *Phaeocystis* spring bloom (Desroy & Denis, 2004). Although the intertidal zone is potentially the most impacted area by foam accumulation, no inter-annual study to date has analysed its impact on fish and macrocrustaceans.

Based on environmental variables, fish and macrocrustaceans collected during spring (from March to June) over an intermittent 11 year period from 2000 to 2013, this study explored (i) changes in the species composition and community structure of an intertidal sandy beach, and (ii) the underlying environmental factors generating inter-annual variability in fish and macrocrustacean communities, including the potential negative impact of *Phaeocystis* spring blooms.

3.2.2. Materials and methods

3.2.2.1. Study area and sampling

This study was carried out on a sandy beach (Sainte Cécile) located near a small estuary (La Canche), on the French coast of the eastern English Channel. The beach is characterised by the presence of bars and pools parallel to the coast with fine and medium sands. The distance between high and low water marks is about 700 m at neap tide and 1500 m at spring tide. The tidal regime is semi-diurnal with an average tidal range of about 7 m on spring tides and 3 m on neap tides.

For 11 years (2000, 2003-2007, and 2009-2013), sampling was conducted weekly (from March to June) at two replicate stations located at 300-400 m from the high tide line (50° 33'N, 1° 35'E), as soon as the meteorological conditions were favorable. On average 13 sampling dates were done during each spring period except during 2007 where only 8 sampling dates were done. Sampling was done with a 1.5 m beam trawl during daylight hours. The trawl had a 5.5 m long net with a mesh size of 8 x 8 mm in the main body, 5 x 5 mm in the cod end, and was equipped with a tickler-chain in the ground rope. Following recommendations by Riley & Corlett (1966), net speed was kept as constant as possible during sampling, about 38 m min^{-1}. The net was pulled by two people in parallel to the shoreline in a water depth <1 m during the ebb tide (high tide +3 h). A meter registered the distance traveled by the trawls. As a result, each trawling represented an average distance of 250 m and a sampling surface of about 400 m^2. Catches of each trawling were stored in plastic bags and sorted within a few hours in the laboratory.

After the catch, the fish were anesthetized with clove oil and transported in plastic bag to the laboratory. All fish and macrocrustaceans were identified to species level and counted. Individual fish were measured (total length, mm). Small-sized crustaceans (e.g. isopods, mysids) were not included in the present study. For each species, density was calculated as trawl catches standardized to numbers of individuals per 1000 m^{-2} trawled and not corrected for net efficiency. Annual species density was *calculated* as the *average density* of all samples across the spring period (from March to June). Before, species densities obtained from the two sampling stations were averaged at each sampling date. The permission to collect fish in the areas under study was issued by the "Direction des Affaires Maritimes DAM" of Boulogne-sur-mer (dram-npe@equipement.gouv.fr). In France there is no need for special approval to catch or kill fish by an ethics committee. The present field study did not involve endangered or protected species.

3.2.2.2. Environmental variables

Daily Seine River runoffs at Poses ($m^3 s^{-1}$) were made freely available by the Public Interest Group Seine-Aval (http://seine-aval.crihan.fr/web/). Data of the NAO winter (December through to March) index (NAO_w) were obtained from the National Center for Atmospheric Research website (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). NAO_w is estimated based on the Sea Level Pressure difference between Lisbon (Portugal) and Stykkisholmur (Iceland) between December and March measured since 1864.

Temperature (T, °C), salinity (S), Suspended Particulate Matter (SPM, $mg.l^{-1}$), chlorophyll-a concentration (Chl-a, $\mu g.l^{-1}$), and *Phaeocystis globosa* abundance were obtained from the national French monitoring network SOMLIT (http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). Temperature and salinity were measured with a CTD probe Seabird CTD25 or SBE19. Hydrological data and water samples for phytoplankton counts were collected with 8 L Niskin bottle fortnightly at high tide in subsurface (-2 m) and near the bottom (~ -20 m) from the permanent coastal station C (50°40’75 N; 1°31’17E) located near the study area. For the present study, data from subsurface and near the bottom were averaged at each sampling date.

Chl-*a* was estimated according to the equations of Lorenzen (1966), after extraction in acetone 90% for 12h at 4°C in the dark. Abundance of *P. globosa* cells was determined under inverted microscopy according to the Utermöhl method from samples preserved with acid Lugol’s iodine solution (2% final concentration) up until 2006, thereafter with 1% (final concentration) Lugol-glutaraldehyde solution. The number of *Phaeocystis* cells of the colonial form was counted separately from free cells within a month after sampling according to biovolume measurements (Schoemann *et al.,* 2005), except for samples from the period 2000-2005 which were counted months to several years after sampling. In this case, the number of *Phaeocystis* cells was counted as a total number of free cells, as Lugol’s iodine solution disintegrates the colony matrix some months after fixation (Chang, 1984). Note that long-term storage in Lugol’s seems do not affect *Phaeocystis* cell abundance. Accordingly, based on cell counts made at 9 sampling dates, a significant relationship (r^2=0.86, p<0.001) with a slope of 1.06 was found between preserved sub-samples with Lugol’s for more one year and those preserved with Lugol-glutaraldehyde counted within a month after sampling. *Phaeocystis* biomass was estimated using a mean carbon conversion factor of 89.5 pg C cell^{-1} (Schoemann *et al.,* 2005). *Phaeocystis* spring biomass was calculated by integrating over time the biomass data for the spring bloom period (Breton *et al.,* 2006). This choice was motivated by the transient nature of such bloom, and the very high range of biomass values in the course of any spring bloom (up to five orders of magnitude).

3.2.2.3. Data analysis

To examine inter-annual variations in environment, a normalized Principal Component Analysis (PCA) was performed to render the environmental variables scale-free and dimensionless (Krebs, 1999). Inter-annual variations in species composition were explored with several indices. Species diversity and evenness were assessed by the Shannon–Wiener and the Pielou’s evenness index, respectively. Similarity in species composition between years was assessed by calculating the Jaccard’s similarity index on presence/absence data for each pair of years (Krebs, 1999). This index ranges from zero (no shared species between years) to one (identical years). In addition, one-way analysis of similarity ANOSIM was performed on species densities to test statistically the variation in spring fish and macrocrustacean assemblages over the 11 years. The test was performed on a Bray-Curtis similarity matrix, calculated using log-transformed data. To examine inter-annual variations in species densities, a centered PCA was chosen to keep variance and dominance among species. Only species with an occurrence >1% in the whole sampling period were considered. To ascertain distinct species assemblages an ascendant hierarchical classification (AHC) with the Ward’s aggregation criterion was built from the first component coordinates from the factorial map of the centered PCA. Temporal trends were tested according to Kendall (1955). In the case of autocorrelation in time-series, variance was corrected according to Hamed & Ramachandra (1998).This methodology is described in detail in Daufresne et al. (2009). Before trend analysis, missing years (2002, 2003, and 2008) were interpolated using distance weighted least squares. Relationships between species densities and environmental variables were explored with two different approaches: (1) a co-inertia analysis was performed with all species for a global measure of co-structure, followed by (2) a generalized linear model (GLM) analysis, both to focus on the dominant species and to determine the relative importance of each significant environmental variable.

Co-inertia analysis consists in finding co-inertia axes, which maximize covariance between row coordinates (years) of environment and species density matrices (Dray *et al.,* 2003). Co-inertia was calculated from the normalized PCA on the environmental variables and from the centered PCA on the species densities. The strength of the relationship (i.e. coupling) between these two data-sets was assessed by calculating a multidimensional correlation coefficient (RV) and by testing the statistical significance using the Monte Carlo permutation procedure with 1000 permutations. Generalized linear models (GLM) were applied assuming a Gaussian distribution. Before GLM analysis, multi-collinearity between the environmental variables was tested with Pearson correlation method. Because of collinearity between salinity and Seine river runoff, this last variable was removed from the GLM analysis. The GLM was built with an additive methodology: environmental variables as predictors were tested independently for significance and subsequently, significant ones were added to determine the residual deviance, as well as the percentage explained by each one and the total percentage of the deviance explained by the model. All environmental variable interactions were initially included in the model. The step AIC function (R package “MASS”, v7.3-5; Kendall, 1955) was used to select the significant environmental variables and to estimate the coefficients of the models. Environmental variables were removed by backward elimination based on Akaike’s information criterion (AIC). AIC balanced the degree of fit of a model with the number of variables, in order to find the most parsimonious model. Once the model with the lowest AIC value was selected, the deviance for each of the significant environmental variables was analyzed. None of the models revealed any major violation of the modeling assumptions (i.e. residual normality, homoscedasticity). Moreover, inspection of autocorrelation plot of the residuals showed no evidence of autocorrelation outside of the Bartlett two-standard-errors limits.

Kruskal–Wallis tests and Mann–Whitney U test for post hoc pairwise comparisons were performed with XLSTAT 2007 and were used to check for differences in fish species densities between years. ANOSIM analyses were performed with PRIMER software package (version 5.0) (Clarke & Warwick, 2001), PCA and co-inertia analyses with ade4 package and GLM with R software (R Development CoreTeam, 2005), and autocorrelation plot with SYSTAT 11. All statistical significance were set at $p < 0.05$.

3.2.3. Results

3.2.3.1. Environmental variables

All environmental variables during the winter/spring period displayed high inter-annual variations over the period 2000-2013. For example, mean temperature, salinity, and the magnitude of *Phaeocystis* spring blooms (Figure 15) varied from 8.5 (2013) to 11.03 °C (2007), from 33.9 (2000) to 34.5 (2010), and from 0.29 (2005) to 112 g C m^{-3} $bloom^{-1}$ (2003), respectively.

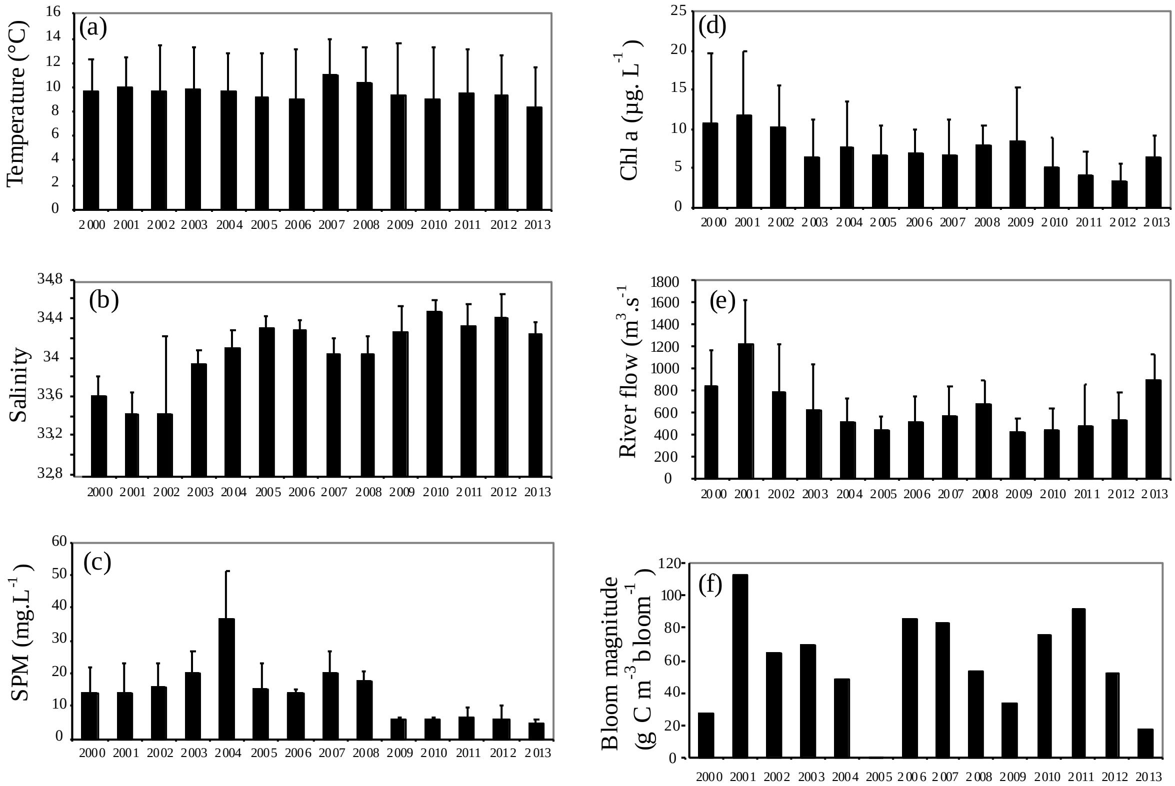

Figure 15. Temporal variations (2000-2013) of environmental variables in coastal waters of the eastern English Channel. (a) temperature, (b) salinity, (c) Suspended Particulate Matter [SPM], (d) chlorophyll-a concentration [Chl-a]), (e) Seine river flow, (f) *Phaeocystis globosa* bloom magnitude.

The first and second principal components (PC1 and PC2) of the PCA on all environmental variables explained 43 and 20% of the total data inertia, respectively (Figure 16). The first principal component (PC1) showed an opposition between salinity and NAOw, Seine River runoff, T, SPM, and Chl-*a* (Figure 16 A). Furthermore, PC1 exhibited a significant increasing temporal trend over the period 2000-2013 (z=2.29, $p < 0.05$, Figure 16B), resulting mainly from the gradual significant increase in salinity (z=3.18, $p < 0.01$) over time, but a progressive decrease in both SPM (z=-2.74, $p<0.01$) and Chl-*a* (z=-2.41, $p<0.05$). By contrast, no significant temporal trends for NAOw, T, Seine River runoff and *Phaeocystis* were detected ($p>0.05$).

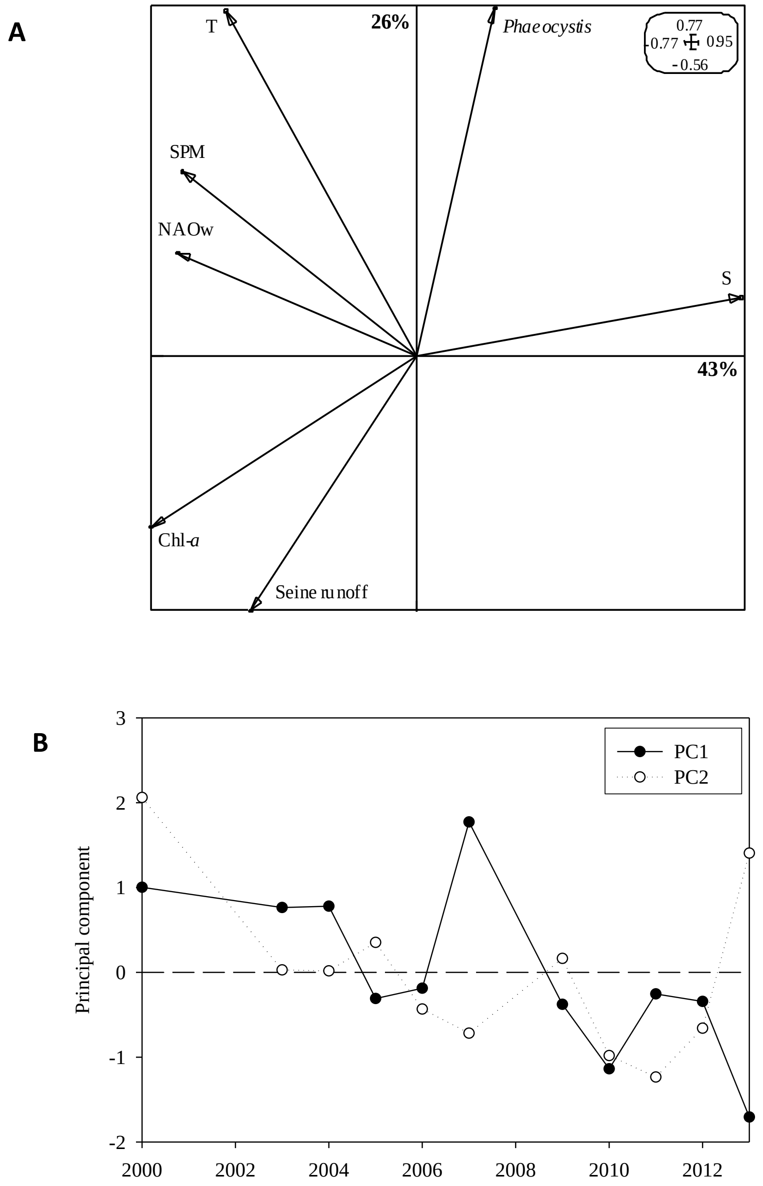

Figure 16. Variations (2000-2013) in climate (NAOw) and environmental variables (Seine River runoff, T, S, SPM, Chl-*a*, and the magnitude of *Phaeocystis* blooms) using a normalised PCA. A. Ordination plot of the variables in the two first principal components (PC1 and PC2). Contribution of each axis to total variance is shown in %. Scales of the axes are given in the boxes. B. Temporal variations in PC1 and PC2. Note that temporal trend in PC1 was highly significant ($r^2=0.65$, $p< 0.001$).

3.2.3.2. Species composition

A total of 28 species (18 fish and 10 macrocrustaceans) belonging to 21 different families, were collected in the intertidal sandy beach over the 11 spring periods (March to June), from 2000–2013 (Table III). The captured fish were mainly represented by juveniles, often from species of commercial importance. Seven fish species were commonly present each year over the studied period. Among them, *Pleuronectes platessa* (exclusively 0-group), *Sprattus sprattus* (post-larvae and juvenile), and *Pomatoschistus microps,* were the most abundant representing 43.3, 39.2, and 13.5% of the total fish catches, respectively. *Crangon crangon* was by far the most abundant species (mean density during the period of study: 1393 ind. 1000 m^{-2}), and contributed to 72 % of the total catches. *Carcinus maenas* was also regularly caught (85 % frequency of occurrence).

Out of the 28 species captured, only six (*P. platessa, P. microps, S. sprattus, Ammodytes tobianus, C. crangon,* and *C. maenas*) dominated the intertidal zone assemblages over the 11 years, and so could be considered as key species. Accordingly, these species represented in total 99.4 % of the total catches, having relative high densities and occurrence during the 11 years studied (Table 3). Average total density of these key species was 1932 ind. 1000 m^{-2}. By contrast, most of the other species occurred in low densities or occasionally, such as *Dicentrarchus labrax*, *Syngnatus acus*, *Psetta maxima*, and *Portumnus latipes*. It should be noted that *Eriocheir sinensis* and *Hemigrapsus sanguineus*, two east-Asian introduced species, were recorded in the intertidal zone from 2011.

Table 3. Species composition, mean densities (ind/1000m²) and occurrence (calculated for the whole study period) of fish and macrocrustaceans along the Sainte Cécile intertidal sandy beach over the period 2000-2013. Note the absence of sampling in the years 2001-2002 and 2008.

Family	Species (abbreviation)		**2000**	**2003**	**2004**	**2005**	**2006**	**2007**	**2009**	**2010**	**2011**	**2012**	**2013**	**(%) occurrence**
Fishes														
Clupeidae	*Sprattus sprattus*	(S spr)	30.5	212.8	46.5	213	215.1	57	49.2	637	119.8	283	161.8	72.48
	Clupea harengus	(C har)	0	0	0	0	0	0	0	0	0	0.1	0	0.65
Gasterosteidae	*Gasterosteus aculeatus*	(G acu)	0	0	0	0	0	0	0	0.1	0	0	0	0.65
Gadidae	*Merlangius merlangus*	(M mer)	0.3	0	0	0	0	0	0	0	0	0	0	1.40
	Trisopterus luscus	(T lus)	0.8	0.3	0	0	0	0	0	0	0	0	0	2.31
Atherinidae	*Atherina presbyter*	(A pre)	0	0	0	0	0.2	0	0	0	0.2	0.1	0.20	2.92
Agonidae	*Agonus cataphractus*	(A cat)	1.3	0	0	0	0	0	0	0	0	0	0	2.10
Moronidae	*Dicentrarchus labrax*	(D lab)	0	0.7	0.3	0.1	0	0	0.5	0.5	0	0.7	1.90	14.85
Gobiidae	*Pomatoschistus microps*	(P mic)	42.1	243.7	198.2	153	37.4	45.4	3.1	1	1.5	70	6.73	76.29
Cottidae	*Cottus gobio*	(C gob)	0	0	0	0	0.2	0	0	0	0	0	0	1.30
Trachinidae	*Echiichthys vipera*	(E vip)	0	0.2	0	0	0	0	0	0	0.1	0	0	1.41
Ammodytidae	*Ammodytes tobianus*	(A tob)	10.2	25.9	39.5	49.9	26.7	5	2.5	1.2	0.6	0.2	0.59	49.18
Syngnatidae	*Syngnathus acus*	(S acu)	1	1.4	4.7	0.4	2	0.3	1.2	4.4	4.1	0.3	2.45	31.24
Pleuronectidae	*Pleuronectes platessa*	(P pla)	509.6	997.2	188.3	294.6	259.7	77.7	63.2	26.5	11.4	69.6	62.16	90.20
	Platichthys flesus	(P fle)	0	0.5	0.4	0	0.1	0	0.3	0.7	0.7	2.1	1.11	19.04
Soleidae	*Solea solea*	(S sol)	1.2	3.4	2.2	0	0	0	0	0	0	0	0.07	7.13
Scophthalmidae	*Psetta maxima*	(P max)	0.1	0	0	0	0	0	1	1.7	2.3	1.6	0.49	15.15
	Scophthalmus rhombus	(S rho)	2.3	0	0	0	0	0	0	0	0.9	0.4	0.20	6.93
Macrocrustaceans														
Crangonidae	*Crangon crangon*	(C cran)	3381.6	756.4	2376.9	1040.9	397.4	847.1	3199.1	431.4	736.3	2260.3	158.92	93.92
Palaemonidae	*Palaemon longirostris*	(P lon)	0	0.5	0	0.1	0.2	0	0	0	0.1	0.2	0.07	5.40
	Palaemon serratus	(P ser)	0	0	0.4	0	0	0	0	0	0	0	0	1.52
Portunidae	*Carcinus maenas*	(C mae)	35.3	79.3	78.3	96.3	158.9	63.9	14.4	11.9	6.8	15.2	17.03	84.91
	Liocarcinus holsatus	(L hol)	1.9	0	0	0	0.1	10.5	0	0.1	0	0	0	8.52
Carcinidae	*Portumnus latipes*	(P lat)	0	2.7	3.9	2.1	0.7	1.2	2.1	0	23.9	2	3.01	30.94
Majidae	*Macropodia longirostris*	(M lon)	0.3	0	0.3	0	0.1	0	0	0	0	0	0	2.86
Porcellanidae	*Pisidia longicornis*	(Pi lon)	0.7	2	1	0	0	0	1.3	0	0.2	0	0.20	5.26
Varunidae	*Eriocheir sinensis*	(E sin)	0	0	0	0	0	0	0	0	0.1	0	0	0.51
	Hemigrapsus sanguineus	(H san)	0	0	0	0	0	0	0	0	0.2	0	0.20	0.98
Total species number			**16**	**15**	**14**	**10**	**14**	**9**	**12**	**12**	**17**	**15**	**17**	

3.2.3.3. Inter-annual variations in community structure and species density

The various diversity indices (species richness S, Shannon-Wiener diversity H' and Pielou's evenness J) exhibited no significant trend ($r^2<0.02$; $p>0.05$) (Figure 17) and species composition stayed rather similar between years. Among years comparisons exhibited high Jaccard's coefficients (0.40 – 0.83) showing that the fish and macrocrustacean species composition was more or less stable between years in a qualitative point of view. Accordingly, only some occasional species (*P. flesus, D. labrax and P. maxima)* occurred more frequently from 2009.

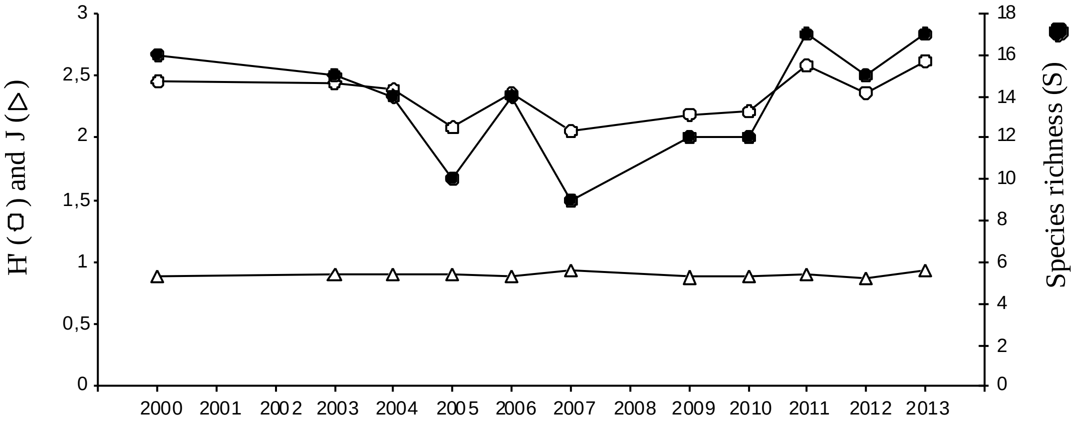

Figure 17. Temporal variations (2000-2013) in species richness (S), diversity (H') and evenness (J) of fish and macrocrustaceans along the Sainte Cécile intertidal sandy beach. Note the absence of sampling in the years 2001-2002, and 2008.

All of the species presented high inter-annual variability in density. One-way ANOSIM indicated a significant change of fish and macrocrustacean assemblages over the 11 years (ANOSIM, *global R* = 0.40, *p* = 0.001). PCA analysis on species density revealed four species assemblages over the 11 years studied (Figure 18A). The first species assemblage positioned along the first principal component (PC1, 58% of total variance) was composed of *P. platessa, P. microps, A. tobianus* and *C. maenas.* The second and third assemblages in opposition along the second principal component (PC2, 12% of total variance) were composed of *S. sprattus* and *C. crangon,* respectively.

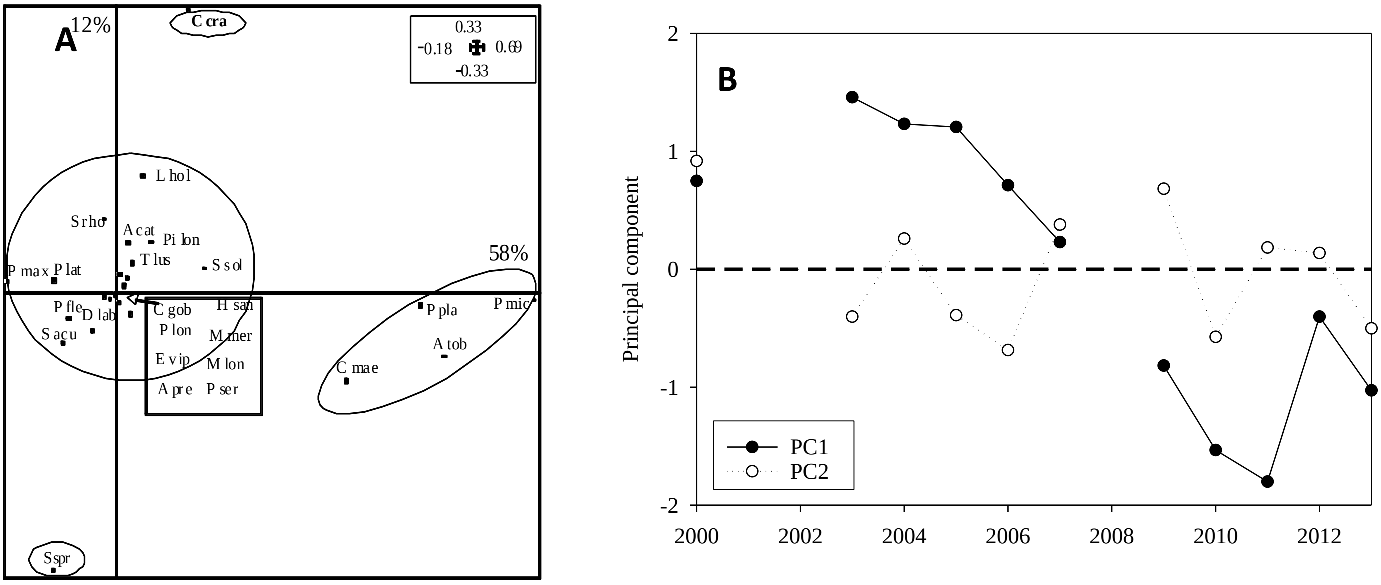

Figure 18. Temporal variations (2000-2013) in fish and macrocrustacean density along the Sainte Cécile intertidal sandy beach using a centred PCA. A. Average position of the species in the two first principal components (PC1 and PC2). Contribution of each axis to total variance is shown in %. Scales of the axes are given in the boxes. Species associations were defined from hierarchical cluster analysis by Ward's method of the species coordinates. See Table 3 for species labels. B. Temporal variations in PC1 and PC2. Note that temporal trend in PC1 was highly significant (r^2=0.68, $p < 0.005$), and the absence of sampling in the years 2001-2002 and 2008.

Density of each of these six dominant species (key species) exhibited significant differences between years (Kruskal-Wallis, $p<0.05$, Figure 19). Furthermore, PC1 exhibited a significant negative temporal trend ($z=-2.96$, $p<0.01$), showing that *P. platessa, P. microps, A. tobianus,* and *C. maenas* progressively declined over the eleven years period. Although PC2 did not display any significant temporal trend, the contribution of *S. sprattus* in the catch increased from 2010 (Mann-Whitney test, $p<0.05$, Figure 19), contributing to 30±22 % of the total catches over the period 2010-2013 against 7±7% previous to this. By contrast, neither *C. crangon* nor the fourth assemblage, which was composed of all the 19 other species (Figure 19A), displayed any significant temporal trend.

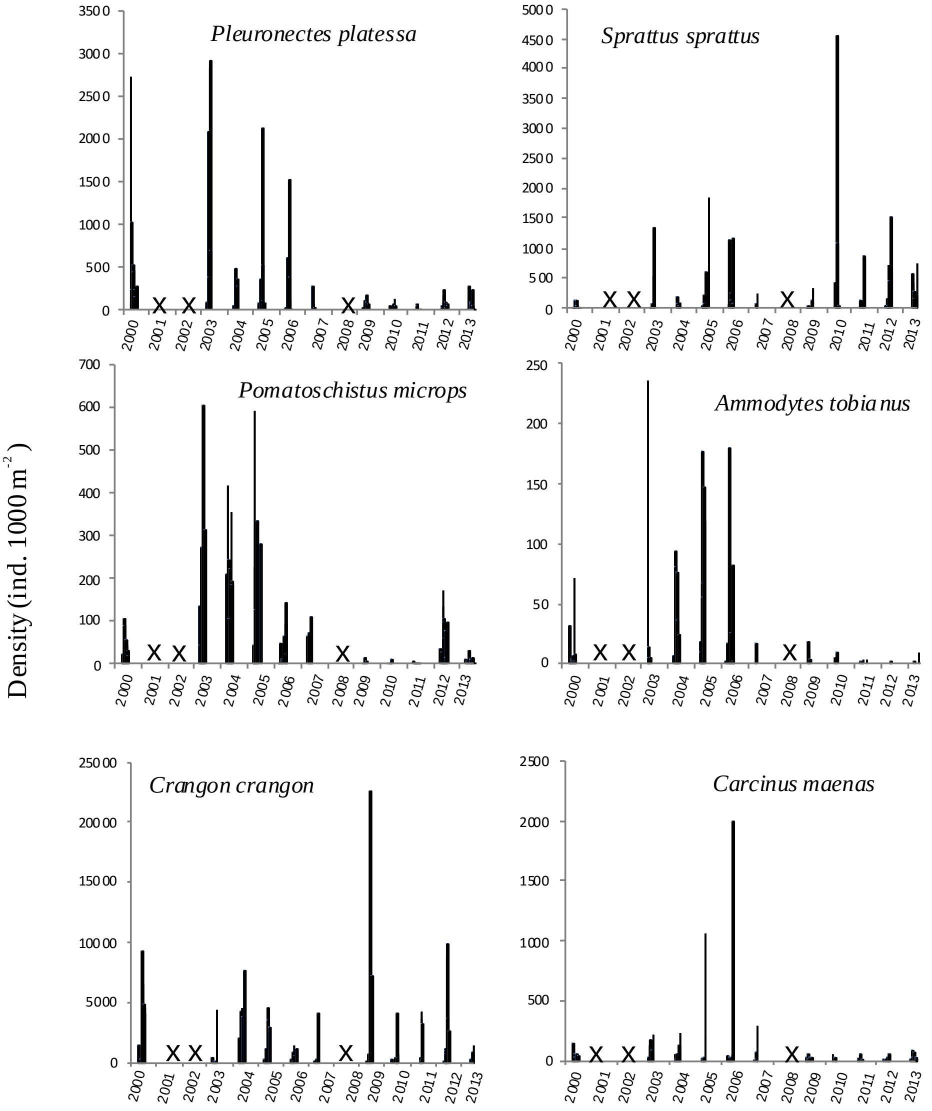

Figure 19. Temporal variations (2000-2013) in densities (ind. 1000 m^{-2}) of the dominant fish and macrocrustacean species along the Sainte Cécile intertidal sandy beach. Each bar represents the density at a sampling date. "X" indicate years with no sampling (2001-2002, and 2008). Note the differences in the y-axis scales.

Altogether, these results showed that the period 2000-2007 was characterized by relative high densities of *P. platessa*, *P. microps*, *A. tobianus*, and *C. maenas* and by a low contribution of *S. sprattus* within the community. By contrast, the period 2010-2013, was characterized by a relatively high contribution of *S. sprattus*, but relatively low densities of *P. platessa*, *P. microps*, *A. tobianus*, and *C. maenas*. Note that although fish and macrocrustacean densities fluctuated inversely from year-to-year over the 11 years period (Figure 20), the negative relationship was not significant (r= 0.15; p=0. 651).

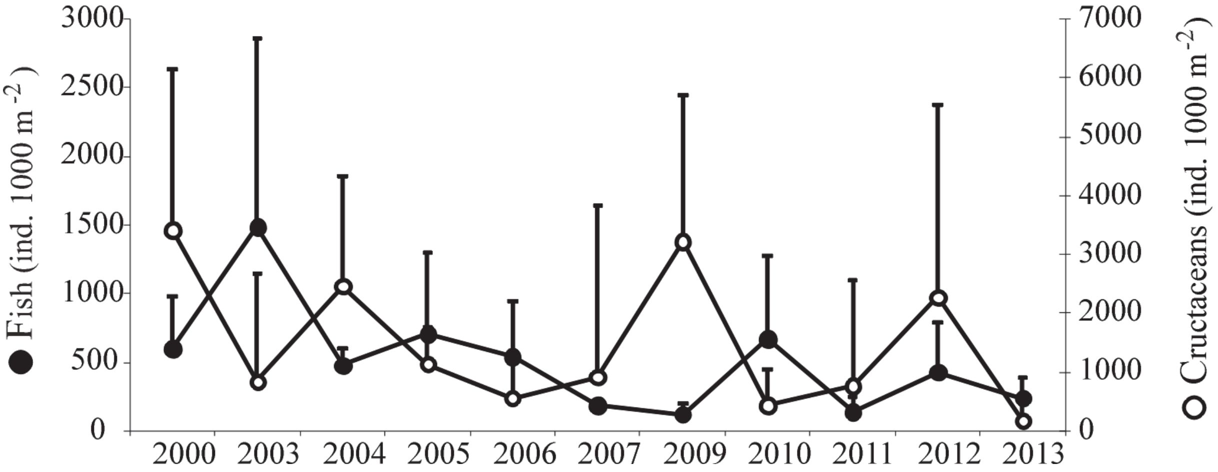

Figure 20. Temporal variations (2000-2013) in mean (+SD) total fish and macrocrustacean densities (ind. 1000 m $^{-2}$) along the Sainte Cécile intertidal sandy beach. Note the absence of sampling in the years 2001-2002, and 2008.

3.2.3.4. Relationships between fish and macrocrustacean spring community-structure, and their environment

Co-inertia analysis (Figure 21) revealed a significant coupling between fish and macrocrustacean spring community-structure, densities and environment (RV=0.59, $p<0.05$). Accordingly, the first axis was clearly dominant, and explained alone 60 % of the total variance. Co-inertia and GLM results indicated that out of the seven environmental variables, NAOw, T, S, Chl-*a*, and SPM were the most important for structuring the inter-annual distribution of fish and macrocrustacean spring community (Figure 21, Table 4). Species such as *P. platessa*, *P. microps, A. tobianus, C. crangon* and *C. maenas* were relatively more abundant during periods of relative high NAOw, T, Chl-*a*, and SPM. *P. platessa* and *A. tobianus* densities were negatively correlated to S, while *S. sprattus* was negatively correlated to T and Chl-*a.* All models explained substantial proportions of the variance in time series (Table 4). The magnitude of the *Phaeocystis* spring blooms was not well represented on the factorial map of the co-inertia analysis and was not a significant predictor in the GLM analysis, indicating its relative lack of importance in explaining intertidal fish and macrocrustacean spring community-structure.

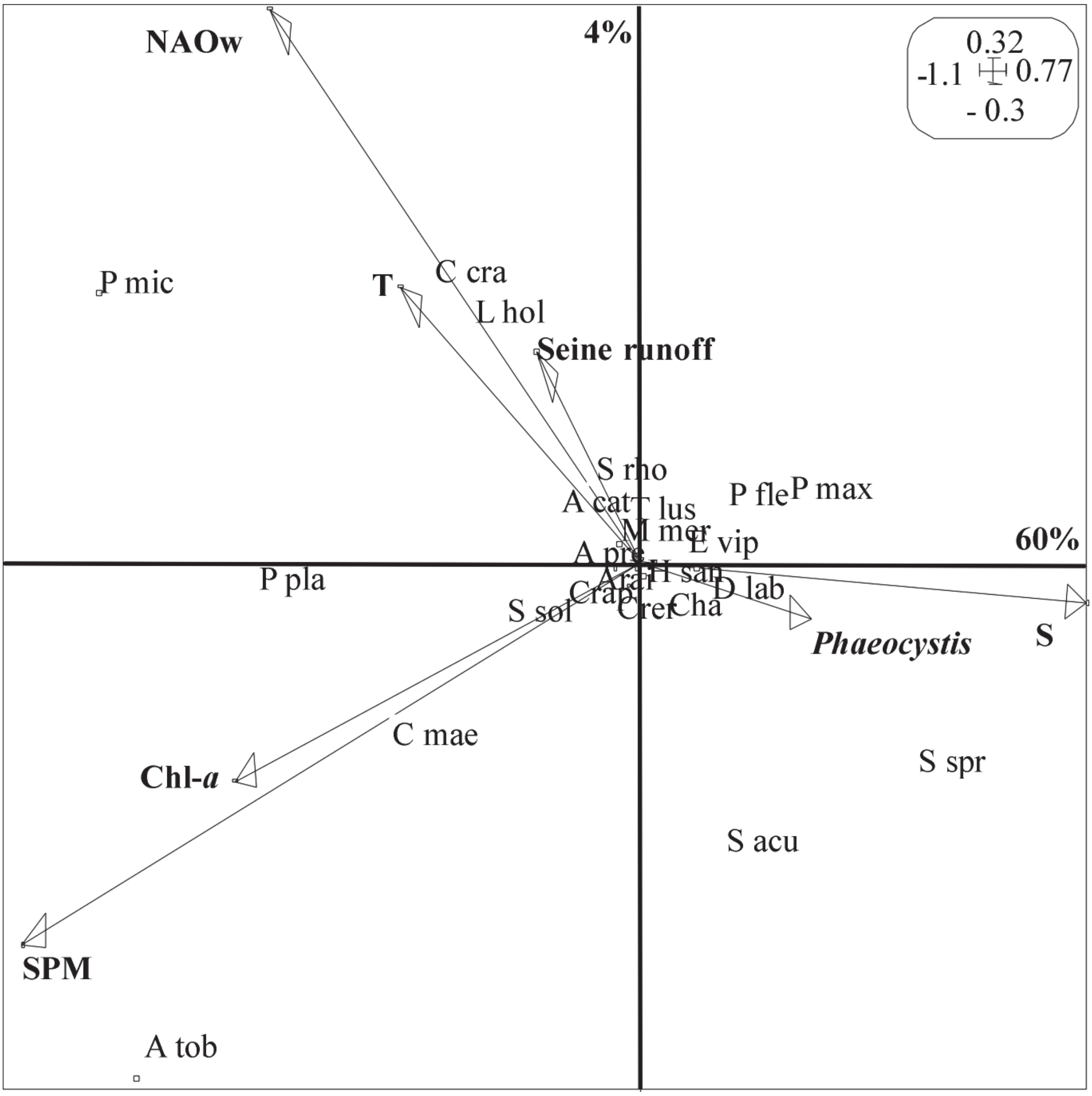

Figure 21. Relationships over the period (2000-2013) between fish and macroscrustacean densities and climate and environmental parameters using a co-inertia analysis. Contribution of each axis to total variance explained is shown in %. Scales of the axes are given in the boxes. See Table 3 for species labels. Note the absence of fish and macrocrustacean species sampling in the years 2001-2002 and 2008.

Table 4. Deviance analysis table of explanatory variables in the Gaussian GLM model for *S. sprattus, P. platessa, P. microps, A. tobianus, C. crangon* and *C. maenas* densities. Values of deviance for each factor, residual deviance (res. dev.), change in deviance, percentage of the total deviance explained by each factor (% Explained), total model (in bold), and p values are presented.

Source of variation		**Deviance**	**Residual dev.**	**Change in dev.**	**% Explained**	**AIC**	***p*-Value**
S. sprattus	NULL		1,64				
	T	0,37	1,27	0,37	23,78		0,044
	Chla	0,76	0,52	0,76	49,22		0,009
	Total model				**73,00**	5,57	
P. platessa	NULL		3,27				
	S	1,52	1,72	1,55	47,10		0,011
	SPM	0,88	0,70	1,02	30,90		0,034
	Total model				**78,00**	12,93	
P. microps	NULL		7,40				
	NAO	2,11	4,64	2,76	37,87		0,005
	SPM	3,91	0,69	3,95	54,13		0,001
	Total model				**92,00**	12,77	
A. tobianus	NULL		6,90				
	S	1,15	5,48	2,36	18,04		0,022
	Chla	0,95	4,54	4,76	36,33		0,031
	SPM	3,81	0,73	4,54	34,63		0,001
	Total model				**89,00**	13,31	
C. crangon	NULL		1,79				
	NAO	0,97	0,83	0,97	24,36		0,010
	Total model				**66,00**	8,72	
C. maenas	NULL		2,04				
	SPM	0,99	1,05	0,99	0,18		0,017
	Total model				**0,56**	11,41	

3.2.4. Discussion

3.2.4.1. Species composition and community structure

Fish and macrocrustaceans are important components of sandy beach fauna. The mobile and relatively homogeneous nature of the substratum on the sandy intertidal zone means that few refuges are available for these species to remain intertidal over the low-tide period. This study found that the great majority of fish and macrocrustaceans were juvenile migrants (Elliott & Dewailly, 1995), and were present only at high tide. In this study, the number of fish species recorded within the intertidal zone (18) was comparable to that in adjacent areas, such as the Canche estuary which was sampled with a 2-m beam trawl in spring over two years (16 species, (Selleslagh & Amara, 2008b). However, it was lower than the collection recorded in the subtidal area with a 3-m beam trawl (26 species, Amara unpublished data). The advantages for marine species using the intertidal zone during part of their life cycle are not well known. However, many authors have reported that intertidal sandy beach areas may provide refuge from predation coupled with high productivity to enhance survival and growth (Amara & Paul, 2003). Species may also use these habitats in search of an optimum physiological environment that promotes maximal growth (Thiel *et al.,* 1995). Juveniles of some abundant species in the studied area, such as *Solea solea*, *Limanda limanda, Buglossidium lutheum* and *Callionymus lyra* (Amara, 2004), remain during spring or summer in the subtidal zone, and are scarcely ever caught intertidally (e.g. *S. solea*). These species are probably less adapted to fluctuating environmental conditions with their resultant physiological demands. Therefore, utilization of the intertidal zone by certain fish species represents an advantage that not only reduces predation and maximises growth but also reduces competition for food in the earliest stages of their life cycle when densities are highest and competition is likely to be greatest in the subtidal zone (Gibson *et al.,* 2002; Banikas & Thompson, 2012).

The species diversity in this studied intertidal zone was similar to that found in the few other published studies undertaken on European intertidal sandy beaches (e.g. 20 species in a Belgian surf zone (Beyst *et al.,* 2001), and 24 species at Porto Pim, Azores (Santos & Nash, 1995). However, 43 species of fish and 16 species of macrocrustaceans were caught during a four year study on a Scottish intertidal sandy beach (Gibson *et al.,* 1993), and 35 species were captured on other Scottish beaches (Poxton, 1992). This high number results from the use of two different sampling gears (seine net and beam trawl), the proximity of the adjacent rocky headlands, and the sampling period (day/night) (Gibson *et al.,* 1996). Although caution is needed when comparing studies in which different types of fishing gear (different type, size or speed) were used, the beam trawl used in this work is considered efficient for catching demersal fish and epibenthic species in shallow coastal waters (Kaiser *et al.*, 1994; Lazzari *et al.*, 1999).

As for other sandy beaches, only few taxa numerically dominated the catch, with most species occurring occasionally or rarely, in low number (Beyst *et al.*, 2001; Gibson *et al.*, 1993; Lazzari *et al.*, 1999). Out of the 28 species captured, only six (*P. platessa, P. microps, A. tobianus, S. sprattus, C. crangon* and *C. maenas*) could be considered as dominant and key species of the intertidal zone. They represented 99.4 % of the total catches during spring, and showed high densities and occurrence during the 11 years studied. Among them, *P. platessa* was the most abundant fish species (43.3% of the total fish catches). As in other shallow waters in northern Europe, *C. crangon* (96% of the total crustaceans) was the dominant mobile epibenthic species. As for *C. maenas*, this macrocrustacean species is highly abundant and an ubiquitous member of the large motile epifauna of shallow soft bottom areas along the European coasts (Beyst *et al.*, 2001; Gibson *et al.*, 1993; Campos *et al.*, 2010; Selleslagh *et al.*, 2009). The temporal structure of epibenthic communities of temperate intertidal sandy beaches is often the result of seasonal settling or consecutive migration waves of the young stages (Gibson *et al.*, 1996; Amara & Paul, 2003). Indeed, most of the species spawn in deeper offshore waters, and invade shallow coastal areas in spring or summer as late larvae or early juveniles, when such areas are relatively warm and rich in food (Santos & Nash, 1995; Amara, 2004; Clark et al.,1996). According to Beck et al. (2001), a habitat can be defined as a nursery of a species if its contribution per area to the production of recruits to the adult population is greater, on average, than the production from all other juvenile habitats. The juvenile density of most of the key species (e.g. *P. platessa* 215 ind. 1000 m^{-2}) in this study's intertidal zone was higher than in the adjacent subtidal area (e.g. *P. platessa* 16.5 ind. 1000 m^{-2}; (Amara, 2004), and in the Canche estuary (e.g. *P. platessa* 17 ind. 1000 m^{-2}, [38]). In the Dutch Wadden Sea, Van der Veer & Witte (1993) observed differences between intertidal and subtidal 0-group plaice growth. These authors showed that growth in the intertidal zone was always higher than in the subtidal one, due to the presence of the prey *Arenicola marina* in the intertidal zone. All these data emphasize the importance of sandy intertidal zone as nursery ground, which allows suitable conditions for juvenile fish development.

3.2.4.2. Temporal community structure evolution and environmental influence

As with previous studies on sandy beaches (e.g. Beyst *et al.,* 2001; Gibson *et al.,* 1993; Lazzari *et al.,* 1999), the fish assemblage in the Canche intertidal zone studied here was dominated by a few abundant species. Gross temporal patterns of change in this assemblage are therefore mainly a result of alterations in the density of these dominant species. High inter-annual variations in density of the key species were associated to low inter-annual variations in species composition. This is typical of many intertidal fish assemblages (Santos & Nash, 1995; Lazzari *et al.,* 1999; Ross *et al.,* 1987) and particularly those inhabiting the rocky intertidal zone (see the review of Gibson & Yoshiyama, 1999). However, in some areas such as the surf zone of the northern New Jersey (USA) shoreline, high inter-annual variations in density of some fish species were associated to high inter-annual variations in species composition (Wilber *et al.,* 2003).

Concerning species composition, these results showed that the fish and macrocrustacean spring community structure in this intertidal zone was stable from year-to-year, and was based on a set of regularly occurring species. Between years comparisons exhibited high Jaccard's similarity coefficients (0.40 – 0.83) and the ANOSIM (based on species densities) showed that the fish and macrocrustacean composition was stable over the 11 years studied. These Jaccard coefficient values were similar to those found on the west coast of Scotland (0.55 to 0.71, Gibson *et al.,* 1993), the Belgian surf zone in (0.3 to 0.8, Beyst *et al.,* 2001), and Maine, USA (0.38 to 0.83, Lazzari *et al.,* 1999). Although all these other studies were undertaken over a shorter time scale (less than 5 years), they indicate that the assemblages of intertidal fish are persistent and resilient to any change, and, therefore, their general taxonomic structure is predictable from year-to-year (Gibson & Yoshiyama, 1999; Jackson & Jones, 1999). In temperate intertidal ecosystems, the major temporal differences in community structure generally occur on a seasonal basis and reflect the breeding cycle of the species (Gibson *et al.,* 1993; Selleslagh & Amara, 2008a; Clark et al.,1996). Nevertheless, some occasional species (*P. flesus, D. labrax, P. maxima)* occurred in this study more frequently from 2009. Moreover, some species such as *E. sinensis* and *H. sanguineus,* which are native to the east coast of Asia, and were introduced into the English Channel during the mid 1930s, and the North Sea during the 1990s (Herborg *et al.,* 2003), were recorded from 2011. Even if these two species are classified as invasive species, they were in low numbers at the beach sampled in our study.

Although temporal variations in shallow coastal epibenthic species densities are well documented, much confusion still prevails over the factors influencing or controlling them. They have been attributed to fluctuations in a wide variety of both biological and physical variables including the timing of spawning seasons and hence the influx (immigration/recruitment) and efflux (emigration) of individuals to and from populations (e.g. Gibson *et al.,* 1993; Herborg *et al.,* 2003), food availability (Costa-Dias *et al.,* 2010), predation pressure (Van der Veer & Bergman, 1987; Pihl, 1990), water temperature (e.g. Beyst *et al.,* 2001; Beukema, 1992), wind speed and direction (e.g. Gibson *et al.,* 1993; Pihl, 1990), turbidity (e.g. Ross *et al.,* 1987), and salinity (e.g. Campos *et al.,* 2010).

Inter-annual variations observed in species density (up by five-fold for the key species), are most likely the result of differences in year-class strength and recruitment success. The fact that fluctuations did not follow the same pattern for all dominant species, suggests that species responded differently to the environmental variables and that the factors contributing to successful recruitment differed between species.

It is now clear that climate variability affects the density and biogeography of marine organisms (Poloczanska *et al.,* 2013). Several recent long-term studies in the English Channel and the North Sea have revealed changes in intertidal beach macrofauna that were directly or indirectly related to climate variability (Schückel & Kröncke, 2013; Kröncke *et al.,* 2013). A study based on a 34-year time series of *C. crangon* abundances in the Dutch Wadden Sea indicated that salinity, freshwater discharge and the NAO were relevant factors affecting its abundance (Campos *et al.,* 2010). The NAO and river flow may influence recruitment success, probably due to their effects on the productivity and growth of coastal organisms (Henderson *et al.,* 2006). Such environmental factors have been recognized as key issues in the estuarine colonization and settlement processes of both marine fish and invertebrate larvae and juveniles (e.g. Amara *et al.,* 2000; Attrill & Power, 2002).

Co-inertia and generalized linear model analyses identified, among the measured environmental variables, winter NAO index, water temperature, salinity suspended particular matter, and chlorophyll-*a* as the major environmental factors to explain these changes. Hydrological and oceanographic features in coastal waters of the EEC depend mainly on the Seine River outflow, which creates a water mass of relatively low salinity and nutrient enrichment known as "*Fleuve côtier"* (Brylinski, 1991), spreading northward parallel to the French coast. This coastal river of relative vertical stability and considered as a productive area, is separated from the offshore waters of Atlantic origin by an unstable and tidally influenced frontal zone (Brylinski, 1991). Since this front has been shown to influence fluctuations of ichthyoplankton assemblages such as offshore/onshore distribution (Grioche & Koubbi, 1997), the observed hydrological change over the period 2000-2013, associated with NAO change, may have affected progressively the recruitment success of species such as *P. platessa, P. microps,* and *A. tobianus.* Density of *S. sprattus,* considered as a cold/temperate water species, was negatively correlated to temperature in our study. This species may have probably found optimal conditions for its development when water temperature decreases. Attrill & Power (2002) illustrated a situation in which climatic oscillations exerted effects on fish assemblages by affecting the suitability of estuarine nursery grounds for marine fish. They found an increase in diversity during high NAO winters, which is partly explained by the increase in the number of rare species. Although species diversity and community structure in our intertidal zone was stable from year-to-year, the NAO was identified as a factor structuring the inter-annual variations in density of some key species such as *P. microps and C. crangon.* The NAO is probably best viewed as a means of describing processes that operate at a higher level of control of oceanographic and atmospheric phenomena rather than as an agent that acts directly on the fish assemblages.

In shallow coastal areas, juvenile fish are exposed to high predation pressure (Amara *et al.*, 2000; Van der Veer *et al.*, 2000). During the 11 years studied, fish and macrocrustacean densities fluctuated from year-to-year, with a slight negative, but not significative correlation. Many studies have showed predator-prey interactions between these two groups of species. Due to its high density (72 % of the total catches in the present study), *C. crangon* is a key component of the trophic web. It is known as an important prey for some fishes (gobies, gadoids, several flatfish and demersal roundfish species), crustaceans and shorebirds (Campos *et al.,* 2010) as well as an important predator of numerous larvae and juvenile stages of several fish and benthic species (Van der Veer & Bergman,1987; Oh *et al.,* 2001). For example, both *C. crangon* and *C. maenas* are the main predators on the early benthic stages of *P. platessa* in April-May (Van der Veer & Bergman,1987).

Finally, despite high inter-annual variations in the magnitude of *P. globosa* spring blooms, by two-orders of magnitude, no effects on either juvenile fish or macrocrustacean species diversity, densities or assemblages were observed. These results concur with those from a recent mesocosm study, which clearly showed that exudates and TEP excreted from decaying *P. globosa* colonies and foam accumulation have no negative effect on juvenile sea bass growth, condition or survival (Amara *et al.,* 2013). However, by supposing similarly high inter-annual variations in foam accumulation on the beach of the magnitude of *P.*

globosa spring blooms, this study's results, differ with those of (Desroy & Denis, 2004). They showed that foam accumulation on the Canche beach, associated with the decline period of the *P. globosa* spring bloom, affected all macrobenthic taxa (potential prey for fish and crustaceans) by reducing both the number of species and their densities (Desroy & Denis, 2004). However, most of these modifications were short-lived, and all systems and organisms came back to their regular activity or displayed their initial properties a few weeks after the end of the bloom (Spilmont *et al.*, 2009). These discrepancies may result from the difference in the ability of these organisms to escape from foam. By contrast to macrobenthic species, fish and macrocrustaceans are motile species, probably giving them the possibilities to avoid foam accumulation on the beach, and unfavourable areas in general.

In conclusion, the fish and macrocrustacean spring community structure in the studied intertidal zone was stable from year-to-year, and was based on a set of regularly occurring species. However, strong inter-annual variations in species density occurred (up by five-fold for the key species), being associated to inter-annual variations in winter NAO index, water temperature, salinity, suspended particular matter and chlorophyll-*a*. No significant relationship between crustaceans and fish were found in the present study but predator-prey interactions should be investigated in more details in future studies. Although the recurrent and dense spring blooms of the Prymnesiophyte *Phaeocystis globosa* is one of the main potential threats in shallow waters of the eastern English Channel, no negative impact of its temporal change was detected on the fish and macrocrustacean spring community structure. More work is necessary both to characterize patterns of faunal change and their linkages with biological and oceanographic changes, and also to understand the causal mechanisms through which fish assemblages are being affected by changing environmental conditions.

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3.3. Seasonal and inter-annual persistence and stability in the community structure of fish and macrocrustacean on an intertidal sandy beach: implications for biological monitoring.

Abstract:

The transitional position of the intertidal zone, between the marine and terrestrial environments, makes it vulnerable to anthropogenic pressure and climate induced sea level rise. Understanding and managing increasing threat on intertidal ecosystem requires impact assessment and monitoring indices that provide accurate quantification of change. Fish assemblages are generally considered as appropriate to develop indicators of ecosystem quality. Persistence, which refer to similarity in species composition over time and stability which refers to constancy in abundance over time should both be considered when assessing temporal change in natural assemblages and evaluating anthropogenic disturbance. We used multivariate statistics (STATIS) and standard qualitative community ecology metrics (species composition, richness, diversity, evenness and similarity) to examine the seasonal and inter-annual persistence and stability in the fish and macrocrustaceans community structure on an intertidal sandy beach. Significant inter-annual variations in both environmental variables and species abundances were observed, with maximum values in spring and summer. However, the various diversity indices exhibited no significant seasonal or inter-annual trend and species composition stayed rather similar between seasons and years. STATIS analysis showed that during the four years of study, both environmental variables and species abundances exhibited a strong common seasonal structure between years. Only 8 species over the 27 identified in the study contributed the most to the seasonal structure. We suggest that the fish and macrocrustacean assemblage properties may be used for assessing intertidal ecosystem change under anthropogenic pressure.

Key words: Intertidal . Fish . Macrocrustaceans . fish assemblages. ecosystem status. Eastern English Channel.

Résumé:

La position de transition de la zone intertidale, entre les milieux marins et terrestres, la rend vulnérable aux pressions anthropiques et climatiques. Afin de comprendre et de gérer la menace croissante sur cet écosystème, il est nécessaire de faire des études d'impact et d'évaluer les indices qui fournissent une quantification précise du changement subit. Les assemblages de poissons sont généralement considérés comme indicateurs de la qualité de l'écosystème. La Persistance, qui se réfèrent à la similitude dans la composition des espèces au fil du temps, et la stabilité, qui se réfère à la constance dans l'abondance des espèces dans le temps, devraient être prises en compte lors de l'évaluation des changements temporels dans les assemblages naturels ainsi que l''évaluation des perturbations anthropiques.

Nous avons utilisé les statistiques multivariées (STATIS) et les mesures écologiques qualitatives standards (la composition des espèces, la richesse spécifique, la diversité, l'équitabilité et l'indice de similarité) afin d'examiner la persistance et la stabilité saisonnière et interannuelle des populations de poissons et de macrocrustacés sur une plage sableuse intertidale. Les variables environnementales et les abondances des espèces observent de significatives variations interannuelles, avec des valeurs maximums au printemps et en été. D'importantes variations interannuelles dans les deux variables de l'environnement et l'abondance des espèces ont été observées, avec des valeurs maximales au printemps et en été. Cependant, les divers indices de diversité ne présentent aucune tendance significative saisonnière ou interannuelle et la composition des espèces est restée assez similaire entre les saisons et les années. L'analyse STATIS a montré que pendant les quatre années de l'étude, les deux variables environnement et abondance des espèces présentaient une forte structure commune saisonnière entre les années. Seules 8 espèces des 27 espèces identifiées dans cette étude ont contribué le plus à la structure saisonnière. Nous suggérons que les propriétés des assemblages de poissons et macrocrustacés peuvent être utilisées dans l'évaluation des changements de la zone intertidale sous l'influence de la pression anthropique.

MOTS CLEF : Zone intertidale. Poissons. Macrocrustacés. Assemblages de poissons. Manche Orientale.

3.3.1. Introduction:

Due to their location between the continent and the sea and their shallow depths, intertidal zone play an important ecological role in coastal ecosystems by providing a collection of habitat types for many species, functioning as nursery areas and feeding grounds for marine opportunistic fish and macrocrustacean species (Beyst *et al.,* 2001; Amara and Paul, 2003, Selleslagh and Amara, 2008). Intertidal habitats have generally been viewed as ecotones where marine organisms encounter harsh and highly variable physical conditions. However many marine species have the ability to use the intertidal zone during high tide. This is not necessarily dependence on the intertidal environment, but opportunistic utilization of near-shore environment offering increased feeding possibilities (Blaber and Blaber, 1980) and refuge from predators, larger and more numerous in the subtidal zone (Gibson and Yoshiyama, 1999). The temporal structure of the communities in the intertidal zone is often the result of seasonal settling or consecutive migration waves of the young stages. Indeed, most of these species spawn in deeper offshore waters and invade, as late larvae or early juveniles, shallow coastal areas in spring and summer, when such areas are relatively warm and rich in food (Edwards & Steele, 1968; Beukema, 1992; Marchand, 1991; Selleslagh and Amara, 2008).

The sandy shorelines are one of the most extensive intertidal systems worldwide (Short, 1999), dominating most of the temperate coastlines (Kotwicki *et al.,* 2005). However, how such unique and vulnerable ecosystems respond to environmental forcing, notably in regards to seasonal and inter-annual community structure, persistence and stability is still poorly understood, particularly for fish and macrocrustacean communities. Exposed sandy beaches are important habitats along the eastern English Channel and southern bight of the North Sea, representing 74% of the mainland coast, and providing important nursery habitat for juvenile fish and macrocrustaceans (Beyst *et al.*, 2001, Amara and Paul, 2003, Selleslagh and Amara, 2008). Therefore, understanding the functioning and the dynamic of sandy beaches intertidal habitats is important regarding the conservation and management of these habitats affected by increasing environmental (e.g. sea rising, storms) and anthropogenic disturbance (pollution, beach replenishment, cleaning,...). Indeed, the transitional position of the intertidal zone, between the marine and terrestrial environments, makes it vulnerable to anthropogenic pressure and climate induced sea level rise. One key aspect is to consider the persistence and stability of the fish assemblage, where persistence refers to similarity in species composition over time and stability refers to constancy in abundance over time

(Connell and Sousa, 1983). The main source of natural variation in the persistence and stability of fish assemblages in undisturbed aquatic habitats is linked to environmental variability (Deegan *et al.,* 1997; Robinson and Yakimishyn, 2013). The persistence and stability of fish assemblages is typically highest where environmental conditions are relatively constant or where conditions change slowly over long time periods (Robinson *et al.,* 2000; Oberdorff *et al.,* 2001). However, in highly variable nearshore marine rocky intertidal habitats fish assemblages were considered relatively stable and resilient (Grossman, 1983; Gibson and Yoshiyama, 1999; Almada and Faria, 2004).

In this context, the present study analyze the seasonal and inter-annual persistence and stability of fish and macrocrustaceans species composition and community structure on an intertidal sandy beaches and, explore their relation with environmental variables. The intertidal studied area (Sainte Cécile beach) is away from anthropogenic pressure and is considered as a low disturbed zone (Amara *et al.,* 2007; Amara *et al.,* 2009). Understanding assemblage properties has important implications for assessing ecosystem status condition and may be useful in further comparative studies on fish and macrocrustaceans assemblages on sandy beaches intertidal habitats subjected to various degrees of disturbance.

3.3.2. Material and methods

3.3.2.1. Study area and sampling

The study area was the intertidal zone of a sandy beach (Sainte Cécile beach) located on the French coast of the eastern English Channel (50°34’00’’N 1°30’52’’E). The beach is characterised by the presence of sand bars and pools parallel to the coast with fine and medium sands. The distance between high and low water mark was about 700 m at neap tide and 1500 m at spring tide. The tidal regime is semi-diurnal with an average tidal range about 7 m at neap tides and 3 m on neap tides (Amara and Paul, 2003).

During four years (2005-2006 and 2012-2013), weekly samples (from early March to late May) followed by monthly sampling the rest of the year were collected in the middle part of the intertidal sandy beach. Sampling was done with a 1.5 m beam trawl during day light hours. The fishing net was 5.5 m long, had a mesh size of 8 x 8 mm in the main body and 5 x 5 mm in the cod end, and was equipped with a tickler-chain in the ground rope. Following recommendations by Riley and Corlett (1966), net speed was kept as constant as possible during sampling, about 38 m.min^{-1}. The net was pulled by two persons parallel to the shore line in a depth of water <1 m during the ebb tide (high tide +3 h). A meter registered the distance travelled by the trawls and each sample represented an average trawling distance of 250 m and a sampling surface of about 400 m^2. Catches were stored in plastic bags and sorted within a few hours in the laboratory. The permission to collect fish in the areas under study was issued by the “Direction des Affaires Maritimes DAM” of Boulogne-sur-mer (dram-npe@equipement.gouv.fr).

At the laboratory, all fishes and macrocrustaceans were identified to species level and counted. All individuals fishes were measured (total length, mm) and small-sized crustaceans (e.g. isopods, mysids) were excluded. For each species, trawl catches were standardized to numbers of individuals per 1000 m^{-2} trawled and not corrected for net efficiency.

3.3.2.2. Environmental variables

Temperature [T], salinity [S], Suspended Particulate Matter [SPM], Particulate Organic Carbon [POC] and chlorophyll a [Chla]) were obtained from the national French monitoring network SOMLIT (http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). These data were collected on board the oceanographic ship Sepia II fortnightly at high tide in subsurface (-2 m) and near the bottom (~ -20 m) from the permanent coastal station C (50°40’75 N; 1°31’17E) located near the study area. For the present study, data from subsurface and near the bottom were averaged for each date. In addition, wind speed was obtained from “Météo France Boulogne Sur Mer”.

Daily Seine estuary runoffs at Poses ($m^3 s^{-1}$) were made freely available by the Public Interest Group Seine-Aval (http://seine-aval.crihan.fr/web/) and daily Somme estuary runoffs were also freely available by Hydro bank (http://www.hydro.eaufrance.fr/).

3.3.2.3. Data analysis:

To examine inter-annual variations in environment, a normalized Principal Component Analysis (PCA) was performed to render the environmental variables scale-free and dimensionless (Legendre and Legendre, 2012). To examine seasonal and inter-annual variations in species composition, species diversity and evenness were assessed by the Shannon–Wiener and the Pielou’s evenness index, respectively. Similarity in species composition between years was assessed by calculating the Jaccard’s similarity index on presence/absence data for each pair of years (Krebs, 1999). This index ranges from zero (no shared species between seasons or years) to one (identical species composition). Out of the 27 species recorded over the 4 years monitored, only those with an occurrence > 1%, were retained for further statistical analysis. Abundances of the resulting total of 17 species were log-transformed to minimize the influence of high values. To depict significant inter-annual variability in the overall species abundances, a between-class covariance analysis was performed on a matrix crossing 4 classes (i.e years) and 17 species. In a first step, a centered Principal Component Analysis (PCA) was performed, and in a second step the sampling dates were projected on the factorial map as supplementary rows. The statistical significance of inter-annual variations in the overall species abundances was tested using Monte Carlo permutation procedure (Manly, 1997) with 1000 permutations. To explore the inter-annual stability of the seasonal structure in species assemblages, the STATIS multitable method (Lavit *et al.,* 1994) was performed. By doing simultaneous principal component analyses (PCA) of several data tables with same variables, this method allows to find a structure common to these tables (called as "compromise"). In our study, compromise represents, therefore, the stable part of the seasonal variability of abundance of each species. The accuracy of the compromise is evaluated by weights and cos2, the first evaluating the contribution of each year to the compromise, and the last measuring the similarity of each seasonal structure with the compromise. Before and after the compromise analysis, an "inter-structure" and "trajectories" analysis allow to studying the similarity between years in the seasonal variability of species, and to depicting differences between years, respectively. STATIS was performed on centred PCA of the species tables to keep variability and dominance (Legendre and Legendre, 1998). In order to investigate the stable part of the relationships between species abundance and environmental variables measured through time, the STATICO method (Dray et al. 2003; Thioulouse, 2011) was first used. STATICO is also based on STATIS method but combined with a co-inertia analysis (Dolédec and Chessel, 1994). The first step is a co-inertia analysis on the environmental matrix and that of species abundance group for each year, which consists in finding co-inertia axes by maximizing covariance between rows coordinates of environment and species abundance matrices. To estimate the strength of the relationship (i.e. coupling) between two tables from each sampling zone, a multidimensional correlation coefficient (RV) was calculated, and the statistical significance was tested using Monte Carlo permutation procedure with 1000 permutations. Then, STATIS analysis was performed to find the stable part of the environment-species among the four years. Because results highlighted strong instability in the relationship between species and their environment, we performed in a second step, simple co-inertia analysis for each year, followed by group of years in order to depict the higher RV value as possible.

3.3.3. Results:

3.3.3.1. Composition of fish and macrocrustaceans assemblages

A total of 27 species (17 fish and 10 macrocrustaceans) belonging to 21 different families, were collected in the intertidal sandy beach with the 174 beam trawl samples carried out during the four years of sampling (Table 5). Most of individuals were young of-the-year (YOY) and juveniles, often from species of commercial importance such as common plaice *Pleuronectes platessa*, sea bass *Dicentrarchus labrax*, sprat *Sprattus sprattus*, turbot *Psetta maxima* or brown shrimp *Crangon crangon*.

The various diversity indices (species richness S, Shannon-Wiener diversity H’ and Pielou’s evenness J) exhibited no significant seasonal or inter-annual trend ($r^2<0.02$; $p>0.001$) (Fig. 22) and species composition stayed rather similar between seasons and years. Among seasons and among years comparisons exhibited high Jaccard’s coefficients (0.44–0.85) showing that the fish and macrocrustacean species composition was more or less stable between season and years in a qualitative point of view. Fish density decreased from 2005 and macrocrustaceans density varied between years with the smallest density in 2013 (232 ind.1000 m^{-2}) (Fig. 23). At the seasonal scale, the highest density of both fish and macrocrustaceans occurred in summer and the lowest in winter (Fig. 23).

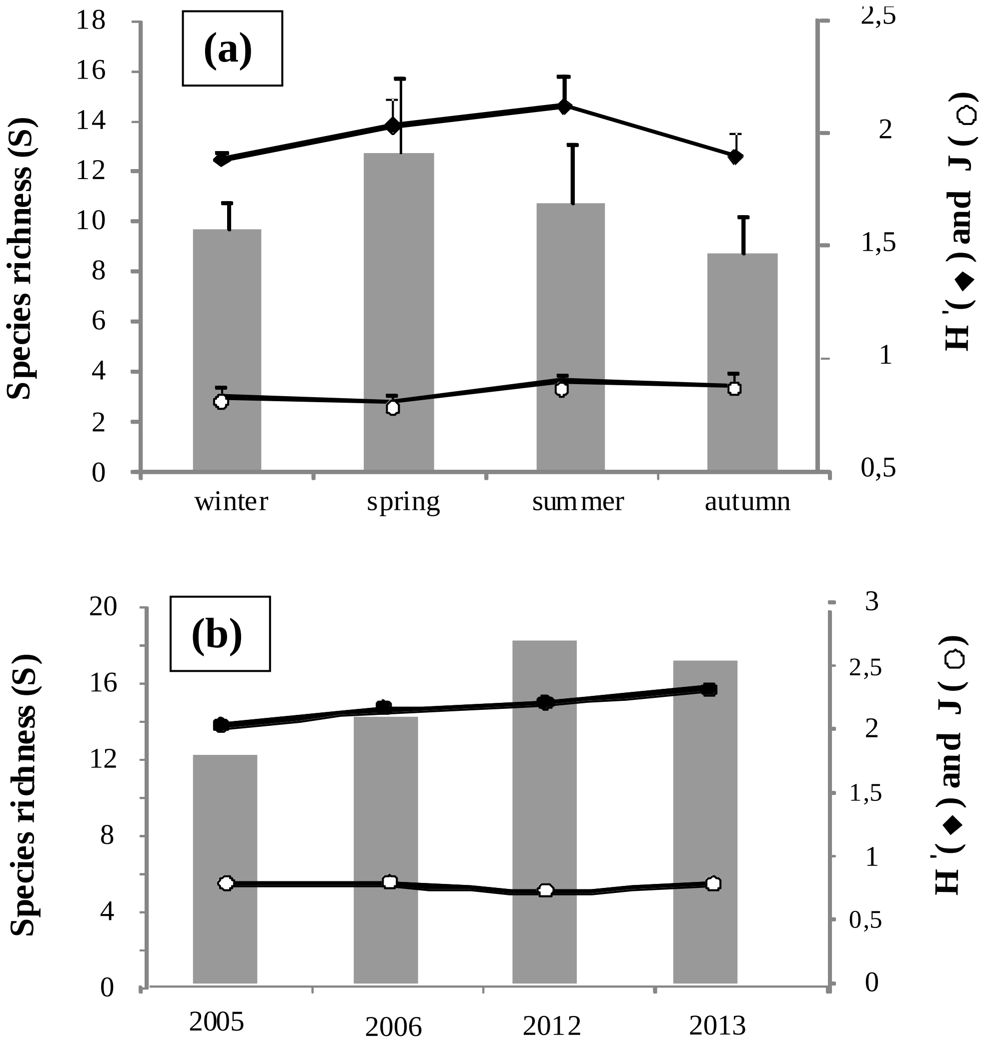

Figure 22. Seasonal (a) and inter-annual (b) variations of species richness S, diversity H' and eveness J during the 4 years of study (2005-2006-2012-2013).

Common plaice, sprat and common goby *Pomatoschistus microps* were the most abundant fish species and made up 94% of the total fish catch. Also these species may be found all year round and they have a clear seasonal peak of abundance. The fish assemblages were dominated by plaice and sprat during the spring and by sprat during summer and common goby during autumn (Table 5). Sand eel *Ammodytes tobianus* was also important components of the fish community but only during spring. The brown shrimp was by far the most abundant species of the macrocrustacean community (mean density during the period of study: 1122 ind.1000m-²) whatever the season (100% frequency of occurrence) and contributed to 94% of the total macrocrustacean catch. Shore crabs *Carcinus maenas* were also regularly caught (87.5% frequency of occurrence) and were abundant mainly during summer. According to their densities and occurrence, plaice, common goby, sprat, brown shrimp and shore crab could be considered as key species of the intertidal fish and macrocrustaceans community. These species showed inter-annual variation in density and for all of them a strong reduction in density occurred in 2013 (Figure 24).

Table 5. Species composition and mean densities (ind/1000 m²) of fish and macrocrustaceans along the Sainte Cécile intertidal sandy beach over the period of sampling (2005-2006-2012-2013).

Family	Species	Abbreviation	2005	2006	2012	2013
Fishes						
Clupeidae	*Sprattus sprattus*	(S spr)	323,8	137,7	117,7	68,7
	Clupea harengus	(C har)	0,0	0,0	0,1	0,0
Cottidae	*ind species (chabot)*	chabot	0,0	0,1	0,0	0,0
Gasterosteidae	*Pungitius pungitius*	(P pun)	0,0	0,0	0,0	0,2
Gadidae	*Ciliata mustela*	(C mus)	0,0	0,0	0,2	0,0
Atherinidae	*Atherina presbyter*	(A pre)	0,5	0,1	0,6	0,0
	ind species (atherine)	atherine	0,0	0,0	0,0	0,1
Moronidae	*Dicentrarchus labrax*	(D lab)	3,7	12,7	5,8	3,8
Mugilidae	*Liza ramada*	(L ram)	0,0	0,0	0,3	0,0
Gobiidae	*Pomatoschistus microps*	(P mic)	86,4	97,3	98,1	23,9
Trachinidae	*Echiichthys vipera*	(E vip)	0,0	0,0	0,1	1,3
Ammodytidae	*Ammodytes tobianus*	(A tob)	16,4	11,0	0,1	0,5
Syngnatidae	*Syngnathus acus*	(S acu)	0,3	9,5	0,1	7,3
Pleuronectidae	*Pleuronectes platessa*	(P pla)	124,3	104,9	24,7	25,6
	Platichthys flesus	(P fle)	0,0	0,0	1,2	0,8
Soleidae	*Solea solea*	(S sol)	0,0	0,0	0,0	0,0
Scophthalmidae	*Psetta maxima*	(P max)	0,8	0,0	1,4	2,2
	Scophthalmus rhombus	(S rho)	0,2	0,4	0,1	0,6
Macrocrustaceans						
Crangonidae	*Crangon crangon*	(C cran)	1028,2	1532,9	1561,9	208,7
Palaemonidae	*Palaemon longirostris*	(P lon)	0,0	0,1	9,4	0,0
	Palaemon serratus	(P ser)	0,0	0,4	0,0	0,0
Portunidae	*aenasCarcinus m*	(C mae)	45,8	170,0	11,5	16,5
	Liocarcinus holsatus	(L hol)	0,0	0,0	0,0	0,0
Carcinidae	*Portumnus latipes*	(P lat)	1,2	4,6	2,8	7,5
Majidae	*Macropodia longirostris*	(M lon)	0,0	0,0	0,0	0,0
Porcellanidae	*Pisidia longicornis*	(Pi lon)	0,0	0,0	0,0	0,1
Varunidae	*Hemigrapsus sanguineus*	(H san)	0,0	0,0	0,0	0,1

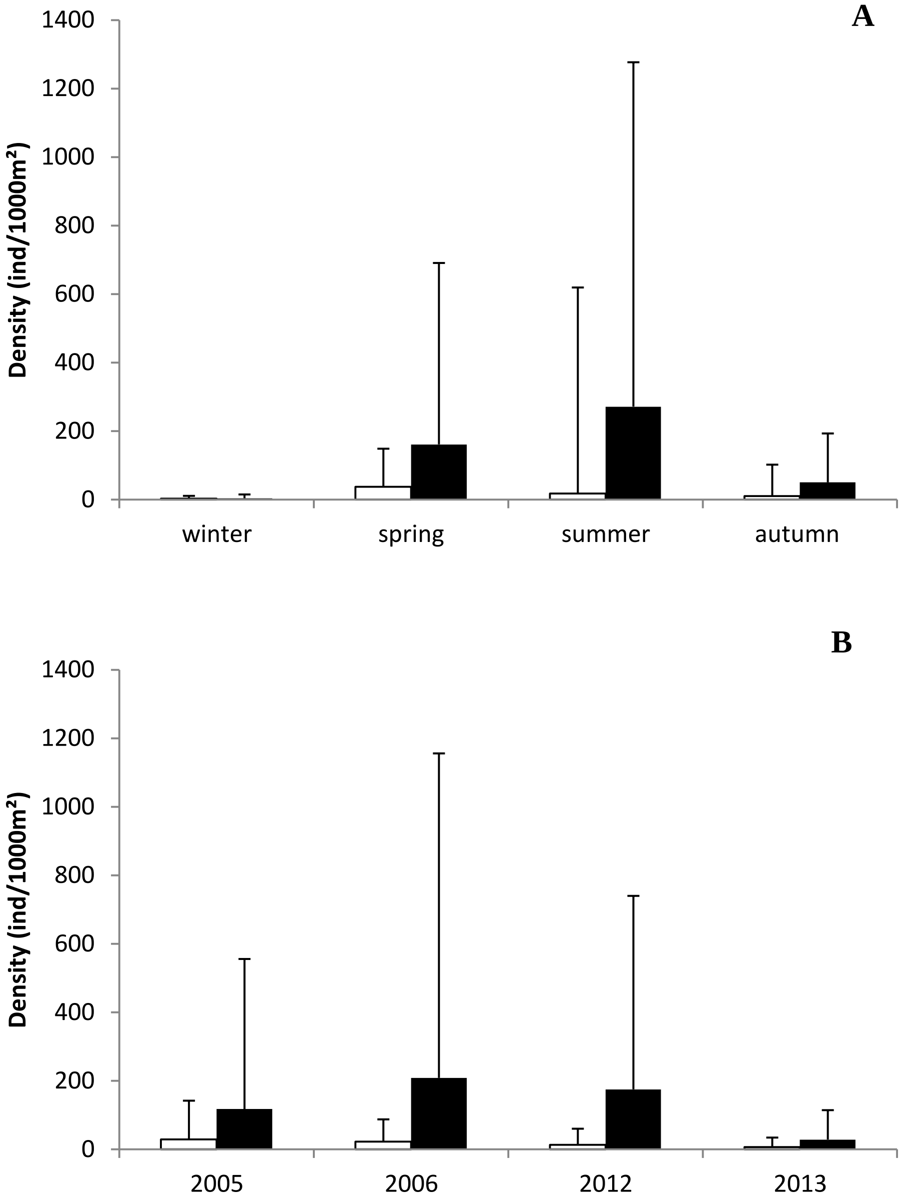

Figure 23. Seasonal (a) and inter-annual (b) variations in fish (white bar) and macrocrustaceans (black bar) densities during the 4 years of study (2005-2006-2012-2013).

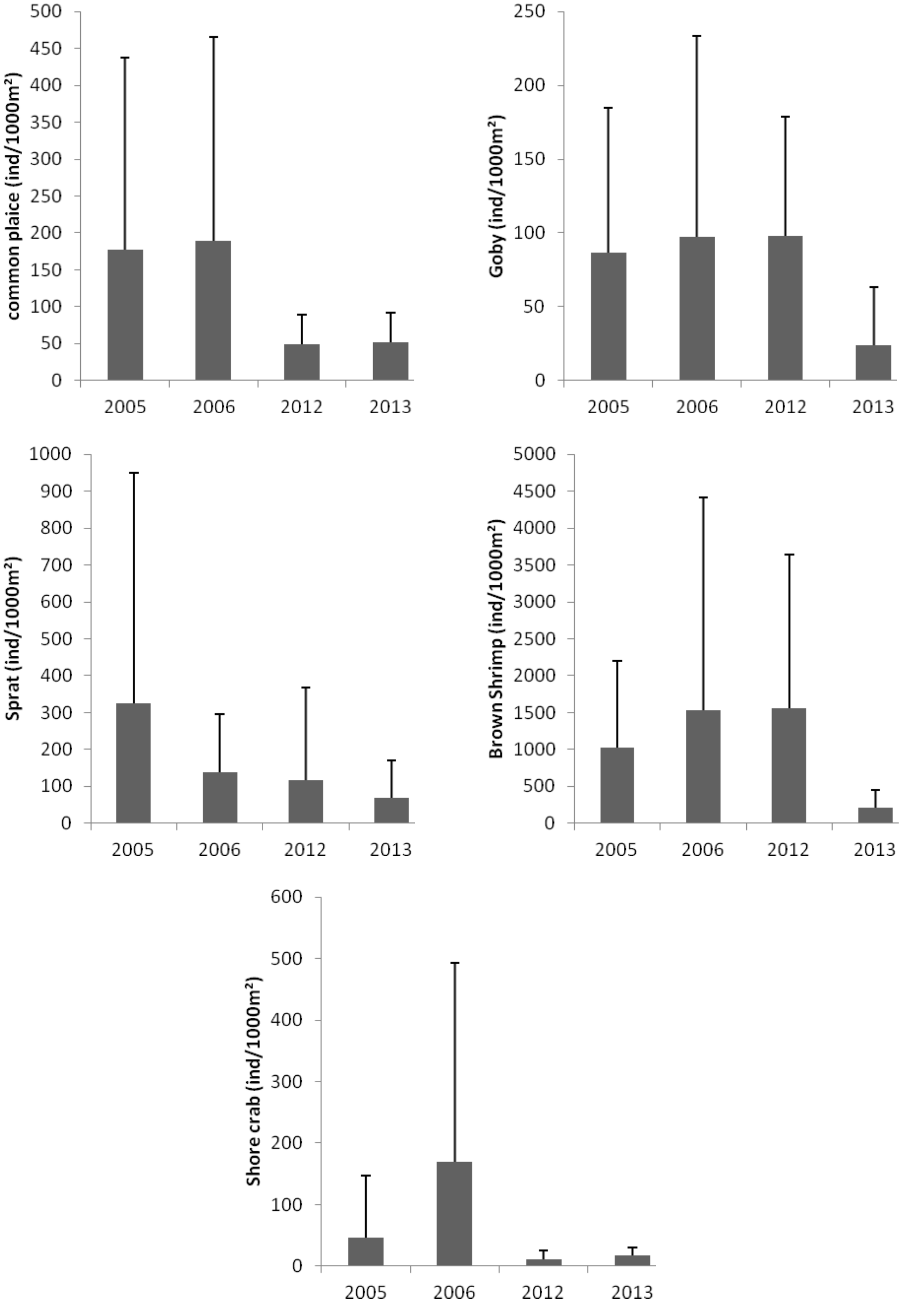

Figure 24. Evolution of the 5 key species mean densities (ind/1000m²) during the 4 years of study (2005-2006-2012-2013)

3.3.3.2. Inter-annual variations of the environment and species assemblages

Environmental variables showed clear seasonal fluctuations characteristic of temperate regions along the 4-year study period (Fig. 25). The between years normalized PCA with environmental variables showed significant inter-annual variations (p< 0.0001, representing 22.7% of the total inertia) (Fig. 27). The first two axes represented 72 and 22% of the total variability in the data, respectively. The first axis showed mainly an opposition between Seine and Somme runoffs and SPM. The second axis showed an opposition between S and POC and chl *a*. The ordination of the years along the first two axes opposed the years 2005 and 2006 to the years 2012 and 2013, by their relative low Seine and Somme runoffs and high SPM content. The second axis opposed the year 2012 to the other ones, by its relative higher S and lower POC and chl *a* content.

As for environmental variables, between-years covariance PCA analysis with species density showed significant inter-annual variations (p< 0.0001, representing 12.5% of the total inertia). The first two planes explained 67 and 27% of total variability in the data, respectively (Fig. 27). As for environmental variables, the years 2005 and 2006 were opposed to the two most recent ones according to the second axis, resulting from their higher abundance in plaice, goby, sprat and sand eel. The first axis opposed the years 2013 to the other ones for their relative lower abundance in brown shrimp, sprat, plaice and gobie, and their relative higher abundance in greater pipefish and flounder.

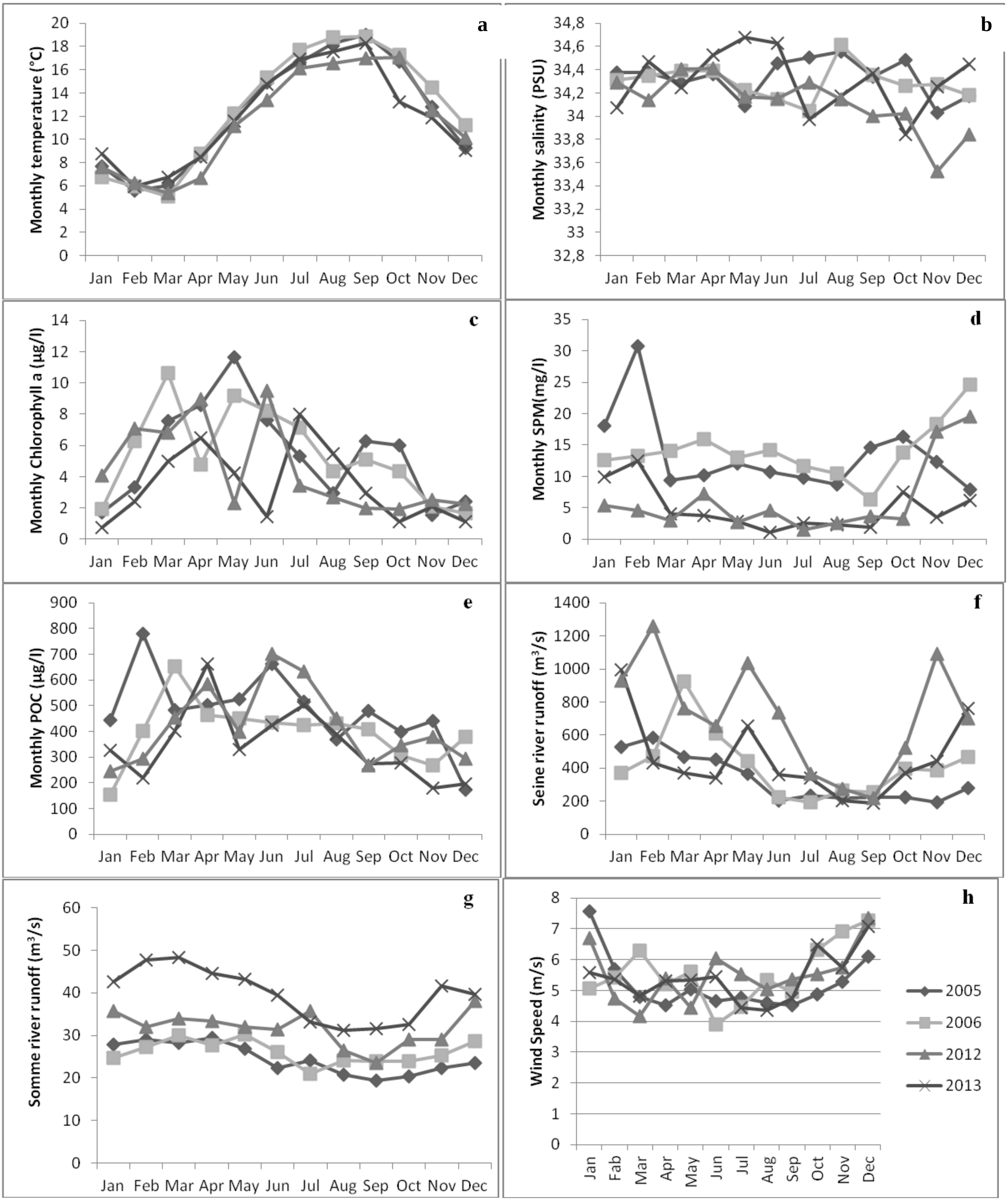

Figure 25. Monthly variation of environmental parameters during 2005-2006-2012-2013. (a) temperature (b) salinity (c) chlorophyll a (d) SPM (e) POC (f) Seine river runoff (g) Somme river runoff (h) Wind speed.

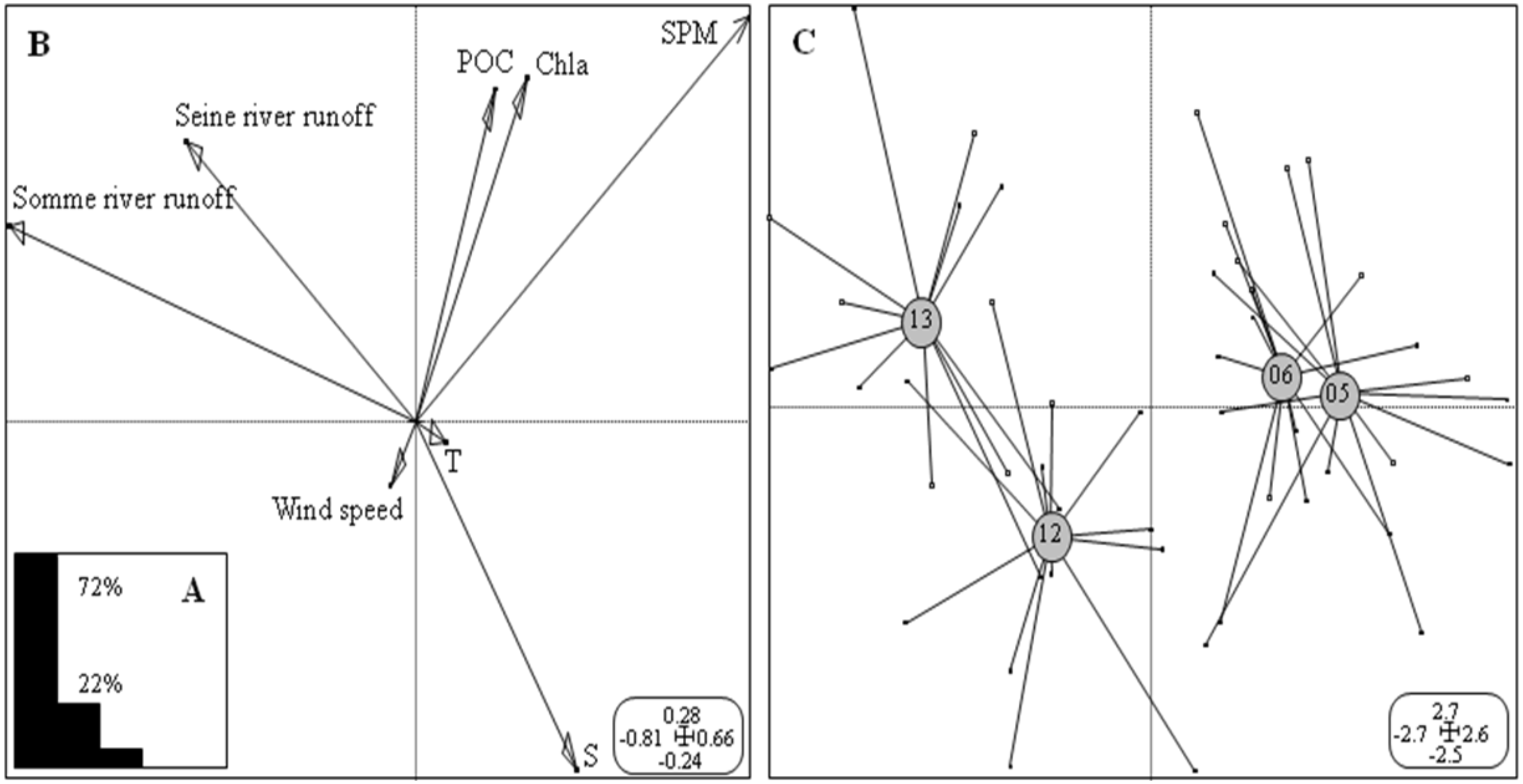

Figure 26. Between-years PCA analysis of environmental variables (wind speed, Seine and Somme river runoffs, T, S, SPM, POC, and Chl *a*). A. Eigenvalue diagram showing that the first factorial plane explains 94% of the total inertia of the data B. Projection of the variables on the first factorial plane C. Projection of the sampling years. Note the different scales.

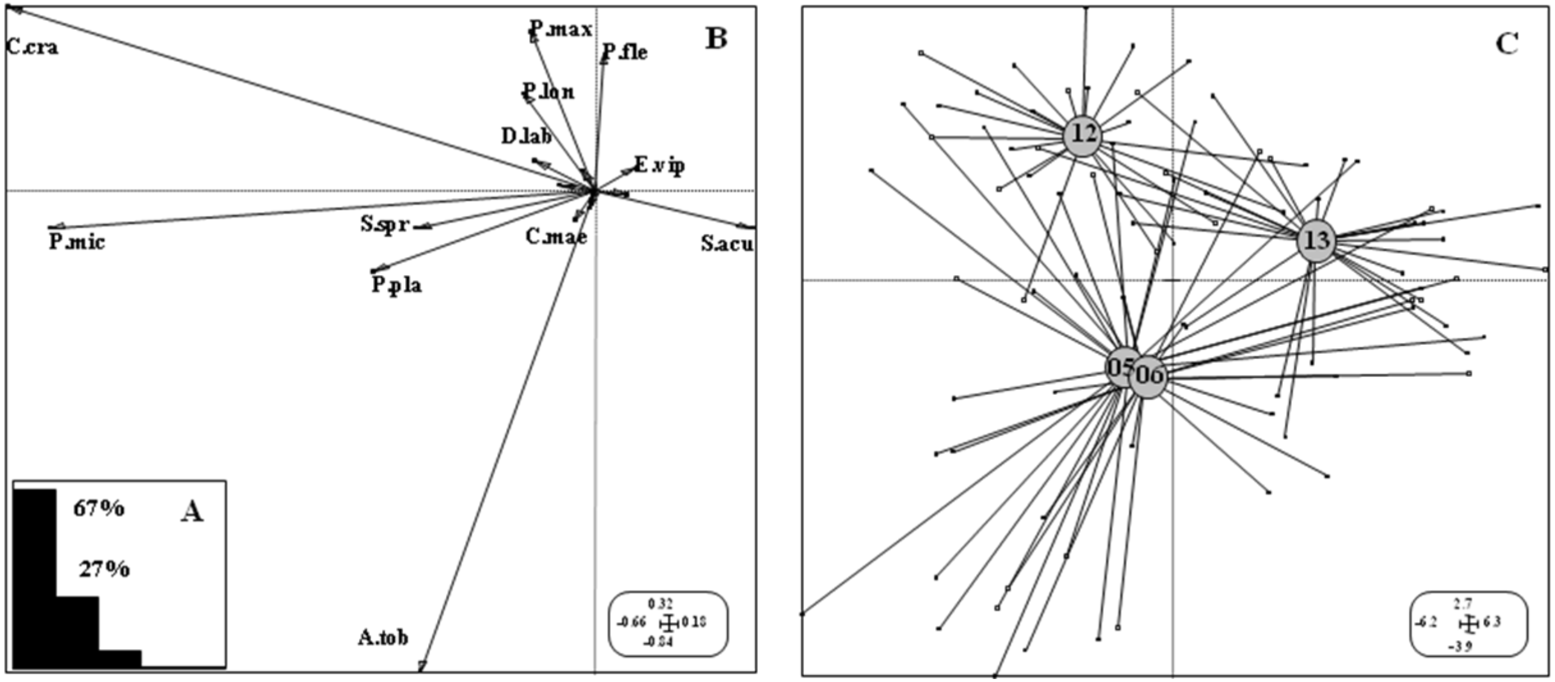

Figure 27. Between-years PCA analysis of fish and macrocrustacean abundances (only the labels of most abundant species are indicated) recorded in the Sainte Cécile intertidal sandy beach in the eastern English Channel. A. Eigenvalue diagram showing that the first factorial plane explains 94% of the total inertia of the data B. Projection of the variables on the first factorial plane C. Projection of the sampling years. Note the different scales.

3.3.3.3. Stability in the seasonal structure of the environment and species assemblages

STATIS analysis with the environmental variables showed a strong common seasonal structure between years (Fig. 28). Accordingly, the first eigenvalue from the inter-structure analysis (Fig. 28A) represented 54% of the total inertia, and the values of the all four years along the first inter-structure factor were high (Fig. 28B). Nevertheless, the second inter-structure factor, which explained 38% of the total inertia, opposed the year 2012 to the other ones, indicating some particular seasonal structure in the year 2012. This was confirmed by the smaller weight and cos2 values of the year 2012 than those of the other ones (Table 6), indicating the smaller contribution of the year 2012 in the construction of the compromise. The common seasonal structure of environmental variables between years, of which the two first axes accounted for 58 and 16.5% of the total inertia, respectively, is presented on Fig. 7C. The first axis of the factorial map allowed to distinguishing autumn and wintertime (from October to February) on the left side of the first axis from spring and summertime (from April to September) on the right side of the first axis. Accordingly, relative strong wind speed, high Seine River runoff and SPM content, but low T, POC and Chl *a* content characterized autumn and wintertime. The second axis of the factorial map opposed the end of winter and spring (from February to May) on the lower side of the second axis to autumn and winter on the upper side of the second axis. Accordingly, relative high S, and POC and Chl*a* content, but low T characterized the end of winter and spring.

Table 6. Values of weights, NS norm and Cos2 found with STATIS analysis on environmental variables.

Years	**Weights**	**NS norm 2**	**Cos2**
2005	4.931 e^{-1}	2.100 e^{-1}	0.508
2006	5.171 e^{-1}	2.165 e^{-1}	0.570
2012	4.648 e^{-1}	2.841 e^{-1}	0.479
2013	5.229 e^{-1}	2.894 e^{-1}	0.560

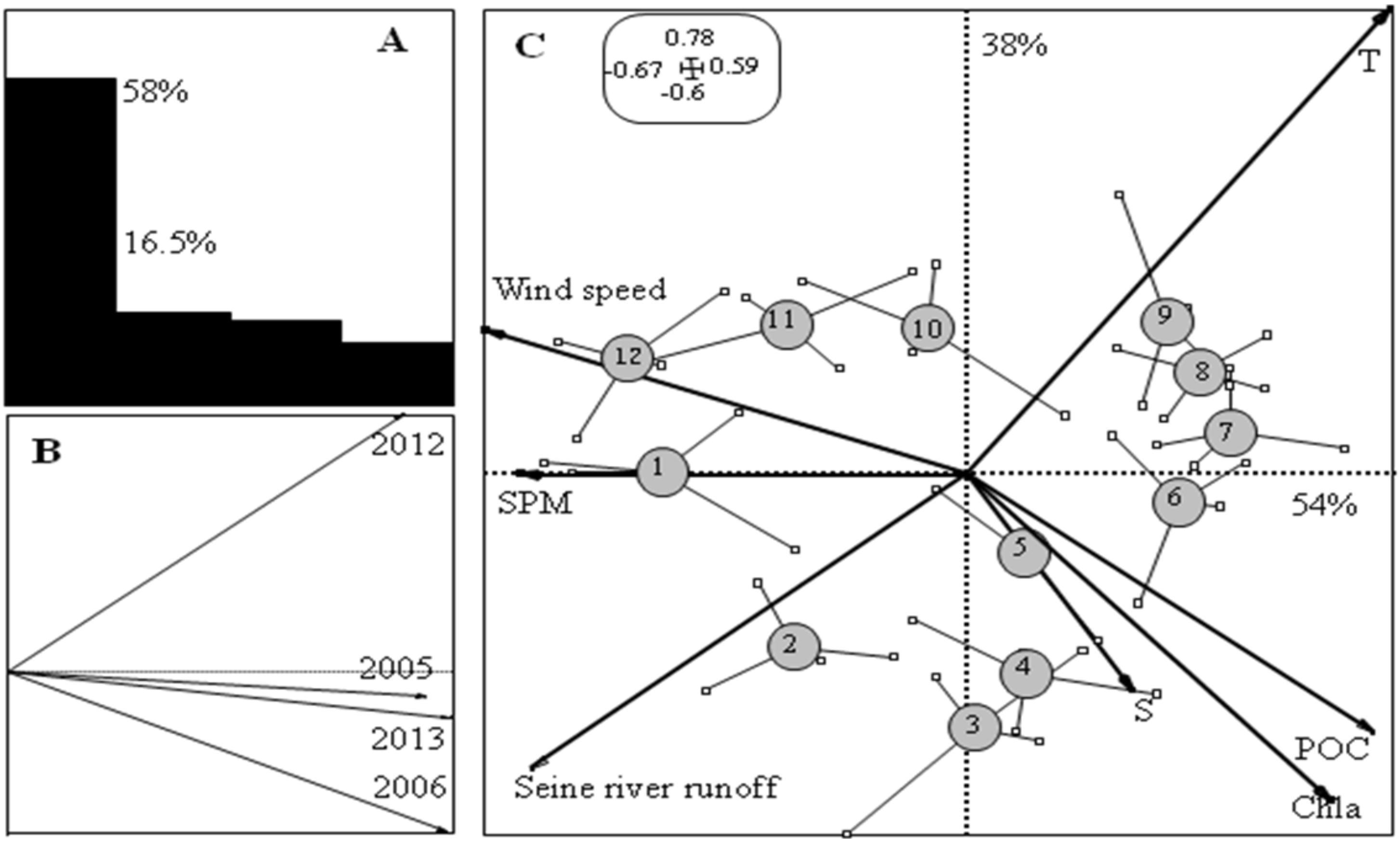

Figure 28. STATIS analysis showing the stable part of the seasonal variations in environmental variables for the years 2005, 2006, 2012, and 2013, recorded at the SOMLIT coastal station in the eastern English Channel. (A) Eigenvalues of the inter-structure analysis, (B) position of the four years on the two first axes and (C) projections of environmental variables, and all the years (white square) and months barycentre (grey circle) on the two first axes.

As for the environment, STATIS analysis with species abundances exhibited a strong common seasonal structure between years. Accordingly, the first eigenvalue represented 72% of the total inertia (Figure 29A), and the values of the all four years along the first inter-structure factor were high (Fig. 29B). The second interstructure factor explained only 9% of the total inertia. Nevertheless, it allowed to separating the two groups of years, i.e. 2005-2006 and 2012-2013. The smaller weight and cos2 values of the year 2013 than those of the other ones (Table 7), indicated that this year exhibited a little particular structure compared to the other ones. Only 8 species over the 27 identified in the study contributed the most to the seasonal structure. However, they represented altogether 99% of the total species abundance over the entire study, and are therefore considered as to be representative of the whole community. The first axis of the compromise (Figure 29), which represented 73% of the total inertia, opposed the dominant species, i.e. plaice, sprat, gobie, brown shrimp and crabe shore to the other ones. The projection of the sampling dates on the factorial map of the compromise showed that all these species were common in spring and summer (from April to July). The second axis of the compromise accounted only for 4.5% of the total inertia. It opposed sea bass, which was common in autumn and winter (September to December), to sand eel, sprat and plaice, which were common in spring and summer.

Table 7. Values of weights, NS norm and Cos2 found with STATIS analysis on species abundances.

Years	**Weights**	**NS norm 2**	**Cos2**
2005	5.030 e^{-1}	8.855 e+00	0.923
2006	5.103 e^{-1}	7.264 e+00	0.935
2012	4.987 e^{-1}	1.027 e+00	0.903
2013	4.878 e^{-1}	1.981 e+00	0.791

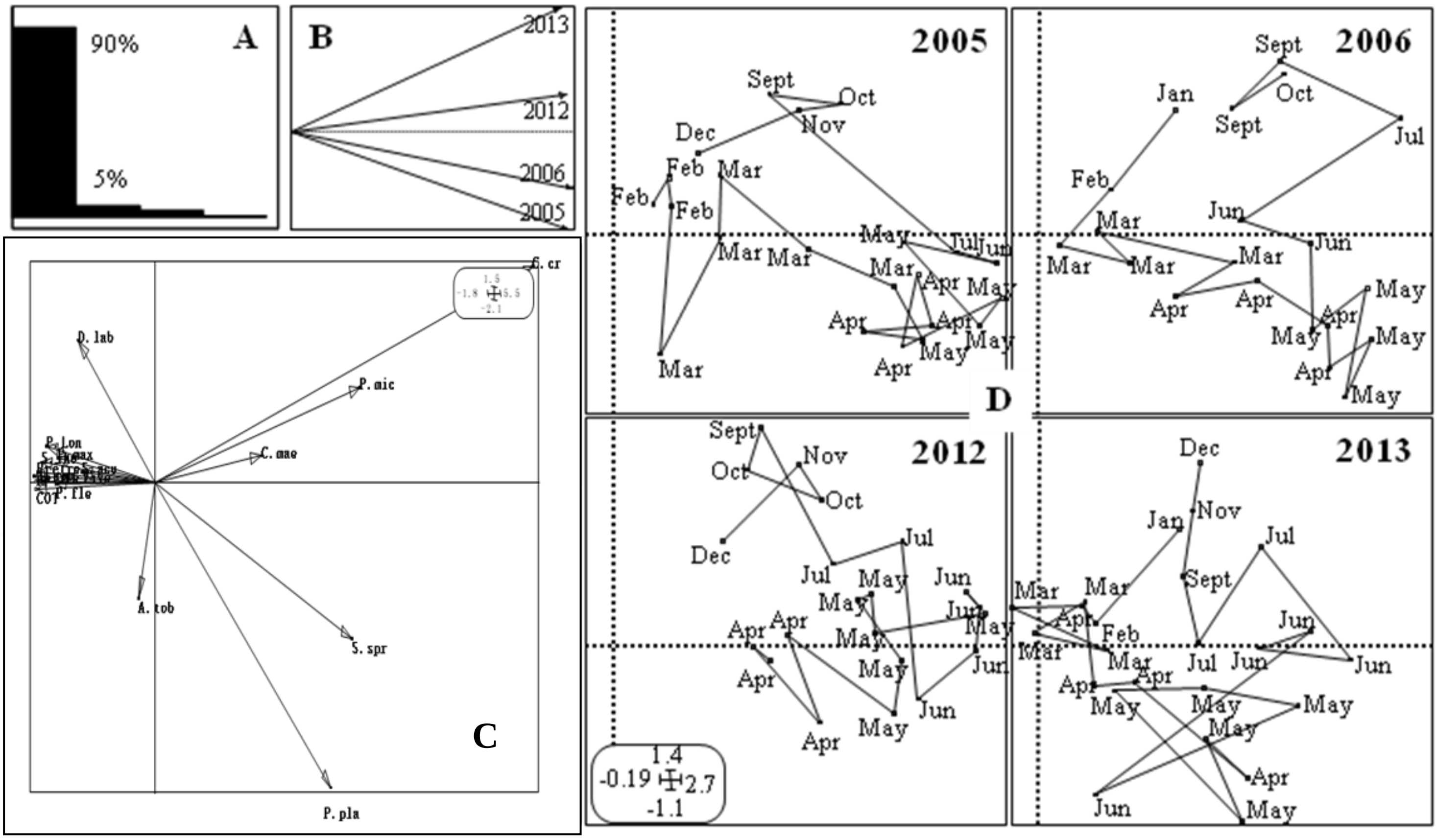

Figure 29. STATIS analysis showing the stable part (compromise step) of the seasonal variations in fish and macrocrustacean assemblages recorded in 2005, 2006, 2012, and 2013 along the eastern English Channel. (A) Eigenvalues of the inter-structure analysis, (B) position of the four years on the two first axes, (C) projections of fish and macrocrustacean species, and (D) the sample months on the two first axes.

3.3.3.4. Relationships between fish and macroscrustacean community-structure and their environment

Co-inertia analysis (Figure 30) revealed a strong seasonal coupling between species abundances and environment (RV=0.67, p<0.005). Accordingly, the two first eigenvalues explained 75 and 24% of the total inertia. The first axis was clearly dominant, and explained alone 69 % of the total inertia. Wind speed, T, SPM, POC, and Chla were the environmental variables contributing the most to the seasonal distribution of the species. The species sprat, plaice, goby, shore crab and brown shrimp were relatively more abundant when wind speed and SPM are low, but SST, POC and chl*a* are relatively high. The second axis explained 22% of the total inertia, with S as the sole explanative environmental variable. Sea bass was abundant when S is low, whereas sand eel was abundant when S is relatively high.

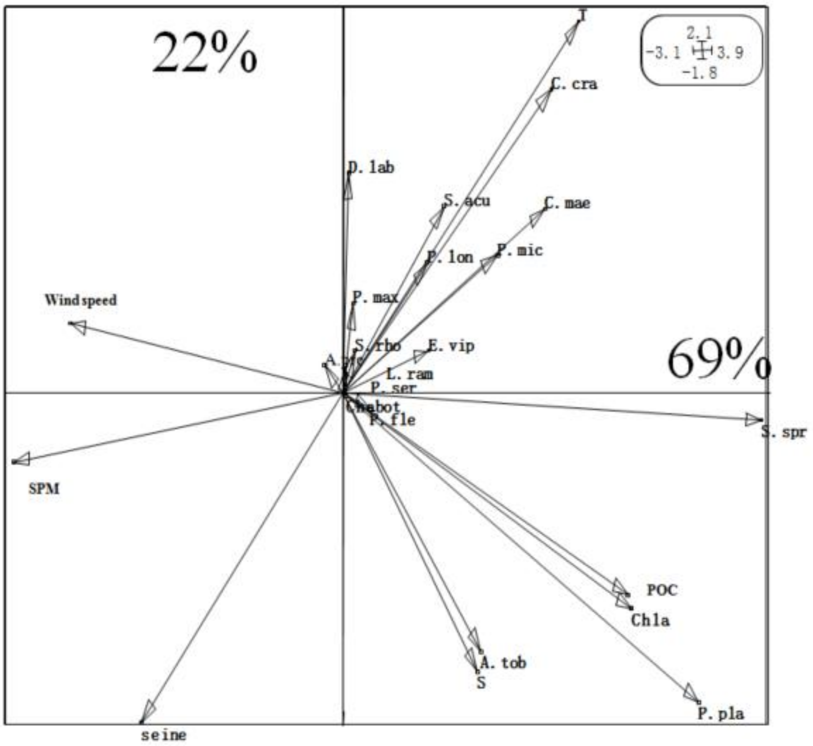

Figure 30. Co-inertia analysis performed on the environmental variables and the fish and macrocrustaceans abundances. Percentage of inertia explained by Factors 1 and 2 are 69 and 22%, respectively.

3.3.4. Discussion

3.3.4.1. Fish and macrocrustacean composition

Many fish species undertake short movements synchronously with the tide to take advantage of the intertidal zone. This study found that the great majority of fish and macrocrustaceans were juvenile migrants. As many living organisms, fish generally select those habitats that optimize their fitness.

The advantages for marine species using the intertidal zone during part of their life cycle are not well known. Of the factors explaining intertidal migration, foraging seems the most important for species such as plaice, goby, brown shrimp and shore crab, for which numerous studies already demonstrated the importance of intertidal areas as feeding grounds (Van der Veer and Witte, 1993; Beyst *et al.,* 2002; Cattrijsse and Hampel, 2006; Leclerc *et al.,* 2014). For example, common plaice are dependent on shallow intertidal sediment substratum as nursery grounds during their early juvenile stage, which is only a small fraction of the species distribution range (Gibson, 1994). Other species on the other hand, can be considered as rather opportunistic migrants taking advantage of the benefits of intertidal migration. Intertidal migration might also be related to predator avoidance as suggested by the low abundance of large predators in shallow waters (Blaber and Blaber, 1980; Gibson, 1994). In contrast to rocky shores, the dynamic and relatively homogeneous nature of substratum on sandy shores means that few refuges are available for fishes to remain intertidal over the low-tide period. Consequently the great majority of species that live on sandy beaches enter and leave the intertidal zone with each tide (Gibson *et al.*, 1993) and the community consists almost solely of transient species.

The number of species (27 species: 17 fish and 10 macrocrustaceans) collected in each season during four years with a sampling effort of 174 beam trawl samples was similar to that found in the few other published studies undertaken on European intertidal sandy beaches (e.g. 20 species in a Belgian surf zone (Beyst *et al.,* 2001), and 24 species at Porto Pim, Azores (Santos and Nash, 1995) and 21 species in Irish Sea (O'Sullivan, 1994). However, 43 species of fish and 16 species of macrocrustaceans were caught during a four year study on a Scottish intertidal sandy beach (Gibson *et al.,* 1993), and 35 species were captured on other Scottish beaches (Poxton, 1992). This high number results from the use of two different sampling gears (seine net and beam trawl), the proximity of the adjacent rocky headlands, and the sampling period (day/night) (Gibson *et al.*, 1996). Although caution is needed when comparing studies in which different types of fishing gear (different type, size or speed) were used, the beam trawl used in this work is considered efficient for catching demersal fish and epibenthic species in shallow coastal waters (Clark *et al.,* 1996; Beck *et al.*, 2001). As for other sandy beaches, only few taxa numerically dominated the catch, with most species occurring occasionally or rarely, in low number (Gibson *et al.,* 1993; Beyst *et al.,* 2001; Lazzari *et al.*, 2003). Out of the 27 species captured, only five (*P. platessa, P. microps, S. sprattus, C. crangon* and *C. maenas*) could be considered as dominant and key species of the intertidal zone. They represented more than 95% of the total catches during winter and autumn and more than spring 99.3 % during spring and summer. Lazzari et al. (1999) found that the low number of species occurring regularly year-round in temperate regions has been attributed to the wide variation in annual water temperature.

3.3.4.2. Temporal community structure evolution and environmental influence

Gross temporal patterns of change in fish and macrocrustacean assemblage are mainly a result of alterations in the density of the dominant species. In the present study, seasonal and interannual patterns in species densities were evident, with maximum values in spring and summer. This seasonality in density of the fish and macrocrustaceans community of the intertidal zone largely reflects the different times of recruitment of different species, as observed in other areas (Amara, 2003; Beyst *et al.,* 2001; Gibson, 1973; Kuipers, 1977). For many species (e.g. plaice, sprat, sea bass) the intertidal zone only functioned as an important area of settlement and nursery for a relatively short period during the first months following settlement. Spring and summer fish collections were dominated by common plaice, common goby and sprat. In autumn, common goby and sprat were the main fish species but sea bass and syngnathe are also important species. Common goby is repeat spawner and is among the most abundant fish of shallow coastal areas, estuaries and marine bays of the European coast (Fonds, 1973; Hamerlynck & Cattrijsse, 1994). In the intertidal zone studied, this specie was present throughout the year but in higher density in autumn. As in other shallow waters in northern Europe, the brown shrimp is the dominant mobile epibenthic species (e.g. Beyst *et al.,* 2001; Kuipers & Dapper, 1984; Pihl & Rosenberg, 1982). This crustacean species which tolerates diverse environmental conditions was present all year round and is a ubiquitous member of the large motile epifauna of shallow water communities (Gibson *et al.,* 1993).

Inter-annual variations observed in species density are most likely the result of differences in recruitment success. The fact that fluctuations did not follow the same pattern for all dominant species, suggests that species responded differently to the environmental variables and that the factors contributing to successful recruitment differed between species. Co-inertia analysis revealed a strong coupling between species densities and environment. Wind speed, water temperature, SPM, POC, and chlorophyll-a were the environmental variables contributing the most to the species densities variations. In a long term study (11 years) conducted in the same intertidal area, inter-annual variations in fish and macrocrustacean spring species density were mostly related to inter-annual variations in winter NAO index, water temperature, salinity, suspended particular matter and chlorophyll-a (Benazza *et al.*, 2015).

3.3.4.3. Persistence and stability in the community structure

One of the remarkable findings of this study is that the fish and macrocrustacean community structure in the Canche intertidal zone was persistent from year-to-year, and was based on a set of regularly occurring species. The diversity index did not vary significantly during the seasons and years. This persistence is due to high dominance of the key species, which were recorded in all seasons and years and accounted for more than 95 % of the total number of individuals over the study period. Seasonal and between years comparisons exhibited high Jaccard's similarity coefficients (0.44–0.85). These Jaccard coefficient values were similar to those found on the west coast of Scotland (0.55 to 0.71, Gibson et al, 1993), the Belgian surf zone in (0.3 to 0.8, Beyst *et al.*, 2001), and Maine, USA (0.38 to 0.83, Lazzari *et al.*, 1999). These results indicate that the composition of intertidal fish and macrocrustaceans are persistent and resilient to any change, and, therefore, their general taxonomic structure is predictable from year-to-year (Jackson and Jones, 1999; Brown and McLachlan, 1990). High seasonal and inter-annual variations in density of the key species were associated to low seasonal and inter-annual variations in species composition. This is typical of many intertidal fish assemblages (Ross *et al.*, 1987; Santos and Nash, 1990; Lazzari *et al.*, 1999) and particularly those inhabiting the rocky intertidal zone (see the review of Gibson and Yoshiyama, 1999).

Significant inter-annual variations in both environmental variables and species abundances were observed. However, during the four years of study, both environmental variables and species abundances exhibited a strong common seasonal structure between years. Only 8 species over the 27 identified in the study contributed the most to the seasonal structure. These species represented altogether 99% of the total species abundance over the entire study, and are therefore considered as to be representative of the whole community. These results confirm those in highly variable nearshore marine rocky intertidal habitats where fish assemblages were considered relatively persistent and resilient (Gibson and Yoshiyama, 1999; Almada and Faria, 2004). Such pattern was also described in many shallow coastal areas such as eelgrass (*Zostera marina*) meadows (e.g. Robinson and Yakimishyn, 2013), and estuaries (Simier *et al.*, 2006; James *et al.*, 2008) where there is a persistence and stability of fish assemblages. For example, Magurran and Henderson (2010) found that the structure of the Bristol Channel fish assemblage has remained essentially unchanged over a 30-years period and that the core species are largely responsible for the maintenance of assemblage structure through time.

3.3.4.4. Fish and macrocrustaceans assemblages for biological monitoring of intertidal ecosystem

The transitional position of the intertidal zone, between the marine and terrestrial environments, makes it vulnerable to anthropogenic pressure and climate induced sea level rise. Understanding and managing increasing threat on intertidal ecosystem requires impact assessment and monitoring indices that provide accurate quantification of change and are readily communicable. As fish integrate a large variety of anthropogenic pressures (Elliott *et al.*, 1988; Karr, 1981), fish assemblages are generally considered as appropriate to develop indicators of ecosystem quality. Consequently, numerous fish-based multimetric indices have been developed in the context of the European Water Framework Directive (WFD) (Pont *et al.*, 2006), especially in transitional waters (e.g. Borja *et al.*, 2004 ; Breine *et al.*, 2007, 2010; Delpech *et al.*, 2010; Tableau *et al.*, 2013). Understanding these assemblage properties has important implications for assessing ecosystem condition, because if fish assemblages are not naturally persistent or stable from year to year, then it will be difficult to assess effect from anthropogenic activities (Robinson and Yakimishyn, 2013).

The seasonal and interannual fish and macrocrustacean community structure in the Canche intertidal zone was persistent from year-to-year, and was based on a set of regularly occurring species. This stability, however, was influenced by unpredictable interannual variation in species abundance related to environmental change. The intertidal studied area is away from anthropogenic pressure and is considered as a low disturbed zone (Amara *et al.*, 2007; Amara *et al.*, 2009). Therefore, our results may be useful for determining reference for intertidal area with minimal anthropogenic activity.

In conclusion, our study has demonstrated that the fish and macrocrustaceans assemblages are persistent in time and predictable, with the same set of species occupying the intertidal zone according to season. The five most abundant species caught were consistently recorded in catches each year, but abundances of individual species varied on an annual basis. We suggest that variability in fish assemblage properties may be used for assessing ecosystem change under anthropogenic pressure.

Acknowledgments

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CHAPITRE 4

Performances physiologiques des juvéniles de la plie commune *Pleuronectes platessa.*

4.1. Introduction :

La fonction des nourriceries intertidales doit permettre l'optimisation des performances physiologiques des juvéniles afin de contribuer au renouvellement des populations adultes. Afin de mieux comprendre ce processus de recrutement des populations ichtyologiques, il est nécessaire d'étudier la dynamique des populations et d'évaluer les facteurs qui la régissent. La variabilité du recrutement des poissons plats est censée être principalement déterminée lors de la phase pélagique avec un certain ajustement des effectifs après la période de colonisation (Van der Veer et al., 1990).

De nombreuses études ont été faites au niveau de la zone intertidale, là où les juvéniles de poissons plats et plus précisément ceux de la plie commune trouvent refuge en période printanière. Néanmoins, les mécanismes de fonctionnement et les processus régissant la survie des individus sont encore peu connus. Dans ces écosystèmes, les facteurs physiques et biologiques qui régulent la croissance et la survie des poissons (par exemple la température, la salinité, l'oxygène dissous, la disponibilité des proies, l'abondance des prédateurs…) varient considérablement dans l'espace et le temps. De ce fait, la croissance et la survie dans ces nourriceries a des implications importantes pour des processus tels que le recrutement dans le stock adulte (Beverton et Iles, 1992; Van der Veer et al., 1990). C'est pour cela que la croissance a été l'un des aspects le plus étudié de la biologie des poissons, et il a été démontré qu'elle dépend essentiellement des conditions de température (Yamashita et al., 2001). Une croissance rapide des juvéniles au niveau des nourriceries augmente la chance de survie des individus en diminuant la prédation (Sogard, 1997; Able et al., 1999), qui est principalement dépendante de la taille des poissons (Van der Veer & Bergman, 1987; Van der Veer et al., 1990; Wennhage, 2000).

La plie européenne *Pleuronectes platessa*, espèce d'importance économique, a été longtemps étudiée dans de nombreuses régions de l'Atlantique nord-est. Les adultes pondent leurs œufs au large (> 20 m de profondeur) dans les premiers mois de l'année. Les œufs et les larves pélagiques peuvent prendre jusqu'à 3 mois pour achever leur développement, au cours duquel ils seront transportés vers les côtes. En général, un grand nombre de juvéniles (14-17 mm) arrive sur les zones d'alevinage au printemps. Il y a des changements interannuels, associés aux variations de température, non seulement dans le nombre total d'individus arrivant dans les nourriceries mais aussi des variations dans les périodes de colonisation. Ces différences peuvent affecter la croissance et la survie des juvéniles et par conséquent influencer la dynamique des nourriceries. Il peut aussi y avoir des différences dans les taux de mortalité subies par les différentes cohortes. Les 1ères cohortes arrivant sur les côtes sont généralement les plus grandes (niveau densités), mais aussi, ce sont celles dont les mortalités sont les plus élevées. Les études à long terme de la colonisation, la croissance et la survie durant les stades juvéniles sont rares, mais très précieux dans l'établissement des niveaux de variabilités naturelles de ces paramètres. A plus large échelle, le succès du renouvellement des populations pourrait dépendre des conditions environnementales (naturelles et/ou anthropiques) rencontrées durant la période juvénile des poissons (Gibson, 1994), autrement dit de leurs performances biologiques.

Le long des côtes de la Manche Orientale, et en particulier dans les zones intertidales adjacentes de l'estuaire de la Canche, la colonisation des juvéniles de la plie commune se fait de Mars à Juin (Amara et Paul, 2003; Selleslagh & Amara, 2008a). Pour qu'un habitat soit qualifié de bonne qualité, on présume que la croissance, la condition et la survie sont optimisées (Gibson, 1994).

C'est pourquoi plusieurs auteurs ont utilisé des indices de croissance et de condition, tels que la croissance récente, l'indice de condition K ou les rapports biochimiques ARN/ADN pour estimer la qualité des nourriceries. Ces indices étant sensibles aux variations environnementales (Adams, 2002), ils permettent de détecter les modifications du milieu et de voir si les conditions sont favorables aux juvéniles de poissons qui les fréquentent durant les premiers mois de leur vie.

Notre objectif dans cette étude était d'analyser et de comparer l'état, la croissance et les indices nutritionnels des cohortes de plie nouvellement installées, recueillies au cours de la période de colonisation (7 ans d'échantillonnage). Cela va nous permettre de caractériser la qualité de l'habitat et de son adéquation temporelle, et d'acquérir une meilleure compréhension de l'influence que la variabilité de l'environnement peut avoir sur le contrôle de la densité de population de plies et donc le recrutement. Nous avons supposé l'existence de variations de performances biologiques des juvéniles de plie récemment établis en zone intertidale, en fonction de leur date de colonisation et la disponibilité en nourriture, qui peut être un facteur limitant à certaines dates.

Cette 2ème étude se focalise sur la dynamique de la colonisation des juvéniles de plie *Pleuronectes platessa* en nourricerie intertidale en relation avec les facteurs environnementaux. Cette partie visera à mieux comprendre le processus de colonisation et à analyser l’importance des événements subis lors de la période de colonisation dans le déterminisme du recrutement de cette espèce de poissons plats. Cette étude permettra de comprendre la variabilité de recrutement de cette espèce en évaluant le lien entre les abondances des juvéniles de plie en zone intertidale et le niveau du recrutement et ainsi d’émettre des hypothèses sur les mécanismes impliqués dans son déterminisme.

En 2$^{\text{ème}}$ lieu, la croissance, la condition et l’état nutritionnel des juvéniles de plie tout au long de la période de colonisation ont été étudiés. Ce travail nous permettra de conclure si les conditions environnementales au niveau des nourriceries intertidales sont bonnes pour le développement des juvéniles de poissons. Cette étude permettra aussi d’évaluer l’importance des facteurs environnementaux, toujours dans une optique d’améliorer la compréhension des processus intervenants dans la variabilité du recrutement de la plie. Ce travail devrait permettre de préciser l’importance des événements subis lors de la phase juvénile dans le déterminisme du recrutement de la plie.

Et enfin, les performances physiologiques (croissance, condition K, le rapport ARN/ADN et la vacuité) des juvéniles de la plie commune ont été examinées.

4.2. Seasonal and interannual variations of biological performances of newly settled juvenile plaice *Pleuronectes platessa* during the spring period on an intertidal sandy beach.

Abstract

Habitat quality of an intertidal nursery ground in the eastern Channel for 0-group plaice *Pleuronectes platessa* was investigated by following settlement, condition and growth during seven years (2005 to 2007 and 2010 to 2013) between March to June. Plaice settlement period extended from mid-March to late May and both date of pic of settlement and plaice densities varied between years. Fulton K, RNA:DNA and recent otolith growth indices were above the established baseline value for nutritional stress, indicating that newly settled plaice were in relatively high condition and that food was not a limiting factor. We did not observe density-dependent growth at our study site, and the relatively high growth rates observed each year suggest minimal competition for food. Our study indicate that the Sainte Cécile nursery areas provide suitable conditions growth and survival of early juvenile stages.

Keywors: plaice, juvenile, settlement, growth, condition.

Résumé :

Dans cette étude, la qualité de l'habitat d'une nourricerie intertidale de la Manche Orientale a été étudiée. Pour ce fait, le suivi de colonisation et indices de condition et de croissance des juvéniles de plie commune *Pleuronectes platessa,* issus d'un échantillonnage de 7 années (2005-2007 et 2010-2013) en période printanière (mars à juin) ont été pris en considération. La colonisation de la zone intertidale par les juvénile de plie s'étend de la mi-Mars à la fin mai, avec des variations interannuelles non seulement dans les dates des pic de colonisation mais aussi dans les densités. Notre étude montre que les valeurs des indices de Fulton K, le rapport ARN:ADN et l'indice de croissance récente (obtenu par otolithométrie) étaient au-dessus de la valeur de base établie pour le stress nutritionnel, ce qui indique que les plies nouvellement installées avaient des conditions relativement élevées et que la nourriture n'était pas un facteur limitant. Nous n'avons pas observé de corrélation entre la croissance et la densité au niveau de notre zone d'étude, et les taux de croissance relativement élevés, observés chaque année suggèrent une compétition minimale pour la nourriture. Notre étude indique que la nourricerie intertidale de la plage sableuse Sainte Cécile offre des conditions de croissance et de survie aux juvéniles.

MOTS CLEF : Plie. Juvénile. Colonisation. Croissance. Condition.

4.2.1. Introduction

Evaluation of the specific factors regulating life history dynamics of marine fish population is essential to understand recruitment. Recruitment variability in flatfish is believed to be mainly determined during the pelagic phase with some further adjustment of year-class strength after settlement (Van der Veer *et al.,* 1990). Although growth limitation and mortality on nursery grounds are thought to contribute to recruitment variability (Rauck and Zijlstra, 1978; Karakiri *et al.,* 1989; Cowen *et al.,* 2000; Grover *et al.,* 2002; Duncan and Holland, 2006), survival processes of the juvenile phase are still not well known and remain controversial in regard to their contribution to recruitment variability (Le Pape and Bonhommeau, 2013).

There has been much research undertaken on flatfish nursery grounds, yet the mechanisms operating and processes governing survival are still poorly known. Recent work on one small nursery ground in the Irish Sea (Nash & Geffen, 2000) suggests that the year class strength of an annual cohort can be determined on the nursery grounds rather than in the pelagic phase. For example, Fonseca *et al.*, (2006) showed that performances of juvenile soles *Solea solea* and *Solea senegalensis* in the Tagus estuary differed according to their arrival date in the nursery ground. It is therefore important to examine the nursery ground phase more critically. Habitat quality of a nursery ground can affect growth rates and survival (Gibson, 1994).

Temperate nearshore areas serve as nurseries for a number of juvenile marine species (Able *et al.,* 1999; Elliott and Dewailly, 1995; Jones *et al.,* 2002; Laegdsgaard and Johnson, 2001; McLusky and Elliott, 2004; Elliott *et al.,* 2007; Franco *et al.,* 2008; Amara *et al.,* 2000; Selleslagh and Amara, 2008) and especially flatfishes (Gibson, 1994; Amara, 2003; Amara and Paul, 2003; Le Pape *et al.,* 2003). Fishes aggregate in these productive areas where their fitness is thought to be enhanced through optimal growth from better feeding conditions (Gibson, 1994; Beck *et al.,* 2001). Within these systems, physical and biological factors that regulate the growth and survival of fishes (e.g. temperature, salinity, dissolved oxygen, prey availability, predator abundance) vary substantially in space and time. In this context, variations in the quality of these habitats, i.e. according to fluctuations in abiotic and biotic factors (e.g. availability of food and density of newly settled fish), into which fish juveniles settle may affect the quality and the nursery function. Growth and survival in these nursery areas has important implications for population processes such as recruitment to the adult population (Beverton and Iles, 1992; Van der Veer *et al.,* 1990). During the juvenile stage, higher condition and growth rate results in successive improvements in feeding (Van der Veer & Witte, 1993), predator avoidance (Gibson *et al.,* 1995; Wennhage, 2000) and ultimately survival (Vethaak, 1992; Islam & Tanaka, 2005).

The European plaice (*Pleuronectes platessa* Linnaeus) are a commercially important common north European flatfish. Plaice early life history has been extensively studied in many areas of the north-east Atlantic. Adult plaice spawn offshore in water >20 m deep in the early months of the year. Pelagic eggs and larvae can take up to 3 mo to complete development during which time they are transported towards coastal nursery grounds where they settle following metamorphosis (Gibson, 1999; Benazza *et al.,* 2015). Settlement of newly metamorphosing plaice onto nursery grounds occurs in pulses over a period of several weeks (Alhossaini *et al.,* 1989; Amara and Paul, 2003; Geffen *et al.,* 2011). In general, large numbers of very small individuals (14–17 mm) arrive on nursery grounds in spring (Nash & Geffen, 2000). There are annual variations in both the overall numbers of individuals arriving on a nursery ground and the settlement patterns or timing (Hyder and Nash, 1998). These aspects of settlement may affect the growth and survival of the juvenile and influence the nursery ground dynamics (Geffen *et al.,* 2011). In some nursery areas, it has been showed that the second sub-cohorts have a higher growth rate than the first and third sub-cohorts, while later sub-cohorts have extremely low growth rates (Al-Hossaini *et al.,*1989 ; Modin and Pihl, 1994; Geffen *et al.,* 2011). This has been associated with increased temperatures as the settlement period progresses. There may also be differences in the mortality rates experienced by the different sub-cohorts (Al-Hossaini *et al.,* 1989).In the Irish Sea, Geffen *et al.,* (2011) noted that the first subcohort is usually the largest and suffers the highest mortality. Long-term studies of settlement, growth, and survival during early life history stages are rare but highly valuable in establishing levels of natural variability (e.g. Sogard *et al.,* 2001).

Along the eastern English Channel coast, and particularly in adjacent intertidal areas of the Canche estuary, settlement of juvenile plaice takes place from March to June (Amara & Paul, 2003; Selleslagh & Amara, 2008a). In this area, Amara and Paul (2003) suggested a food limitation only for newly settled plaice. Because environmental factors which regulate growth, condition and survival of fishes are highly variable during the plaice settlement period (Selleslagh & Amara, 2008a, b), patterns of habitat suitability for newly settled juveniles may also be dynamic.

Our objective in this study was to analyse and compare condition, growth and nutritional indices of newly settled plaice sub-cohorts collected during the settlement period during seven years. This will allow us to characterise the habitat quality and the temporal suitability of nursery habitat for newly settled plaice, and gain a better understanding of the influence that environmental variability may have on controlling population density of juvenile plaice and hence recruitment. We hypothesised the existence of variations of biological performances of newly settled juvenile plaice according to their settlement date and that food may be a limiting factor at certain dates.

4.2.2. Materials and methods

4.2.2.1. Study area and sampling

Newly settled juvenile of *Pleuronectess platessa* were collected on the surf zone of the sandy beach of Sainte Cecile, which is located near the north of Canche estuary, between Hardelot in the north and Etaple in the south, on the French coasts of the English channel (50°34’00’’ N 1°30’52’’ E) (figure 31). The beach is characterised by the presence of sand bars and pools parallel to the coast with fine and medium sands. The distance between high and low water mark was about 700 m at neap tide and 1500 m at spring tide. Sampling was done weekly at two replicate stations during the settlement period (from March to June) during 7 years (from 2005 to 2007 and from 2010 to 2013).

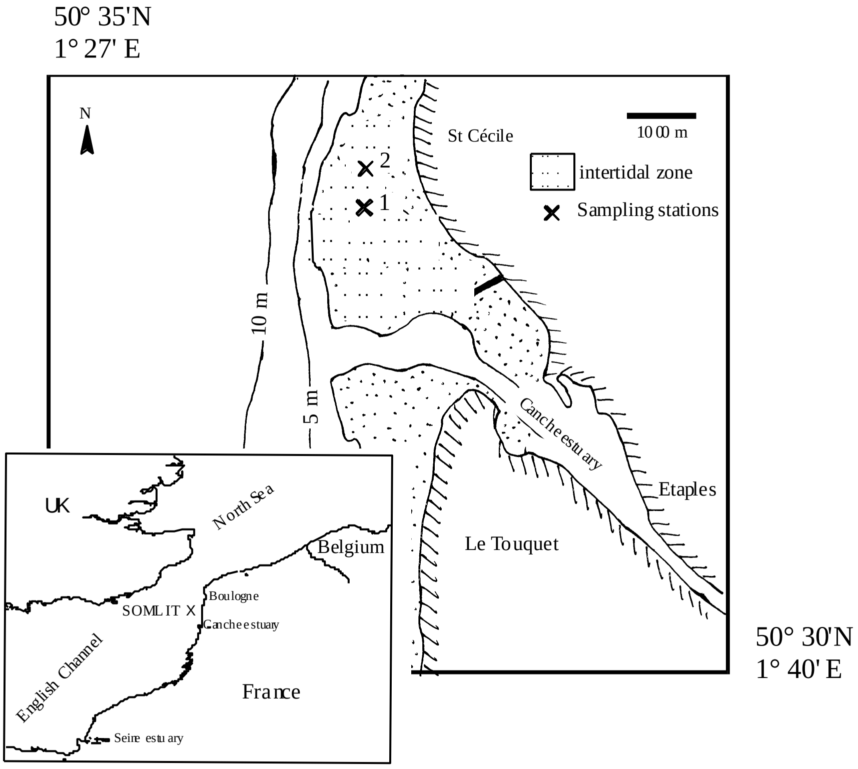

Figure 31. Location of the study area and the two sampling stations (X) along the Sainte Cécile intertidal sandy beach. The location of the SOMLIT coastal station for environmental parameters is also indicated.

Sampling was done with a 1.5 m beam trawl, during daylight hours at 2 to 3 hours after the high tide. The fishing net was 5.5 m long with a mesh size of 8x8 mm in the main body and 5x5 m long in the cod end, and was equipped with a tickler-chain in the ground rope. Following recommendations by Riley and Corlett (1966), net speed was kept as constant as possible during sampling, about 38m min-1. The net was pulled by two people in parallel to the shoreline in a water depth <1 m during the ebb tide (high tide +3 h). A meter registered the distance traveled by the trawls. As a result, each trawling represented an average distance of 250 m and a sampling surface of about 400 m^2.

After catch, plaice juveniles were sorted in plastic bags full of seawater and transported to the laboratory for measuring (total length (TL) and weight). Newly settled individuals (total length < 25 mm) were frozen at -20°C for later biological analysis.

Plaice density was calculated as trawl catches standardized to numbers of individuals per 1000 m^{-2} trawled and not corrected for net efficiency. Before, plaice densities obtained from the two sampling stations were averaged at each sampling date.

4.2.2.2. Environmental variables

Physico-chemical variables, temperature (°C), salinity, pH and turbidity (NTU) were measured at each sampling date using a Tetracon 325 and Cyberscan multiprobe. Chlorophyll-a concentration (Chl-a, µg.l-1), and Phaeocystis globosa abundance were obtained from the national French monitoring network SOMLIT (http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). Water samples for phytoplankton counts were collected with 8 L Niskin bottle fortnightly at high tide in subsurface (-2 m) and near the bottom (~ -20 m) from the permanent coastal station C (50°40’75 N; 1°31’17E) located near the study area. For the present study, data from subsurface and near the bottom were averaged at each sampling date. Chl-a was estimated according to the equations of Schoemann *et al.*(2005), after extraction in acetone 90% for 12h at 4°C in the dark. Abundance of *P. globosa* cells was determined under inverted microscopy according to the Utermöhl method from samples preserved with 1% (final concentration) Lugolglutaraldehyde solution. The number of Phaeocystis cells of the colonial form was counted separately from free cells within a month after sampling according to biovolume measurements (Schoemann *et al.*, 2005).

4.2.2.3. Growth and condition indices

Three biological indices were calculated: RNA/DNA ratio, recent growth and Fulton’s K condition indices as described below.

4.2.2.3.1. RNA:DNA ratios

Whole-body and white muscle RNA:DNA ratios have been widely used to assess the condition and growth of fishes in both field and laboratory studies. RNA:DNA ratio reflects variations in growth–related protein synthesis (Chicaro and Chicaro, 2008). The quantity of ribonucleic acid (RNA) varies with the rate of protein synthesis while the amount of esoxyribonucleic acid (DNA) per cell is species-constant in somatic tissue (Buckley & Bulow, 1987; Chicharo and Chicharo, 2008). RNA:DNA ratio was calculated as a reliable indicator of recent growth and nutritional condition of larval and juvenile fish (Rooker and Holt; 1996; Clemmesen *et al.,* 1997; Chicharo, 1998; Buckley *et al.,* 1999; Heyer *et al.,* 2001; Peck *et al.,* 2003; Buckley *et al.,* 2004; Caldarone *et al.,* 2006; De Raedemaecker *et al.,* 2012; Kerambrun *et al.,* 2012). Fish in good condition tend to have higher RNA:DNA ratios than those in poor condition.

To determine the individual RNA:DNA ratio based on the fluorometric methods described by Clemmesen (1993) and Caldarone et al. (2001), 25 g of white muscle tissue of the fish was used and extracted in 300 µl N-lauroylsarcosine (final concentration 1%) in Tris-EDTA buffer (pH 7.5). After diluting and centrifuging the muscles for 15min at 14 000 g at 4°C, 75 µl of the supernatant was combined in a microplate with the fluorophore BET, and the total nucleic acid fluorescence was recorded with a microplate fluorometer. RNase was then added to each well, and the plate was incubated with shaking for 20 min at room temperature before being read a second time. The resulting fluorescence was attributed to DNA. RNA concentrations were calculated from the difference in fluorescence between the first and second readings (Caldarone *et al.,* 2001; Caldarone *et al.,* 2006). RNA and DNA content in tissue samples was calculated from calibration curves determined with a series of dilutions of pure calf-thymus DNA and baker’s yeast RNA and adjustment to dilution factors.

4.2.2.3.2. Fluton’s K condition index

Fulton’s K condition index is considered a good indicator of the general welfare of the fish (Lambert & Dutil, 1997). This morphometric index assumes that heavier fish for a given length are in better condition. It was calculated with the following formula:

$$\mathbf{K\ (mg/mm^3) = (W/TL^3)\ x100}$$

Where W is the weight (mg) and TL the total length (mm) (Ricker, 1975).

4.2.2.3.3. Recent growth

The recent growth index (RG; mm) was determined by measuring the width of the peripheral daily increments of the otoliths. We used daily otolith increments from the last 5 days before capture as an indicator of recent growth (mean distance between the margin of the otolith back to the 5th ring). Sagittae (because they are the biggest otoliths and with distinct daily increments) were removed from the head and mounted on microscope slides, sulcus side up, with cyanocrilate glue (Amara & Paul, 2003). They were polished with a series of abrasive paper (from 5 to 0.1 mm grain size) until the accessory primordia and the increments at the outer edge were visible. Otoliths were analyzed under transmitted light at 400 magnifications, using a video system fitted to a compound microscope. All the measurements were done along the same axis (anteroposterior) using an Image Analysis System (TNPC, 5.0, NEOSIS).

4.2.2.3.4. Feeding analysis

The guts (stomach and intestine) content of juveniles' plaice were dissected and analysed under stereomicroscope. The empty coefficient which is the percentage of the empty stomachs to the total number of stomachs examined was calculated to analyse seasonal and interannual differences in feeding intensity.

4.2.2.4. Data analysis

Results did not match the parametric assumption of normality (Shapiro-Wilk test, $p > 0.05$) and homoscedasticity (Levene's F test, $p > 0.05$). Kruskal Wallis (KW) non-parametric comparison tests were thus used to compare environmental conditions and fish growth and condition both between sampling date of the same year or between years. When needed, the KW test was followed by a pairwise Wilcoxon test (pW). A significance level of 5% was considered in all statistical analysis. XLSTAT software was used to perform all the statistical analysis.

4.2.3. Results:

4.2.3.1. Environmental conditions:

All the parameters analyzed showed temporal variations but without tendency. During the 7 years of study (from 2005 to 2007 and from 2010 to 2013), the temperature shows a classical increase during spring period from about 6°C in March to 15°C at the end of June (figure 32). Mean temperatures and their variations shows no significant differences between years during the spring period ($P>0.05$). However, spring temperatures are lower in 2013 and higher in 2007. Mean salinity showed significant differences between years ($p=0.026$). The differences are between 2007 and the years 2010 ($p=0.008$) and 2012 ($p=0.046$) and varied between 33.86 (April 2007) and 34.68 (May 2012). The Chlorophyll a vary from 1.96 µg/l (May 2010) to 18.02 µg/l (May 2007). The results of Kruskal Wallis showed differences between years (p=0.029) and the post hoc separated 2005 and 2007 from 2010, 2011 and 2012, and the year 2006 from 2010 (p<0.05).

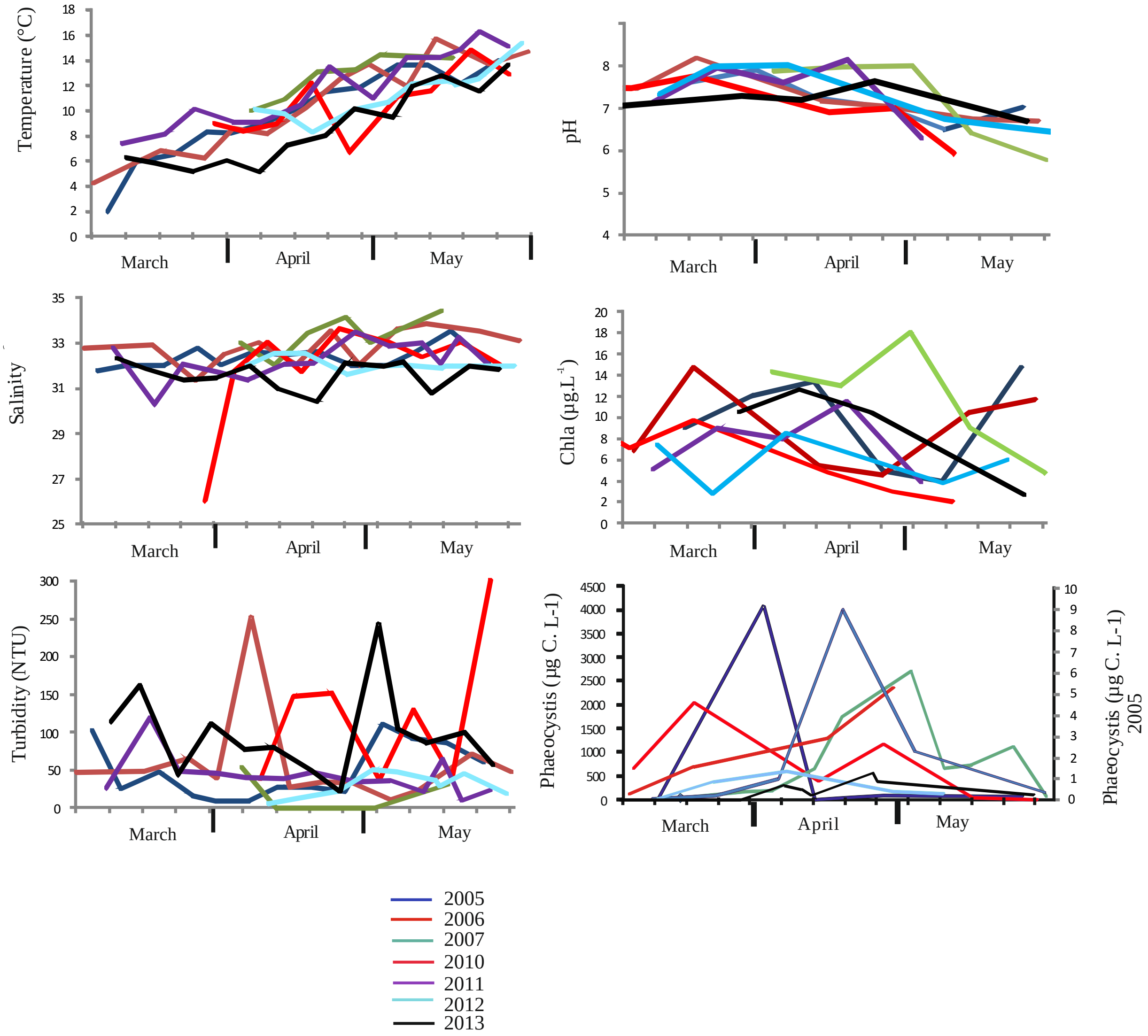

Figure 32. Temporal variations (2005, 2006,2007, 2010, 2011, 2012, 2013) of environnemental variables.

4.2.3.2. Plaice settlement and densities

During the seven years analysed, plaice settlement started in early April and finished in late May (Figure 33). There was important inter annual differences in plaice densities and date of peak of settlement. Peak of settlement occurred earlier (April) during the years 2007, 2010, 2011 and 2013 and later (May) in 2005, 2006 and 2012. Maximum densities during the peak of settlement varied between 2120 ind. 1000 m^{-2} during 2005 to 66 ind. 1000 m^{-2} during 2011.

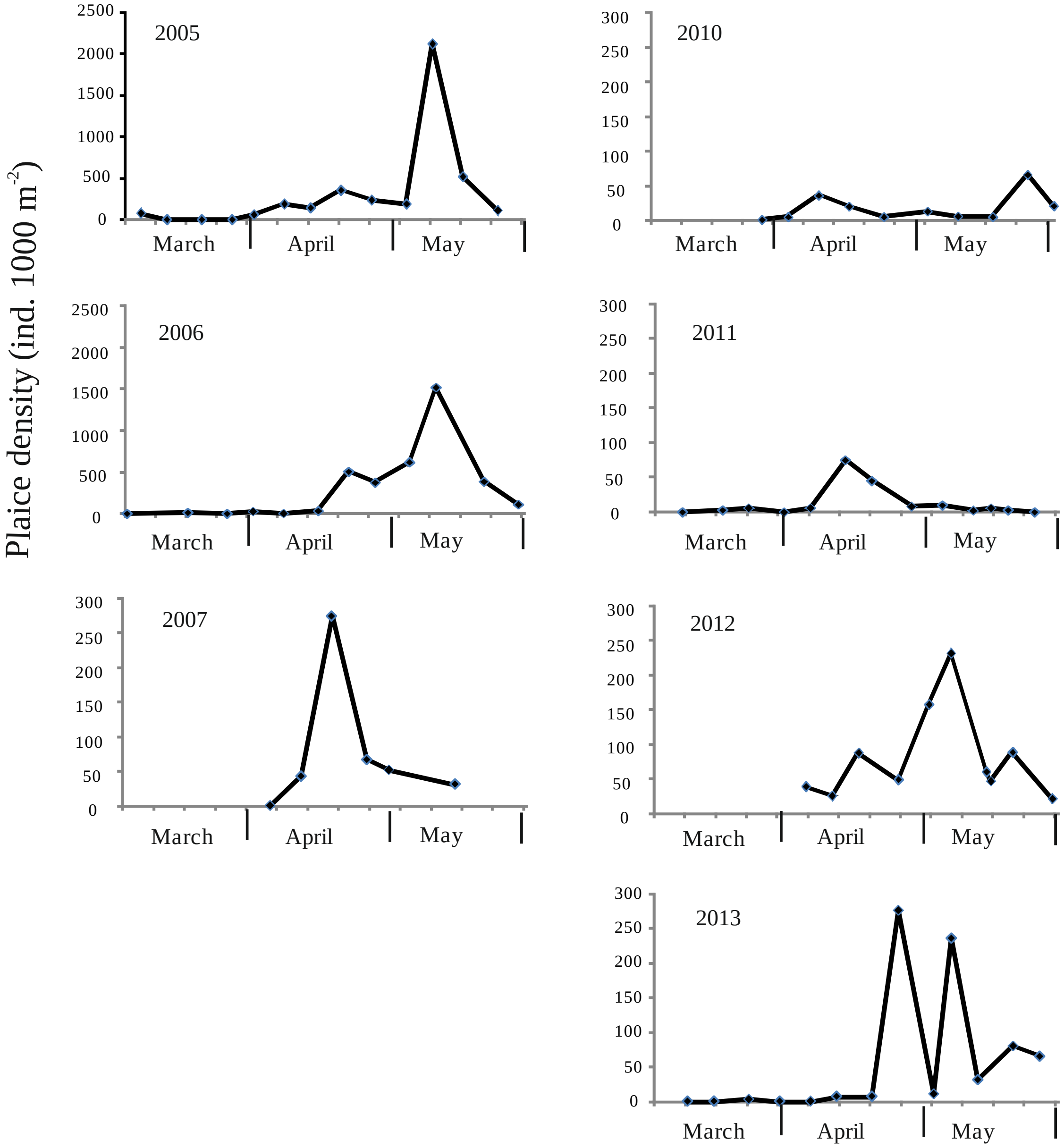

Figure 33. Temporal variations of plaice density (ind.1000 m^{-2}).

4.2.3.3. Condition and growth indices

There were no clear patterns in the average condition and growth indices of fish for any of the years analyzed. For a same year, Fulton's K was generally not significantly different during the settlement period (KW, $P>0.05$) (Figure 34). The values of this index ranged from 0.60 in March 2010 to 1.27 in June 2013. Except for May 2013, mean Fulton's K displayed no significant variability between years (Kruskal-Wallis KW, $P>0.05$).During the study, the mean Fulton's K was 1.03 mg.mm^{-3} and was generally higher than 0.9 mg.mm^{-3} except at two dates: 1st May 2010 and 5 May 2011.

RNA:DNA ratios of juvenile plaices collected from 2005 to 2007 and from 2010 to 2013 ranged from 0.58 in May 2012 to 3.82 in April 2010 (Figure 34). During the study, the mean RNA:DNA ratios was 1.50. Significant differences exist both between sampling dates of a same year or between years but without any tendency (Kruskal-Wallis KW, $P<0.05$).

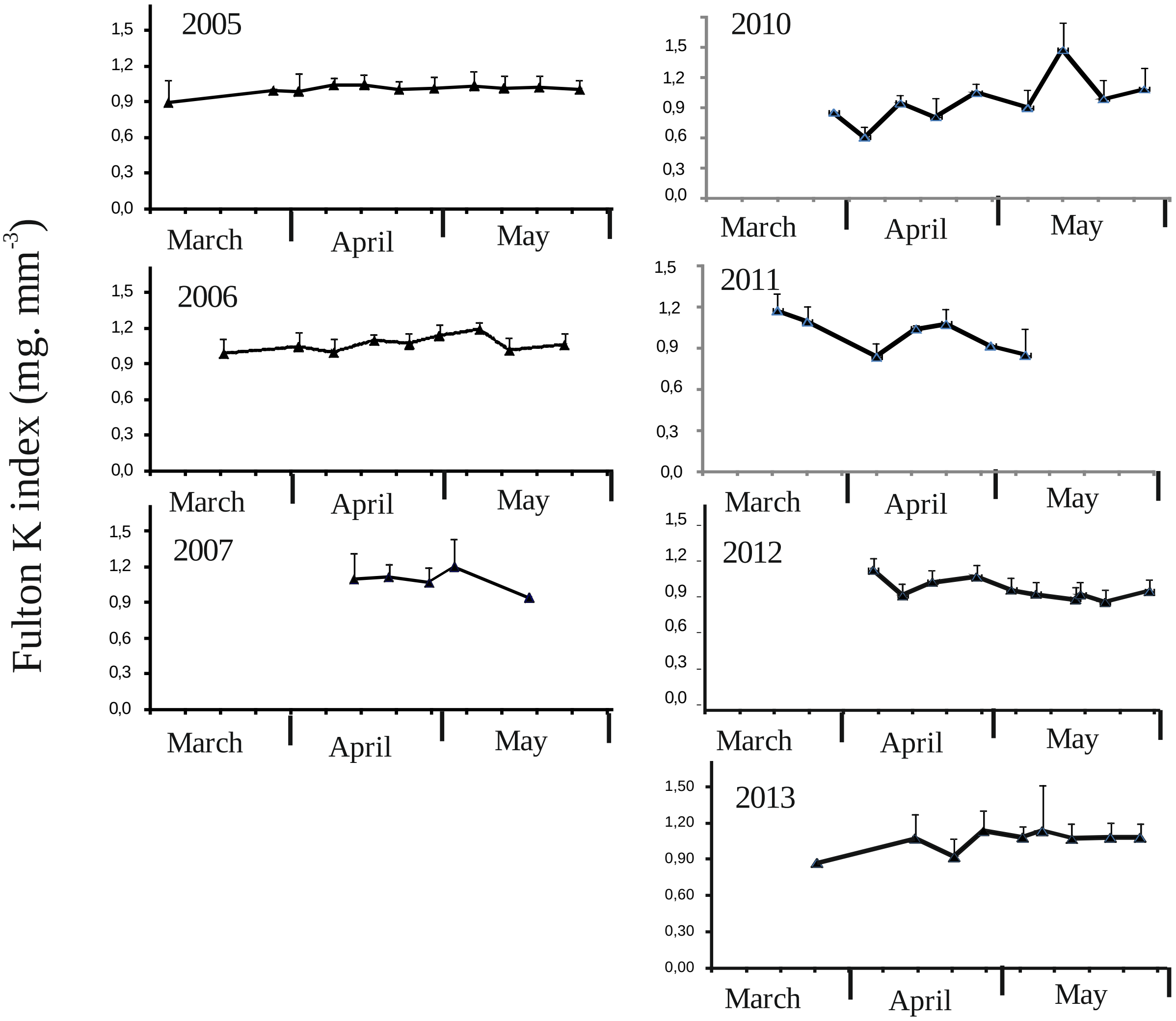

Figure 34. Temporal variations of mean (+ sd) Fulton K index (mg.mm^{-3}).

The same variations were observed for the recent otolith growth index. This index varied between 1.98 µm/day (10 May 2010) and 6.41 µm/day (26 March 2010) (figure 35).

The coefficient of vacuity showed significant differences between years (p=0.02) with differences between 2011 with 2005, 2006 and 2013 with 2005, 2006 (Figure 36).

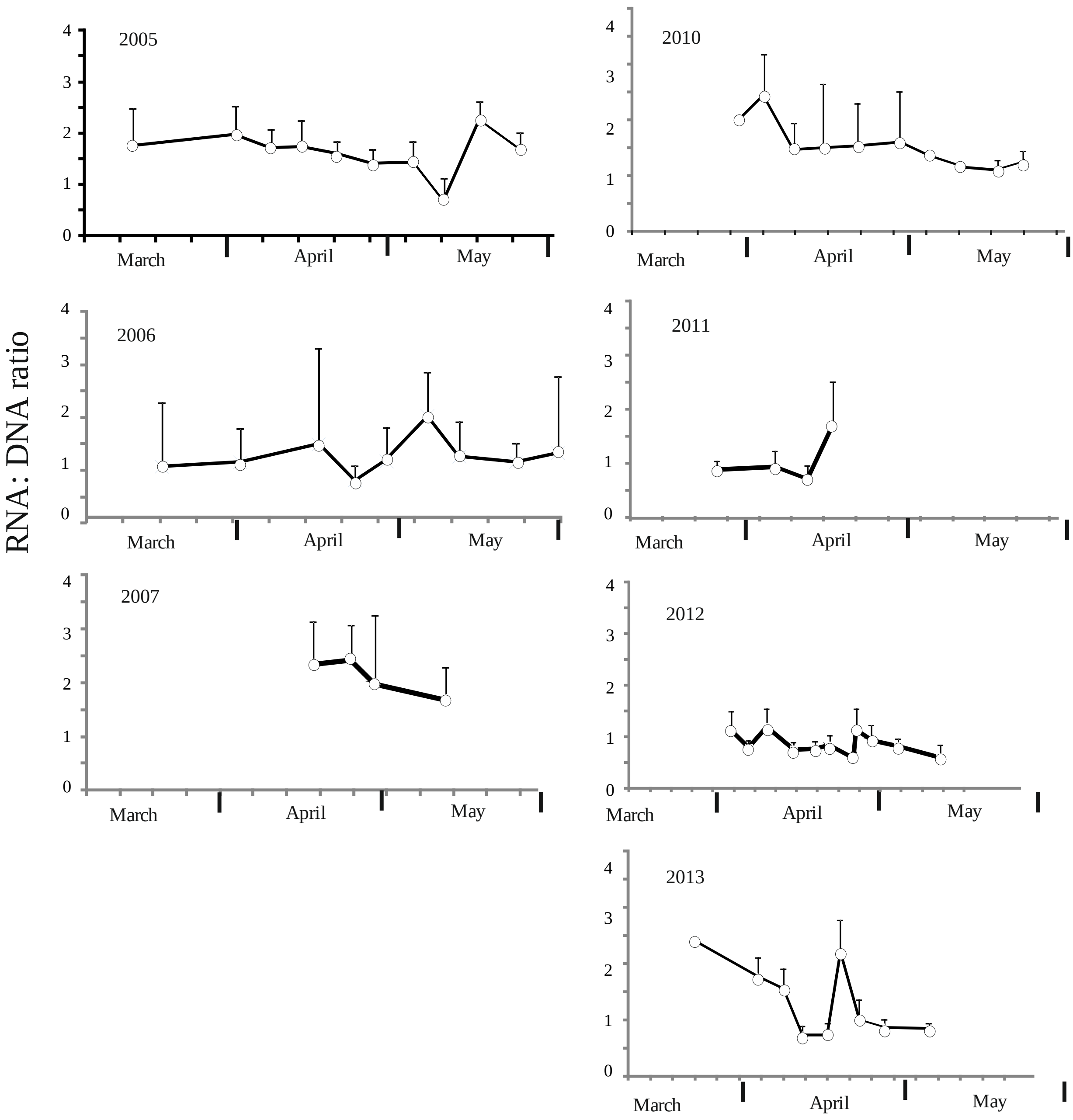

Figure 35. Temporal variations of mean (+ sd) RNA:DNA ratio.

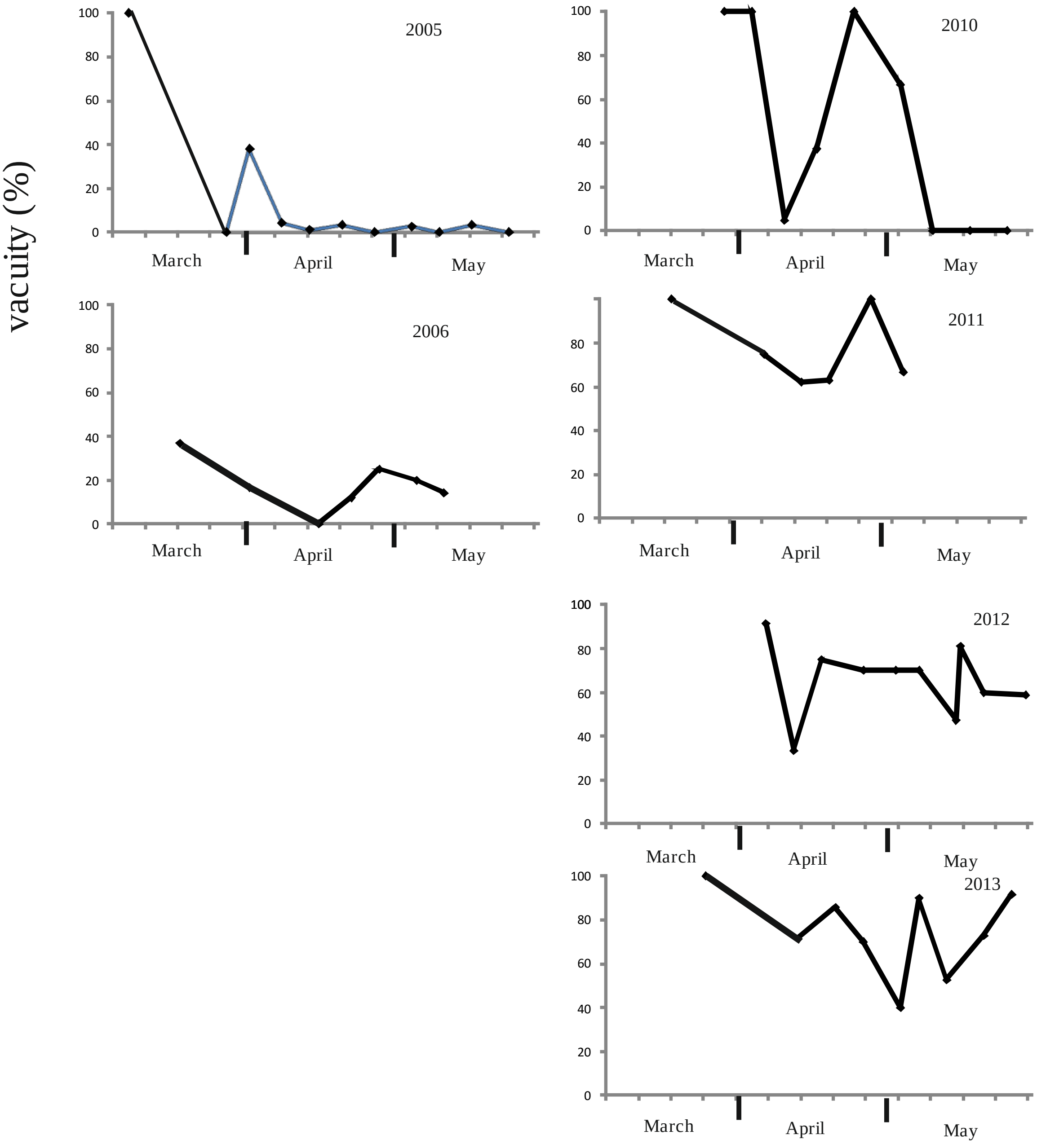

Figure 36. Temporal variations of plaice vacuity index (%).

There was no significant relationship ($p<0.05$) between plaice densities and Fulton k ($r^2=0.06$), or RNA:DNA ration ($r^2 = 0.001$) or recent otolith growth ($r^2=0.02$) or the vacuity index ($r^2=0.19$) (Figure 37).

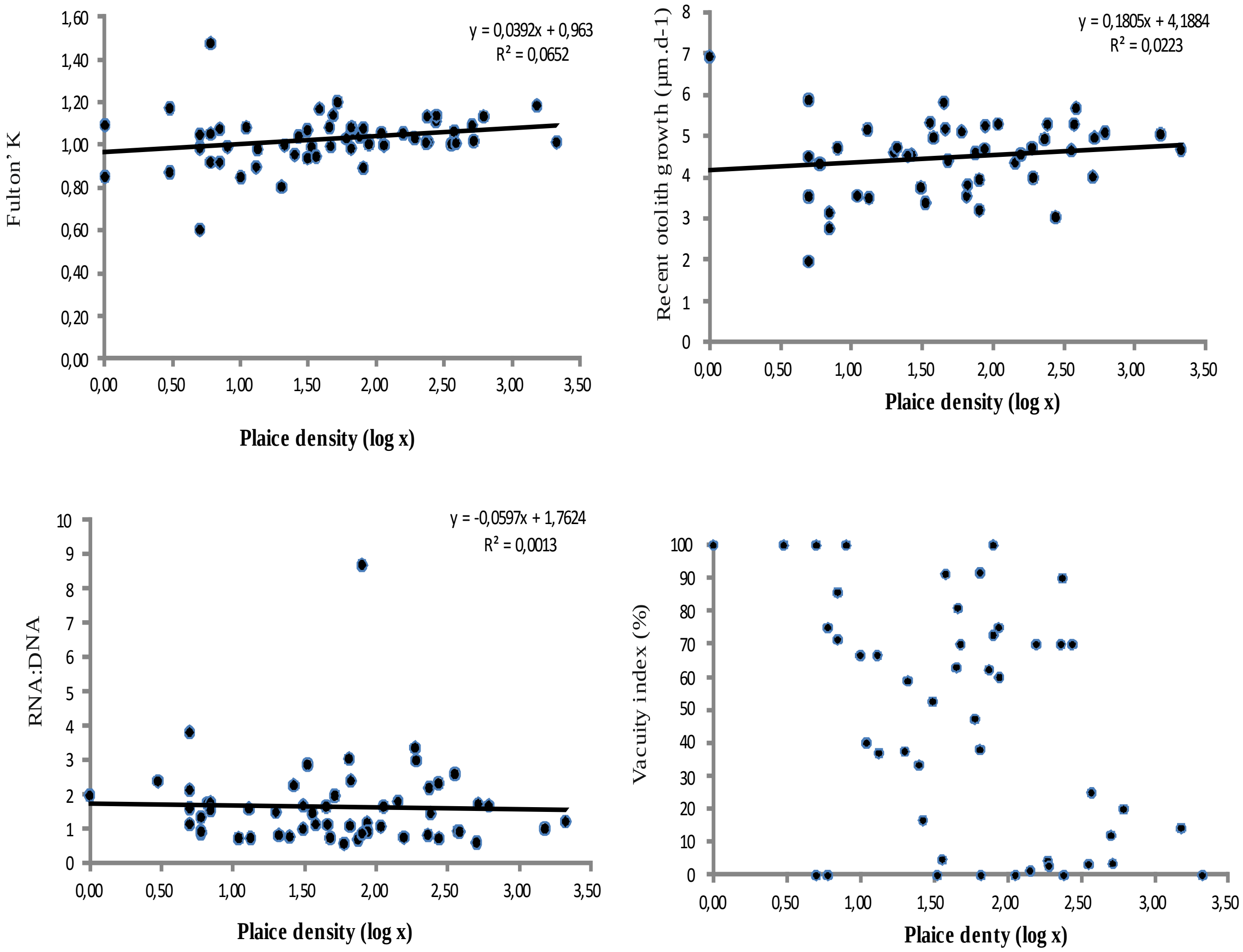

Figure 37. Relationship between newly settled juvenile plaice densities and Fulton K, RNA:DNA, Recent otolith growth and vacuity index.

There was no significant relationship (p<0.05) between the three analyzed growth and condition indices (Figure 38).

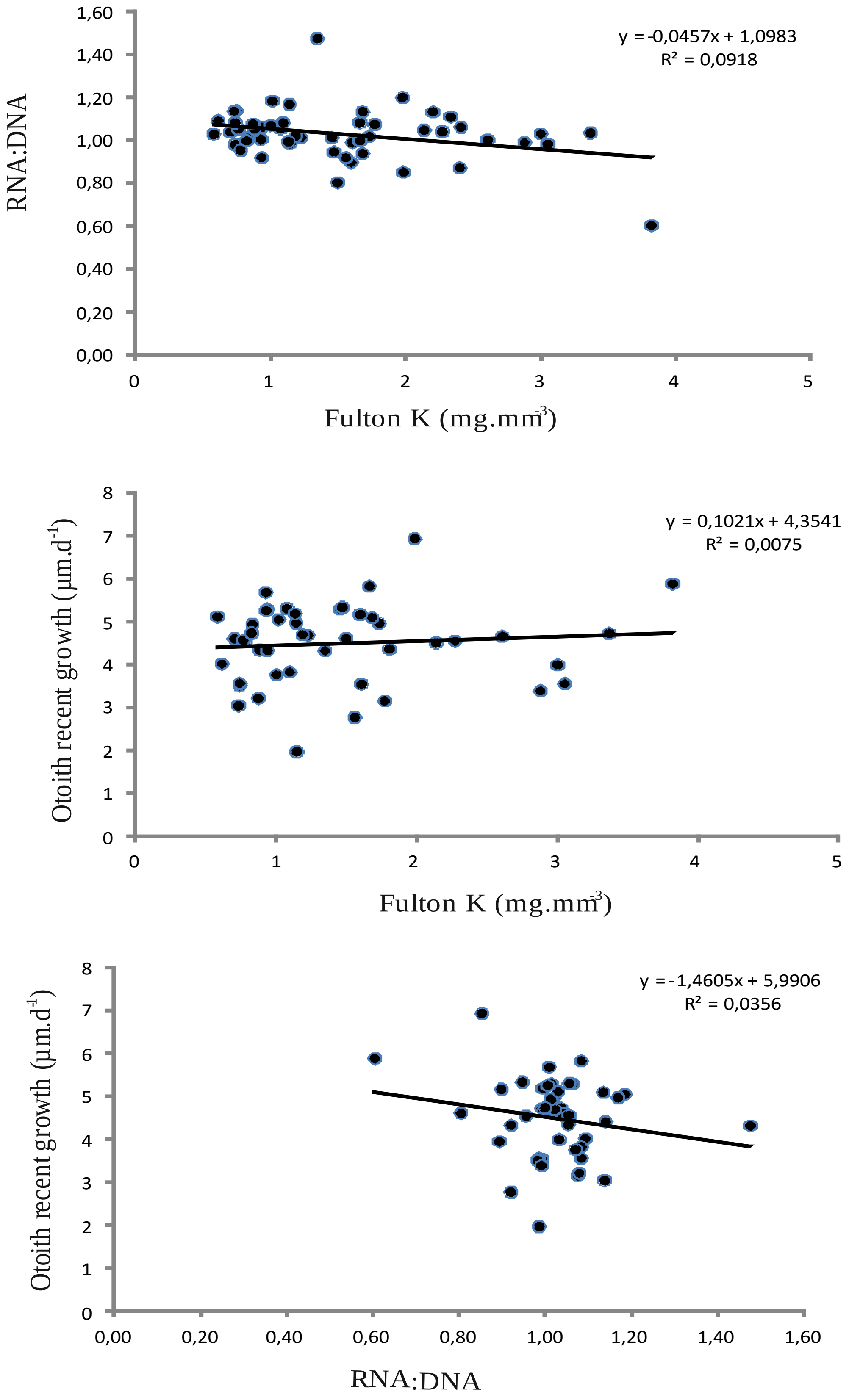

Figure 38. Relationship between the three growth and condition indices.

4.2.4. Discussion

Plaice settlement period extended from mid-March to late May. A similar period of settlement has been observed in other areas (Bergman *et al.,* 1988; Edwards & Steele, 1968; Pihl, 1990; Van der Veer, Pihl, & Bergman, 1990). However, in this study, the peak of settlement occurred earlier (in late April-mid May) as compared in more northern areas such as to the West coast of Scotland (early June, Edwards & Steele, 1968), the Wadden Sea (mid-May or early June; Berghahn, Ludemann, & Ruth, 1995; Bergman *et al.,* 1988; Van der Veer & Witte, 1993) in Icelandic waters and in northern Norway (end of June; Hjörleifsson & Palsson, 2001; Freitas *et al.,* 2010). In the present study the time of year that plaice settle on the beaches varies from year to year as observed in other areas (Riley and Corlett, 1966; Lockwood, 1974; Alhossaini *et al.,* 1989; Hyder and Nash, 1998). This pattern in settlement is generally related to the spawning season and to water temperatures during egg and larval development (Van der Veer and Witte, 1999).

There has been much research undertaken on flatfish nursery grounds, yet the mechanisms operating and processes governing survival are still poorly known. Recent work on one small nursery ground in the Irish Sea (Nash & Geffen, 2000) suggests that the year class strength of an annual cohort can be determined on the nursery grounds rather than in the pelagic phase. It is therefore important to examine the nursery ground phase more critically. Habitat quality of a nursery ground can affect growth rates and survival (Gibson, 1994). Probably the most important factors for juvenile fish are food availability, predation and temperature.

Considerable debate has focused on the ‘maximum growth and optimal food condition’ hypothesis (Karakiri *et al.,* 1991; Van der Veer & Witte, 1993), which states that food in juvenile *P. platessa* habitats is always plentiful and non-limiting and that temperature alone controls growth rate (Steele & Edwards, 1970; Rauck & Zijlstra, 1978; Zijlstra *et al.,* 1982; Karakiri *et al.,* 1989, 1991; Van der Veer *et al.,* 1990; Van der Veer & Witte, 1993; Modin & Pihl, 1994; Berghahn *et al.,* 1995; Hjörleifsson & Palsson, 2001). Tests of this hypothesis at discrete *P. platessa* nurseries around Europe using otolith and size-frequency analysis have produced contradictory results, in some cases supporting the concept of maximum growth (Zijlstra *et al.,* 1982; Van der Veer *et al.,* 1990; Karakiri *et al.,* 1991;

Hjörleifsson & Palsson, 2001; Freitas *et al.,* 2010) while in others invoking density-dependent (Steele & Edwards, 1970; Modin & Pihl, 1994; Teal *et al.,* 2008) or density-independent (Van der Veer & Witte, 1993) food limitation. In the eastern channel, food limitation has been postulated for newly settled individuals at the beginning of the settlement season (Amara & Paul 2003). Whether food limitation occurs at a particular site is presumably the result of the range of settlement intensity experienced (Nash *et al.,* 2007) interacting with the local carrying capacity. However, Kuipers (1977) working in the Wadden Sea, demonstrated that because of high production to consumption ratios, food limitation at that site was unlikely.

Nursery grounds can be defined generally as habitats that enhance the growth and survival of juveniles (Gibson, 1994), or more specifically as habitats that make a greater than average contribution to the recruitment of the adult population compared to other juvenile habitats (Beck *et al.*, 2001). Growth condition during the early juvenile stage may be determinant for the survival and recruitment success. Faster growth experienced by juvenile flatfish on the nursery will reduce the time during which an individual is vulnerable to predation (Taylor, 2003). Hence, survival will be greatest on nursery grounds where juvenile flatfish experience rapid growth (Gibson, 1994; Sogard *et al.*, 2001).

Growth and condition of juvenile fish are assumed to be a comprehensive indicator of habitat quality and individual health (Gibson, 1994), as it integrates environmental conditions (e.g. food resources, salinity and temperature) and individual performances (e.g. Able *et al.,* 1999; Meng *et al.,* 2000). Many fish-based indices (morphometric, histological, biochemical and growth indices) have been used to evaluate biological performances of fish (see review in Ferron & Leggett, 1994). Among them, condition indices such as RNA:DNA ratio, Fulton's K condition index and recent otolith growth are efficient proxies for growth rate and nutritional status and provide information on fishes' responses to habitat quality and environmental conditions (Gilliers *et al.,* 2004; Islam & Tanaka, 2005; Amara *et al.,* 2007; Vasconcelos *et al.,* 2009).

Although some variations were observed, there were no clear patterns in the average condition and growth indices of fish for any of the years analyzed. In a recent experimental study with newly settled juvenile plaice, Selleslagh and Amara (2012) clearly showed that the recent otolith growth, the Fulton's K condition index and the RNA:DNA ratio were sensitive to starvation. Values of 0.32 for RNA:DNA, 0.83 mg. mm3 for Fulton's K index, and 3.99

mm for recent otolith daily growth were defined as critical threshold values below which juvenile plaice can be classified as ‘starving’. In the present study, Fulton K, RNA:DNA and recent otolith growth indices were above the established baseline value for nutritional stress, indicating that newly settled plaice were in relatively high condition and that food was not a limiting factor. Our study indicates that the Sainte Cécile nursery areas provide suitable conditions growth and survival of early juvenile stages.

We did not observe density-dependent growth at our study site, and the relatively high growth rates observed each year suggest minimal competition for food. In other flatfish species, there is evidence for both the presence (Shaw and Jenkins, 1992; Nash *et al.,* 1994) and absence (Hagen and Quinn, 1991; Rijnsdorp and Van Beek, 1991; Van der Veer and Witte, 1993; Gibson, 1994; Rogers, 1994; Van der Veer *et al.*, 1994; Haynes *et al.,* 2012) of density-dependent growth. Modin and Pihl (1994) concluded that competitive effects generating density dependence in juvenile plaice are likely unimportant until extremely high densities are attained.

The lack of a direct correlation between the growth and condition indices is consistent with some previous studies (Gilliers *et al.,* 2004; Vasconcelos *et al.,* 2009; Walther *et al.,* 2010; De Raedemaecker *et al.,* 2012). RNA:DNA ratio and Fulton’s K condition index were more sensitive to the nutritional conditions than growth index (Selleslagh and Amara, 2012). This is explained by the fact that growth could be less responsive or less sensitive than biochemical indices (Haines, 1973).

CHAPITRE 5

Conclusion Générale

Ce dernier chapitre synthétise les résultats obtenus au cours de cette thèse et expose les perspectives qui s'en dégagent.

1. La composition du peuplement en zone intertidale et l'influence de l'environnement

Il est nécessaire de démontrer la dépendance des juvéniles de poissons et de macrocrustacés vis-à-vis des nourriceries intertidales et qui résulte d'un compromis entre les contraintes de ce milieu générateur de stress et la survie du poisson.

L'abondance des juvéniles de poissons en zone intertidale est notée par de nombreux auteurs (Gibson, 1973 ; Eleftheriou & McIntyre, 1976 ; Ross, 1983 ; Ross et all., 1987 ; Henderson, 1989 ; Costa & Elliott, 1991 ; McBride & Conover, 1991 ; Poxton, 1992 ; Beyst *et al.*, 2001 ; Wilber *et al.*, 2002 ; Amara & Paul, 2003). Cette abondance peut être examinée pour sa signification vis-à-vis des stratégies de renouvellement des espèces ou bien pour la contribution des espèces au bon fonctionnement de leur milieu. Les ressources disponibles convenant aux régimes alimentaires des espèces, sont suffisamment abondantes pour limiter les compétitions au sein d'un même niveau trophique. De même que la pression de prédation est assez faible, soit en raison de protections particulières offertes par l'environnement, soit tout simplement en raison d'une moindre abondance des prédateurs. Outre les risques d'échec lors du transport des zones du large vers les zones intertidales, les conditions particulières et souvent variables dans ces milieux amènent à s'interroger sur la signification écologique de leur utilisation par les espèces.

Les assemblages décrits sont des groupes d'espèces qui ont tendance à évoluer ensemble, soit parce qu'ils ont des préférences d'habitats similaires soit parce qu'ils interagissent ensemble biologiquement parlant. Ces espèces sont ainsi considérées comme des indicateurs de l'hétérogénéité de l'habitat (Noss, 1990 ; Kremen, 1992 ; Monaco *et al.*, 1992 ; Bulger *et al.*, 1993).

La faune peuplant ces zones a été étudiée à maintes reprises, particulièrement en Afrique du sud, en Australie et aux Etats Unis (Brown & McLachlan, 1991). Par contre, en Europe du nord, ce genre d'étude reste relativement rare et souvent limité aux espèces dominantes tels que les poissons plats, incluant les espèces d'importance économique (Salvat, 1962 ; Beukema, 1974, 1976 ; Eleftheriou & Nicholson, 1975 ; Angus, 1979 ; Eleftherious & Robertson, 1988 ; Ansell & Gibson, 1990, Dexter, 1990 ; Amara & Paul, 2003 ; Selleslagh &

Amara, 2008). En plus de cela, ces études sont des études à court terme, se limitant à une année ou à une saison.

Au cours de notre étude, la composition des peuplements observés au niveau de la zone intertidale de la plage sableuse de Sainte Cécile est comparable à d'autres zones intertidales nord européennes (Gibson, 1973 ; Santos and Nash, 1995 ; Beyst *et al.*, 2001).

Les modèles saisonniers sont observés non seulement au niveau des densités des espèces mais aussi leur diversité. Ceci reflète les différents temps de recrutement des différentes espèces dues aux périodes de pontes différées. En effet, la période de recrutement chez les poissons plats est observée en période printanière en raison de la ponte effective en période hivernale au large des côtes (Bromley, 2000). Après l'éclosion, les larves sont alors transportées vers les zones intertidales grâce aux mouvements de la marée (Daan *et al.*, 1990 ; Cattrijsse *et al.*, 1997).

Dans notre étude, les gobies *Pomatoschistus microps* sont les espèces les plus abondantes et sont présentes en toute saison avec des pics de densité au printemps, à cause des flux migratoires de juvéniles issus de différentes périodes de ponte. Les sprats *Sprattus sprattus* sont aussi une espèce importante dans la composition des peuplements en zone intertidale et spécialement en période printanière. Les densités de macrocrustacés quand à elles observent les mêmes évolutions que les densités de poissons, avec une nette domination de la crevette grise *Crangon crangon* et du crabe vert *Carcinus maenas.* Les études montrent aussi qu'il n'y a pas de changements entre les années : les communautés sont persistantes d'année en année. Par contre, au sein d'une même année, le peuplement change d'une saison à une autre. Par exemple, les assemblages printaniers persistent d'année en année, il n'y a que les densités qui diffèrent.

Une fois les communautés peuplant la zone intertidale définies, l'un des principaux buts de ce travail était de définir l'impact des paramètres environnementaux sur les assemblages de poissons et de macrocrustacés.

Dans cette étude, les principaux facteurs abiotiques qui expliquent les tendances et les assemblages de poissons et de macrocrustacés en période printanière sont la NAOw, la Température, la Salinité, la Chlorophylle a et les particules en suspension.

Les espèces telles que les plies communes *Pleuronectes platessa,* les gobies, les sprats, les lançons *Ammodytes tobianus,* les crevettes grises et les crabes verts sont plus abondantes en période de fortes NAOw, de température, de chlorophylle a et de particules en suspension. Néanmoins, il y a des corrélations négatives entre la plie et le lançon avec la salinité, tandis qu'il y une corrélation négative entre les deux paramètres la température et la chlorophylle avec le sprat.

L'étude montre aussi qu'en Manche orientale, les zones intertidales sont des zones riches et capables d'accueillir de nombreuses espèces de poissons et de macrocrustacés. Étant donné que chaque espèce a, en général, un régime alimentaire spécifique, il n'y a pas de compétition intraspécifique.

2. Les paramètres environnementaux : impact sur les performances physiologiques de la plie commune

Les impacts naturels et humains sont connus pour avoir des effets sur la structure et le fonctionnement des zones intertidales, considérées comme nourriceries (Blaber *et al.*, 2000 ; Cabral *et al.*, 2001 ; Whitfield and Elliott, 2002 ; Martinho *et al.*, 2007 ; Courrat *et al.*, 2009). Par conséquent, la croissance et la survie des larves et juvéniles des espèces qui vivent dans cet écosystème seront affectés (Vasconcelos *et al.*, 2007, Amara *et al.*, 2009).

L'application des indicateurs de condition des poissons est ainsi nécessaire afin de déterminer et de protéger la qualité de l'habitat de la nourricerie.

Dans ce travail, les mécanismes écologiques qui affectent les conditions de nutrition (déterminé par le rapport ARN/ADN) et la condition morphométrique (représentée par l'indice K de Fulton) de la plie commune durant la période de colonisation ont été étudiés. Le choix de l'espèce réside dans le fait que les juvéniles de ce poisson plat sont les plus abondants au niveau de la plage Sainte Cécile en plus de leur importance économique et l'intérêt de protéger leurs stocks.

Il a été démontré que la croissance et la survie sont conditionnés par physicochimique de l'environnement dans lequel les juvéniles vivent (Fry, 1971). L'indice K de Fulton est un indice facile à mesurer et un outil efficace dans l'évaluation de la condition des poissons plats. La variabilité observée dans cet indice est largement expliquée par les composantes biotiques et abiotiques de l'habitat. Le ratio ARN/ADN est plus difficile à obtenir. En effet, cet indice est largement lié à la taille du poisson, la température, la variabilité interspécifique et la détermination expérimentale d'un seuil critique de cet indice. Néanmoins, dans les habitats naturels affectés par l'homme ou d'intenses fluctuations naturelles, le ratio R/D procure une information fiable pour la détection des périodes de faible croissance.

La faible corrélation entre les deux indices coïncide avec d'autres études (Gilliers *et al.*, 2004 ; Vasconcelos *et al.*, 2009 ; Walther *et al.*, 2010 ; De Raedemaecker *et al.*, 2010, 2012).

En conclusion, les résultats de l'étude montrent une relation effective entre les variations environnementales et les indices de conditions et de nutrition des juvéniles de plie commune en zone intertidale. La sensibilité du rapport ARN/ADN aux fluctuations environnementales récentes est liée au fait que le taux de ARN change sensiblement suivant la disponibilité de la nourriture. Tandis que l'indice de Fulton donne une information sur la croissance en général. L'étude montre l'importance d'étudier ces indices et leur rôle dans la détermination de la qualité de la nourricerie qui procurera par la suite une croissance rapide, une survie optimale des juvéniles et le bon recrutement dans les stocks d'adultes.

Nos résultats ont montré que les performances des juvéniles de plies pêchés en baie de Canche sont élevées tout au long de la période printanière, période critique de colonisation. Ceci reflète le bon fonctionnement de l'habitat, favorable au développement et à la survie des poissons.

3. Zones de nourriceries en Manche orientale, impacts anthropiques et changements environnementaux :

L'estran est un écosystème biologique d'interface : c'est la transition entre le milieu aquatique marin et le milieu aérien terrestre, et facteur d'enrichissement de la haute mer. Cette zone intertidale, de balancement des marées, est localisée entre l'étage supralittoral (zone des embruns) et l'étage infralittoral constamment immergé. C'est le lieu de transfert des matières minérales et organiques du système terrestre au système marin littoral. La zone intertidale, en alternance émergée et immergée, est un milieu qui subit de grandes variations physico-chimiques en fonction de la marée et de son amplitude (modifications de la salinité, de la température, de la luminosité, etc.). Cette particularité, donne à ce milieu un caractère unique et fragile avec des conditions de vie particulières.

La zone intertidale est une mosaïque de niches écologiques très sensibles aux changements environnementaux et aux pollutions provoquées par l'anthropisation des côtes d'où l'intérêt de se préoccuper de leur protection. Sachant que l'utilisation de l'estran présente des avantages aux juvéniles tels que la disponibilité en nourriture et un refuge améliorant la survie et de bonnes conditions pour une croissance rapide (Lenanton & Potter, 1987; Beck *et al.,* 2001) et la moindre perturbation, qu'elle soit environnementale et/ou issue de l'activité humaine, peut diminuer les conditions générale des larves et juvéniles de poissons et de macrocrustacés.

Dans ce travail, nos résultats confirment et supportent le fait que l'utilisation d'indices de croissance, biochimiques et morphométriques est un outil adéquat pour identifier le statut global du rôle d'une nourricerie (Gilliers, 2004).

Pour la 2eme fois, l'impact des blooms de *Phaeocystis globosa,* non seulement sur la composition des peuplements de l'estran mais aussi sur les performances de la plie commune, a été étudié. Le rapprochement a été établi, du fait que les efflorescences de *Phaeocystis* se produisent en période printanière lors de la colonisation de la zone intertidale. Notre étude rejoint d'autres études faites sur ce sujet et qui montrent qu'il n'y a aucun effet ni sur la dynamique de colonisation des juvéniles, ni sur les densités, ni sur les indices de diversité, ni sur les performances physiologiques des poissons. Ceci est expliqué par le fait que *P.globosa* ne produit pas de substances chimiques toxiques.

4. Perspectives de travail :

L'objectif global de la thèse étant d'étudier l'influence de l'environnement sur la dynamique des populations et des assemblages de poissons et de macrocrustacés présents en zone intertidale, on peut considérer avoir répondu aux questions posées. Néanmoins il reste certaines zones d'ombre qui méritent quelques éclaircissements.

Lors de l'étude des performances physiologiques de la plie commune, il a été établi qu'il y avait une corrélation entre les différents paramètres mesurés (indice de vacuité, Fulton's K et le rapport ARN/ADN) et la présence de crevette grise *Crangon crangon* et de gobie *Pomatoschistus microps* dans le milieu. En effet, si les crevettes et les gobies sont considérées comme des prédateurs de la plie commune pendant la période de colonisation de la zone intertidale, il serait intéressant d'approfondir les recherches sur la prédation de la plie commune par la crevette grise et le gobie et de déterminer, par analyse des contenus stomacaux du crustacé et du poisson, le taux de prédation et le temps de détection de l'ADN de la plie dans leurs estomacs. Ces perspectives de travail permettront de conclure quant à l'importance de la prédation par la crevette et le gobie sur la mortalité des plies dans le milieu naturel et par conséquent sur les processus intervenant dans le recrutement.

Au cours d'une thèse défendue en 2008 (Selleslagh, 2008), l'impact des perturbations environnementales sur les performances physiologiques des plies communes en couplant des études *in situ* et expérimentales, a été étudié. N'ayant pas pu poursuivre cette étude, il serait intéressant de poursuivre continuer cette étude en introduisant d'autres variables environnementales, telles que la pollution chimique (métaux lourds et hydrocarbures) ou encore les rejets de dragage, afin de calibrer et d'établir des seuils de référence pour les indicateurs physiologiques en fonction de différents stress. Cela permettrait de mieux appréhender l'effet des différents stress environnementaux et par conséquent de mieux les identifier en milieu naturel.

Il serait intéressant aussi de poursuivre sur quelques années encore, la colonisation en période printanière de la zone intertidale de la baie de Canche et d'étendre l'étude sur d'autres plages de la côte française en Manche Orientale et voir la possibilité de prédire le recrutement des poissons. Ces données pourraient être utilisées dans la gestion des pêcheries.

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ANNEXES

RESEARCH ARTICLE

Environmental Control on Fish and Macrocrustacean Spring Community-Structure, on an Intertidal Sandy Beach

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Abstract

The inter-annual variability of the fish and macrocrustacean spring community on an intertidal sandy beach near the Canche estuary (North of France) was studied from 2000 to 2013 based on weekly spring sampling over an 11-year period. Twenty-eight species representing 21 families were collected during the course of the study. The community was dominated by a few abundant species accounting for $>$ 99% of the total species densities. Most individuals caught were young-of-the-year indicating the importance of this ecosystem for juvenile fishes and macrocrustaceans. Although standard qualitative community ecology metrics (species composition, richness, diversity, evenness and similarity) indicated notable stability over the study period, community structure showed a clear change since 2009. Densities of *P. platessa*, *P. microps* and *A. tobianus* decreased significantly since 2009, whereas over the period 2010-2013, the contribution of *S. sprattus* to total species density increased 4-fold. Co-inertia and generalised linear model analyses identified winter NAO index, water temperature, salinity and suspended particular matter as the major environmental factors explaining these changes. Although the recurrent and dense spring blooms of the Prymnesiophyte *Phaeocystis globosa* is one of the main potential threats in shallow waters of the eastern English Channel, no negative impact of its temporal change was detected on the fish and macrocrustacean spring community structure.

Introduction

Intertidal ecosystems are dynamic interfaces between the land and the sea. Although these particular environments display harsh and highly variable hydrodynamic conditions, they support a diverse and heterogeneous fauna, and are thought to be highly productive [1,2]. Among intertidal systems worldwide, sandy shorelines are one of the most extensive, dominating most of the temperate coastlines [3]. These ecosystems are important temporary habitats for the life cycle of many marine organisms such as juvenile fish, and consequently, are considered to play an important role for coastal fisheries [4]. Many authors have reported that intertidal areas provide a refuge from predators, abundant food resources and favorable environmental conditions, which promote growth and survival (see [5]).

However, how such unique and vulnerable ecosystems respond to environmental forcing, notably in regards to inter-annual community structure, dynamics and persistence is still poorly understood, particularly for fish and macrocrustacean communities. Indeed, while many marine fish and macrocrustacean species have the ability to use the intertidal zone during high tide, most studies have concentrated on meiofauna and macrobenthos and more recently on birds (e.g. [6]). In addition, the majority of the studies on fish have been conducted on rocky intertidal ecosystems (e.g. [7,8]). This is especially the case for European coasts, where only a few studies have been conducted on exposed sandy beach fish and macrocrustacean communities [2,9,10,11,12]. Furthermore, these studies have mainly been undertaken over a short timescale, no more than 5 years (e.g. [9]). Long-term studies have focused either on population dynamics of one of the dominant species, typically flatfishes [13], or the most abundant motile macrocrustacean groups, in particular crabs and shrimps [14].

Long-term studies are essential to assess the effect of environmental changes and human activities on intertidal fauna communities. Several recent studies revealed changes in coastal sandy shore macrofaunal communities which were directly or indirectly related to long-term climate variability (e.g. [15,16]). Because of its relatively sessile habit, benthic macrofauna is regarded to be a good indicator for environmental changes and disturbances in the marine environment [17] and references therein). However, knowledge on how such environmental changes affect intertidal sandy beach motile fauna, such as fish and macrocrustaceans, is still limited. In the subtidal, many studies have observed and described during the past decade the effects of disturbance and environmental changes on fish, macrocrustacean community structure, and diversity in the English Channel and North Sea (e.g. [18,19,20]). Variations have been related mainly to those of: climate (i.e. the North Atlantic Oscillation (NAO) index), hydrological conditions (temperature and salinity), food, and/or predator abundances. For example, in the eastern English Channel (EEC) hydrological conditions have dramatically changed since the beginning of the 2000s, being influenced by the reduction of freshwater discharge by the main river (the Seine river) [21]. These environmental conditions changes (i.e. lower river discharge and increase of the salinity) have been suggested as the major cause of the suprabenthic faunal changes in the Seine estuary [21]).

Exposed sandy beaches are important habitats along the EEC and southern bight of the North Sea, representing 74% of the mainland coast, and providing important nursery habitat for juvenile fish and macrocrustaceans [2,12,22]. One of the main threats affecting shallow waters of the EEC is the recurrent and dense algal spring bloom of the Prymnesiophyte *Phaeocystis globosa*, which induce foam accumulation on the surface of the sea and beaches by the release of mucilaginous polysaccharides. Colony proliferation affects the penetration of light in the water column, thus seriously impacting on the abundance, metabolism, growth, feeding and behaviour of marine organisms [23]. Both macrobenthic species richness (potential prey for fish and crustaceans) and densities have been simultaneously reduced during a *Phaeocystis* spring bloom [24]. Although the intertidal zone is potentially the most impacted area by foam accumulation, no inter-annual study to date has analysed its impact on fish and macrocrustaceans.

Based on environmental variables, fish and macrocrustaceans collected during spring (from March to June) over an intermittent 11 year period from 2000 to 2013, this study explored (i) changes in the species composition and community structure of an intertidal sandy beach, and (ii) the underlying environmental factors generating inter-annual variability in fish and macrocrustacean communities, including the potential negative impact of *Phaeocystis* spring blooms.

Materials and Methods

The permission to collect fish in the areas under study was issued by the "Direction des Affaires Maritmes DAM" of Boulogne-sur-mer (dram-npe@equipement.gouv.fr). In France there is no need for special approval to catch fish by an ethics committee. The present field study did not involve endangered or protected species. This study was conducted in accordance with European Commission recommendation 2007/526/EC, on revised guidelines for the accommodation and care of animals used for experimental and other scientific purposes.

Study area and sampling

This study was carried out on a sandy beach (Sainte Cécile) located near a small estuary (La Canche), on the French coast of the eastern English Channel. The beach is characterised by the presence of bars and pools parallel to the coast with fine and medium sands. The distance between high and low water marks is about 700 m at neap tide and 1500 m at spring tide. The tidal regime is semi-diurnal with an average tidal range of about 7 m on spring tides and 3 m on neap tides.

For 11 years (2000, 2003–2007, and 2009–2013), sampling was conducted weekly (from March to June) at two replicate stations located at 300–400 m from the high tide line (50° 33'N, 1° 35'E), as soon as the meteorological conditions were favorable. On average 13 sampling dates were done during each spring period except during 2007 where only 8 sampling dates were done. Sampling was done with a 1.5 m beam trawl during daylight hours. The trawl had a 5.5 m long net with a mesh size of 8 x 8 mm in the main body, 5 x 5 mm in the cod end, and was equipped with a tickler-chain in the ground rope. Following recommendations by [25], net speed was kept as constant as possible during sampling, about 38 m min^{-1}. The net was pulled by two people in parallel to the shoreline in a water depth <1 m during the ebb tide (high tide +3 h). A meter registered the distance traveled by the trawls. As a result, each trawling represented an average distance of 250 m and a sampling surface of about 400 m^2. Catches of each trawling were stored in plastic bags and sorted within a few hours in the laboratory.

After the catch, the fish were anesthetized with clove oil and transported in plastic bag to the laboratory. All fish and macrocrustaceans were identified to species level and counted. Individual fish were measured (total length, mm). Small-sized crustaceans (e.g. isopods, mysids) were not included in the present study. For each species, density was calculated as trawl catches standardized to numbers of individuals per 1000 m^{-2} trawled and not corrected for net efficiency. Annual species density was *calculated* as the *average density* of all samples across the spring period (from March to June). Before, species densities obtained from the two sampling stations were averaged at each sampling date.

Environmental variables

Daily Seine River runoffs at Poses (m^3 s^{-1}) were made freely available by the Public Interest Group Seine-Aval (http://seine-aval.crihan.fr/web/). Data of the NAO winter (December through to March) index (NAO_w) were obtained from the National Center for Atmospheric Research website (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). NAO_w is estimated based on the Sea Level Pressure difference between Lisbon (Portugal) and Stykkisholmur (Iceland) between December and March measured since 1864.

Temperature (T,°C), salinity (S), Suspended Particulate Matter (SPM, $mg.l^{-1}$), chlorophyll-a concentration (Chl-a, $\mu g.l^{-1}$), and *Phaeocystis globosa* abundance were obtained from the national French monitoring network SOMLIT (http://somlit-db.epoc.u-bordeaux1.fr/download.php?serie=ST). Temperature and salinity were measured with a CTD probe Seabird CTD25 or SBE19. Hydrological data and water samples for phytoplankton counts were collected with 8 L

Niskin bottle fortnightly at high tide in subsurface (-2 m) and near the bottom (~ -20 m) from the permanent coastal station C (50°40'75 N; 1°31'17E) located near the study area. For the present study, data from subsurface and near the bottom were averaged at each sampling date.

Chl-*a* was estimated according to the equations of [26], after extraction in acetone 90% for 12h at 4°C in the dark. Abundance of *P. globosa* cells was determined under inverted microscopy according to the Utermöhl method from samples preserved with acid Lugol's iodine solution (2% final concentration) up until 2006, thereafter with 1% (final concentration) Lugol-glutaraldehyde solution. The number of *Phaeocystis* cells of the colonial form was counted separately from free cells within a month after sampling according to biovolume measurements [26], except for samples from the period 2000–2005 which were counted months to several years after sampling. In this case, the number of *Phaeocystis* cells was counted as a total number of free cells, as Lugol's iodine solution disintegrates the colony matrix some months after fixation [27]. Note that long-term storage in Lugol's seems do not affect *Phaeocystis* cell abundance. Accordingly, based on cell counts made at 9 sampling dates, a significant relationship ($r^2 = 0.86$, $p<0.001$) with a slope of 1.06 was found between preserved sub-samples with Lugol's for more one year and those preserved with Lugol-glutaraldehyde counted within a month after sampling (S1 Fig.). *Phaeocystis* biomass was estimated using a mean carbon conversion factor of 89.5 pg C $cell^{-1}$ [26]. *Phaeocystis* spring biomass was calculated by integrating over time the biomass data for the spring bloom period [28]. This choice was motivated by the transient nature of such bloom, and the very high range of biomass values in the course of any spring bloom (up to five orders of magnitude).

Data analysis

To examine inter-annual variations in environment, a normalized Principal Component Analysis (PCA) was performed to render the environmental variables scale-free and dimensionless [29]. Inter-annual variations in species composition was explored with several indices. Species diversity and evenness were assessed by the Shannon–Wiener and the Pielou's evenness index, respectively. Similarity in species composition between years was assessed by calculating the Jaccard's similarity index on presence/absence data for each pair of years [30]. This index ranges from zero (no shared species between years) to one (identical years). In addition, one-way analysis of similarity ANOSIM was performed on species densities to test statistically the variation in spring fish and macrocrustacean assemblages over the 11 years. The test was performed on a Bray-Curtis similarity matrix, calculated using log-transformed data. To examine inter-annual variations in species densities, a centered PCA was chosen to keep variance and dominance among species. Only species with an occurrence >1% in the whole sampling period were considered. To ascertain distinct species assemblages an ascendant hierarchical classification (AHC) with the Ward's aggregation criterion was built from the first component coordinates from the factorial map of the centered PCA. Temporal trends were tested according to [31]. In the case of autocorrelation in time-series, variance was corrected according to [32]. This methodology is described in detail in [33]. Before trend analysis, missing years (2002, 2003, and 2008) were interpolated using distance weighted least squares. Relationships between species densities and environmental variables were explored with two different approaches: (1) a co-inertia analysis was performed with all species for a global measure of co-structure, followed by (2) a generalised linear model (GLM) analysis, both to focus on the dominant species and to determine the relative importance of each significant environmental variable.

Co-inertia analysis consists in finding co-inertia axes, which maximize covariance between row coordinates (years) of environment and species density matrices [34]. Co-inertia was calculated from the normalized PCA on the environmental variables and from the centered PCA on the species densities. The strength of the relationship (i.e. coupling) between these two data-sets was assessed by calculating a multidimensional correlation coefficient (RV) and by testing the statistical significance using the Monte Carlo permutation procedure with 1000 permutations.Generalized linear models (GLM) were applied assuming a Gaussian distribution. Before GLM analysis, multi-collinearity between the environmental variables was tested with Pearson correlation method. Because of collinearity between salinity and Seine river runoff, this last variable was removed from the GLM analysis. The GLM was built with an additive methodology: environmental variables as predictors were tested independently for significance and subsequently, significant ones were added to determine the residual deviance, as well as the percentage explained by each one and the total percentage of the deviance explained by the model. All environmental variable interactions were initially included in the model. The step AIC function (R package "MASS", v7.3–5) was used to select the significant environmental variables and to estimate the coefficients of the models. Environmental variables were removed by backward elimination based on Akaike's information criterion (AIC). AIC balanced the degree of fit of a model with the number of variables, in order to find the most parsimonious model. Once the model with the lowest AIC value was selected, the deviance for each of the significant environmental variables was analysed. None of the models revealed any major violation of the modeling assumptions (i.e. residual normality, homoscedasticity). Moreover, inspection of autocorrelation plot of the residuals showed no evidence of autocorrelation outside of the Bartlett two-standard-errors limits.

Kruskal–Wallis tests and Mann–Whitney U test for post hoc pairwise comparisons were performed with XLSTAT 2007 and were used to check for differences in fish species densities between years. ANOSIM analyses were performed with PRIMER software package (version 5.0) [35], PCA and co-inertia analyses with ade4 package and GLM with R software (R Development CoreTeam, 2005), and autocorrelation plot with SYSTAT 11. All statistical significance were set at $p < 0.05$.

Results

Environmental variables

All environmental variables during the winter/spring period displayed high inter-annual variations over the period 2000–2013 (S1 Table). For example, mean temperature, salinity, and the magnitude of *Phaeocystis* spring blooms (Fig. 1) varied from 8.5 (2013) to 11.03°C (2007), from 33.9 (2000) to 34.5 (2010), and from 0.29 (2005) to 112 g C m^{-3} $bloom^{-1}$ (2003), respectively. The first and second principal components (PC1 and PC2) of the PCA on all environmental variables explained 43 and 20% of the total data inertia, respectively (Fig. 2). The first principal component (PC1) showed an opposition between salinity and NAOw, Seine River runoff, T, SPM, and Chl-*a* (Fig. 2A). Furthermore, PC1 exhibited a significant increasing temporal trend over the period 2000–2013 ($z = 2.29$, $p < 0.05$, Fig. 2B), resulting mainly from the gradual significant increase in salinity ($z = 3.18$, $p < 0.01$) over time, but a progressive decrease in both SPM ($z = -2.74$, $p < 0.01$) and Chl-*a* ($z = -2.41$, $p < 0.05$). By contrast, no significant temporal trends for NAOw, T, Seine River runoff and *Phaeocystis* were detected ($p > 0.05$).

Species composition

A total of 28 species (18 fish and 10 macrocrustaceans) belonging to 21 different families, were collected in the intertidal sandy beach over the 11 spring periods (March to June), from 2000–2013 (Table 1). The captured fish were mainly represented by juveniles, often from species of commercial importance. Seven fish species were commonly present each year over the studied

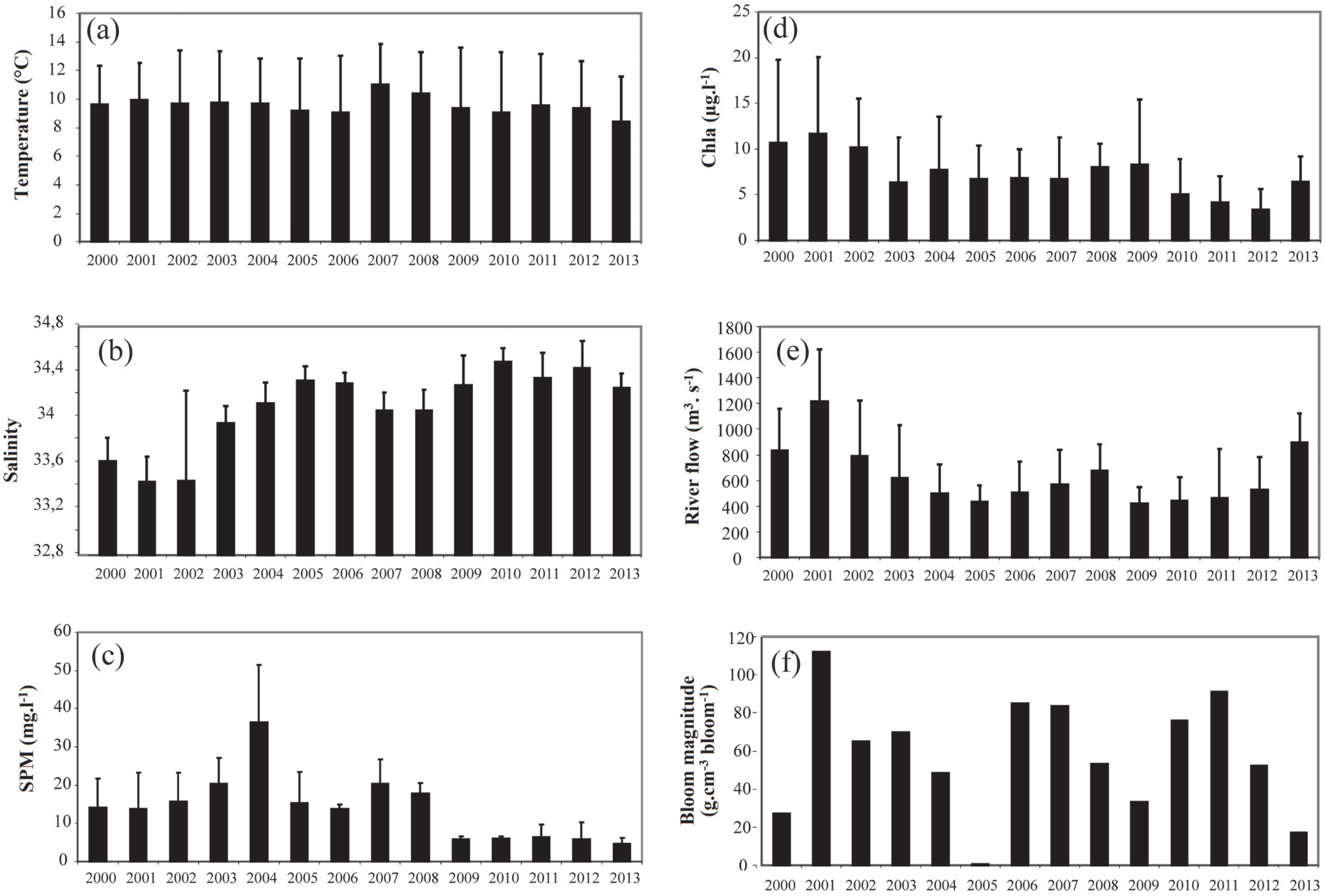

Figure 1. Temporal variations (2000–2013) of environmental variables in coastal waters of the eastern English Channel. (a) temperature, (b) salinity, (c) Suspended Particulate Matter [SPM], (d) chlorophyll-a concentration [Chl-a]), (e) Seine river flow, (f) *Phaeocystis globosa* bloom magnitude.

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period. Among them, *Pleuronectes platessa* (exclusively 0-group), *Sprattus sprattus* (post-larvae and juvenile), and *Pomatoschistus microps*, were the most abundant representing 43.3, 39.2, and 13.5% of the total fish catches, respectively. *Crangon crangon* was by far the most abundant species (mean density during the period of study: 1393 ind. 1000 m^{-2}), and contributed to 72% of the total catches. *Carcinus maenas* was also regularly caught (85% frequency of occurrence).

Inter-annual variations in community structure and species density

The various diversity indices (species richness S, Shannon-Wiener diversity H' and Pielou's evenness J) exhibited no significant trend ($r^2<0.02$; $p>0.05$) (Fig. 3) and species composition stayed rather similar between years. Among years comparisons exhibited high Jaccard's coefficients (0.40–0.83) showing that the fish and macrocrustacean species composition was more or less stable between years in a qualitative point of view. Accordingly, only some occasional species (*P. flesus*, *D. labrax and P. maxima)* occurred more frequently from 2009.

All of the species presented high inter-annual variability in density. One-way ANOSIM indicated a significant change of fish and macrocrustacean assemblages over the 11 years (ANOSIM, *global* $R = 0.40$, $p = 0.001$). PCA analysis on species density revealed four species

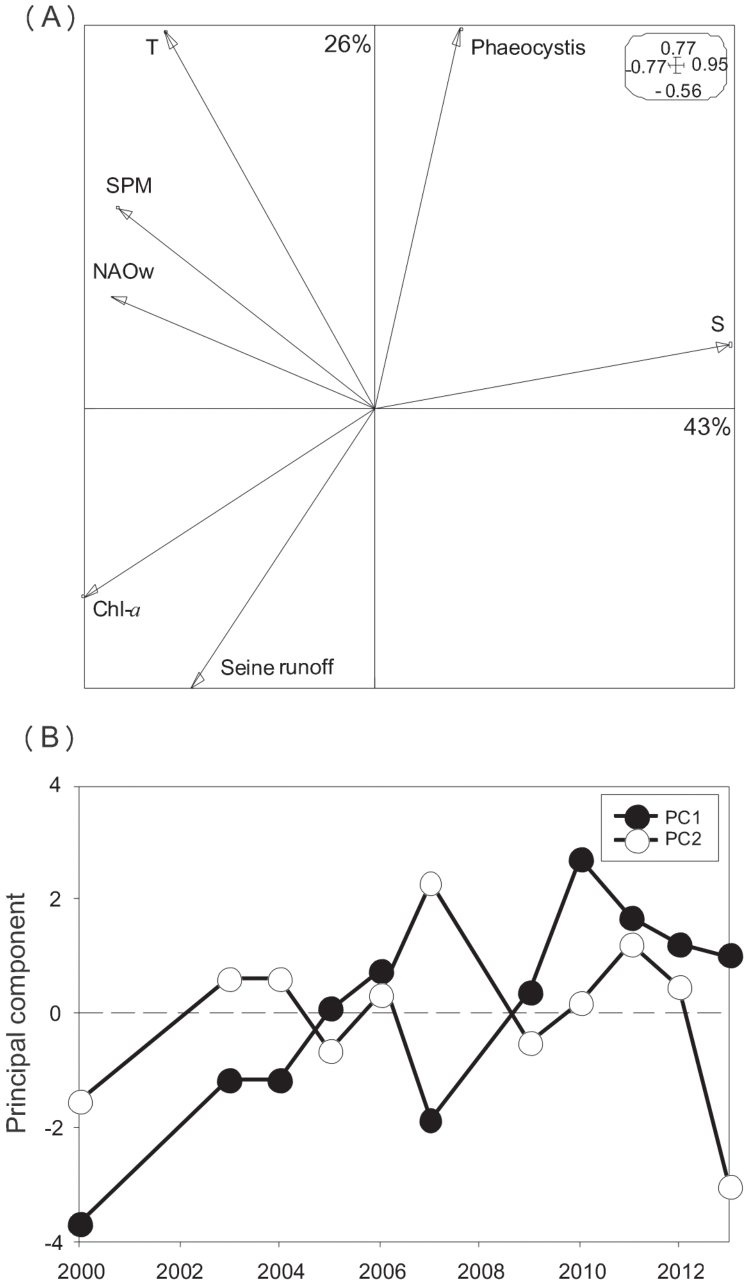

Figure 2. Variations (2000–2013) in climate (NAOw) and environmental variables (Seine River runoff, T, S, SPM, Chl-*a*, and the magnitude of *Phaeocystis* blooms) using a normalised PCA. A. Ordination plot of the variables in the two first principal components (PC1 and PC2). Contribution of each axis to total variance is shown in %. Scales of the axes are given in the boxes. B. Temporal variations in PC1 and PC2. Note that temporal trend in PC1 was highly significant ($r^2 = 0.65$, $p < 0.001$).

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assemblages over the 11 years studied (Fig. 4A). The first species assemblage positioned along the first principal component (PC1, 58% of total variance) was composed of *P. platessa*, *P. microps*, *A. tobianus* and *C. maenas*. The second and third assemblages in opposition along the second principal component (PC2, 12% of total variance) were composed of *S. sprattus* and *C. crangon*, respectively. Density of each of these six dominant species (key species) exhibited

Table 1. Species composition, mean densities (ind/1000m²) and occurrence (calculated for the whole study period) of fish and macrocrustaceans along the Sainte Cécile intertidal sandy beach over the period 2000–2013.

Family	Species (abbreviation)		2000	2003	2004	2005	2006	2007	2009	2010	2011	2012	2013	(%) occurrence
Fishes														
Clupeidae	Sprattus sprattus	(S spr)	30.5	212.8	46.5	213	215.1	57	49.2	637	119.8	283	161.8	72.48
	Clupea harengus	(C har)	0	0	0	0	0	0	0	0	0	0.1	0	0.65
Gasterosteidae	Gasterosteus aculeatus	(G acu)	0	0	0	0	0	0	0	0.1	0	0	0	0.65
Gadidae	Merlangius merlangus	(M mer)	0.3	0	0	0	0	0	0	0	0	0	0	1.40
	Trisopterus luscus	(T lus)	0.8	0.3	0	0	0	0	0	0	0	0	0	2.31
Atherinidae	Atherina presbyter	(A pre)	0	0	0	0	0.2	0	0	0	0.2	0.1	0.20	2.92
Agonidae	Agonus cataphractus	(A cat)	1.3	0	0	0	0	0	0	0	0	0	0	2.10
Moronidae	Dicentrarchus labrax	(D lab)	0	0.7	0.3	0.1	0	0	0.5	0.5	0	0.7	1.90	14.85
Gobiidae	Pomatoschistus microps	(P mic)	42.1	243.7	198.2	153	37.4	45.4	3.1	1	1.5	70	6.73	76.29
Cottidae	Cottus gobio	(C gob)	0	0	0	0	0.2	0	0	0	0	0	0	1.30
Trachinidae	Echiichthys vipera	(E vip)	0	0.2	0	0	0	0	0	0	0.1	0	0	1.41
Ammodytidae	Ammodytes tobianus	(A tob)	10.2	25.9	39.5	49.9	26.7	5	2.5	1.2	0.6	0.2	0.59	49.18
Syngnatidae	Syngnathus acus	(S acu)	1	1.4	4.7	0.4	2	0.3	1.2	4.4	4.1	0.3	2.45	31.24
Pleuronectidae	Pleuronectes platessa	(P pla)	509.6	997.2	188.3	294.6	259.7	77.7	63.2	26.5	11.4	69.6	62.16	90.20
	Platichthys flesus	(P fle)	0	0.5	0.4	0	0.1	0	0.3	0.7	0.7	2.1	1.11	19.04
Soleidae	Solea solea	(S sol)	1.2	3.4	2.2	0	0	0	0	0	0	0	0.07	7.13
Scophthalmidae	Psetta maxima	(P max)	0.1	0	0	0	0	0	1	1.7	2.3	1.6	0.49	15.15
	Scophthalmus rhombus	(S rho)	2.3	0	0	0	0	0	0	0	0.9	0.4	0.20	6.93
Macrocrustaceans														
Crangonidae	Crangon crangon	(C cran)	3381.6	756.4	2376.9	1040.9	397.4	847.1	3199.1	431.4	736.3	2260.3	158.92	93.92
Palaemonidae	Palaemon longirostris	(P lon)	0	0.5	0	0.1	0.2	0	0	0	0.1	0.2	0.07	5.40
	Palaemon serratus	(P ser)	0	0	0.4	0	0	0	0	0	0	0	0	1.52
Portunidae	Carcinus maenas	(C mae)	35.3	79.3	78.3	96.3	158.9	63.9	14.4	11.9	6.8	15.2	17.03	84.91
	Liocarcinus holsatus	(L hol)	1.9	0	0	0	0.1	10.5	0	0.1	0	0	0	8.52
Carcinidae	Portumnus latipes	(P lat)	0	2.7	3.9	2.1	0.7	1.2	2.1	0	23.9	2	3.01	30.94
Majidae	Macropodia longirostris	(M lon)	0.3	0	0.3	0	0.1	0	0	0	0	0	0	2.86
Porcellanidae	Pisidia longicornis	(Pi lon)	0.7	2	1	0	0	0	1.3	0	0.2	0	0.20	5.26
Varunidae	Eriocheir sinensis	(E sin)	0	0	0	0	0	0	0	0	0.1	0	0	0.51
	Hemigrapsus sanguineus	(H san)	0	0	0	0	0	0	0	0	0.2	0	0.20	0.98
Total species number			16	15	14	10	14	9	12	12	17	15	17	

Note the absence of sampling in the years 2001–2002 and 2008.

Out of the 28 species captured, only six (*P*. *platessa*, *P*. *microps*, *S*. *sprattus*, *Ammodytes tobianus*, *C*. *crangon*, and *C*. *maenas*) dominated the intertidal zone assemblages over the 11 years, and so could be considered as key species. Accordingly, these species represented in total 99.4% of the total catches, having relative high densities and occurrence during the 11 years studied (Table 1). Average total density of these key species was 1932 ind. 1000 m^{-2}. By contrast, most of the other species occurred in low densities or occasionally, such as *Dicentrarchus labrax*, *Syngnatus acus*, *Psetta maxima*, and *Portumnus latipes*. It should be noted that *Eriocheir sinensis* and *Hemigrapsus sanguineus*, two east-Asian introduced species, were recorded in the intertidal zone from 2011.

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significant differences between years (Kruskal-Wallis, $p<0.05$, Fig. 5). Furthermore, PC1 exhibited a significant negative temporal trend ($z = -2.96$, $p<0.01$), showing that *P*. *platessa*, *P*. *microps*, *A*. *tobianus*, and *C*. *maenas* progressively declined over the eleven years period. Although PC2 did not display any significant temporal trend, the contribution of *S*. *sprattus* in the catch increased from 2010 (Mann-Whitney test, $p<0.05$, Fig. 5), contributing to 30±22% of the total catches over the period 2010–2013 against 7±7% previous to this. By contrast, neither *C*. *crangon* nor the fourth assemblage, which was composed of all the 19 other species

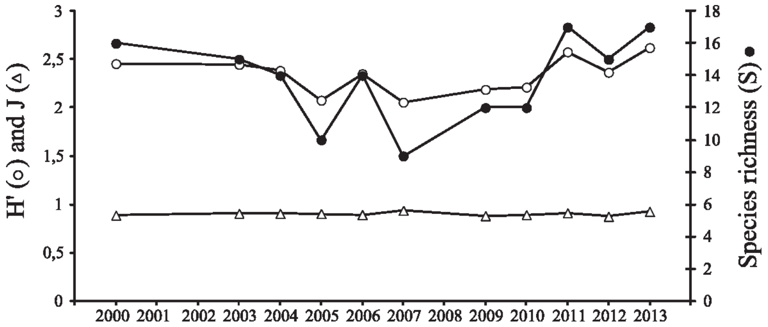

Figure 3. Temporal variations (2000–2013) in species richness (S), diversity (H') and evenness (J) of fish and macrocrustaceans along the Sainte Cécile intertidal sandy beach. Note the absence of sampling in the years 2001–2002, and 2008.

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(Fig. 5A), displayed any significant temporal trend. Altogether, these results showed that the period 2000–2007 was characterized by relative high densities of *P. platessa*, *P. microps*, *A. tobianus*, and *C. maenas* and by a low contribution of *S. sprattus* within the community. By contrast, the period 2010–2013, was characterized by a relatively high contribution of *S. sprattus*, but relatively low densities of *P. platessa*, *P. microps*, *A. tobianus*, and *C. maenas*. Note that although fish and macrocrustacean densities fluctuated inversely from year-to-year over the 11 years period (Fig. 6), the negative relationship was not significant (r = 0.15; p = 0. 651).

Relationships between fish and macroscrustacean spring community-structure, and their environment

Co-inertia analysis (Fig. 7) revealed a significant coupling between fish and macrocrustacean spring community-structure, densities and environment (RV = 0.59, $p<0.05$). Accordingly, the first axis was clearly dominant, and explained alone 60% of the total variance. Co-inertia and GLM results indicated that out of the seven environmental variables, NAOw, T, S, Chl-*a*, and SPM were the most important for structuring the inter-annual distribution of fish and macrocrustacean spring community (Fig. 7, Table 2). Species such as *P. platessa*, *P. microps*, *A. tobianus*, *C. crangon* and *C. maenas* were relatively more abundant during periods of relative high NAOw, T, Chl-*a*, and SPM. *P. platessa* and *A. tobianus* densities were negatively correlated to S, while *S. sprattus* was negatively correlated to T and Chl-*a*. All models explained substantial proportions of the variance in time series (Table 2). The magnitude of the *Phaeocystis spring blooms was* not well represented on the factorial map of the co-inertia analysis and was not a significant predictor in the GLM analysis, indicating its relative lack of importance in explaining intertidal fish and macrocrustacean spring community-structure.

Discussion

Species composition and community structure

Fish and macrocrustaceans are important components of sandy beach fauna. This study found that the great majority of fish and macrocrustaceans were juvenile migrants. The advantages for marine species using the intertidal zone during part of their life cycle are not well known. Many authors have reported that intertidal sandy beach areas may provide refuge from predation coupled with high productivity to enhance survival and growth [36,37]. Species may also use these habitats in search of an optimum physiological environment that promotes maximal growth [38]. Juveniles of some abundant species in the studied area, such as *Solea solea*,

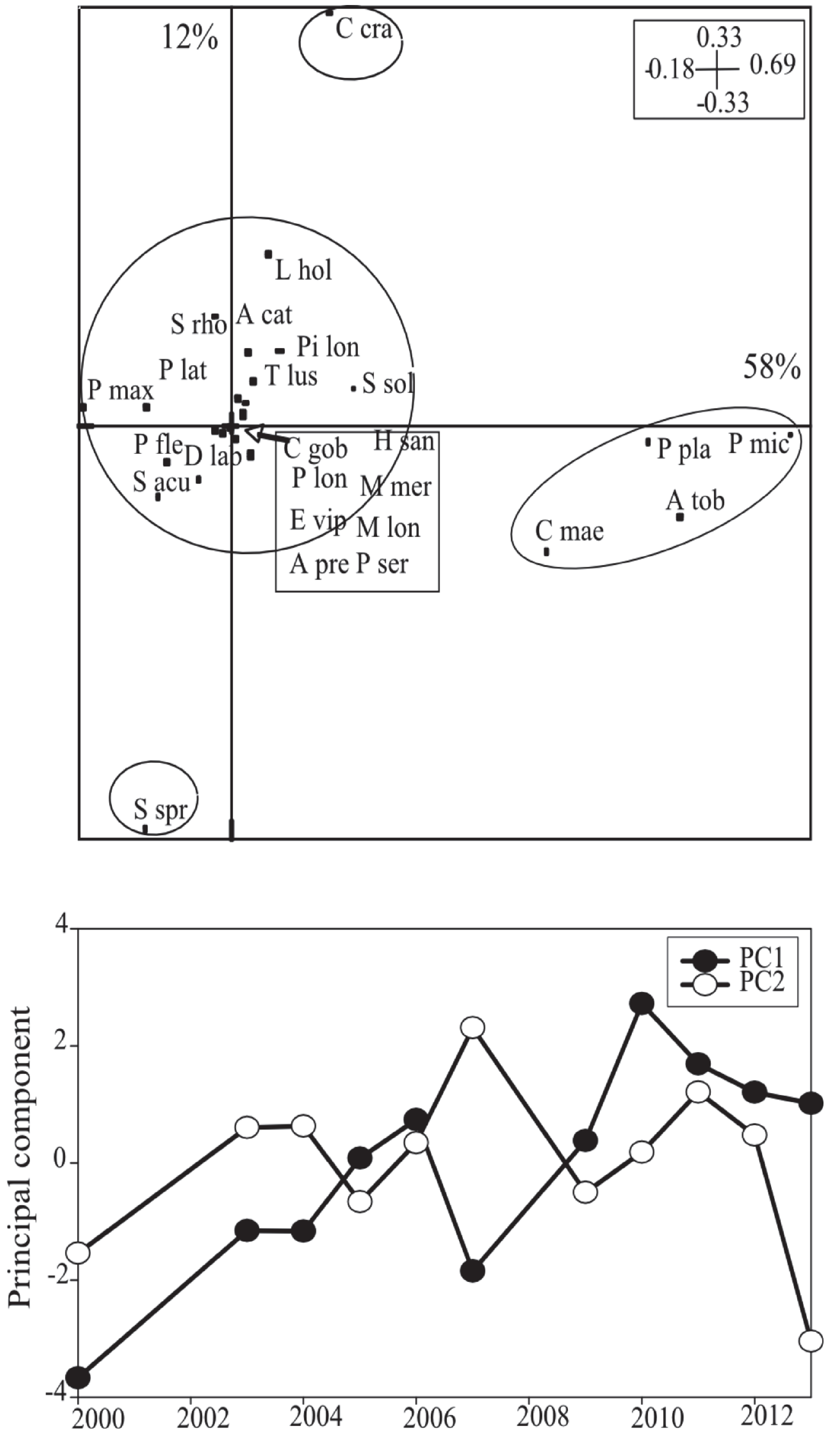

Figure 4. Temporal variations (2000–2013) in fish and macrocrustacean density along the Sainte Cécile intertidal sandy beach using a centred PCA. A. Average position of the species in the two first principal components (PC1 and PC2). Contribution of each axis to total variance is shown in %. Scales of the axes are given in the boxes. Species associations were defined from hierarchical cluster analysis by Ward's method of the species coordinates. See Table 1 for species labels. B. Temporal variations in PC1 and PC2. Note that temporal trend in PC1 was highly significant ($r^2 = 0.68$, $p < 0.005$), and the absence of sampling in the years 2001–2002 and 2008.

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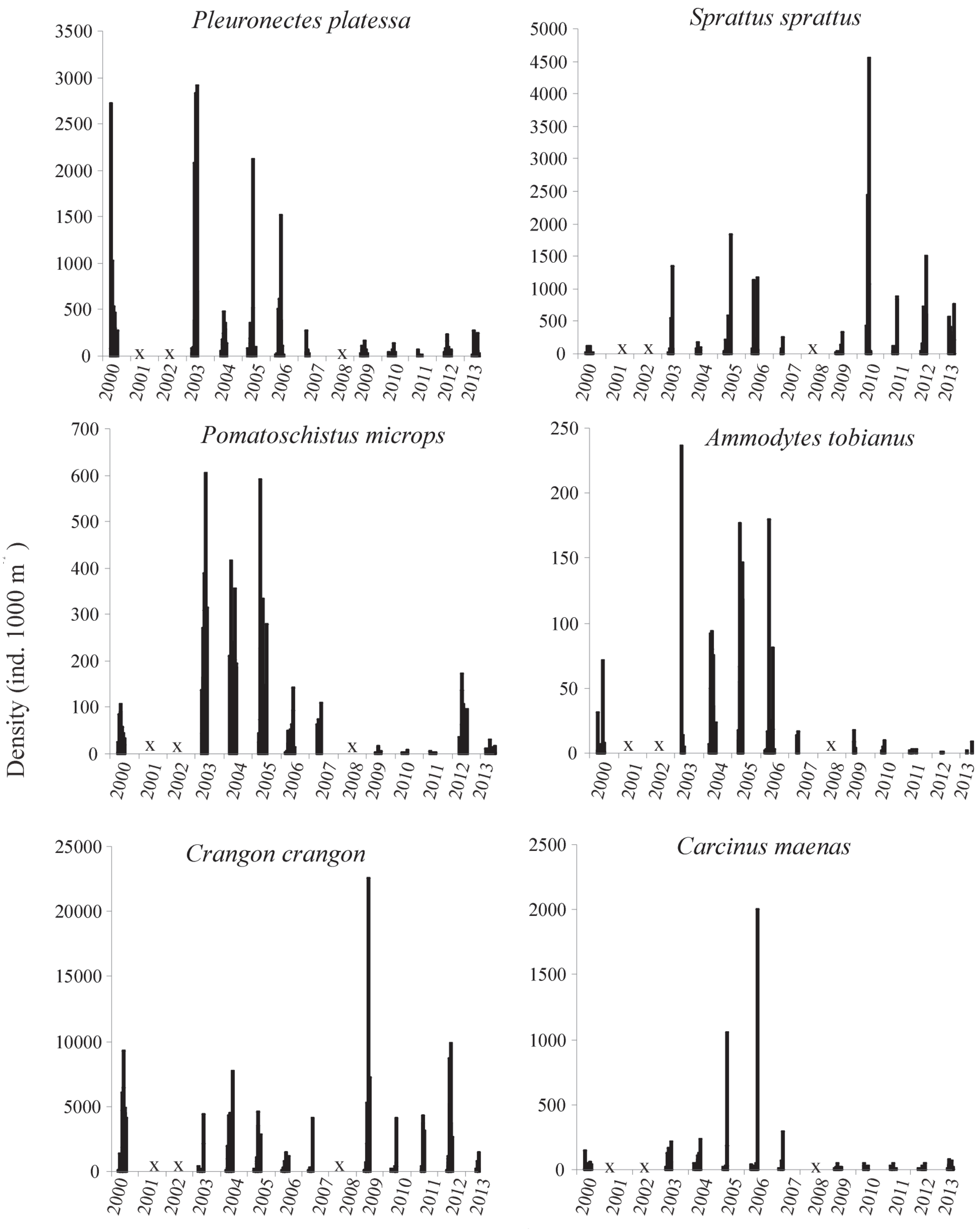

Figure 5. Temporal variations (2000–2013) in densities (ind. 1000 m^{-2}) of the dominant fish and macrocrustacean species along the Sainte Cécile intertidal sandy beach. Each bar represent the density at a sampling date. "X" indicate years with no sampling (2001–2002, and 2008). Note the differences in the y-axis scales.

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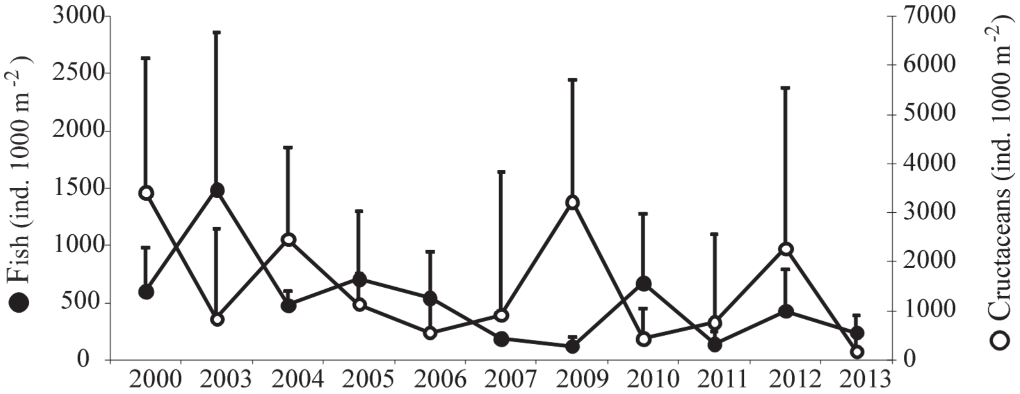

Figure 6. Temporal variations (2000–2013) in mean (+SD) total fish and macrocrustacean densities (ind. 1000 m^{-2}) along the Sainte Cécile intertidal sandy beach. Note the absence of sampling in the years 2001–2002, and 2008.

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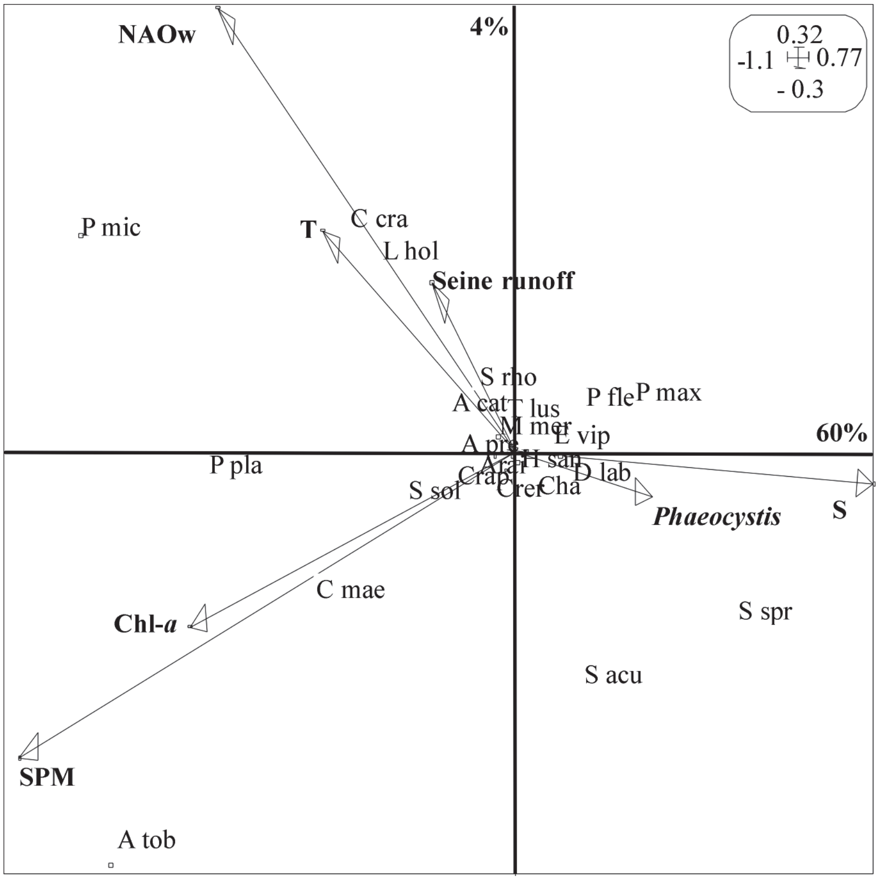

Figure 7. Relationships over the period (2000–2013) between fish and macroscrustacean densities and climate and environmental parameters using a co-inertia analysis. Contribution of each axis to total variance explained is shown in %. Scales of the axes are given in the boxes. See Table 1 for species labels. Note the absence of fish and macrocrustacean species sampling in the years 2001–2002 and 2008.

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Table 2. Deviance analysis table of explanatory variables in the Gaussian GLM model for *S. sprattus*, *P. platessa*, *P. microps*, *A. tobianus*, *C. crangon* and *C. maenas* densities.

Source of variation		Deviance	Residual dev.	Change in dev.	% Explained	AIC	*p*-Value
S. sprattus	NULL		1,64				
	T	0,37	1,27	0,37	23,78		0,044
	Chla	0,76	0,52	0,76	49,22		0,009
	Total model				73,00	5,57	
P. platessa	NULL		3,27				
	S	1,52	1,72	1,55	47,10		0,011
	SPM	0,88	0,70	1,02	30,90		0,034
	Total model				78,00	12,93	
P. microps	NULL		7,40				
	NAO	2,11	4,64	2,76	37,87		0,005
	SPM	3,91	0,69	3,95	54,13		0,001
	Total model				92,00	12,77	
A. tobianus	NULL		6,90				
	S	1,15	5,48	2,36	18,04		0,022
	Chla	0,95	4,54	4,76	36,33		0,031
	SPM	3,81	0,73	4,54	34,63		0,001
	Total model				89,00	13,31	
C. crangon	NULL		1,79				
	NAO	0,97	0,83	0,97	24,36		0,010
	Total model				66,00	8,72	
C. maenas	NULL		2,04				
	SPM	0,99	1,05	0,99	0,18		0,017
	Total model				0,56	11,41	

Values of deviance for each factor, residual deviance (res. dev.), change in deviance, percentage of the total deviance explained by each factor (% Explained), total model (in bold), and p values are presented.

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Limanda limanda, *Buglossidium lutheum* and *Callionymus lyra* [22], remain during spring or summer in the subtidal zone, and are scarcely ever caught intertidally. These species are probably less adapted to fluctuating environmental conditions with their resultant physiological demands. Therefore, utilization of the intertidal zone by certain fish species represents an advantage that not only reduces predation and maximises growth but also reduces competition for food in the earliest stages of their life cycle when densities are highest and competition is likely to be greatest in the subtidal zone [36,39].

The species diversity in this studied intertidal zone was similar to that found in the few other published studies undertaken on European intertidal sandy beaches (e.g. 20 species in a Belgian surf zone [2], and 24 species at Porto Pim, Azores [10]. However, 43 species of fish and 16 species of macrocrustaceans were caught during a four year study on a Scottish intertidal sandy beach [9], and 35 species were captured on other Scottish beaches [40]. Although caution is needed when comparing studies in which different types of fishing gear (different type, size or speed) were used, the beam trawl used in this work is considered efficient for catching demersal fish and epibenthic species in shallow coastal waters [41].

As for other sandy beaches, only few taxa numerically dominated the catch, with most species occurring occasionally or rarely, in low number [2,9,42]. Out of the 28 species captured, only six (*P. platessa*, *P. microps*, *A. tobianus*, *S. sprattus*, *C. crangon* and *C. maenas*) could be considered as dominant and key species of the intertidal zone. They represented 99.4% of the total catches during spring, and showed high densities and occurrence during the 11 years studied. Among them, *P. platessa* was the most abundant fish species (43.3% of the total fish catches). As in other shallow waters in northern Europe, *C. crangon* (96% of the total crustaceans) was the dominant mobile epibenthic species. This macrocrustacean species is highly abundant and an ubiquitous member of the large motile epifauna of shallow soft bottom areas along the European coasts [2,9,14,43]. The temporal structure of epibenthic communities of temperate intertidal sandy beaches is often the result of seasonal settling or consecutive migration waves of the young stages [11,37]. Indeed, most of the species spawn in deeper offshore waters, and invade shallow coastal areas in spring or summer as late larvae or early juveniles, when such areas are relatively warm and rich in food [10,22,44]. According to [45], a habitat can be defined as a nursery of a species if its contribution per area to the production of recruits to the adult population is greater, on average, than the production from all other juvenile habitats. The juvenile density of most of the key species (e.g *P. platessa* 215 ind. 1000 m^{-2}) in this study's intertidal zone was higher than in the adjacent subtidal area (e.g. *P. platessa* 16.5 ind. 1000 m^{-2}; [22], and in the Canche estuary (e.g. *P. platessa* 17 ind. 1000 m^{-2}, [46]). In the Dutch Wadden Sea, [47] observed differences between intertidal and subtidal 0-group plaice growth. These authors showed that growth in the intertidal zone was always higher than in the subtidal one, due to the presence of the prey *Arenicola marina* in the intertidal zone. All these data emphasize the importance of sandy intertidal zone as nursery ground, which allows suitable conditions for juvenile fish development.

Temporal community structure evolution and environmental influence

The fish and macrocrustacean spring community structure in the Canche intertidal zone was stable from year-to-year, and was based on a set of regularly occurring species. Nevertheless, some occasional species (*P. flesus*, *D. labrax*, *P. maxima)* occurred in this study more frequently from 2009. Moreover, some species such as *E. sinensis* and *H. sanguineus*, which are native to the east coast of Asia, and were introduced into the English Channel during the mid 1930s, and the North Sea during the 1990s [48], were recorded from 2011. Even if these two species are classified as invasive species, they were in low numbers at the beach sampled in our study.

Between years comparisons exhibited high Jaccard's similarity coefficients (0.40–0.83) and the ANOSIM (based on species densities) showed that the fish and macrocrustacean composition was stable over the 11 years studied. These Jaccard coefficient values were similar to those found on the west coast of Scotland (0.55 to 0.71, [9]), the Belgian surf zone in (0.3 to 0.8, [2]), and Maine, USA (0.38 to 0.83, [42]). Although all these other studies were undertaken over a shorter time scale (less than 5 years), they indicate that the assemblages of intertidal fish are persistent and resilient to any change, and, therefore, their general taxonomic structure is predictable from year-to-year [5,49]. In temperate intertidal ecosystems, the major temporal differences in community structure generally occur on a seasonal basis and reflect the breeding cycle of the species [9,12,44].

Gross temporal patterns of change in fish and macrocrustacean assemblage are mainly a result of alterations in the density of the dominant species. High inter-annual variations in density of the key species were associated to low inter-annual variations in species composition. This is typical of many intertidal fish assemblages [10,42,50] and particularly those inhabiting the rocky intertidal zone (see the review of [5]). Although temporal variations in shallow coastal epibenthic species densities are well documented, much confusion still prevails over the factors influencing or controlling them. They have been attributed to fluctuations in a wide variety of both biological and physical variables including the timing of spawning seasons and hence the influx (immigration/recruitment) and efflux (emigration) of individuals to and from populations (e.g. [9,51]), food availability [52], predation pressure [53,54], water temperature (e.g. [2,55]), wind speed and direction (e.g. [9,54]), turbidity (e.g. [50]), and salinity (e.g. [14]).

Inter-annual variations observed in species density (up by five-fold for the key species), are most likely the result of differences in year-class strength and recruitment success. The fact that fluctuations did not follow the same pattern for all dominant species, suggests that species responded differently to the environmental variables and that the factors contributing to successful recruitment differed between species. It is now clear that climate variability affects the density and biogeography of marine organisms [56]. Several recent long-term studies in the English Channel and the North Sea have revealed changes in intertidal beach macrofauna that were directly or indirectly related to climate variability [15,16]. A study based on a 34-year time series of *C. crangon* abundances in the Dutch Wadden Sea indicated that salinity, freshwater discharge and the NAO were relevant factors affecting its abundance [14]. The NAO and river flow may influence recruitment success, probably due to their effects on the productivity and growth of coastal organisms [57]. Such environmental factors have been recognized as key issues in the estuarine colonization and settlement processes of both marine fish and invertebrate larvae and juveniles (e.g. [58,59]).

Co-inertia and generalised linear model analyses identified, among the measured environmental variables, winter NAO index, water temperature, salinity suspended particular matter, and chlorophyll-*a* as the major environmental factors to explain these changes. Hydrological and oceanographic features in coastal waters of the EEC depend mainly on the Seine River outflow, which creates a water mass of relatively low salinity and nutrient enrichment known as "*Fleuve côtier*" [60], spreading northward parallel to the French coast.. Since this frontal zone has been shown to influence fluctuations of ichthyoplankton assemblages such as offshore/onshore distribution [61], the observed hydrological change over the period 2000–2013, associated with NAO change, may have affected progressively the recruitment success of species such as *P. platessa*, *P. microps*, and *A. tobianus*. Density of *S. sprattus*, considered as a cold/temperate water species, was negatively correlated to temperature in our study. This species may have probably found optimal conditions for its development when water temperature decreases. [59] illustrated a situation in which climatic oscillations exerted effects on fish assemblages by affecting the suitability of estuarine nursery grounds for marine fish. They found an increase in diversity during high NAO winters, which is partly explained by the increase in the number of rare species. Although species diversity and community structure in our intertidal zone was stable from year-to-year, the NAO was identified as a factor structuring the inter-annual variations in density of some key species such as *P. microps and C. crangon*. The NAO is probably best viewed as a means of describing processes that operate at a higher level of control of oceanographic and atmospheric phenomena rather than as an agent that acts directly on the fish assemblages.

In shallow coastal areas, juvenile fish are exposed to high predation pressure [58,62]. During the 11 years studied, fish and macrocrustacean densities fluctuated from year-to-year, with a slight negative, but not significative correlation. Many studies have showed predator-prey interactions between these two groups of species. Due to its high density (72% of the total catches in the present study), *C. crangon* is a key component of the trophic web. It is known as an important prey for some fishes (gobies, gadoids, several flatfish and demersal roundfish species), crustaceans and shorebirds [14] as well as an important predator of numerous larvae and juvenile stages of several fish and benthic species [53,63]. For example, both *C. crangon* and *C. maenas* are the main predators on the early benthic stages of *P. platessa* in spring [53].

Finally, despite high inter-annual variations in the magnitude of *P. globosa* spring blooms, by two-orders of magnitude, no effects on either juvenile fish or macrocrustacean species diversity, densities or assemblages were observed. These results concur with those from a recent mesocosm study, which clearly showed that exudates and TEP excreted from decaying *P. globosa* colonies and foam accumulation have no negative effect on juvenile sea bass growth, condition or survival [64]. By contrast to macrobenthic species [24] which can be affected by foam accumulation, fish and macrocrustaceans are motile species, probably giving them the possibilities to avoid foam accumulation on the beach, and unfavourable areas in general.

In conclusion, the fish and macrocrustacean spring community structure in the studied intertidal zone was stable from year-to-year, and was based on a set of regularly occurring species. However, strong inter-annual variations in species density occurred (up by five-fold for the key species), being associated to inter-annual variations in winter NAO index, water temperature, salinity, suspended particular matter and chlorophyll-*a*. No significant relationship between crustaceans and fish were found in the present study but predator-prey interactions should be investigated in more details in future studies. Although the recurrent and dense spring blooms of the Prymnesiophyte *Phaeocystis globosa* is one of the main potential threats in shallow waters of the eastern English Channel, no negative impact of its temporal change was detected on the fish and macrocrustacean spring community structure. More work is necessary both to characterise patterns of faunal change and their linkages with biological and oceanographic changes, and also to understand the causal mechanisms through which fish assemblages are being affected by changing environmental conditions.

Supporting Information

S1 Fig. Comparison of *Phaeocystis* cell counts in replication samples preserved with Lugol's for more one year and Lugol-glutaraldehyde preserved less than one month after sampling.
(TIF)

S1 Table. Mean values of environmental data recorded during the first six months (January to June) from 2000 to 2013.
(XLSX)

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Author Contributions

Conceived and designed the experiments: RA. Performed the experiments: RA JS AB KR VC EL. Analyzed the data: MB EB AB RA. Contributed reagents/materials/analysis tools: KR EL JS MB. Wrote the paper: RA EB AB.

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