UNIVERSITE DES ANTILLES ET DE LA GUYANE

HABILITATION A DIRIGER DES RECHERCHES

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Ifremer

Biodiversité halieutique : impacts de la pêche et des changements climatiques
-
Conséquences économiques pour les pêcheries

Présentée le 23 janvier 2014, devant le jury constitué de :

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Sommaire

I - Curriculum Vitae

Fabian BLANCHARD

Né le 16 juin 1970

Formation

→ Doctorat Océanographie Biologique, Université de Bretagne Occidentale, 14 septembre 2000

Titre : impact de l'exploitation par la pêche sur la dynamique de diversité des peuplements de poissons démersaux (sous la direction de Jean Boucher)

→ DEA Océanographie Biologique, Paris VI-UBO, « gestion des écosystèmes côtiers en terme de ressources », juin 1995, mention Bien.

→ Maîtrise Sciences de l'Environnement – mention Océanologie, Université Bordeaux I, juin 1994, mention Bien.

→ Licence Sciences Naturelles, Université Bordeaux I, juin 1993

Postes occupés

→ Délégué Régional Ifremer en Guyane, Chef de station et chef de l'unité Biodiversité Halieutique de Guyane depuis octobre 2008

→ Ifremer, Chercheur Ecologue Halieute, Laboratoire des Ressources Halieutiques de Guyane, (septembre 2005 – septembre 2008) : approche écosystémique des pêches (interactions climat/biodiversité/pêche)

→ Ifremer, Chercheur Ecologue Halieute, Laboratoire des Ressources Halieutiques, Plouzané (octobre 2000-août 2005) : impact du changement climatique et de la pêche sur la structure et la biodiversité des peuplements de fond, poissons et invertébrés, conséquences économiques

→ Ifremer, VAT Biostatisticien, Laboratoire des Ressources Halieutiques de Guyane (décembre 1995 – avril 1997) : les ressources de la pêche côtière traditionnelle et leur exploitation

Langues, logiciels

Anglais (lu, écrit, parlé), Espagnol (lu, parlé), Portugais (lu, parlé-notions), Créole guyanais (notions)

S+, R, Statistica, Spad, Arcview

II - Résumé

Recruté en tant que Cadre de Recherche en écologie halieutique au Laboratoire des Ressources Halieutiques de l'Ifremer à Brest en octobre 2001, puis affecté au Laboratoire des Ressources Halieutiques de l'Ifremer en Guyane en septembre 2005, mes activités des 10 dernières années, 2003-2012, ont été consacrées au montage, à la conduite et animation d'actions pluri-disciplinaires de recherche dans le cadre d'appels d'offres nationaux et européens sur le thème des impacts de la pêche et du changement climatique sur les peuplements de fonds exploités, ainsi que des conséquences économiques pour les pêcheries. A partir de 2008, une partie de mon activité est consacrée à la représentation de l'Ifremer en tant que Délégué Régional en Guyane, à la direction de la station Ifremer de Guyane et du Laboratoire des Ressources Halieutiques. En 2011, l'Ifremer a été restructuré en quatre grands départements et les laboratoires en unités de recherche. J'ai alors proposé que le laboratoire des Ressources Halieutiques de Guyane que j'animais devienne l'Unité Biodiversité Halieutique de Guyane, appellation plus conforme aux approches développées.

Les actions de recherche ont été menées en partenariat avec des halieutes, écologues marins, statisticiens, modélisateurs et économistes ; partenaires au sein de l'Ifremer, d'organismes de recherche - IRD, CNRS, Institut National de Recherche Halieutique du Maroc - , et d'Enseignement Supérieur - Université de Bretagne Occidentale, Université du Littoral Côte d'Opale, Ecole Nationale d'Ingénieur de Brest, Université des Antilles et de la Guyane. Ces actions ont permis de consolider une communauté pluri-disciplinaire nationale pour aborder les questions de l'analyse intégrée et de la modélisation à l'échelle écosystémique de la durabilité écologique et économique de l'exploitation des ressources halieutiques dans un contexte climatique changeant. Elles ont permis par ailleurs une première application formelle significative au sein de l'Ifremer, de l'approche écosystémique des pêches en contexte tropical (Guyane).

Les méthodes d'analyse utilisées ont en premier lieu été développées pour le cas du plateau continental du Golfe de Gascogne. Ces méthodes ont ensuite été étendues et appliquées à d'autres plateaux continentaux dont les caractéristiques étaient très différentes en termes climatique, de fonctionnement physique, bio-géographique, d'exploitation halieutique, économique et de gestion de la pêche : au Maroc dans la zone sous influence d'un up-welling, et en Guyane sous l'influence de l'estuaire de l'Amazone. Des actions lancées en 2009 et en 2010, reprennent ces méthodes pour des cas d'application à un autre plateau continental, dans la région tropicale du nord de l'Australie, et pour des cas en zones littorales, en Guyane et aux îles Salomon.

Les principaux résultats obtenus sont i) l'identification de changements dans la structure des peuplements de poissons de fond : l'analyse des l'évolution temporelle des caractéristiques des peuplements de fond notamment en terme de taille individuelle, de niveau trophique, d'affinité thermique des espèces (origine biogéographique) a montré l'existence d'effets conjoints de la pêche (sur-exploitation et effets écosystémiques) et des changements climatiques, en région tempérée comme en région tropicale ; ii) l'identification de changements dans la structure en espèce des débarquements des pêcheries à l'échelle des dernières décennies, ainsi que la diminution de leur valeur économique totale, à la fois conséquence des changements dans les peuplements mais conséquence aussi des changements intervenus dans les marchés internationaux des produits de la mer ; iii) Le poids des différent facteurs (pêche, climat, marchés…) est variable selon les cas d'étude, mais ceux qui sont décrit ici sont ceux, communs aux différents systèmes, qui semblent prépondérants ; iv) l'adaptation de modèles existants ainsi que le développement de nouveaux modèles maintenant opérationnels, depuis des échelles permettant une utilisation en terme d'expertise et de recommandation de gestion des pêcheries à court terme, jusqu'à des échelles permettant des projections exploratoires à long terme visant à comprendre les effets conjoints du climat, de la pêche et des marchés.

Ces actions ont été valorisées par de nombreuses publications. Depuis 2003, j'ai personnellement contribué en premier auteur et en tant que co-auteur, à 15 publications scientifiques de rang A et 16 communications orales lors de colloques nationaux et internationaux. Des stagiaires de fin d'études d'ingénieur, Mastères 2, doctorants, post-doctorants ont été formés. J'ai personnellement encadré ou co-encadré 7 étudiants en Mastère Professionnel ou Recherche, un post-doctorant. Deux thèses de l'UAG dont je suis co-encadrant ont débuté fin 2009 et deux autres ont commencé en 2010 et 2012 (dont une UAG et une avec l'Université de la Sorbonne), avec des bourses de thèse dont le financement a été acquis dans le cadre d'AAP de l'ANR et de la Direction Régionale de l'Environnement (maintenant DEAL) en Guyane, de la région Guyane et de l'Ifremer.

III - Principaux résultats des travaux menés

1. Introduction : de l’approche halieutique classique à l’approche écosystémique des pêches ou approche intégrée, maximisation vs viabilité

La gestion des pêches repose sur les modèles halieutiques représentant la dynamique d’une population exploitée (recrutement, croissance, mortalité), considérée à l’équilibre avec son milieu. Ces modèles permettent de trouver un maximum de production soutenable (ou RMD, rendement maximum durable) par la population. Cependant, le recrutement fluctue d’une année sur l’autre, voire peut montrer une tendance temporelle liée à des modifications environnementales ou des équilibres d’interactions trophiques concernant la population considérée. Le RMD calculé, considéré à l’équilibre n’est alors plus valable. Le RMD peut ne pas être compatible non plus avec la viabilité des populations non ciblées, captures accessoires, avec la viabilité des populations qui subissent un impact suite au passage des engins de pêche, avec la viabilité des populations qui subissent un impact via leurs interactions trophiques avec les espèces directement impactées par la pêche ; le RMD peut ne pas être compatible non plus avec la préservation des habitats exploités qui subissent l’impact physique des engins de pêche. Par ailleurs, le rendement économique maximum d’une pêcherie est souvent réalisé pour des valeurs d’effort de pêche inférieures à celles permettant d’obtenir le RMD : au-delà d’une certaine valeur de l’effort de pêche, le coût économique d’une unité supplémentaire d’effort est inférieur au gain observé. Ainsi, le RMD peut théoriquement être incompatible avec la réalité économique des entreprises de pêche, ce qui semble être le cas pour la pêcherie crevettière de Guyane dont la dynamique d’exploitation est autant économique que biologique.

Le passage à une approche plus écosystémique, et intégrée, c’est-à-dire passer d’un rendement maximum pour une pêcherie exploitant une ou plusieurs espèces, à un rendement viable écologiquement et économiquement, s’impose donc progressivement, mais reste loin de l’opérationnalité. Ce passage nécessite de comprendre les impacts de la pêche sur les ressources, la biodiversité associée, les habitats qui permettent leur maintien, mais qui subissent dans le même temps les forçages climatiques s’accentuant dans le contexte du changement climatique, et de comprendre les conséquences de ces impacts pour les pêcheries en regard des facteurs économiques tels que les marchés et des facteurs institutionnels tels que la régulation de l’accès aux ressources dans le déploiement de l’effort de pêche. Les disciplines à mobiliser en premier lieu sont donc l’écologie des écosystèmes, des peuplements, la macro-écologie, les sciences économiques, et la modélisation des systèmes, capable de faire l’interface entre les disciplines et de formaliser l’ensemble des processus.

2. Biodiversité halieutique et approche intégrée

La biodiversité halieutique peut être définie comme l'ensemble des espèces commerciales ; des espèces non commerciales mais capturées systématiquement car faisant partie du même peuplement ; des espèces capturées accidentellement, comme par exemple les oiseaux, les mammifères ou reptiles marins ; des espèces non capturées mais impactées par le passage des engins de pêche ; des espèces non capturées mais en interaction écologique de premier niveau (prédateurs, proies, compétiteurs directs) avec les espèces directement impactées. Dans une démarche écosystémique pour l'analyse des pêcheries, cette notion définit une limite du sujet d'étude, bien qu'une certaine vision plus holistique de l'approche écosytémique de pêches englobe le fonctionnement complet de l'écosystème, considérant que les impacts indirects peuvent atteindre les premiers échelons du réseau trophique, la production primaire. C'est cette notion de biodiversité halieutique qui a orienté mes travaux et qui en est ainsi le premier fil conducteur.

S'il est nécessaire de rendre la pêche durable d'un point de vue environnemental, cela ne sera possible que dans la mesure où persiste une rentabilité économique. Il faut donc trouver les modalités et les niveaux d'exploitation permettant de concilier les deux objectifs : rentabilité économique non nulle et maintient de la biodiversité halieutique. La recherche par des modèles dynamiques intégrés, de niveau d'exploitation viable écologiquement et économiquement (noyau de co-viabilité) et de manière plus générale la bio-économie des pêcheries est le second fil conducteur ayant orienté mes travaux au cours des dernières années.

Ainsi, dans un premier temps ont été décrits dans ce document mes travaux visant à identifier les impacts de la pêche sur la biodiversité halieutique (peuplements de poissons de fonds, peuplements d'invertébrés benthiques et deux espèces de la faune « charismatique »), ainsi que les effets conjoints du changement climatique, à partir i) de données de campagnes menées en mer, et ii) d'un modèle individu-centré intégrant ces effets dans la dynamique des espèces simulées. Dans un second temps, des analyses de données visant à montrer comment ces modifications se traduisent en termes de valeur économique de la production ont été décrites, nécessitant toutefois de tenir compte de facteurs forçants économiques tels que la mondialisation des marchés des produits de la mer. Enfin, la compréhension ainsi acquise du système biodiversité/pêcherie a permis de simuler des scénarios de gestion ou de trajectoires probables de ce système à différentes échelles (évolution attendue de la filière crevettière et de la pêche côtière).

3. Impacts de la pêche sur la biodiversité halieutique et effets conjoints du changement climatique

3.1. Structure et dynamique des peuplements de fond exploités : le cas du plateau continental du Golfe de Gascogne

Peu de résultats d'impacts attribuables au seul impact de la pêche sur les peuplements de poissons de fond ont été obtenus. En effet, d'une part des changements peuvent en théorie être masqués par la variabilité spatio-temporelle de la biodiversité des peuplements et d'autre part, l'analyse des changements porte sur une série temporelle de données disponible à partir de la fin des années quatre-vingt, donnant vraisemblablement l'image de peuplements ayant déjà atteint un nouvel équilibre suite aux impacts en question. Par ailleurs, c'est au cours de cette même période que se manifeste le changement climatique sur le milieu marin, facteur d'impact supplémentaire rendant plus difficile la discrimination de celui lié à l'exploitation.

Ce premier point est analysé dans les publications suivantes présentées en annexe.

Blanchard, F. et Boucher, J., 2001. Dynamics of the demersal fish community in the Bay of Biscay. Proceedings of the 7th International Symposium on Oceanography of the Bay of Biscay, Biarritz, 4-6 Avril 2000. Actes Colloques Ifremer, 31 : 181-186.

Blanchard, F., 2001. Approche de la dynamique des peuplements de poissons démersaux exploités : analyse comparée de la diversité spécifique dans le golfe de Gascogne (océan Atlantique) et dans le golfe du Lion (mer Méditerranée). Aquatic Living Resources, 14: 29-40.

Souissi, S., Ibanez, F., Ben Hamadou, R., Boucher, J., Cathelineau, A.C., **Blanchard, F**., Poulard, J.C. 2001. New method for multivariate cartography : application to study species assemblages and their habitats by using bottom trawl surveys in the Bay of Biscay (France). Sarsia, 86: 527-542.

Blanchard, F. and Boucher, J., 2001. Temporal variability of total biomass in harvested communities of demersal fishes. Fisheries Research, 49: 283-293.

Poulard, J.C., **Blanchard, F**., Boucher, J., Souissi, S., 2003. Variability in the demersal fish assemblages of the Bay of Biscay during the 1990s. ICES Marine Science Symposia, 219: 411-414.

Duplisea, **D., Blanchard, F**. 2005. Relating species and community dynamics in a heavily exploited marine fish community. Ecosystems, 8 : 899-910.

3.2. Impacts de la pêche au chalut sur les peuplements de la macrofaune d'invertébrés benthiques : le cas du plateau continental du Golfe de Gascogne

Sur les plateaux continentaux, la pêche au chalut de fond est une source de perturbation chronique qui affecte les habitats benthiques, ainsi que les peuplements qui les habitent. Ces peuplements constituent une partie du régime alimentaire des espèces exploitées par la pêche telles que les poissons démersaux, en particulier dans leur phase juvénile, mais aussi les poissons benthiques, parfois y compris à l'âge adulte. Le plateau continental Nord Gascogne, et particulièrement la Grande Vasière, est exploité par une importante pêcherie démersale française, notamment la pêcherie langoustinière. L'analyse de l'impact de la pêche chalutière sur le benthos a été menée conjointement avec les benthologues de l'IUEM (Lemar) dans le cadre du chantier Gascogne du PNEC (figure 1).

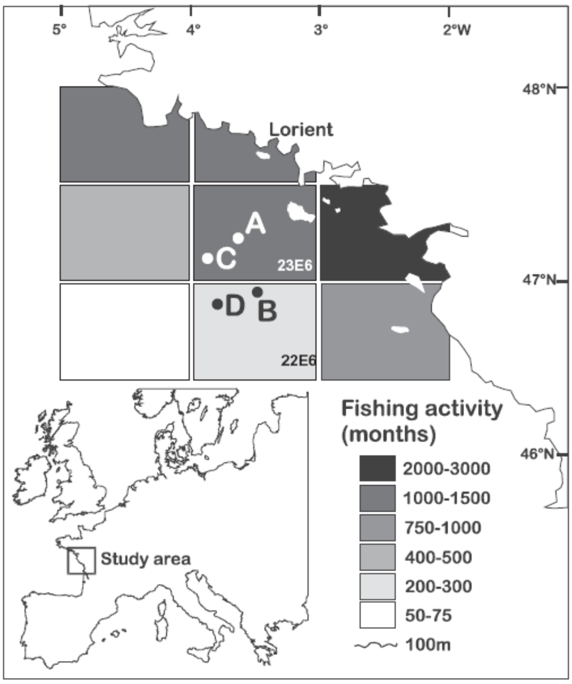


Figure 1. Position des zones d'échantillonnage du benthos (petit chalut à perche et benne) dans le Golfe de Gascogne en 2001 et 2003, et effort de pêche des chalutiers de fond (en mois*bateaux) au sein des rectangles statistiques CIEM pour l'année 2001 (données Ifremer- SIH). Blanchard *et al.*, 2004.

La comparaison des peuplements benthiques actuels et ceux de 1966 montre une évolution à long terme très nette des entités bio-sédimentaires du plateau continental Nord Gascogne. Les tendances générales mises en évidence sont une homogénéisation du type sédimentaire sur la Grande Vasière alors que les sédiments de la marge externe apparaissent plus stables. Des modifications de la composition spécifique des peuplements de la macrofaune benthique ont également été décelées, conduisant à des changements d'identité des entités bio-sédimentaires (Le Loc'h et al., 2005). Les causes des évolutions observées sont multiples et la déconvolution des signaux climatiques et anthropiques est encore difficile à appréhender.

Le passage des chaluts sur le fond a un effet direct sur les populations dont les individus sont capturés, sur les populations non capturées mais dont les individus, fixés ou non sur le sédiment sont abîmés, voire cassés par le contact de l'engin de pêche. Il peut exister aussi un effet indirect : les individus fragilisés car abîmés ou cassés, les individus morts, sont des proies plus facilement accessibles pour des prédateurs et pour les nécrophages. Nous avons ainsi pu montrer, que au sein de l'épifaune (les organismes non enfouis), l'abondance, la biomasse et la diversité des espèces les plus fragiles (squelette externe fin, bivalves) étaient plus faibles dans les zones les plus fortement exploitées (figure 2), tandis qu'à l'inverse, les espèces opportunistes étaient favorisées (Blanchard *et al.*, 2004, Vergnon et Blanchard, 2006).

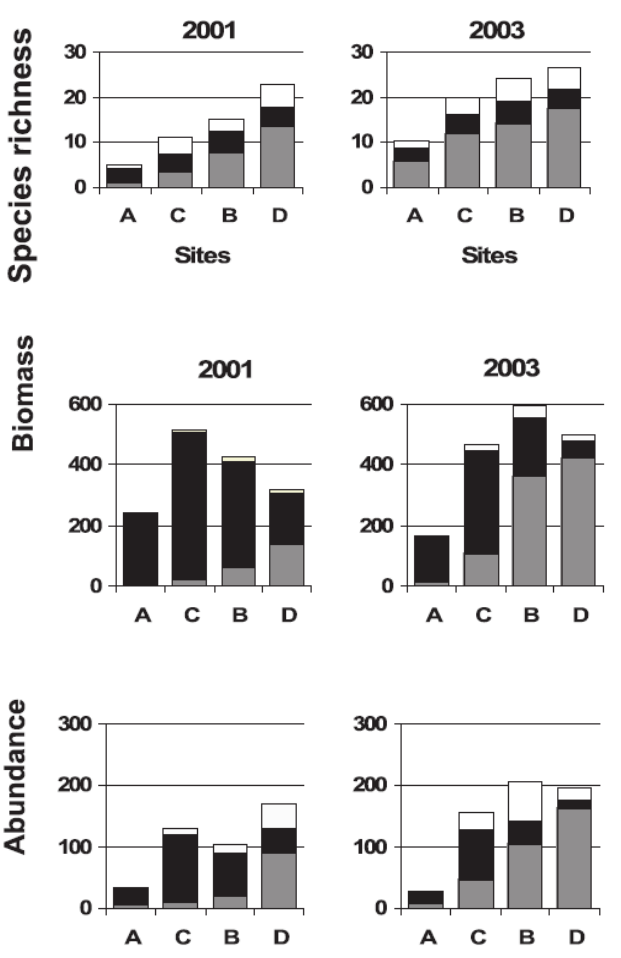


Figure 2. Richesse spécifique (nombre d'espèces), biomasse (poids humide en g/1000m²) et abondance (nombre d'individus/1000m²) des espèces sensibles par leur caractéristiques physiques et écologiques (en gris), des espèces opportunistes (en noir) et des espèces indifférentes (en blanc) au sein d'une zone fortement exploitée (sites AC) et modérément exploitée (sites BD), *cf.* carte figure 1. Vergnon et Blanchard, 2006.

Au sein de l'épifaune, les espèces sessiles (fixées) sont en moyenne deux fois plus impactées que les espèces vagiles (mobiles). De tels résultats étaient seulement connus pour la Mer du Nord et étaient donc mis en évidence pour la première fois dans un autre écosystème.

Nous avons montré aussi que la structure du peuplement benthique au sein de la zone moins exploitée pouvait être considérée comme écologiquement en bon état. Les peuplements d'invertébrés benthiques pourraient donc supporter une certaine pression de pêche, valeur au-delà de laquelle la communauté change de structure. Il pourrait ainsi être imaginé de répartir spatialement l'effort de pêche de manière à ne pas dépasser cette valeur par unité de surface.

Ces résultats sont détaillés dans les publications suivantes présentées en annexe.

Blanchard, F., LeLoc'h, F., Hily, C., Boucher, J., 2004. Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Marine Ecology Progress Series, 280 : 249-260.

Vergnon, R; **Blanchard, F**., 2006. Evaluation of trawling disturbance on macrobenthic invertebrate communities in the Bay of Biscay, France: Abundance Biomass Comparison (ABC method). Aquatic living resources. Vol. 19, no. 3, pp. 219-228.

3.3. Interactions pêche et faune « charismatique » : le cas des tortues et oiseaux marins en Guyane

Les interactions entre les activités de pêche et la faune marine telle que mammifères marins, oiseaux et tortues font l’objet de travaux dont les répercussions dans les médias sont fortes. Des règlementations sont mises en œuvre pour limiter ces interactions, qu’elles soient positives ou négatives.

En Guyane, la pêcherie crevettière est en interaction avec les tortues et les oiseaux marins. La pêcherie chalutière génère des rejets important en raison de captures accessoires fortes : de 7 à 9 kg de captures accessoires pour 10 kg de capture totale (Vendeville et *al.*, 2008., Durabilité des activités halieutiques et maintien de la biodiversité marine en Guyane, rapport final, IFOP-CPER Guyane).

Ces captures accessoires sont rejetées mortes en majeure partie et bénéficier aux populations d’oiseaux marins, notamment la frégate superbe (*Fregata magnificens*). Bénéficiant d’une alimentation à moindre dépense énergétique, la population a augmenté et est devenue sensible aux variations de l’effort de pêche. Lorsque l’effort de pêche diminue, les rejets diminuent aussi. Ainsi les jeunes oiseaux sont carencés (les adultes préfèrant conserver la nourriture pour eux-mêmes), ce qui les rend sensibles à un herpes-virus déjà présent chez ces oiseaux, et finissent par mourrir.

Parmi les captures accessoires, la tortue luth *Dermochelys coriacea* est identifiée. En saison de ponte, cette espèce resterait à proximité du fond pour se nourrir de méduses entre deux pontes ; elle devient ainsi capturable aisément. Des travaux ont été réalisés pour mettre en place des dispositifs de sélectivité permettant d’éviter les captures de grands animaux (tortues, poissons), dispositifs rendus obligatoires dès 2010 par délibération du Comité Régional des Pêches de Guyane.

Ces travaux sont abordés dans les publications suivantes présentées en annexe.

De Thoisy, B., Lavergne, A., Semelin, J., Pouliquen, J.-F., **Blanchard, F**., Hansen, E., Lacoste, V., 2009. Herpesvirus outbreaks in a colony of Magnificent Frigate birds (*Fregata magnificens*) in French Guiana. Journal of Wildlife Diseases, 45(3): 802-807.

Fossette, S., Girard, C., Bastian, T., Calmettes, B., Ferraroli, S., Vendeville, P., **Blanchard, F**., Georges, J.-Y., 2009. Thermal and trophic habitat of the leatherback turtle during the nesting season in French Guiana. Journal of Experimental Marine Biology and Ecology, 378: 8-14.

3.4. Effets conjoints de la pêche et du changement climatique sur les peuplements de poissons de fond : le cas du plateau continental du Golfe de Gascogne et de la Guyane

L'analyse de la structure des peuplements de fond et de leurs changements au cours du temps a été conduite à partir de données de campagnes expérimentales de chalutage de fond dans le Golfe de Gascogne et sur le plateau de Guyane. Ces peuplements dont les caractéristiques écologiques sont différentes montrent tous deux des changements qui peuvent s'interpréter en regard du réchauffement des eaux et de l'impact de la pêche.

3.4.1. Les SST

Si l'augmentation des températures de surface était publiée dans le golfe de Gascogne depuis 1998, il n'existait pas de résultats concernant toute la colonne d'eau sur le plateau continental. Le réchauffement touche en fait toute la colonne d'eau sur le plateau du golfe de Gascogne (Blanchard et Vandermeirsch, 2005): entre 1970 et 2000, un réchauffement de 1.5°C est observé dans la masse d'eau comprise entre 0 et 50 mètres de fond et de 0.8°C dans la masse d'eau comprise entre 50 et 200 mètres de fond. Ce réchauffement est particulièrement sensible après 1987/1988.

En revanche, sur le plateau des Guyanes, région tropicale, un réchauffement des eaux de surface est mis en évidence et une première quantification et donnée. Il est du même ordre de grandeur que dans le Golfe de Gascogne (figure 3). Une augmentation des valeurs minimales, maximales et moyennes est à noter (figure 4).

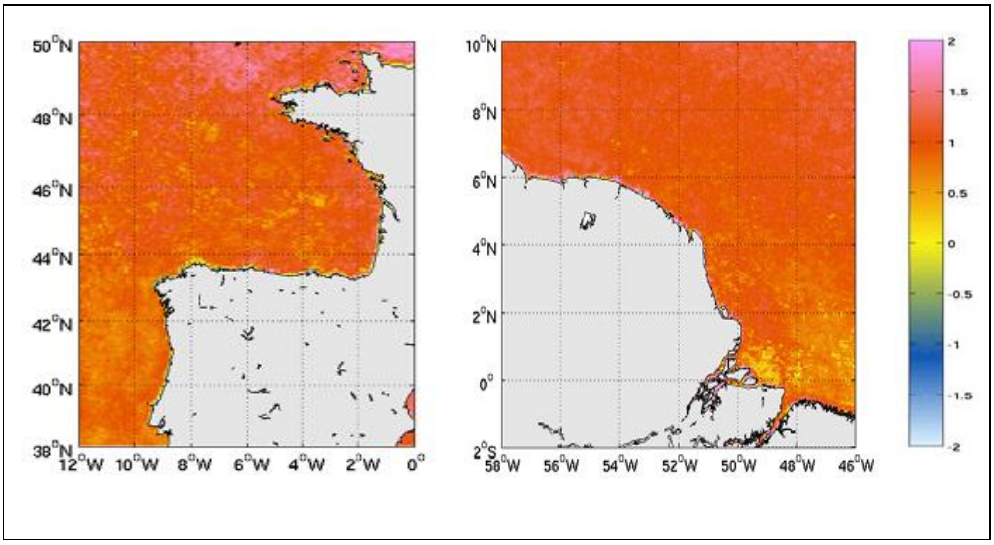


Figure 3. Variations de la température de surfaces par rapport à la moyenne 1985-2006 (données satellites) en °C (source données : Physical Oceanography Distributed Active Archive Center).

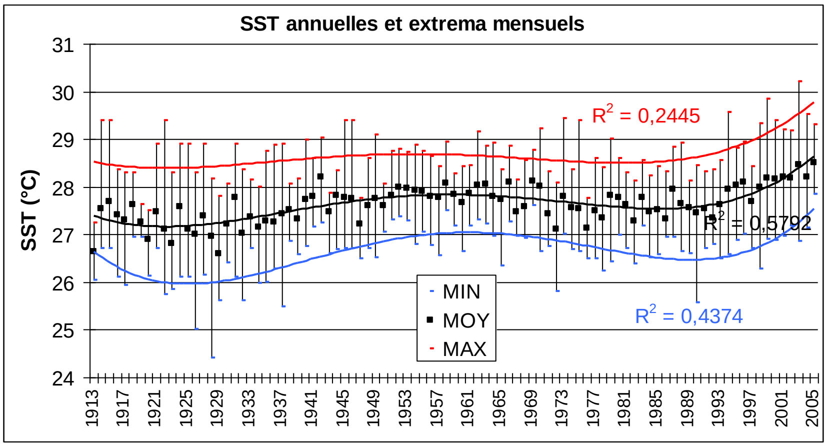


Figure 4. Variations temporelles de la température de surface moyenne annuelle ("MOY"), des valeurs moyennes du mois le plus froid (min) et du mois le plus chaud (max) sur le plateau continental guyanais (données ICOADS).

3.4.2. Les peuplements écologiques de fond

Géographiquement le Golfe de Gascogne se présente comme une entité bien individualisée. Bien que rattaché à l'Atlantique N.-E., sa position et la morphologie de ses côtes vis-à-vis de la circulation générale en font une entité particulière. Il est possible d'identifier un schéma général de circulation, de cycle annuel des communautés planctoniques, de distribution des communautés de poissons. C'est une zone de mélange de la faune tempérée classique avec des groupes d'affinité boréale, subtropicale et tropicale (figure 5). De telles zones de mélange sont considérées comme susceptibles de répondre plus rapidement que d'autres zones à de faibles variations climatiques. Sur une centaine d'espèces présente chaque année dans les campagnes expérimentales de chalutage de fond menées entre 20 et 200m de fond, ces trois groupes d'espèces sont représentés avec une richesse spécifique différentes : le groupe des espèces subtropicales est le plus important avec 62 espèces, le groupe tempéré est représenté par 27 espèces, et le groupe boréal est représenté par 24 espèces (figure 6).

Le plateau continental de Guyane est situé en zone tropicale. Il est bordée par le courant nord-Brésil sur la pente continental du sud-est au nord-ouest, et soumis aux influences des eaux dessalées et chargées en matière en suspension en provenance de l'estuaire de l'Amazone. Deux saisons rythment le fonctionnement de l'écosystème: la saison humide de décembre à juillet, et la saison sèche d'août à novembre. Cette région est classée, à comparaison des autres grands écosystèmes marins, parmi les plus productifs. Des espèces tropicales et sub-tropicales s'y rencontrent. Les campagnes expérimentales de chalutage de fond menées entre 10 et 60 m de fond permettent de dénombrer environ 150 espèces de poissons. On dénombre autant d'espèces tropicales que d'espèces subtropicales.

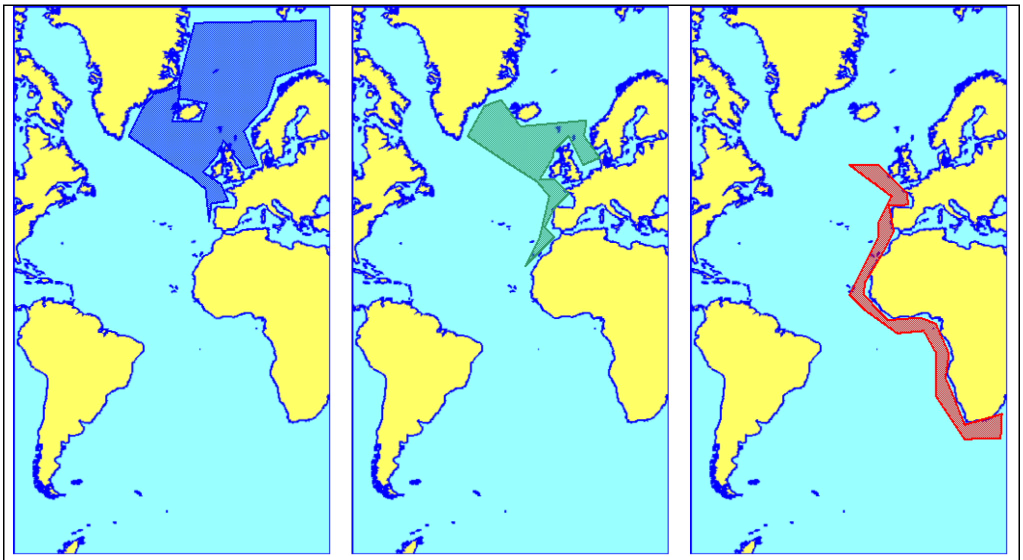


Figure 5. Aires biogéographique des espèces échantillonnées dans le golfe de Gascogne au cours des campagnes de chalutage scientifiques : espèces boréales (en bleue à gauche), espèces tempérées (en vert au centre) et espèces subtropicales (en rouge à droite).

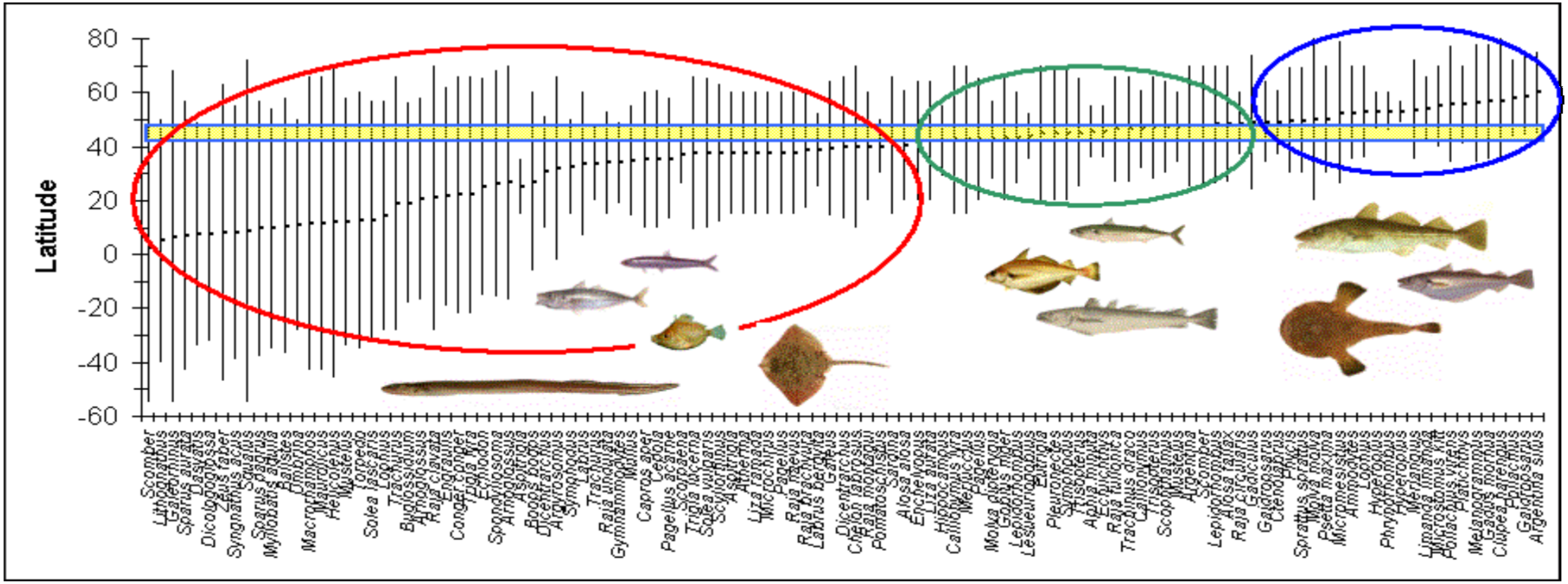


Figure 6. Aire de répartition (latitude haute, basse, médiane) des espèces échantillonnées dans le golfe de Gascogne, dont la position latitudinale est repérée en jaune, au cours des campagnes de chalutage scientifiques: espèces boréales (en bleue), espèces tempérées (en vert) et espèces subtropicales (en rouge).

3.4.3. Changements au sein des peuplements

3.4.3.1. Sur le plateau continental du Golfe de Gascogne

Dans le Golfe de Gascogne, les variations temporelles de l'abondance totale des espèces subtropicales, boréales et tempérées montrent des tendances différentes selon les groupes (figure 7). Conformément aux hypothèses d'un effet du réchauffement, l'abondance totale des espèces subtropicales augmente significativement de façon exponentielle après 1992 soit environ quatre ans après le réchauffement (le coefficient de détermination de la régression linéaire est de 0.6). Il n'y a pas d'effet significatif sur l'abondance totale des espèces tempérées. En revanche, un effet négatif était attendu sur l'abondance des espèces boréales, ce qui n'est pas observé (pas de tendance significative). Le cas particulier du sanglier, *Capros aper* est caractéristique : cette espèce était rare au début de la série temporelle ; elle est maintenant un espèce dominante (Blanchard and Vandermeirsch, 2005). Le sanglier n'est pas la seule espèce à montrer une tendance temporelle de son abondance.

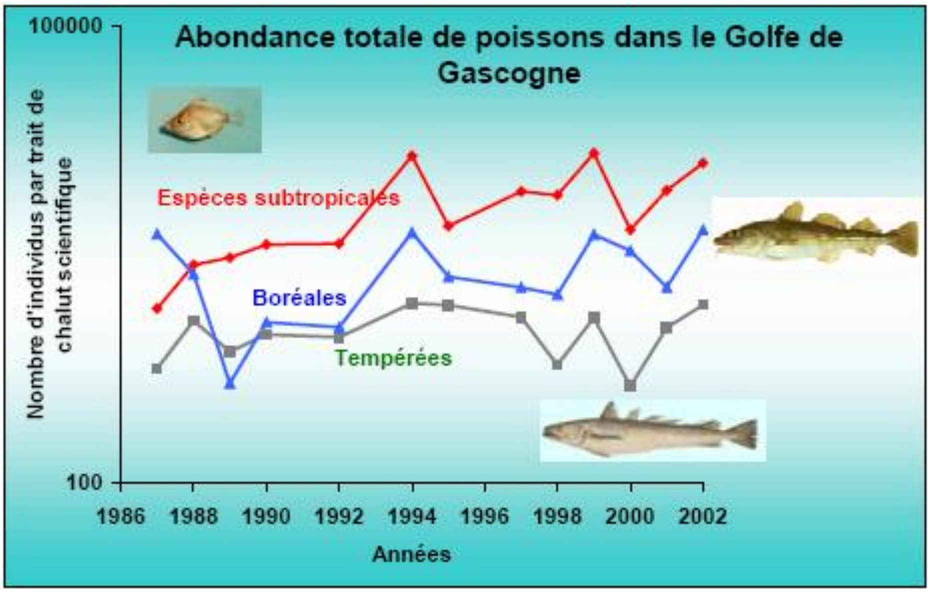


Figure 7. Variations temporelles de l'abondance totale des espèces subtropicales, boréales et de transition ou tempérées (échelle logarithmique, nombre d'individus par trait de chalut, campagnes Ifremer "EVHOE", N/O Thalassa).

Une analyse des correspondances a été conduite sur les données standardisées afin de regrouper les espèces dont les trajectoires temporelles se ressemblent (figure 8). Les caractéristiques de distribution en latitude de ces espèces ont été ajoutées dans l'analyse en tant que variables supplémentaires illustratives (non utilisées pour le calcul des axes mais projetées dans le plan factoriel). Deux principaux groupes apparaissent dans le premier plan factoriel expliquant 34% de la variance: l'un est constitué d'espèces dont l'abondance a diminué, l'autre est constitué d'espèces dont l'abondance a augmenté. Le premier groupe, dont l'abondance des espèces a diminué regroupe des espèces dont le centre de l'aire de répartition se situe à une latitude plus haute que le golfe de Gascogne (affinité froide) et qui sont aussi les espèces exploitées de grande taille dont le diagnostic est celui de la sur-exploitation ou de pleine exploitation, tandis que l'autre groupe, dont l'abondance des espèces a augmenté regroupe les espèces dont le centre de l'aire de répartition est à une latitude plus basse que celle du golfe de Gascogne (affinité chaude) et qui sont soit beaucoup moins exploitées, soit moins fragiles face à l'exploitation car ayant des stratégies vitales permettant de supporter des taux de mortalité par pêche plus élevés.

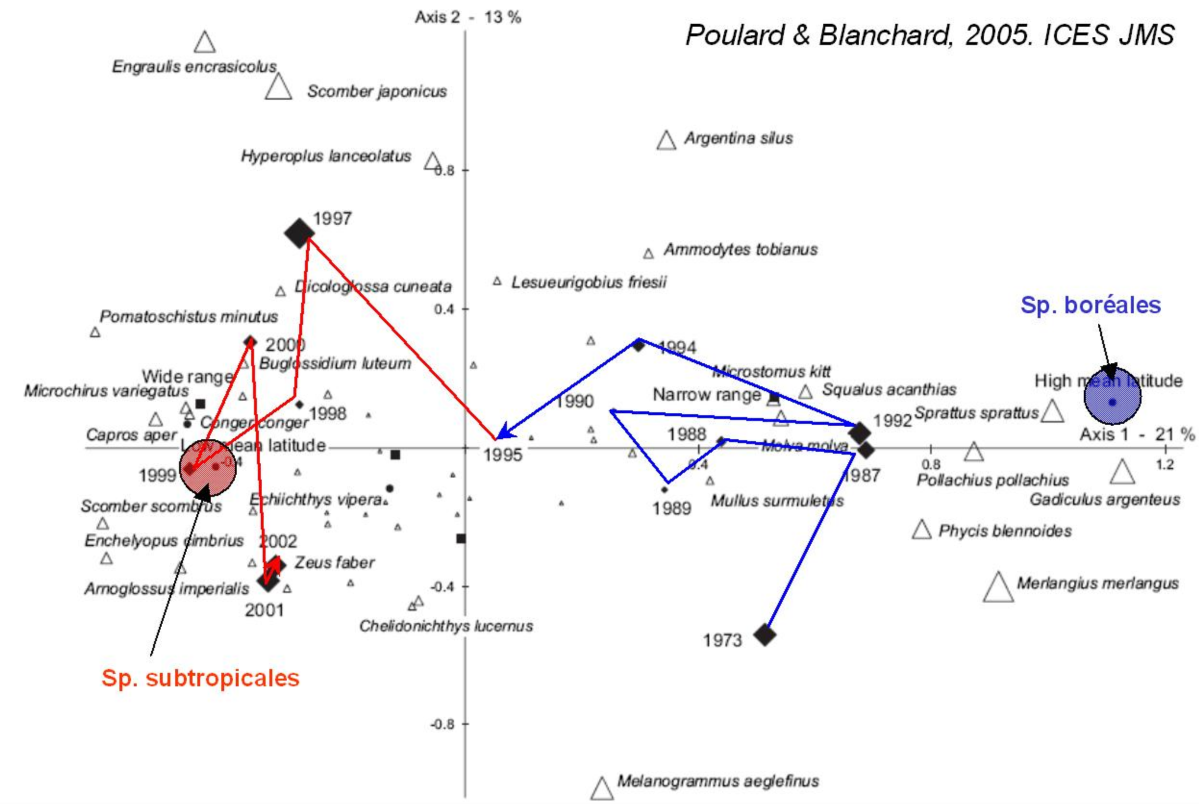


Figure 8. Projection des variables espèces dans le premier plan de l'analyse des correspondances (AC), des campagnes (de 1973 à 2002) et des positions latitudinales du centre de l'aire de répartition des espèces (origine biogéographique des espèces).

Ces résultats sont détaillés dans les publications suivantes présentées en annexe.

Poulard, J-C., **Blanchard, F.** 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. ICES Journal of Marine Science, 62: 1436-1443.

Blanchard, F., Vandermeirsch, F., 2005. Warming and exponential abundance increase of the subtropical fish *Capros aper* in the Bay of Biscay (1973–2002). Comptes-Rendus Biologies 328 : 505-509.

3.4.3.2. Sur le plateau continental de la Guyane

En Guyane, des modifications dans la structure du peuplement de fond ont pu être mises en évidence par comparaison des données issues de campagnes expérimentales menées en saison sèche et saison humide en 1993, 1994 à celles issues de campagnes menées avec le même protocole en 2006 et 2007 dans le cadre du programme ANR-Chaloupe (figure 9, 10).

Un indicateur de l'affinité thermique des espèces a été proposé. Il s'agit de la température de surface (SST) observée à l'échelle de l'aire de répartition. Cette donnée est en effet disponible facilement dans les bases de données internationales accessibles gratuitement via internet (telle ICOADS par exemple) et est disponible pour toutes les régions. Si cet indicateur, ou proxy, reste grossier, il ne permet pas une analyse fine espèce par espèce. En revanche, nous postulons qu'il permet une analyse à l'échelle macro-écologique, des peuplements. L'affinité thermique est alors caractérisée par un optimum, moyenne annuelle des SST sur l'aire de répartition, un minimum et un maximum, respectivement plus faible et plus forte SST en moyenne mensuelle. Le peuplement de poissons de Guyane montre ainsi deux principaux groupes en termes d’affinité thermique (figure 9a). Des espèces pour lesquelles les températures de surface moyennes annuelles observées en Guyane depuis 1980 correspondent à leur optimum, et des espèces pour lesquelles les températures observées en Guyane sont au-delà de leur optimum.

L'analyse des correspondances (figure 9b et c) montre i) que les espèces dominantes dans les années 90 et 2000 ne sont plus les mêmes, ii) que les espèces dominantes actuellement sont celles qui ont les affinités thermiques les plus chaudes, et iii) que ces dernières voient leur biomasse augmenter, tandis que les premières voient leur biomasse diminuer.

Parallèlement, la pression de pêche exercée sur le plateau guyanais a été divisée par deux entre les deux périodes temporelles analysées. Hormis la pêcherie de ligneurs, relativement sélective en terme d'espèce, et qui cible le vivaneau (lutjanidés), la seule pêcherie exerçant une pression sur le peuplement de poissons analysé est la flottille chalutière crevettière de Guyane. Celle-ci connaît en effet une situation économique défavorable (baisse de la valeur de la crevette sur le marché international et augmentation des coûts de production en raison du prix du carburant; la viabilité économique de la filière n'est maintenue qu'au prix d'une réduction de la flotte, cf. analyse en section 5.2). Ainsi, les espèces les plus sensibles à la pression de pêche (espèces de grande taille, longévives, à première reproduction tardive, à faible maturité…) ayant des affinités thermiques élevées seraient favorisées, tandis que les espèces moins sensibles à la pression de pêche et dont les affinités thermiques sont plus basses, seraient défavorisées. Les modifications du peuplement résulteraient des effets combinés d’une réduction de la mortalité par pêche et du changement des températures. Cette hypothèse reste à approfondir. Une publication est en préparation.

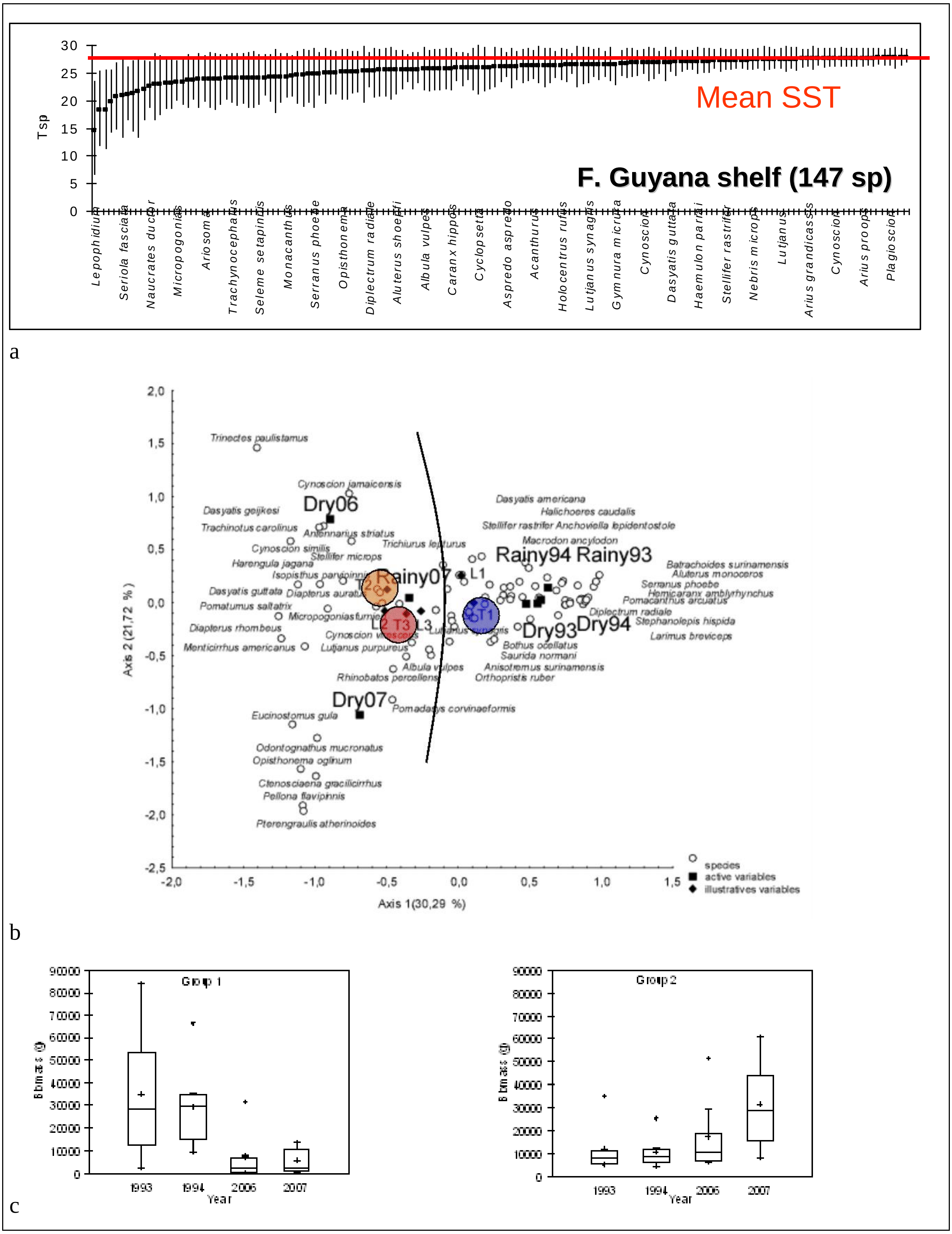


Figure 9. a. Affinité thermique des espèces échantillonnées sur le plateau Guyanais et SST moyennes. b. Projection des variables espèces dans le premier plan de l'analyse des correspondances (AC), des saisons (sèches et humides 1993-1994, 2006-2007) et des affinités thermiques des espèces (T1: élevées; T3, basses, T2, intermédiaires). c. Biomasse totale des espèces du groupe 1 (coordonnées positives sur le 1er axe) et du groupe 2 (coordonnés négatives sur le 1er axe).

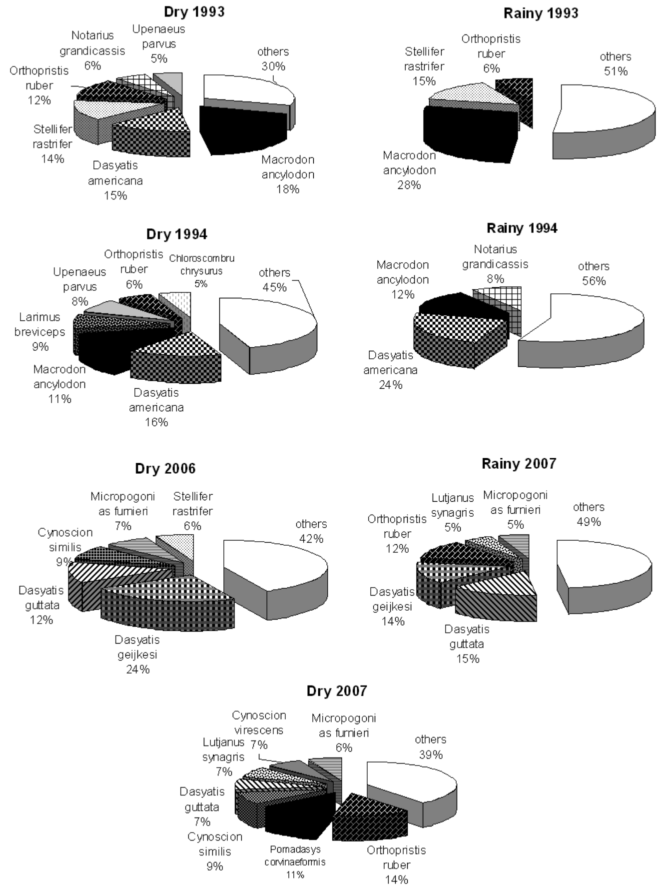


Figure 10. Composition spécifique relative (en biomasse) du peuplement de poissons de fond du plateau de Guyane échantillonné en saison sèche et humide, en 1993, 1994, 2006 et 2007.

3.5. Un modèle individu-centré pour l'analyse des impacts du réchauffement et des activités de pêche sur les peuplements de poissons.

Le modèle représente les processus de croissance individuelle, de prédation, de reproduction dépendant de la température, de survie dépendant de l'habitat (figure 11). Le modèle est paramétré à partir de données acquises lors de campagnes expérimentales et à partir des données issues du site Fishbase.org. Neuf espèces ont été représentées pour leur importance en biomasse dans les campagnes et/ou pour leur importance commerciale. La capacité du modèle à représenter les trajectoires observées à l'échelle du Golfe et d'une vingtaine d'années est testée. Ensuite, les effets des deux facteurs (pêche et réchauffement) sur des indicateurs écosystémiques sont testés (longueur moyenne des individus dans le peuplement, niveau trophique et affinité thermique).

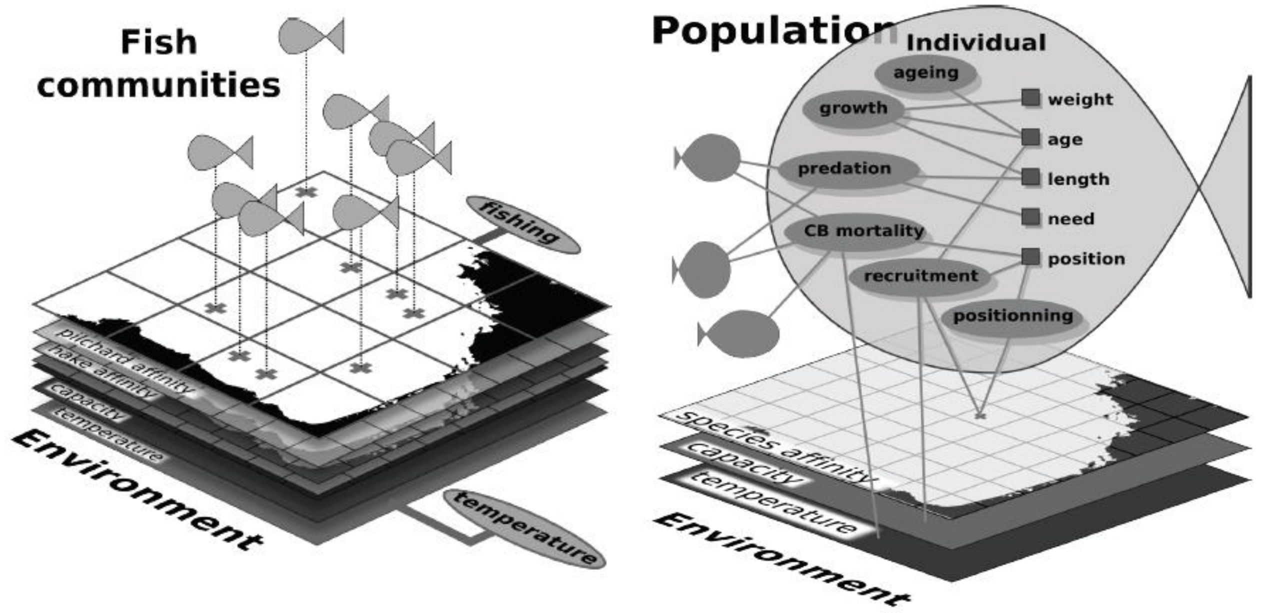
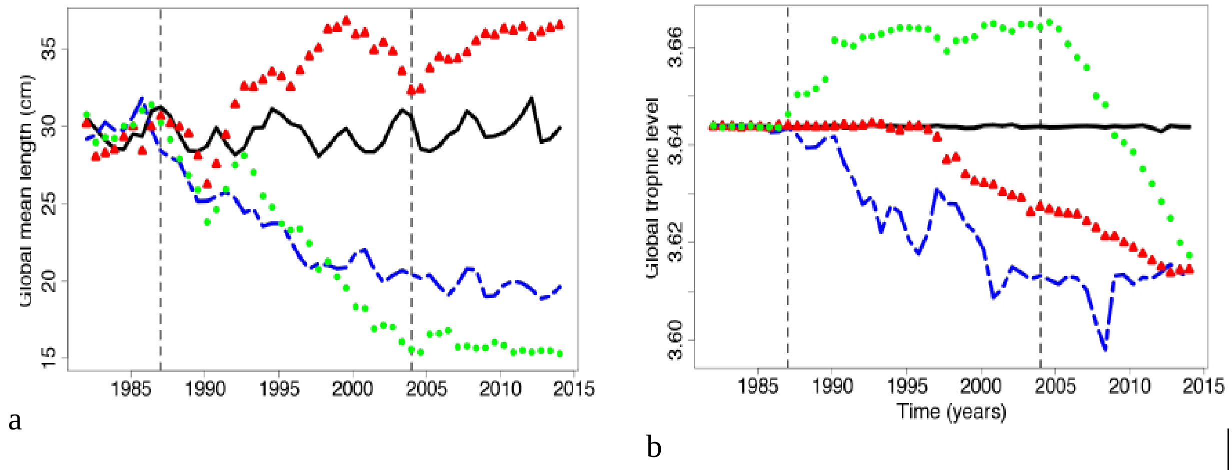


Figure 11. Représentation schématique du modèle et d’un individu modélisé. L’environnement contient des informations et des processus pouvant modifier le comportement des individus (CB pour « Capacity based »).

Quatre scénarios sont présentés ici (figure 12) : le scénario 1, sans pêche et sans réchauffement, le scénario 2 avec pêche et sans réchauffement, le scénario 3 avec réchauffement et sans pêche et le scénario 4 combinant réchauffement des eaux et exploitation par la pêche. Le réchauffement simulé est comparable à celui-observé dans le Golfe de Gascogne. Les résultats obtenus avec le scénario pêche sont conformes à ce qui est attendu (baisse des tailles et des niveaux trophiques), de même que ceux obtenus avec le scénario réchauffement en terme de latitude médiane (plus forte dominance d’espèces de basse latitude). En revanche, le scénario avec réchauffement (n°3) a aussi pour conséquence de baisser le niveau trophique, comme l’impact de la pêche. Il existe ensuite des interactions, effets synergiques ou antagonistes d’interprétation peu intuitive, qui ne seront pas détaillées ici. Il sera simplement conclu que les indicateurs retenus répondent tous deux aux deux facteurs, soit directement, soit indirectement, et qu’ils ne peuvent ainsi pas aisément être utilisés pour détecter des impacts de l’un ou l’autre facteur.



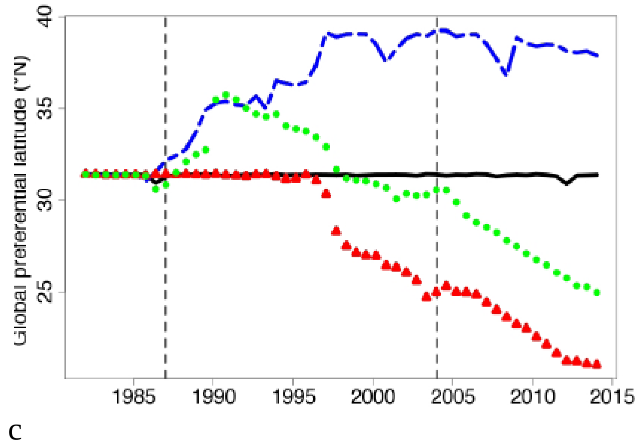


Figure 12. Variations temporelles issues des simulations par le modèle individu-centré VirtuOcean pour quatre scenarios différents. a, b : Longueur individuelle moyenne et niveau trophique dans le peuplement. c : Latitude médiane moyenne du centre de l'aire de répartition toutes espèces confondues dans le peuplement.

Scénario 1 : sans pêche et sans réchauffement (trait noir) ;
Scénario 2 : pêche sans réchauffement (pointillés bleus) ;
scénario 3, réchauffement sans pêche (triangles rouges) ;
Scénario 4, réchauffement et pêche (ronds verts).

Ces travaux sont détaillés dans le document de travail suivant présenté en annexe.

Bonneaud, S., Desmeulles, G., **Blanchard, F.**, Chevaillier, P., 2009. An individual-based model to study the impacts of global warming and fishing activities on fish communities. Working paper, projet ANR "Chaloupe". 13pp.

4. Changements dans la structure et la valeur économique des débarquements de la pêche dans le Golfe de Gascogne et en Guyane : conséquences de la sur-exploitation ou du contexte économique ?

Des modifications des peuplements de poissons ont été identifiées. Les pêcheries subissent-elles directement ces modifications, ou sont-elles capables d'une adaptation ? Les facteurs économiques liées aux marchés ou encore les régulations institutionnelles mises en place sont-ils dominant dans la dynamique des pêcheries au point de masquer les conséquences des effets de changements au sein de la ressource en terme de rendements des pêcheries ? Ces questions ont été analysées au regard des cas du Golfe de Gascogne et du plateau de la Guyane française.

Une baisse de la valeur de la production totale de l'ensemble des pêcheries du Golfe de Gascogne est mise en évidence (Steinmetz *et al.*, 2008). Une modification de la structure des débarquements est associée à cette baisse (figures 13, 14) : dans les années 70-80, les débarquements concernent particulièrement des espèces de grande taille, d'affinité boréales, de haut niveau trophique, et de forte valeur commerciale. Par les effets de la sur-exploitation induisant une baisse de la production de ces stocks de pêche, associés à des changements environnementaux (réchauffement des eaux) à la fin des années 90 et début des années 2000, l'exploitation se concentre sur des espèces de plus petite taille, d'affinité plutôt tempérée, voire subtropicale, de bas niveau trophique et de valeur commerciale moindre. De plus, la raréfaction des ressources dans les années 80 a induit une augmentation des prix moyens. Puis, suite d'une part à l'ouverture du marché européen à l'Irlande et à l'Espagne apportant des produits de la mer à moindre coût, et d'autre part, à l'arrivée sur le marché de produits d'aquaculture tel que le saumon de Norvège, les prix moyens des produits de la pêche ont fortement diminué. Ainsi, il est possible de montrer que la baisse de valeur totale est une conséquence de la baisse de la production et des prix unitaires, et des changements de la structure des peuplements au profit d'espèces à faible valeur.

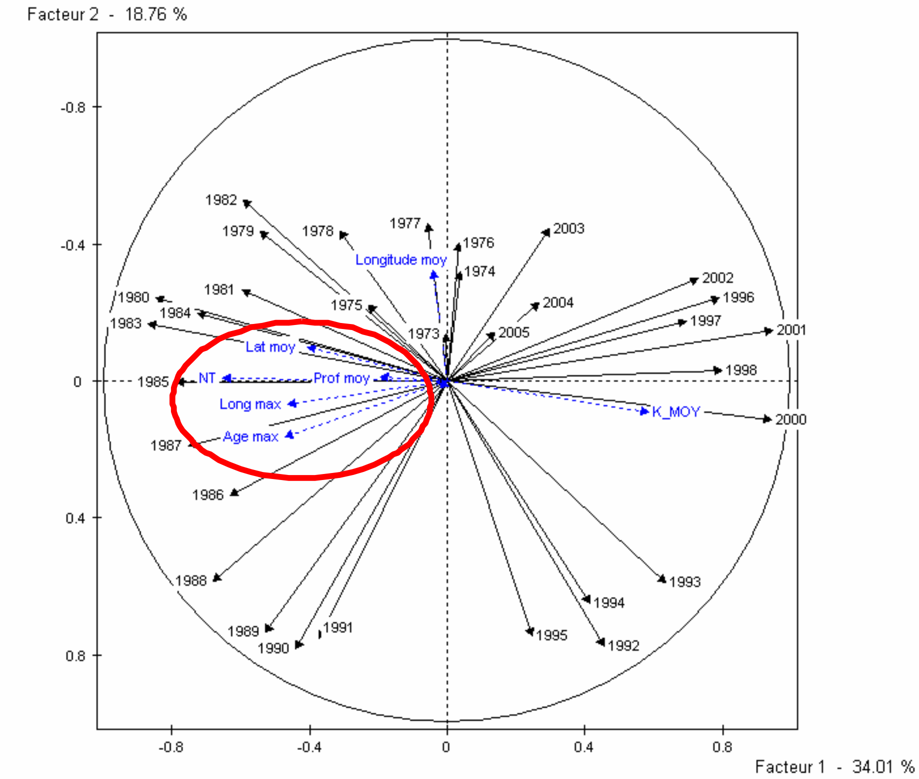


Figure 13. ACP des données débarquements des pêcheries du Golfe de Gascogne : projection dans le premier plan (53 % de la variance expliquée) des variables actives (années) et illustratives : Lat et Longitude moy, positions latitudinales et longitudinales du centre de l'aire de répartition des espèces ; prof moy, profondeur moyenne ; Long max, longueur maximale que l’espèce peut atteindre, NT, niveau trophique de l’espèce.

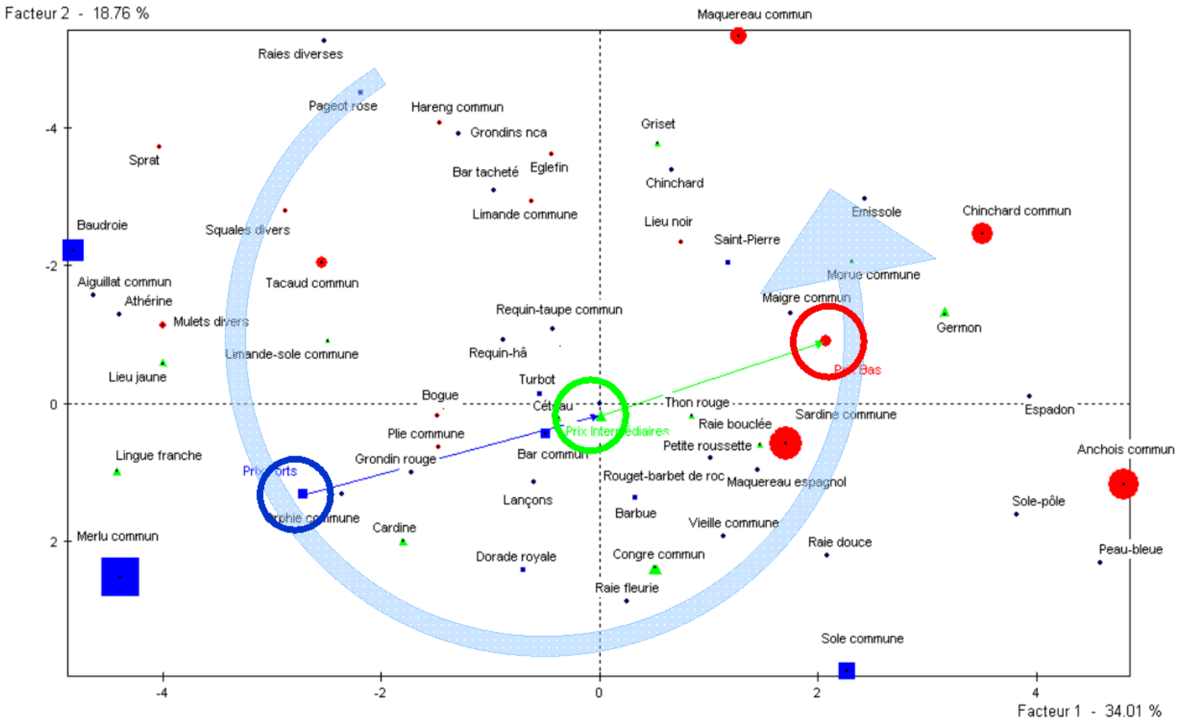


Figure 14. ACP des données débarquements des pêcheries du Golfe de Gascogne : projection dans le premier plan de l’ACP (53 % de la variance expliquée) des espèces débarquées, de la valeur moyenne des espèces (prix forts en bleu, prix intermédiaire en vert, prix bas en rouge ; euro constant 2005). La flèche circulaire indique le sens chronologique, de 1973 à 2002. La taille des symboles est proportionnelle à la contribution de l’espèce aux facteurs. Steinmetz, F., Thébaud, O., Blanchard, F., Le Floc’h, P., Bihel, J., 2008.

De même, une baisse de la valeur totale des débarquements de la pêche crevettière guyanaise est mise en évidence (Chaboud *et al.*, 2009), en raison d'une diminution de la production et de la baisse de la valeur de la crevette en Guyane liée aux changements du marché (figure 15). D'un point de vue écologique, le succès de la reproduction, ou le recrutement, montre de fréquents incidents depuis 1999 (figure 16a). Des explications sont cherchées dans les changements des facteurs environnementaux : augmentation des températures diminuant la reproduction, ou encore baisse des vents de surface induisant les courants favorables pour emmener les larves dans les zones de nurseries (figure 16b, c). D'un point de vue économique, le principal facteur est l'évolution du marché mondial de la crevette depuis le milieu des années 90. Après la francisation de la pêcherie, la plupart des captures a été exportée vers le marché intérieur français. Les crevettes guyanaises complétaient l'importation des pêcheries de Madagascar ou de l'Afrique de l'ouest. Après 1995, le marché mondial de la crevette tend à être dominé par la croissance de l'aquaculture. En 2006, l'aquaculture représente 80% des apports mondiaux en crevettes pénéidées. Ce changement a de dramatiques conséquences sur les pêcheries de crevettes tropicales qui faisaient déjà face à une stagnation des débarquements (due à la pleine exploitation de la plupart des stocks de crevette) et l'augmentation de coût du gasoil. Le prix mondial unitaire de crevette, calculé à partir des données de la FAO sur les échanges commerciaux internationaux a diminué depuis 1995. Le prix courant en 2003 (6,5 US $/ kg) est moins élevé que le prix observé en 1986 (7 US $/ kg). La production guyanaise n'est pas suffisante à l'échelle mondiale pour avoir un effet sur les prix ; elle en subit donc les variations. De plus, durant ces dernières années, l'augmentation des coûts du gasoil touche fortement les résultats économiques déjà en déclin.

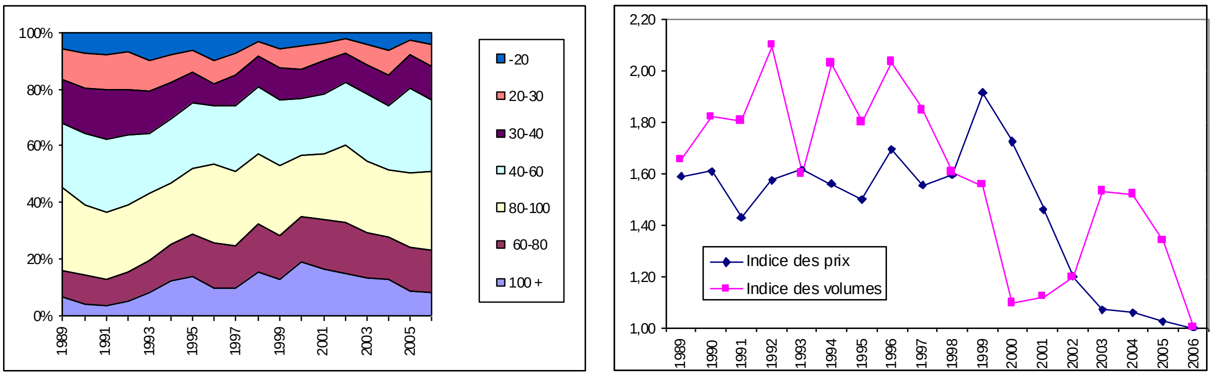
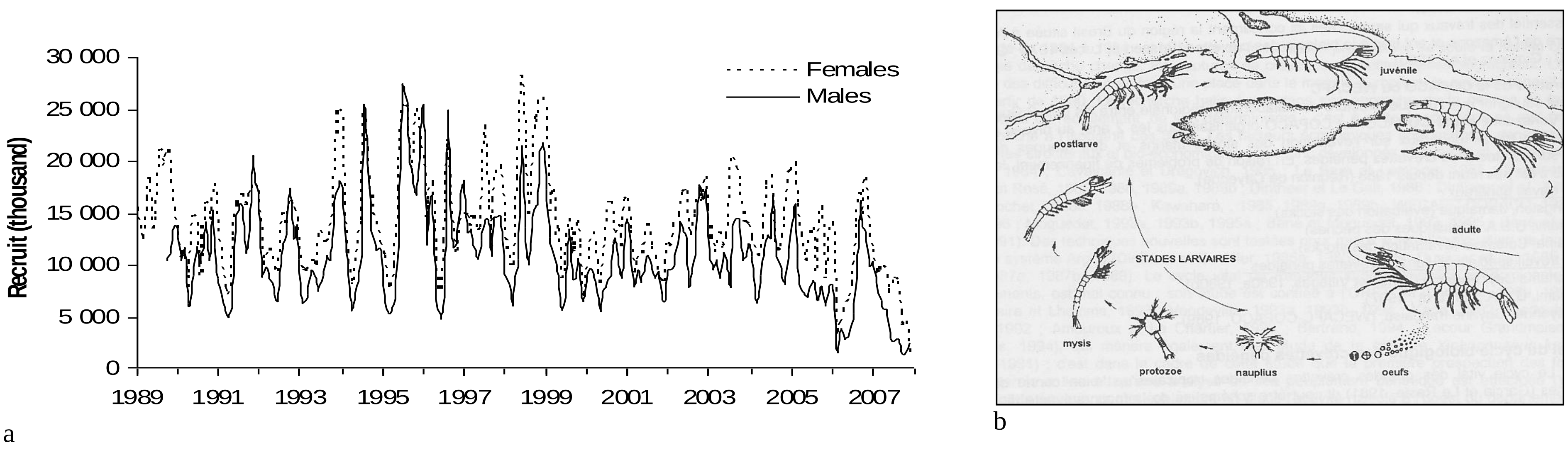


Figure 15. Variations temporelles de la composition relative de la capture des chalutiers crevettiers guyanais par catégorie commerciale (en nombre moyen de crevette/Kg), de l'indice de Fisher des quantités débarquées et des prix moyen de la production au Kg.



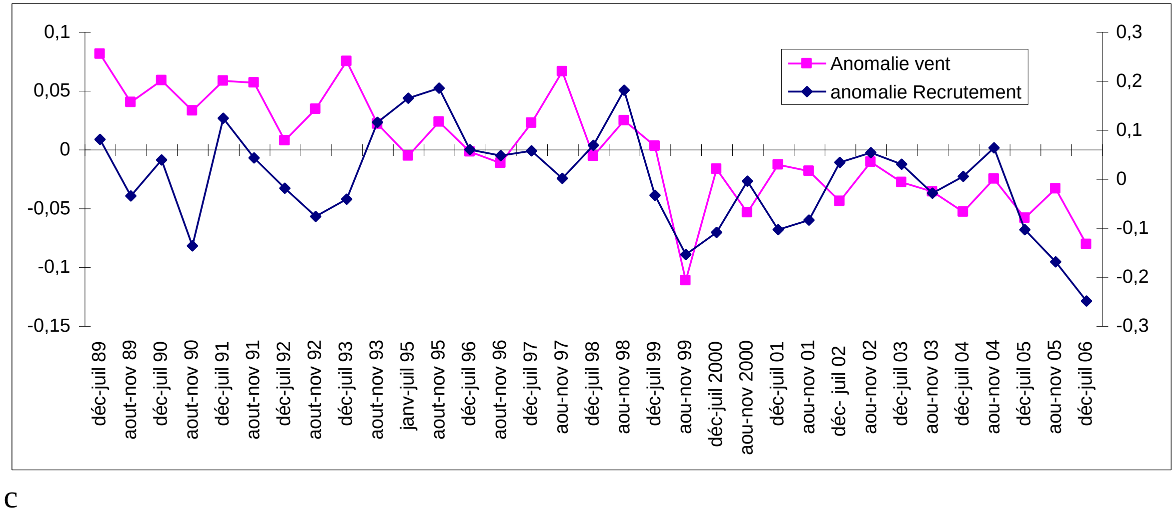


Figure 16. a. Variations temporelles du recrutement de *Farfantepeneus subtilis* obtenues par Analyse Virtuelle des Populations (VPA) sur un pas mensuel. b. Représentation des migrations au cours des écophases de la crevette (œufs pondus au large, dérive des larves vers les nurseries littorales, développement des juvéniles sur le littoral et migration des adultes vers le large). c. Variations temporelles des anomalies de recrutement cumulé sur 6 mois et des vents du nord induisant le courant e surface depuis le large vers le littoral (données tri-horaire Météo-France, station Iles du Salut).

Dans deux cas très différents de pêcheries (l'ensemble des pêcheries du Golfe vs une pêcherie chalutière en Guyane), dans des contextes environnementaux très différent (respectivement tempéré et tropical), des points communs sont mis en évidence : baisse de la production, de la valeur totale de la production, de la valeur unitaire des produits de la pêche. Ces évolutions communes ont des interprétations comparables (changements dans la disponibilité des ressources pour des raisons de surexploitation et/ou environnementales, changements dans les marchés).

Ces travaux sont détaillés dans les publications suivantes, présentées en annexe.

Thébaud, O., **Blanchard, F**., 2011. Fishing the food web - Integrated analysis of changes and drivers of change in fisheries of the Bay of Biscay. In "World Fisheries : a social-ecological analysis", first edition. Edited by Ommer, Perry, Cochrane and Cury. © 2011 Blackwell Publishing Ltd. Published 2011 by Blackwell Publishing Lltd. Chapter 5, pp. 90-104.

Steinmetz, F., Thébaud, O., **Blanchard, F**., Le Floc'h, P., Bihel, J., 2008. A bio-economic analysis of long term changes in the fisheries production of the Bay of Biscay. Aquatic Living resources, 21 : 317-327.

Le Floc'h, P., Poulard, J.C , Thébaud, O., **Blanchard, F**., Bihel, J., Steinmetz, F., 2008. Analyzing the market position of fish species subject to the impacts of long-term changes in marine fish communities: an application to the French fisheries of the Bay of Biscay. Aquatic Living resources, 21: 307-316.

5. Modélisation intégrée : scénarios de viabilité écologique et économique

5.1. Introduction

Dans un objectif *in fine* de gestion halieutique, le niveau de complexité des modèles qui ont été développés depuis le début du XXème siècle s'est accru (figure 17). Cette complexité croissante a été rendue possible par la meilleure compréhension écologique des systèmes, permettant de formaliser et paramétrer les processus, et par des moyens informatiques plus performants. Dans le cadre de l'action de recherche ANR-Chaloupe que j'ai coordonnée, douzes modèles de niveau de complexité variée on été développés et/ou appliqués aux cas d'étude avec pour objectif d'analyser par des cas d'application, leur niveau d'opérationnalité en terme de gestion écosystémique des ressources ou de recherche plus exploratoire (figure 18).

Trois modèles bio-économiques appliqués à la Guyane, auxquels j'ai contribué sont présentés ici de manière synthétique ;

i) un modèle de la pêcherie crevettière a été implanté pour tester des scénarios d'évolution environnementale, économique et réglementaire ;

ii) un modèle couplant la pêcherie crevettière et son impact sur la population de frégates a été développé pour analyser les conséquences du déclin de cette pêcherie pour la gestion d'une réserve naturelle accueillant ces oiseaux ;

iii) un modèle de la pêcherie côtière artisanale intégrant les treize principales espèces et leurs interrelations trophiques, ainsi que les quatre flottilles qui les exploitent, a été développé pour tester la viabilité écologique et économique de scénarios d'évolution de la pêcherie qui sera confrontée à une demande accrue (en raison d'une croissance démographique forte).

Les publications correspondantes et qui suivent offrent une description plus détaillée des modèles.

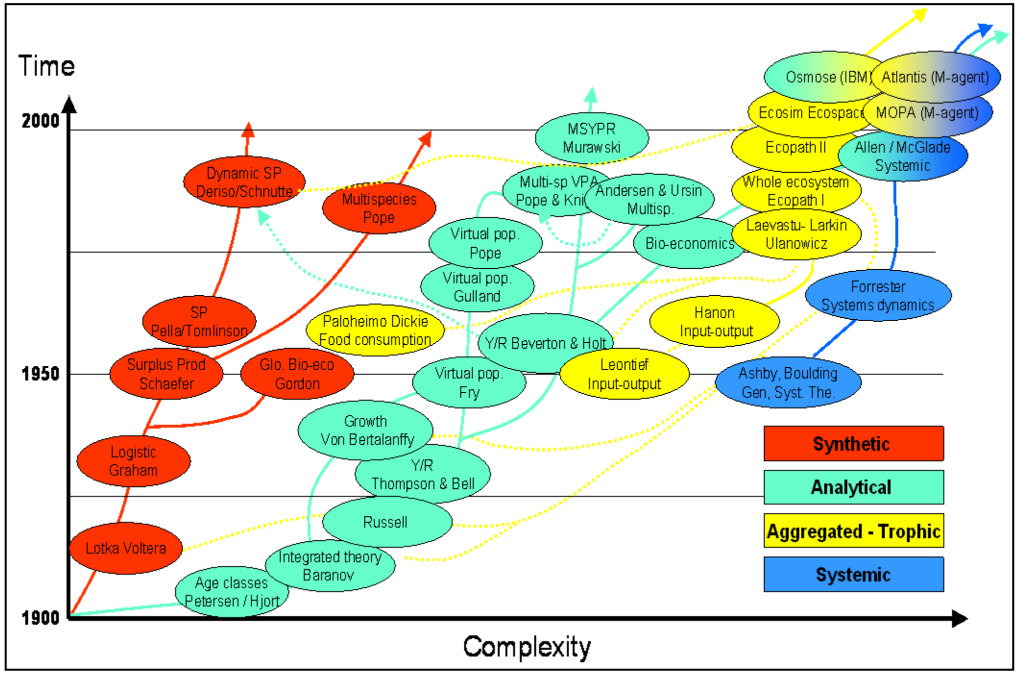


Figure 17. Synthèse de l'évolution temporelle de la modélisation en regard de la complexité, selon Garcia et Charles, présenté à ICES International Symposium on Fisheries Management Strategies, Galway, Ireland, 27-30 June 2006. Garcia, S., Charles, A.T., 2008. Fishery systems and linkages: Implications for science and governance. Ocean and Coastal Management, 51: 505-527.

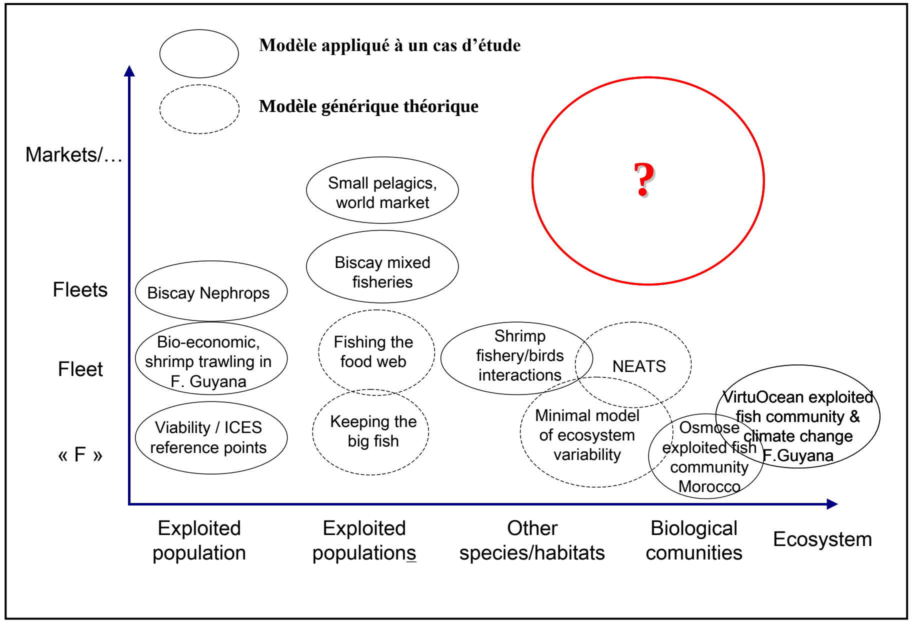


Figure 18. Typologie des modèles développés dans le cadre de l'action ANR « Chaloupe » en regard de la complexité des processus représentés, sur une dimension bio-écologique en abscisse et économique en ordonnée. Le point d'interrogation montre que la modélisation des systèmes complexes intégrant l'écologie à l'échelle des peuplements et l'économie n'a pas pu être mis en œuvre. Blanchard et Thébaud, 2009, présenté au séminaire Franco-Australien de bio-économie, Brest, France, septembre 2009. En préparation pour publication.

5.2. Modélisation bio-économique, outil d'intégration pour évaluer la dynamique des pêcheries face aux changements économiques et environnementaux : le cas de la pêcherie crevettière en Guyane.

Plusieurs analyses de données sur les captures et effort de pêche ont été menées pour alimenter le modèle en données et paramètres. Quelques études spécifiques ont été nécessaires pour obtenir les paramètres de coût et de prix pour l'année 2006. Le modèle est composé de différents modules associés. Toutes les variables monétaires sont exprimées en termes constants (€ année 2006), utilisant l'index des prix guyanais comme déflation pour les années passées. Tout d'abord, le modèle prévoit de représenter les dynamiques des pêcheries pendant la période de 1994 à 2006. Des projections peuvent être faîtes pour une période de 10 ans suivant la période précédente, basées sur des hypothèses concernant l'évolution temporelle des paramètres biologiques et économiques. Le pas de temps du modèle est un jour. Le module ressource a utilisé un modèle de structure en âge, avec des cohortes mensuelles de mâles et de femelles. Deux types de stratégie de pêche ont été distinguées : la pêche côtière (de 30 à 50 m de fond) et au large (plus de 50 m de fond). Les stratégies sont caractérisées par différentes capacités de captures des espèces cibles. Un calcul des captures est fait pour chaque cohorte par espèce et par sexe, et le total des captures instantanées est obtenu par une somme parmi les différentes cohortes.

La qualité du modèle est évaluée par sa capacité à reproduire les dynamiques antérieures de la pêcherie pendant la période de 1994-2006. Au travers de cette période, le modèle donne d'assez bons résultats sur le total des captures en crevette et sur la biomasse du stock (figure 19). D'un point de vue économique, les deux principales crises (2000-2001) et 2006 sont aussi recréées par la simulation. Des scénarios peuvent alors être testés.

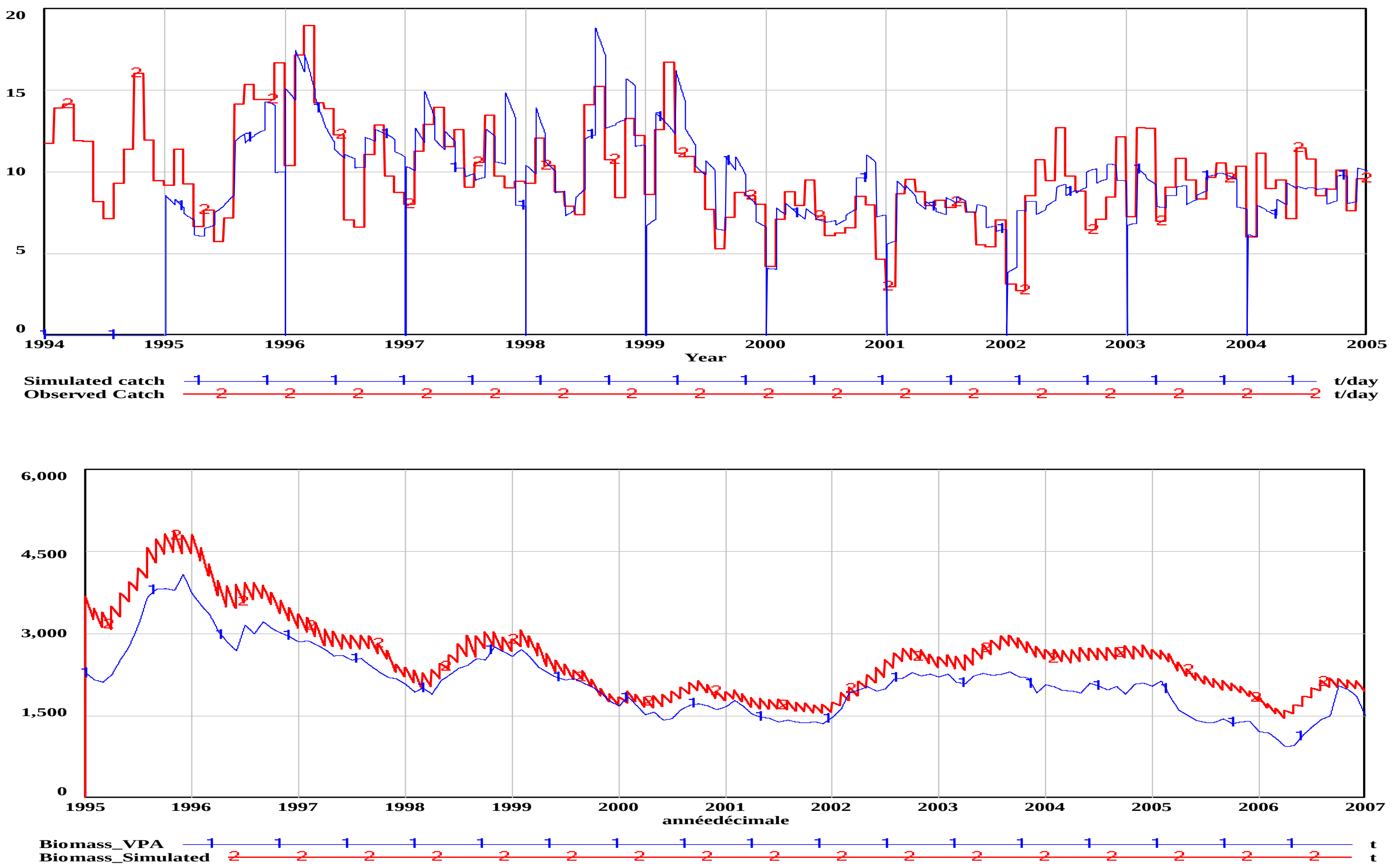


Figure 19. Résultats des simulations réalisées avec le modèle bio-économique de la pêcherie crevettière de Guyane comparés aux observations. a. Variations temporelles des captures totales observées (en rouge) et simulées à partir du modèle (en bleu), en tonnes par jour. b. Variations temporelles de la biomasse totale du stock calculée par VPA (en bleu) et simulée par le modèle (en rouge), en tonnes.

La pêcherie a connu simultanément des changements écologiques et économiques : principalement baisse du recrutement, augmentation des coûts de carburant et baisse du prix de vente de la crevette. Seuls les résultats de deux scénarios de gestion combinant changements écologiques et économiques sont montrés ici. D'une part, une diminution de 50% de la subvention Poseidom[1] actuelle est simulée, et d'autre part une modification de la subvention pour inciter à moins pêcher les petites crevettes. Pour le prix du gasoil, nous avons utilisé un taux d'augmentation de 15% par an. Ces scénarios économiques sont complétés par un scénario de recrutement de crevettes basé sur les données de la période 2004-2007, c'est-à-dire de très mauvais recrutements. La prise en compte simultanée des deux types de changement mène à une réduction de la flotte de 18 à 10 bateaux en 2016 (figure 20). Le comportement autorégulant permet un renouvellement très important de la ressource, en dépit d'un « régime » de mauvais recrutement utilisé dans cette simulation. Ce résultat souligne le risque de non viabilité économique pour la pêcherie, si les tendances actuelles des prix de la crevette et du gasoil ne se stabilisent ou ne s'inversent pas.

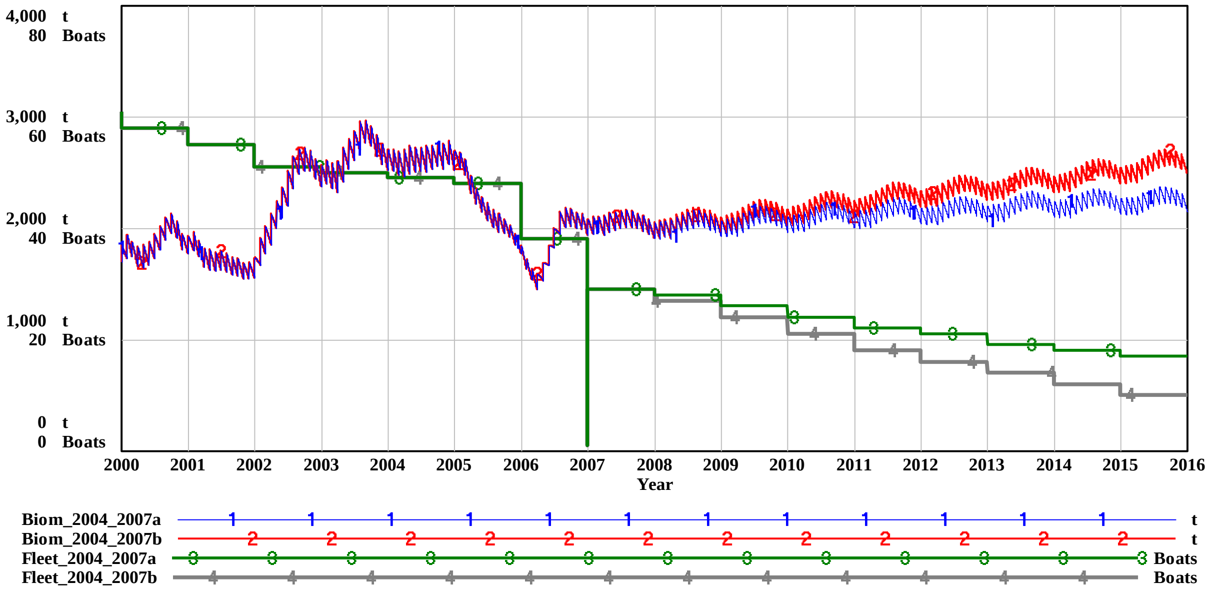


Figure 20. Impacts de changements économiques et environnementaux sur la biomasse du stock de crevettes et sur la flottille crevettière de Guyane tels que simulés à partir du modèle selon deux scénarios : augmentation du prix du gasoil et baisse de la subvention Poseidom (courbes 1 et 3), augmentation du prix du gasoil et prime plus forte pour les gros calibres (courbes 2 et 4).

Ces travaux sont détaillés dans la publication suivante présentée en annexe.

Chaboud, C., Vendeville, P., Viera, A., **Blanchard, F.**, 2009. Global economic and environmental changes and fisheries viability: the case of the French Guyana shrimp fishery.

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[1] Le POSEIDOM est un programme européen de prime à la production à l'exportation pour compenser les surcoûts liés à l'éloignement des territoires. Les rendements seraient plus forts si l'on cible les crevettes de petit calibre, que l'on trouve moins au large, permettant d'obtenir plus de subventions.

5.3. Externalités d’une pêcherie en termes de biodiversité : le cas de la pêcherie crevettière de Guyane et de son impact sur les oiseaux marins

La gestion durable des ressources naturelles, et notamment la pêche, doit tenir compte de plusieurs objectifs contradictoires. C'est le cas de la pêcherie de crevettes Guyane française dont un objectif de rentabilité impliquer une réduction de l'activité de pêche. D'une part, cette pêche a des externalités négatives sur la biodiversité des écosystèmes marins en raison de rejets, et d'autre part, cette pêche a des externalités positives sur l'économie de la communauté locale et aussi sur une espèce d'oiseaux protégées dans la région (la Frégate superbe, *Fregata magnificens*) qui se nourrit des rejets). Dans l’article ci-après (Martinet and Blanchard, 2009), nous examinons la viabilité de ce système considérant deux objectifs : un objectif économique en termes de rentabilité de l'activité de pêche, et un objectif de conservation en termes de population de Frégate. Dans ce but, nous avons développé un modèle dynamique de ce système bio-économique permettant ici l'étude des compromis entre les deux objectifs contradictoires. Ce travail confirme la pertinence de l'approche « viabilité » pour la gestion des ressources naturelles, qui devrait conduire à la mise au point de nouveaux outils pour l'arbitrage des objectifs de durabilité contradictoires. En particulier, de tels outils peuvent être utilisés comme base quantitative pour les analyses de type coûts-avantages prenant en compte les externalités environnementales.

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Analysis

Fishery externalities and biodiversity: Trade-offs between the viability of shrimp trawling and the conservation of Frigatebirds in French Guiana

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ABSTRACT

Sustainable management of natural resources, and in particular fisheries, must take into account several conflicting objectives. This is the case in the French Guiana shrimp fishery for which profitability objectives imply a reduction in the fishing activity. On the one hand, this fishery has negative externalities on marine biodiversity due to discards. On the other hand, this fishery has positive externalities on the economy of the local community and interestingly enough on a protected seabird species in the area (the Frigatebird that feeds on discards). In this paper, we examine the viability of that system considering two sustainability objectives: an economic objective in terms of the profitability of the fishing activity, and a conservation objective in terms of the Frigatebird population. For that purpose, we have developed a dynamic model of that bioeconomic system and study here the trade-offs between the two conflicting objectives. It provides a means to quantify the necessary give and takes involving the economic and ecological objectives that would ensure a viable management solution. Our study confirms the relevance of the viability approach to address natural resource management issues, which should lead to the development of new tools for the arbitration of conflicting sustainability objectives. In particular, such tools could be used as a quantitative basis for cost–benefit analysis taking into account environmental externalities.

1. Introduction

Fishery activities generate externalities on biodiversity. On the one hand, there are numerous negative externalities linked to fishery discards in terms of bycatch species and loss of marine biodiversity. Indeed, eliminating discards is currently a major political objective (CEC, 2007). On the other hand, one potential positive externality of these discards is that they may play a fundamental role in marine bird feeding (Furness, 2003). According to Furness (1999), reducing fishery discards may dramatically reduce some seabird populations. This is also the case when discards are reduced due to an adjustment of fishing activities related to the economic context. For example, the prior level of fishing activity of the French Guiana shrimp fishery is no longer economically viable given the present prices, costs, and amount of subsidies. The recent reduction in that fishing activity has resulted in a high rate of Frigatebird chick mortality and has triggered a conflict between the ecological objective of the Frigatebird conservation program off the Caribbean coast of French Guiana and the economic objective of the fishery. Managing fishery activities in a sustainable way must thus take into account conflicting objectives that would ensure economic viability while preserving marine and bird biodiversity.

In ecological economics, it is now recognized that multicriteria modeling, and especially the viability approach (Aubin, 1991), are well-suited to address sustainability issues (De Lara and Doyen, 2008). The aim of the viability approach is to study the consistency between a dynamic model and a set of constraints. It involves defining the conditions such that the constraints are satisfied at all times. In particular, thanks to the viability approach, it is possible to characterize the dynamics of a bio-economic system in terms of its capacity to achieve, in the long-run, sustainability objectives represented by ecological and economic constraints. Béné et al. (2001), Doyen and Béné (2003) and Eisenack et al. (2006) have used the viability approach to investigate natural resource management issues. Cury et al. (2005) have argued that the application of the viability approach is relevant for an ecosystem management of fisheries. Indeed, the viability of fisheries has recently been studied by Doyen et al. (2007), Martinet et al. (2007) and Chapel et al. (2008), among others. In particular, Béné and Doyen (2000) study the viability of the French Guianese shrimp fishery in terms of economic issues alone, without accounting for environmental externalities.

Viability studies usually account for constraints with given levels. It may result in problems with no viable solutions. Martinet and Doyen (2007, appendix A.1.5) introduced the idea that relaxing some constraints would be one way to overcome from such non-viable solutions. It may also be necessary to conciliate ecological and economic requirements for particular ecological economic states to

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be viable. In this study, we follow this lead to investigate a way to account for potential interactions between constraint levels, using the French Guiana case-study. It is a means to provide much needed information about trade-offs between sustainability objectives. In the example of the shrimp fishery and Frigatebirds, it allows us to describe the trade-offs between ensuring the viability of the shrimp trawling and maintaining the bird population which feeds on fishery discards.

To this end, we have developed a dynamic bioeconomic model of a fishery that generates discards which are a source of food for a bird population. We account for two sustainability objectives (represented by constraints): an economic constraint on the profitability of the fishing activity and a conservation constraint of the bird population. We examine how these sustainability objectives are compatible one with respect to the other, and if there are trade-offs between both viability constraint levels. In other words, we are dealing with how to cope with two seemingly different objectives at the same time, and more specifically with the give and take in the level of constraints that must be worked out to be able to reach these objectives.

The paper is organized as follows. In Section 2, we present a model based on the Guianese shrimp fishery. In Section 3, we address the co-viability issue of achieving at the same time economic and ecological objectives in a dynamic way. In Section 4, we extend this viability analysis by describing the trade-offs between economic and biological objectives. We also define the economic conditions that are necessary (including the minimum amount of subsidies) if the Guianese fishing activity is to be viable while maintaining a targeted Frigatebird population level. In Section 5, we discuss how this approach fits into the literature on biodiversity conservation. In Section 6, we conclude on the potential use of the viability approach as a tool that provides a well-grounded basis for arbitration between conflicting sustainability objectives. Parameter values and mathematical proof are provided in the appendix.

2. Model of a fishery interacting with a seabird population

2.1. The French Guiana case study

The shrimp fishery in French Guiana is composed of trawlers fishing for shrimp on the continental shelf. Two main species are involved: *Farfantepeneus subtilis* and *F. brasiliensis*. Only *F. subtilis* was accounted for. It is the species caught the most often and, since the eighties, it has been thoroughly investigated by Ifremer (the French institute of research for the exploitation of the sea) providing solid knowledge of the population and exploitation dynamics. From a historical point of view, the economic dynamics of the fishery have been characterized by a decrease in the fishing activity for profitability purposes. In turn, the amount of catch has dramatically decreased, and actually it is about half the Maximum Sustainable Yield (MSY). This decrease in fishing activity has meant a decrease in discard.

The Frigatebird *Fregata magnificens* population in French Guiana is the most important colony of this seabird species from northern Brazil to Venezuela. The colony is located in a natural reserve on "Le Grand Connetable", a small island which makes survey easy. They are exceptional birds, because of their low reproduction rate, their long period of parental care (the longest of any bird), and their long life spent (more than 30 years) (Weimerskirch at al., 2003). Before the development of the shrimp fishery (and associated discards), the Frigatebird population was stable, with about 180 nesting couples managing to raise their chick. Since it is not possible here to represent the Frigatebird population in a dynamic way in our case (sufficient long-run data is not yet available to assess the dynamics), the number of breeding bird couples serves as a proxy for the Frigatebird population.

Calixto-Albarran and Osorno (2000) have found a correlation between the variety of fish in the diet of Frigatebird population on Isla Isabel (off the Pacific coast of Mexico) and species discarded by prawn-fishing trawlers in the area, thereby assuming an opportunistic feeding during nesting period. Based on personal field observation that found 120 Frigatebirds feeding on the discard of a sole shrimp trawler, the same correlation is assumed to hold for the Guianese population. A strong correlation has been also observed between chick mortality during breeding and periods of reduced fishing activity (and associated decreasing discards) within the area of bird foraging (unpublished data). Until recently, the decrease in discard had no impact on the Frigatebird population, but the ongoing decline of the fishery and the associated observed mortality of chicks now jeopardize the conservation program. In the 2007 economic context, some of the 639 surveyed couples were not able to feed their chick. Understanding the interactions between economic dynamics and the conservation objectives is therefore necessary. For that purpose, we have developed a bioeconomic model of the fishery.

2.2. The bioeconomic model

We consider a single stock fishery, characterized every year t by the biomass B_t of the resource stock (shrimp in our case study). The dynamics of the bio-economic system is controlled by the fishing effort E_t, following Clark (1985). The global harvest is defined by $H_t = qB_tE_t$, where the constant parameter q represents the catchability of the resource. Using a discrete time version of the "logistic model" to represent the growth function of the shrimp stock, the dynamics of the resource stock is given by

$$B_{t+1} = B_t + R(B_t) - H_t = B_t + rB_t\left(1 - \frac{B_t}{B_{\text{sup}}}\right) - qB_tE_t \qquad (1)$$

where B_{sup} is the carrying capacity of the ecosystem, and r the natural growth rate of the resource stock ($r<1$).

The fishery is characterized by profit given as

$$\pi_t = (p + \tau)H_t - cE_t = (p + \tau)qB_tE_t - cE_t \qquad (2)$$

where p is an exogenous resource price, τ is a production subsidy and c is the per effort unit cost.

This fishery generates discards of bycatch species. These discards depend on the fishing effort E_t. A part of these discards is used by seabirds to feed themselves and to feed newborns during the breeding season (Frigatebirds in our case study). We define the quantity of discards available for birds as $D_t = dE_t$, where d is a discard constant, i.e., the quantity of discarded biomass that birds can eat per unit of fishing effort. An important point is that the discards are made up of bycatch species (fish, squid, starfish, crabs, jellyfish), hence not proportional to the catches of the targeted species (to the shrimp biomass) but to the fishing effort (the overall number of trawler's haul).

We are interested in the number of Frigatebird couples that make a nest and find enough food to raise the chick until it can leave the nest.[1] We assume the following relationship between discards and Frigatebird nests

$$F_t = sD_t + F_0 \qquad (3)$$

where F_0 is the number of Frigatebird couples that raised a chick successfully before fishing began in the area and there was no discard. s is a constant parameter describing the effect of the new food source provided by discards.

2.3. The viability constraints

In the present analysis, we will focus on two viability constraints.

On the one hand, the economic viability of the shrimp fishery depends on its profit that has to be positive, i.e., $\pi_t \geq 0$.

---

[1] Using breeding units as a proxy for the population size is usual when the ecological dynamics is unknown. See, for example, Montgomery et al. (1999).

Defining the catch per unit of effort $h_t = H_t/E_t$ (for $E_t > 0$), and using the profit definition (Eq. (2)), leads to the following

$$\pi_t \geq 0 \;\Rightarrow\; h_t \geq \frac{c}{p+\tau}$$

The catch per unit of effort $h_t = qB_t$ must therefore be greater than a threshold $h_{\min} = \frac{c}{p+\tau}$ for the fishing activity to be profitable. This threshold depends on the economic context (resource price, subsidies level, and cost structure).The viability constraint representing that economic objective is thus defined as

$$h_t \geq h_{\min}. \tag{4}$$

On the other hand, an ecological objective is to protect the Frigatebird population. For that purpose, a minimum number of couples able to feed chicks is targeted. The viability constraint representing this ecological objective is thus defined as

$$F_t \geq F_{\min}. \tag{5}$$

We aim at defining bioeconomic configurations that make it possible to satisfy both the constraints in a dynamic way.

3. Co-viability analysis

3.1. The viability framework of analysis

To develop our analysis, we have adopted the viability approach. The purpose of our analysis is to determine if there are inter-temporal viable exploitation decisions $E(.)$ that make it possible to satisfy both the economic objective (Eq. (4))and the conservation objective (Eq. (5)), at all times $t \geq t_0$, given the dynamics of the fishery (Eq. (1)).

The approach is based on the definition of states B and controls E, satisfying dynamics (1) resulting in trajectories that respect constraints (4) and (5). We define the set of states B from which there exist inter-temporal decisions resulting in viable trajectories. Formally, this set, called the viability kernel of the problem, is defined by

$$Viab(h_{\min}, F_{\min}) = \left\{ B_0 \;\middle|\; \begin{array}{l} \exists E(.) \text{ and } B(.) \text{ starting from } B_0 \\ \text{satisfying dynamics (1)} \\ \text{and constraints (4) and (5) } \forall t \geq t_0. \end{array} \right\} \tag{6}$$

The viability kernel of our problem is determined in subsection 3.2. From any state inside the viability kernel, there exists at least one viable decision driving the dynamic system on a viable trajectory, i.e., a trajectory that respects the constraints at all times. On the contrary, if the state is outside the viability kernel, or if the trajectory leaves it, there are no decisions making it possible to respect the constraints forever, and at least one of the constraints will be violated within a finite time. It means that if state B is not in the viability kernel, the viability objectives cannot be achieved intertemporally. As a consequence, if the viability kernel is empty, there are no bioeconomic states of the fishery that allows the satisfaction of both economic and ecological constraints in the long run.[2] It means that the sustainability objectives are too ambitious and could never be achieved in the long run, whatever the initial condition of the system. To avoid such an unviable situation, one can relax one of the constraints (Martinet and Doyen, 2007). We will use that approach in Section 4.

3.2. The viability kernel

We provide here the viability kernel of our problem. The proof and mathematical details are in Appendix A.

The expression of the viability kernel depends on the condition

$$F_{\min} \leq \frac{rsd}{q}\left(1 - \frac{h_{\min}}{qB_{\sup}}\right) + F_0 \tag{7}$$

An interpretation of this condition is given in the following subsection presenting a sensitivity analysis.

If ($h_{\min}$, $F_{\min}$) satisfy condition (7), the viability kernel is the set

$$Viab(h_{\min}, F_{\min}) = [\underline{B}\,(h_{\min}), B_{\sup}] \tag{8}$$

where

$$\underline{B}\,(h_{\min}) = \frac{h_{\min}}{q}. \tag{9}$$

The associated viable decisions E^{viab} must satisfy conditions $\underline{E}\,(F_{\min}) \leq E^{\mathrm{viab}} \leq \overline{E}\,(B, h_{\min})$, where

$$\underline{E}\,(F_{\min}) = \frac{F_{\min} - F_0}{sd} \tag{10}$$

and

$$\overline{E}\,(B, h_{\min}) = \frac{1}{q}\left(1 + r\left(1 - \frac{B}{B_{\sup}}\right) - \frac{h_{\min}}{q}\frac{1}{B}\right) \tag{11}$$

If ($h_{\min}$, $F_{\min}$) do not satisfy condition (7), the viability kernel is empty (Viab($h_{\min}$, $F_{\min}$) = ∅).

When it is not the empty set, the viability kernel is as represented on Fig. 1.

3.3. Sensitivity analysis

When the viability kernel is not empty (i.e., if condition (7) holds), it expression depends on the constraint threshold $h_{\min}$ (see Eq. (8)).

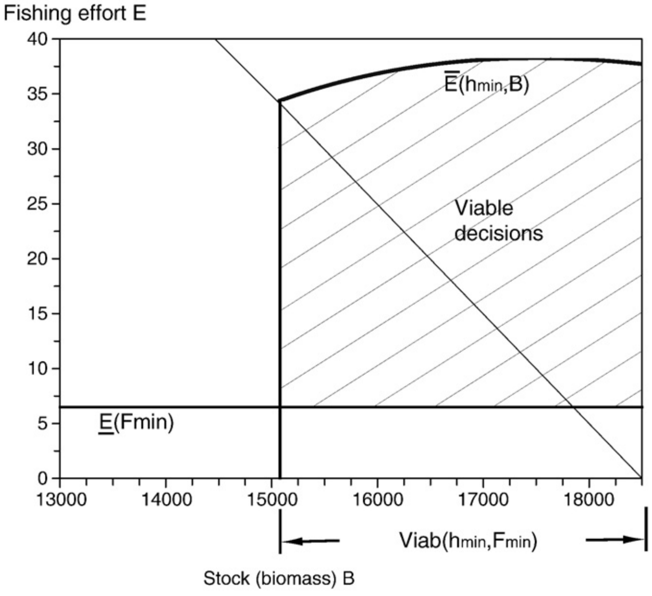

Fig. 1. Viability kernel (stock biomass) associated with economic constraint $h_{\min}$ and conservation objective $F_{\min}$, and associated viable decisions (fishing effort). The straight oblique line represents the stationary state effort-biomass relationship.

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[2] From a mathematical point of view, the viability kernel is a weakly invariant set. It is the biggest set of states such that from any of those states there are admissible decisions resulting in dynamics that both satisfy the viability constraints and remain within the set. This means that from any viable state, at least one dynamic path remains within the viability kernel. Viable decisions are thus defined such that the viability constraints are satisfied and the state of the system stays within the viability kernel.

Moreover, viable decisions depend on both $h_{\min}$ and $F_{\min}$ (see Eqs. (10) and (11)).

In our viability problem, the economic constraint (4) corresponds to a viability condition depending on the economic context. This context may change (if prices, subsidies, or costs change), resulting in a change in the viability kernel. In a similar way, the ecological constraint (5) is an ecological objective that may be adjusted. We provide here a sensitivity analysis of the results with respect to the levels of the constraints.

From Eq. (9), one can see that $\underline{B}(h_{\min})$ increases with $h_{\min}$, which means that the higher the economic constraint (the worse the economic context), the higher the induced stock constraint, and then the smaller the viability kernel.

Fig. 2 represents this result. We consider two economic contexts, $h_{\min}1$ and $h_{\min}2$, with $h_{\min}2>h_{\min}1$ meaning that the economic context is more favorable to the fishery in case 1 (higher price and/or subsidy, and/or lower costs); and two ecological objectives $F_{\min}1$ and $F_{\min}2$, with $F_{\min}2>F_{\min}1$, meaning that one wants to maintain a higher Frigatebird population in situation 2.

In Fig. 2, the higher the economic constraint level, the smaller the viability kernel. Moreover, as the threshold $\underline{E}(F_{\min})$ linearly increases with respect to the constraint level, the viable decisions are reduced when the ecological objective increases.

If the conservation objective is too high, it is not possible to reach the ecological objective for the given economic constraint; the viability kernel is empty (no state makes it possible to satisfy both the constraints over time). From dynamical perspective, if the economic context is degraded (i.e., if $h_{\min}$ increases) the maximum viable effort $\overline{E}(\underline{B})$ decreases, inducing a lower potential conservation of the bird population. There is thus a trade-off between economic viability and ecological conservation. In the next section, we study that point in more detail.

As regards condition (7), we can say that the conservation objective must be lower than a threshold depending on the economic context. The higher $h_{\min}$ is, the lower $F_{\min}$ must be for the viability kernel not to be empty. As we shall see, this condition will play a crucial role in the trade-offs between sustainability objectives.

4. Trade-off between sustainability objectives

In this section, we discuss the consequences of the economic viability of the fishery on the conservation objective of the Frigatebird population. We first provide an analysis describing trade-offs between the economic objective and the biodiversity conservation objective. We then define the economic incentive that would make it possible to reach a given conservation objective, when it is not possible in the initial economic context, and the associated cost.

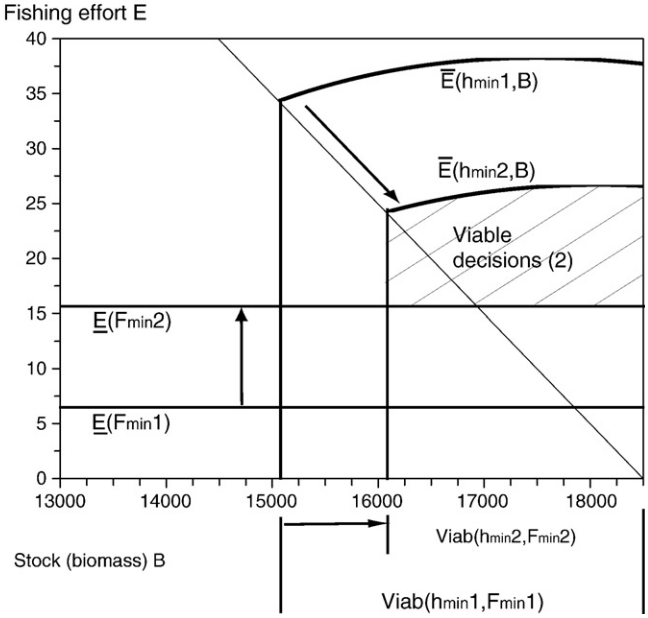

Fig. 2. Sensitivity of the viability kernel Viab($h_{\min}$,$F_{\min}$) to the constraints levels. $h_{\min}2>h_{\min}1$ and $F_{\min}2>F_{\min}1$. The higher the constraints, the smaller the kernel and the more restricted the associated viable decisions.

4.1. Set of reachable objectives

In a given economic context (i.e., for $h_{\min}$ corresponding to given prices, costs and subsidy levels), it would be interesting to know how large a Frigatebird population can be in the long run. To obtain this information, we compute the maximum conservation objective for which the viability kernel is not empty. We define the maximum reachable conservation objective with respect to $h_{\min}$ as follows:

$$\mathcal{F}(h_{\min}) = \max\{F_{\min} \,|\, Viab(h_{\min}, F_{\min}) \neq \emptyset\} \tag{12}$$

The non-emptiness of the viability kernel depends on relationship (7). The maximum level $F_{\min}$ that satisfies this condition is

$$\mathcal{F}(h_{\min}) = \frac{rsd}{q}\left(1 - \frac{h_{\min}}{qB_{\text{sup}}}\right) + F_0 \tag{13}$$

According to our calculation, given the 2007 economic context, the maximum number of Frigatebird couples expected to successfully breed is (around) $\mathcal{F}(h_{\min})=478$ couples, meaning that some of the 639 Frigatebird couples surveyed in 2007 would lose their chick during the nesting period.

We have exhibited a trade-off between the economic constraint $h_{\min}$ and the ecological constraint $F_{\min}$. Achievable conservation objectives must satisfy $F_{\min} \leq \mathcal{F}(h_{\min})$. To increase the level of one of the constraints above the threshold given by compatibility relationship (13), it is necessary to reduce the level of the other.

To provide more information about trade-offs between sustainability objectives, in the following section we examine the give and takes between the conservation objective $F_{\min}$ and the economic objective $h_{\min}$.

4.2. Equivalent economic incentives: One of the costs of biodiversity conservation

In our case study, the economic constraint is defined by the economic context. This constraint can be modified by changing the subsidy level (increasing it or decreasing it). The ecological objective is more flexible as it is a chosen target. It can be adapted in order to have a non-empty viability kernel.

It is possible to define the necessary economic conditions to be able to reach a given conservation objective $F_{\min}$, that is to say to look for the economic conditions resulting in a $h_{\min}$ such that the viability kernel is not empty. For this purpose, we define the reciprocity of relationship (13), i.e., the maximum level of $h_{\min}$ that is compatible with an ecological constraint $F_{\min}$:

$$\mathcal{H}(F_{\min}) = \max\{h_{\min} \,|\, Viab(h_{\min}, F_{\min}) \neq \emptyset\} \tag{14}$$

We have

$$\mathcal{H}(F_{\min}) = qB_{\text{sup}}\left(1 - \frac{q(F_{\min} - F_0)}{rsd}\right) \tag{15}$$

This level corresponds to the worst economic context compatible with the Frigatebird population objective $F_{\min}$. If the economic situation is worse, i.e., if the economic proxy $h_{\min} = \frac{c_t}{p_t + \tau_t}$ is higher than the threshold $\mathcal{H}(F_{\min})$, the viability constraints cannot be satisfied. It means that to be able to reach a conservation objective $F_{\min}$, it is necessary to modify the viability constraint $h_{\min}$ (by changing the economic context, adjusting the subsidy level) so that the viability kernel is not empty.

As the level of the economic proxy depends on the economic context, one can compute the equivalent shrimp price (including subsidies) at which a given ecological viability objective $F_{\min}$ would be reachable[3]

$$h_{\min} \leq \mathcal{H}(F_{\min}) \Leftrightarrow \frac{c}{(p+\tau)} \leq qB_{\sup}\left(1 - \frac{q\,(F_{\min} - F_0)}{rsd}\right)$$

$$\Leftrightarrow (p+\tau) \geq \frac{c}{qB_{\sup}}\left(\frac{1}{1 - \frac{q(F_{\min} - F_0)}{rsd}}\right) \tag{16}$$

To achieve the conservation objective $F_{\min}$, a minimum fishing activity is needed. That level of fishing activity is profitable only if the selling price (price plus subsidy) is higher than the threshold defined in Eq. (16). As this selling price includes the exogenous market price p_t and the subsidy τ_t, the minimum level of the subsidy that will result in a non-empty viability kernel is defined as

$$\tau^*(F_{\min}) = \frac{c}{qB_{\sup}}\left(\frac{1}{1 - \frac{q(F_{\min} - F_0)}{rsd}}\right) - p \tag{17}$$

This level of subsidy[4] can be interpreted as follows: If a conservation objective $F_{\min}$ higher than the value $\mathcal{F}(h_{\min})$ (with $h_{\min} = \frac{c_t}{p_t + \tau_t}$) is to be reached, it is necessary to provide an economic incentive at a level τ^*, instead of the initial level τ_t. In a symmetric way, note that when the viability kernel is not empty (when economic constraint $h_{\min}$ is lower than $\mathcal{H}(F_{\min})$, it is possible to reduce subsidy level from τ_t to τ^* in order to reduce bycatch while still satisfying the conservation objective $F_{\min}$.

By construction, if $\tau = \tau^*(F_{\min})$, then $h_{\min} = \mathcal{H}(F_{\min})$ (the expression of which is given by Eq. (15)). It is possible to compute the minimum cost of such an incentive program by multiplying the subsidies level τ^* by the minimum quantity of shrimp $\underline{H}$ harvested in the viability kernel, i.e., at the equilibrium state $\underline{B}(h_{\min})$ which is associated to effort $\underline{E}(F_{\min})$. It reads $\underline{H} = q\underline{B}(h_{\min})\underline{E}(F_{\min})$. Moreover $h_{\min} = \underline{H}/\underline{E}$, which leads to $\underline{H} = \mathcal{H}(F_{\min})\underline{E}$. As from Eq. (17) $\tau^* = \frac{c}{\mathcal{H}(F_{\min})} - p$, the expression of the minimum total subsidy cost $\mathcal{S}(F_{\min})$ can be written as

$$\mathcal{S}(F_{\min}) = \left(\frac{c}{\mathcal{H}(F_{\min})} - p\right)\mathcal{H}(F_{\min})\underline{E}\,(F_{\min}) \tag{18}$$

$$= \left(c - pqB_{\sup}\left(1 - \frac{q(F_{\min} - F_0)}{rsd}\right)\right)\frac{F_{\min} - F_0}{sd} \tag{19}$$

Eq. (19) only depends on exogenous parameters and on the viability target $F_{\min}$. It is a parabola which is equal to zero when the target $F_{\min}$ is the natural level F_0. Fig. 3 represents that cost with respect to the viability constraint $F_{\min}$.

Thanks to our viability analysis, we are able to describe quantitative trade-offs between sustainability objectives. In particular, we can relate the Frigatebird preservation objective to a monetary cost of subsidies and a quantitative environmental cost of discards. In the next section, we discuss how this kind of analysis fits into the broader issue of biodiversity conservation.

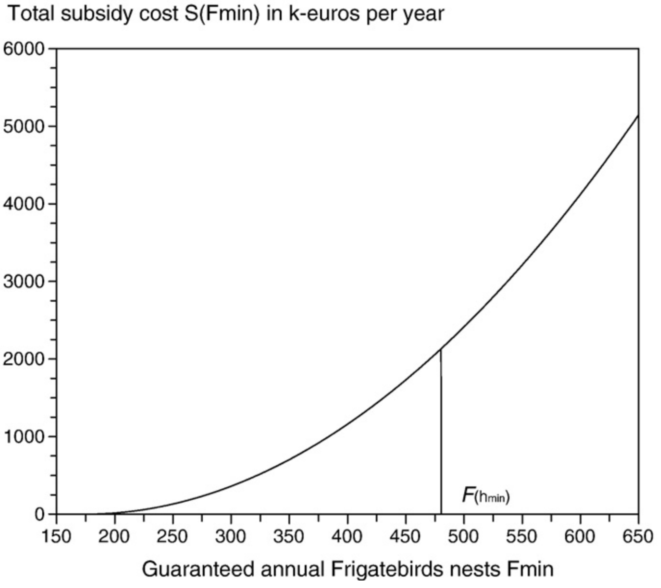

Fig. 3. Total annual cost of a subsidy program $\mathcal{S}(F_{\min})$ with respect to the Frigatebirds conservation objective $F_{\min}$. As a benchmark, $\mathcal{F}(h_{\min})$ is the maximum conservation objective that is reachable in the present economic context (without modifying the subsidy level).

5. Discussion

Human activities generate externalities on ecosystems and modify natural equilibria (Crocker and Tschihart, 1992). Worm et al. (2006) emphasize the negative consequences of biodiversity loss in marine ecosystems on the productivity and stability of these ecosystems. The main externality of fisheries on seabird population is negative and due to bycatch (Wilcox and Donlan, 2007). Nevertheless, positive externalities also occur when seabirds feed on discards (Furness, 2003). These externalities should be accounted for in ecosystem approaches to fishery management, considering all the activities that take place in the marine environment and their interdependencies and competition for the ocean space (Pascoe, 2006). To protect biodiversity, seen as a public good, it may be efficient to regulate economic activities to provide good incentives, reducing negative externalities or enhancing positive ones (Bayon et al., 2000). Perhaps the simplest approach to providing correct incentives to private agents is to align private incentives with public economic interest, using Pigouvian compensations.[5] This requires setting prices that equate the marginal willingness to pay for biodiversity to the marginal cost of maintaining it (Montgomery et al., 1999). The issue is then to determine at which level biodiversity should be "produced." In particular, the benefits in maintaining or enhancing biodiversity need to be compared with the cost of stopping or maintaining related activities, these costs being direct or indirect. Valuing these different costs and benefits is not easy, especially when one considers non-market goods such as biodiversity. In our case study, the task is all the harder as the objective to maintain a large Frigatebird population conflicts with the objective to reduce bycatch to protect marine biodiversity. According to Eppink and van den Bergh (2007, p.291) "… within particular groups of fragile species and ecosystems, trade-offs in conservation of specific species can be made that may improve the efficiency and effectiveness of conservation efforts, with an eye to the

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[3] The same kind of analysis could have been done on cost structure c_t with a discussion on the evolution of fishing costs, such as oil, and potential specific subsidies.

[4] From an economic point of view, a negative subsidy is a tax. In the following analysis, this case is not excluded. Our result can also be interpreted as follows: what is the maximum tax level (in order to reduce fishery's activity and bycatch level) that would be compatible with a given conservation objective of the Frigatebird population?

[5] Taxes or subsidies.

net effect on biodiversity functions and welfare impact". This raises the important question of how to deal with conflicting biodiversity preservation objectives.

Metrick and Weitzman (1998) argue that the relevant solution concept to account for biodiversity preservation is the cost–benefit ranking criterion. However, such an approach should rely on "revealed preferences". Economics provides an important theoretical framework for such valuation and comparison.[6] In economics, the value of a species is often related to its contribution to biodiversity (Brock and Xepapadeas, 2003; Weikard, 2002; Weitzman, 1992, 1998). When based on species preservation, valuation studies focus on a single species, revealing individual willingness to pay to avoid a loss of the given species. This approach may be particularly relevant for endangered or 'emblematic' species, to reveal their existence value, even if the result can be biased,[7] but valuing the existence of one particular species is not the same as valuing its contribution to biodiversity. These economic valuation methods provide at least a monetary indicator of preservation value, which can be used in cost–benefit analysis. The main conclusion of Nunes and van den Bergh (2001, p.218) is that "monetary valuation of changes of biodiversity can make sense, if a clear life diversity level is chosen, a concrete biodiversity change scenario is formulated, and a multidisciplinary approach is used."

The economic modeling approach for biodiversity conservation, including cost-effectiveness models (with a budget constraint), makes it possible to define the "production possibility frontier" of ecological and economic objectives (Eppink and van den Bergh, 2007). Pradhan and Leung (2006) present a way to account for a fishery externality (negative externality of longliners on sea turtles) in a multi-objective fishery management framework. Such an approach makes it possible to assess the success of fishery management within a multi-criteria framework, taking into account the constraints managers face (Ward and Kelly, 2009). According to Wätzold et al. (2006), ecological–economic modeling is a promising way to develop multidisciplinary frameworks. Based on such interdisciplinary ecological–economic approaches, we argue that Viability, which models both economic dynamics and ecological processes, is well-suited to describe the trade-offs between objectives in ecological economic models addressing biodiversity loss and conservation issues, and this from a sustainability perspective, the objectives being met at all times. As suggested by Martinet and Doyen (2007) we extended the viability analysis to describe the necessary trade-offs between conflicting objectives and the quantitative relationships between them. Our results indicate that there is a trade-off between, on the one hand, an increase in fleet profit and thereby a reduction in bycatch and, on the other hand, Frigatebird population size. The preservation of a high population level of Frigatebirds on "Le Grand Connetable" may serve as a source to restore declining populations elsewhere, ensuring their safeguard. The problem is that it implies the reduction in some marine species populations, which has to be taken into account. We are able to quantify this trade-off, giving an expression of the annual cost of Frigatebirds conservation (with respect to the population level) both in terms of required subsidies and discard levels. In particular, we have founded that there is an increasing cost of conservation, with decreasing marginal returns to conservation expenditures. This cost of conservation would be enhanced by a monetary valuation of the negative externalities on marine biodiversity and reduced to account for the positive externalities on employment and support to the local community, and compared to the marginal contribution of this Frigatebird population to the species contribution to biodiversity value. By focusing on the relationship connecting local management practice (linked with externalities in the environment of a protected area) to the population of individual species, we do not address the entire chain that connects management decisions to biodiversity.[8] An important issue may be to evaluate the contribution of that Frigatebird population to the safekeeping of the species. In particular, one should take into account ecological threshold effects (Perrings and Pearce, 1994), and the interaction with other (declining) populations, in the strategy of conservation.

According to Metrick and Weitzman (1998, p.21), "Decision about endangered species reflects the values, perception, uncertainties, and contradictions of the societies that make them". In practice, the expenditures for biodiversity and ecosystem preservation are much lower than the revealed willingness to pay, suggesting that "we do not really care about Biodiversity" (Pearce, 2007). In our case, incentive measures favorable to the Frigatebird population would also have positive social externalities (and micro-economic interests once the fishery gets subsidies). However, negative externalities on marine ecosystem should not be neglected, even if it does not affect emblematic species.[9]

6. Conclusion

Several seabird species feed on the discards of fisheries. If the fishery's activity declines for economic reasons, the bird population could decline. In this paper, we focus on the particular and unusual relationship between the subsidized Guianese shrimp fishery and the protected Frigatebird population. The recent decline in the trawling activity has been correlated with an increased Frigatebird chick mortality rate. Using a bioeconomic model describing the dynamics of the shrimp fishery and its interactions with the Frigatebird population, we have accounted for two apparently conflicting sustainability objectives represented by constraints: an economic constraint on the profitability of the fishing activity, and a conservation constraint of the bird population. Using the viability approach, we have examined how these sustainability objectives are compatible one with respect to the other, and if there are trade-offs between both viability constraint levels. More specifically, we have investigated the give and takes in the level of constraints that must be worked out to be able to reach these objectives.

In our case study, the maximum Frigatebird population that can be conserved depends on the fishing activity that is limited by the economic context of the fishery. It would be possible to conserve a larger population if subsidies were granted to increase the shrimp trawling. Thanks to our approach, we are able to determine the lowest level of subsidies needed to ensure the economic viability of the fishery while maintaining a targeted Frigatebird population. Moreover, we came to understand that if that level is lower than the current amount of subsidies, it would be possible to further reduce the subsidy level without harming the bird population. On the contrary, if that level is higher than the current level, it would amount to what we call

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[6] This holds true even if valuation of non-market environmental services is better established in terrestrial environment than in marine environment (Pascoe, 2006).

[7] The assessment of biodiversity values may lead to a large range of monetary indicators, depending on the biodiversity value type under assessment (e.g., existence value or use value) and the selection of the valuation method, and the interpretation of single species valuation studies should be done with care when the results are used to policy design. Spash and Hanley (1995) emphasize that the monetary willingness to pay revealed by valuation methods (and especially by Contingent Valuation) fails as a measure of welfare change due to the fact that preferences on biodiversity are lexicographic, and it does not allow trade-offs between biodiversity and other market goods. As cost–benefit analysis requires such valuation, it makes it difficult to apply these approaches, and thus to value the benefits of biodiversity preservation (Hanley et al., 1995).

[8] This chain includes the links between the population of the species and likelihoods of survival, likelihoods of survival and contributions to biodiversity, and these contributions and the value society places on it (Montgomery et al., 1999).

[9] Note that willingness to pay for squid may be lower than that for Frigatebirds.

an “extra-cost”. In this case, it appears that the managers of the conservation program should be aware of this when they define their ecological objective in terms of population number. To sum up, the objectives of a conservation program (within a protected area) cannot be defined without taking into account potential interactions with ecological and economic dynamics outside the protected area.

Our study confirms the relevance of the viability approach to account for ecological and economic objectives in the case of natural resource management issues. Applying this approach makes it possible to define the bioeconomic conditions for several objectives, represented by constraints and given target levels, to be met at all times. We have shown that viability analysis can be extended to account for the give and takes of the constraint levels, making it possible to determine the set of achievable objectives and pinpoint trade-offs between sustainability targets. This extended approach would provide policymakers with thorough knowledge of all the possible achievable objectives, including trade-offs between conflicting ones, and therefore provide a quantitative tool for arbitration. In our study, the description of the trade-offs between sustainability objectives could be a starting point for a broader environmental economic analysis aiming to define the socially optimal level of an incentive program. The cost of fishery subsidies has to be compared to i) its benefits in terms of social externalities (communities support and employment) and ecological positive externalities (Frigatebird conservation), and ii) its costs in terms of negative externalities on marine biodiversity.

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Appendix A

A.1. Parameter values

We present here the way parameters were obtain, and the hypothesis underlying our model.

A.1.1. Economic and biological parameters for the shrimp fishery

Biological parameters of the shrimp fishery were estimated using LPUE series (landings per unit of effort) as an index of abundance. These LPUE were computed using information from fishing companies log books on fishing time and landings. We used non linear parameter estimation techniques to find the best fit of the predicted LPUE, given the observed LPUE. The fitting criterion is the minimization of the square deviation, using the methods provided by Hilborn and Walters (1992).

Economic parameters (costs, prices, and subsidies) in the 2007 economic context were computed by Huber Fayet.[10] In 2007, the economic context was $p_{2007} = 7$ k-euros per ton; $\tau_{2007} = 1.1$ k-euros per ton; $c_{2007} = 641.893$ k-euros. These values were defined from economic surveys carried out in May 2007 within the Chaloupe project, in the three major shrimp fishing companies. In the 2007 economic context, the minimum catches per unit of effort ensuring profitability was 79.246 tons of shrimps per effort unit (it corresponds to a resource stock $B = 16{,}074$ tons). The related viability constraint is $h_{\min} = 79.246$. Note that without subsidies (i.e., if $\tau = 0$), the fishery would not be profitable at all at the 2007 price and costs.

A.1.2. Frigatebird and fishery interaction parameters

The parameters of the interaction between the Frigatebird population and fishery discards were obtained by Fabian Blanchard and Julien Semelin.[11] We explain here the basic idea underlying relationship (3).

In our model, the fishing effort unit has been defined as the total effort developed by a vessel during one year. Taking into account the maximum individual size of a fish a Frigatebird is capable of swallowing, a trawler haul generates 11.2 kg of discarded biomass the birds can feed on. Computing the mean number of days at sea per vessel and per year (which is quite constant around 258 days at sea per vessel per year in our case study, as climatic conditions in this area are quite similar from one year to another), and accounting for two trawling haul per day, each fishing effort unit E generates $d = 5.78$ tons of discards available as a source of food for birds per year. Given the facts that the bird species has a long life time and a late maturity age, and that data on the population size are available only for recent years, it is not possible to model, according to current knowledge, the population dynamics and the influence of discard on it. We thus have to make some strong assumption on the relationship between discard and reproduction success. The number of nests in natural conditions (the one observed before the development of the fishery in the 60s) is about 180 couples succeeding in reproduction each year. This leads to our reference population F_0. Given recent data on discard and Frigatebird population survey, chick mortality occurs every time the quantity of discards decreases below 336 kg per couple. In particular, 215 tons of discards made it possible to ensure the viability of the 639 nests surveyed in January 2007. We assume that discards have a linear effect on reproduction success, and consider two reference points: 180 couples are viable with no discard, 639 couples are viable with 215 tons of discards. It gives us a slop of 2.135 for the linear relationship linking bird couples to discard. Hence the parameters of Eq. (3).

The 2007 survey of Frigatebird population leads to an evaluation of the population size of 639 couples (two adults and a nest). A total conservation objective would results in a threshold $F_{\min} = 639$ (this objective would require to maintain a quantity of discards available for feeding of 215 tons each year).

The following table gives the parameters value for our case study.

Parameter	Name	Value	(Units)
r	Resource growth rate	0.91	
B_{sup}	Environmental carrying capacity	18,500	(tons)
q	Resource catchability	$4.93 * 10^{-3}$	$(\text{year})^{-1}$
d	Rate of “available” discards	5.78	(tons) $(\text{year})^{-1}$
s	“Feeding on discards” effect	2.135	(bird couples) $(\text{tons})^{-1}$
F_0	“Natural bird population”	180	(bird couples)

A.2. Computation of the viability kernel

We refer to De Lara and Doyen (2008) for the resolution of viability problems in a discrete time framework.

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[10] Huber Fayet (2007) *Modélisation bioéconomique de la pêcherie crevettière de Guyane Française*, Master thesis, under the supervising of Christian Chaboud (IRD).

[11] Blanchard F. and Semelin J. (2008) Impact of fishery discards on the population dynamics of a tropicalmarine bird species (*Fregate magnificiens*) in French Guiana: when fishermen strike affects the bird reproduction success. Unpublished work. Chaloupe working paper.

Consider the viability problem defined by the dynamics (1) and the constraints (4) and (5). The aim of the analysis is to define the viability kernel (Eq. (6)) $\mathrm{Viab}(h_{\min},F_{\min}) \subseteq \mathbb{B} = [0, B_{\sup}]$.

Constraint (4) results in the necessary condition

$$B_t \geq \frac{h_{\min}}{q} \tag{A.1}$$

We define the threshold value $\underline{B}(h_{\min}) = \frac{h_{\min}}{q}$. The economic constraint (Eq. (4)) is thus equivalent to the state constraint $B_t \geq \underline{B}(h_{\min})$. This constraint is stationary through time.

According to Aubin (1991) and De Lara and Doyen (2008), the viability kernel of the problem is the biggest weakly invariant set within the constrained set $[\underline{B}(h_{\min}),B_{\sup}]$, in the sense that:

- from any state $B_0 \in \mathrm{Viab}$ there are trajectories staying within Viab and respecting the constraints forever (weak invariance of the viability kernel)
- from any state $B_0 \in \mathbb{B} \setminus \mathrm{Viab}$ there are no trajectory satisfying the constraint forever.

To prove the results presented in Section 2, we will proceed as follows:

- We introduce some preliminary results
- We then show that the whole constrained domain $[\underline{B}(h_{\min}),B_{\sup}]$ is viable if condition (7) holds.
- We last prove that the viability kernel is empty if condition (7) does not hold.

Step 1: Preliminary results

- Given the ecological constraint (5) and the definition (3), any viable decision must satisfy $E_t \geq \underline{E}(F_{\min})$, with

$$\underline{E}(F_{\min}) = \frac{F_{\min} - F_0}{sd} \tag{A.2}$$

- For any $B_t \geq B(h_{\min})$, we define the fishing effort $\overline{E}(h_{\min}, B_t)$ such that $B_{t+1} = \underline{B}(h_{\min})$. Given the dynamics (1), it reads

$$\overline{E}(h_{\min},B_t) = \frac{1}{q}\left(1 + r\left(1-\frac{B_t}{B_{\sup}}\right) - \frac{h_{\min}}{q}\frac{1}{B_t}\right)$$

$\overline{E}(h_{\min}, B_t)$ satisfies the three following properties:

i) As the dynamics (1) is decreasing with the effort (the higher E_t the lower B_{t+1}), for any $B_t \in [\underline{B}(h_{\min}),B_{\sup}]$, if $E_t \leq \overline{E}(h_{\min},B_t)$ then $B_{t+1} \geq \underline{B}(h_{\min})$; respectively, we have: if $E_t \geq \overline{E}(h_{\min},B_t)$ then $B_{t+1} \leq \underline{B}(h_{\min})$.

ii) We have $\overline{E}(h_{\min},\underline{B}(h_{\min})) = \frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right)$ which is equivalent to

$$r\underline{B}(h_{\min})\left(1-\frac{\underline{B}(h_{\min})}{B_{\sup}}\right) = q\underline{B}(h_{\min})E_t$$

It means that for $B_t = \underline{B}$ and $E_t = \overline{E}(h_{\min}, \underline{B}(h_{\min}))$, the growth of the natural resource is equal to the catches; we have a stationary state, and the resource stock remains at $\underline{B}(h_{\min})$, resulting in an equilibrium.

iii) Note that $\overline{E}(h_{\min},B_t)$ is an inverted U-shape parabola.
On the interval $[\underline{B}(h_{\min}), B_{\sup}]$, its minimum value is at one of the boundary of the definition set.
Standard computation gives $\overline{E}(h_{\min},\underline{B}(h_{\min})) = \frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right)$, and

$$\overline{E}(h_{\min},B_{\sup}) = \frac{1}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right).$$

As $r < 1$, we have $\overline{E}(h_{\min},\underline{B}(h_{\min})) < \overline{E}(h_{\min},B_{\sup})$, which means that

$$\underset{B \in [\underline{B}(h_{\min}),B_{\sup}]}{\operatorname{argmin}} \overline{E}(h_{\min},B) = \underline{B}(h_{\min}).$$

Step 2: Proof that the viability kernel is $[\underline{B}(h_{\min}),B_{\sup}]$ when condition (7) holds.

We assume that $F_{\min} \leq \frac{rsd}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right) + F_0$ (condition (7)).

From relation (A.1), we know that the $\mathit{Viab} \subseteq [\underline{B}(h_{\min}),B_{\sup}]$. To prove our claimed result, we need to prove that $[\underline{B}(h_{\min}),B_{\sup}] \subseteq \mathit{Viab}$, which leads to the equality of the sets. For that purpose, we only have to show to that there exists (at least) one decision rule that keeps the state of the system within the set $[\underline{B}(h_{\min}), B_{\sup}]$ while respecting the constraint.

Let us define the following closed-loop decision rule: $E_t = \overline{E}(h_{\min}, B_t)$, defined at step 1 above.

From any initial state $B_t \in [\underline{B}((h_{\min}),B_{\sup}]$, we have $B_{t+1} = \underline{B}(h_{\min})$, by definition of $\overline{E}(h_{\min},B_t)$. Then, according to the properties ii) of $\overline{E}(h_{\min},\underline{B}(h_{\min}))$ described at step 1, the trajectory is stationary at $\underline{B}(h_{\min})$.

Along this particular trajectory, as $B_t \geq \underline{B}(h_{\min})$ for any t, the economic constraint (4) is satisfied at any time.

Moreover, along that trajectory, for any time t, we have $E_t = \overline{E}(h_{\min},B_t)$.

Using the result iii) exhibited in step 1 that $\overline{E}(h_{\min},B_t) \geq \overline{E}(h_{\min},\underline{B}(h_{\min}))$ for all $B \in [\underline{B}(h_{\min}),B_{\sup}]$, we have for all times $E_t \geq \overline{E}(h_{\min},\underline{B}(h_{\min}))$, where $\overline{E}(h_{\min},\underline{B}(h_{\min})) = \frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right)$ (see step 1, point ii) above).

The condition (7) is equivalent to $\frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right) \geq \frac{F_{\min}-F_0}{sd}$.

We thus get $E_t \geq \frac{F_{\min}-F_0}{sd}$, which implies that the biological constraint (5) is satisfied, according to the result (A.2) presented at step 1.

For any state within $[\underline{B}(h_{\min}),B_{\sup}]$, the proposed decision rule leads to a trajectory satisfying the viability constraints at all times.

We thus have $[\underline{B}(h_{\min}),B_{\sup}] \subseteq \mathit{Viab}(h_{\min},F_{\min})$. □

The viable decisions associated with a given viable states $B \in \mathrm{Viab}(h_{\min},F_{\min})$ are $\underline{E}(F_{\min}) \leq E(B) \leq \overline{E}(h_{\min},B)$. The first inequality is required to the satisfaction of the ecological constraint (see first point of step 1), and the second inequality is required to maintain the state B within the viability kernel (see step 1, point i)).

Step 3: Proof that the viability kernel is empty when condition (7) does not hold.

To prove that the viability kernel is empty in that case, we will show that any fishing effort satisfying the ecological constraint (5) would result in a trajectory which would violate the economic constraint (4) in a finite time, whatever the initial condition of the biomass B_0 such that $B_0 \in [\underline{B}(h_{\min}), B_{\sup}]$.

First note that if condition (7) does not hold, we have

$$F_{\min} > \frac{rsd}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right) + F_0 \Leftrightarrow \frac{F_{\min}-F_0}{sd} > \frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right).$$

It means that there exist $\varepsilon > 0$ such that

$$\frac{F_{\min}-F_0}{sd} = \frac{r}{q}\left(1-\frac{h_{\min}}{qB_{\sup}}\right) + \varepsilon \tag{A.3}$$

Assume for a while that the viability kernel is not empty. It would mean that there is at least one initial state B_0 such that, from that state, there are admissible decisions resulting in a trajectory that satisfies the constraints forever. We will show that any trajectory satisfying the ecological constraint (5) would then eventually violate the biomass constraint (A.1), and thus the economic constraint (4). Hence a contradiction.

According to step 1 (A.2), to satisfy the ecological constraint a viable fishing effort must satisfy $E_t \geq \frac{F_{\min} - F_0}{sd}$. Given the biomass dynamics (1), for all $B_t \in [\underline{B}(h_{\min}), B_{\sup}]$, we have

$$B_{t+1} - B_t = rB_t\left(1 - \frac{B_t}{B_{\sup}}\right) - qB_tE_t$$

$$\Leftrightarrow B_{t+1} - B_t \leq rB_t\left(1 - \frac{B_t}{B_{\sup}}\right) - qB_t\frac{F_{\min} - F_0}{sd}$$

$$\Leftrightarrow B_{t+1} - B_t \leq rB_t\left(1 - \frac{B_t}{B_{\sup}}\right) - qB_t\left(\frac{r}{q}\left(1 - \frac{h_{\min}}{qB_{\sup}}\right) + \varepsilon\right)$$

$$\Leftrightarrow B_{t+1} - B_t \leq \frac{rB_t}{B_{\sup}}\left(\frac{h_{\min}}{q} - B_t\right) - qB_t\varepsilon$$

On $[\underline{B}(h_{\min}), B_{\sup}]$, we obviously have $B_t \geq \underline{B}((h_{\min})$, where $\underline{B}(h_{\min}) = \frac{h_{\min}}{q}$. It means that, for any fishing effort satisfying the ecological constraint (5), at each time period, whatever the biomass stock $B_t \in [\underline{B}(h_{\min}), B_{\sup}]$, the biomass is necessarily decreasing. Moreover, we also have

$$B_{t+1} - B_t \leq - h_{\min}\varepsilon \tag{A.4}$$

which means that the quantity of resource depleted is larger than the strictly positive level $h_{\min}\varepsilon$. There is thus a finite time T such that $B_T < B(h_{\min}) + h_{\min}\varepsilon$. The biomass constraint (A.1) will then be violated either in T or in $T+1$.[12] □

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[12] It is even possible to give an upper value for T. Given Eq. (A.4), for any $B_0 \in [\underline{B}\,(h_{\min}), B_{\sup}]$, we have $B_t \leq B_0 - h_{\min}\varepsilon t$. The condition $B_t < \frac{h_{\min}}{q} + h_{\min}\varepsilon$ is thus reached for any $t > \frac{B_0 - h_{\min}/q}{h_{\min}\varepsilon} - 1$. We thus have $T \leq \frac{B_0 - h_{\min}/q}{h_{\min}\varepsilon} - 1$.

5.4. Exploitation d'espèces en interactions par quatre flottilles artisanales : le cas de la pêche côtière en Guyane

Le modèle développé est un modèle multi espèces – multi flottilles en temps discret qui intègre les dynamiques des stocks exploités avec des interactions trophiques de type Lotka-Volterra. Treize espèces ou groupes d'espèces sont retenues, en groupant les espèces de croupias, les espèces de requins et les espèces de loubines, auxquelles est ajoutée une quatorzième espèce pour représenter le reste du réseau trophique. Il y a en particulier une importance des crevettes dans le régime alimentaire des espèces. Les populations sont également en interactions par l'intermédiaire des captures par les différents navires. Quatre flottilles sont représentées, les pirogues (P), les canots créoles (CC), les canots créoles améliorés (CCA) et les tapouilles (T). Ce modèle donne pour chaque mois de la simulation, l'état (en biomasse et en abondance) des stocks de poissons, ainsi que les captures pour chaque espèce de poisson et les revenus par flottille.

Les données utilisées pour paramétrer le modèle sont estimées à partir de résultats provenant des observations quotidiennes réalisées auprès des pêcheurs sur les points de débarquements en termes d'effort de pêche, de caractéristique des moyens mis en œuvre pour les opérations de pêche et les débarquements par espèce. Ces enquêtes sont mises en place par l'Ifremer depuis 2006. Après exploitation de ces données, les valeurs de débarquement par espèce et par navire ainsi que celles des efforts de pêches (2006-2009), ont pu être calculées. Les valeurs des taux de croissance intrinsèque par mois proviennent de la base de données fishbase (http://www.fishbase.org). Les valeurs des autres paramètres du modèle ont étés identifiées par optimisation (minimisation de l'écart entre les valeurs des débarquements observés pour 48 mois et les valeurs simulées par le modèle).

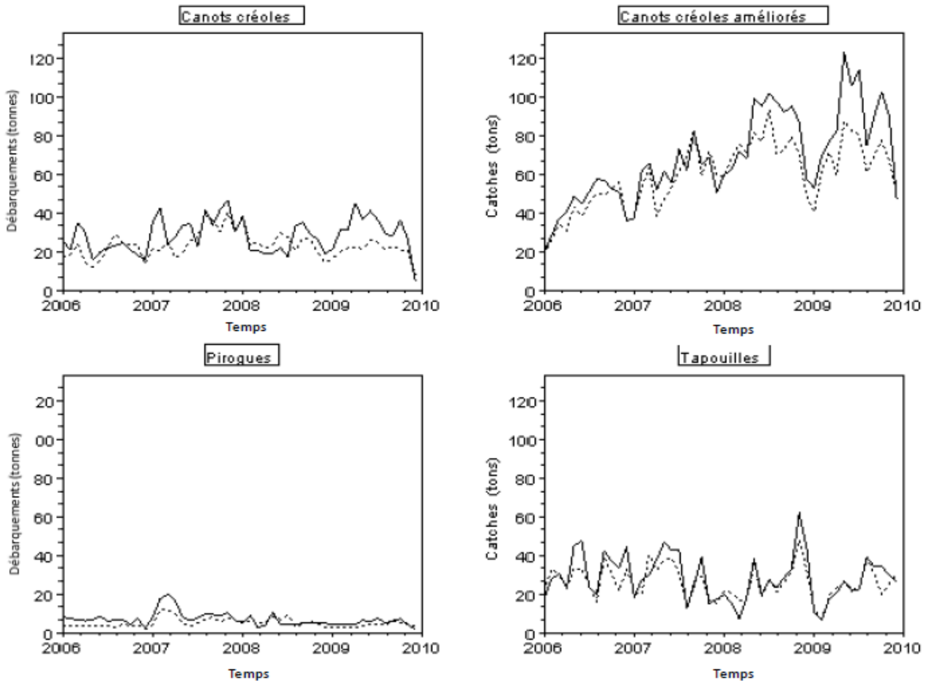

Figure 21. Débarquements observés par flottille entre 2006 et 2009 (traits pleins) et simulés à partir du modèle (traits pointillés) après calibration.

Sur les quatre scenarios testés sur des périodes de quarante ans détaillés dans la publication qui suit, seuls les scénarios status quo (SQ : maintien de la pression de pêche actuelle), et de co-viabilité (CVA : quelle pression de pêche par flottille pour assurer une viabilité économique, en limitant l'impacter sur la biodiversité et satisfaire la demande alimentaire, considérant une augmentation des apports de 3% par an, équivalente à l'augmentation de la population), sont présentés ici.

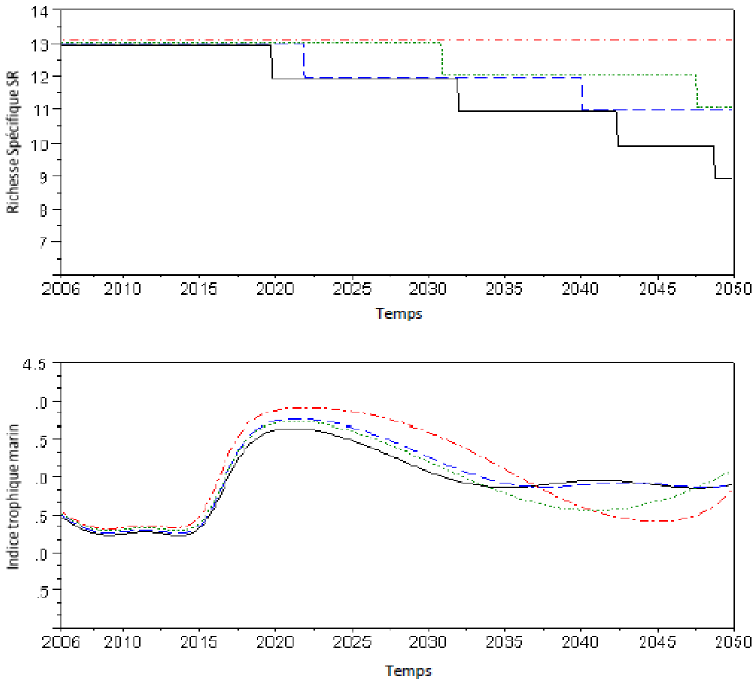

Figure 22. Performances écologiques des scénarios de gestion, en termes de richesse spécifique (figure du haut) et de niveau trophique moyen du réseau d'espèces exploitées (figure du bas) : scénario SQ (trait plein noir), scénario CVA (tirets bleus). Les deux autres figurés correspondent à deux autres scénarios à titre illustratif, arrêt total de la pêche (tirets et pointillés rouges) et maximisation des profits (pointillés verts).

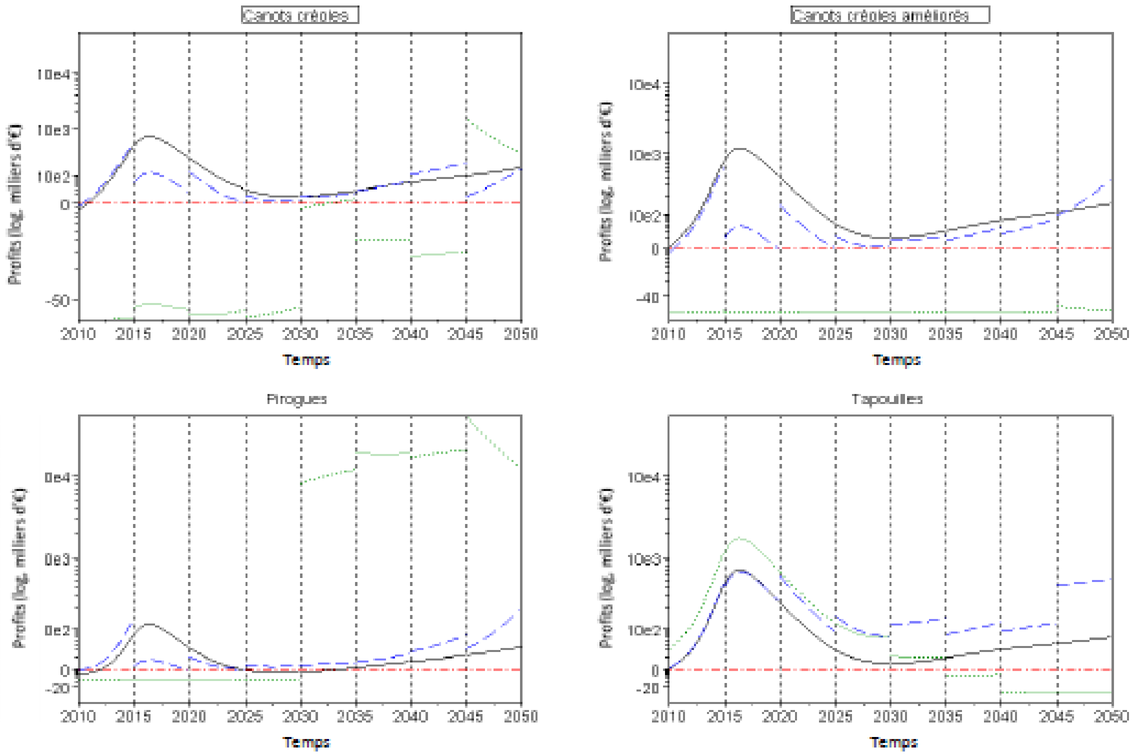

Figure 23. Comparaison des trajectoires temporelles des profits par flottille selon les scénarios, SQ (trait plein noir), scénario CVA (tirets bleus). Le troisième figuré corresponde à un scénario, à titre illustratif, de maximisation des profits de la pêcherie (pointillés verts).

Le modèle montre des résultats très proches des observations (figure 21). Celui-ci peut donc être utilisé même s'il doit être amélioré, en particulier en ce qui concerne les paramètres biologiques. Ceux-ci sont en effet issus de la littérature et devraient être confrontés à des paramètres mesurés sur les populations de poissons des eaux guyanaises. Les scénarios de gestion proposés sont, d'une part le scénario *status quo*, on maintient et on fige les modalités d'exploitation, telles qu'elles sont observées actuellement, et d'autre part, un scénario où l'on cherche à minimiser l'impact sur l'écosystème tout en continuant à générer du profit et en répondant à la demande alimentaire croissante, scénario de co-viabilité. C'est un scénario de développement durable de la pêcherie. Le scénario *status quo* obtient de moins bonnes performances économiques et écologiques que le scénario co-viabilité (Figures 22 et 23).

Ces travaux sont détaillés dans la publication suivante présentée en annexe.

Cissé, A.A., Gourguet, S., Doyen, L., **Blanchard, F**., Pereau, J.C. A bio-economic model for the ecosystem-based management of the coastal fishery in French Guiana. Environment and Development Economics 00: 1–25 © Cambridge University Press 2013, doi:10.1017/S1355770X13000065

6. Discussion

Des modifications de la biodivesité : pêche ou climat ?

Dans le cadre de l'évaluation des écosystèmes pour le millénaire « Millenium Ecosystem Assessment », des experts ont réalisé un diagnostic à l'échelle mondiale de l'état de la biodiversité et des facteurs qui l'altèrent, à l'échelle spatiale des grands biomes (forêt, montagnes, océans côtiers et hauturiers, déserts…) et à l'échelle temporelle de la seconde moitié du vingtième siècle. La diminution du nombre d'espèces et celle de l'abondance des populations qui les composent sont dues à leur exploitation, à la dégradation des habitats, à l'augmentation des espèces envahissantes, au réchauffement climatique et à la pollution. Il est nécessaire d'affiner ces observations, aux échelles spatiales des écosystèmes qui doivent être gérés (conservation, exploitation…) et aux échelles temporelles compatibles avec la gestion des écosystèmes et en particulier celles des politiques publiques. Pour les écosystèmes marins, des travaux ont montré, principalement en Mer du Nord, les impacts de l'exploitation par la pêche sur l'écosystème marin. Parallèlement, les impacts du réchauffement des eaux et des autres modifications de facteurs physiques associés au changement climatique, commencent à être connus. Un débat existe parfois entre les « défenseurs » des impacts de la pêche et les « défenseurs » des impacts climatiques : l'impact de la pêche étant le plus fort et celui sur lequel on peut agir par une réduction de la pression de pêche, l'impact du changement climatique ne serait pas important car moindre et non réductible à court et moyen termes. De fait, les impacts de la pêche liés à une augmentation de la pression de pêche visible depuis la seconde moitié des années 70 ont précédé ceux du changement climatique survenant de façon significative dans le milieu marin à la fin des années 80. Il existe peu de travaux traitant en même temps de ces deux facteurs d'impact. Cependant, nous montrons par nos travaux, non seulement que les deux facteurs, pêche et climat, interviennent, avec parfois des mêmes effets sur un indicateur, ou des effets contraires. La part de facteurs dans les changements écosystémiques observés reste donc difficile à quantifier. Cet impact climatique ne peut donc être ignoré, car si l'on ne peut le modérer, au moins peut-on s'y adapter à condition d'être capable de l'observer et/ou le prévoir.

En termes de conséquences pour les pêcheries, l'interprétation des changements observés dans la structure des captures, en poids et en valeur, nécessite en plus une compréhension de la dynamique des marchés et des facteurs de production. La mondialisation du marché des produits en est un facteur essentiel. Dans les deux cas traités en exemple, les changements dans les peuplements et populations exploitées se surajoutent aux facteurs économiques, aboutissant à une baisse de la valeur de la production halieutique, autrement dit, une baisse de la valeur de ce service écosystémique.

Du simple au complexe, de l'opérationnel à l'exploratoire, du culturalisme à l'universalisme: réconcilier écologie et halieutique

Le développement de nombreux modèles appliqués à différent cas d'étude et pour répondre à différentes questions ont permis de formaliser ici un lien entre leur niveau de complexité et la nature de leur utilisation en terme de gestion opérationnelle des pêcheries ou d'outil exploratoire par la simulation pour la compréhension du fonctionnement des systèmes (figure 24). Les modèles de complexité moindre introduisent des processus bien connus, dont les variables sont souvent mesurées et qui peuvent donc être calibrés. Ils correspondent à des échelles temporelles de l'ordre du mois, de la saison de l'année, et des échelles spatiales correspondant à celle de la distribution spatiale du stock exploité modélisé. Ces modèles sont donc opérationnels comme base de gestion car leur contenu, bien que simplificateur est bien quantifié et donc convaincant pour les décideurs et usagers. Les modèles plus complexes introduisent des variables représentant des processus connus, bien que peu mesurés et donc mal quantifiés. Bien que théoriquement plus réalistes, leur validation est difficile. Ils correspondent à des échelles temporelles de l'ordre de l'année, d'une ou plusieurs décennies et à l'échelle spatiale d'un écosystème. Ils sont donc plus utilisés pour comprendre le fonctionnement des systèmes.

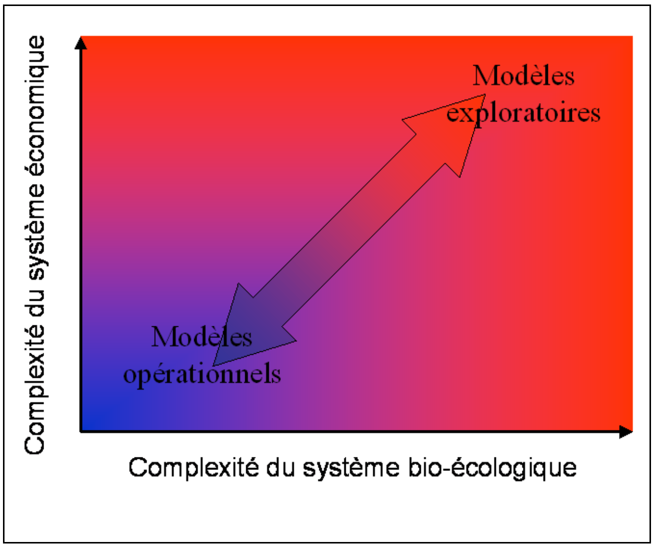

Figure 24. Type d'utilisation des modèles selon le niveau de complexité des processus représentés, processus biologiques et écologiques en abscisse, processus d'exploitation et économiques en ordonnée.

Ce développement pose la question de la multiplication du nombre de modèle : doit-on construire un nouveau modèle à chaque question ? A chaque nouveau cas d'application ? Pour chaque nouvelle action de recherche ? La question de fond est ainsi celle de la généricité des modèles. Peut-on considérer que chaque système ressource/exploitation est suffisamment identique à un autre en termes de trajectoire et de fonctionnement pour que le même modèle soit applicable ? Quelle est l'échelle de complexité du système considéré qui permet la généricité (un stock/un métier ? un écosystème/un ensemble de flottes de pêche ?). Le débat en Sciences Humaines entre la notion de culturalisme, qui considère que chaque groupe humain est avant tout un groupe homogène ayant ses caractéristiques propres et donc différent d'un autre groupe, et celle d'universalisme, considérant avant tout les caractéristiques communes à tout groupe humain malgré les différences propres à chaque groupe, peut être éclairant. La démarche de l'écologue théoricien, l'universaliste, est celle d'une recherche de généralisation de ses observations réalisées à des échelles spatiales et temporelles assez grandes (« Fishing down the food web » de Daniel Pauly, 1996[1], ou encore « la disparition des grands poissons en 2048 » de Boris Worm, 2006[2]). Ces observations aboutissent donc à des modèles plutôt exploratoires selon l'exposé du paragraphe précédant, bien que les écologues produisent des recommandations mais qui restent assez générales (diminuer globalement l'effort de pêche, restaurer les écosystèmes). La démarche de l'ingénieur halieutique, le culturaliste pour continuer le parallèle, est celle de la compréhension d'un système particulier qui doit être géré à court terme et qui n'entre pas toujours bien dans le cadre de la généralisation proposée par les écologues. Il s'en suit souvent une incompréhension entre les deux approches qu'il faut pourtant concilier.

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[1] Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing Down Marine Food Webs. Science, 279: 860-863.

[2] Worm, B., Barbier, E.B., Beaumont, N., Duffy, E., Folke, C., Halpern, B.S., Jackson, J., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science, 314: 787-790.

Plus qu'une opposition, il y a complémentarité des approches, avec la nécessité de réconcilier la gestion au quotidien des stocks de pêche et des pêcheries qui les exploitent, par les modèles halieutiques classiques opérationnels basés sur la dynamique des populations exploitées, avec une gestion à long terme des écosystèmes marins qui supportent la production des ressources halieutiques par des modèles plus exploratoires, basés sur les connaissances acquises en macro-écologie, en écologie des écosystèmes et des peuplements.

Approche intégrée et concept de développement durable

Ce concept, dont le premier énoncé reconnu le plus souvent est celui de Bruntland (1987), indique qu'une activité humaine économique, telle que la pêche, pour se développer durablement, doit être économiquement viable, ne pas altérer l'environnement, être socialement juste et respecter l'équité intergénérationnelle. Dans le contexte des activités de pêche, cela signifie que les armements doivent être rentables, que les dommages causés par l'exploitation sur les populations marines, la biodiversité associée et les habitats doivent être limités de manière à ne pas modifier les équilibres écologiques et le fonctionnement des écosystèmes et enfin que le niveau de vie, les pratiques, la culture des communautés de pêcheurs doivent être respectés ; la génération suivante devant tirer de la pêche les mêmes bénéfices que leurs aînés. On cherchera donc à évaluer l'état, ou encore le coût, bio-écologique, économique et social de la pêcherie en question et à trouver les modalités de pêche compatibles avec un bon état dans ces trois dimensions. En effet, le rendement économique maximal n'est pas toujours compatible avec le rendement biologique maximal à court terme. De même ce dernier n'est pas toujours compatible avec la préservation de la biodiversité, des habitats. Enfin, l'un et l'autre ne sont pas toujours compatibles avec le partage équitable des revenus de la pêche entre les différents acteurs et leur famille (armateur, capitaine, marins, transport, commercialisation). En revanche, il s'agit de trouver les modalités d'exploitation, sinon optimales dans les trois dimensions, du moins acceptables, trouver les compromis permettant de rendre compatible les objectifs sociaux, économiques et écologiques. La capacité de mettre en œuvre ces modalités, de trouver ces compromis, est maintenant perçue comme l'achoppement de la gestion actuelle des pêches (Boucher et Cury, 2005[3]). Si les méthodologies ont progressés pour qualifier et quantifier l'état bioécologique en relation à l'exploitation, ce sont les domaines de l'halieutique et de l'écologie halieutique, et l'état économique des pêcheries, en revanche la qualification et quantification de l'état social des communautés de pêcheurs et celles qui y sont liées, reste un domaine peu avancé. Cette idée est développée dans l'article suivant présenté en annexe.

Blanchard, F., Maneschy, M.-C., 2010. Vers un développement durable des pêcheries traditionnelles côtières amazoniennes : intégrer les sciences humaines, les sciences naturelles et économiques. Amaz'Hommes, sous la direction de Egle Barone-Visigalli et Anna Roosevelt, 371-382.

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[3] Boucher, J., Cury, P., 2005. Biodiversité : défis pour la gestion des pêches, *in* Biodiversité, Science et Gouvernance, Actes de la Conférence Internationale, Paris, 24-28 janvier 2005, sous la direction de R. Barbault, MNHN, Le Duc J.P. (Ed) : 208-211.

Apports de l’analyse de deux cas d’étude : les plateaux continentaux du Golfe de Gascogne et de la Guyane

1. Approche comparée

De manière générale, la portée des résultats de travaux scientifiques dépend i) de leur apport en termes de nouvelles connaissances, par exemple les populations exploitées répondent significativement au changement climatique ii) de leur apport en soutien à une théorie, par exemple, les peuplements bentho-démersaux se structurent non seulement selon les espèces mais selon la taille individuelle iii) de leur généricité (un modèle écosystémique est applicable à différents cas d’écosystèmes) et encore iv) de leur intérêt en termes d’application dans notre cas à la gestion de la pêche.

Les travaux de recherche présentés ici ont été menés dans deux contextes écologiques différents (tropical vs. tempéré) mais ayant des caractéristiques communes, permettant une certaine généralisation : le plateau continental du Golfe de Gascogne, et celui de la Guyane. D’un point de vue du fonctionnement écologique, ce sont deux cas de zones océaniques ouvertes de grande échelle spatiale comparable (légèrement inférieure à l’échelle des Large Marine Ecosystems). Les espèces y sont nombreuses, le plus souvent peu spécialisées en termes d’habitat et de régime alimentaire. Les flux entrant de nutriments proviennent principalement des fleuves. Les résultats obtenus dans nos deux cas d’analyse, dans la mesure où ils sont identiques, pourraient être vérifiables ailleurs dans le monde dans ce type d’écosystèmes qui se retrouve dans tous les océans. En revanche, les résultats ne seraient donc pas a priori applicables sans vérification à d’autres types d’écosystèmes moins ouverts tels que la Mer Baltique, les lacs, les plateaux continentaux des îles volcaniques (Martinique ou Guadeloupe par exemple), ou encore aux écosystèmes dont les principaux apports en nutriments proviennent du fond via un up-welling.

D’un point de vue du contexte socio-économiques, les pêcheries observées dans les deux cas d’étude sont dépendantes des mêmes règlementations européennes et nationales, avec toutefois un marché local beaucoup plus restreint en Guyane (250 000 habitants) et un marché national et européen éloigné (surcoût, méconnaissance des produits).

L’analyse de deux cas d’étude ayant quelques caractéristiques communes et quelques autres différentes a donc pour intérêt de montrer dans quelle mesure les résultats obtenus, concernant les dynamiques écologiques, les dynamiques économiques et les méthodes développées seraient généralisables à d’autres cas ayant ces mêmes caractéristiques communes.

2. Quels résultats généralisables et retombées en termes de gestion

2.1. Dynamiques écologiques : synergie pêche et climat

Il a été montré que l'exploitation par la pêche modifiait la biodiversité des peuplements bentho-démersaux, réduction du nombre d'espèces, espèces opportunistes et/ou de petite taille favorisées. Quant au réchauffement des eaux, il favoriserait, en contexte tempéré, les espèces à affinité chaude, *i.e.* les espèces sub-tropicales dans le Golfe de Gascogne, sachant que les espèces de petite taille réagissent plus rapidement, ce sont les espèces sub-tropicales de petite taille dont l'abondance augmente. Du point de vue de la structure en taille individuelle des peuplements, pêche et réchauffement climatique agissent de façon synergique. En Guyane, la pression de pêche diminuant, les populations d'espèces de grandes taille devraient se reconstituer, tandis que le réchauffement climatique défavoriserait les espèces-subtropicales. Ainsi, en Guyane, si les espèces à réagir les premières sont celles de petite taille alors, les espèces sub-tropicales de petite taille devraient être défavorisées, ce qui, synergiquement avec l'augmentation des espèce de grande taille se reconstituant suite à la baisse de la pression de pêche devrait modifier la structure en taille de façon inverse en comparaison du Golfe de Gascogne. Cela reste à démontrer, nécessitant de nouvelles campagnes sur le plateau de Guyane, avec les même protocoles que ceux qui ont déjà été mis en œuvre dans le passé.

2.2. Dynamiques économiques : la tragédie des communs exacerbée par le réchauffement et la mondialisation du marché des produits de la mer

Dans le Golfe de Gascogne, comme en Guyane, pour les pêcheries considérées, respectivement l'ensemble des pêcheries et la pêcherie crevettière, les quatre mêmes facteurs principaux expliquent la baisse de la valeur totale de la production et de la rentabilité : i) baisse de la production totale (surexploitation des stocks et conséquences du changement climatique), ii) baisse de la valeur unitaire liée à l'importation en Europe de produits d'élevage (saumon de Norvège, crevettes d'Asie du Sud-Est) dont la production se fait à coût moindre en comparaison de la pêche, iii) changement de biodiversité (modification de la composition spécifique, i.e., la part relative des espèces dans le peuplement) avec augmentation de la part des espèces de petite taille dont la valeur économique est moindre et iv) augmentation des coûts d'exploitation (carburant).

Cette baisse de rentabilité n'encourage pas à court termes une pêche responsable. A la difficulté classique de gestion d'une ressource commune, la course au poisson, induisant surcapacité, surexploitation et diminution des ressources, s'ajoute celle du changement climatique. Il devient nécessaire de mieux appréhender les effets de ce changement en passant d'une échelle macro-écologique (bio-géographie, écologie des peuplements), à une échelle géographique correspondant à celle de la gestion, d'un territoire, d'un écosystème, et des populations exploitées

2.3. Méthodologie

Les approches intégrées « écologique-économique », en statistiques, faisant appel aux biostatistiques en écologie couplées à l'économétrie en économie, ou par modélisation bio-économique ont permis de mieux comprendre les impacts conjoints des dynamiques écologiques et économiques sur l'évolution des pêcheries (baisse de la valeur et de la rentabilité) et de la biodiversité halieutique (altération, remplacement…). Dans ces conditions, le seul contrôle de la capacité de pêche ou de la production pour atteindre (revenir) le RMD pour une espèce donnée risque de ne pas être efficace à long termes, non durable donc. Par exemple, le TAC défini en Guyane pour la crevette n'est pas viable économiquement : la rente obtenu par navire dans le cas d'une consommation totale du TAC serait nulle voire négative, le TAC n'est donc jamais atteint et des licences de pêche restent disponibles. L'analyse économique ne doit pas venir a posteriori d'une recommandation basée sur une analyse biologique : on recommande un TAC pour atteindre le RMD, puis on analyse éventuellement les conséquences économiques d'une telle recommandation si l'on a les données et si les enjeux en termes socio-économiques sont *a priori* non négligeables. En effet, il serait plus pertinent de proposer directement un ensemble de scénarios viables écologiquement et socio-économiquement. De plus, l'appropriation par les professionnels de la pêche sera sans doute plus aisée si on leur présente des contraintes qui tiennent compte de la rentabilité. Les résultats de nos travaux dans ce domaine montrent que la méthodologie contribuant aux approches intégrées avance rapidement en ce sens (cas de la crevette et de la pêche côtière en Guyane) et contribuent à une mise en œuvre opérationnelle de l'approche écosystémique des pêches.

IV - Animation d'actions de recherche au cours des 10 dernières années

Coordination, au sein du Laboratoire des Ressources Halieutiques de l'Ifremer à Brest, de l'action de recherche « Impacts de la pêche et du changement climatique sur le peuplement de poissons du Golfe de Gascogne et conséquences pour la pêche » financée à hauteur de 15 k€ sur les années 2004 et 2005, dans le cadre de l'AAP 2003 « Biodiversité et Changement global » de IFB-GICC, en partenariat avec le Service d'Economie Maritime de l'Ifremer et le Laboratoire d'informatique Industrielle de l'Ecole Nationale d'Ingénieurs de Brest (ENIB).

Coordination au sein du Laboratoire des Ressources Halieutiques de l'Ifremer en Guyane, de l'action de recherche « Chaloupe : changement global, dynamique de la biodiversité marine exploitée et viabilité des pêcheries », financée à hauteur de 850 k€ sur les années 2006-2009, dans le cadre de l'AAP Biodiversité 2005 de l'ANR et de la labellisation par le pôle de compétitivité Mer, en partenariat avec l'UMR d'économie Ifremer/UBO « AMURE », le Département Ecologie et Modèles pour l'halieutique de l'Ifremer, l'IRD, l'ENIB, le laboratoire d'Informatique de l'Université du Littoral Côte d'Opale, de l'UMR de biologie de la conservation CNRS/MNHN « CERESP », l'Institut National de Recherche Halieutique du Maroc. Http://www.projet-chaloupe.fr

Coordination au sein du Laboratoire des Ressources Halieutiques de l'Ifremer en Guyane, de l'action de recherche « GECO : gestion durable des pêcheries côtières de Guyane », financée à hauteur de 19 k€ sur les années 2009-2010, dans le cadre de l'AAP Recherche 2008 du Secrétariat d'Etat à l'Outre-Mer, en partenariat avec le Département d'Economie Maritime de l'Ifremer, l'UMR de biologie de la conservation CNRS/MNHN « CERESP », le GREThA, centre d'Economie théorique et appliquée de l'Université Montesquieu-Bordeaux IV, et le laboratoire de l'Economie du Développement de l'Université des Antilles et de la Guyane.

Coordination au sein du Laboratoire des Ressources Halieutiques de l'Ifremer en Guyane, de l'action de recherche « Depeche : développement durable de la pêche côtière en Guyane, potentiel écologique et éonomique », financée à hauteur de 200 k€ sur les années 2009-2011, dans le cadre de l'axe Recherche du PO-Feder de la Guyane, en partenariat avec le Département d'Economie Maritime de l'Ifremer, et le laboratoire de l'Economie du Développement de l'Université des Antilles et de la Guyane.

Coordination de la tâche « écologie » de l'action de recherche « ADHOC : modèles de co-viabilité biodiversité marine et pêcheries » coordonnée par l'UMR de biologie de la conservation CNRS/MNHN « CERESP », financée sur les années 2010-2013, dans le cadre de l'AAP 2009 « 6ème extinction » de l'ANR, en partenariat avec le Département d'Economie Maritime de l'Ifremer, le GREThA, centre d'Economie théorique et appliquée de l'Université Montesquieu-Bordeaux IV, le World Fish Center, le CSIRO (Australie).

Coordination scientifique du programme de recherche « Mérou » porté l'ONCFS en Guyane financée à hauteur de 200 k€ sur les années 2009-2012, dans le cadre de l'AAP « Biodiversité Marine» de la Diren en Guyane, en partenariat avec l'Université de Floride et l'Université des Antilles et de la Guyane.

V - Expertise

Depuis 2009, réponses à la demande d'avis de la DRIRE de Guyane concernant les travaux d'exploration pétrolière dans la ZEE guyanaise. A titre d'exemple :

Dreves L., Roest Walter R., et **F. Blanchard**, 2009.- Demande d'autorisation d'ouverture de travaux dans le cadre du Permis d'Exploration Guyane Maritime. Direction Régionale de l'Industrie, de la Recherche et de l'Environnement Antilles-Guyane.

En 2009, réponses à une demande d’avis de la Direction Régionale des Affaires Maritimes de Guyane concernant l’état du stock de crevettes de Guyane en vue du renouvellement des licences de pêche crevettière, et à une saisine de la Direction des Pêches Maritimes du Ministère de l’Agriculture et de la Pêche, concernant i) la quantification de l’activité informelle de la petite pêche côtière en vue d’une augmentation de la capacité de la flotte, et ii) l’adéquation de l’état de la ressource en vivaneau avec l’entrée en flotte de nouveaux navires caseyeurs venus des Antilles.

En 2008/2009/2010/2011/2012, réponse à une demande d’avis de la Direction Régionale des Affaires Maritimes de Guyane concernant l’état du stock de crevettes de Guyane en vue du renouvellement des licences de pêche crevettière

En 2003, participation avec le Ministère des Affaires Etrangères à la session de juillet de l’Organisation Maritime Internationale à Londres, sur la demande française de mise en place d’une zone maritime écologiquement sensible et vulnérable en vue d’y interdire le passage des pétroliers à simple coque.

VI - Communications

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De Thoisy, B., Lavergne, A., Semelin, J., Pouliquen, J.-F., **Blanchard, F**., Hansen, E., Lacoste, V., 2009. Herpesvirus outbreaks in a colony of Magnificent Frigate birds (*Fregata magnificens*) in French Guiana. Journal of Wildlife Diseases, 45(3): 802-807.

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Interviews pour le journal "Le Marin", numéro du 1er novembre 2002, janvier 2010, pour l’hebdomadaire « la semaine Guyanaise » février 2010, pour le magazine Sciences Ouest, numéro de mai 2004 (impacts du climat et de la pêche), pour RFO « paroles de scientifique » en 2006, 2008, pour le journal télévisé de Guyane première (changement climatique) en 2012.

Sensibilisation sur le thème science – environnement – éthique auprès de classes de 1ères et terminales, sous forme d’exposés et discussions, 1996-1997, Cayenne, Guyane française.

VII - Cours donnés à l’université

Licence professionnelle, protection de l’environnement, Université des Antilles et de la Guyane, 2005-2009 : écologie appliquée, impacts de la pêche et du climat sur le biodiversité marine, les ressources halieutiques et les pêcheries de Guyane.

Mastere 1 - Biologie - Chimie- Environnement, Université des Antilles et de la Guyane, 2012-2013 : Ecosystèmes marins tropicaux.

Mastere 2 - biodiversité marine, Université de Lille, 2004-2005 : impacts de la pêche et du climat sur le biodiversité marine, introduction à la gestion des pêcheries, problématique des aires marine protégées.

Mastere 2 - économie, gestion et financement du développement durable, Université des Antilles et de la Guyane, 2010-2011, 2011-2012, 2012-2013 : dynamiques économiques et écologiques des pêcheries.

VIII - Responsabilités, relations internes et externes

Délégué Régional depuis le 01/10/08, j'assure la représentation de l'Ifremer en Guyane. Cette représentation est à la fois locale et régionale.

Chef de la station Ifremer de Guyane depuis le 01/10/08, j'assure la responsabilité de l'implantation Ifremer en Guyane.

Chef du laboratoire Ressources Halieutiques de Guyane, depuis le 01/10/08, devenu unité biodiversité halieutique en 2011, j'encadre une équipe constituée d'un agent administratif, de trois chercheurs, d'un technicien, de trois doctorants, de deux VSC (volontaires service civil de niveau cadre, en contrat de 12 mois renouvelable une fois), auxquels s'ajoutent le suivi de la sous-traitance d'une partie de la collecte de données du système national d'information halieutique en Guyane réalisée par six agents ainsi que des stagiaires. En 2012, l'unité est donc composée d'une équipe de dix personnes à laquelle s'ajoute le suivi de la sous-traitance.

Un site internet de la délégation a été conçu et mis en ligne a mon initiative :
http://www.ifremer.fr/guyane

IX - Comités scientifiques, de relecture

Membre du Comité Scientifique du GIP Pôle Universitaire Guyanais depuis sa création en 2007 jusqu'à sa fin.

Membre du conseil de l'école doctorale de l'UAG.

Membre du CSRPN de Guyane depuis janvier 2013.

Régulièrement sollicité pour relire des articles soumis pour publication pour ICES Journal of Marine Science, Journal of Marine Systems, Marine Ecology Progress Series, Fisheries Oceanography, Cybium, Chemistry and Ecology, Estuarine, Coastal and Continental Shelf Sciences.

X - Encadrements et co-encadrements d'étudiants au cours des dernières années

Nom Etudiant	Niveau	Intitulé du diplôme/thème	Etablissement	Année	Valorisation
Fran Decoster	Licence Professionnelle	Protection Environnement	Université des Antilles et de la Guyane	2008	Restitution orale et rapport écrit pour les

Rebecca Brumelot	Licence Professionnelle	Protection Environnement	Université des Antilles et de la Guyane	2008	représentants professionnels et plaisanciers de la pêche en Guyane
Pierre Hélaouët	Diplôme d'Université	Dynamique spatiale de la diversité du peuplement de poissons de fond du Golfe de Gascogne	Université de Bretagne Occidentale	2004	
Rémi Vergnon	Mastère Recherche	Océanographie Biologique	Paris VI – Université de Bretagne Occidentale	2004	Une communication orale (colloque International Shellfish Restoration), une publication rang A (Aquat. Liv. Resources, 2006)
Caroline Bernard	Mastère Professionnel	Génie des Anthroposystèmes littoraux	Université La Rochelle	2006	Restitution orale pour les gestionnaire et professionnels de la pêche en Guyane
Antoine Rivierre	Mastère Professionnel	Biodiversité Tropicale	Université des Antilles et de la Guyane	2007	Une communication orale (colloque franco-brésilien EcoLab)
Aurore Faulin	Mastère Professionnel	Génie des Anthroposystèmes littoraux	Université La Rochelle	2007	Restitution orale et rapport écrit pour les représentants professionnels et plaisanciers de la pêche en Guyane
Abdoul Cissé	Mastère Professionnel et Mastère Recherche	Economie du Développement et de l'Environnement	Université des Antilles et de la Guyane	2009	Restitution orale au Comité Régional des Pêches de Guyane
Lazare Charles	Mastere Professionnel	Gestion et Financement du développement durable	Université des Antilles et de la Guyane	2012	
Nadia Justable	Mastere Professionnel	Gestion et Financement du développement	Université des Antilles et de la Guyane	2013	

		durable			
Jean-Bernard Victor	Doctorat	Pêche et économie en Guyane	Université des Antilles et de la Guyane	2008	
Abdoul Cissé	Doctorat	Evaluation et modélisation bio-économique de la pêche côtière en Guyane	Université des Antilles et de la Guyane	2010	Colloques : 4 communications orales 1 publication de rang A1
Celine Artero	Doctorat	Bio-Ecologie du Mérou Géant en Guyane	Université des Antilles et de la Guyane	2010	
Lea Bomier	Doctorat	Politiques publiques de gestion du ecteur minier : le cas de l'or et du pétrole en Guyane	Université de Paris-Sorbonne	2010	
Ivaneide Jaussaud	Post-Doctorat	Changements à long terme de la structure du peuplement de poissons de fond du plateau guyanais	Ifremer	2009	

XI - Perspectives

Un partenariat en sciences économiques a été construit avec l'UAG en Guyane, sur le thème de l'économie de l'environnement, concernant les dynamiques économiques des pêcheries guyanaises, dans le cadre des actions de recherche DEPECHE (financements des Fonds Européens pour le Développement des Régions, Guyane), GECO (financements du Secrétariat d'Etat à l'Outre-Mer), ADHOC (financements ANR-AO « 6ème extinction »), BIOMER (financements 1er AO recherche de la FRB). Un partenariat Ifremer, UAG, CNRS, Université Bordeaux IV (laboratoire Gretha) est donc en place. Dans ce contexte un candidat s'est inscrit en thèse d'économie à l'UAG en 2008 (formation des prix, dynamique des marchés des produits de la mer en Guyane). Un second s'est inscrit en 2009 et est hébergé et co-encadré à l'Ifremer (évaluation économique de la pêche côtière et modélisation bio-économique de sa viabilité), avec une bourse financée par le projet ANR ADHOC. Un troisième s'est inscrit en 2010, avec co-un encadrement UAG et Ifremer sur une espèce d'intérêt particulier de cette pêcherie côtière (le mérou géant, *Epinephelus itajara*), avec une bourse financée par la Diren-Guyane. Enfin, un quatrième doctorant (bourse acquise) est inscrit à l'UAG depuis septembre 2012 et est accueilli au CEREGMIA pour un travail en économétrie des pêches guyanaises. Cette thématique est donc mobilisatrice. Un pôle économie de l'environnement s'intéressant au milieu marin, en particulier à l'approche intégrée de l'halieutique, pourrait donc être renforcé et pérennisé en Guyane, permettant aussi d'alimenter les enseignements à des niveaux licence professionnelles et masteres.

Les analyses menées en Guyane concernant la gestion des ressources marines et de leur exploitation dans le contexte du changement global, doivent être menées de concert avec les équipes brésiliennes du nord qui interviennent sur les mêmes sujets. Une première action de coopération est en cours dans le cadre du projet OSE-GUYAMAPA porté par l'IRD. Une première thèse portant sur la résilience du système pêcheries côtières et peuplements écologiques côtiers pourrait être hébergée au sein de l'unité Biodiversité Halieutique de l'Ifremer en Guyane et inscrite en co-tutelle entre l'UAG et une université brésilienne.

A terme, des approches méthodologiques développées actuellement pourraient aussi être appliquées aux pêcheries antillaises, permettant aussi des approches comparées. Il devrait ensuite être envisageable d'organiser une communauté scientifique, internationale (Brésil), autour de la question des approches intégrées pour la gestion écosystémique des pêcheries, avec des applications tropicales.

XII – Annexes

Principales publications

Dynamique des peuplements de poissons démersaux et impact de la pêche dans le golfe de Gascogne : voies d'analyse

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Résumé

La dynamique des peuplements de poissons démersaux du golfe de Gascogne est analysée à partir des indices de diversité spécifique et de la variabilité temporelle de biomasse. La structure de diversité est caractérisée par une forte dominance de quelques espèces dans tout le golfe. Les variations annuelles de biomasse des espèces sont plus fortes que les variations de la biomasse totale. Outre l'effet de compensations aléatoires, ceci indique qu'il existe des compensations entre espèces qui seraient dues à des interactions biotiques. Les enseignements sur la dynamique des peuplements de poissons démersaux exploités obtenus à partir de ces analyses sont discutés.

Abstract

The dynamics of the demersal fish community in the bay of Biscay is investigated by analysing species diversity and biomass variability. A strong dominance of a few species in the whole bay of Biscay is the main pattern of species diversity. The species biomass shows greater annual variations than the total biomass. Apart from the averaging effect, this is usually interpreted as evidence of compensations between species because of energy limitation at the system level. Conclusions about the interest of this approach to address community dynamics and fishing impact are brought.

Introduction

Des auteurs analysent la dynamique des peuplements de poissons démersaux, intégrant l'effet de la pêche. Différentes approches sont utilisées dans ce but : indices de diversité, modélisation, spectre multispécifique de taille, variabilité temporelle de biomasse (Greenstreet & Hall, 1996 ; Rice & Gislason, 1996 ; Duplisea *et al.*, 1997).

La dynamique du peuplement de poissons démersaux du golfe de Gascogne est étudiée selon deux approches à partir de données issues de campagnes scientifiques réalisées de 1987 à 1995. L'analyse de la structure de diversité spécifique constitue la première approche. En effet, cette structure de diversité est issue d'une dynamique particulière. L'analyse de la variabilité de biomasse totale et par espèce constitue la seconde approche.

Les espèces peuvent être contraintes par la capacité d'accueil du milieu qui induit des relations entre elles et régule leur dynamique. Dans ce cas, les compensations entre espèces peuvent se traduire par une faible variabilité de biomasse totale comparée à la variabilité des espèces.

Matériel et méthodes

Les données utilisées sont issues de campagnes scientifiques de chalutage de fond (Evhoe) menées par l'Ifremer dans le golfe de Gascogne entre 1987 et 1995.

La structure de diversité dépend pour partie du type de dynamique à l'œuvre dans le peuplement, telles les perturbations ou les interactions entre espèces (Huston, 1994). Les variations de la diversité et de la biomasse sont analysées pour trois assemblages d'espèces définis selon les travaux de Poulard & Boucher (1997) : côtier (0-50 m), plateau (50-150 m) et pente continentale (profondeur supérieure à 150 m). Les indices de diversité de Hill (1973), N1et N2, sont choisis :

$$N1 = \exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right) \qquad N2 = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

avec p_i, proportion de l'espèce i en abondance et S le nombre d'espèces dans l'échantillon. Les modèles classiques d'accumulation d'espèces (Lande, 1996) sont ajustés pour s'affranchir de l'effet de l'effort d'échantillonnage. Afin de dissocier l'effet du nombre d'espèces et celui de leur abondance relative dans les variations de N1, un abaque est construit : N1 s'exprime aussi sous la forme suivante :

$$N1 = \exp(J' \ln S)$$

avec J', indice de Pielou (1975) exprimant la régularité de distribution des individus en espèces. La régularité J' est calculée pour toute valeur de N1 et S. N1 est représenté en ordonnée, S en abscisse et J' sous forme d'isoplèthes. Pour comparer les indices de diversité, le test-t et le test de Tukey sont utilisés par plusieurs auteurs (Iglesias, 1981 ; Greenstreet & Hall, 1996 ; Ungaro *et al.*, 1998). Ici, les différences entre années et entre assemblages sont testées par analyse de variance à deux critères de classification des indices N1 et N2.

Duplisea *et al.* (1997) ont montré que la variabilité temporelle de la biomasse totale de poissons démersaux est plus faible que la variabilité de biomasse par espèce sur le plateau de la Nouvelle-Écosse. Ceci serait dû aux interactions entre espèces. Le coefficient de variation temporelle de la biomasse totale de poissons démersaux (CVt) est comparé au coefficient de variation des espèces (CVi) dans chacun des trois assemblages :

$CV = (100\sigma)/\bar{x}$, avec σ, l'écart type et $\bar{x}$, la biomasse moyenne. La biomasse totale est estimée par la somme des biomasses des espèces échantillonnées au cours d'une campagne, divisée par la surface chalutée pour chacun des trois assemblages.

Résultats

Analyse de la structure de diversité

Les valeurs de N1 et S sont simulées à partir des modèles d'accumulation d'espèces pour un « 10 traits » de chalut dans chaque assemblage et pour chaque année (fig. 1). Selon l'analyse de variance à deux critères de N1 et N2, les différences entre années et entre assemblages ne sont pas significatives (tab.).

Analyse de variance à deux critères de N1 et N2, années et assemblages d'espèces (zones).

	N1			N2		
	ν	F	P	ν	F	P
Année	6	0,75	0,62	6	0,77	0,61
Zone	2	0,49	0,62	2	2,82	0,11

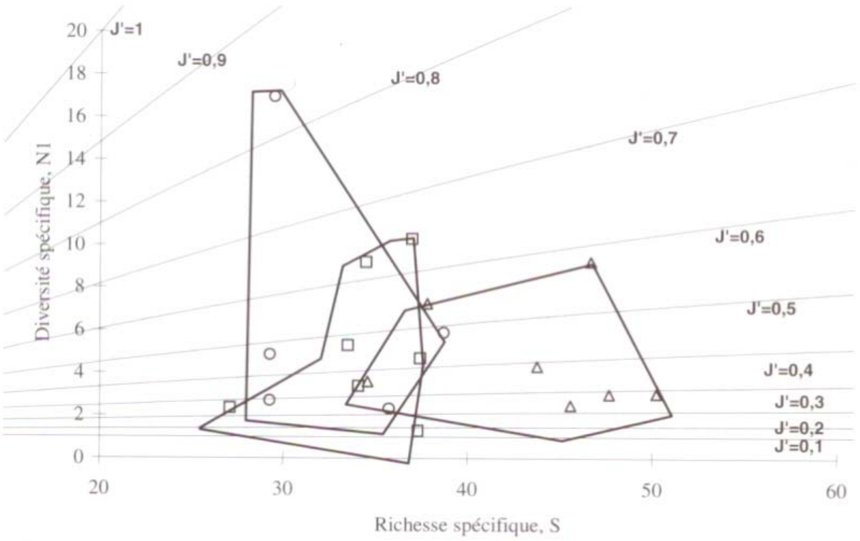

Figure 1 - Relation entre N1, S et J' dans le golfe de Gascogne. Les isoplèthes de valeurs de J' sont reportées par pas de 0,1 (trait plein et fin). Valeurs annuelles pour l'assemblage d'espèces, Δ : de la côte; □ : du plateau; O : de la pente continentale. Les valeurs sont regroupées par assemblage (trait gras continu).

Analyse de la variabilité de la biomasse totale et par espèce

Le coefficient de variation CVt de la biomasse totale est, respectivement dans les assemblages de la côte, du plateau et de la pente, de 33 %, 35 % et 43 pour cent. Le coefficient de variation CVi par espèce varie de 27 à 192 pour cent. Quatre-vingt douze pour cent des espèces ont un coefficient CVi plus fort que celui de la biomasse totale (fig. 2).

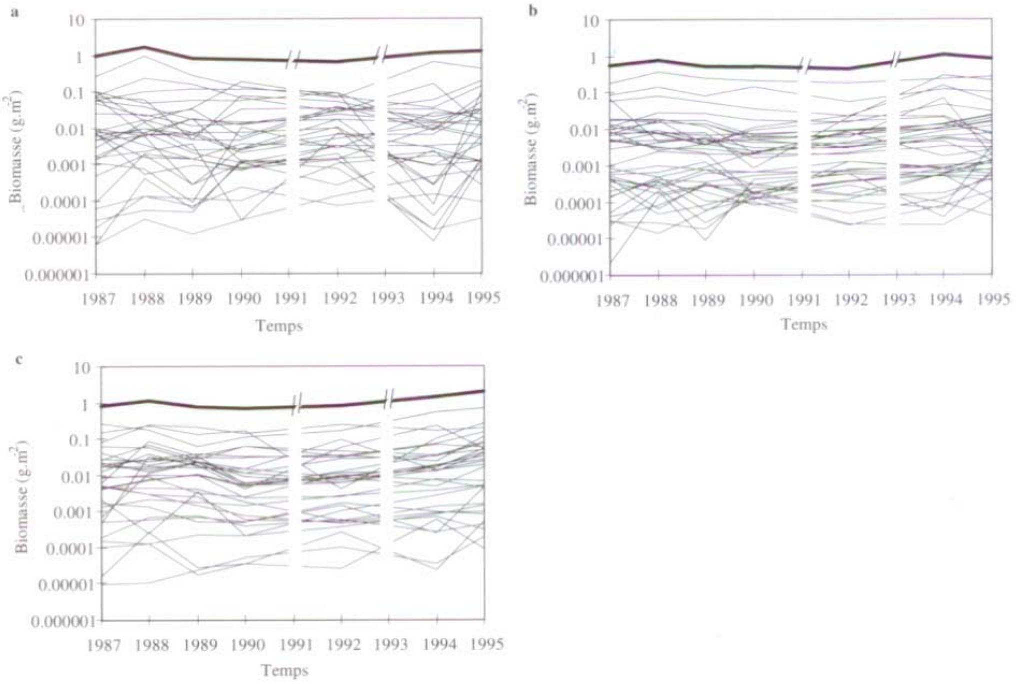

Figure 2 · Variations temporelles de la biomasse totale de poissons démersaux (trait gras) en g.m^{2} et de la biomasse par espèce (traits fins) dans les trois assemblages du golfe de Gascogne. a : assemblage côtier ; b : assemblage du plateau ; c : assemblage de la pente.

Discussion

Des grandes caractéristiques de la diversité apparaissent. Il n'y a pas de différences entre les assemblages. Une même dynamique régulerait donc les assemblages selon cette approche. La variabilité de la biomasse totale est plus faible que celle de la biomasse des espèces. L'effet statistique et les interactions entre espèces expliquent cette observation (Tilman, 2000).

Huston (1994) donne une interprétation de la structure de diversité par une approche comparative, selon la dynamique des peuplements. C'est en comparant, soit plusieurs peuplements de diversité différente, les uns par rapport aux autres, soit un même peuplement pendant une période d'évolution significative, que la dynamique peut être interprétée. Dans le cas du golfe de Gascogne, aucune différence de diversité n'étant observée, il est possible de conclure qu'une même dynamique régule l'ensemble du peuplement, mais sans que l'on puisse définir la nature des processus dominants dans cette dynamique. En revanche, l'analyse de la variabilité de la biomasse totale en regard de celle de la biomasse par espèce permet de mettre en évidence le rôle des interactions biotiques comme processus régulant la dynamique.

Conclusion

À l'échelle d'une décennie, dans le golfe de Gascogne, la diversité ne varie pas. La réponse du peuplement à l'impact de la pêche est probablement déjà intégrée. C'est à une échelle géographique plus vaste et à une échelle temporelle plus grande qu'il faut donc rechercher un impact de la pêche à l'aide des indicateurs de diversité spécifique. La variabilité temporelle de la biomasse totale pourrait être un indicateur du rôle des interactions entre espèces dans la dynamique des peuplements. Or, selon l'hypothèse de Levine (1976), une prédation continue (la pêche peut être considérée comme une prédation continue) pourrait altérer l'intensité des interactions de compétition. Une comparaison de la variabilité de la biomasse totale entre peuplements où le niveau d'exploitation est différent, ou au sein d'un même peuplement avec des séries historiques, permettrait d'analyser l'impact de l'exploitation sur la dynamique des peuplements.

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Une approche de la dynamique des peuplements de poissons démersaux exploités : analyse comparée de la diversité spécifique dans le golfe de Gascogne (océan Atlantique) et dans le golfe du Lion (mer Méditerranée)

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Abstract – Dynamics of harvested demersal fish communities: analysis of the species diversity in the Bay of Biscay (Atlantic Ocean) and in the Gulf of Lions (Mediterranean Sea). Species diversity variations between the demersal fish assemblages of the Bay of Biscay (Atlantic Ocean) and of the Gulf of Lions (Mediterranean Sea) are analysed on a decade scale. The aim of this study is to interpret the dynamics of these two communities characterised by different level of fishing intensity. Data come from trawl surveys carried out for the direct evaluation of the demersal stocks abundance from 1983 to 1997. Diversity indices used are the Hill's indices N1 and N2, the species richness S, the evenness J', the K-dominance curves and the life strategy of the dominant species. Three demersal fish assemblages are defined in the community of the Bay of Biscay and in that of the Gulf of Lions: coastal, continental shelf, and continental slope. There are neither significant differences between the assemblages of the Bay of Biscay nor between those of the Gulf of Lions. There are no significant differences between years. The assemblages of the Gulf of Lions are characterised by higher values of N2 and S than the assemblages of the Bay of Biscay. The K-dominance curves show that there is a lower number of dominant species in the Bay of Biscay than in the Gulf of Lions. Finally, there are more long-lived species among the dominant one in the Gulf of Lions than in the Bay of Biscay. Then the community of the Bay of Biscay corresponds to a system adjusted to perturbations (unpredictable mortalities) while the Gulf of Lions corresponds to a system adjusted to a less perturbed environment. There is no interpretation of the relationship between the level of fishing intensity and the chosen indices at the scale of this study. It is concluded that dynamics patterns of the communities can be interpreted from the species diversity indices when associated with K-dominance curves and life strategy characteristics. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

species diversity / community dynamics / demersal fish / Bay of Biscay / Gulf of Lions

Résumé – Les variations de la diversité spécifique entre les assemblages de poissons démersaux du golfe de Gascogne (océan Atlantique) et du golfe du Lion (mer Méditerranée) sont analysées à l'échelle d'une décennie. L'objectif est d'interpréter la dynamique de ces peuplements dont les niveaux d'exploitation par la pêche diffèrent. Les données utilisées sont issues des campagnes de chalutages réalisées de 1983 à 1997 pour l'évaluation des stocks de poissons démersaux. Les indicateurs de diversité analysés sont les indices *N1* et *N2* de Hill, la richesse spécifique *S*, la régularité *J'*, les courbes K-dominance et les stratégies démographiques des principales espèces. Chacun des deux peuplements est constitué de trois assemblages d'espèces (assemblage côtier, du plateau et de la pente continentale). Il n'existe de différence significative ni entre les assemblages du golfe de Gascogne, ni entre ceux du golfe du Lion. Il n'y a pas non plus de différence significative entre les années. L'ensemble du golfe du Lion est caractérisé par des valeurs *N2* et des indices *S* plus élevés que dans le golfe de Gascogne. *S*elon les courbes K-dominance, le peuplement du golfe de Gascogne est caractérisé par un plus petit nombre d'espèces dominantes que dans le golfe du Lion. Enfin, les espèces dominantes du golfe du Lion sont caractérisées par une longévité et/ou une taille maximale plus grande que celles du golfe de Gascogne. Le golfe de Gascogne correspondrait à un système adapté à l'existence de perturbations (mortalités imprévisibles), tandis que le golfe du Lion correspondrait à un système adapté à un environnement moins perturbé. Un impact de l'exploitation n'a pu être interprété à partir des indices choisis, utilisés à cette échelle. Toutefois, lorsque les indices de diversité sont mis en relation avec la stratégie démographique des espèces, des éléments de dynamique des peuplements sont mis en évidence. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

diversité spécifique / dynamique des peuplements / poissons démersaux / golfe de Gascogne / golfe du Lion

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1. INTRODUCTION

Devant l'obligation de préserver la biodiversité (convention de la diversité biologique, 1992) et face à l'exploitation des écosystèmes marins par la pêche, il est nécessaire de connaître la diversité des espèces et les processus qui assurent son maintien. Ainsi, des méthodes de mesure de la biodiversité permettant

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d'établir un diagnostic de l'état des peuplements exploités sont recherchées.

Dans cette perspective récente particulière, les principaux indicateurs de la diversité spécifique utilisés conjointement sont notamment la richesse spécifique, les indices de diversité spécifique de Shannon et de Hill, les indices de dominance. L'évolution temporelle de la diversité mesurée par ces indicateurs est analysée, parfois depuis la première moitié du siècle (Greenstreet et Hall, 1996 ; Rice et Gislason, 1996 ; Rogers et Ellis, 2000), ou au cours de la seconde moitié (Xianshi et Qisheng, 1996 ; Lekve et al., 1999 ; Bianchi et al., 2000), voire depuis 2000 ans (Wolff, 2000a, b). D'autres analyses mettent en évidence des variations spatiales de la diversité (McClanahan, 1994 ; Jennings et Polunin, 1997 ; Ungaro et al., 1998). Dans chacune de ces analyses, des changements de la diversité, en relation avec l'exploitation, sont mis en évidence à partir de l'un ou l'autre des indices, mais jamais de l'ensemble de ceux utilisés. De plus, les changements observés sont parfois contradictoires selon les études (augmentation ou diminution de la diversité). Outre l'effet de l'exploitation, il n'y a pas d'interprétation écologique de ces résultats dans ces travaux.

D'autres auteurs analysent la diversité dans la perspective d'identifier les facteurs qui déterminent ses variations. À l'échelle spatiale des grands bassins, tels que les océans et mers, c'est l'effet de la latitude (Horn et Allen, 1978 ; Macpherson et Duarte, 1994) ou de l'histoire biogéographique sur la diversité (Garibaldi et Caddy, 1998) qui est évoqué (Gaston, 2000). À une échelle spatiale plus fine, l'échelle d'un peuplement, l'effet de la profondeur sur la diversité est mis en évidence (Sanchez-Gil et al., 1981 ; McClatchie et al., 1997). Dans ce cas, les perturbations physiques de l'environnement et la productivité seraient les facteurs explicatifs liés à la bathymétrie. La composition et la distribution des sédiments influent aussi la diversité spécifique des peuplements de poissons démersaux (Rodriguez-Capetillo et al., 1987). Toutefois, les perturbations et la productivité sont des variables difficiles à mesurer (Boucher, 1997). Ainsi, il existe peu d'analyses de la diversité intégrant à la fois une interprétation écologique et l'impact de l'exploitation par la pêche.

Frontier et Pichod-Viale (1991) donnent une interprétation écologique de la dynamique des peuplements à partir de la structure de diversité spécifique selon une succession écologique. Un peuplement au stade pionnier, soumis à des perturbations, est constitué d'un nombre relativement faible d'espèces à multiplication rapide. Si les perturbations cessent, le peuplement se diversifie par apparition d'espèces à croissance plus lente, c'est le stade mature. Ainsi, selon ces auteurs, la stratégie démographique des espèces dominantes est un élément qui permet une première interprétation de la dynamique à partir de la structure de diversité sans avoir à mesurer des facteurs tels que la productivité et les perturbations.

Deux types d'effets de l'exploitation par la pêche sont mis en évidence sur les stratégies démographiques des espèces. D'une part, une diminution de l'âge et une augmentation de la taille à première maturité des populations exploitées est observée à court terme (Rochet, 1998). D'autre part, une décroissance de l'abondance des espèces ayant une croissance lente et un âge à première maturité tardif est mise en évidence en mer du Nord (Jennings et al., 1999). L'analyse des stratégies démographiques, utilisée en complément des indices de diversité spécifique, dans le cadre de l'interprétation donnée par Frontier et Pichod-Viale (1991), pourrait donc contribuer à l'interprétation des observations et à établir un diagnostic sur la dynamique des peuplements exploités.

Des éléments de la dynamique des peuplements de poissons démersaux du golfe du Lion et du golfe de Gascogne sont analysés par Blanchard et Boucher (2001) à partir des variations annuelles de la biomasse, pour une décennie. L'exploitation, mesurée par les débarquements commerciaux par unité de surface, plus forte dans le golfe du Lion que dans le golfe de Gascogne, modifie pour partie la dynamique des peuplements, en diminuant le rôle des interactions biotiques entre les espèces. Toutefois, la diversité n'est pas analysée.

Ici, l'objectif est d'interpréter la dynamique des peuplements exploités par la pêche à partir de la théorie de Frontier et Pichod-Viale (1991) à l'aide des indicateurs de diversité spécifique cités, complétés des stratégies démographiques des espèces.

Dans cette optique, l'existence de tendances temporelles ou spatiales, de variations de la diversité des poissons démersaux à l'échelle d'une décennie dans le golfe du Lion et dans le golfe de Gascogne est recherchée. La possibilité de mettre ces tendances en relation avec l'exploitation est discutée. Les variations de la diversité sont établies à partir des données de campagnes de chalutage scientifique menées de 1983 à 1997, pour les différents assemblages d'espèces du golfe du Lion et du golfe de Gascogne. Les indices de diversité spécifique utilisés sont les indices de Hill, de richesse spécifique, de dominance et les courbes K-dominance. Les stratégies démographiques des espèces dominantes dans chaque assemblage sont établies à partir de la longévité et de la longueur maximale à l'âge adulte (Adams, 1980).

2. MATÉRIEL ET MÉTHODES

2.1. Données

Trois séries de données indépendantes issues de campagnes scientifiques de chalutage de fond menées par l'Ifremer pour l'évaluation des stocks halieutiques sont utilisées. La première série (EVHOE) est issue de 7 campagnes menées dans le golfe de Gascogne, en octobre/novembre, de 1987 à 1990, en 1992, 1994 et 1995. De 101 à 142 traits de chalut sont réalisés pendant chaque campagne. Les deux autres séries sont issues de campagnes menées dans le golfe du Lion en mai/juin 1983, de 1985 à 1987, et en 1992 pour la seconde série (CHALIST) et de 1994 à 1997 pour la troisième série (MEDITS). De 57 à 110 traits de chalut sont réalisés pendant chaque campagne. Seules les espèces démersales communes aux échantillonnages de la deuxième et troisième série sont retenues dans nos analyses. L'échantillonnage ciblant les espèces démersales, les espèces pélagiques trouvées dans les échantillons ne sont prises en compte pour aucune des campagnes dans nos analyses.

Les stations sont réparties aléatoirement dans des strates définies selon la profondeur, de 10 à 600 m. Le nombre de stations est le même dans chaque strate. Le protocole d'échantillonnage des campagnes EVHOE est décrit par Amara et al. (1998). Les protocoles d'échantillonnage des campagnes CHALIST et MEDITS sont décrits respectivement par Gaertner et al. (1998) et Bertrand et al. (1997).

2.2. Répartition géographique des assemblages

Le peuplement de poissons démersaux du golfe de Gascogne, ainsi que celui du golfe du Lion, est constitué de plusieurs assemblages d'espèces (Poulard et Boucher, 1997 ; Gaertner et al., 1998). Ces assemblages sont définis par analyse factorielle et classification hiérarchique. Le nombre d'assemblages définis au sein d'un peuplement dépend du choix de niveau de coupure du dendrogramme obtenu. Une coupure en trois assemblages est retenue par Gaertner et al. (1998) : un assemblage côtier de 0 à 80 m, un assemblage du plateau continental de 80 à 150 m et un assemblage de la pente continentale au-delà de 150 m. Ce niveau de coupure, cohérent avec les résultats de Poulard et Boucher (1997) pour le golfe de Gascogne, est retenu ici. En effet, ce gradient bathymétrique pourrait induire un gradient de facteurs susceptibles de faire varier la diversité spécifique entre les assemblages. Ainsi, les variations annuelles de la diversité, sur la période de 1983 à 1997, sont analysées pour chacun de ces 6 assemblages d'espèces.

2.3. Indices de diversité

En mer du Nord, les indices de diversité *N1* de Hill, fonction exponentielle de l'indice *H'* de Shannon, et *N2,* réciproque de l'indice de Simpson, ont été choisis (Greenstreet et Hall, 1996) pour leur complémentarité. En effet, l'indice *N2* est sensible à la présence des espèces les plus abondantes puisque chaque proportion est élevée au carré, tandis que *N1* l'est moins car dans ce cas chaque proportion est pondérée par son logarithme (Hill, 1973). *N1* et *N2* dépendent de la richesse spécifique (*S*), soit le nombre d'espèces, et de la régularité (*J'*) de répartition des individus en espèces. Lorsque toutes les proportions sont identiques, *J'* = 1.

$$N1 = \exp\left(- \sum_{i=1}^{S} p_{\mathrm{i}} \ln p_{\mathrm{i}} \right) \qquad (1)$$

$$N2 = \frac{1}{\sum_{i=1}^{S} p_{\mathrm{i}}^{2}} \qquad (2)$$

$$J' = \frac{\ln N1}{\ln S} \qquad (3)$$

avec p_{i}, proportion de l'espèce i en abondance et *S* le nombre d'espèces dans l'échantillon.

L'indice de diversité *N1* et la richesse spécifique (*S*) sont sensibles à l'effort d'échantillonnage, mais non l'indice *N2* (Hill, 1973 ; Lande, 1996). L'effort n'est pas le même dans les 6 assemblages géographiques définis. La méthode de raréfaction, classiquement utilisée, permet de modéliser les relations entre la richesse spécifique (*S*), l'indice *N1* et l'effort d'échantillonnage (*f*). Ainsi, les valeurs de *S* et *N1* sont calculées pour un effort identique entre campagnes de chalutage et assemblages (Lande, 1996 ; Warwick et Clarke, 1995 ; cf. annexes 1 et 2).

Les différences entre les années et entre les assemblages sont testées par analyse de variance à deux critères de l'indice *N1, N2, S* et *J'* (Scherrer, 1983). Lorsque des différences sont significatives, le test de rangs multiples basé sur la plus petite différence significative permet de classer les valeurs (Scherrer, 1983).

2.4. Courbes K-dominance

En complément de ces mesures univariées, la représentation graphique des distributions de fréquence cumulée par ordre décroissant des espèces est présentée (Lambshead et al., 1983). Les distributions en abondance et en biomasse peuvent être présentées sur un même graphique (Warwick, 1986 ; Warwick et al., 1987 ; Warwick et Clarke, 1991). Lorsque la courbe de biomasse est plus élevée que la courbe d'abondance, l'assemblage est dominé par des espèces dont les individus sont peu nombreux mais de forte masse corporelle observée. À l'inverse, lorsque la courbe de biomasse est moins élevée que la courbe d'abondance, l'assemblage est dominé par des espèces dont les individus sont nombreux mais de faible masse corporelle.

Ces distributions sont calculées par campagne, pour l'ensemble des traits de chalut agrégés par assemblage. Chaque assemblage est caractérisé par ses distributions moyennes. La représentation graphique des distributions par campagne permet d'établir une éventuelle évolution temporelle.

2.5. Traits démographiques des espèces dominantes

Pour caractériser les stratégies démographiques des espèces, la longévité et la longueur maximale sont deux traits démographiques classiquement utilisés. Ces paramètres sont utilisés pour établir le type de stratégie démographique des espèces dominantes dans chaque assemblage. Ils doivent aider à l'interprétation de la dynamique (Frontier et Pichod-Viale, 1991) : un assemblage dont les espèces dominantes ont une petite taille, une croissance rapide et une longévité courte (stratégie r), serait plus perturbé qu'un assemblage où dominent des espèces de taille plus grande, de croissance lente et de forte longévité (stratégie K).

La composition spécifique relative est déterminée dans chaque assemblage, à partir de la moyenne interannuelle des abondances et des biomasses par espèce. Les stratégies démographiques sont susceptibles d'être modifiées à court terme par un effet de la pêche (Rochet, 1998). Toutefois, il ne s'agit pas ici de mesurer des changements de stratégies liés à la plasticité pour des mêmes espèces entre deux régions, mais de mettre en évidence une différence de type d'espèces dominantes selon leur stratégie sur un gradient r–K. La précision et l'actualité des données de longévité et de taille maximale de l'espèce (longueur standard ou totale) données par Quéro (1984) et Whitehead et al. (1986) pour l'Atlantique Nord-Est et la Méditerranée sont donc adaptées pour ce travail.

3. RÉSULTATS

3.1. Indices de diversité spécifique

Les paramètres des modèles de raréfaction ajustés aux données sont indiqués en annexe 1 et 2. L'indice *N1* de diversité de Hill et la richesse spécifique (*S*), sont simulés à partir de ces modèles pour un même effort d'échantillonnage, soit 100 traits de chalut.

Aucune tendance dans le temps n'est visible graphiquement pour *N1*, *N2*, *S* et *J'* (*figure 1*). Trois analyses de variance à deux critères, assemblages et années, sont réalisées pour chaque indice *N1*, *N2*, *S* et *J'* (*tableau I*) : une analyse avec les 6 assemblages, une analyse dans le golfe du Lion et une dans le golfe de Gascogne. Les analyses de l'indice *N1* et de l'indice *J'* n'indiquent de différences, ni entre années, ni entre zones. L'analyse de variance de l'indice *N2* pour les 6 assemblages indique des différences significatives entre zones, tandis que les analyses pour chacun des golfes n'indiquent pas de différences. Il existe donc des différences selon l'indice *N2* entre les assemblages du golfe du Lion et ceux du golfe de Gascogne. Les analyses de variance de l'indice *S* pour les 6 assemblages, pour le golfe de Gascogne et le golfe du Lion indiquent des différences entre zones. Le test de rangs multiples de l'indice *S* indique que le nombre d'espèce est plus grand dans le golfe du Lion.

L'indice *N2* permet de mettre en évidence une différence de diversité entre le golfe du Lion et le golfe de Gascogne, contrairement à l'indice *N1*. *N2* étant plus sensible que *N1* aux espèces les plus abondantes, une différence entre ces deux systèmes biogéographiques serait donc liée à la présence de quelques espèces dominant fortement dans le système où *N2* est plus faible, dans le golfe de Gascogne. L'indice *S* permet de mettre en évidence que le nombre d'espèces est plus grand dans le golfe du Lion.

3.2. Courbes K-dominance

Les distributions moyennes en biomasse et abondance permettent de savoir si les individus des espèces dominantes sont de petite taille observée et en forte abondance ou de forte taille observée et de faible abondance (*figure 2*). Dans le golfe de Gascogne, la distribution en abondance des espèces est plus élevée que la distribution en biomasse dans les trois assemblages, indiquant une forte dominance d'espèces dont les individus sont nombreux et de faible masse corporelle. Dans le golfe du Lion, la distribution en abondance et la distribution en biomasse des assemblages de la côte et du plateau sont quasiment confondues. L'assemblage de la pente continentale du golfe du Lion est caractérisé par des distributions similaires à celle du golfe de Gascogne. Le gradient de profondeur n'induit pas de tendance cohérente des distributions K-dominance pour les deux golfes. Selon cette méthode, le peuplement du golfe de Gascogne est carac-

Tableau I. Analyse de variance à deux critères de *N1*, *N2* (indices de diversité de Hill), *S* (richesse spécifique) et *J'* (régularité de Piélou), entre années et assemblages d'espèces (zones), générale (golfe du Lion et golfe de Gascogne) et par région.

Table I. Two-ways analysis of variance of *N1*, *N2*, *S* and *J'*, between years and species assemblages (zones), global (Gulf of Lions and Bay of Biscay) and within each area.

			N1		*N2*		*S*		*J'*	
	Critère	ν	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Globale	Année	11	1,15	0,36	2,01	0,07	2,4	0,04	0,48	0,9
	Zone	5	2,6	0,05	12,32	0*	12,6	0*	1,5	0,21
golfe du Lion	Année	8	1,5	0,26	2,48	0,08	1,76	0,19	0,97	0,5
	Zone	2	4,8	0,03	0,71	0,51	8,7	0,005*	2,6	0,12
golfe de Gascogne	Année	6	0,59	0,73	0,77	0,61	2,31	0,11	0,49	0,8
	Zone	2	0,35	0,71	2,82	0,11	17,9	0*	0,49	0,63

* différence significative ($P < 0.01$). * significant difference ($P < 0.01$).

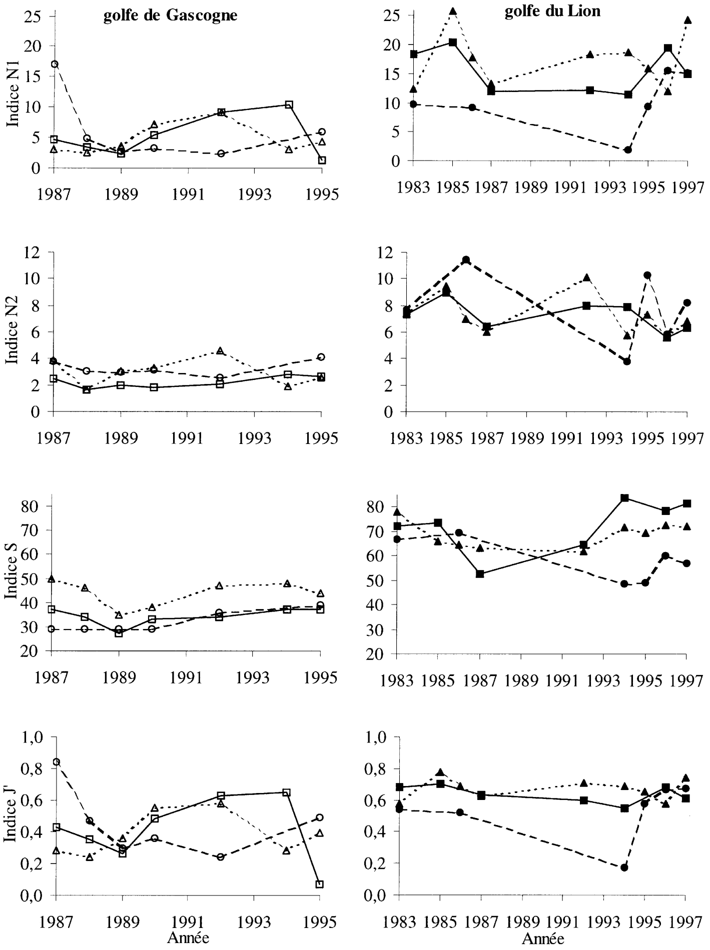

Figure 1. Temporal variations of the species diversity *N1* and *N2* indices, the species richness *S* index, the evenness *J'* index in the demersal fish assemblages of the Bay of Biscay: △, coastal assemblage; □, continental shelf assemblage; ○, continental slope assemblage; and of the Gulf of Lions: ▲, coastal assemblage; ■, shelf assemblage; ●, slope assemblage.

Figure 1. Variations temporelles des indices *N1*, *N2* de diversité spécifique de Hill, de l'indice *S* de richesse spécifique et de l'indice de régularité *J'* de Piélou dans les assemblages de poissons démersaux du golfe de Gascogne : △, assemblage de la côte ; □, assemblage du plateau ; ○, assemblage de la pente ; et du golfe du Lion : ▲, assemblage de la côte ; ■, assemblage du plateau ; ●, assemblage de la pente.

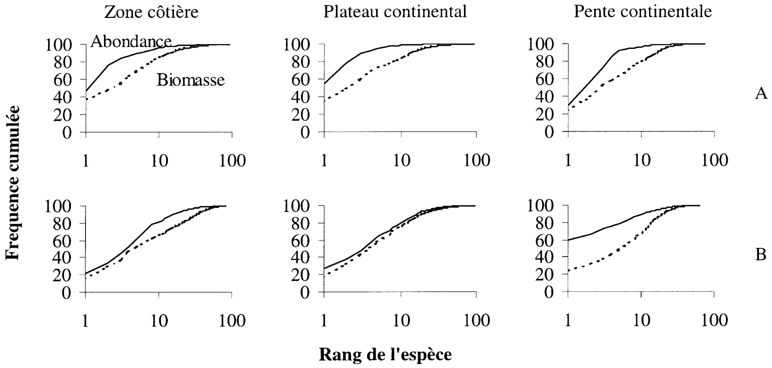

Figure 2. Average K-dominance curves in abundance (solid line) and biomass (dotted line) in the demersal fish assemblages of the Bay of Biscay (A) and of the Gulf of Lions (B).

Figure 2. Courbes K-dominance moyennes en abondance (trait plein) et en biomasse (trait pointillé) pour les assemblages de poissons démersaux du golfe de Gascogne (A) et du golfe du Lion (B).

térisé par des espèces dominantes dont les individus sont plus nombreux en proportion que dans le golfe du Lion et de plus petite taille.

L'ordonnée à l'origine des distributions annuelles en abondance de chaque assemblage varie au cours de la décennie analysée sans montrer de tendance (*figure 3*). L'assemblage de la pente du golfe du Lion est caractérisé par des variations plus fortes que les autres assemblages. Les 4 distributions de l'assemblage de la pente continentale du golfe du Lion dont les ordonnées à l'origine sont les plus élevées, correspondent aux campagnes MEDITS tandis que les 2 distributions dont les ordonnées à l'origine sont les plus basses, correspondent aux campagnes CHALIST. Bien que dans les assemblages de la côte et du plateau du golfe du Lion, il n'y ait pas de variations explicables par les différences de protocole entre les deux types de campagnes, il n'est pas exclu que les différences de distributions observées à la pente soient dues aux différences de protocole.

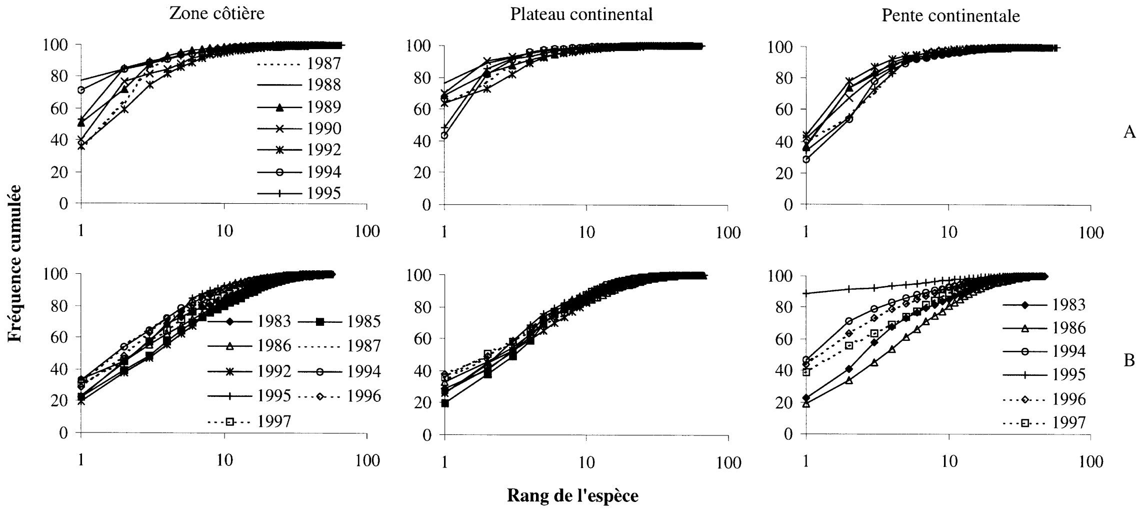

Figure 3. Courbes K-dominance annuelles en abondance pour les assemblages de poissons démersaux du golfe de Gascogne (A) et du golfe du Lion (B).

Figure 3. Yearly K-dominance curves in abundance in the demersal fish assemblages of the Bay of Biscay (A) and of the Gulf of Lions (B).

Les courbes K-dominance annuelles ne montrent pas de tendance dans le temps. Le golfe de Gascogne est caractérisé par des courbes K-dominance indiquant un système dominé par quelques espèces dont les individus sont de petite taille. Il s'agit soit d'espèces représentées par les juvéniles ou des espèces de stratégie démographique de type r. Le golfe du Lion est caractérisé par des courbes K-dominance indiquant un système dominé par des espèces dont les individus sont de plus grande taille. Il s'agit soit d'espèces représentées par les adultes ou des espèces de stratégie démographique de type K.

3.3. Composition relative en espèces et stratégies démographiques

La composition en espèces, en abondances et biomasses relatives (moyennes pour la période étudiée) permet d'identifier les espèces dominantes dont la stratégie démographique doit être analysée. Pour plus de lisibilité des graphiques, seuls 90% de la biomasse et de l'abondance des assemblages sont représentés.

Dans le golfe de Gascogne (*figure 4a*), 5 espèces constituent plus de 50% de la biomasse et de l'abondance. Les assemblages sont donc dominés par un petit nombre d'espèces : le tacaud commun (*Trisopterus luscus*), le petit tacaud (*Trisopterus minutus*), le sanglier (*Capros aper*), la grande argentine (*Argentina silus*) et le merlu européen (*Merluccius merluccius*).

Dans le golfe du Lion (*figure 4b*), 11 espèces constituent plus de 50% de la biomasse et de l'abondance. Le petit tacaud (*Trisopterus minutus capelanus*), la rascasse du nord (*Helicolenus dactylopterus*), le gadicule argenté (*Gadiculus argenteus*), le grondin gris (*Eutrigla gurnardus*), la petite roussette (*Scyliorhinus canicula*), le congre (*Conger conger*), le merlu européen (*Merluccius merluccius*), la baudroie rousse et la baudroie commune (*Lophius budegassa* et *L. piscatorius*), le chien espagnol (*Galeus melastomus*) et le grenadier (*Trachyrhynchus trachyrhynchus*).

Les traits démographiques de ces espèces sont donnés : la taille maximale et la longévité que l'espèce peut atteindre (*tableau III*). Les espèces dominantes du golfe de Gascogne sont caractérisées par une taille maximale plus petite et une longévité plus faible que les espèces dominantes du golfe du Lion. Pour illustrer ce propos, la taille moyenne des espèces dominantes est calculée dans les 2 golfes, soit la somme des tailles individuelles figurant au *tableau III*, divisée par le nombre d'espèces concernées (5 pour le golfe de Gascogne et 11 pour le golfe du Lion). Cette taille moyenne est environ de 50 cm pour les espèces dominantes du golfe de Gascogne et environ de 100 cm pour les espèces dominantes du golfe du Lion.

4. DISCUSSION

Les grandes caractéristiques des variations de la diversité apparaissent. La variabilité interannuelle est forte quel que soit l'assemblage et les indices n'indiquent pas de tendance croissante ou décroissante dans le temps. Il n'y a pas de gradient de diversité selon la bathymétrie correspondant aux assemblages choisis. La diversité spécifique est plus élevée dans le golfe du Lion selon l'indice *N2* et l'indice *S* que dans le golfe de Gascogne. A l'exception de l'assemblage de la pente continentale, fortement dominé par une espèce de petite taille (*Gadiculus argenteus*), les assemblages du golfe du Lion sont caractérisés par des espèces dominantes dont les individus sont de plus forte taille observée que ceux des espèces dominantes du golfe de Gascogne. Enfin, parmi les espèces dominantes, la proportion d'espèces de forte longévité, de croissance

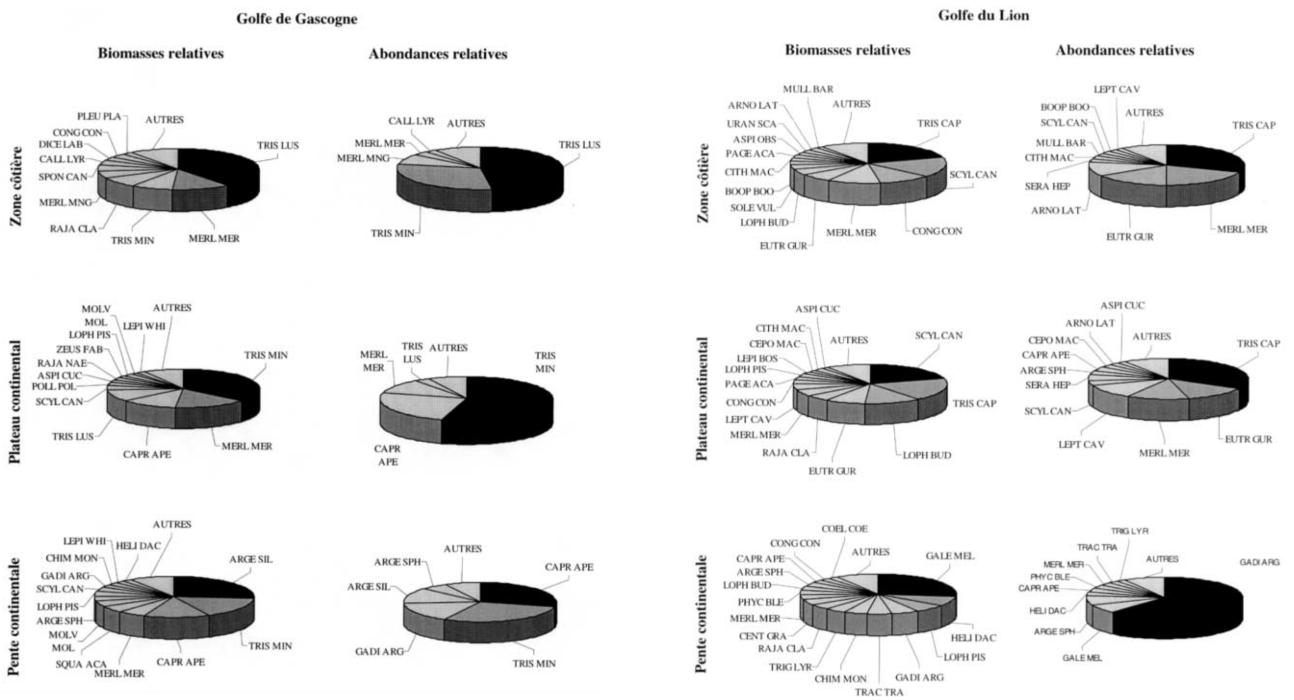

Figure 4. Biomasses et abondances relatives des espèces des trois assemblages de poissons démersaux du golfe de Gascogne et du golfe du Lion. La signification des codes est donnée dans le *tableau II*.

Figure 4. Relative biomass and abundance of species in the three demersal fish assemblages of the Bay of Biscay and of the Gulf of Lions. Species codes, scientific and common names are given in *table II*.

plus lente et d'âge à maturité plus tardif, est plus grande dans le golfe du Lion que dans le golfe de Gascogne. Même si des modifications par l'exploitation ont pu intervenir et réduire les longévités, des espèces comme *Lophius piscatorius*, *L. budegassa*, *Galeus melastomus* et *Conger conger*, dominantes dans le golfe du Lion, restent des espèces de stratégie démographique de type K comparées à des espèces telles que *Trisopterus minutus* et *T. luscus*, dominantes dans le golfe de Gascogne.

Ainsi, selon les principes énoncés par Frontier et Pichod-Viale (1991), le golfe de Gascogne, où les espèces dominantes sont de faible taille et de longévité courte, correspondrait à un système adapté à l'existence de perturbations. Le golfe du Lion, plus diversifié, où dominent des espèces de forte longévité et de taille plus grande, correspondrait à un système moins perturbé. Les perturbations sont définies ici par la mortalité due à l'environnement hydroclimatique (tempêtes, anomalies de températures, de vents) et aux activités anthropiques (pollution, surexploitation). Le peuplement du golfe de Gascogne est donc un système adapté à des mortalités plus fortes et/ou plus fréquentes que le peuplement du golfe du Lion. Une analyse de la variabilité des biomasses, à partir de ces mêmes données, a permis de mettre en évidence une différence du rôle des interactions biotiques entre les espèces dans la dynamique de ces peuplements (Blanchard et Boucher, 2001). Ici, c'est le rôle du régime de perturbations dans la dynamique des peuplements qui est mis en évidence.

La pression de pêche exercée sur les stocks de poissons démersaux est généralement maximale pour les gros individus. Ainsi, la proportion d'espèces dominantes de stratégie r, petite taille et faible longévité, devrait théoriquement augmenter avec l'intensité l'exploitation (Jennings et Kaiser, 1998). La pression de pêche est plus forte dans le golfe du Lion que dans le golfe de Gascogne, comme le montrent les débarquements commerciaux en poissons démersaux, rapportés à la surface de la région exploitée (Blanchard et Boucher, 2001). Ainsi, à cause de l'exploitation, la proportion d'espèces de stratégie r devrait théoriquement augmenter plus fortement dans le golfe du Lion que dans le golfe de Gascogne. Toutefois, selon nos résultats, la proportion de telles espèces est plus forte dans le golfe de Gascogne que dans le golfe du Lion. De plus, à l'échelle de temps de cette étude, une décennie, il n'y a pas d'augmentation de la proportion d'individus de petites tailles. La structure de diversité observée ici serait donc indépendante de l'effet de l'exploitation. Dans le golfe du Lion, le nombre d'espèces de poissons démersaux est stable entre 1957 et 1994 (Aldebert, 1997). Seul le nombre d'espèces de sélaciens, espèces de stratégie de type K, diminue. Cette tendance décroissante intervient principalement entre les années 60 et les années 80, soit avant la période étudiée dans notre analyse. De même, une

Tableau II. Liste des espèces et codes utilisés (*figure 4*) pour le golfe du Lion (L) et le golfe de Gascogne (G).
Table II. Species codes and names used (*figure 4*), for the Gulf of Lions (L) and the Bay of Biscay (G).

Code	Nom scientifique	Nom vernaculaire	Zone
ARGE SPH	*Argentina sphyraena*	Petite argentine	GL
ARGE SIL	*Argentina silus*	Grande argentine	G
ARNO LAT	*Arnoglossus laterna*	Fausse limande	L
ASPI CUC	*Aspitrigla cuculus*	Grondin rouge	G L
ASPI OBS	*Aspitrigla obscura*	Grondin sombre	L
BOOP BOO	*Boops boops*	Bogue	L
CALL LYR	*Callionymus lyra*	Dragonet lyre	G
CAPR APE	*Capros aper*	Sanglier	GL
CENT GRA	*Centrophorus granulosus*	Squale-chagrin commun	L
CEPO MAC	*Cepola macrophtalma*	Cépole commune	L
CHIM MON	*Chimaera monstrosa*	Chimère commune	G L
CITH MAC	*Citharus macrolepidotus*	Feuille	L
COEL COE	*Coelorhynchus coelorhynchus*	Grenadier raton	L
CONG CON	*Conger conger*	Congre	G L
DICE LAB	*Dicentrarchus labrax*	Bar commun	G
EUTR GUR	*Eutrigla gurnardus*	Grondin gris	L
GADI ARG	*Gadiculus argenteus*	Merlan argenté	G L
GALE MEL	*Galeus melastomus*	Chien espagnol	L
HELI DAC	*Helicolenus dactylopterus*	Rascasse du Nord	G L
LEPI BOS	*Lepidorhombus boscii*	Cardine quatre taches	L
LEPI WHI	*Lepidorhombus whiffiagonis*	Cardine	G
LEPT CAV	*Lepidotrigla cavillone*	Cavillone	G
LOPH BUD	*Lophius budegassa*	Baudroie rousse	L
LOPH PIS	*Lophius piscatorius*	Baudroie commune	G L
MERL MER	*Merluccius merluccius*	Merlu européen	G L
MERL MNG	*Merlangius merlangus*	Merlan	G
MOLV MOL	*Molva molva*	Grande lingue	G
MULL BAR	*Mullus barbatus*	Rouget de vase	L
PAGE ACA	*Pagellus acarne*	Pageot acarné	L
PHYC BLE	*Phycis blennoides*	Mostelle de vase	L
PLEU PLA	*Pleuronectes platessa*	Plie	G
POLL POL	*Pollachius pollachius*	Lieu jaune	G
RAJA CLA	*Raja clavata*	Raie bouclée	G L
RAJA NAE	*Raja naevus*	Raie fleurie	G
SCYL CAN	*Scyliorhinus canicula*	Petite roussette	G L
SERA HEP	*Serranus hepatus*	Tambour	L
SOLE VUL	*Solea vulgaris*	Sole commune	L
SPON CAN	*Spondyliosoma cantharus*	Dorade grise	G
SQUA ACA	*Squalus acanthias*	Aiguillat commun	G
TRAC TRA	*Trachyrhynchus trachyrhynchus*	Grenadier	L
TRIG LYR	*Trigla lyra*	Grondin lyre	L
TRIS CAP	*Trisopterus minutus capelanus*	Capelan	L
TRIS LUS	*Trisopterus luscus*	Tacaud commun	G
TRIS MIN	*Trisopterus minutus minutus*	Petit tacaud	G
URAN SCA	*Uranoscopus scaber*	Rascasse blanche	L
ZEUS FAB	*Zeus faber*	Saint-Pierre	G

disparition de sélaciens est observée dans le golfe de Gascogne, au large du bassin d'Arcachon, au cours des 3 derniers siècles (Quéro et Cendrero, 1996). Ainsi, l'image de la diversité des peuplements, observée entre 1993 et 1997 intègre déjà probablement un impact de l'exploitation.

Une explication des caractéristiques de diversité peut alors être cherchée dans la biogéographie de ces régions (Boucher, 1997). La région Méditerranéenne–Atlantique appartient à la province tempérée nord-est atlantique. La sous-province chaude méditerranéenne a son équivalent en atlantique, c'est la sous-province chaude lusitanienne, des Canaries et Açores jusqu'au nord de la péninsule ibérique (St Jean de Luz). Le golfe de Gascogne appartient à la sous-province tempérée moyenne, mais c'est une région qui est une zone de transition entre la sous-province lusitanienne et la sous-province tempérée moyenne (boréale) qui n'apparaît réellement qu'au nord du golfe de Gascogne (Glémarec, 1988). Tortonese (cité par Briggs, 1974) compare la faune ichtyologique de la côte Atlantique (Portugal) à celle de Méditerranée. Il dénombre 362 espèces à la côte en Méditerranée pour 248 au Portugal. Seules 30 espèces trouvées au Portugal ne sont pas répertoriées en Méditerranée. Parmi ces 30, 17 sont distribuées vers le nord, dans des eaux plus froides, 9 sont des espèces tempérées à affinité chaude qui atteignent la limite nord de leur distribution

Tableau III. Traits démographiques des espèces dominantes (représentant plus de 50% de la biomasse et de l'abondance totale) du golfe de Gascogne et du golfe du Lion*.

Table III. Life history traits of the dominant species (more than 50% of the total biomass and abundance) in the Bay of Biscay and in the Gulf of Lions*.

Nom commun	Nom scientifique	*Tmax* (cm)	Longévité (an)	Région
Merlan argenté	*Gadiculus argenteus*	15 (*SL*)	nd	L
Sanglier	*Capros aper*	16 (*SL*)	nd	G
Petit tacaud	*Trisopterus minutus*	26 (*SL*)	4 à 6	G, L
Rascasse du Nord	*Helicolenus dactylopterus*	44 (*TL*)	5	L
Tacaud commun	*Trisopterus luscus*	45 (*SL*)	4 à 5	G
Grenadier	*Trachyrhynchus trachyrhynchus*	50 (*TL*)	nd	L
Grondin gris	*Eutrigla gurnardus*	50 (*TL*)	7	L
Grande argentine	*Argentina silus*	60 (*TL*)	20	G
Chien espagnol	*Galeus melastomus*	61 à 90 (*TL*)	nd	L
Petite roussette	*Scyliorhinus canicula*	100 (*TL*)	nd	L
Baudroie rousse	*Lophius budegassa*	100 (*SL*)	25	L
Merlu européen	*Merluccius merluccius*	120 (*SL*)	20	G, L
Baudroie commune	*Lophius piscatorius*	200 (*SL*)	25	L
Congre	*Conger conger*	300 (*TL*)	15	L

* D'après Quéro, 1984 ; Whitehead et al., 1986. *Tmax*, longueur maximum atteinte par l'espèce. *SL*, longueur standard ; *TL*, longueur totale ; nd, non déterminée ; Région : région où l'espèce est observée (G, golfe de Gascogne ; L, golfe du Lion).
* From Quéro, 1984; Whitehead et al., 1986. *Tmax*, maximum length *SL*, standard length; *TL*, total length; nd, not determined; Région: area where the species is observed (G, Bay of Biscay; L, Gulf of Lions).

au Portugal et 3 peuvent être qualifiées d'espèces tempérées au sens large ou tempérées chaudes. Si la plupart des espèces tropicales atteignent leur limite nord à Gibraltar, on peut encore trouver quelques espèces tempérées chaudes dans le golfe de Gascogne, ce qui confirme le caractère transitoire de ce secteur. Ainsi, la Méditerranée est plus riche en espèces que la côte Atlantique. Cette tendance de la richesse spécifique est retrouvée au niveau du golfe de Gascogne et du golfe du Lion.

Une analyse comparée entre régions est souvent confrontée à la difficulté posée par l'utilisation de protocoles d'échantillonnage différents (Bianchi et al., 2000). Les problèmes d'estimation de la diversité, liés à un effort d'échantillonnage différent selon les années et les zones, ont été résolus par l'utilisation de modèles (cf. annexe 1 et 2). Les données analysées sont issues de deux types de campagnes pour le golfe du Lion, de 1983 à 1992 (CHALIST) et de 1994 à 1997 (MEDITS), la principale différence étant un changement de maillage du chalut. L'existence d'une tendance temporelle pourrait ainsi être masquée par le changement de protocole. Toutefois, il n'y a pas non plus de tendance temporelle observable dans le golfe de Gascogne échantillonné de 1987 à 1995 sans changement de protocole. Il est donc plus probable que l'absence de tendance, à l'échelle annuelle sur la période considérée (de 1983 à 1997), soit due à une indépendance de ces indices vis-à-vis de l'exploitation à l'échelle temporelle de l'étude, plutôt qu'au changement de protocole. D'autre part, les protocoles d'échantillonnage du golfe de Gascogne et du golfe du Lion sont différents par la saison d'échantillonnage et par le maillage du chalut utilisé. En 1988, une campagne de chalutage de fond a été menée au printemps dans le golfe de Gascogne, en plus de la campagne d'automne, selon le même protocole. Le nombre d'espèces échantillonnées au printemps n'est pas significativement différent du nombre d'espèces échantillonnées pendant la campagne d'automne. Ainsi, même si un recrutement de certaines espèces a pu intervenir entre les deux saisons, le nombre d'espèces présentes ne change pas, ce qui signifie que sont toujours présent, soit les adultes, soit les juvéniles, soit les adultes et les juvéniles en même temps. Ainsi, il est peu probable que la différence de saison entre les campagnes de printemps, menées dans le golfe du Lion, et les campagnes d'automne, menées dans le golfe de Gascogne, soit à l'origine de la différence du nombre d'espèces trouvé entre ces deux zones géographiques. De plus, la différence du nombre d'espèces observées correspond bien à une différence observée par d'autres auteurs à l'échelle biogéographique. Enfin, la représentation graphique des distributions des fréquences relatives de classes de poids individuel (distribution moyenne sur les années concernées) par type de chalutage permet de les comparer visuellement (*figure 5*). Le type de chalutage mené dans le golfe de Gascogne (EVHOE) permet un meilleur échantillonnage des petites classes de poids que les campagnes CHALIST mais moins bon que les campagnes MEDITS menées dans le golfe du Lion. Ainsi, la dominance par des espèces de faible poids individuel, observée dans le golfe de Gascogne n'est pas lié au protocole d'échantillonnage.

Selon les arguments apportés, les différences de diversité observées ne semblent liées, ni aux protocoles d'échantillonnage, ni à l'exploitation par la pêche. Ainsi, le golfe de Gascogne et le golfe du Lion sont deux systèmes écologiques dont les structures de diversité diffèrent. Par conséquent, les dynamiques diffèrent aussi. L'utilisation des indices de diversité

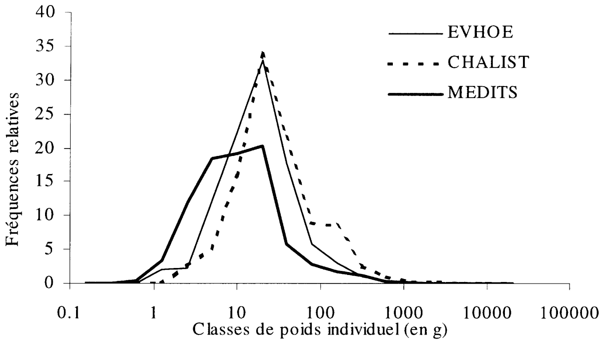

Figure 5. Fréquences relatives toutes espèces confondues (poissons démersaux) par classe de poids individuel dans les échantillonnages réalisés dans le golfe de Gascogne, campagnes EVHOE (1987 à 1995) et dans le golfe du Lion, campagnes CHALIST (1983 à 1992) et campagnes MEDITS (1994 à 1997).

Figure 5. Percent abundance distribution of the demersal fish communities by log10 weight classes (g), in the surveys EVHOE (thin solid line) carried out in the Bay of Biscay, and CHALIST (dashed line) and MEDITS (bold solid line) carried out in the Gulf of Lions.

(*N1*, *N2*, *S* et *J'*) permettent de mettre en évidence une différence entre les deux peuplements. Dans les analyses réalisées par d'autres auteurs, les différences sont attribuées soit à un impact de l'exploitation (Greenstreet et Hall, 1996 ; Bianchi et al., 2000), soit à des facteurs écologiques (McClatchie et al., 1997) ou encore biogéographiques (Garibaldi et Caddy, 1998). Ici les trois aspects sont pris en compte. L'impact de l'exploitation n'a pas pu être mis en évidence. La biogéographie permet d'interpréter les différences de diversité spécifique et l'utilisation des courbes K-dominance en abondance et en biomasse, ainsi que l'analyse des stratégies démographiques, permet d'intégrer un facteur écologique : le régime de perturbations.

Allen et al. (1999) concluaient que l'utilisation du seul indice de diversité taxonomique ne constituait qu'un indicateur ambigu de l'intégrité biologique des lacs. Cette conclusion peut être étendue aux indices de diversité spécifique pris indépendamment les uns des autres pour les assemblages de poissons marins. En revanche, c'est l'utilisation conjointe des indices de diversité spécifiques de Hill et des courbes K-dominances, associée aux traits démographiques des principales espèces qui a permis ici de décrire des éléments de la dynamique des peuplements selon l'interprétation de Frontier et Pichod-Viale (1991).

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ANNEXES

Annexe 1. Les modèles de raréfaction sont de la forme :

$$S_i = a \log_{10} (f_i) + b \qquad (4)$$

$$H'_i = Hm \left(1 - \exp \left(- c(f_i - d) \right) \right) \qquad (5)$$

avec *a*, *b*, *c*, *d*, constantes, *f*, le nombre de traits de chalut et *Hm*, la valeur maximale calculée. La relation (4) est ajustée par régression linéaire et la relation (5), modèle asymptotique, est ajustée avec l'algorithme de Marcardt. Le critère d'ajustement utilisé classiquement est le coefficient de détermination R^2. *N1* et *S* sont estimés à partir de ces modèles pour chaque année et assemblage.

Paramètres du modèle (4) ajusté par année dans les assemblages côtiers, du plateau et de la pente continentale du golfe de Gascogne et du golfe du Lion.

Parameter values of the model (4) fitted within years and within coastal, continental shelf and continental slope assemblages of the Bay of Biscay and of the Gulf of Lions.

		Zone côtière			Plateau continental			Pente continentale		
	Année	*a*	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2
golfe du Lion	1983	32,1	13,5	0,95	23,5	25	0,97	19,8	27,2	0,97
	1985	30,1	5,7	0,98	23,1	27,3	0,96	–	–	–
	1986	26,6	11,4	0,97	24,7	14,2	0,96	23,3	22,9	0,93
	1987	23,4	16,3	0,92	21,8	8,9	0,93	–	–	
	1992	23,5	14,9	0,97	27	10,5	0,95	–	–	
	1994	25,5	20,6	0,94	32,8	17,8	0,97	11,2	26,1	0,86
	1995	23,6	22,1	0,97	29,3	21,6	0,98	14,2	20,5	0,87
	1996	28	16,6	0,97	29,4	19,5	0,98	17	26,3	0,89
	1997	30,9	10,1	0,96	37,4	6,9	0,97	14,1	28,4	0,94
golfe de Gascogne	1987	43,9	6,3	0,91	30,6	6,8	0,97	16,4	13,1	0,95
	1988	33,3	12,2	0,98	32,4	1,6	0,93	20,1	9,1	0,92
	1989	24	10,5	0,95	29,3	–2,2	0,92	23,8	5,4	0,98
	1990	35,6	2,2	0,96	21,9	11,6	0,93	23,8	5,4	0,99
	1992	36,5	10,1	0,95	30,8	3,6	0,96	24,2	11,5	0,95
	1994	35,6	12,1	0,98	31,2	5,7	0,98	24,7	13,6	0,93
	1995	39,5	4,2	0,91	36,6	0,7	0,9	28,2	10,5	0,96

Annexe 2. Paramètres du modèle (5) ajusté par année dans les assemblages côtiers, du plateau et de la pente continentale du golfe de Gascogne et du golfe du Lion. * modèle non utilisé pour la simulation de la diversité par faiblesse de l'ajustement. *Hm*, *c* et *d* sont les paramètres du modèle définis en *annexe 1*.

Annex 2. Parameter values of the model (5) fitted within years and within coastal, continental shelf and continental slope assemblages of the Bay of Biscay and of the Gulf of Lions. * model with weak goodness of fit, non used for the simulations of diversity. *Hm*, *c* and *d* are the parameters of the model defined in *annexe 1*.

		Côte				Plateau				Pente			
	Année	*Hm*	*c*	*d*	R^2	*Hm*	*c*	*d*	R^2	*Hm*	*c*	*d*	R^2
golfe du Lion	1983	2,5	0,23	–3	0,92	2,9	0,47	–1,71	0,93	2,3	0,7	–2,1	0,99
	1985	3,2	0,36	–0,4	0,97	3	0,19	–7,2	0,98	–	–	–	–
	1986	2,8	0,13	–6,1	0,98	2,4	0,39	–1,1	0,8	2,2	0,6	–2,1	0,52
	1987	2,6	0,46	–0,7	0,97	2,5	0,44	–0,4	0,96	–	–	–	–
	1992	2,9	0,18	–5,7	0,96	2,5	0,08	–15,3	0,97	–	–	–	–
	1994	2,9	0,15	–9	0,96	2,4	0,08	–12,9	0,9	0,67	0,7	–1,3	0,91
	1995	2,8	0,27	–5,1	0,95	3,4	0,002	–365	0*	2,4	0,02	–15,2	0,78
	1996	2,5	0,25	–4,6	0,96	3	0,1	–9,4	0,99	2,7	1,2	–0,2	0,99
	1997	3,2	0,13	–7,4	0,99	2,7	0,2	–1,2	0,94	2,7	0,8	–1,3	0,98
golfe de Gascogne	1987	1,14	0,29	–1,7	0,92	1,9	0,08	–10,6	0,94	2,9	0,24	–3,4	0,97
	1988	1,03	0,17	–2,2	0,94	1,8	0,05	–10,9	0,94	2,5	0,02	–31,1	0,96
	1989	1,6	0,02	–79,3	0,85	1,5	0,04	–14,3	0,84	1,2	0,07	–14,1	0,66
	1990	2,3	0,16	–2,2	0,98	1,9	0,04	–34,7	0,8	1,7	0,02	–50,7	0,35
	1992	2,5	0,12	–9	0,7	2,6	0,06	–22,2	0,99	1,3	0,04	–16,3	0,94
	1994	1,5	0,06	–10	0,91	2,6	0,1	–12,5	0,97	0,7	0,03	–64,3	0,01*
	1995	1,9	0,04	–26,8	0,92	0,29	0,08	–17,5	0,96	1,9	0,12	–9,7	0,91

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A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France)

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SARSIA

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This new numerical approach proposes a solution to a fundamental and difficult question in ecology, consisting of the correct geographical representation of multidimensional structures. Firstly, transformation was applied to the original matrix (*n* sites x *q* variables) in order to satisfy the condition of multinormality. Then, a hierarchical cluster analysis was used and each hierarchical level was studied and characterised by a certain probability level. For each cut off level an algorithm based on the computation of the Bayesian probabilities produced a smaller matrix (*n* sites × *c* groups). These conditional probabilities measure the chance that each site has in belonging to a predefined group of sites. Spatial distributions of these probability values for each group of sites were mapped using kriging interpolation. Finally, the maps were used to define homogenous zones on a single map by superimposing one map on the other. The maximal value of interpolated probability was used as criterion to assign each point of the map to the zones predefined by this classification.

This method was applied to map demersal fish habitats by using a dataset from bottom trawl surveys in the Bay of Biscay (France) during October 1990. The boundaries between habitats were identified objectively. Then, the indicator species and species assemblages characterising the different habitats were identified by using an indicator value index. This index integrates the specificity and the fidelity quantities calculated for each species in each habitat. The obtained results showed that this method presented a robust tool to describe the habitat of exploited species. The obtained habitats were validated by their correspondence with depth strata, sediment type and also by the biological characteristics of the indicator species.

The proposed method is useful in the study of temporal variations of habitats with regards to species assemblages and can also be generalised to other multivariate databases of different descriptors (physical, chemical, biological, etc.).

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INTRODUCTION

Considerable developments have occurred in both data acquisition and in the modelling of spatial patterns of marine systems (Ault & al. 1999). Generally however, spatialized data bases covering long periods of time are still often treated separately from one another. This has lead to a necessary development of adequate numerical methods resulting in better understanding of the spatial and temporal variability in marine ecosystems. Moreover, the need for marine habitat classification and mapping is important as a result of increasing activities of the international conventions on Biodiversity (Rio), the Protection of Species and Habitat (OSPAR), the FAO Code of Conduct for Responsible Fisheries (Cancun), and the Jakarta Mandate for Marine Protected Areas.

Consequently, the rich source of ecological information available from scientific surveys carried out in different exploited areas has been increasingly analysed to define habitat and species changes after anthropogenic or environmental impact (Greenstreet & Hall 1996; Greenstreet & al. 1999; Jennings & al. 1999a, b; Rogers & Ellis 2000).

Recently Mahon & al. (1998) used a large data set collected by demersal research trawl surveys from 1970 to 1994 on the east coast of North America in order to study assemblages and biogeography of demersal fishes. The approach of pooling all the data from different surveys together in order to carry out multivariate analysis can however be confusing as both spatial and temporal factors are mixed. It is thus necessary to map each trawl survey fish habitat separately in order to efficiently assess spatial and temporal effects (Gaertner & al. 1998). Moreover, species assemblages should be considered in order to define the habitat dynamics.

Multivariate regionalization techniques are necessary in the study of spatial structure of large datasets. Several methods have been developed in spatialized disciplines (e.g. geology, climatology, terrestrial vegetation, etc.) including Principal Components Analysis (Richman & Lamb 1985; Boyer & al. 1997; Comrie & Glenn 1998), multivariate classification (Oliver & Webster 1989; Bourgault & al. 1992; Souissi & al. 2000). However until now, visual appreciation has been the primary means by which groups of sites have been assimilated to ecosystem regions after using regionalization methods. Spatial contiguity is not necessarily the rule in marine ecology especially when characterised by high levels of spatial heterogeneity due to accidental topography and to non-linear hydrodynamical properties. Therefore, the constrained cluster analysis often used in terrestrial ecology (Dufrêne & Legendre 1991) may not be necessarily justified in marine habitat studies.

This paper describes a new algorithm combining both multivariate hierarchical classification techniques and spatial models of regionalized variables. This combination goes further than the separation of groups of sites as with ordinary classification since interpolation is used resulting in a more refined mapping. A one year bottom trawl survey in the bay of Biscay is used as an example to illustrate the different steps and results obtained with this algorithm. This study of demersal species habitats has four main aims: 1) to identify the spatial structure of demersal communities at different scales. 2) To establish how the definition of the boundaries between these sub-areas can be carried out objectively. 3) To define the characteristic species assemblages for each area. 4) To assess the ecological interpretations after using this method.

The data set was first subdivided into two matrices representing the dominant species and the secondary species. A classification of sites after hierarchical cluster analysis was applied to the matrix of dominant species. Then, successive levels of hierarchical classification were considered. For each regionalization level, the study area was divided into different habitats corresponding to the number of clusters. The interpolation of each point within its identified habitat was obtained by using the theory of regionalized variables based on a Bayesian probability. These techniques were initially developed for geological applications (Harff & Davis 1990; Harff & al. 1993). Finally, the indicator species for each group of sites were identified by computing the indicator value index proposed by Dufrêne & Legendre (1997).

MATERIAL AND METHODS

DATA SOURCES

The developed method was applied to a set of data collected during the groundfish survey carried out by IFREMER in the Bay of Biscay. The EVHOE survey series began in 1987 (Poulard 1989; ICES 1991, 1997; Amara & al. 1998). The survey area was between 48°30'N in the north and the northern margin of Gouf de Cap Breton in the south. The area was stratified according to latitude and depth. A 36/47 GOV trawl was used with a 20 mm mesh codend liner. The haul duration was 30 minutes long with a towing speed of 4 knots. Fishing was mainly restricted to daylight hours. Catch weights and catch numbers were recorded for all species, all finfish and a selection of shellfish were measured. The data obtained from the 135 hauls carried out between 25 September and 25 October 1990 were used to illustrate the different steps of the method. The biology of the species, alimentary diet, behaviour and habitat, is given by the FAO world fish fauna (Fisher & al. 1987).

SPECIES SELECTION AND MATHEMATICAL TRANSFORMATION

The abundance indices of pelagic species are better estimated by acoustic surveys (Massé 1996) and pelagic trawls than bottom trawls, so these species (e.g. anchovy, sardine, mackerel, etc.) were eliminated from this analysis. Species present in more than 5 % of the tows were retained (Fig. 1A). The data was transformed by a double square root for two reasons, firstly to minimise the effects of high values and secondly to satisfy the multinormality of the data, a required condition before using the regionalized variables (Harff & Davis 1990). In order to accomplish the latter condition, the sum of the total abundances for each selected species was computed. After this, species were ranked following their contribution to the global sum of the data (Fig. 1B). The contribution level of 0.5 % separated the species into two groups: the dominant species (Table 1) and the secondary species (Table 2).

The multinormality of transformed data was tested with the Dagnelie method (Dagnelie 1975 in Legendre & Legendre 1998) based on the Mahalanobis generalized distance (see Eq. 6). Generalized distances are computed between each object (site) and the multidimensional mean of all objects. Then the values of the skewness and kurtosis were computed and their deviation compared to a theoretical normal distribution was tested (CEA 1986; Legendre & Legendre 1998). The null hypothesis of normality of the distribution of both parameters tested could not be rejected (p = 0.289 and 0.122 for skewness and kurtosis, respectively). Thus the multinormality of the data was confirmed.

METHOD

The different steps of the numerical method are shown in Fig. 2. Only the stages after species selection have been detailed. In this case the inputs of the analysis are the sites-species matrices A and B (Fig. 2), corresponding to dominant species and secondary species, respectively.

Step 1: cluster analysis

The matrix A was used in a cluster analysis. First, the species abundances were transformed ($x^{0.25}$) before computing a similarity coefficient between sites (matrix S). The Bray-Curtis similarity coefficient and clustering strategy of flexible links with beta set at the value of –0.25 (Legendre & Legendre 1998) were used.

Instead of studying one spatial configuration with a fixed number of clusters, a hierarchical tree with successive cutting off levels was used. Consequently, for the same data set different spatial organization patterns of assemblages were studied.

Step 2: expression of conditional probabilities

For each level of the hierarchical classification a number of clusters was obtained. The level of heterogeneity between each site and properties of each group was assessed with one value of a conditional Bayesian probability. This method, originally developed in geology (Harff & Davis 1990; Harff & al. 1993), was adapted for the purposes of this study.

Each object (site) X_i is a q-dimensional variable, where q is the number of the selected dominant species (A in Fig. 2):

$$X_i = \{x_{i,1}, x_{i,2}, ..x_{i,j}, ..x_{i,q}\} \qquad (1)$$

where $x_{i,j}$ is the transformed abundance of species j in the site i.

For each cut off level (c) of the hierarchical tree, a partition Z_c^Q of groups of sites G_j can be considered,

$$Z_c^Q = \{G_1, G_2, ..G_j, ..G_c\} \qquad (2)$$

of which each element is defined by a number of sites

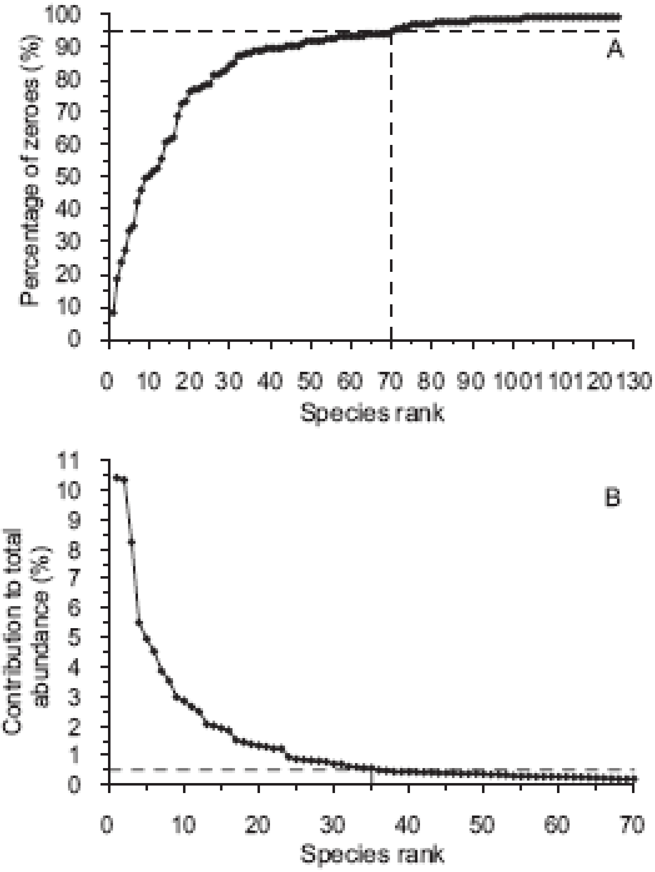

Fig. 1. Numerical criteria of species selection. A) the percentage of zeroes in the 135 sites for different species are sorted in ascending order. The threshold level of 95 % is considered. B) Contribution of each selected species in the total abundance. The 70 species selected in the step (A) are ranked according their contribution. At the level of 0.5 % the selected species are subdivided into two groups: the dominant species (Table 1) and the secondary species (Table 2).

n_j^Q, a centroid of the group m_j^Q and a covariance matrix Σ_j:

$$G_j : \left(n_j^Q, m_j^Q, \Sigma_j\right) \qquad j \in \Gamma^c, \Gamma^c = \{1, ..., c\} \qquad (3)$$

Where j is a group of sites obtained from a hierarchical classification and Γ^c is the set of groups of sites containing c elements, where c is the cut off level. The centroid is the data point (vector) that is the mean of the abundance values of each species among the sites belonging to the considered group. The covariance matrix represents the within dispersion of a group G_j.

The partition Z_c^Q is termed the model and each one of its elements G_j is termed a j-model (Harff & Davis 1990). It should be noted that the number of elements in each partition depends on the level c of the hierarchical classification (Fig. 2). In general, the spatial coherence of a j-model emerges from the contagiousness of the ecological processes involved. In this case this concerns the habitats of demersal species characterising a typical species association. Depending on the composition of each site X_i (Eq. 1), its conditional probability of membership to a *j*-model is expressed by Bayes' relationship (Harff & al. 1993):

$$P(X_i \in G_j) = \frac{p_j \left|\Sigma_j\right|^{-1/2} \exp\left(-d_j^2(i)/2\right)}{\sum_{k \in I^C} p_k \left|\Sigma_k\right|^{-1/2} \exp\left(-d_k^2(i)/2\right)} \qquad (4)$$

where p_j is an *a priori* probability of the *j*-model, which represents the proportion of the number of sites in the cluster *j* versus the total number of sites:

$$p_j = \frac{n_j^G}{\sum_{k \in I^C} n_k^G} \qquad (5)$$

and $d_j^2(i)$ is the generalised Mahalanobis distance between G_j and X_i:

$$d_j^2(i) = (X_i - m_j^G)' \; \Sigma_j^{-1} (X_i - m_j^G) \qquad (6)$$

Assuming that the dispersion matrices are equals (Harff & Davis, 1990),

$$\sum_i = \sum_j = \sum_0 \qquad \forall i, j \in I^K$$

Table 1. List of dominant demersal species selected for mapping their habitats in the Bay of Biscay and the South Celtic Sea. All species were present in the 135 stations selected from the autumn survey of 1990 with a frequency greater than 5 % and a total abundance contribution greater than 0.5 %. The species are subdivided into 4 groups: Sharks and Rays, Bony fishes, Crustacea and Cephalopoda.

Group & Family	Label	(%)	Species
Sharks and Rays			
Scyliorhinidae	SCYLCAN	2.48	*Scyliorhinus canicula* (Linné., 1758)
Rajidae	RAJANAE	0.70	*Raja naevus* Müller & Henle, 1841
Bony fishes			
Argentinidae	ARGESIL	0.87	*Argentina silus* (Ascanius, 1775)
Argentinidae	ARGESPH	4.52	*Argentina sphyraena* Linné, 1758
Gadidae	GADIARG	3.86	*Gadiculus argenteus* Guichenot, 1850
Gadidae	MERLMNG	1.38	*Merlangius merlangus* (Linné, 1758)
Gadidae	MICRPOU	10.35	*Micromesistius poutassou* (Risso, 1827)
Gadidae	TRISLUS	2.97	*Trisopterus luscus* (Linné, 1758)
Gadidae	TRISMIN	10.42	*Trisopterus minutus* (Linné, 1758)
Lotidae	MOLVMOL	0.56	*Molva molva* (Linné, 1758)
Merlucciidae	MERLMCC	8.23	*Merluccius merluccius* (Linné, 1758)
Zeidae	ZEUSFAB	0.78	*Zeus faber* Linné, 1758
Caproidae	CAPRAPE	2.84	*Capros aper* (Linné, 1758)
Triglidae	ASPICUC	2.01	*Aspitrigla cuculus* (Linné, 1758)
Sparidae	SPONCAN	0.80	*Spondyliosoma cantharus* (Linné, 1758)
Mullidae	MULLSUR	0.58	*Mullus surmuletus* Linné, 1758
Callionymidae	CALLLYR	2.65	*Callionymus lyra* Linné, 1758
Callionymidae	CALLMAC	1.29	*Callionymus maculatus* Rafinesque, 1810
Gobiidae	LESUFRI	0.83	*Lesueurigobius friesii* (Malm, 1874)
Gobiidae	POMAMIN	0.71	*Pomatoschistus minutus* (Pallas (ex Gronovius), 1770)
Scophthalmidae	LEPIWHI	1.92	*Lepidorhombus whiffiagonis* (Walbaum, 1792)
Bothidae	ARNOIMP	1.23	*Arnoglossus imperialis* (Rafinesque, 1810)
Bothidae	ARNOLAT	1.22	*Arnoglossus laterna* (Walbaum, 1792)
Soleidae	MICRVAR	0.93	*Microchirus variegatus* (Donovan, 1808)
Crustacea			
Nephropidae	NEPHNOR	1.32	*Nephrops norvegicus* (Linné, 1758)
Galatheidae	MUNIBAM	1.51	*Munida bamffia* (Pennant, 1777)
Cancridae	CANCPAG	0.62	*Cancer pagurus* Linné, 1758
Cephalopoda			
Sepiidae	SEPIELE	1.45	*Sepia elegans* Blainville, 1827
Sepiidae	SEPIORB	0.60	*Sepia orbignyana* Ferussac, 1826
Sepiolidae	SEPISPP	2.05	*Sepiola* spp. & *Sepietta* spp.
Loliginidae	ALLOSPP	5.50	*Alloteuthis* spp.
Loliginidae	LOLIFOR	3.52	*Loligo forbesi* Steenstrup,1856
Loliginidae	LOLIVUL	1.84	*Loligo vulgaris* Lamarck, 1798
Ommastrephidae	ILLECOI	4.95	*Illex coindeti* (Verany, 1839)
Ommastrephidae	TODAEBL	0.84	*Todaropsis eblanae* (Ball, 1841)

a pooled variance-covariance matrix Σ_p (Cooley & Lohnes 1971; Legendre & Legendre 1998) was used as a substitute of the normal dispersion matrix Σ in the d^2 computation.

Step 3: cartography of regionalized variables

Harff & al. (1993) considered that the conditional probability (Eq. 4) may be treated as a regionalized variable, because the stochastic features of X_i were retained. Thus geostatistical tools can be applied to matrices P_c of conditional probabilities (Fig. 2). In this way the spatial distributions of the conditional probability for each group of sites were mapped. An interpolated regular grid of 0.025 longitude by 0.025 latitude degrees corresponding to the study area limits was obtained by using a spherical variogram model and the kriging method (Matheron 1962). The probability data are assumed to be isotropic. For each point z in space (one node of the regular interpolated grid) a vector of conditional probabilities obtained by interpolation can be associated:

Table 2. List of secondary demersal species considered in the study of indicator species at the local scale when habitats are identified using the dominant species shown in Table 1. All species were present in the 135 stations selected from the autumn survey of 1990 with a frequency greater than 5 % and a contribution to total abundances of under 0.5 %. The selected species are subdivided into 5 groups: Sharks and Rays, Bony fishes, Crustacea, Cephalopoda and Bivalves.

Group & Family	Label	(%)	Species
Sharks and Rays			
Rajidae	RAJACLA	0.30	*Raja clavata* Linnaeus, 1758
Rajidae	RAJAMON	0.22	*Raja montagui* Fowler, 1910
Scyliorhinidae	GALEMEL	0.45	*Galeus melastomus* Rafinesque, 1810
Bony fishes			
Congridae	CONGCON	0.39	*Conger conger* (Linnaeus, 1758)
Lophiidae	LOPHBUD	0.20	*Lophius budegassa* Spinola, 1807
Lophiidae	LOPHPIS	0.39	*Lophius piscatorius* Linnaeus, 1758
Sebastidae	HELIDAC	0.43	*Helicolenus dactylopterus* (Delaroche, 1809)
Triglidae	EUTRGUR	0.42	*Eutrigla gurnardus* (Linnaeus, 1758)
Triglidae	TRIGLUC	0.20	*Trigla lucerna* Linnaeus, 1758
Cepolidae	CEPORUB	0.44	*Cepola rubescens* Linnaeus, 1766
Pleuronectidae	MICRKIT	0.39	*Microstomus kitt* (Walbaum, 1792)
Pleuronectidae	PLEUPLA	0.27	*Pleuronectes platessa* Linnaeus, 1758
Pleuronectidae	LIMALIM	0.26	*Limanda limanda* (Linnaeus, 1758)
Soleidae	SOLEVUL	0.38	*Solea vulgaris* Quensel, 1806
Soleidae	BUGLLUT	0.29	*Buglossidium luteum* (Risso, 1810)
Soleidae	DICOCUN	0.22	*Dicologoglossa cuneata* (Moreau, 1881)
Trachinidae	TRACDRA	0.42	*Trachinus draco* Linnaeus, 1758
Trachinidae	ECHIVIP	0.45	*Echiichthys vipera* (Cuvier, 1829)
Bothidae	LEPIBOS	0.40	*Lepidorhombus boscii* (Risso, 1810)
Gadidae	PHYCBLE	0.35	*Phycis blennoides* (Brünnich, 1768)
Gadidae	POLLPOL	0.26	*Pollachius pollachius* (Linnaeus, 1758)
Gadidae	ENCHCIM	0.29	*Enchelyopus cimbrius* (Linnaeus, 1758)
Moronidae	DICELAB	0.34	*Dicentrarchus labrax* (Linnaeus, 1758)
Sparidae	BOOPBOO	0.25	*Boops boops* (Linnaeus, 1758)
Ammodytidae	AMMOTOB	0.53	*Ammodytes tobianus* (Linnaeus, 1758)
Ammodytidae	HYPELAN	0.27	*Hyperoplus lanceolatus* (Le Sauvage, 1824)
Mugilidae	LIZARAM	0.47	*Liza ramada* (Risso, 1826)
Macrouridae	MALALAE	0.28	*Malacocephalus laevis* (Lowe, 1843)
Crustacea			
Portunidae	MACRPUB	0.38	*Macropipus puber* (Linnaeus, 1758)
Crangonidae	CRANCRA	0.35	*Crangon crangon* (Linnaeus, 1758)
Cephalopoda			
Octopodidae	ELEDCIR	0.23	*Eledone cirrhosa* (Lamarck, 1798)
Octopodidae	OCTOSPP	0.28	*Octopus* sp.
Sepiidae	SEPIOFF	0.37	*Sepia officinalis* Linnaeus, 1758
Ommastrephidae	TODASAG	0.29	*Todarodes sagittatus* (Lamarck, 1798)
Bivalves			
Pectinidae	PECTMAX	0.20	*Pecten maximus* (Linnaeus, 1758)

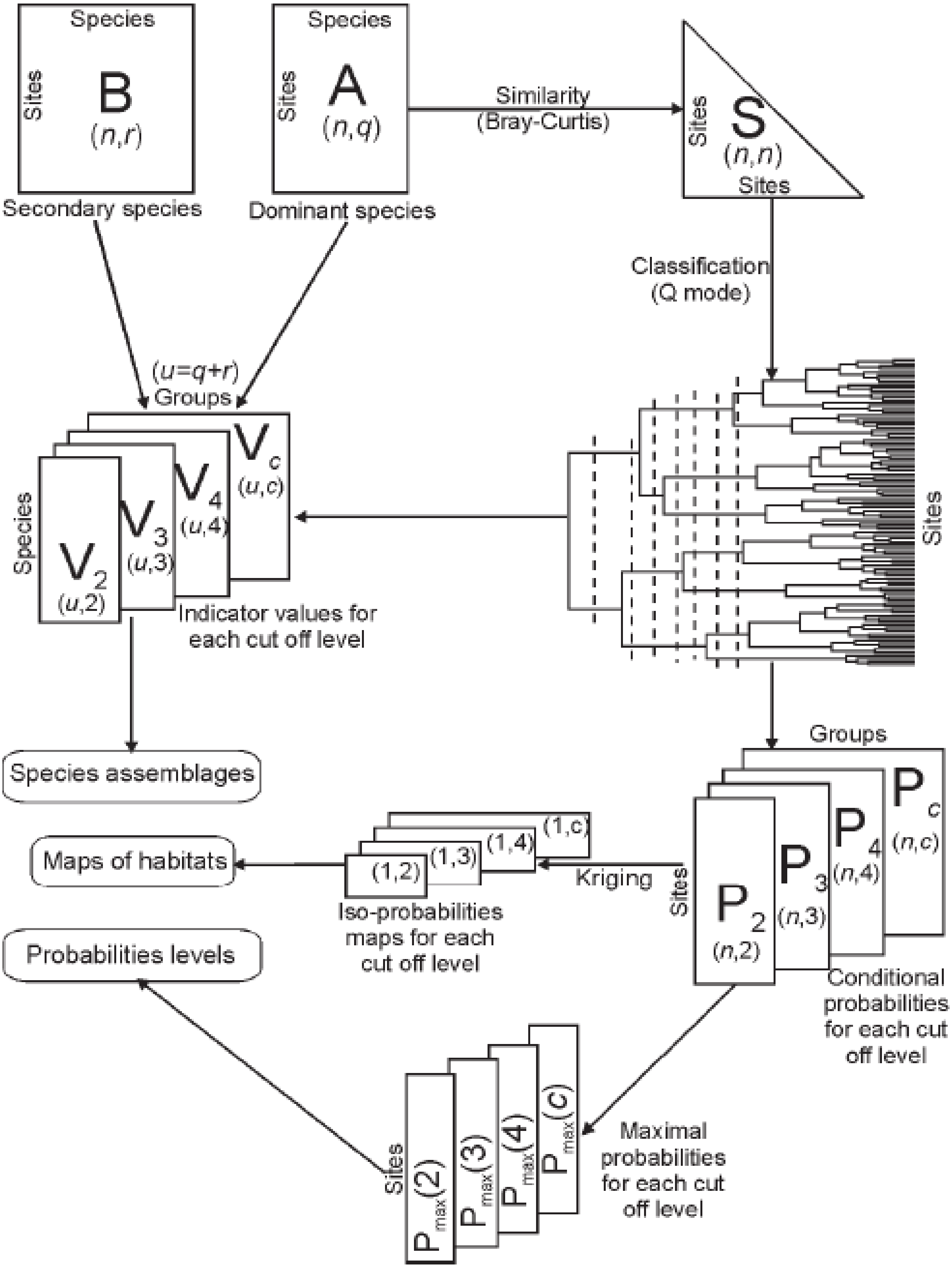

Fig. 2. Diagram of the analysis steps for the multivariate mapping method. The different steps explaining the connections between the input matrices A(*n*: sites, *q*: dominant species) and B(*n*: sites, *r*: secondary species) and the final resulting map of fish habitats and indicator species for each hierarchical level. The different steps of the diagram are detailed in Materials and Methods section.

$$p_z = \left\{p_z(1), p_z(2), \ldots, p_z(c)\right\} \quad (7)$$

So z belongs to the area j representative of the group of sites G_j if its conditional probability is the largest for that group (Eq. 8).

$$p_z(j) = \max(p_z) \quad (8)$$

Step 4: characterisation of the different zones

After mapping the different habitat zones, it is necessary to identify the species that characterise each habitat. The indicator value index proposed by Dufrêne & Legendre (1997) was used to identify the indicator species and the significant assemblages for each habitat and spatial organization (Fig. 2). The specificity and fidelity of each species s compared to each cluster of sites G_j can be measured by the values $SP_{j,s}$ and $FI_{j,s}$, respectively:

$$\begin{cases} SP_{j,s} = NI_{j,s} / NI_{+j} \\ FI_{j,s} = NS_{j,s} / NS_{j+} \end{cases} \quad (9)$$

where $NI_{j,s}$ is the mean abundance of species s across the sites relating to G_j, NI_{+j} which is the sum of the mean abundances of species s within the various groups in the partition. At the same time $NS_{j,s}$ is the number of sites in G_j where the species s is present and NS_{j+} is the total number of sites in that group. The specificity value ($SP_{j,s}$) is maximum when species s is present in group G_j only, whereas the fidelity value ($FI_{j,s}$) is maximum when species s is present in all sites of G_j. The specificity and fidelity represent information independently from one another, their product multiplied by 100 produces a percentage of the indicator value $IV_{j,s}$:

$$IV_{j,s} = 100 SP_{j,s} FI_{j,s} \quad (10)$$

Dufrêne & Legendre (1997) proposed to retain the maximum indicator value for each species s among all groups.

$$IV_j = \max(IV_{j,s}) \quad (11)$$

For this study, only species having an indicator value greater than 25 %, being the threshold level used by Dufrêne & Legendre (1997), were retained in the assemblages. Furthermore, the indicator value indices were computed for each level of the hierarchical classification. The analysis of the variation of indicator value as the number of groups increased point out the characteristic species for each hierarchical level. For the highest hierarchical levels, when the indicator values of all species are decreasing, the clustering method does not often offer any additional information. So, this analysis provides an *a posteriori* criterion to define the highest significant hierarchical level (Dufrêne & Legendre 1997).

Moreover, a new criterion for characterising each hierarchical level by one probability value was added. For each probability matrix (P_k, $k = 2$ to c in Fig. 2) a vector $P_{\max}(k)$ representing the maximal probability for each site was computed.

$$P_{\max}(k) = \max(P'_k) \quad (12)$$

where P'_k is the transposed sites-probabilities matrix for the cutoff level k.

Then each level of hierarchical classification k was characterised by one probability value $P_M(k)$ estimated from the median of the vector $P_{\max}(k)$:

$$P_M(k) = median\left(P_{\max}(k)\right) \quad (13)$$

$P_M(k)$ can be interpreted as being an average measure of the within-groups homogeneity for each hierarchical level.

The different steps of the method (shown in Fig. 2) were programmed with Matlab Software.

RESULTS

GLOBAL ANALYSIS OF SITE GROUPS AT DIFFERENT HIERARCHICAL LEVELS

Nineteen different partitions of groups of sites corresponding to increasing levels from 2 to 20 clusters were considered after hierarchical classification (Fig. 3). The corresponding $P_M(k)$ (Eq. 13) quantities were computed, and then plotted in Fig. 4. The median probability that a site belongs to its group of sites for the first cut off level was equal to 0.86. Then, $P_M(3)$ increased to the value of 0.89. For the next aggregation level, with 4 site groups, the median probability $P_M(4)$ decreased slightly to the value of 0.88. The highest amplitude of increase in P_M values was obtained for the five site group hierarchical level, where the associated probability ($P_M(5)$) overcame the threshold of 0.9. Then, the values of P_M increased slightly for the next levels 6 and 7. The threshold value of 0.95 was first reached for the eight cluster aggregation (Fig. 4). The probabilities P_M continued increasing with the number of clusters showing a plateau around 1.0 for the highest number of clusters. According to this first characterisation, the spatial organization patterns of species assemblages for the first seven partitions (from 2 to 8 clusters indicated with discontinuous lines in Fig. 3) were arbitrarily retained for the following detailed analyses.

Mapping of the different zones

Starting with the second hierarchical level, a matrix of conditional probabilities (135 sites × 2 site groups) was computed. The maps of the iso-probability contours for each zone are shown in Fig. 5A-B. The probability levels are shown by a colour scale increasing from white to one characteristic colour. For example the median depth of the first zone (Fig. 5A) is equal to 62 m, which corresponds to the green colour according to the depth colour scale. This representation facilitates the interpretation of the geographical representation of habitat zones and their

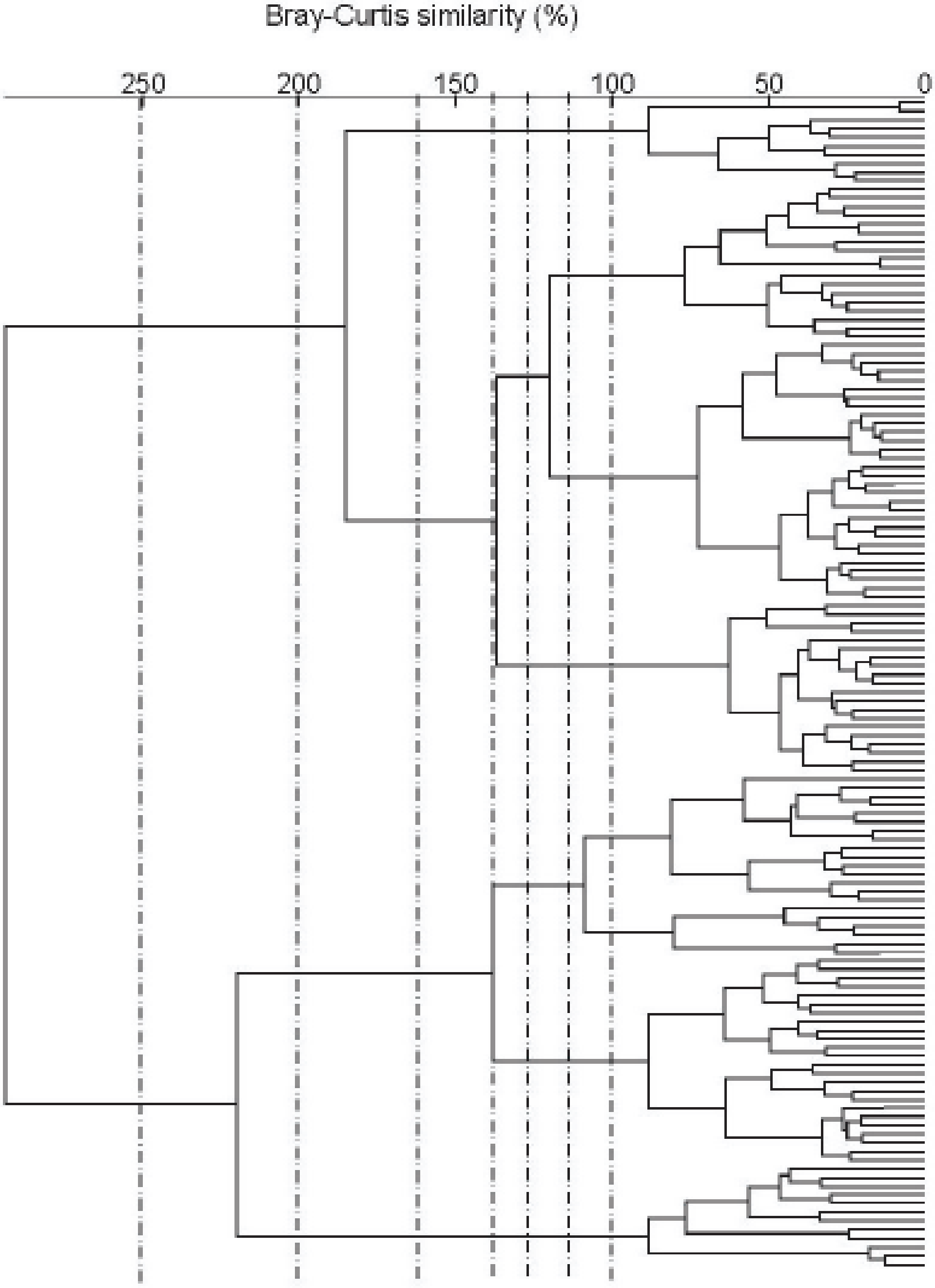

Fig. 3. Classification of the sampling sites for the bottom trawl survey carried out between 25 September and 25 October 1990, using Bray-Curtis dissimilarity coefficient and clustering strategy of flexible links with beta equal to –0.25. The first seven hierarchical levels giving from 2 to 8 site groups were indicated with discontinuous lines.

average depth properties. The probability of correct classification of each point within a zone is assessed by applying the maximal probability value criterion (Eq. 8). Fig. 5C shows the final map of both habitats. The method does not introduce any spatial contiguity constraints, however the obtained zones are contiguous. They clearly represent a separation between the coastal zone in the bay of Biscay and the rest of the study area including the southern part of the Celtic Sea.

Fig. 6 shows the final maps obtained for a number of habitats starting from 3 and continuing up to 8. The first habitats identified from the hierarchical classification are those of the bay of Biscay shallow water (Fig. 6A) and the slope of the shelf-break (Fig. 6B). It must be pointed out however that the resulting mapped group formations from one level to the next one, may subtly differ (particularly at group boundaries) from the groups formed after IndVal calculation using hierarchical clustering since interpolation is used. In fact the boundaries may change altogether, this is particularly noticeable for sites occurring near the boarders of each group. An example is shown for the passage from 4 zones (Fig. 8B) to 5 zones (Fig. 8C). The newly appeared zone III (Fig. 8C) is represented by two separate areas. This is directly due to the procedure of computing new conditional probabilities and identifying, through interpolation, new boundaries between the different zones.

The subdivision of the studied area into 6 groups is characterised by a clearcut separation between the central bay of Biscay zone and the southern Celtic Sea zone (Fig. 6D). By increasing the number of habitats, we obtain first a separation between the central Bay of Biscay zone (zone IV in Fig. 6E) and the continental slope zone (zone VI in Fig. 6E). The last subdivision concerns the coastal area, which is characterised by 4 different habitats for the 8 site groups level (Fig. 6F).

The increase of the number of zones resulted in a decrease of both spatial heterogeneity (in terms of average probability, Fig. 4) and spatial contiguity between zones (Fig. 6).

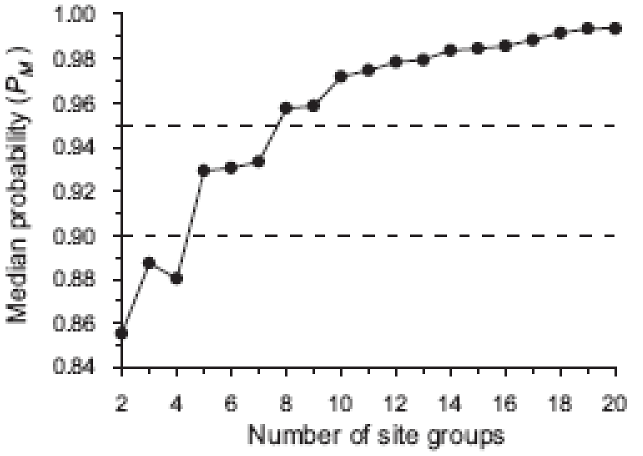

Fig. 4. Variation of the median probability (P_M) as a function of the number of site groups. Vectors of maximal probabilities (P_{max} in Fig. 2) were used in the computation of P_M at the considered 19 hierarchical levels. The probability levels of 0.9 and 0.95 are shown with discontinuous horizontal lines.

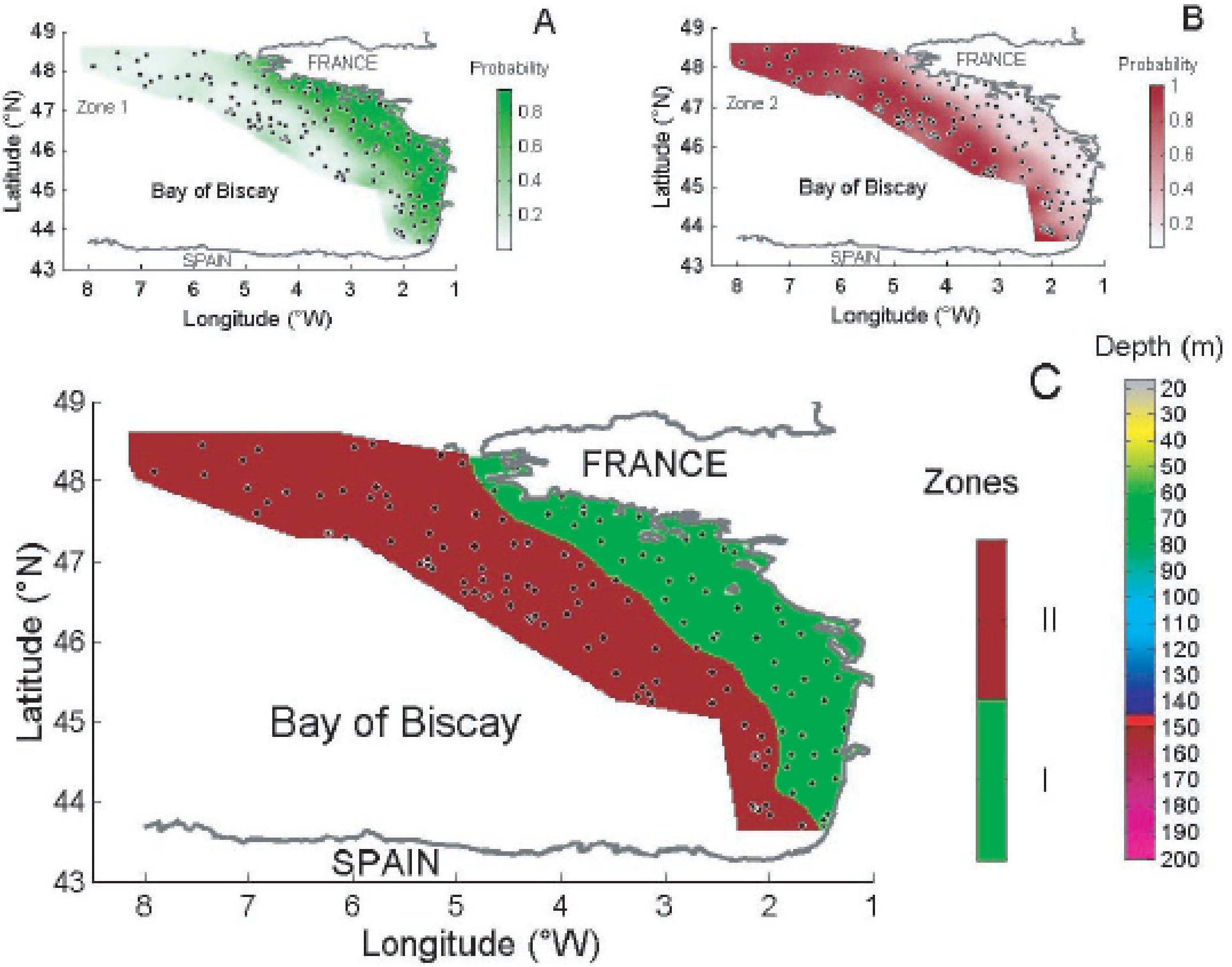

Fig. 5. Iso-probability maps for the coastal zone (A) and the offshore zone (B). Each map represents a spatial distribution of the probabilities of being a member of one group of sites identified in Fig. 3 for the two site groups hierarchical level. The probability levels are represented by a colour scale bar increasing from white ($P = 0$) to a characteristic colour ($P = 1$) depending on the median depth of the site group. The depth colour bar shown in (C) was truncated over 200 m depth.

C) Final map of the two habitats zones. The positions of the sampling sites in the Bay of Biscay are indicated by black symbols.

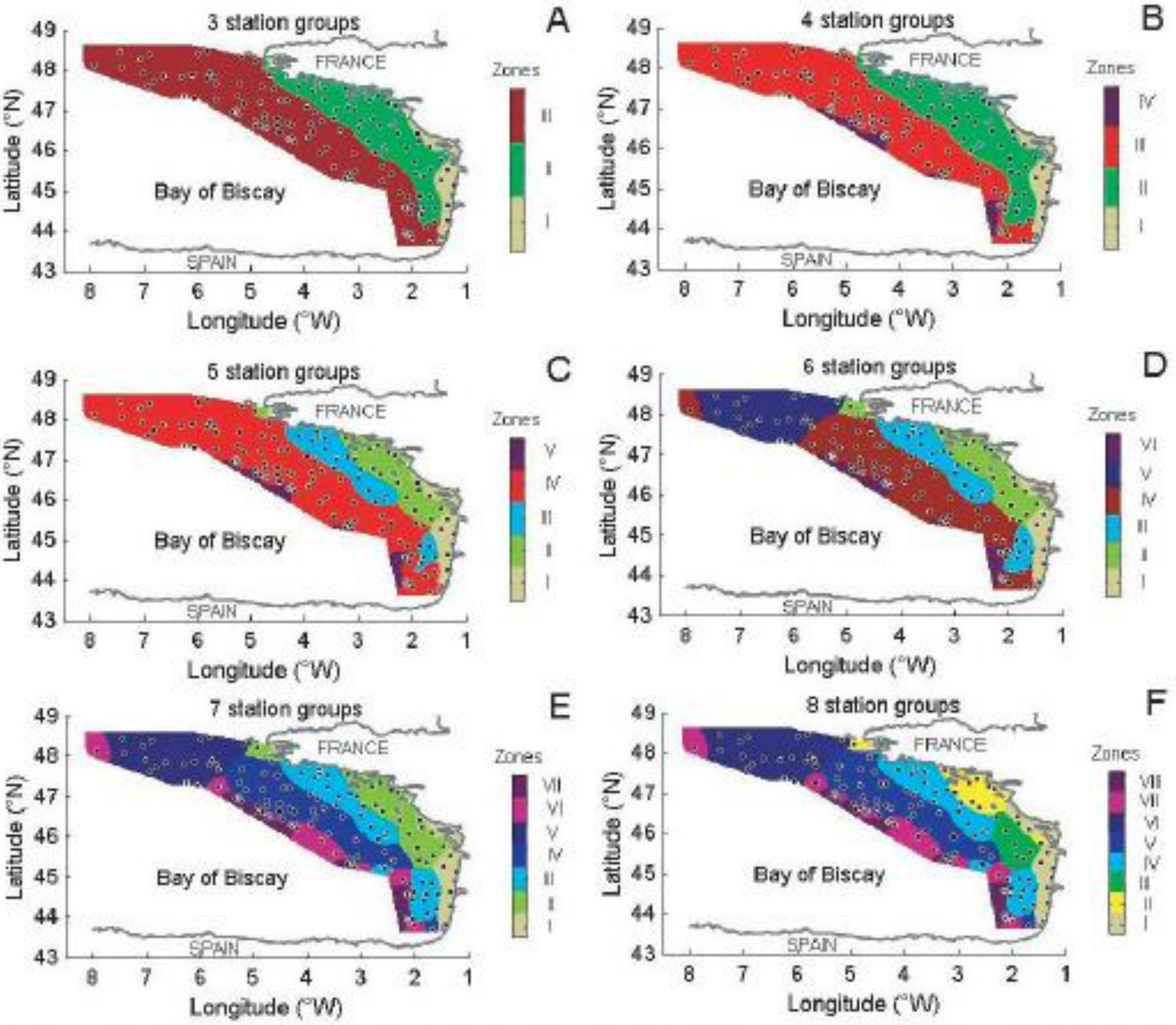

Fig. 6. Maps of the different habitat zones for the following hierarchical levels: 3(A), 4(B), 5(C), 6(D), 7(E) and 8(F). Each colour represents the median depth according to colour scale bar of Fig. 5. Dark violet colour indicates the deeper sites (median depth = 375 m).

BATHYMETRIC REGIONALIZATION OF THE SAMPLED AREA

As a first criterion for characterising the spatial patterns of site groups, the average depth distributions were calculated for different site groups using Box-and-whiskers plots (Fig. 7). When only two groups of sites were considered, their depths were distributed around two median values: 62 m and 150 m. For this level, the boxes of depth-distribution did not overlap (Fig. 7), so, the bathymetry can be considered as a good discriminator between these habitats. When increasing the hierarchical level, the more heterogeneous group was split into two new site groups. For example, the third hierarchical level was characterised by the isolation of the shallow coastal and estuarine site group (25 m median depth) from the other coastal sites of intermediate depths (77 m median depth). The group of deepest sites, characterised by a high variability of depths around a median of 375 m corresponding to the slope of the shelf-break, formed the next cut off level (Fig. 7). The four identified site groups were sorted according to a bathymetric gradient. Five depth strata were distinguished around the following median values: 25 m, 51 m, 99 m, 145 m and 375 m. The higher hierarchical levels of 6 and 7 groups, showed a subdivision of the 145 m deep group. This group was subdivided into two groups with similar depth distributions (Fig. 7), one of these groups (141 m median depth) was then further subdivided into shallower sites (132 m median depth) and deeper sites (172 m median depth). The last subdivision concerned the coastal group of median depth 51 m, which was split into two groups having 36 m and 62 m median depths, respectively. While bathymetry appeared to be a good structuring factor, additional information was derived from the study of the assemblages and indicator species for each aggregation level.

INDICATOR SPECIES AND SPECIES ASSEMBLAGES

The indicator values (Eq. 11) for both dominant species (Table 1) and secondary species (Table 2) were computed for the seven levels of the hierarchical structure of site clustering. The threshold level of 25 % for the index chosen by Dufrêne & Legendre (1997) was used in this analysis. The characteristic species for each site group and the values of the index are shown in Table 3. For the first hierarchical subdivision in two groups, only 69 % of the total number of the dominant species were retained

Table 3. Variations of the indicator value (Eq. 10) with hierarchical levels shown in Fig. 3. Only species having indicator values greater than 25 % were retained. Species labels for dominant species and rare species are those of Tables 1 and 2, respectively. The indicator value is shown between parentheses and preceded by the number of the site group.

	Number of site groups						
Species label	2	3	4	5	6	7	8
Dominant species							
ALLOSPP	I(68)	II(69)	II(67)	III(44);II(32)	III(42);II(31)	III(39);II(29)	III(42)
ARGESIL			IV(48)	V(48)	VI(44)	VII(31)	VIII(31)
ARGESPH	II(70)	III(67)	III(77)	IV(67)	IV(55)	VI(38);IV(31)	VII(35);V(29)
ARNOIMP	II(46)	III(46)	III(53)	IV(52)	V(72)	V(61)	VI(61)
ARNOLAT	I(27)	II(32)	II(31)	III(29)	III(27)		III(37)
ASPICUC	II(46)	III(40)	III(44)	IV(38)	V(65)	V(57)	VI(54)
CALLLYR	I(51)	II(38)	II(37)	II(73)	II(64)	II(63)	II(63)
CALLMAC	II(25)		III(28)		IV(27)	IV(27)	
CAPRAPE	II(74)	III(74)	III(77)	IV(77)	V(67)	V(46);VI(33)	VI(46);VII(33)
GADIARG	II(62)	III(61)	IV(86)	V(84)	VI(80)	VII(70)	VIII(69)
ILLECOI	II(83)	III(82)	III(76)	IV(72)	IV(67)	VI(70)	VII(69)
LEPIWHI	II(63)	III(61)	III(39)	IV(37)	IV(30)	VI(32)	VII(32)
LESUFRI	I(31)	II(35)	II(35)	III(59)	III(59)	III(59)	IV(58)
LOLIFOR	II(58)	III(53)	III(41)	IV(35)	V(62)	V(59)	VI(58)
LOLIVUL	I(44)	I(80)	I(80)	I(66)	I(66)	I(66)	I(54);II(26)
MERLMCC	I(69)	II(76)	II(72)	III(74)	III(69)	III(61)	IV(58)
MERLMNG	I(49)	I(25)	I(25)	II(54)	II(54)	II(54)	II(53)
MICRPOU	II(97)	III(97)	III(72)	IV(71)	IV(74)	VI(83)	VII(83)
MOLVMOL					V(43)	V(40)	VI(40)
MULLSUR		I(56)	I(56)	I(48)	I(48)	I(47)	I(43)
MUNIBAM	II(26)	III(26)	IV(47)	V(46)	VI(45)	VII(42)	VIII(42)
NEPHNOR		II(28)		III(47)	III(44)	III(40)	IV(40)
POMAMIN		II(26)	II(26)	II(46)	II(46)	II(46)	II(39)
RAJANAE	II(32)	III(32)			V(36)	V(30)	VI(30)
SCYLCAN	II(49)	III(27)	III(27)				
SEPIELE	II(44)	III(42)	III(49)	IV(40)	V(49)	V(41)	VI(33)
SEPISPP				III(30)	III(26)	IV(25)	
SPONCAN	I(30)	I(81)	I(81)	I(71)	I(71)	I(71)	I(65)
TRISLUS	I(50)	I(41)	I(41)	I(32);II(27)	I(31);II(26)	I(30);II(25)	II(40);I(26)
TRISMIN	I(55)	II(70)	II(68);III(25)	II(61)	II(49)	II(47)	II(57)
Secondary species							
BOOPBOO		I(57)	I(57)	I(55)	I(55)	I(55)	I(53)
CEPORUB		II(27)	II(26)	III(28)	III(27)	III(26)	
ELEDCIR					V(33)	V(32)	VI(32)
GALEMEL			IV(89)	V(89)	VI(89)	VII(85)	VIII(85)
HELIDAC			IV(53)	V(53)	VI(47)	VII(41)	VIII(41)
HYPELAN		I(36)	I(36)	I(30)	I(30)	I(30)	
LEPIBOS			IV(54)	V(54)	VI(52)	VII(44)	VIII(44)
LIMALIM				II(32)	II(32)	II(32)	II(45)
LIZARAM		I(55)	I(55)	I(53)	I(53)	I(53)	I(50)
MALALAE			IV(66)	V(66)	VI(64)	VII(58)	VIII(58)
OCTOSPP			IV(33)	V(32)	VI(31)	VII(28)	VIII(27)
PHYCBLE			IV(58)	V(57)	VI(57)	VII(56)	VIII(56)
SOLESOL		I(28)	I(28)				II(27)
TODASAG			IV(45)	V(45)	VI(43)	VII(36)	VIII(36)
TRACDRA		I(38)	I(38)	I(34)	I(34)	I(34)	I(32)

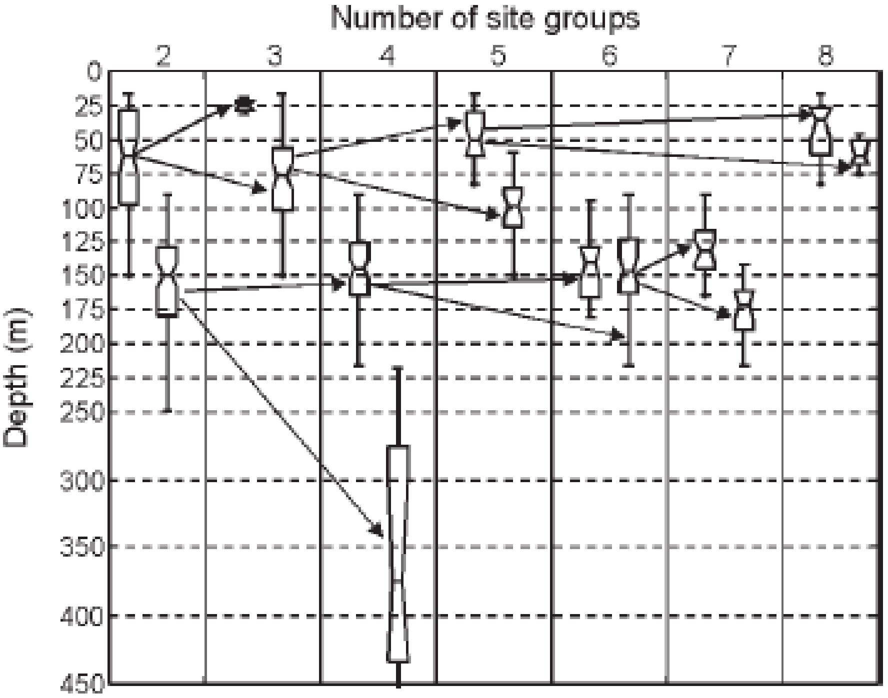

Fig. 7. Detailed representation of depth distributions of the two newly obtained groups of sites at each hierarchical level using box-and-whisker plots. For each aggregation level only the two newly obtained groups of sites were shown. Arrows indicated the hierarchical link between the different groups.
The box has lines at the lower quartile, median, and upper quartile values (representing the 25th, 50th and 75th percentiles of the sample, respectively). The whiskers are lines extending from each end of the box to show the extent of the rest of the data.

(see Table 1). Both zones (Fig. 5C) were dominated by species with wider spatial distribution patterns, such as blue whiting *Micromesistius poutassou* with an index value of 97 % for the second zone (Table 3). Almost all the blue whiting individuals were in the offshore zone and were present in all of these sites. This species is associated with *Illex coindeti*, *Capros aper*, *Argentina sphyraena*, *Lepidorhombus whiffiagonis*, *Gadiculus argenteus* and *Loligo forbesi*. The indicator values of these species were equal to or greater than 58 %. Another group of seven species (*Scyliorhinus canicula*, *Aspitrigla cuculus*, *Arnoglossus imperialis*, *Sepia elegans*, *Raja naevus*, *Munida bamffia* and *Callionymus maculatus*) with lower indicator values for the same zone was also distinguished. On the other hand, ten species characterised the coastal zone (Table 3). The highest indicator value of 69 % was obtained for hake *Merluccius merluccius*. The maximum indicator value for most characteristic species was obtained for higher hierarchical levels, this is an indication of the heterogeneity of the coastal habitats. For example, the species association of *Spondyliosoma cantharus*, *Loligo vulgaris* and *Mullus surmuletus* characterised the shallow water habitat for the third hierarchical level. For the same level, the indicator values of three characteristic species (*Merluccius merluccius*, *Trisopterus minutus* and *Alloteuthis* spp.) of the second coastal zone reached their maximum. The isolation of smaller site groups made the apparition of secondary species in the list of indicator species possible (Table 3). For example, after the third hierarchical level, seven secondary species (*Boops boops*, *Liza ramada*, *Trachinus draco*, *Hyperoplus lanceolatus*, *Dicologoglossa cuneata*, *Trigla lucerna* and *Solea solea*) were identified as indicators of the shallow coastal zone.

The first subdivision of the offshore zone isolated the break-shelf sites, characterised by the association of three dominant species (*Gadiculus argenteus*, *Argentina silus* and *Munida bamffia*) with seven secondary species (Table 3). The highest indicator value for this group was obtained for the secondary species *Galeus melastomus* (89 %). The characteristic species of zone III (Fig. 6B) were *Capros aper* and *Argentina sphyraena*, as their maximal indicator value (77 %) was reached at this level. The characteristic species of the next hierarchical level (5 site groups) were indicators of the newly isolated groups: *Callionymus lyra* for zone II (Fig. 6C) and *Lesueurigobius friesii* for zone III (Fig. 6C). The separation between the Southern Celtic Sea and the Bay of Biscay habitats occurred in the sixth hierarchical level (Fig. 6D). Table 3 shows the difference between these zones in terms of assemblages of indicator species. With the exception of the species *Capros aper*, the maximal indicator values for the Southern Celtic Sea zone were obtained at this hierarchical level (Table 3).

The next levels did not result in any increase of indicator values for any of the species. So, it was assumed that the highest significant hierarchical level was attained for the six site groups.

DISCUSSION

The development of remote sensing techniques has significantly globalised approaches in spatially orientated ocean research. Considering the development of techniques using ocean colour detectors to estimate the primary productivity (Antoine & al. 1995) and water circulation (Taupier-Lepage & Millot 1988), extrapolation to estimate the productivity of the higher trophic levels (in particular the exploited resources) remains currently difficult. All mono-species and non spatialized approaches used in the past for fisheries management have shown their limitations (Gunderson & al. 1995; Parsons 1995), as an alternative the integrated ecosystem approaches (Christensen & al. 1996; Larkin 1996) and spatially based approaches (Ault & al. 1999) have been developed. In order to improve these approaches, it is necessary to develop broad scale monitoring and surveys of marine resources. At present, there is an increasing demand to study species assemblages in relationships with their habitats and to study their temporal evolution or change with respect to both fishing pressure and environmental change (Gomes & al. 1995; Mahon & al. 1998). However the current techniques used to analyse the databases coming from bottom trawl surveys or catch data are based on strong assumptions. These assumptions can go from sampling programs involving *a priori* selected areas (Iglesias 1981) up to the visual delimitation of homogenous regions after random sampling (Gomes & al. 1995). In the absence of an objective statistical approach to separate spatially homogenous zones according to their species assemblages, the comparison of the temporal evolution of these habitats and their biodiversity remains unsatisfactory.

The regionalization of habitats based on the properties of their inhabitants is a classical approach in ecology (Dufrêne & Legendre 1997). However, this approach is limited because it relies too much on ecologically meaningful descriptors, because the species compositions and spatial distributions of species populations do not only vary with the habitat type. The other direct approach consisting in the description of all the characteristics of a habitat is also limited as much by the knowledge of the relevant characteristics of these habitats as that of the volume of work needed. Until now, both approaches have come up against difficulties in geographically representing the properties defined in a multidimensional mathematical space. Mahon & al. (1998) used principal component analysis (PCA) and cluster analysis (CA) to map fish assemblages from large spatio-temporal datasets. In their study, assemblages were identified using arbitrary threshold levels of species loadings on the principal components (PCs). The top 5 % of the site scores for each PC, were also arbitrarily used in identifying the main sites of each assemblage. So, the same site can belong to more than one map, increasing the difficulty in defining clear boundaries between the biogeographical zones (see Fig. 3 in Mahon & al. 1998). Moreover, the authors did not perform any statistical tests showing the robustness of their results based on the use of one random subset of 10 % of the data in CA. Mahon & al. (1998) considered their results as being too preliminary to permit them to conclude with serious management implications. They also showed the necessity of the use of such results (assemblage maps) in the definition of boundaries for large marine ecosystems. Although the notion of boundaries is important, it is difficult to separate these objectively in the previous studies, especially if the number of site groups is low. Colvocoresses & Musick (1984) performed CA on a pooled sites-species matrix constructed from bottom trawl surveys over a 9-year period. They used different symbols to map the various site groups. This classically used representation is also limited when clear boundaries have to be drawn or if seasonal (or inter-annual) comparison between maps is to be made (for example see figs 4 & 6 in Colvocoresses & Musick 1984).

In this paper the proposed method overcomes these limitations and proposes an objective technique for defining boundaries after regionalization of spatialised databases. The first originality of the method is the application of the regionalized variables theory to map demersal species habitats. These techniques developed for geological applications (Harff & Davis 1990; Harff & al. 1993) are powerful tools for use in answering a host of ecological questions that deal with the mapping of multivariate databases. The computation of conditional Bayesian probabilities for each site showed several advantages. Firstly, it was used to assess the level of within-group heterogeneity. For example, for homogenous site groups, each site is characterised by high conditional probabilities of belonging to the same site groups. In other situations, when one or more sites again show high probabilities but this time in other site groups, the technique reallocates them. In other words, the conditional probability is a measure of the power of belonging of a site to a particular site group. In this paper, the vectors of maximal probabilities of sites were used to characterise each level of hierarchical classification by an average probability value (see Figs 3-4). Another advantage of the use of conditional probabilities came from the objective method in the establishment of boundaries between the different zones (Fig. 5).

The method can be separated into three steps: i) the clustering of site groups, ii) the calculation of conditional probabilities, and, iii) the identification of assemblages and indicator species. The last two steps were applied to each hierarchical level. Each single step of the method is not new in itself, however, the combination between these different multivariate techniques developed for different disciplines may be considered as a new applied approach. This originality is further strengthened by the flexibility of the algorithm and the numerous extensions possible not to mention the use of various powerful multivariate analyses. For this application, a hierarchical cluster analysis was used in the first step to classify the different sites. However, all methods which are able to produce a partition of sites into groups, such as k-means or probabilistic clustering for example, may be used in the first step of this method (see Legendre & Legendre 1998). It is also possible to include partitions obtained from other environmental data sets (Souissi & al. 2000) or at least *a priori* partitions. In all cases, the homogeneity of biological characteristics (e.g. demersal assemblages in this paper) in the initial spatial partition can be assessed by the computation of conditional probabilities. In the example shown here, since the first regionalization level (2 site groups), the computed average probability was relatively high (Fig. 3).

Several methods for regionalization have been developed in other spatially oriented disciplines e.g. soil science (Goovaerts 1992), climate science (Comrie & Glenn 1998), water quality management (Boyer & al. 1997) and recently in the monitoring of coastal ecosystems (Souissi & al. 2000). The present algorithm can be further applied to these studies. However, only multinormally distributed data can be used in order to compute the conditional probabilities (Harff & Davis 1990). Several mathematical transformation are proposed for hydrological and physical parameters (Hernandez Encinas 1994; Sokal & Rohlf 1995). When species catches data were used (e.g. the present application) only dominant species (low percentage of zeroes) were used to compute conditional probabilities. In most multivariate analyses, the elimination of secondary species is frequent (Ibanez & al. 1993; Fromentin & al. 1997; Dufrêne & Legendre 1997; and others). In this application, the secondary species matrix was also used in identifying indicator species. It was shown that some secondary species were indicators of the shallower coastal habitats while others characterised the deeper habitat (see Table 3). This remains a good demonstration of the role of considering both global and local scales in studying the spatial organisation of demersal and benthic communities.

Instead of using the same cluster analysis approach in the R mode (classification of species), indicator values were used to discriminate between abundance in all sites and the spatial heterogeneity of species distributions. The added advantages of using indicator values are discussed in Dufrêne & Legendre (1997).

The objective choice of cut off level of a dendrogram is a common asked question in ecology. Few methods are proposed in terms of numerical techniques (Feoli & Lausi 1980; Legendre & Legendre 1998), and the common protocol is to use visual criteria and *a priori* knowledge of the system studied (Hosie & al. 1997). In the present study the solution of studying several successive hierarchical levels was adopted (Dufrêne & Legendre 1991). The first analysis of variation in average probability value as a function of the hierarchical level (Fig. 4) allowed for the selection of levels 2 to 8 site groups to take place. Then, the indicator value criteria showed that the only significant hierarchical levels were those from 2 to 6 site groups (Table 3). The bathymetry seems to have been the most structuring factor for the demersal species habitats, with the exception of the isolation of the southern Celtic Sea group (Fig. 7). According to the indicator values (Table 3), the last group was mainly characterised by 5 demersal fish species (*Arnoglossus imperialis*, *Capros aper* and *Aspitrigla cuculus*, *Molva molva* and *Raja naevus*). The first two and the fifth are subtropical species, the third is a temperate one and the fourth is boreal. As southern and northern species coexist in this group, biogeography may obviously not justify the separation of this group from the other groups of the Bay of Biscay. So, an explanation must be sought at the ecological level. These 5 species are most often associated with hard substrate bottoms such as rock, gravel and sand (in FishBase, Froese and Pauly 2001). The bottoms of the Bay of Biscay are mainly muddy while hard bottoms dominate in the Celtic Sea probably because of the strong hydrodynamical properties of this sea. Perhaps these species are found in the Celtic Sea rather than in the Bay of Biscay as a result of their bottom preferences. The characterisation of the southern Celtic Sea area by this group of species may therefore provide evidence for an ecological pattern so far unnoticed.

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Temporal variability of total biomass in harvested communities of demersal fishes

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Abstract

The biomass variability of the demersal fish communities of the Bay of Biscay and the Gulf of Lions is analysed on a decadal scale using scientific surveys and fisheries data. The coefficient of variation of the total biomass is lower than the coefficient of variation of species biomass in both areas. Previous analyses from the Scotian Shelf have demonstrated that the total biomass of demersal fish is quite stable relative to individual species biomass. This result was interpreted as demonstrations of interactions between species due to energy limitation of systems. Moreover, the total biomass variability is lower in the Bay of Biscay than in the Gulf of Lions. As the distribution of the coefficients of variation of species in the Bay of Biscay does not differ from that in the Gulf of Lions, the difference of total biomass variability is not explained by the variability of species. Further, harvesting is investigated as a source of difference of total biomass variability between the Bay of Biscay, the Gulf of Lions and the Scotian Shelf. The mean of total biomass is the lowest in the area where the harvesting level is the highest (Gulf of Lions) and is the highest where harvesting is the lowest (Scotian Shelf), while the total biomass variability increases with the harvesting level. A hypothesis on fishing impact on the community dynamics is discussed and the total biomass variability is proposed to be a broad indicator of the fisheries impact on the demersal fish communities.

Keywords: Demersal fish biomass; Community dynamics; Energy limitation; Fishing impact

1. Introduction

Sissenwine and Daan (1991) stated that "it is hard to justify accepting models which we know are wrong (i.e. single species models, etc.) because we are not sure that the alternative models (i.e. multispecies models) are right". More knowledge about community dynamics is required (May et al., 1979; Pimm and Hyman, 1987; Wilson et al., 1991a; Hall, 1999). The main theories developed to explain community dynamics involve abiotic environmental processes (Conover et al., 1995; Ottersen and Sundby, 1995), biotic processes or a balance between the two (see Barbault (1992) and Huston (1994) for a general review).

With these theories in view, on the basis of studies of the fisheries landings of the Gulf of Maine and Georges Bank, Sutcliffe et al. (1976), Hennemuth (1979) and Murawski et al. (1991) showed that the temporal variability of the total biomass is lower than that of the individual species. Sutcliffe et al. (1976) interpret this observation as resulting from the different climatic "preferences" of species, while Hennemuth (1979) attributes this to a limiting carrying

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capacity, competition and predation relationships. However, these authors used data from commercial catches. Fisheries data may contain ecological information and information on the patterns of harvesting (May et al., 1979; Hilborn and Walters, 1987). Therefore, the patterns of harvesting may hide ecological information. Duplisea et al. (1997) show from scientific surveys carried out on the Scotian Shelf (the same biogeographic region as the Gulf of Maine and Georges Bank) that the annual variability of the total biomass of demersal fishes is lower than the variability of the seven families making up the assemblage. This result is interpreted according to the hypothesis of energy limitation (Steele, 1965; Barbault, 1992), as evidence that energy supply is a limiting factor at the community scale. The low variability of the total biomass relative to the species variability may therefore reflect the very nature of the community dynamics independent of harvesting patterns: the energy limitation leads to dynamics regulated by interactions between species.

McGrady-Steed and Morin (2000) state that in aquatic microcosms, the densities of nearly half of the species declined as species richness increased, demonstrating broad community-wide density compensation that resulted from more abundant competitors and predators. Moreover, the temporal variation of entire functional groups composed of multiple species decreased as species richness increased and they conclude that interspecific interactions contribute to the reduced temporal variability of functional groups. A corollary to this is that the removal of biomass by fisheries could move the community below an energy limitation process by increasing the energy available to every species. Then, the role of interactions in the dynamics of species could decrease, allowing species to fluctuate independently from each other, inducing an increase of the total biomass variability.

As the works quoted are confined to a limited zone, Scotian Shelf, Georges Bank and Gulf of Maine (southeast Canada), a question arises: Do the dynamics of the demersal fish community in other geographic areas exhibit the same regulation pattern? Then, two more preliminary questions arise from the previous assumptions: Are these other communities characterised by different values of the total biomass variability? If so, could these differences be related to the harvesting level?

To answer these questions, the biomass variability of harvested demersal fish communities of two other biogeographic areas, the Bay of Biscay and the Gulf of Lions (France) are analysed. The total and individual (by species) biomass variability of demersal fishes are compared within and between both areas with scientific survey data set to avoid the bias induced by the patterns of harvesting. The characteristics of biomass variability are then examined with a data set of small-scale trawlers of La Rochelle (Bay of Biscay). Then, the relationships between total biomass, total variability, species variability and the harvesting level (defined by Caddy et al. (1995) as the fisheries productivity) are investigated.

2. Materials and methods

2.1. Data

The variability of individual species biomass and total biomass is analysed using independent data sets (Table 1). The first set is landings and CPUE (catch per unit of effort), annual yields in weight, provided by the small-scale trawlers fleet of La Rochelle (Bay of Biscay) from 1982 to 1993. A set of seven scientific surveys EVHOE was carried out in the Bay of Biscay (43–49°N, France) for the direct evaluation of demersal stocks abundance every year in October/November from 1987 to 1990 and in 1992, 1994 and 1995. From 101 up to 142 hauls within 1 year are available. The third set stems from nine scientific surveys CHALIST and MEDITS carried out in the Gulf of Lions for the direct evaluation of demersal stocks abundance in May/June 1983, then from 1985 to 1987, in 1992 and from 1994 to 1997. From 57 to 110 hauls are

Table 1
Number of scientific surveys, total number of trawl hauls, number of total landing years and number of landing years from La Rochelle (LR) trawlers

	Bay of Biscay	Gulf of Lions	Scotian Shelf (Duplisea et al., 1997)
Surveys	7	9	22
Trawl hauls	866	618	Not reported
Total landing years	3	9	10
LR landing years	12		

available in each survey. Details of the EVHOE survey procedures are provided in ICES (1991) and by Amara et al. (1998). The CHALIST and MEDITS surveys are described, respectively, by Gaertner et al. (1998) and Bertrand et al. (1997).

The annual landings of demersal fishes from the whole Gulf of Lions, Bay of Biscay and Scotian Shelf are available, respectively, from 1983 to 1989 (FAO, 1991), from 1982 and 1984 (Dardignac, 1988), and from 1980 to 1989 (http://www.ncr.dfo.ca).

2.2. Biomass variability

The total biomass variability and the species variability in the Bay of Biscay and the Gulf of Lions are compared to test whether the same patterns as in the Scotian Shelf may be observed in these areas. Then, the distribution of species variability of the Bay of Biscay and the Gulf of Lions are compared to test whether the difference in total variability between areas may be due to differences in species variability.

The biomass per species is estimated within each scientific survey by the sum of a species biomass per standard trawl haul divided by the trawled area. The total biomass within each survey is the sum of all species biomass. The trawled area is the product of the ship speed, the trawling time, the trawl horizontal opening and the number of hauls. The annual CPUE estimates the species biomass from the data of the small-scale trawlers. The CPUEs are the production to fishing effort ratio. The annual production is the sum of the monthly landings of a species. The total production is the sum of all the monthly landings. The fishing effort is the product of the fishing time (hours) of the year and the mean engine power (kW) of the fleet (Guillou and Njock, 1978).

The coefficient of variation of biomass in time is used to assess variability. It is computed for every species ($\mathrm{CV_i}$) and for the sum of species ($\mathrm{CV_t}$):

$$\mathrm{CV} = \frac{100\sigma}{\bar{x}}$$

where σ is the standard deviation and $\bar{x}$ the mean of the measured variable (biomass landings, CPUE and biomass). The coefficients of variation are primarily calculated with the scientific survey data set from the Bay of Biscay and the Gulf of Lions. As the presence of zero for some years increases artificially the CV, the less abundant species that are not sampled every year are removed from the calculation. The coefficients of variation are again calculated with the annual biomass landings and CPUE fisheries to check whether the variability characteristics remain true in spite of the harvesting patterns.

The *t*-test is used to compare the species coefficient of variation between areas, after checking the homoscedasticity and the normality of distributions (Scherrer, 1983).

2.3. Fisheries removal

Removal of biomass by fisheries could move the community below an energy limitation process by increasing the energy available to every species. Therefore, the role of interactions in the community could decrease and the fluctuations become more independent from each other; consequently, the total variability should increase. The fishery productivity as the harvesting level is calculated to test whether it may be related to differences in mean and variability of total biomass. The values of biomass and $\mathrm{CV_t}$ provided by Duplisea et al. (1997) for the Scotian Shelf are integrated in the analysis.

The values of total biomass are compared between the Gulf of Lions, the Bay of Biscay and the Scotian Shelf. As the number of values is low (seven in the Bay of Biscay and nine in the Gulf of Lions), the non-parametric test of Kruskal–Wallis (KW), suitable for low strength samples, is applied.

A global index of harvesting level is computed according to the work of Charbonnier and Garcia (1985) and Caddy et al. (1995). According to these authors, the landings per surface area increase with the fishing effort. Hence, the fishery productivity, annual landings of demersal fishes per surface area of the continental shelf may be used as an index of harvesting level. This measurement expresses the biomass harvested by unit area.

3. Results

3.1. Biomass variability

3.1.1. Scientific surveys data

In the Bay of Biscay, 65 species of demersal fishes are sampled in every scientific survey. The mean of total biomass is 2.89 g m^{-2}, CV_t is 32.3%. CV_i varies from 18.4 to 140.5%. Only three species (*Lophius budegassa*, *Scyliorhinus canicula* and *Trisopterus minutus*) are characterised by a CV_i lower than that of total biomass one. The ratio of species having a CV_i higher than that of the total biomass is 95% (Table 2).

Table 2
Species list, individual and total coefficient of variation in the demersal fishes assemblages

Species	Bay of Biscay	Gulf of Lions
Ammodytes tobianus	118.9	
Argentina sphyraena	68.6	101.2
A. silus	82.0	
Arnoglossus laterna	79.2	80.0
A. rueppelli		82.1
A. thori		50.9
A. imperialis	39.0	
Aspitrigla cuculus	48.3	35.5[a]
A. obscura		76.4
Bathysolea profundicola	117.1	
Blennius ocellaris		35.9[a]
Boops boops	101.9	71.4
Buglossidium luteum	111.0	121.9
Callionymus lyra	123.1	
C. maculatus	92.6	
Capros aper	69.6	162.2
Cepola rubescens	59.4	79.2
Chimaera monstrosa	76.9	
Citharus macrolepidotus		50.0
Coelorhynchus coelorhynchus	81.9	
Conger conger	44.9	27.4[a]
Dicentrarchus labrax	73.5	
Dicologoglossa cuneata	55.9	
Diplodus annularis		94.8
Echiichthys vipera	43.8	
Enchelyopus cimbrius	93.7	
Etmopterus spinax	97.4	
Eutrigla gurnardus	103.5	53.1
Gadiculus argenteus	108.6	
Galeus melastomus	91.3	84.4
Helicolenus dactylopterus	49.8	105.1
Hyperoplus lanceolatus	130.9	
Labrus bergylta	71.4	
Lepidorhombus boscii	50.8	24.1[a]
L. whiffiagonis	36.6	
Lepidotrigla cavillone		48.8
Lesueuriogobius friesii	97.7	
Lophius budegassa	32.1[a]	31.2[a]
L. piscatorius	49.6	65.4
Macrorhamphosus scolopax	140.5	186.7
Malacocephalus laevis	63.4	
Melanogrammus aeglefinus	102.8	
Merluccius merluccius	42.6	47.4
Merlangius merlangus	39.6	
Microstomus kitt	49.0	
Microchirus variegatus	72.4	65.3
Molva molva	42.6	
Mullus barbatus		71.6
M. surmuletus	80.9	60.9
Pagellus acarne	85.5	66.4
P. bogaraveo		84.5
P. erythrinus		50.3
Phycis blennoides	66.1	68.8
Phrynorhombus norvegicus	114.5	
Pleuronectes platessa	66.0	
Pollachius pollachius	121.9	
Pomatoschistus minutus	122.2	
Psetta maxima	88.8	
Raja clavata	45.4	50.2
R. fullonica	124.5	
R. montagui	50.4	
R. naevus	56.0	
Scorpaena elongata		75.8
S. notata		60.8
Scyliorhinus canicula	31.3[a]	76.4
Serranus cabrila		45.2
S. hepatus		61.7
Solea vulgaris	43.4	52.5
Sparus aurata	127.5	
Spondyliosoma cantharus	61.8	
Squalus acanthias	133.5	126.4
Syngnathus acus	140.2	
Torpedo marmorata	85.6	
Trachinus draco	56.6	57.6
Trigla lucerna	69.3	74.0
T. lyra		78.1
Trigloporus lastoviza	78.4	72.0
Trisopterus minutus capelanus		28.8[a]
T. luscus	71.6	
T. minutus	18.4[a]	
Uranoscopus scaber		37.6[a]
Zeus faber	91.4	40.3
CV_t	32.3	40.3

[a] The species CV_i are smaller than the total biomass CV_t.

In the Gulf of Lions, 45 species are sampled in every scientific survey. The mean of total biomass is 2.52 g m^{-2}, CV_t is 40.3%. CV_i ranges from 24.1 to 186.7%. Only seven species are characterised by a CV_i lower than that of total biomass one: *Aspitrigla*

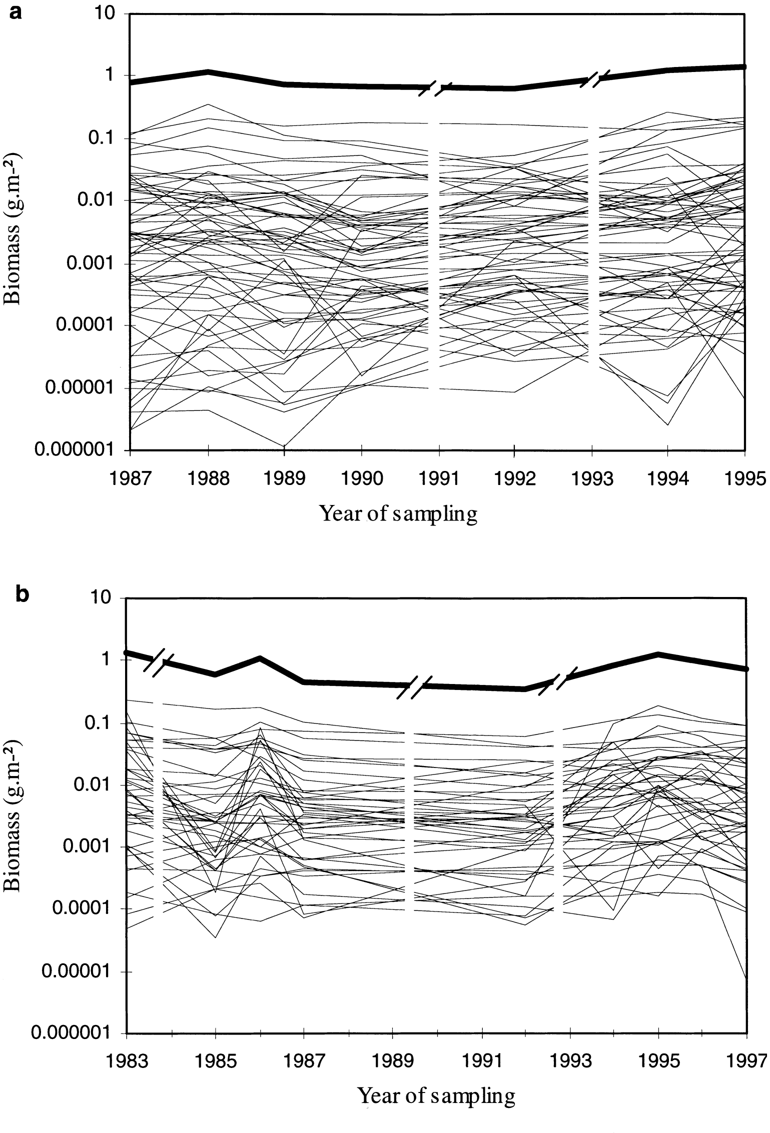

Fig. 1. Total biomass (bold line) and variations of individual species biomass (thin lines) in g m^{-2}: (a) in the Bay of Biscay; (b) in the Gulf of Lions.

cuculus, *Blennius ocellaris*, *Conger conger*, *Lepidorhombus boscii*, *L. budegassa*, *T. capelanus* and *Uranoscopus scaber*. The ratio of species having a CV_i higher than that of the total biomass is 84% (Table 2). The variability of the total biomass appears low as compared to the species temporal variability in both the geographic areas (Fig. 1). From 22 to 65% of the species, respectively, in the Gulf of Lions and the Bay of Biscay, are characterised by a CV twice as high as that of the total biomass.

According to the Kolmogorov–Smirnov test, the theoretical normal distribution fits well the two distributions of species variability (KS statistic is 0.06 in the Bay of Biscay and 0.08 in the Gulf of Lions, $p<0.05$). The mode of the distribution is 72 in the Bay of Biscay and 65 in the Gulf of Lions. The *t*-test does not detect differences between species variability in the two areas (t is -1.44, $p<0.05$).

The characteristic of higher individual species variability than total variability in the Scotian Shelf area is also observed within two other biogeographic areas from the Bay of Biscay and the Gulf of Lions. Moreover, the total variability is higher in the Gulf of Lions than in the Bay of Biscay and this is not caused by higher species variability.

3.1.2. Fisheries data

The analysis of the commercial landings and CPUE variability is carried out with 18 species retained (Table 3). It concerns 15 species or family of fishes, one species of crustacean and two families of cephalopod. These species represent more than 90% of the biomass of the commercial landings. The mean value of total annual landings of the small-scale trawlers of La Rochelle is 2032 t. The total biomass CV_t (25%) is lower than the CV_i of each species or family (from 28 to 68%) except the sole (21%). The biomass is divided by the fishing effort providing CPUE. The mean value of the annual CPUE is 96 kg 1000 h^{-1} kW^{-1}. The annual CPUE variability remains lower (CV_t of 11%) than the species CPUE variability (CV_i from 14 to 63%). The total commercial landings and CPUE variability of the small-scale trawlers of La Rochelle is therefore lower than the individual species landings and CPUE variability (Fig. 2). The characteristic of low total biomass variability and high species biomass variability is observed in the Bay of Biscay from both scientific surveys data and from fisheries data.

Table 3
Species list, individual and total coefficient of variation computed with landed production data (CV_{prod}) and yields (CV_{CPUE}) of the small-scale trawlers of La Rochelle (Bay of Biscay)

Family or species	CV_{prod}	CV_{CPUE}
Rajidae	56.4	59.1
A. cuculus	68.1	62.8
Scomber scombrus	63.7	47.9
S. canicula	62.8	59.6
P. pollachius	58.8	47.7
M. merluccius	47.2	39.3
D. cuneata	46.8	45.6
M. merlangus	45.1	48.9
Trachurus trachurus	45.0	35.6
M. barbatus and *M. surmuletus*	43.6	30.8
D. labrax	36.2	18.4
T. luscus	33.4	21.5
L. piscatorius and *L. budegassa*	31.9	22.5
C. conger	31.0	20.9
S. vulgaris	21.1[a]	14.0
Nephrops norvegicus	49.9	34.8
Sepiidae	45.0	32.8
Loliginidae	28.0	35.6
Total biomass	25.1	10.9

[a] The species CV is smaller than the total biomass CV.

3.2. Fisheries removal

The difference of the mean total biomass between the Bay of Biscay (2.89 g m^{-2}), the Gulf of Lions (2.52 g m^{-2}) and the Scotian Shelf (4.69 g m^{-2}) is tested. The distribution equality hypothesis is rejected by the KW test (statistical observed value of 19.09 and critical value of 9.21 at 1%). The non-parametric *U*-test of Wilcoxon, Mann and Whitney, same test as KW but for only two samples, is used to test which pairs are different. This test indicates rejection of the equality hypothesis of biomass distributions of the Bay of Biscay and the Gulf of Lions (statistical observed value of 7.9 and critical value of 12 at 5%). As there are more differences between the two other pairs, the test is not performed between these pairs. The total biomass values for the Bay of Biscay, the Gulf of Lions and the Scotian Shelf are different. In the Bay of Biscay the value of CV_t is 32, in the Gulf of Lions CV_t is 40 and on the Scotian Shelf CV_t is 22. The fishery productivity, the mean of annual landings of demersal fishes divided by the shelf area, is 0.85 t km^{-2} in the Gulf of Lions, 0.38 t km^{-2} in the Bay of Biscay and 0.2 t km^{-2} on the Scotian Shelf (Table 4).

The total biomass and the fishery productivity exhibit an inverse relationship (Fig. 3a). The total biomass decreases when the harvesting level increases. Finally, the total variability and the fishery productivity exhibit a relationship (Fig. 3b). The variability increases with the harvesting level.

4. Discussion

4.1. Biomass variability

4.1.1. Scientific surveys data

Duplisea et al. (1997) first observed higher biomass variations of demersal fish species group than total biomass in the Scotian Shelf using scientific survey

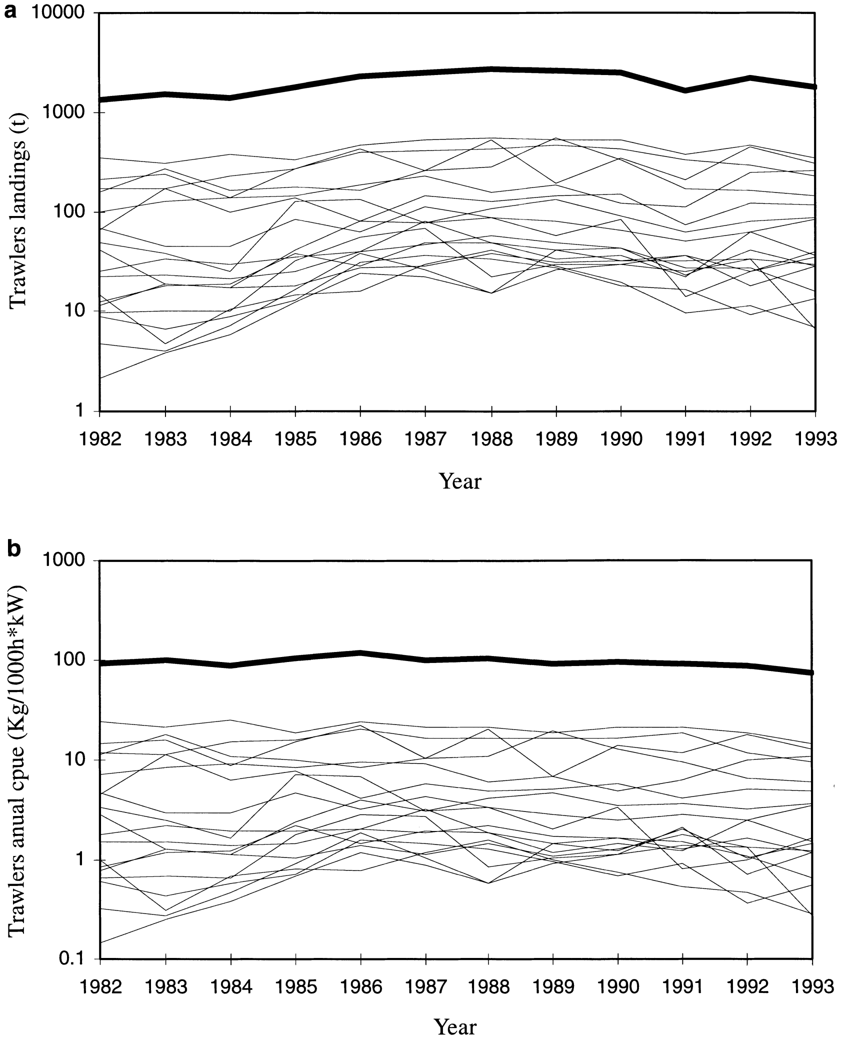

Fig. 2. Total biomass (bold line) and individual biomass variations by species (thin lines) in the landings and CPUE of the small-scale trawlers of La Rochelle: (a) annual landings (t); (b) annual CPUE (kg 1000 h^{-1} kW^{-1}).

Table 4

Summary of the values for landings, continental shelf area, total biomass, fishery productivity and coefficient of variation of the total biomass (CVt) for the 3 systems analysed (Bay of Biscay, Gulf of Lions and Scotian Shelf)

	Bay of Biscay	Gulf of Lions	Scotian Shelf
Mean of annual demersal fisheries landings (t)	64499 (Dardignac, 1988)	11860 (FAO, 1991)	73748 (Statistical Services, Fisheries and Oceans Canada, http://www.ncr.dfo.ca)
Area of continental shelf (km^2)	170000	14000	370000
Biomass ($g\ m^{-2}$)	2.9	2.5	4.7 (Duplisea et al., 1997)
Fishery productivity ($t\ km^{-2}$)	0.38	0.85	0.2
CV_t	32	40	22

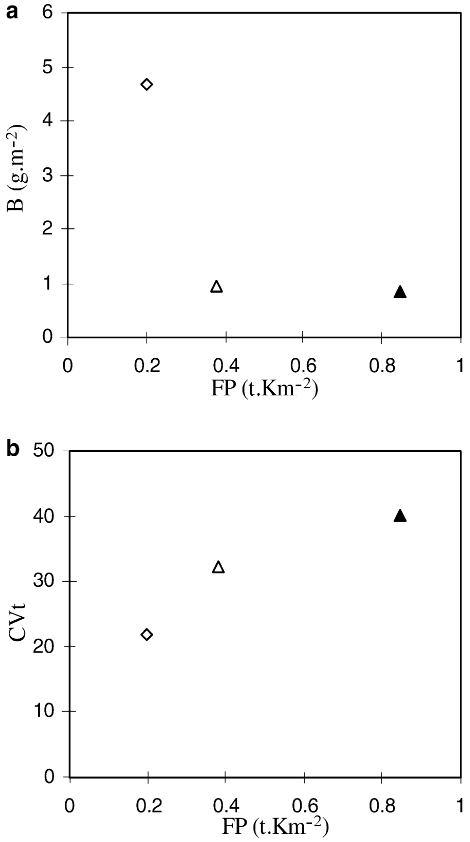

Fig. 3. (a) Relationship between the total biomass, B, and the harvesting level, fishery productivity, FP (total landings by unit of area in $\mathrm{t\,km^{-2}}$); (b) relationship between the coefficient of variation $\mathrm{CV_t}$ of total biomass and the fishery productivity, FP; in the Gulf of Lions (full triangle), the Bay of Biscay (empty triangle) and the Scotian Shelf (empty lozenge).

data. They interpret the low total biomass variability from Steele's (1965) hypothesis of energy limitation that is a carrying capacity of the ecosystem leading to tropic interactions between species. The same patterns of dynamics regulation are observed in the Bay of Biscay and in the Gulf of Lions. The dynamics of the demersal fish communities from these three different biogeographic areas could then be regulated by energy limitation.

Results from works dealing with demersal fish community dynamics are consistent with the hypothesis of interactions between species. Modelling approaches suggest that interactions may account for observed variability in demersal fish assemblages (Ursin, 1982; Sissenwine et al., 1984; Overholtz and Tyler, 1986). Time series analysis approaches are also consistent with species interactions (Myers and Cadigan, 1993; Pope and Macer, 1996; Fromentin et al., 1997). Results from our approach are also consistent with the hypothesis that energy limitation could be a conservative property of demersal fish community dynamics in temperate areas.

However, the total biomass variability is higher in the Gulf of Lions than in the Bay of Biscay. This could be due to a decrease of the role of interactions in the community of the Gulf of Lions. Moreover, the distributions of species variability are identical. Although the nature of the processes involved in the species dynamics is not tackled here, the role of the physical factors could explain why the distributions of the species variability remain identical: in the systems where interactions play the main role in dynamics, the variability of species should be induced by interactions; in the systems where the role of interactions decreases, the role of the physical factors could increase, both processes could then induce the species variability.

4.1.2. Fisheries data

May et al. (1979) put forward three possibilities with regard to the changes of species composition in the fisheries landings of the North Sea without change in total biomass: compensatory shifts in population densities, changes in patterns of harvesting and coincidental environmental effects. Actually, on account of low CPUE (between year variability or rarefaction trend of species), fishermen may land species usually thrown back because of their moderate or low economic value. In the same way Van Densen and Buijse (1992) considered that imposing an effort limitation damps variations in the annual catches. Moreover, authors think that the fishermen attempt to maximise their yields (Beverton and Holt, 1957; Hilborn and Walters, 1987; Pikitch, 1987; Marchal and Horwood, 1996). However, the low total biomass variability and the high individual species variability are observed here not only with fisheries landing data but also with scientific survey data, released from the behaviour of fishermen. Therefore, the low variability of the total biomass observed in the landings data would not be induced by the harvesting patterns but by the community dynamics. This result allows to establish the low total biomass variability pattern from the fisheries data as well as from the scientific survey data.

4.1.3. Species replacement

One aim of the work of Duplisea et al. (1997) was to explain the total biomass stability in spite of a change in the species composition observed by Pope et al. (1988). They find "no evidence of consistent species replacement trends on the shelf-wide scale and conclude that diffuse replacement best describes species succession on the Scotian Shelf as a whole". The analysis reported in the present paper defends the compensatory shift hypothesis. The work of Quéro and Cendrero (1996) in the Bay of Biscay bring evidence of long-term trends of rarefaction (from 1727 to the present day) of species that have become extinct by now. On the scale of the present study, no trend is reported by these authors. Moreover, the timescale of our study may be too short to find evidence of such trends. Similarly, absence of species replacement in the Gulf of Lions is shown in the work of Gaertner et al. (1998) in the concerned period. Therefore, biomass variability quantified here by the coefficient of variation does not reflect trends but annual variations.

4.2. Fisheries removal

4.2.1. Fishing effect

Welcomme (1985) defended the hypothesis that the total annual catches vary more in over-exploited ecosystems because the yield consists of fewer and mainly short-lived species. Van Densen and Buijse (1992) added that the catch of over-exploited species consists of relatively few year-classes. They argue that in these situations, environmental variability, which induces variation in population parameters, probably has a more pronounced influence on the variation in the annual catch. In the present study, the total biomass variability increases with the fishery productivity. An alternative effect of fishing could be proposed: exploitation may decrease population biomass moving the community away from its density-dependent limitation; therefore, the role of interactions in species dynamics could decrease when harvesting increases. As the species may then fluctuate more independently from each other, the CV_t would consequently increase. In fact, biomass decreases and total variability increases when the harvesting level increases. According to Caddy and Garibaldi (2000), the effects of fishing on multispecies landings from 14 world areas are consistent with the present work.

However, other effects of fishing could be addressed. By selecting species, fisheries could alter the abundance ratio of species and thereby alter or emphasise the biotic interactions in the community. As weak or strong interactors may induce fluctuations or may stabilise species biomass (McCann et al., 1998; Berlow, 1999; Berlow et al., 1999), the variability of the total biomass may change. Moreover, fishing alters the demographic structure of species by decreasing the number of age groups in such a way that the group of recruits becomes more dominant in biomass. As physical factors, such as temperature or wind, may control the recruitment in a population (Ellersten et al., 1989; Dickson and Brander, 1993; Ottersen and Sundby, 1995), the whole biomass of the population may fluctuate according to these physical factors.

4.2.2. Fishery productivity and biomass estimations

In other aspects, the same energy limitation, whatever be the region, is assumed to measure distance from the density-dependence threshold using total biomass. This assumption is reasonable insofar as the three areas concerned are located in the same latitudes (from 40 to 50°N). Hence, the harvesting level sustained by the community, quantified by the total fishing landings by unit of continental shelf surface, is comparable between areas. The values of fishery productivity computed by Caddy et al. (1995, 1998) and the values computed here are of the same magnitude. They have observed an increase of the fishery productivity in the Mediterranean and interpret this as a consequence of a nutrient enrichment brought by about anthropogenical runoffs. So, we may wonder if the highest value of the fishery removal reached in the Gulf of Lions is due to this enrichment or to higher fishing effort. This increase is observed in the Gulf landings in the last 3 years of the time series, 1987, 1988 and 1989 (Caddy et al., 1995). However, when these years are removed, the fishery productivity remains the highest ($0.61\ \text{t}\,\text{km}^{-2}$ vs 0.38 and $0.2\ \text{t}\,\text{km}^{-2}$).

The demersal fish monitoring are carried out in the Bay of Biscay, the Gulf of Lions and the Scotian Shelf with different fishing gears in different seasons. The estimated value of biomass is probably sensitive to the fishing gear characteristics and subject to seasonality. Though according to Pope and Knights (1982) and Pope et al. (1988), the less-exploited Faroe Bank and Georges Bank have more large piscivores and less fish preys than the heavily exploited northern North Sea. Moreover, Duplisea et al. (1997) give the modal body weight of all fish species as 180 g, while it is only 37 g in the Bay of Biscay and 32 g in the Gulf of Lions (unpublished data). These arguments support the hypothesis of higher biomass in the Scotian Shelf than in the Bay of Biscay and in the Gulf of Lions.

5. Conclusions

There are three conclusions. The total biomass variability is lower than the species biomass one, not only on the Scotian Shelf but also in the Bay of Biscay and the Gulf of Lions. This characteristic is established both with scientific survey data and fisheries data. These two conclusions tend to confirm that this characteristic is a pattern of the dynamics regulation and could be a conservative property of demersal communities. This regulation pattern is consistent with the hypothesis of energy limitation despite the fact that interactions are not identified or measured. With a generalisation of low total biomass variability in demersal communities, this pattern could then become a main criterion of validation of multispecies models or be used as an input constraint (Wilson et al., 1991b).

The third conclusion is the possible relationship between the total variability and the harvesting level. This could indicate a decrease of the role of interactions in species dynamics by fisheries removal. Despite the difficulties to demonstrate the underlying processes, the conservative patterns of biomass variability and the possible relationships between exploitation and total biomass variability are consistent with the total biomass variability, being a broad indicator of the fishing impact on the community.

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Variability in the demersal fish assemblages of the Bay of Biscay during the 1990s

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Data were collected during autumn groundfish surveys carried out on the eastern continental shelf of the Bay of Biscay from 1987 to 2000. The spatial organization of the demersal fish assemblages is examined using multitable factorial analysis. It shows the species assemblages are organized according to three major spatial structuring factors. Two are orientated mainly along a bathymetric gradient, while the third is linked to a large muddy bottom area near 100 m depth. These features fit well with the 11 surveys analysed. Of the 49 species considered in this study, 11 exhibited limited temporal variations in their abundance and spatial distributions. The variability of mesoscale hydrodynamic features has no measurable effect on the scale of species assemblages, but large-scale hydroclimatic changes seem to affect those species that are at the limit of their distribution range in the Bay of Biscay.

Keywords: Bay of Biscay, demersal fish assemblage, multitable factorial analysis.

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Introduction

The spatial pattern of groundfish distribution is influenced by the physical, environmental, and habitat characteristics. In the case of shelf and upper-slope demersal assemblages, depth is often the main gradient along which faunal changes occur.

Data collected during annual autumn surveys are used to analyse the spatial organization of species assemblages on the eastern continental shelf of the Bay of Biscay in the period 1987–2000. The study of the multispecies spatial structures over time requires the combined analysis of different tables of species density sampled at different stations. This is done using multitable factorial analysis.

Available data

Data were collected during the 11 groundfish surveys carried out by IFREMER since 1987 in the Bay of Biscay from October to December (ICES, 1997). The survey area is between 48°30′N and 43°30′N. The sampling scheme is stratified according to latitude and depth. A 36/47 GOV trawl is used with a 20-mm mesh codend liner. Haul duration is 30 min at a towing speed of 4 knots. Fishing is mainly restricted to daylight hours.

Three changes occurred in the sampling procedure beginning in 1997: (a) a stratified random scheme replaced the fixed station sampling strategy used since 1987; (b) the number of hauls made per survey decreased from about 120 to 80; and (c) operations were carried out from a different research vessel.

The data obtained from 1163 hauls were analysed. A total of 209 fish species were caught but only 49 demersal fish species, present on average in at least 5% of the tows, were included in the analysis. The numbers per tow were log-transformed before conducting the analysis to minimize the dominant effect of exceptional catches.

Data analysis

The analysis methods used are described in Gaertner *et al.* (1998). The table of the total number of individuals per survey and per species (matrix with 11 surveys and 49 species) was used as input in a between-class correspondence analysis (CoA) to test the existence of a survey effect in the overall species composition. The significance of between-survey differences was checked by means of a permutation test.

The CoA version (Gaertner *et al.*, 1998) of the STATIS multitable method (Lavit, 1988) was then used to describe the stable part and the variable part of the spatial structuring of the assemblages. The first stage of the STATIS method consists of calculating a distance matrix between species for each survey. This allows comparison between surveys by calculation of a distance matrix between surveys. The 11 elements of the first eigenvector of the diagonalized between-survey distance matrix are then used to weight the 11 species distance matrices to construct a mean table of maximum inertia (compromise table). The analysis (correspondence analysis) of the compromise table defines axes and components, which express the stable part of the spatial structures. In addition, the projection of the 11 matrices into the compromise space allows a plot of the species trajectories. These represent the temporal variations of each species with respect to the common structure and identify the relative location of the sampling stations.

Results

The inter-survey CoA demonstrates the occurrence of weak but significant temporal variations ($p<0.05$) in overall species composition between the surveys at the scale of the Bay of Biscay.

Table 1. STATIS analysis: contribution of each survey to the construction of the compromise table (weight) and fit of each survey to the compromise (Cos^2).

Survey	No. of sampled stations	Weight	Cos^2
1987	127	0.30	0.61
1988	132	0.32	0.75
1989	139	0.30	0.66
1990	135	0.31	0.71
1992	105	0.30	0.63
1994	101	0.30	0.66
1995	112	0.31	0.77
1997	89	0.31	0.74
1998	74	0.29	0.63
1999	70	0.29	0.65
2000	79	0.29	0.61

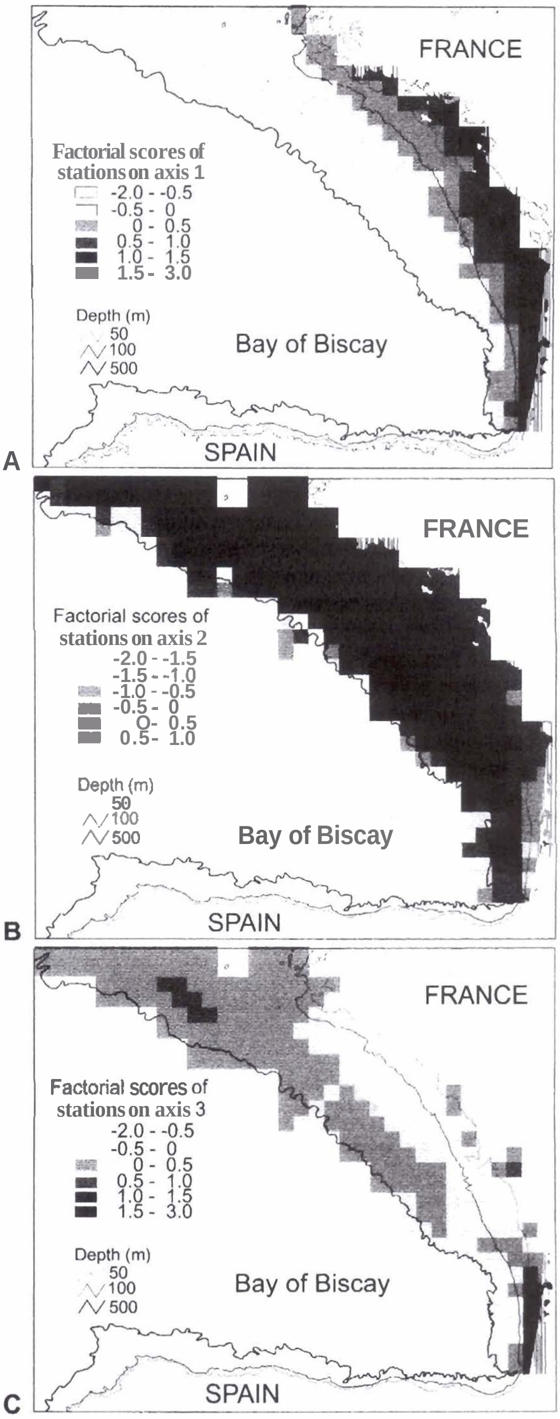

Figure 1. Map of the stable structure of the demersal fish assemblages and of the factorial scores of the sampling stations on the first three axes (A to C) of the correspondence analysis of the STATIS compromise table.

Table 2. Main indicator species defining the first three components of the stable structure of the spatial organization of the assemblages from the STATIS compromise table analysis.

Axis	Species	Coordinate sign
	Spondyliosoma cantharus	+
	Mullus surmuletus	+
	Trachinus draco	+
	Argentina silus	–
	Gadiculus argenteus	–
	Capros aper	–
	Trisopterus minutus	+
	Capros aper	+
2	*Aspitrigla cuculus*	+
	Galeus melastomus	–
	Argentina silus	–
	Chimaera monstrosa	–
	Trachinus draco	+
	Roops boops	+
3	*Liza ramada*	+
	Merlangius merlangus	–
	Pomatoschistus minutus	–
	Lesueuriogobius friesii	–

The STATIS results (Table 1) show that the contribution of the different surveys to the construction of the compromise table is well balanced. The fit of each survey to the compromise table is relatively constant and does not exhibit temporal trends.

The first three axes of the correspondence analysis of the compromise table explain more than one-third of the inertia of the stable part of the spatial structuring of the assemblages. They represent the main spatial organizational directions of the species assemblages. Axis 1 (Figure 1A) shows that the depth gradient is the main structuring factor over the survey area. In the shallower part of the continental shelf (less than 100 m) a weak latitude gradient also exists. The indicator species of gradient extreme values are listed in Table 2. On axis 2 (Figure 1B), positive scores demarcate the central part of the continental shelf. High positive scores in the northern part of the shelf are associated with ***Aspitrigla cuculus*** and ***Capros aper.*** High negative scores on axis 3 (Figure 1C) are closely related to the spatial distribution of *Lesueuriogobius friesii* and encompass the muddy bottoms, which occur between 60 and 120 m depth.

Eleven 'species mainly contributed to the inter-survey variations (Figure 2). Their positions with respect to the gradients and in relation to other species show, however, that variations were confined to species natural ranges. Five species were widely distributed over the outer part of the continental shelf, while the spatial distributions of the six other species were restricted to shallower waters. Changes in abundance or spatial distribution patterns were identified. They were temporary for some species and exhibited time trends for others.

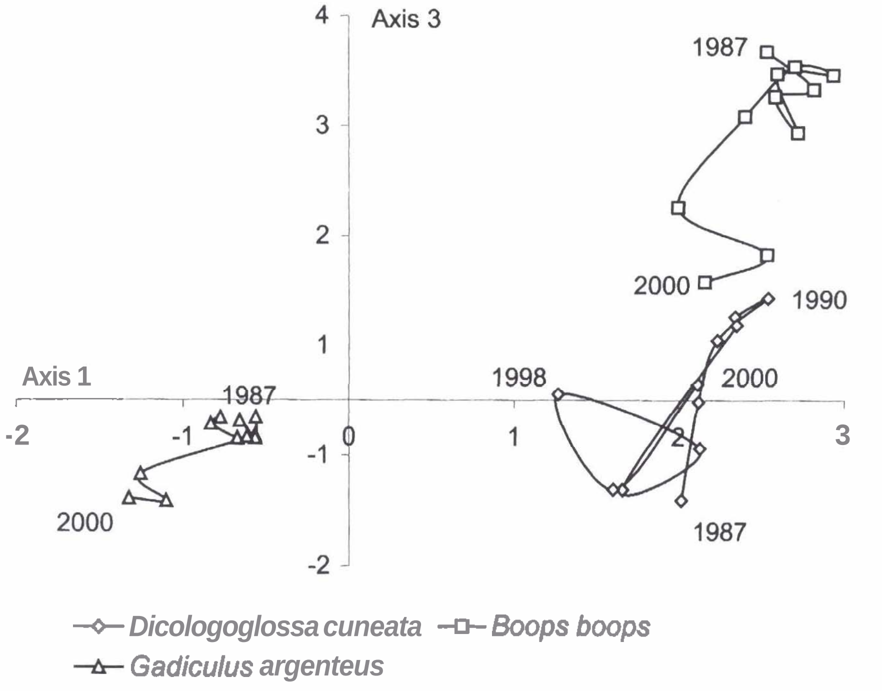

Figure 2. Details of the projection of the trajectories over time of some of the 11 characteristic species on the factorial plane 1–3 of the STATIS compromise.

Synthesis and conclusion

The demersal fish species assemblages on the Bay of Biscay eastern continental shelf are spatially organized according to depth, latitude, and substrate type represented by the large muddy bottom area near the 100 m depth contour. A common structure is identified over the 11 autumns sampled in the period 1987–2000. Small inter-survey variations are shown. They are linked to changes occurring in the abundance or the spatial distribution patterns over time of 11 species.

The relative stability of the demersal fish communities throughout the study period contrasts with the strong variability of some mesoscale hydrodynamic features (upwellings, lower salinity water lenses, and cold pool) encountered on the French continental shelf of the Bay of Biscay (Puillat *et al.*, 2003). These changes seem not to have measurable effects at the scale of the demersal fish species assemblages because they were too short in duration, not intense enough, too small spatially, or some combination of these.

On the other hand, large-scale hydroclimatic changes, as indicated by increases in sea surface temperature (Planque *et al.*, 2003), seem to affect species that are at their limit of distribution range in the Bay of Biscay. *Dicologglossa cuneata* and *Boops boops*, two shallow-water species having their northern distribution limit in the Bay of Biscay, show increasing abundance trends and increases in their areas of distribution over the study period in response to the observed warming.

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ECOSYSTEMS

Relating Species and Community Dynamics in an Heavily Exploited Marine Fish Community

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ABSTRACT

We examined the dynamics of fish species and how they relate to species assemblage coherence in the heavily exploited Georges Bank fish community. Coherence is defined as reduced temporal variability of total assemblage biomass. We assumed that a higher degree of compensation hence coherence occurs within competitively coupled species assemblages; therefore, fisheries may directly alter the dynamics of certain targeted species sizes but assemblage structure will be relatively more stable owing to compensatory interactions. Species-sizes were grouped, based on negative covariance coupling in biomass time series from survey data. Assemblages representing benthic feeders were clearly identified by this method; furthermore, the most heavily exploited species-sizes were decoupled from other species-sizes suggesting that fisheries have diminished their potential to compensate or to be compensated for by competitive interactions. Biomass of species-sizes within known trophic guilds strongly compensated other guild-member biomass fluctuations if the diet of guild members was more specialized. This is an indication that more competitive conditions (more specialization) foster greater compensatory responses between competitors biomass fluctuations.

Key words: goal function; thermodynamics; emergent property; energy flow; species replacement; diversity-stability.

INTRODUCTION

Determining the impact of a single species fishery on aggregate fish community properties is a difficult problem that has received considerable attention (Duplisea and others 1997; Kerr and Dickie 2001; Jennings and others 2002; Rochet and Trenkel 2003; Trenkel and Rochet 2003). It is often assumed that fisheries control the dynamics of exploited fish communities, yet multispecies interactions can also strongly affect exploited fish species population dynamics (Magnússon 1995). Clearly, there is a need to understand species dynamics within a community perspective, even in the less than ideal situation where human activities affect outcomes.

Relating species and community dynamics is difficult because species are parts of ecosystems that contain many causal loops, which invalidates purely piecewise, species by species analyses and projections in all but the very short term (days to weeks). This is because ecosystems are complex self-organizing systems (Kay 1990). This does not mean that we cannot study community level phenomena, we can but we need to develop means to analyze structure at these higher levels rather than building from the base up.

Higher level system phenomena in fish ecology are usually examined using measures of the aggregated community such as total biomass (Duplisea and others 1997), biomass size spectra (Rice and Gislason 1996; Bianchi and others 2000) or

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mean trophic level of the community (Pauly and others 1998). These measures are able to show what the impacts of fishing have been on the aggregated community rather than just a single or group of species. These are useful phenomenological descriptors of systems but remain post hoc and provide little predictive capacity; however, these descriptors are still useful for drawing generalities on how fish assemblages are organized and how they are likely to respond to fishing.

One such generality that has arisen out of size spectrum studies is that total system biomass is much less variable than biomass of component species; furthermore, that biomass at size usually has a consistent pattern over time and space (Sheldon and others 1977). These patterns are present even in the face of large fisheries which undoubtedly affect community interactions; however, fish communities readily cope with fisheries perturbations in terms of preserving system energy flow function. The altered exploited fish community, however, may not be desirable in a socio-economic sense owing to community shifts from commercially desirable species often to lower value and less charismatic species. It has also been shown that biomass in an ecological sub-grouping of benthic feeding fish, that contained evolutionarily distant species, was remarkably constant in biomass (Duplisea and others 1997). This preservation of the benthic fish collective structure suggests that species replacement occurs in fish assemblages such that if one species decreases in abundance one or more other species usually increase in abundance to compensate (Duplisea and others 1997). General phenomena such as these are referred to as emergent properties, and arise out of huge numbers of interactions between components but are difficult to predict simply from studying many components (Ulanowicz 1986).

Although it may be difficult to predict assemblage phenomena from component dynamics, it is still desirable to know how phenomena at the aggregated and disaggregated scales relate to each other. To this end, our knowledge of general phenomena have sometimes been taken as starting points for predicting system dynamics. For example, Ulanowicz (1997) derived Ascendancy (**A**) as a measure of ecosystem maturity that accounts for the number of interacting components and linkage strength between components. **A** is posited to be higher in old undisturbed systems than new or ephemeral systems. Another example is the system wide production to biomass ratio (P/B), which tends to be lower in mature ecosystems than in ecosystems in early successional stages (Margalef 1968; Matsuno 1978). Clearly, one could maximize **A**, minimize P/B, or optimize any system property as a means to understand ecosystem organization.

Trophic competition is a known structuring mechanism in animal assemblages and species that have the greatest diet overlap are considered the strongest competitors with each other (Simberloff and Dayan 1991; Wilson 1999; Blanchard 2001). Groups of species with similar diets are referred to as trophic guilds. It is logical that one or more species in a trophic guild are most likely to compensate biomass fluctuations of other species in the same guild under competitive conditions of limited food resource. Hence, it is likely that given a time series of biomass of a species assemblage, the competitive species pairs are most likely to show combined biomass constancy and also a covariance structure that maintains that biomass (Cottingham and others 2001).

Given perturbations on individual species both natural and man induced, one might expect that compensation will occur between trophically similar species. This indeed has been observed in the Georges Bank fish assemblage (Murawski and Idoine 1992). We have used this observation of biomass constancy as a optimization criterion for determining which species interact and compensate each others' biomass fluctuations to achieve a relatively stable trophic guild biomass.

In the present marine fish study, we suggest that biomass constancy in systems is most likely to be apparent within competitively structured trophic guilds. We hypothesize that temporal variation in species biomass within a guild is most likely to be compensated by an opposite biomass fluctuation of one or more other species within the same guild; therefore, species within the same guild are most likely to have coupled covariance in biomass such that their aggregate biomass is relatively constant. Here we explore methods for understanding how biomass compensations may occur in an exploited fish community and how compensations relate to known trophic guilds of species-sizes.

Our study unfolds within a series of steps where we:

1. Develop a method that examines covariance between species and aggregates of other species to determine covariance groupings to be considered a tentative assemblage structures,
2. Examine how the most heavily exploited species in the system fit into these covariance groupings,
3. From trophic guild structure determined by diet studies, test for significance of species compen-

Table 1. Stepped Procedure of the Covariance Grouping Method

Step	Operation
1	Create a matrix of biomass estimates over time for each species.
2	Choose a starting species.
3	Compute the covariance in the time series of this species with every other species.
4	Aggregate the biomass of the start species with the species that has the largest negative covariance with it.
5	Name this aggregated time series, aggregate 1.
6	Remove from the community matrix the component species that made up aggregate 1.
7	Start again at point 3 but with aggregate 1 as the chosen species.
8	Keep aggregating until the decrease in temporal variance (CV) of the aggregate caused by adding a new species is 0.
9	When aggregation no longer reduces temporal variance, start the procedure again at 2 but with the reduced community matrix.
10	Follow steps from 3–9 until there are no species left that have not been assigned to an aggregate group.
11	Start at 2 again but with a different start species than has been chosen before.
12	Go from 2 to 10 until every species in the matrix has been the start species.
13	Compute the number of times each pair of species appears with each other in the same group.
14	Create a clustering and dendogram based on the similarity matrix determined from 13.

sation in that guild's biomass and examine results in relation to specialization versus generality of the guild diet.

This work sequence goes from the most general to the most specific in an attempt to understand how the Georges Bank fish community copes with perturbation such as fishing, then subsequently tease apart this response such that the aggregate response can in some manner be seen as a manifestation of individual species responses.

METHODS

Data

We used size and abundance data collected through statistically rigorous groundfish sampling surveys for the Georges Bank conducted by the Canadian Department of Fisheries and Oceans and for the North Sea collected by CEFAS. The Georges Bank survey is conducted in February each year using a stratified random sampling design (Doubleday 1981) and a Western IIa trawl with 19 mm cod-end mesh (Carrothers 1988). STRAP averages (Smith and Somerton 1981), area weighted averages based on a stratified random design, are reported here. We included fish only in the size range 15–120 cm, as fish of this size should be captured consistently over the time series. We divided each species into size categories and calculated the biomass in each species-size category for each surveyed year (Appendix A). The size categories chosen were as in Garrison and Link (2000). For most species, small was from 10–20 cm, medium from 21–40 cm, large from 41–80 cm and extra large was larger than 80 cm. Additionally, we report the potential impacts of directed commercial fishing on various species using the US National Marine Fisheries Service system, which is based on ratio of the current biomass (B) to the estimated biomass at the maximum sustainable yield (Bmsy) point (Appendix A, Murawski and Almeida (2000)). The potential impact by catch in the large scallop fishery on Georges Bank is also considered (Appendix A, NEFMC (2003)). We excluded species-sizes from the analysis if they appeared in less than half of the number of survey years as they are quite rare and therefore do not have much influence on the species-size covariance structure.

Covariance Grouping Method

We developed a method of grouping species-sizes based on their largest negative covariance (Table 1). Because the most tightly coupled competitors are most likely to show compensatory biomass trajectories, this should appear as the largest negative covariance in a community covariance matrix. Therefore, we chose a starting species and calculated the covariance between it and every other species-size group. We then aggregated with this starting species-size, the species-size that had the largest negative covariance minus the time series variance of the starting species group:

$$\Phi = \mathrm{Min}(\mathrm{cov}_{i,j} - \mathrm{var}_i) \text{ for all } j \qquad (1)$$

Where the species-size j which has the value ϕ and is chosen to aggregate with i. These two species-sizes are then removed from the matrix as separate entities but instead appear as a summed aggregate entity. The procedure is repeated until an amalgamation criterion is no longer satisfied. As our premise is that competitively determined groupings will have relatively more stable biomass than components, we chose an amalgamation termination criterion that dictates addition of a new species-size to the group must reduce the temporal variance of the aggregate and when it no longer does, terminate the amalgamation sequence. This termination criterion is consistent with the premise that species-sizes in the same guild are most likely to compensate each other's biomass fluctuations in time. We measured the temporal variance of the aggregate as the CV over time. A group is defined at the termination of an amalgamation sequence. The procedure then looped with the reduced community matrix. After all species-sizes in the matrix were assigned to a group, the entire procedure is looped using a different starting species-size. This was continued until every species-size had been the starting species once. The starting species-size loop is necessary because the procedure can be sensitive to starting species given that multiple species-size contingencies can exist and affect amalgamation order hence group membership.

The solution provided by this method is just one of several depending on the degree of contingency considered. That is, a hierarchical scheme where a new starting species is at every single step would account for more contingency but this is a factorial problem and quickly could become computationally intractable. The degree of contingency in species interactions is like the contingency in an assembly sequence (Law and Morton 1996) and the greater the contingency, the greater the number of possible sequences, hence the greater the computation time. Our method has not accounted for the entire range of possible assembly sequences yet by allowing each species to appear as the starting species once, we have accounted for a great many possible outcomes.

If we started with X number of species-sizes then we end up with X number of realizations of the method which could theoretically all be the same or quite different depending on the strength of the contingent species-size covariance. We therefore, brought these together to form a dendogram by creating a distance matrix based on the number of times a species-size pair grouped together over all the realizations of the method. If these species were often grouped together, then they had a high affinity with each other (compensatory trajectories) and were not overly affected by the presence or absence of other species. We call the strength of this affinity the group fidelity.

We examined the groups resulting from this analysis for their general diet preference, for example, benthic feeders, to see if the grouping made sense. Additionally, because the method could potentially reveal the complementary biomass trajectories between predator–prey pairs, it is important to examine the relative body sizes of the group components where a prey and predator pair is unlikely to occur in groupings when the constituents are all of the same size category. Finally, we tested for spurious groupings by using a null model test (below). In this instance, this test is not one of significance but one of spuriosity. Because the groups were defined by complementary covariance, we expect a significant result for compensation in the null model test. If the null model test for complementary covariance does not confirm it, then it is valid to conclude that a particular group is a spurious group resulting from the method.

Null Model (Monte Carlo) Testing of the Biomass Constancy of Known Trophic Guilds

Garrison and Link (2000) provided careful analyses of the diets of several Georges Bank fish species by size category. They performed multivariate analyses to group these into trophic guilds based on their diets. As we have a survey time series for Georges Bank species, we examined the hypothesis that biomasses of species-size groups within a Garrison-Link guild (GLG) are ordered such that the sum is compensatory; hence, temporal variability of biomass is reduced in a GLG more than would be expected if biomass configurations of GLG components were random.

Ho: biomass is randomly configured amongst guild components hence the CV of temporal variance within the guild is close to random, that is, $CV \approx 50\% \equiv 5\% > CV < 95\%$.

Ha1: biomass is configured amongst guild components such that the sum within years is relatively constant and the CV of temporal variance within the guild is significantly smaller than if biomass configurations were random, that is $CV \leq 5\%$.

Ha2: biomass is configured amongst guild components such that the sum within years is significantly variable; hence, the CV of temporal variance within the guild is significantly greater than if biomass configurations were random, that is, $CV \geq 95\%$.

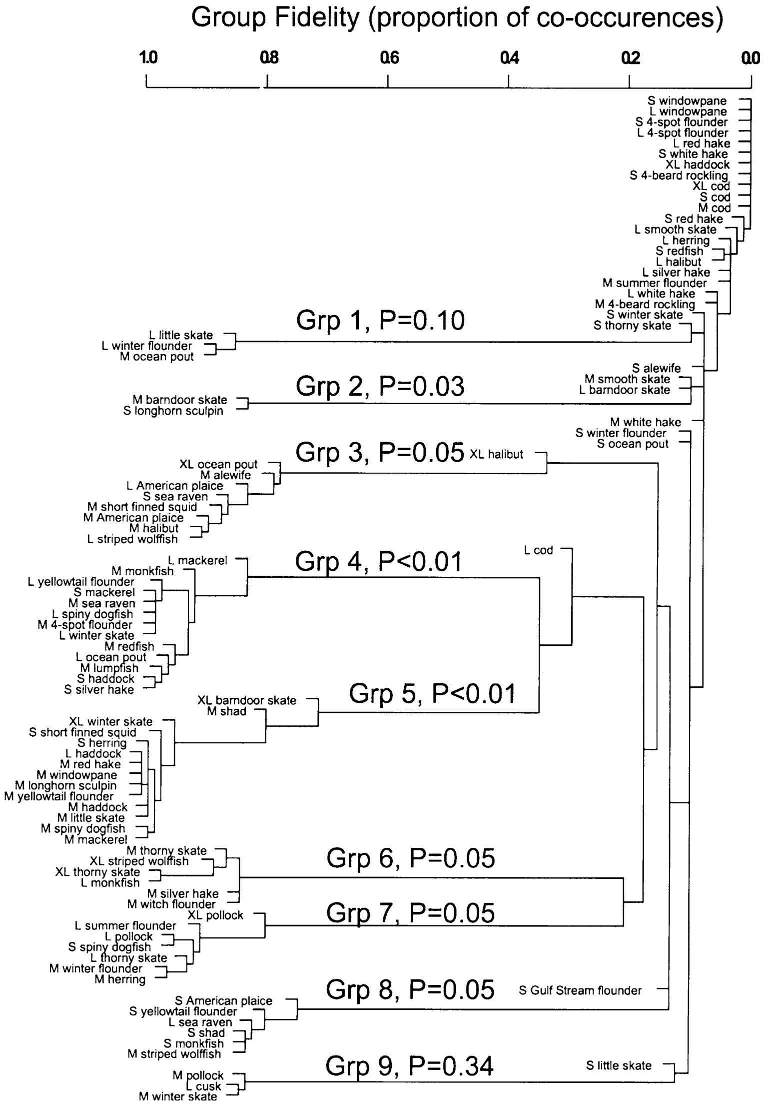

Figure 1. A dendogram of Georges Bank species groups divided into four size classes based on similarities determined from time series covariance grouping method, where most dissimilar species (greatest negative covariance) were grouped with each other. Groups and the significance level for spuriosity (where $P > 0.05$ indicates a spurious grouping) are shown on the figure.

We examine these results in relation to the diversity of the diet of GLG members as a measure of prey switching potential, hence the generality of the diet and an indicator of the potential for a competition for food to occur amongst guild members. Diet diversity was calculated as the Shannon–Wiener index of fish stomach content differentiated into species (Garrison and Link 2000). By using the original matrix for null model testing we are controlling for the effects of random statistical cancellation (Margalef 1974; Doak and others 1998), sometimes referred to as the "portfolio effect" (Tilman and others 1998) and provides a useful analogy to better understand what is implied by the above hypotheses:

Ho is the null hypothesis where nothing interacts and guild components appear to be randomly co-occurring. Therefore, if the actual configuration of a guild's components' biomasses are neither more nor less variable than those same biomasses randomly configured over all years, then we cannot reject the null model (that is, no evidence of interaction is occurring). This is the classic portfolio effect where compensation in fluctuations is merely the result of random statistical cancellation and the greater the number of components, the greater the potential for overall constancy. Generally this is what a safe financial investing strategy aims to do, where the investment is spread over multiple sectors and regions to buffer individual fluctuations and addition of wealth comes about through overall economic growth rather than selection of particular fast growing subsectors or regions.

Ha1 is where the actual biomass configuration of components is less variable than one finds with random permutations of the component biomasses. Such a situation might occur in a financial portfolio by investing in different yet competing industries in the same sector. A simplistic example might be to invest in the long distance transportation sector with a two fold investment strategy such that both the high speed rail industry and the domestic airline industry split the total investment. The probability for one of these industries to increase when the other decreases is higher than for just two random industries over all economic sectors. This is a situation of hyperstability in the transportation portfolio, however is does not buffer against total decline in the transport sector owing to other external circumstances, for example, the general decline in the transportation sector following the events of 11 September 2001.

Ha2 is where the actual biomass configuration is more variable than random configurations of the biomass. In a portfolio this is called ''putting all your eggs in one basket'': there can be great rewards in particular sector upturns but there is also great loss on sector downturns. This is a boom-bust investing strategy.

RESULTS

Time Series Covariance Grouping Method

The time series covariance grouping method aggregated Georges Bank species into nine major groups (Figure 1). Application of the null model spuriosity test showed that species-sizes in groups 2–8 were not spurious groups ($P < 0.05$) while groups 1 and 9 were. More than 75% of the constituent species in Groups 1, 6, 7 and 8 are strongly associated with the benthos. Other groups contained various pelagics and predators such as herring and dogfish, respectively; therefore, it is not possible to make a clear designation for these groups. Several species-sizes in this analysis were grouped with other species only with a very low group fidelity based on complementary time series biomass. Fishing activities strongly influences many of the lone species such as cod, flounders and skates. Most groupings have a fidelity of more than 0.8 indicating that time series complementarity between group and species-size biomass was relatively insensitive to starting species-size.

Over all realizations of the method, 80% of the groups formed contained only one species-size while less than 5% contained between 10 and 14 species sizes (Figure 2a). Of the groups formed in all realizations, each contained less than 5% of the community biomass 90% of the time. On four realizations of the method, however, a single group was formed that contained more than 70% of the community biomass and on one occasion between 75 and 80% (Figure 2b).

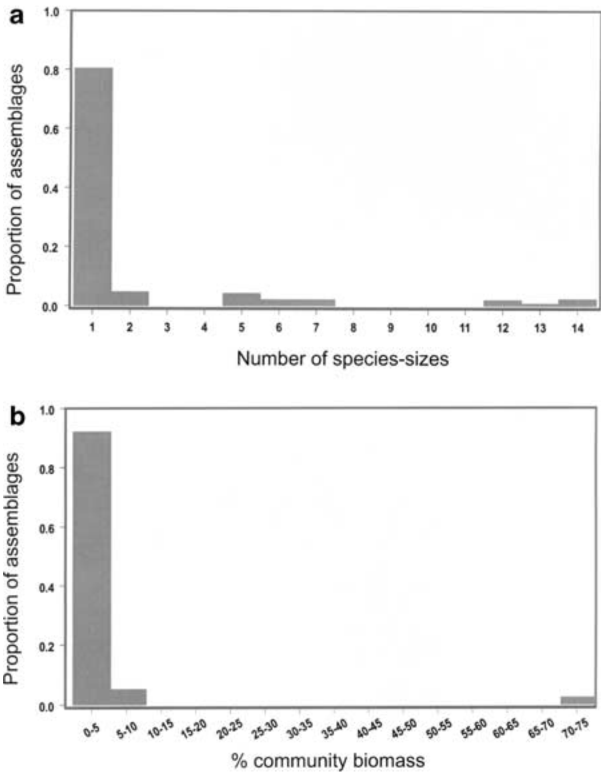

Figure 2. **A** Histogram of number of species-size categories from Georges Bank in groups and **B** proportion of biomass in groups as determined from the time series covariance grouping method. These histograms are produced from all realizations of the covariance grouping method rather than from the summary dendogram of those realizations shown in Figure 1.

Null Model Guild Temporal Stability

The Monte Carlo method of examining variability of combined GLG biomass against the null model showed that two of the nine GLG on which the null model analysis could be performed had a significantly small CV value while five of the nine had a significantly large CV (Table 2). That is, the null hypothesis that species-size biomasses within GLG are independent of each other, was rejected in eight of the nine cases thus suggesting that species biomass trajectories in GLG were either more or less variable than would be expected if biomasses of species-sizes were random.

The two GLG which had a significantly small CV (demersal benthivores and general piscivores) were also the multispecies GLG where diet diversity was also the smallest (Table 2), that is, for which the specificity for a particular type of food was greatest. To the contrary, the six GLG with significant large

CV usually had high diet diversity (less dependence on specific prey types). Four of these high CV GLG (three omnivore GLG and sea raven piscivores) consisted of only one biological species, although of two or three different sizes of each; hence, these cannot be considered multispecies guilds and direct recruitment-growth links exist between sizes of each of these species. Because of these links, it is not valid to search for compensation with the null model test when only one biological species constitutes a guild. The one remaining significantly high CV GLG, pelagic planktivores, consisted of mackerel, herring and small pollock and had a relatively high diet diversity. The pelagic planktivore GLG also had the highest temporal variance relative to other guilds and not just in relation to its null model CV. The one guild for which the null hypothesis was not rejected was GLG I, shrimp and amphipod predators, which consisted of 11 species-sizes and had a high diet diversity and a small CV relative to other GLG. Therefore, the covariance structure of biomass time series of different species-sizes in GLG I could not be distinguished from a random assemblage.

DISCUSSION

Phenomena such as conservative biomass at size distributions are commonly observed for exploited fish communities (Kerr and Dickie 2001). These phenomena or emergent properties, are thought to arise out of competitive interactions between species, sizes and life histories compounded with individual and population responses to perturbation. The overall sum of these interactions is identifiable (they emerge) and relatively constant. Emergent properties have been used to characterize systems and are now taking on a greater importance as ecological system indicators (Rochet and Trenkel 2003) as they represent the result of huge numbers of interactions without recourse to studying the dynamics of the components. The present study adopts a similar approach in that it recognizes structure at these aggregated levels (in this case the observation of biomass constancy in guilds). We go further, however, by imposing a pseudo-mechanism on sub-components where we aggregate using certain criteria to manifest the phenomenon of biomass constancy within guilds. Specifically, we have imposed an interaction criterion stating that species within the same guild are most likely to be competitors hence their biomass trends should be complementary with negative covariance. In so doing, we have created a model by which sub-community components must interact to come into congruence with observations at an aggregated level of biomass constancy. This model describes how various players could function together to produce this phenomenon of biomass constancy at an aggregated level.

Through imposing this criterion we have been able to show that the most heavily fished species in the Georges Bank fish community appear removed from other species in the system. We further show that species in more specialized trophic guilds show stronger compensatory covariance structure and species-size group time series characteristics are more similar for species within the same guild than for species between guilds.

The iterative method of aggregating species and groups of species with largest negative covariance created reasonable aggregations of species such as a group of fishes that live and feed on similar benthic food sources even though the constituent species were very different taxonomically (for example, haddock, flounders and skates). This method indicated that some of the species that are most heavily exploited like large cod and haddock (Appendix A, Mertz and Myers (1998)) are also species that were rarely or never assigned to an aggregation of other species. This suggests that the biomass time series of these heavily exploited species are erratic relative to other species in the system and are, in a sense, out of harmony with the rest of the system. This method can produce spurious groups (for example, groups 1 and 9) but application of the null model test can help to eliminate these. Some of the groups formed contain potential predator–prey pairs, for example, Group 7 contains both large spiny dogfish and small haddock whose complementary biomass trajectories are more likely to arise from a predator–prey coupling than a competitive coupling. Predator–prey groups appear less common than competitive groupings because fish predators and prey usually have a size difference of about 10:1 (Floeter and Temming 2003) yet most of the species-sizes assigned to the same group do not have this size differential suggesting that the groupings contain trophic competitors rather than predator–prey pairs. Additionally, it is more likely that predator and prey cycles lag in time hence they would be less apparent in the present method. Nevertheless, this is a potential confounding factor in the groupings and any applied use of these groupings would need to closely consider this.

Well established concepts such as competitive guilds (Simberloff and Dayan 1991; Wilson 1999) suggest that time series compensation should be manifest between species within a competitive guild. Competitive structuring of species' biomasses

Table 2. Results of Null Model Analyses of Significance in Temporal Variability of Biomass in Known Trophic Guilds of Species-sizes and the Corresponding Diet Diversity of these Guilds

Guild Symbol	Guild Description	Diet Diversity	Number of Species-sizes	Multi-species	CV	*P* value of CV
I	Shrimp and amphipod predators	3.68	11	Yes	0.29	0.586
IIa	Pelagic shrimp predators	3.35	4	Yes	0.94	0.914
IIb	Pelagic planktivores	3.04	5	Yes	2.22	0.986
IIIa	Demersal benthivores	1.83	3	Yes	0.63	0.012
IIIb	Benthic amphipod predator (haddock)	1.26	1	No	0.96	–
IVa	Omnivores (dogfish)	3.14	3	No	1.14	0.993
IVb	Omnivores (winter skate)	3.36	2	No	0.98	1.000
IVc	Omnivores (cod)	3.92	3	No	0.55	1.000
Va	Piscivores (sea raven)	2.47	2	No	0.23	0.962
Vb	Piscivores (general)	2.55	6	Yes	1.56	0.047

Trophic guild classification and calculations of diet diversity were taken from data in (Garrison and Link 2000). Multispecies refers to biological species rather than just different size of the same species. Significant values (>0.95, <0.05) are underlined.

in the face of natural and fishery induced species fluctuation suggests that compensation in biomass is likely to occur between species within the same guild. Our null model tested for evidence that species-size biomass time series were not simply random. We found that the species-size biomass configurations were dependent on the diversity of the guild members' diets. More compensation appeared to occur for guilds with specialized diets, suggesting that competition for the more specialized food resources forced a tighter coupling of competitors' biomass trajectories.

The pelagic planktivore guild showed the opposite of compensation as the guild biomass configuration was significantly more variable than expected if random. Such a situation can certainly arise when large scale drivers affect all components of a group in a similar manner. Such might be the case with an environmental driver such as temperature. Indeed most components of the Georges Bank pelagic planktivore community (mostly pelagic fishes) increase in biomass at the same time (Overholtz and others 2000). It is likely that shorter lived pelagics strongly affected by environmental drivers will not show trends in compensation consistent with a competitive structuring mechanism and more likely will appear to follow boom-bust cycles (Ha2, see Methods).

We found that when a guild contained only one biological species, but with two or more sizes of that species, the configurations were more variable than random. This can be expected, as the biomass in these categories are not random as cohorts grow and move to larger sizes leading to autocorrelated time series. We did not attempt to remove the autocorrelation as this is essentially the signal we are using to create groups.

It has been speculated in the past that total community biomass variability is limited by variability of the energy input drivers and is less variable than component biomasses (Duplisea and others 1997). We found, however, that for the total sampled Georges Bank fish community the configurations of species-size biomasses in any one year were such that the variability of the community over the time series was close to random. However, we showed that known trophic guilds within this community can be significantly nonrandom. We performed the same analysis with the English groundfish survey data of the North Sea (data courtesy of the Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK) and found that the species-size biomass configuration was significantly more variable than would be expected if random. This indicates that the time trajectories of species-group biomasses are random on Georges Bank but trajectories are shared in the North Sea fishes. The degree of trajectory sharing between biomasses of species-sizes is not clear but likely it is related to the strength of environmental drivers in the systems and also fishing. Large multispecies fisheries exist in the North Sea and a diversity of economic subsidies keep fisheries open on so many species that the entire system dynamics may be far more a result of fishing than anything else.

The method of aggregating species with other species or groups of species based on their covariance relationship appeals to the concept of compensation within competitive guilds. The method explicitly considers that species compensation need not occur in a pairwise fashion but can and probably does occur diffusely within assemblages (Duplisea and others 1997). For this reason, it is not obvious that aggregations relevant to species compensation could be determined from standard multivariate statistical methods, which usually creates a multivariate pairwise distance matrix, applied to abundance data. Although this sort of method can reveal valuable information about co-occurrence of species in time and space (Mahon and Smith 1989) it is a statistical observation that is not necessarily theory driven. We performed a series of standard and non-standard multivariate clusterings of these data based on various sorts of pairwise distance measures and the results were quite different from the covariance method outlined here.

The strength of Lotka–Volterra competition in modeled communities does not affect the overall stability of the community (Ives and others 1999). Random factors mimicking environmental drivers were shown to be more important in the total biomass variability which accords with some of the results found here. In experimental studies, however, inter-specific competition has been shown to be a stabilizing factor for community biomass (Tilman 1996; Brown and others 2001). Brown and others (2001) suggest that the pairwise view of competition and species interaction is too simple to capture the complexity of competition in natural communities and therefore we need to examine natural assemblages in their entirety to understand how competition is manifest in communities.

Our use of a goal function of minimizing biomass variability is a key factor allowing us to determine group structure; however, is not the only goal function that can be used. Minimizing production to biomass ratio (P/B) may also be a more appropriate system goal function (Margalef 1968) and it is interpreted in a thermodynamic framework (Matsuno 1978). Certainly, improvement on searching for thermodynamic structures in ecosystem data can be made by considering one or more goals.

In studies such as this, where we try to relate observations at the large scale to dynamics at the small scale, can be identified as the inverse problem (Enting 2002) that pervades every scientific field where measurements are made on parts of larger systems. Identification of appropriate parts to measure, characterizing the nature of their interactions and relating some of these interactions to system dynamics is a very difficult problem but it is not intractable. Enting (2002) quotes in his abstract: ''In systems characterized by high levels of contingency, inversion techniques, using observations as boundary conditions can provide an alternative to reductionist approaches''. We have followed Enting here by using observation of biomass constancy to impose a condition by which interacting components must be bound in the entirety of their interactions. Rather than insisting that this pattern is a mechanism operating in the community we have simply used it to help us understand how species-size might interact and be affected by fisheries in an exploited fish community.

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Appendix A. List of Species and their Size Divisions, Trophic Guild Designation used in the Present Analysis and Resource Status

Common English Name	Latin Name	Trophic Guild Designation (Garrison and Link 2000)	Exploitation Status	By-catch in Scallop Fishery %	Potential Bycatch Impact
L cod	*Gadus morhua*	IVc	oe	0.1	Low
M cod	*G. morhua*	IVc	oe	0.1	low
S cod	*G. morhua*	I	oe	0.1	low
XL cod	*G. morhua*	IVc	oe	0.1	low
M 4-beard rockling	*Enchelyopus cimbrius*			0	low
S 4-beard rockling	*E. cimbrius*			0	low
L haddock	*Melanogrammus aeglefinus*	Vb	fe	<0.1	low
M haddock	*M. aeglefinus*	IIIb	fe	<0.1	low
S haddock	*M. aeglefinus*	III	fe	<0.1	low

Appendix A. Continued

Common English Name	Latin Name	Trophic Guild Designation (Garrison and Link 2000)	Exploitation Status	By-catch in Scallop Fishery %	Potential Bycatch Impact
XL haddock	*M. aeglefinus*	Vb	fe	<0.1	low
L white hake	*Urophycis tenuis*	Vb	oe	0.1	med
M white hake	*U. tenuis*	Vb	oe	0.1	med
S white hake	*U. tenuis*	II	oe	0.1	med
L red hake	*Urophycis chuss*	Vb	ue	0.1	med
M red hake	*U. chuss*	I	ue	0.1	med
S red hake	*U. chuss*	I	ue	0.1	med
L summer flounder	*Paralichthys dentatus*		oe	0.8	med
M summer flounder	*P. dentatus*		oe	0.8	med
L 4-spot flounder	*Paralichthys oblongus*	II		0.5	med
M 4-spot flounder	*P. oblongus*	I		0.5	med
S 4-spot flounder	*P. oblongus*	I		0.5	med
L windowpane	*Scophthalmus aquosus*	II	fe	0.5	med
M windowpane	*S. aquosus*	IIa	fe	0.5	med
S windowpane	*S. aquosus*	IIa	fe	0.5	med
L silver hake	*Merluccius bilinearis*	Vb	oe	0.1	low
M silver hake	*M. bilinearis*	Vb	oe	0.1	low
S silver hake	*M. bilinearis*	I	oe	0.1	low
L cusk	*Brosme brosme*			<0.1	low
L pollock	*Pollachius virens*	IIa	fe	<0.1	low
M pollock	*P. virens*	IIa	fe	<0.1	low
XL pollock	*P. virens*	IVc	fe	<0.1	low
L barndoor skate	*Raja laevis*		fe	0.1-11	very high
M barndoor skate	*R. laevis*		fe	0.1–11	very high
XL barndoor skate	*R. laevis*		fe	0.1–11	very high
L thorny skate	*Raja radiata*	Vb	fe	0.3–11	very high
M thorny skate	*R. radiata*	IIIa	fe	0.3–11	very high
S thorny skate	*R. radiata*	I	fe	0.3–11	very high
XL thorny skate	*R. radiata*	Vb	fe	0.3–11	very high
L smooth skate	*Raja senta*		fe	0.4–11	very high
M smooth skate	*R. senta*		fe	0.4–11	very high
L little skate	*Raja erinacea*	IIIa	fe	11.7	very high
M little skate	*R. erinacea*	I	fe	11.7	very high
S little skate	*R. erinacea*	I	fe	11.7	very high
L winter skate	*Raja ocellata*	IVb	fe	1.3–11	very high
M winter skate	*R. ocellata*	I	fe	1.3–11	very high
S winter skate	*R. ocellata*	I	fe	1.3–11	very high
XL winter skate	*R. ocellata*	IVb	fe	1.3–11	very high
L spiny dogfish	*Squalus acanthias*	IVa	oe	0.4	med
M spiny dogfish	*S. acanthias*	IVa	oe	0.4	med
S spiny dogfish	*S. acanthias*	IVa	oe	0.4	med
M redfish	*Sebastes marinus*		fe	<0.1	low
S redfish	*S. marinus*		fe	<0.1	low
M longhorn sculpin	*Myoxocephalus octodecemspinosus*			0.1	low
S longhorn sculpin	*M. octodecemspinosus*			0.1	low
L halibut	*Hippoglossus hippoglossus*			<0.1	low
M halibut	*H. hippoglossus*			<0.1	low
XL halibut	*H. hippoglossus*			<0.1	low
L sea raven	*Hemitripterus americanus*	Va		0.3	med
M sea raven	*H. americanus*	Va		0.3	med
S sea raven	*H. americanus*	Va		0.3	med
L monkfish	*Lophius americanus*	Vb	oe	9.7	very high

Appendix A. Continued

Common English Name	Latin Name	Trophic Guild Designation (Garrison and Link 2000)	Exploitation Status	By-catch in Scallop Fishery %	Potential Bycatch Impact
M monkfish	*L. americanus*	Vb	oe	9.7	very high
S monkfish	*L. americanus*	Vb	oe	9.7	very high
L American plaice	*Hippoglossoides platessoides*		oe	0.1	med
M American plaice	*H. platessoides*		oe	0.1	med
S American plaice	*H. platessoides*		oe	0.1	med
M witch flounder	*Glyptocephalus cynoglossus*		oe	0.1	med
L yellowtail flounder	*Pleuronectes ferrugineus*	IIa	fe	0.9	med
M yellowtail flounder	*P. ferrugineus*	IIIa	fe	0.9	med
S yellowtail flounder	*P. ferrugineus*	I	fe	0.9	med
L winter flounder	*Pseudopleuronectes americanus*	IIa	oe	0.5	med
M winter flounder	*P. americanus*	IIIa	oe	0.5	med
S winter flounder	*P. americanus*	I	oe	0.5	med
S Gulf Stream flounder	*Citharichthys arctifrons*			<0.1	low
M short finned squid	*Illex illecebrosis*		fe	<0.1	low
S short finned squid	*I. illecebrosis*		fe	<0.1	low
M lumpfish	*Cyclopterus lumpus*		fe	<0.1	low
L striped wolffish	*Anarhichas lupus*		oe	<0.1	low
M striped wolffish	*A. lupus*		oe	<0.1	low
XL striped wolffish	*A. lupus*		oe	<0.1	low
L herring	*Clupea harengus*	IVa	ue	<0.1	low
M herring	*C. harengus*	IVa	ue	<0.1	low
S herring	*C. harengus*	IIb	ue	<0.1	low
M shad	*Alosa sapidissima*		fe	<0.1	low
S shad	*A. sapidissima*		fe	<0.1	low
M alewife	*Alosa pseudoharengus*		oe	<0.1	low
S alewife	*A. pseudoharengus*		oe	<0.1	low
L ocean pout	*Macrozoarces americanus*		oe	0.1	med
M ocean pout	*M. americanus*		oe	0.1	med
S ocean pout	*M. americanus*		oe	0.1	med
XL ocean pout	*M. americanus*		oe	0.1	med
L mackerel	*Scomber scombrus*	IIb	ue	<0.1	low
M mackerel	*S. scombrus*	IIb	ue	<0.1	low
S mackerel	*S. scombrus*	IIb	ue	<0.1	low

The trophic guild classification from Garrison and Link (2000). Blanks in the trophic guild designation indicates that species-size was not examined by Garrison and Link (2000). Resource status was assessed by comparing 1997 population status with modeled potential stock production in accordance with the standard procedure and rankings used by the US National Marine Fisheries Service (Murawski and Almeida 2000).

ue = under exploited, fe = fully exploited, oe = over exploited.

Bycatch impact potential is a ranking based on observed by-catch as a percentage of scallop catch by weight (NEFMC 2003) and qualitatively takes into account the abundance of the population.

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Fishing effects on diversity, size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France

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ABSTRACT: Within the framework of the 'dynamic equilibrium model', we tested the hypothesis that fishing causes major disturbance to benthic communities on deeper bottoms of the continental shelf. Benthic megafauna on the Bay of Biscay coast of France was sampled on fishing grounds subject to various conditions of exploitation. Samples were taken at around 100 m depth to avoid strong natural disturbances. Species diversity and the largest body mass class of invertebrates were smaller in strongly exploited areas than in moderately exploited ones. Biomass size spectra in strongly exploited areas were characterised by a comparatively large biomass of small invertebrates, hence the K-dominance curve of abundance was either above the biomass curve, or the curves intersected. In moderately exploited areas, the K-dominance biomass curves were above the abundance curves; the dominant species were a commercial species and a benthic species sensitive to the physical effects of the fishing gears. In the heavily exploited areas, the dominant species were opportunistic carnivorous species of minor or no commercial interest. There were no dominant fish species in the most strongly exploited areas, while 2 fish species were found in the moderately exploited areas. No fragile species were found in the most exploited areas, whereas 6 fragile species were found in the moderately exploited ones. It is concluded that the differences between the most strongly exploited and the moderately exploited areas were consistent with the hypothesis.

KEY WORDS: Benthic communities · Community dynamics · Disturbance · Diversity · Size spectrum

INTRODUCTION

International concern and systematic research on the physical effects of trawling on the seabed and on benthic communities date from the 1970s, after the rapid expansion of fishing fleets, accompanied by technological innovations. Fishing gear used to catch demersal fish and shellfish often disturb both the seabed and the organisms living within or on it. For the most part the response of benthic communities to fishing disturbance is consistent with the generalised model of disturbance, i.e. increased dominance of small, fast-growing species, and general reductions in species diversity and evenness (Hall 1999).

However, not all communities are equally affected. The findings of empirical studies have not been consistent (Collie et al. 2000), mainly for 3 reasons: (1) non-linearity of the diversity–disturbance relationship, (2) different levels of natural disturbance, (3) different spatial scales of the studies. Diversity is highest at intermediate levels of disturbance (Connell 1978). At low natural disturbance, the additional disturbance of fishing may lead to a diversity increase, whereas diversity may decrease when natural disturbance is intermediate, and it may remain unchanged when natural disturbance is high. Most studies have investigated the effects of fishing on benthic communities on the continental shelf at depths <60 m in shallow seas of northern

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Europe and eastern North America (Collie et al. 2000). Benthic communities in these environments experience continuous disturbance at various scales, from a few centimetres in the case of bioturbation by infauna, through metre scales for feeding by predators on the seabed, up to large-scale natural disturbances such as seasonal storms, strong tidal currents, severe winters, or iceberg scouring (see Hall 1994 for a review). The intensity and frequency of natural disturbances therefore vary between the locations analysed. Effects of fishing disturbance on community structure and diversity are then not only likely to depend on the intensity and frequency of fishing, but also on the initial condition of the habitat (Jennings et al. 2002). The effects of trawling on infauna are more noticeable in areas where levels of natural disturbance are low (Brylinsky et al. 1994, Kaiser & Spencer 1996), because in high-disturbance areas the community is already adapted to disturbance (Jennings & Kaiser 1998). Finally, studies have to date been carried out at various spatial scales, but Kaiser (2003) has argued that detecting effects of fishing disturbance is strongly scale-dependent.

The dynamic equilibrium model of Huston (1994) provides a theoretical framework to analyse the effect of fishing disturbance on benthic communities and to reconcile apparently inconsistent findings. At a given productivity level, this model predicts that under conditions of high disturbance frequency and/or intensity, the few species present will be those that are able to complete their life cycles between disturbances and grow rapidly enough for their population size to recover. Under conditions of low disturbance, species whose life history is characterised by slow growth, late reproduction, large size, and efficient resource use will dominate the community. Diversity is then highest at intermediate levels of disturbance.

We conducted surveys on the Bay of Biscay coast of France at around 100 m depth to avoid interference of strong natural disturbances. Benthic megafauna, probably the most vulnerable part of the benthic communities directly impacted by fishing gears, was sampled on fishing grounds subject to different fishery impacts. If the dynamic equilibrium model holds true, then structural differences must be found between heavily fished and moderately fished communities. The following statements were tested: high fishing effort (1) reduces diversity and evenness, (2) reduces the observed maximum body mass, (3) favours a few body mass classes, (4) increases the steepness of the slope of number–size spectra, (5) shifts abundance and biomass distributions among species toward those typical of a disturbed community, (6) changes species composition.

MATERIALS AND METHODS

Sampling strategy. The study zone is located around 47° N and extends between 3 and 4° W off the western Atlantic coast of France (Fig. 1). A bottom trawl survey was carried out with RV 'Côtes de la Manche' during the last week of May and the first week of June 2001. A 2 m beam trawl was used to sample the invertebrate magafauna and demersal fishes (Kaiser et al. 1994, Jennings et al. 1999, Ellis et al. 2000). This proved to be an efficient method for large and rare species and for the integration of small-scale seabed patchiness (Frauenheim et al. 1989). The beam trawl was fitted with a chain mat and a 20 mm mesh liner. During sampling (20 min), warp length was 3 times water depth, the towing speed was 2 knots and the distance trawled was measured by the ship's differential GPS. A Reineck corer was used for sediment determinations. We sampled 8 stations within 4 areas around the 100 m isobath (about 2500 m^2 per haul): 1 station in Area A, 3 in Area B, 2 in Area C, and 2 in Area D. Stratification was based on the spatial variations in the fishing effort of the bottom trawlers in the year of sampling (2001), as determined by ICES statistical rectangle, from data of the Fisheries Monitoring System of IFREMER; the

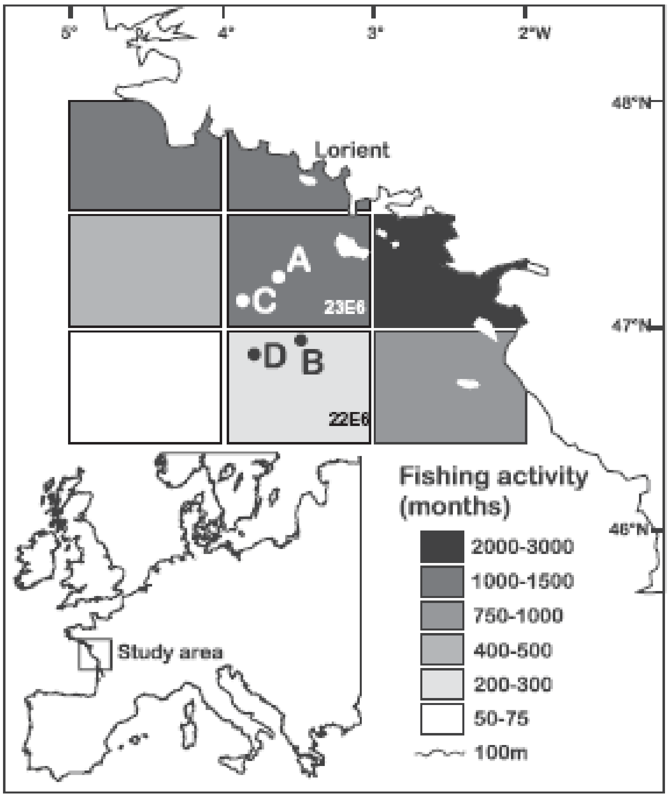

Fig. 1. Location of the 4 areas sampled in the Bay of Biscay and fishing effort of the bottom trawlers (in boat-months) in the ICES statistical rectangles for the year 2001, with n = 1 haul for A, n = 3 for B, n = 2 for C and n = 2 for D

entire study zone is used by the fishery, i.e. unfished areas do not exist

Benthic fauna, invertebrates and fishes, were sorted, identified to the lowest possible taxonomic level (usually species), counted and weighed. The species biomass was determined in each sample as wet weight.

Faunal diversity. Species diversity is classically assessed with the species richness S, the Shannon-Wiener diversity index H' and the Pielou evenness index J'. S is the number of species. H' was calculated as:

$$H' = -\sum_{i=1}^{S} p_i \mathrm{Log} p_i \qquad (1)$$

where p_i is the abundance ratio of the species i. J' was calculated as follows:

$$J' = \frac{H'}{\mathrm{Log} S} \qquad (2)$$

The diversity indices N1 and N2 of Hill (1973) were also assessed, as they are less sensitive to the dominant species and to the sampling effort, respectively, than the previous ones (Lande 1996):

$$\mathrm{N1} = \exp\left(-\sum_{i=1}^{S} p_i \ln p_i\right) \qquad (3)$$

$$\mathrm{N2} = \frac{1}{\sum_{i=1}^{S} p_i^2} \qquad (4)$$

Finally, indices of the taxonomic diversity Δ and distincness Δ* (Warwick & Clarke 1995) were assessed. These indices are less influenced by sample size than the other indices.

$$\Delta = \frac{\sum\sum_{i<j} w_{ij} x_i x_j}{\sum\sum_{i<j} x_i x_j + \sum_i x_i (x_i - 1)/2} \qquad (5)$$

$$\Delta^* = \frac{\sum\sum_{i<j} w_{ij} x_i x_j}{\sum\sum_{i<j} x_i x_j} \qquad (6)$$

Δ is the average (weighted) path length between every pair of individuals, where w_{ij} is the weight given to the path length linking species i and j in the hierarchical classification and x_i denotes the abundance of the ith species ($i = 1, \ldots, S$). Δ* is the average (weighted) path length, ignoring paths between individuals of the same species. All the indices were calculated separately for each replicate tow, and results were tested for significant differences (ANOVA) between ICES statistical rectangles subject to high and low fishing effort.

Size structure of the macrobenthos. Trawling leads to mortality in benthic invertebrates and fishes, but the rates may be lower for the smallest individuals within and among species, as small organisms may be pushed aside by the pressure wave in front of the trawl (Gilkinson et al. 1998), or escape from the trawl through the mesh. Larger individuals usually suffer higher mortality when they are in the path of the trawl (Bergman & van Santbrink 2000). Hence, fishing activity may change the community size spectrum structure (Rice & Gislason 1996, Bianchi et al. 2000, Duplisea et al. 2002).

Biomass size spectra were constructed by summing individual biomass in body mass classes arranged on an octave scale, as in Platt & Denman (1978). An increasing octave series means that the nominal weight for each class is double that of the previous one. Biomass size spectra were calculated for each area by pooling data from the respective stations. The normalised number–size spectra were determined by regressing, from the modal class to the largest one, the log of the total number in body mass class against the log of body mass class. The slopes of these regression lines characterise abundance trends across the size spectrum and simplify comparisons between areas (Sheldon et al. 1977, Pope & Knights 1982, Sprules & Munawar 1986, Pope et al. 1988). Differences among slopes were tested by ANCOVA.

Abundance–biomass comparison (ABC method). Combined K-dominance plots for species biomass and numbers may assume 3 possible forms, representing undisturbed, moderately disturbed and strongly disturbed macrobenthic communities (Warwick 1986, Warwick et al. 1987). A relative biomass curve above the relative numbers curve throughout its entire length is expected for undisturbed communities, where biomass is dominated by one or a few large species represented by few individuals. At moderate disturbance, the large competitively dominant species are eliminated, and the inequality in size between the numerically dominant species and the species with high biomass is reduced, so that biomass and number curves (in %) are close and may intersect. As disturbance increases, communities become dominated numerically by one or a few small species. Then the abundance curve is above the biomass curve throughout its length.

Numbers and biomass curves of the most strongly exploited areas (A and C) were compared to the curves of the moderately exploited areas (B and D). The W statistic (Clarke 1990) was calculated for each replicate tow separately and results were tested for significant differences (ANOVA) between ICES statistical rectangles subject to high and low fishing effort.

$$W = \frac{\sum_{i=1}^{S}\left[\left(\sum_{j=1}^{i} b_j\right) - \left(\sum_{j=1}^{i} a_j\right)\right]}{50(S-1)} \qquad (7)$$

where W is the standardised sum of the differences between each pair of species cumulative biomass

$(\sum_{j=1}^{i} b_j)$ and cumulative abundance $(\sum_{j=1}^{i} a_j)$ value ranked in decreasing order.

Species composition. Biological and ecological characteristics of the species make it possible to group the species according to the potential impact of fishing. Such groups have been defined recently for invertebrates (ICES 2003): scavenger, opportunistic, fragile and sensitive species. Here we have grouped scavengers with opportunistic species and added one more group, the unaffected species. Scavengers have been found more frequently in recent years in the southern North Sea (Lindeboom & de Groot 1998). Apart from possible climate effects, this can be attributed to the fishery impact, as discards and by-catch together with the crushed and broken animals provide large amounts of additional food to scavenging species on the sea floor. Scavengers migrate rapidly into areas of fishing disturbance, where they feed on animals damaged by trawls (Ramsay et al. 1996). Moreover, these species are often not injured by the passage of a trawl. Species with those characteristics sampled here were termed 'opportunistic species', e.g. *Liocarcinus depurator* and *Munida bamffia*. Some species are particularly sensitive to physical injury, as they are characterised by rigid bodies or tubes, and are sessile or slow-moving (MacDonald et al. 1996). Species with those characteristics were termed 'fragile species'; filter feeders were also part of this group, as they are sensitive to particles resuspended by the passage of the trawl, e.g. *Leptometra celtica* and *Virgularia mirabilis*. Species with a hard body that are not scavengers, and species that can escape from the haul after having been caught were termed 'unaffected species', e.g. *Alphaeus glaber*. Species not included in these groups may be affected, but less so than the fragile ones. These species were termed 'sensitive', e.g. *Macropodia tenuirostris*. The ratio (in species number) of fragile, sensitive, unaffected and opportunictic species as defined here were computed *a priori* for each sector and compared between ICES rectangles.

RESULTS

Sediment characteristics

According to the classification of the Bay of Biscay by Chassé & Glémarec (1976), the sediments sampled correspond to the muddy sand and sandy mud type with a silt fraction between 10.0% at Stn C3 to 34.9% at Stn B3, and a median particle size between 109 µm at Stn B3 to 201 µm at Stn CC1 (Table 1). Sampling stations were in the depth range from 106 to 129 m.

Table 1. Sediment characteristics of the sampling stations. Sediment type as defined in Chassé & Glémarec (1976). FV: muddy sand; VS: sandy mud; SHV: heterogeneous muddy sand

Stn	Depth (m)	Silt fraction <63 µm (%)	Median grain size (µm)	Sediment type
AA1	106	12.0	153	FV
BB1	109	15.3	157	FV
B2	109	32.5	115	VS
B3	112	34.9	109	VS
CC1	116	25.1	204	SHV
C3	117	10.0	201	FV
D1	129	11.8	169	FV
DD1	118	12.4	186	FV

Fishing effort

Apart from dredges that are used at depths greater than 50 to 60 m, the only bottom trawl gears used in grounds of 100 m depth in 2001 were otter trawls. Fishing effort of the bottom trawlers was actually lower in Rectangle 22E6, with 299 month-boats, than in Rectangle 23E6, with 1242 month-boats. This is consistent with a previous analysis (Berthou et al. 2000), which showed that fishing effort in 1996 was lower in Rectangle 22E6 (between 130 and 590 month-boats) than in Rectangle 23E6 (between 1900 and 2800 month-boats). In Rectangles 22E6 and 23E6, 4 main 'métiers' (the association of a gear and a species or group of species) accounted for more than 60% of the activity. These were the *Nephrops* twin bottom trawls, the fish twin bottom trawls, the fish bottom otter trawls and the sole twin bottom trawls (Table 2). The reason why fishing effort was lower in Rectangle 22E6 was its greater distance from the main fishing harbour at Lorient, compared to Rectangle 23E6 (Fig. 1); most of the boats are rather small, so that costs increase with distance. The main species landed from Rectangles 22E6 and 23E6 are, in decreasing order: anchovy, horse mackerel, Norway lobster, hake, common sole, and cuttlefish. These 6 species represented 50% of the total landings from these areas in 2001.

Faunal diversity

Of the 58 species sampled in this study, 15 were fishes and 43 were invertebrates (Table 3). Differences between the most strongly exploited areas and the moderately exploited ones are shown in Table 4. Although the species richness was greater in the moderately exploited areas (B and D; between 22 and 33 species) than in the most strongly exploited ones (A and C; between 13 and 23 species), the difference

Table 2. Fishing effort in 2001 for the various 'métiers' (association of a gear, and a species or group of species) in ICES Rectangles 22E6 and 23E6 in number of months (number of boats). BOT: bottom otter trawl; TBT: twin bottom trawl. © IFREMER, Fisheries Monitoring System

Métier	22E6	23E6
Bass BOT	0	3 (2)
Squid BOT	1 (1)	21 (7)
Horse mackerel BOT	0	20 (5)
Bream BOT	0	11 (3)
Fish BOT	16 (4)	192 (31)
Gadoid BOT	0	9 (4)
Pollack BOT	1 (1)	3 (3)
Nephrops BOT	16 (3)	41 (7)
Anglerfish BOT	2 (1)	0
Mackerel BOT	0	23 (7)
Hake BOT	4 (2)	34 (8)
Whiting BOT	0	16 (6)
Skate BOT	2 (1)	0
Gurnard BOT	1 (1)	4 (2)
Cuttlefish BOT	14 (4)	48 (14)
Sole BOT	17 (4)	41 (9)
Bass pair BOT	1 (1)	1 (1)
Nephrops pair BOT	0	2 (2)
Squid TBT	4 (1)	4 (3)
Fish TBT	26 (8)	155 (21)
Nephrops TBT	133 (35)	495 (67)
Anglerfish TBT	11 (3)	23 (5)
Hake TBT	12 (6)	24 (6)
Flatfish TBT	1 (1)	2 (2)
Cuttlefish TBT	13 (4)	27 (12)
Sole TBT	24 (12)	43 (21)
Total	299 (93)	1242 (248)

was not statistically significant (Table 5). There were no significant differences for evenness. On the other hand, diversity *H'* was significantly greater in the moderately exploited rectangle (0.97 to 1.15), than in the strongly exploited one (0.68 to 0.89). The same holds true with regard to the N1 index (2.64 to 3.16 in the moderately exploited rectangle, and 1.97 to 2.43 in the strongly exploited one), and the N2 index (5.9 to 9.99 in the moderately exploited rectangle, and 2.44 to 5.56 in the strongly exploited one). No significant differences were found for the indices Δ and Δ^*.

Size structure

Biomass distribution was more similar to a Gaussian one in the moderately exploited areas (B and D) than in the most strongly exploited areas (A and C; Fig. 2). Biomass distributions in Areas A and C were characterised by a large contribution to the total biomass of one body mass class of invertebrates (5 and 2.5 g, respectively). The largest observed body mass class for invertebrates in the moderately exploited areas (B and D) were 10 and 20 g, respectively, while it was smaller in the most exploited areas (A and C; 5 and 10 g, respectively). The largest observed body mass class for fishes in areas (A, B, C and D) were 80, 20, 40 and 40 g, respectively. There were no clear

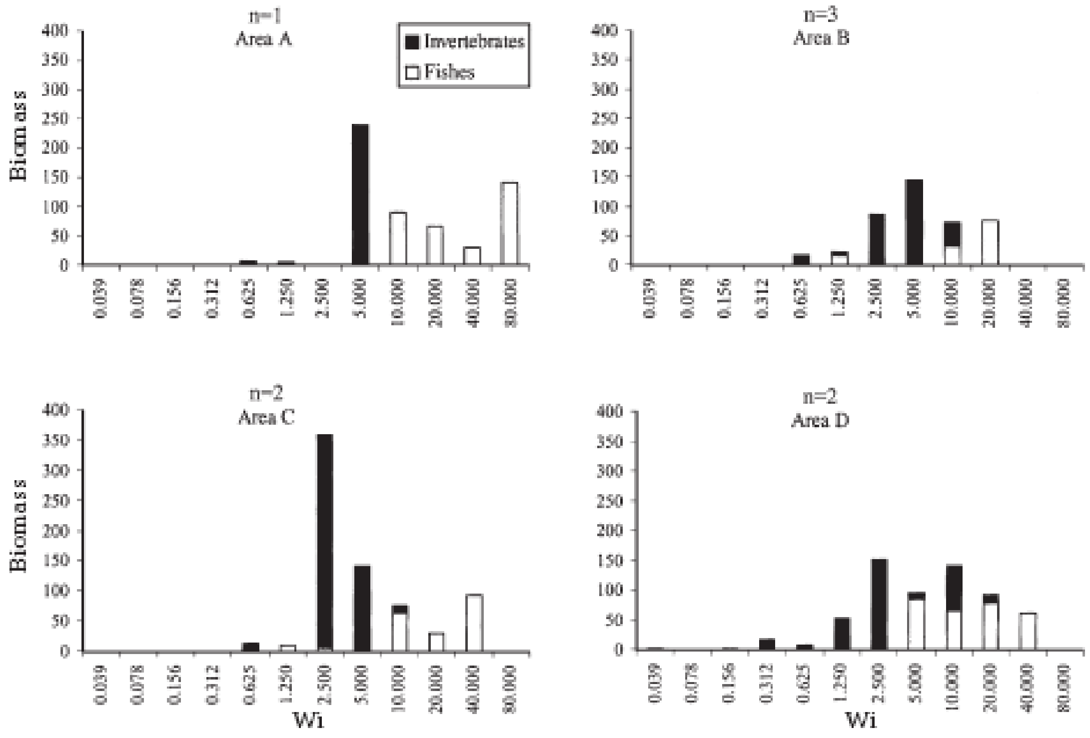

Fig. 2. Mean biomass size spectra for the benthic megafauna of invertebrates and fishes. Biomass and size classes (Wi) are in g wet weight. The number of hauls each panel is indicated above

Table 3. List of species and their abbreviated codes, and taxonomic group (invertebrates [Inv] and fish), abundance (ind.) and biomass (wet weight in g per 1000 m^2) in Areas A, B, C and D. SENS: sensitivity of invertebrates (except cephalopods) to physical effects of bottom fishing gears defined *a priori*; f: fragile; s: sensitive; u: unaffected; o: opportunistic

Code	Species	Taxon group	Abundance A	Abundance B	Abundance C	Abundance D	Biomass A	Biomass B	Biomass C	Biomass D	SENS
ACD	*Actinauges richardi*	Inv	0	0	0	0.55	0	0	0	12.47	s
ADP	*Adamsia carcinopados*	Inv	0	1.28	0	0.25	0	3.75	0	0.11	s
ALD	*Alcyonium digitatum*	Inv	0	0.12	0	1.78	0	0.48	0	0.49	f
ALGL	*Alphaeus glaber*	Inv	0	8.19	3.32	4.33	0	6.9	2.28	2.75	u
ALV	*Anapagurus laevis*	Inv	0	0	0	4.31	0	0	0	0.91	s
AMU	*Amphicteis gunneri*	Inv	0	0.91	1.52	0	0	0.01	0	0	s
APE	*Apporhais pespelicani*	Inv	0	0.25	0	0	0	0.51	0	0	u
ARLA	*Arnoglossus laterna*	Fish	2.55	1.61	4.36	12.59	36.5	19.7	47.72	84.41	
ARSP	*Argentina sphyraena*	Fish	0	0	0.38	0	0	0	1.91	0	
ASL	*Astacilla longicornis*	Inv	0	0	0	7.73	0	0	0	0.56	s
ASY	*Astropecten* spp.	Inv	0	0	0	29.53	0	0	0	71.58	s
BRLY	*Brissopsis lyrifera*	Inv	0	0.41	0	0.55	0	5.27	0	1.38	f
CAAP	*Capros aper*	Fish	0	0.5	1.32	0.25	0	1.43	4.03	0.97	
CALY	*Callionymus lyra*	Fish	0.64	0.12	0.38	0	22.84	2.89	10.26	0	
CAMA	*Callionymus maculates*	Fish	0	0	0.66	0.76	0	0	2.28	3.18	
CAO	*Calliostoma granulatum*	Inv	0	0	0	1.85	0	0	0	7.6	u
CERU	*Cepola rubescens*	Fish	0	0	0.33	0	0	0	7.87	0	
CHCR	*Chlorotocus crassicornis*	Inv	0	1.82	0.38	1.64	0	3.32	0.79	1.86	s
CRAL	*Crangon allmanni*	Inv	5.11	6.91	5.35	1.27	5.64	6.3	5.1	0.77	s
CUCU	*Cuspidaria cuspidate*	Inv	0	0.25	0	0	0	0.22	0	0	s
CUP	*Phaxas pellucidus*	Inv	0	0	0	0.25	0	0	0	0.03	f
D	*Dichelopandalus bonnieri*	Inv	0	0	0.38	0	0	0	0.47	0	s
ENCI	*Enchylopsus cimbrius*	Fish	1.28	2.32	0.33	1.6	43.75	74.5	16.79	46.04	
EUGU	*Eutriglia gurnardus*	Fish	0.64	0	0	1.02	29.54	0	0	62.51	
GADI	*Galathea dispersa*	Inv	0	0	0	1.02	0	0	0	0.01	o
GLR	*Glycera rouxii*	Inv	0	0	0.38	0	0	0	0.01	0	s
GORH	*Goneplax rhomboids*	Inv	0	6.34	2.94	7.86	0	38.24	15.85	26.07	s
GVU	*Gaidropsarus vulgaris*	Fish	0	0.16	0	0	0	2.16	0	0	
HEMA	*Heterocrypta maltzani*	Inv	0	0	0	0.55	0	0	0	0.22	s
IND	*Inachus dorsettensis*	Inv	0	0	0	0.25	0	0	0	1.2	s
LEFR	*Lesueurrigobius friesii*	Fish	1.28	7.37	3.17	0.25	2.64	18	7.25	0	
LID	*Liocarcinus depurator*	Inv	14.68	13.04	9.35	2.4	144.84	61.75	94.86	0.67	o
LOPI	*Lophius piscatorius*	Fish	0	0	0.38	0.51	0	0	5.29	0.61	
LWH	*Lepidorhombus whiffiagonis*	Fish	0	0.33	0	12.29	0	4.67	0	36.17	
MAN	*Macropodia tenuirostris*	Inv	0	1.28	0.38	20.24	0	1.29	0.01	10.97	s
MATU	*Macropipus tuberculatus*	Inv	0	0	0	1.31	0	0	0	5.03	o
MME	*Merluccius merluccius*	Fish	0.64	0.49	1.8	1.27	87.67	0.68	77.11	43.08	
MUBA	*Munida bamffia*	Inv	5.11	23.01	76.44	15.18	28.11	79.21	251.37	35.74	o
MVA	*Microchirus variegatus*	Fish	3.19	1.78	1.09	3.67	52.83	27.57	21.25	56.3	
NEE	*Nephthys caeca*	Inv	0	0.25	0	9.45	0	0.01	0	86.27	s
NENO	*Nephrops norvegicus*	Inv	7.02	29.62	23.84	0.55	66.83	196.27	135.65	1.21	o
NUSU	*Nucula sulcata*	Inv	0.64	7.08	4.36	0.55	0.91	5.92	3.83	3.62	u
PAP	*Pagurus pridauxi*	Inv	0	0.58	0	0.55	0	8.66	0	0.3	o
PEPH	*Pennatula phosphorea*	Inv	0	0.25	0	2.28	0	0.13	0	0.56	f
POHE	*Polybius henslowi*	Inv	0	0.41	0	28.48	0	4.31	0	1.7	o
POPU	*Porania pulvillus*	Inv	0	0	0	0.25	0	0	0	4.2	u
POSP	*Pontophilus spinosus*	Inv	0	0	0	0.51	0	0	0	1.07	s
PRNO	*Processa nouvelli*	Inv	0	1.49	0	0.55	0	0.36	0	1.58	s
PTH	*Pteria hirundo*	Inv	0	0	0	2.28	0	0	0	0.56	f
Scal.	*Scalpellum* spp.	Inv	0	0	0	0.51	0	0	0	1.72	u
Sepiola	*Sepiola* spp.	Inv	0	0.25	0.38	6.21	0	0.84	0.28	2.96	
SOME	*Solenocera membranacea*	Inv	0	0	0	5.46	0	0	0	4.56	s
SQDE	*Squilla desmaresti*	Inv	0	0.66	1.47	0	0	2.19	4.74	0	o
STS	*Sternaspis scutata*	Inv	0	0.37	0.33	0	0	0.59	0.25	0	s
SVU	*Solea vulgaris*	Fish	0.64	0	0	0	54.73	0	0	0	
TUC	*Turritella communis*	Inv	0	0	0.38	0	0	0	0.42	0	u
VEOV	*Timoclea ovata*	Inv	0	1	0.71	0	0	0.75	0.52	0	u
VIMI	*Virgularia mirabilis*	Inv	0	0.5	0	0	0	0.96	0	0	f

Table 4. Species richness (*S*), Evenness index (*J'*), Shannon diversity index (*H'*), Hill diversity indices (N1 and N2), and taxonomic diversity and distincness indices (Δ and Δ*) in each replicate of Areas A, B, C and D

Stn	*S*	*J'*	*H'*	N1	N2	Δ	Δ*
Strongly exploited							
AA1	13	0.8	0.89	2.43	5.56	3.77	4.19
CC1	23	0.61	0.83	2.29	3.72	3.03	4.12
C3	18	0.54	0.68	1.97	2.44	2.69	4.51
Moderately exploited							
BB1	23	0.76	1.04	2.83	6.8	3.67	4.26
B2	22	0.72	0.97	2.64	5.9	3.43	3.99
B3	23	0.72	0.98	2.66	6.46	3.99	4.69
D1	26	0.82	1.15	3.16	9.99	4.8	5.31
DD1	33	0.76	1.15	3.16	8.54	4.16	5.02

differences in maximal body mass for fishes between the most exploited areas (A and C) and the moderately exploited areas (B and D) for fishes.

The fitted linear relationships between abundances and body mass explained a substantial proportion of the variance (Fig. 3). The r^2 values were 0.8, 0.92, 0.89 and 0.98, respectively, in Areas A, B, C and D. The steepest slope was in one of the most strongly exploited areas (C: –1.62) while the flattest one was in a moderately exploited area (D: –1.26). However, there were no significant differences among slopes ($F_{\text{observed}} = 0.38$, $\nu_1 = 3$, $\nu_2 = 14$, $F_{0.05} = 3.34$) or among intercepts ($F_{\text{observed}} = 0.07$, $\nu_1 = 3$, $\nu_2 = 14$, $F_{0.05} = 3.34$).

Abundance–biomass comparison (ABC method)

The communities in the moderately exploited areas (B and D) showed an undisturbed pattern with the biomass curve above the abundance curve (Fig. 4). On the other hand, the communities in the most strongly exploited areas (A and C) showed a disturbed pattern (abundance curve above the biomass curve) and a moderately disturbed pattern with (intersecting curves), respectively. The differences in the abundance/biomass dominance curve between the 2 rectangles were significant (ANOVA, *W* statistic: Table 5).

Species composition

Relative species abundance (Fig. 5) shows differences in dominance between the rectangles: 7 and 8 species, respectively, represent >75% of the total abundance in Areas B and D, while only 5 and 4 species attain 75% in Areas A and C. The most dominant species in Area B (moderately exploited) is the Norway

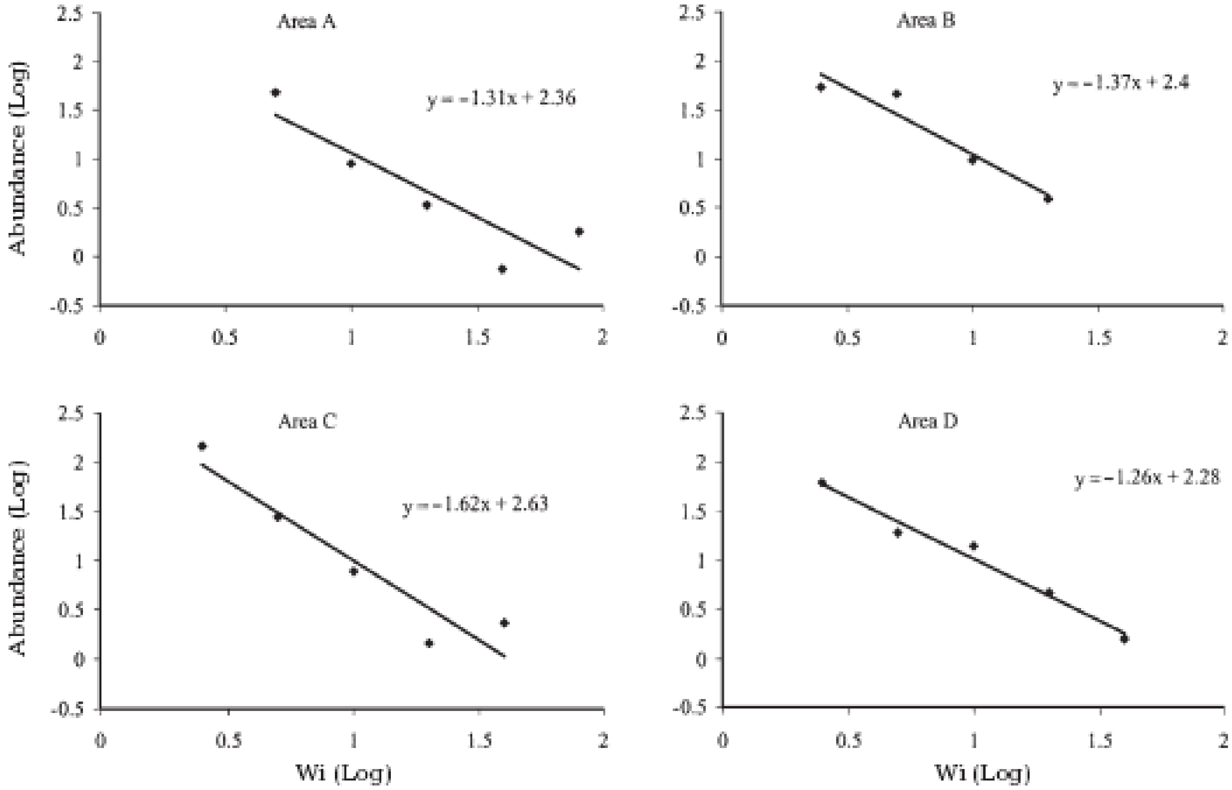

Fig. 3. Normalised size spectra for the benthic megafauna in the 4 areas: abundance vs wet weight (Wi) in g

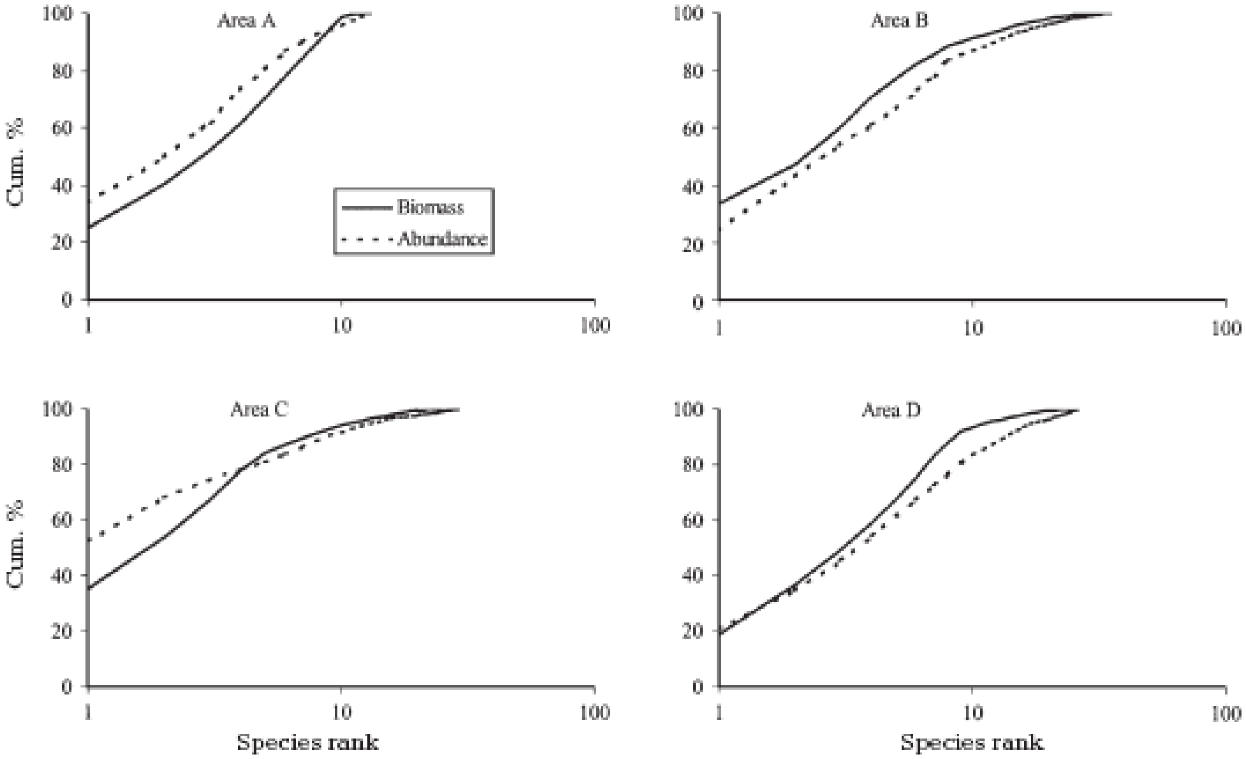

Fig. 4. Cumulative% dominance curves in abundance and biomass of the benthic megafauna communities of fishes and invertebrates from the most exploited areas (A and C) and from the moderately exploited areas (B and D)

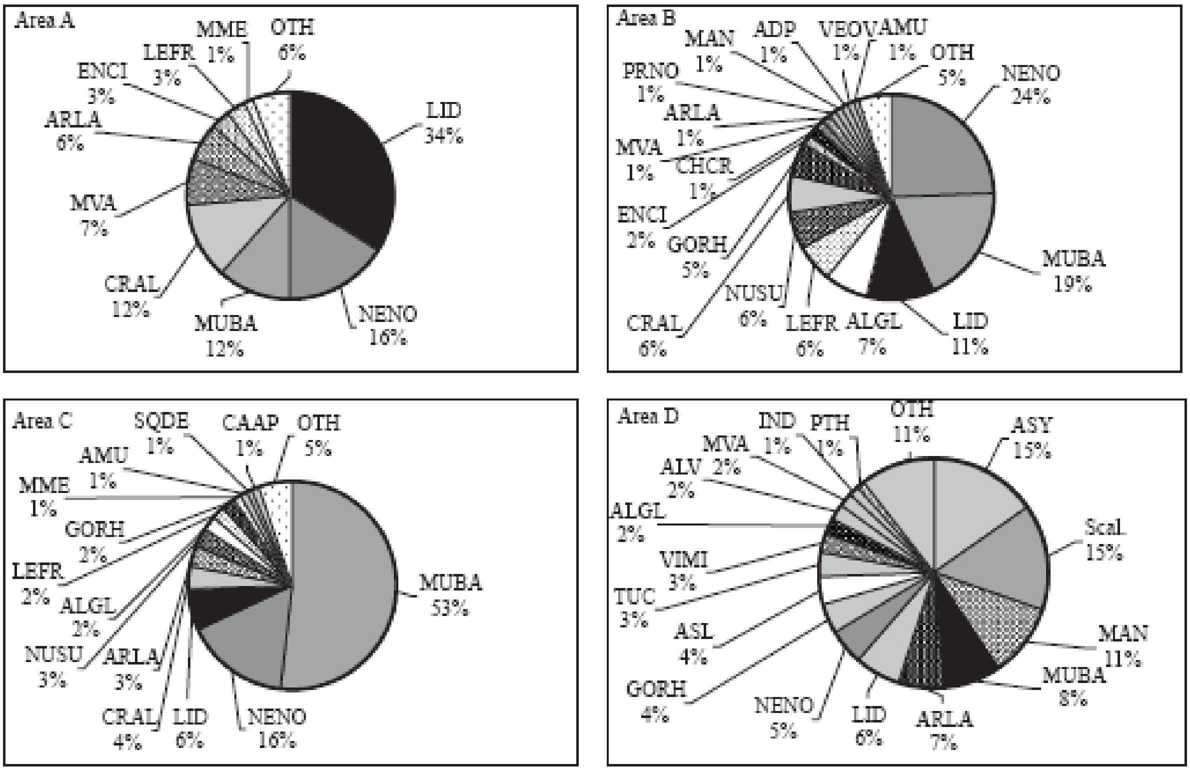

Fig. 5. Relative abundance of species. See Table 3 for the code significance of species (OTH: other species)

Table 5. ANOVA of diversity indices *S*, *J'*, *H'*, N1, N2, Δ, Δ* and of the *W* statistic of the abundance/biomass dominance curves, between rectangles with high and low fishing effort; *significant

	F	p
S	4.096	0.073
J'	2.945	0.137
H'	13.75	0.01*
N1	13.03	0.011*
N2	9.087	0.024*
Δ	4.47	0.079
Δ*	0.71	0.43
W	15.009	0.0082*

lobster *Nephrops norvegicus*, an opportunistic commercial species found in all areas of this study. In Area D (moderately exploited), the dominant species is a sensitive echinoderm genus (*Astropecten* spp.); Area D is the only one where this species was found. In the heavily exploited areas, the 2 dominant species are opportunistic carnivores, the blue-leg swimming crab *Liocarcinus depurator* in Area A, and *Munida bamffia*, a crustacean of minor commercial interest, in Area C. These 2 species were found in all areas of this study. There is no fish species within the first 75% of the total abundance in the most strongly exploited areas (A and C), while 2 small non-commercial fish species are found in the first 75% in the moderately exploited area: Fries's goby *Lesueurigobius friesii* and the scaldfish *Arnoglossus laterna*.

In the most strongly exploited areas (A and C), the opportunistic species were dominant in species number and fragile species were absent (Fig. 6), while sensitive species were dominant and some fragile species were present in the moderately exploited areas (B and D). However, ANOVA showed significant differences between the most strongly exploited areas (A and C) and the moderately exploited areas (B and D), only for fragile species (Table 6).

Table 6. Frequency of fragile, sensitive, unaffected and opportunistic species in the samples and ANOVA between the most exploited rectangle (Areas A and C) and the moderately exploited one (Areas B and D). (*Significant difference between rectangles, H_0 rejected)

Stn	Fragile	Sensitive	Unaffected	Opportunistic
AA1	0	20	20	60
CC1	0	46.67	26.67	26.67
C3	0	30	30	40
BB1	6.25	43.75	12.5	37.5
B2	12.5	37.5	18.75	31.25
B3	15.79	47.37	21.05	15.79
D1	13.64	45.45	22.73	18.18
DD1	15	40	20	25
F-value	31.32	2.95	4.26	3.52
p	0.001*	0.137	0.085	0.11

DISCUSSION

Sediment properties are factors influencing the benthic fauna (Basford et al. 1990, Kühne & Rachor 1996, Rees et al. 1999), although the relationship is clearer for infauna than for the epifauna that was the focus in this study (Duineveld et al. 1991). Moreover, the sampling scale of a beam trawl is orders of magnitude larger than that of corers, so that small-scale heterogeneity is integrated (Callaway et al. 2002). To minimise these effects, benthic communities were only sampled on sandy mud and muddy sand. Furthermore, there are no hydrographic features or other environmental factors in this area that could lead to differential settlement of post-larval juveniles, so that fishing effort consitutes the major source of spatial variation.

However, sampling with bottom trawls usually implies high variance, due to a number of factors such as the patchy distribution of various species. Because of the limited sampling carried out in this study, 8 hauls might not have a representative species composition. Long-term surveys would be required to test the relia-

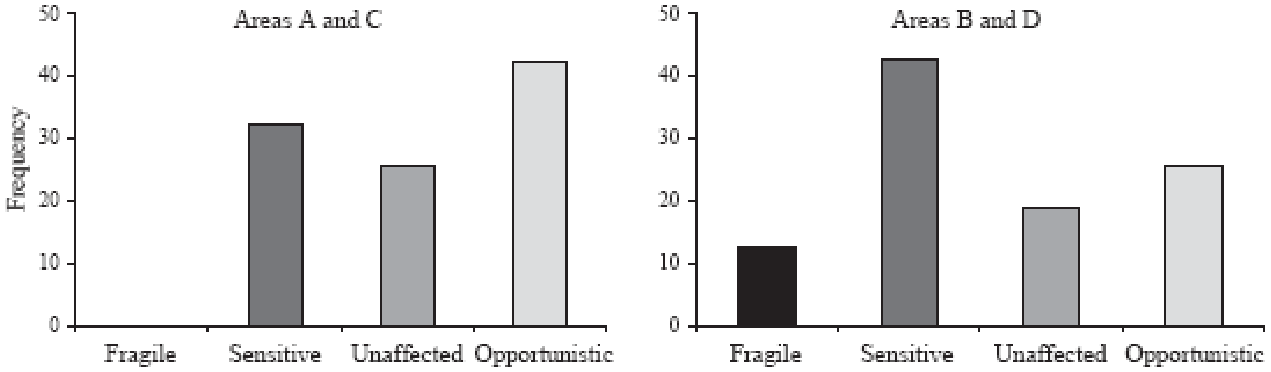

Fig. 6. Averaged frequency (in species number) of fragile, sensitive, unaffected and opportunistic species in the most exploited rectangle (Areas A and C) and in the moderately one (Areas B and D). See the text for the definition of these groups

bility of the data, and caution is in order before generalising or extrapolating the results to the whole region. Our study is probably more useful in detecting patterns of change in community structure according to theoretical ecological guidelines, rather than in really testing an ecological hypothesis.

Species diversity

The diversity indices *H'*, N1 and N2 confirmed the disturbance effect of fishing on the community. Results on species richness, evenness, taxonomic diversity and distinctness were less clear. Species diversity was lower where fishing disturbance was high, but it is difficult to conclude whether this is due to a decrease in slow growing sessile fauna and/or to avoidance of the vagile fauna, which is replaced by a few opportunist species. However, the numbers of both sessile and vagile fragile invertebrate species were lower in the most strongly fished areas (C. Hily pers. obs) so that both processes may apply. No differences were apparent from taxonomic indices; these indices are useful for macrofauna, but our study also included fish megafauna. Taxonomic distances between fishes and invertebrates are huge, compared to distances between invertebrate species, and the values of the taxonomic indices can be so high as to obscure the small spatial differences in taxonomic diversity of invertebrates. These indices should be computed separately for invertebrate and fish species.

Size spectra

Biomass size spectra are widely used to describe the structure of pelagic food chains, demersal fish communities and benthic communities of invertebrates, and sometimes related to the productivity of the ecosystems (Sheldon et al. 1977, Macpherson & Gordoa 1996, Saiz-Salinas & Ramos 1999). Normalised number–size spectra have been used to analyse the impact of fishing on demersal fish communities (Pope & Knights 1982, Pope et al. 1988, Murawski & Idoine 1992, Rice & Gislason 1996, Bianchi et al. 2000), showing an increase in the abundance of the smallest body mass classes and a decrease in the largest ones, probably due to: (1) differential mortality, as fishing gears select large individuals; (2) release from predation of small individuals that are prey to the large ones; (3) recovery from continuous fishing mortality by species with early reproduction and fast growth (*r*-strategists). Although there were no significant differences among slopes of the normalised number–size spectra, different biomass-size structures among areas were found, consistent with the previously quoted fishing effects on demersal fish communities: one small size class was dominant in the most exploited areas compared to the moderately exploited ones.

Abundance–biomass comparison (ABC method)

The ABC method (Warwick 1986) was originally designed to detect pollution effects on macrobenthic invertebrate communities, and then generalised to other physical and biological disturbances (Warwick et al. 1987) and applied to fishery impacts (Lindeboom & de Groot 1998). The method was designed on the basis of the ecological succession theory: after a strong disturbance, (small) opportunistic species are the first to recolonise the habitat, and then (large) conservative species tend to replace them. The ABC method is rarely applied to fishing disturbances in megabenthic communities of invertebrates and fishes, and this study shows that the method can be applied to a wide range of individual sizes, taxa and disturbances. Our results support the hypothesis that fishing acts on communities like a physical disturbance, as well as the underlying theory of ecological succession. Only 3 discrete disturbance levels are defined in this method: highly disturbed, moderately disturbed and undisturbed, whereas in the dynamic equilibrium model, disturbance is a continuous variable. The intercalibration between a discrete variable of disturbance and a continuous one remains to be tackled.

Species composition

Dominant species in the moderately exploited areas were a commercial crustacean species and a sensitive echinoderm, while the dominant species in the most exploited areas were crustacean opportunistic carnivores of minor or no commercial interest. Fishing gear effects may favour scavengers and opportunistic carnivores attracted by crushed organisms, and eliminate fragile species. However, it remains unclear whether increases in scavenger abundance are the result of migration or of population growth. Commercial species such as Norway lobster may be depleted and replaced by a potential competitor such as *Munida bamffia*. Actually, the stock biomass of *Nephrops norvegicus* in the ICES Division VIIIa,b (Bay of Biscay) is at or near the lowest known level and this is attributed to the high exploitation rate and/or fishing patterns that cause high mortality in juveniles (ICES 2002).

We assumed that few differences in grain size of the sediment exist in the study area, so that no natural spatial variation was expected. However, Norway lobster is the dominant species in Area B, but not in Areas A, C and D (it is second in abundance in Areas A and C, and the 7th in the moderately exploited Area D). Relationships between *Nephrops norvegicus* density and sediment grain size have been shown for several stocks: density increases with particle size up to an optimum particle size value, then decreased for larger particle sizes; the optimum particle size differs between stocks (Afonso-Dias 1997). Moreover, the grain size range may be huge in some cases. The relationship between *N. norvegicus* density and particle size in the Bay of Biscay is unknown. It is therefore difficult to conclude whether the variation in the abundance rank of *N. norvegicus* is really a consequence of fishing or rather of small grain size variations or interactions between both factors. The sensitive species *Astropecten* is only dominant in Area D and is not found anywhere else. This could be due to interactions between small sediment variations and fishing effects. No fragile species were found in the most strongly exploited areas, while 6 species were observed in the moderately exploited ones, and this is more probably due to fishing effects than to sediment grain size. Moreover, there is no fish species among the first 75% of the total abundance in the most strongly exploited area, while 2 fish species are found among the top 75% in the moderately exploited area. Heavy fishing activity in the most exploited areas probably drives fishes out of the area.

Community dynamics

Indices of species diversity, size structure, and abundance–biomass distributions among species proved useful to demonstrate fishing impacts on the benthic communities at low and moderate levels of natural disturbance, when used in the framework of the dynamic equilibrium model.

Management requires quantitative methods that predict changes in communities. Size-based models (Duplisea et al. 2002) have to be designed. However available knowledge of trawling disturbance impacts is based primarily on empirical studies. Then models are only empirical, without strong theoretical underpinnings about the ecological processes involved in community dynamics, or with underpinnings not yet fully acknowledged by the scientific community. More theoretical works on community dynamics supported by empirical analyses are then needed to design convincing and effective management strategies of environmental impacts of fishing.

Community dynamics can theoretically be regulated by competitive interactions or ecological disturbances (including environmental and predation factors). Fishing effects as predation disturbance (removal of individuals) have been hypothesised (Blanchard 2001). In communities regulated by interspecific interactions a high intensity of predation can alter the strength of competitive interactions and allow for increased coexistence of competitive species (Levine 1976, Vandermeer 1980). Fishing exploitation could have similar effects, i.e. benthic community dynamics under low conditions of exploitation and low or moderate levels of natural disturbance is probably regulated by competitive interactions, and fishing leads to a shift toward community dynamics regulated by fishing disturbance. This underscores the importance of analysing fishing effects as physical disturbances (break and crush effects of gears). Theories on community dynamics that include ecological disturbance, whether physical or predation disturbance, is a promising theoretical framework to analyse the effects of fishing.

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Evaluation of trawling disturbance on macrobenthic invertebrate communities in the Bay of Biscay, France: Abundance Biomass Comparison (ABC method)

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Abstract – The necessity to move from a traditional fishery management to an ecosystem approach is now acknowledged. Indicators are required to support the development of this approach. For example, community indicators have been proposed to assess the impact of fishing. We tested here the applicability of one such community indicator, the abundance-biomass comparison (ABC method), as a measure of the impact of bottom trawling (years of sampling: 2001 and 2003) on the benthic invertebrates – typically starfishes, crabs, squat lobsters, shrimps and large hard-shelled molluscs- of "Grande Vasière", a major French fishing zone, in the Bay of Biscay. The ABC method is generally used as an impact indicator for different types of physical, biological and anthropogenic disturbances on benthic communities. This method is based on the assumption that increasing disturbance shifts communities from dominance by large-bodied species with low turnover rates toward dominance by small-bodied species with high turnover rates. At less disturbed areas the average biomass of individuals is greater than at more heavily disturbed areas. The ABC method measures this effect by comparing the ranked distributions of abundance and biomass within a given community. We applied the ABC method and compared the size structure and the species diversity at two areas exposed to moderate and high bottom trawl effort. Species diversity was lower in the most exploited area. The highly trawled area was dominated by opportunistic organisms, mainly one species of swimming crab *Liocarcinus depurator*, one species of squat lobster *Munida rugosa* and Norway lobsters *Nephrops norvegicus*, which are large-bodied species. Consequently, the results of the ABC method were inconsistent with the theoretical expectation for these particular macrofaunal communities and the measured levels of fishing intensity.

Key words: Bottom trawl survey / Indicator / Fishing impact/ ABC method / Macrobenthos / Density / Inter-annual variability / Atlantic Ocean

Résumé – Évaluation de la perturbation due au chalutage fond sur une communauté de macro-invertébrés benthiques dans le golfe de Gascogne, France : comparaison abondance-biomasse (méthode ABC). La nécessité de passer d'une gestion monospécifique des pêches à une approche écosystémique est largement reconnue. Pour mettre en place une telle approche, des indicateurs ont été proposés afin d'estimer l'impact de la pêche sur les communautés. Nous avons testé l'efficacité de l'un de ces indicateurs, la comparaison abondance-biomasse (méthode ABC), pour mesurer l'impact du chalutage de fond (année d'échantillonnage : 2001 et 2003) sur les communautés de la macrofaune benthique de la Grande Vasière, golfe de Gascogne (typiquement des crabes, étoiles de mer, des galathées, de gros mollusques à coquille dure). La méthode ABC est généralement utilisée comme un indicateur d'impact de différents types de perturbations physiques, biologiques et anthropiques sur les communautés benthiques. Cette méthode est basée sur l'hypothèse qu'un régime de perturbation croissant entraîne une modification de la structure des communautés qui deviennent graduellement dominées par des espèces opportunistes de petite taille caractérisées par un renouvellement rapide. Dans une communauté modérément perturbée, la biomasse moyenne des individus est ainsi plus grande que dans une communauté fortement perturbée. La méthode ABC mesure cet effet en comparant les distributions en biomasse et densité dans chaque communauté. Nous avons appliqué la méthode ABC et étudié la structure en taille et la diversité spécifique des communautés benthiques en comparant deux zones, l'une soumise à un effort de pêche modéré et l'autre à un important effort de pêche. La diversité spécifique était plus faible sur les sites fortement chalutés. Ces sites étaient dominés par des organismes opportunistes de grande taille, principalement une espèce de crabe nageur *Liocarcinus depurator*, une espèce de galathée *Munida rugosa* et des langoustines *Nephrops norvegicus*. Dans ces conditions, les résultats de la méthode ABC n'étaient pas cohérents avec la théorie pour ces communautés de macro-invertébrés benthiques et les efforts de pêche mesurés.

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1 Introduction

The abundance-biomass comparison (ABC method) has been first used to detect and measure the effects of pollution on macrobenthic communities (Warwick 1986). Its applications have been progressively extended to other communities submitted to physical, biological (Warwick et al. 1987) and anthropic disturbances (Lindeboom and de Groot 1998; Kaiser et al. 2000). In theory, this graphic indicator does not need any control data (undisturbed state) to provide measures of community health. It has then appeared very attractive for monitoring and assessing impact at ecosystem scales because control sites undisturbed by human impact are increasingly difficult to find.

The ABC method assumes that the distributions of biomass and abundance in benthic communities show a differential response to disturbance. Results are presented as combined K-dominance plots for species biomass and abundance. For each of the two parameters, the K-dominance curve is built by plotting on the *Y*-axis the relative contribution of each species ranked on the *X*-axis, by decreasing order of importance.

According to the ecological succession theory – the predicted evolution of community structure with disturbance (Connell 1978) – Warwick proposed three different forms of combined K-dominance plots figuring increasing levels of disturbance (Fig. 1). Undisturbed communities tend to be dominated by large-bodied, long-lived species represented by a small number of individuals with low turnover rates. The biomass curve lies then above the abundance curve throughout its entire length – reflecting the larger average size of each individual. In moderately disturbed communities, the frequency and intensity of disturbance impose sufficient mortality to eliminate the large species with lower population growth rates. The remaining community is dominated by smaller-bodied, short-lived species with high population growth rates and the difference between the biomass curve and the abundance curve decreases toward zero. In grossly disturbed communities, the domination of small-bodied species increases and the abundance curve lies above the biomass curve throughout its entire length.

Soft bottom communities support productive fisheries for crustaceans, flatfishes and some demersal roudfishes, such as hake (*Merluccius merluccius*). Benthic trawling is a major disturbance source of disturbance in soft-sediment communities. The massive increase of fishing effort and trawling has modified the structure of benthic communities (Kaiser et al. 1998, 2000; Jennings 2001) through differential mortalities depending on individual size, life mode, morphology and demography. Overexploitation removes the most sensitive species, which may indirectly modify food web functioning by favouring opportunistic species which are able to feed on the additional trophic resources represented by discards and organisms killed or injured by the gears (Bergmann 2002b). The alteration of the structural and functional integrity of benthic habitats by trawling could then have consequences for fisheries productivity. Furthermore, the ecosystem approach to fisheries management aims to managing exploitable resources while retaining important biodiversity. Thus, it would be relevant to measure the fishing impact on the benthic communities (Hall 1999).

In order to measure fishing impacts on ecosystems, a wide range of quantitative indicators are being developed (Cury and Christensen 2005). One such indicator, the ABC method, appears to have some promise for measuring fishing effects and its implementation had been proposed (Lindeboom and de Groot 1998; Tuck et al. 1998; Kaiser et al. 2000; Blanchard et al. 2004). Although the majority of exploited benthic species belongs to large macrofauna (organisms which size is greater than 1 cm), the ABC method had not been applied yet to this group of organisms. We assessed the impact of moderate and high levels of bottom trawling on benthic macrofaunal communities using both the ABC method and measures of diversity and size structure. The benthic macrofaunal communities subject to a high and a moderate fishing effort were sampled in May 2001 and November 2003 on the Grande Vasière (Bay of Biscay, France). To estimate whether the ABC method could be used as an ecological measure of fishing impact, structural differences between moderately and highly exploited communities were analysed. We compared species richness, mean individual weights, and ranked species distributions of biomass and abundance (ABC method).

2 Materials and methods

2.1 Study area

The "Grande Vasière" study area is located on the continental shelf of the Bay of Biscay around 47°N and extends between 3 and 4°W off the French Atlantic coast. The "Grande Vasière", muddy sediment, is one of the most important fishing zone in France, where the main commercial species is the Norway lobster *Nephrops norvegicus*. In the Bay of Biscay, *Nephrops* is exploited by otter trawl gear, a 1 tonne mobile bottom trawl with a horizontal opening of 10 m, and a 70 mm mesh. Otter trawls are designed to target efficiently large epibenthic species and penetrate the sediment to a depth of a few centimeters only (Lindeboom and de Groot 1998). The Bay of Biscay is subdivided in ICES-statistical rectangles wherein fishermen have to declare their catches. The Norway lobster fleet fishing effort is concentrated in the north part of the Bay of Biscay. The catches are landed in the French (Brittany) harbours: Saint-Guénolé, Le Guilvinec, Loctudy, Lesconil, Concarneau, Lorient and Quiberon.

2.2 Sampling strategy

In May 2001, a bottom sampling survey (INTRIGAS II) was carried out in the study area with RV *Côtes de la Manch*e and replicated in November 2003 by the RV *Thalassa* (EVHOE 2003 survey) using a 2 m beam trawl with a 20 mm codend mesh. The gear was towed for 20 min at a speed of 2 knots. The prospected areas were measured precisely with the ship's Differential Global Positioning System. Pressure captors were placed on the trawl. This gear is appropriate for sampling large epibenthic invertebrate species, which are typically patchily distributed over a large area, as the beam trawl integrates this small-scale patchiness (Fraueheim 1989; Jennings 1999). The beam trawl sampled macrobenthic

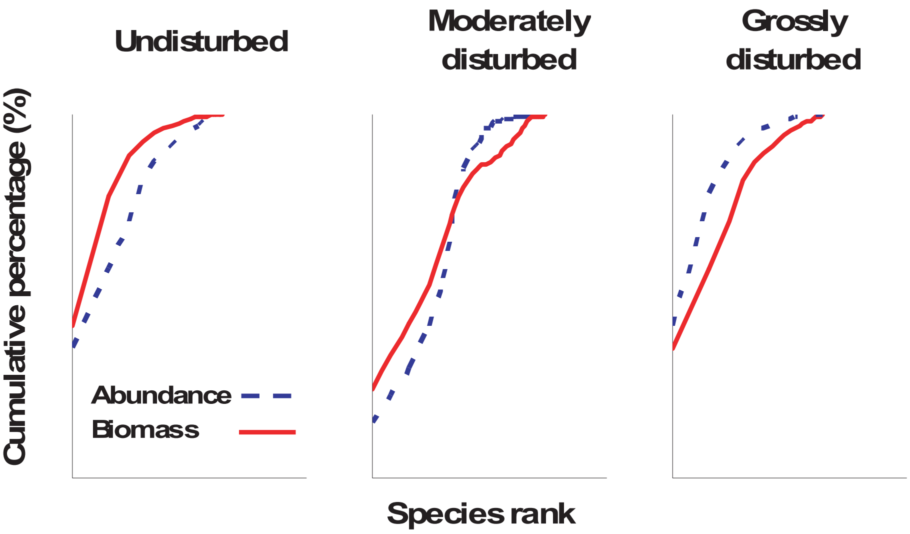

Fig. 1. Theoretical ABC plots for undisturbed, moderately disturbed and grossly disturbed communities. The solid line represents the ranked distribution of biomass in the community and the dashed one represents the ranked distribution of abundance.

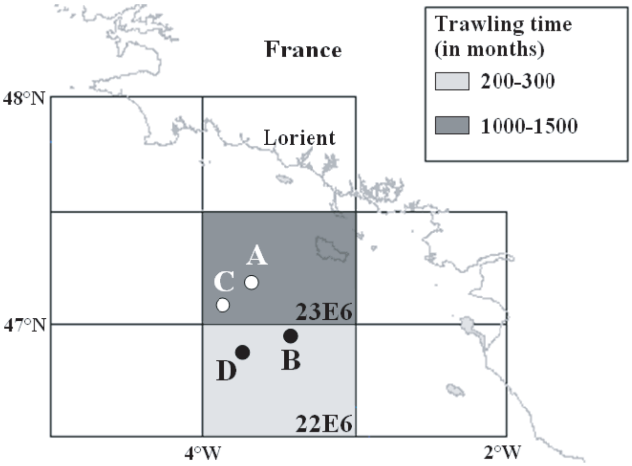

Fig. 2. Locations of the four sampled sites in the Bay of Biscay in 2001 and 2003. Sites A and C are located in a highly fished zone where the time actually spent trawling stands between 1000 and 1500 months per year. B and D are located in a moderately fished zone where the time actually spent trawling stands between 200 and 300 months per year.

invertebrates living on the seabed and to a few centimetres deep in the sediment. Organisms were identified to the specific level. Eight stations were sampled (about 2500 m^2 per haul) in 2001 and eleven in 2003. At each station, and for each species, biomass density and numerical density (respectively biomass and abundance hereafter) were measured and expressed for standard 1000 m^2 areas. Species richness was also measured.

Stations are distributed near the 100 m isobath within four different sites called A, B, C and D, two in each of the two areas of differing trawling intensity (Fig. 2). The location of each site was based on the spatial variation in fleet fishing effort in 2001. Fleet fishing effort was not available for the year 2003 but both the exploited areas and the fishing fleets were the same than in 2001 (pers. comm Leloch). Effort data estimated by the Fisheries Monitoring System of IFREMER in each ICES statistical rectangle were first used. Trawling effort expressed as the time actually spent trawling was between 1000–1500 months per year at the two high fishing pressure sites: A and C, in ICES rectangle 23E6. At the moderately trawled sites B and D (ICES 22E6), trawling effort was between 200 and 300 months per year. This large scale measure of effort may not capture the finer-scalepatchiness of trawling activities within a statistical rectangle so we also estimated the local fishing effort. Relative exploitation levels in A-C, and B-D were calculated by assuming that the fishing effort was lower for sites further from a given harbour. Vessels exploiting each sites were identified and numbered and their contributions to the overall effort were estimated by taking into account their technical features (mean ship speed, mean cruise duration, mean number of hauls per cruise, mean fishing season duration) (pers comm. Ollitraut). All the sites were used by the fishery i.e. there was no unfished site. Our results (not shown here) confirmed that A-C is actually more frequently trawled than B-D. Besides, the four sites presented similar hydrological and sedimentary features.

2.3 Analysis of the community structure

Invertebrate species were sorted *a priori* in categories considering their potential sensitivity to trawling (Table 1 and Blanchard et al. 2004). These categories were defined taking into account both the direct impact of the gear on the seabed and the subsequent ability of a trawled population to recover (ICES 2003).

- Sensitive species are negatively affected by trawling. They are vulnerable to the direct action of the trawl and their ability to recover is limited.
- Indifferent species are not affected by trawling due to a specific life style or morphology.
- Opportunistic species are sensitive to the physical action of the trawl but they are also mobile scavengers able to profit from the post disturbance conditions, feeding on the organisms returned to the sea or killed by the gear.

For each station, biomass, abundance and number of species were measured in each category.

Table 1. List of species (codes and taxonomic groups) and their sensitivity to trawling; Indifferent: white; Sensitive: light grey; Opportunistic: dark grey.

Code	Species	Class
ACD	*Actinauges richardi*	Hexocorallia
ADP	*Adamsia carcinopados*	Hexacorallia
ALD	*Alcyonium digitatum*	Octocorallia
ALGL	*Alpheus glaber*	Crustacea
ALV	*Anapagurus laevis*	Crustacea
APE	*Apporhais pespelicani*	Gastropoda
ARBA	*Arcopagia balaustina*	Bivalvia
ARLO	*Armina loveni*	Gastropoda
ASL	*Astacilla longicornis*	Crustacea
ASY	*Astropecten* spp.	Asteroidea
ATRO	*Atelecyclus rotundatus*	Crustacea
ATUN	*Atelecyclus undecimdentatus*	Crustacea
AZCH	*Azorinus chamasolen*	Bivalvia
BRLY	*Brissopsis lyrifera*	Echinoidea
CAO	*Calliostoma granulatum*	Gastropoda
CHCR	*Chlorotocus crassicornis*	Crustacea
CAPA	*Cancer pagurus*	Crustacea
CRAL	*Crangon allmanni*	Crustacea
CUCU	*Cuspidaria cuspidata*	Bivalvia
CURO	*Cuspidaria rostrata*	Bivalvia
CUP	*Phaxas pellucidus*	Bivalvia
DEEN	*Dentalium entalis*	Scaphopoda
DIBO	*Dichelopandalus bonnieri*	Crustacea
DOLU	*Dosinia lupinus*	Bivalvia
EBCR	*Ebalia cranchi*	Crustacea
GADI	*Galathea dispersa*	Crustacea
GASQ	*Galathea squamifera*	Crustacea
GORH	*Goneplax rhomboides*	Crustacea
HEMA	*Heterocrypta maltzani*	Crustacea
IND	*Inachus dorsettensis*	Crustacea
LECE	*Leptometra celtica*	Crinoidea
LEEL	*Leptopentacta elongata*	Holothurioidea
LID	*Liocarcinus depurator*	Crustacea
LIH	*Liocarcinus holsatus*	Crustacea
MAN	Macropodia tenuirostris	Crustacea
MATU	*Macropipus tuberculatus*	Crustacea
MUBA	*Munida rugosa*	Crustacea
NENO	*Nephrops norvegicus*	Crustacea
NUSU	*Nucula sulcata*	Bivalvia
OPOP	*Ophiura ophiura*	Ophiuroidea
PAP	*Pagurus pridauxi*	Crustacea
PEPH	*Pennatula phosphorea*	Octocorallia
PHEC	*Philocheras echinulatus*	Crustacea
PIRU	*Pitar rudis*	Bivalvia
POHE	*Polybius henslowi*	Crustacea
POPU	*Porania pulvillus*	Asteroidea
POSP	*Pontophilus spinosus*	Crustacea
PRNO	*Processa nouvelli*	Crustacea
PTH	*Pteria hirundo*	Bivalvia
SCA	*Scalpellum* spp.	Crustacea
SCAR	*Scyllarus arctus*	Crustacea
SOME	*Solenocera membranacea*	Crustacea
SQDE	*Squilla desmaresti*	Crustacea
THPU	*Thracia pubescens*	Bivalvia
TUC	*Turritella communis*	Gastropoda
VEOV	*Timoclea ovata*	Bivalvia
VIMI	*Virgularia mirabilis*	Octocorallia
UPDE	*Upogebia deltaurea*	Crustacea

For benthic organisms not living too deep in the sediment, direct fishing mortality, i.e. mortality caused by both physical damages and captures, is higher for larger individuals, as smaller ones are pushed aside by the pressure created in front of the moving trawl (Collie et al. 2000). Therefore, one could expect that large organisms may be rarer in highly trawled sites. We used the mean individual weight (the averaged weight of all individuals in a given community) as an additional parameter to analyse the response of communities to bottom trawling. The mean weight of opportunistic organisms was also monitored.

2.4 ABC method

The average abundance and biomass were calculated for each species and for each of the four sites in 2001 and 2003. Average ABC plots were then built and differences between biomass and abundance curves were quantified by the measure of W (Warwick and Clarke 1994):

$$W = \frac{\sum_{j=1}^{S}\left[\left(\sum_{j=1}^{i} b_j\right) - \left(\sum_{j=1}^{i} a_j\right)\right]}{50(S-1)}$$

where W is the standardised sum of the differences between each pair of species of cumulative biomass $\left(\sum_{j=1}^{i} b_j\right)$ and cumulative abundance $\left(\sum_{j=1}^{i} a_j\right)$ values ranked in decreasing order.

W values in highy and moderately exploited sites were statistically compared in 2001 and 2003. The robustness of the ABC method was investigated by comparing sites submitted to similar fishing efforts in 2001 and 2003.

3 Results

All the statistical tests performed were realized by comparing stations using one way ANOVAs. Mean sites'results are presented below.

3.1 Community structure

Abundance and biomass

Average values are shown in Table 2. In 2001, total biomass strongly differed among sites (Fig. 4). Fishing effort did not significantly account for those variations ($F = 0.212$; $p = 0.661$). Three opportunistic large species, *Munida rugosa, Nephrops norvegicus* and *Liocarcinus depurator*, dominated biomass distibutions in all four sites. The domination of opportunistic species was higher in higly trawled sites while the biomass of sensitive organisms was lower. Consequently, the opportunistic/sensitive biomass ratio was significantly higher in A-C ($F = 19.782$; $p = 0.004$).

Variations of total abundance among the different sites were not explained by the fishing effort distribution ($F = 0.808$; $p = 0.403$). Generally, abundance distributions were

Table 2. Abundance (mean number per 1000 m^2) and biomass (mean wet weigth in g per 1000 m^2) of each species collected in 2001 and 2003, in each site (A, B, C and D). Codes and Latin names of species are listed in Table 1. Indifferent species: white, Sensitive: light grey, Opportunistic species: dark grey.

	2001							
	Abundance				Biomass			
	Sites				Sites			
Species	A	B	C	D	A	B	C	D
LID	14.68	13.04	9.35	12.29	144.84	61.75	94.86	36.17
NENO	7.02	29.62	23.84	9.45	66.83	196.27	135.65	86.27
CRAL	5.11	6.91	5.35	1.27	5.64	6.30	5.10	0.77
MUBA	5.11	23.01	76.44	15.18	28.11	79.21	251.37	35.74
NUSU	0.64	7.08	4.36	0	0.91	5.92	3.83	0
ALGL	0	8.19	3.32	4.33	0	8.19	2.28	2.75
GORH	0	6.34	2.94	7.86	0	38.24	15.85	26.07
CHCR	0	1.82	0.38	1.64	0	3.32	0.79	1.86
PRNO	0	1.49	0	0	0	0.36	0.00	0
MAN	0	1.28	0.38	20.24	0	1.29	0.01	10.97
ADP	0	1.28	0	0.25	0	3.75	0.00	0.11
VEOV	0	1.00	0.71	0.00	0	0.75	0.52	0.00
SQDE	0	0.66	1.47	0.51	0	2.19	4.74	1.72
PAP	0	0.58	0	0.00	0	8.66	0.00	0
VIMI	0	0.50	0	5.46	0	0.96	0.00	4.56
BRLY	0	0.41	0	0.55	0	5.27	0.00	1.38
POHE	0	0.41	0	0	0	4.31	0.00	0
CUCU	0	0.25	0	0	0	0.22	0.00	0
APE	0	0.25	0	0	0	0.51	0.00	0
PEPH	0	0.25	0	0.55	0	0.13	0.00	1.21
ALD	0	0.12	0	1.78	0	0.48	0.00	0.49
TUC	0	0	0.38	6.21	0	0	0.42	2.96
DIBO	0	0	0.38	0.00	0	0	0.47	0
ASY	0	0	0	29.53	0	0	0	71.58
SCA	0	0	0	28.48	0	0	0	1.70
ASL	0	0	0	7.73	0	0	0	0.56
ALV	0	0	0	4.31	0	0	0	0.91
IND	0	0	0	2.40	0	0	0	0.67
PTH	0	0	0	2.28	0	0	0	0.56
CAO	0	0	0	1.85	0	0	0	7.60
MATU	0	0	0	1.31	0	0	0	5.03
GADI	0	0	0	1.02	0	0	0	0.01
HEMA	0	0	0	0.55	0	0	0	0.22
SOME	0	0	0	0.55	0	0	0	1.58
POSP	0	0	0	0.55	0	0	0	0.30
POPU	0	0	0	0.55	0	0	0	3.62
ACD	0	0	0	0.55	0	0	0	12.47
LECE	0	0	0	0.51	0	0	0	0.61
CUP	0	0	0	0.25	0	0	0	0.03
HIA	0	0	0	0.25	0	0	0	0
HEN	0	0	0	0.25	0	0	0	1.20
	2003							
LID	10.08	11.56	22.45	4.53	59.89	66.07	117.17	24.86
MUBA	6.16	16.03	50.72	2.52	69.30	64.14	193.13	10.07
CRAL	3.80	1.30	28.41	0	1.53	0.48	12.62	0
NENO	3.08	3.39	5.83	2.18	18.39	35.05	26.75	11.75
ALGL	1.54	15.22	13.42	2.49	1.09	13.10	10.17	1.09
SOME	0.59	2.31	2.53	4.03	0.71	4.03	2.81	5.88
GORH	0.59	25.15	3.64	11.18	3.76	146.61	16.58	50.29
POSP	0.47	2.94	4.44	3.34	0.17	2.44	2.57	1.77
MAN	0.47	0.66	0	2.83	0.15	0.49	0	1.21
SQDE	0.24	1.93	0.22	2.00	0.59	3.63	0.41	3.65
BRLY	0.24	3.77	2.99	2.85	6.51	61.91	69.78	37.77
LIH	0.24	0	0	0.00	2.37	0	0	0
OPOP	0.12	0	0	2.97	0.84	0	0	21.37

Table 2. continued.

	2003 (continued)							
	Abundance				Biomass			
	Sites				Sites			
Species	A	B	C	D	A	B	C	D
ATRO	0.12	0.00	0	0.63	0.59	0	0	0.89
NUSU	0.12	0.56	7.66	0.17	0.13	0.48	7.63	0.17
VEOV	0.12	2.59	4.98	1.85	0.09	1.91	4.38	1.23
ALV	0.12	2.15	0.52	3.66	0.08	1.15	0.43	1.52
ADP	0.12	0	0	0	0.19	0	0	0
ARBA	0.12	0	0.29	0.50	0.09	0	0.47	0.67
ASY	0	48.16	0.21	54.51	0	105.98	1.04	147.34
CAPA	0	0.08	0	0.16	0	20.60	0	30.23
PAP	0	2.52	0	1.72	0	20.48	0	4.77
TUC	0	44.86	0.23	10.47	0	18.49	0.17	5.59
PRNO	0	12.14	0.61	17.87	0	13.38	0.43	16.46
CAO	0	1.26	0.18	3.59	0	10.82	0.89	13.04
PEPH	0	3.04	0.18	0.17	0	2.04	0.16	0.12
CHCR	0	1.47	0.93	3.19	0	1.69	1.41	3.69
ARLO	0	0.37	0	0	0	0.93	0	0
PIRU	0	0.32	0	0.84	0	0.33	0	1.09
GASQ	0	0.56	0.10	1.68	0	0.29	0.19	1.18
AZCH	0	0.16	0	0.50	0	0.28	0	0.55
ALD	0	0.32	0	2.01	0	0.27	0	9.23
PHEC	0	1.08	1.20	0.50	0	0.24	0.22	0.08
CURO	0	0.11	0	0	0	0.07	0	0
THPU	0	0.08	0	0	0	0	0	0
CUCU	0	0	0.22	0	0	0	0.15	0
EBCR	0	0	0.11	0	0	0	0.02	0
SCAR	0	0	0.11	0	0	0	0.01	0
IND	0	0	0.11	0.16	0	0	0.01	0.02
UPDE	0	0	0.10	0	0	0	0.27	0
LECE	0	0	0	24.06	0	0	0	43.58
SCA	0	0	0	0.47	0	0	0	1.71
POPU	0	0	0	0.16	0	0	0	1.55
LEEL	0	0	0	0.17	0	0	0	0.34
DOLU	0	0	0	0.17	0	0	0	0.27
ATUN	0	0	0	0.17	0	0	0	0.15
DEEN	0	0	0	0.17	0	0	0	0.08
CUP	0	0	0	0.34	0	0	0	0.03

more homogeneous than biomass distributions. *Munida rugosa*, *Nephrops norvegicus* and *Liocarcinus depurator* were the dominant species in sites A, B and C. In D, a sensitive starfish, *Astropecten irregularis*, and an indifferent cirriped *Scalpellum scalpellum* dominated the distribution of abundance. The opportunistic/sensitive abundance ratio was significantly higher in AC ($F = 14.273$; $p = 0.009$).

In 2003, the total biomass and the total abundance appeared not to be linked to fishing effort ($F = 2.336$; $p = 0.161$; $F = 2.832$; $p = 0.127$). Opportunistic/sensitive biomass ratios were significantly higher in A-C ($F = 8.586$; $p = 0.017$). Opportunistic/sensitive abundance ratios were also higher in A-C but the trend was not significant ($F = 4.501$; $p = 0.063$). In A-C, *Munida rugosa*, *N. norvegicus* and *L. depurator* dominated biomass distributions. In moderately exploited sites, dominant species were sensitive organisms. Thus, in B, *Astropecten irregularis* and decapod crustacean *Goneplax rhomboides* were the major species, and in site D, *A. irregularis*, *G. rhomboides* and crinoïde *Leptometra celtica* dominated. In site B, the sensitive species *A. irregularis*, and the indifferent gastropoda *Turittela communis* represented 42% of the total abundance. In site D, *A. irregularis* and *L. celtica* strongly dominated the abundance distribution.

In all prospected sites in 2001 and 2003, relative biomass and abundance of indifferent species did not differ significantly between moderately and highly exploited sites (in 2001, $F = 5.871$; $p = 0.052$; $F = 2.682$; $p = 0.153$. In 2003, $F = 2.180$; $p = 0.174$; $F = 1.788$; $p = 0.214$).

Species richness

For the two sampling years, the number of opportunistic and indifferent species (in 2001, $F = 1.670$, $p = 0.244$ and $F = 1.260$, $p = 0.305$; in 2003, $F = 1.990$, $p = 0.193$ and $F = 3.710$, $p = 0.086$) did not differ in a significant way between A-C and B-D (Fig. 3). However, the number of sensitive species (in 2001, $F = 11.49$, $p = 0.015$; in 2003, $F = 10.25$,

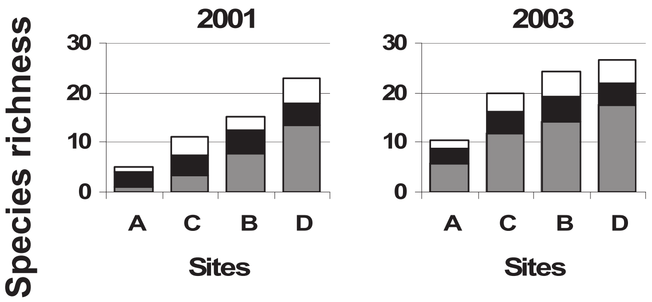

Fig. 3. Species richness of sensitive (▩ Sen), opportunistic (■ Opp) and indifferent (☐ Ind) organisms in highly (A-C) and moderately (B-D) exploited sites in 2001 and 2003.

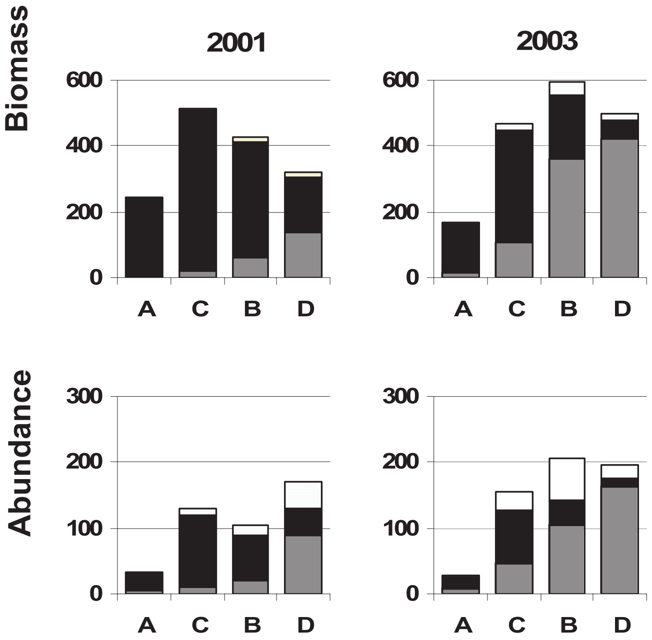

Fig. 4. Biomass (wet weight in g per 1000 m^2) and abundance (number of individuals per 1000 m^2) of sensitive ▩ Sen), opportunistic (■ Opp) and indifferent (☐ Ind) organisms in highly (A-C) and moderately (B-D) exploited sites in 2001 and 2003.

p = 0.011) and the total species richness (in 2001, F = 9.452, p = 0.022; in 2003, F = 10.115, p = 0.011) was significantly lower in highly trawled stations. The total number of species sampled in sites A-C and B-D showed a non significative increasing trend (F = 2.220, p = 0.155) between 2001 and 2003.

Size structure

Mean individual weights (Table 3) were not significantly different between moderately and higly exploited sites (in 2001, F = 0.064, p = 0.132; in 2003, F = 0.820, p = 0.391), suggesting that higher fishing efforts did not imply the disappearance of large organisms. Regarding the opportunistic species, the mean weigth was higher than the mean individual weight in both moderately and highly exploited sites.

Table 3. Biomass (wet weight in g per 1000 m^2, mean ± SD) of individual and opportunistic species in moderately and highly trawled sites in 2001 and 2003.

	Sampling years			
	2001		2003	
	Benthic Trawling Intensity			
	Moderate	High	Moderate	High
Individual weight	3.3 ± 1.3	5.3 ± 2.0	3.1 ± 1.0	4.3 ± 3.0
Opportunist weight	6.1 ± 1.8	7.0 ± 1.8	5.4± 1.0	5.3 ± 2.6

Table 4. Values of W-statistics, ranked in decreasing order, in 2001 and 2003.

Stations	$W-$statistics
2001	
AA1	0.248
BB1	0.110
B2	0.099
B3	0.127
CC1	0.024
C3	0.024
D1	0.129
1DD1	0.119
2003	
AA1	0.122
AA2	0.155
AA3	0.404
BB1	0.089
B2	0.101
B3	0.024
C1	0.121
C2	0.007
C3	0.226
DD1	0.064
D1	0.033

3.2 Abundance-biomass comparison

In 2001, A, B and D sites showed undisturbed patterns with the biomass curve above the abundance curve (Fig. 5). C appeared as a moderatly disturbed community with biomass and abundance curves crossing each other. Values of W-statistics (Table 4) for A-C and B-D were not significantly different (F = 0.112, p = 0.750). In 2003, A and C showed undisturbed patterns, whereas B and D appeared as moderatly disturbed. The differences between A-C and B-D were not significantly different (F = 3.188, p = 0.108). The highly exploited sites A and C showed similar patterns between the two sampling years (F = 0.621, p = 0.457). On the contrary, B and D patterns differed significantly between 2001 and 2003 (F = 11.644, p = 0.009).

4 Discussion

In 2001 and 2003, opportunistic species strongly dominated distributions of biomass and abundance at highly trawled sites. Furthermore, total species richness and sensitive species richness were higher at moderately trawled sites. These results support the hypothesis that benthic trawling is a major source

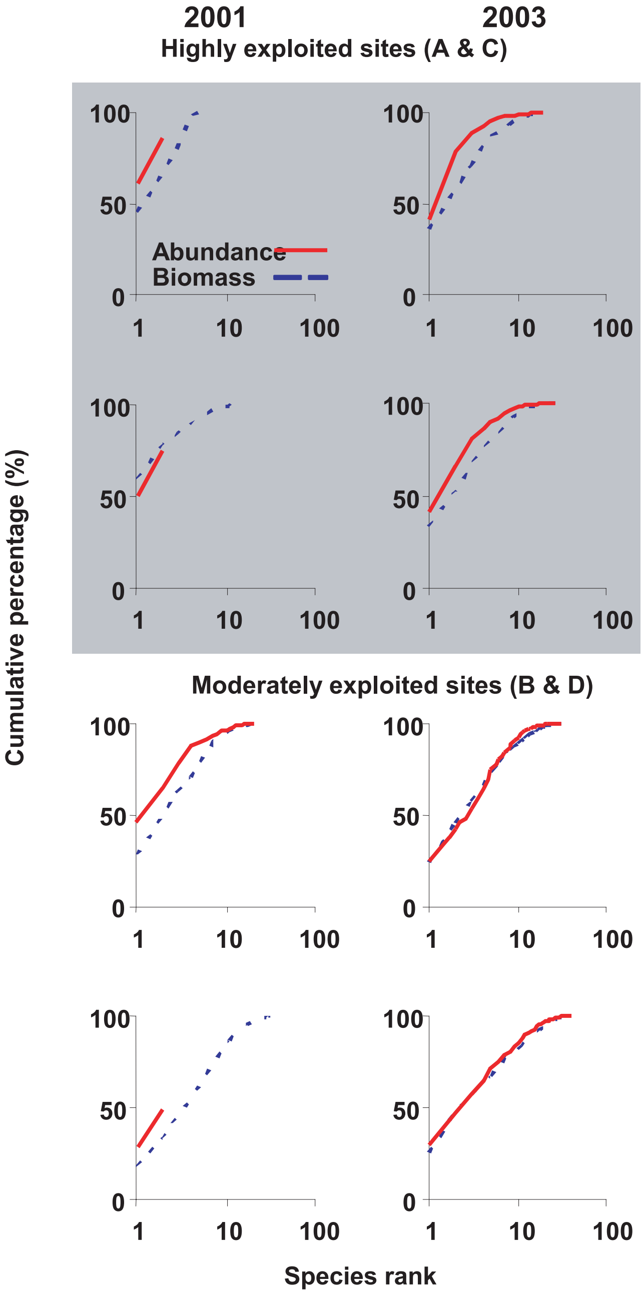

Fig. 5. ABC plots in highly (A-C) and moderately (B-D) exploited sites in 2001 and 2003. The solid line represents the ranked distribution of biomass in the community and the dashed one represents the ranked distribution of abundance.

of disturbance for soft-bottom communities. The mean opportunist weight was also shown to be higher than the mean individual weight at all sites, which is not consistent with the theory underlying the ABC method.

Inter-annual variability

Sampling with benthic trawls usually implies high variability among replicates (Blanchard et al. 2004) and it is then necessary to discuss the reliability of our data set before analysing any result. In particular, the temporal variability in biomass dominance observed at the two moderately trawled sites (a domination of opportunistic species in 2001 followed by a domination of sensitive species in 2003) should be reexamined. The sampling effort developed for this study may have been inappropriate to draw an acurrate picture of benthic macrofaunal communities. Such an assumption finds support in the higher species richness observed in 2003 at all sites. At least two hypothesis related to sampling could be proposed to explain this high inter-annual variability. First, the sampling effort may have failed to integrate the scattered spatial distribution of large epibenthic organisms. As an extreme example, one of the dominant species collected at moderately trawled sites, *Astropecten irregularis*, has a very patchy spatial distribution due to its tendency to aggregate (Leloch 2004). Limited sampling may underestimate the abundance of such patchily distributed species. Indeed, the probability to "miss" partially such populations aggregated on restricted areas is not negligible. Secondly, the trawling effort actually experienced by benthic organisms in sites A, B, C or D might differ from our expectations. In addition with sampling considerations, a natural seasonal variation of the species composition between May 2001 and November 2003 appears as an obvious potential reason of the variability between the two surveys. Yet most large macrofaunal species live several years so that adult benthic stages are present over the whole year within communities. Some of the collected species may undertake seasonal migrations, leading to high temporal variability in biomass and abundance. *Astropecten irregularis* has been reported to migrate seasonally in coastal zones (Freeman 2001). However, the seasonal environmental variability which triggers these migrations is strongly dampened at 100 m deep and is therefore unlikely to affect population dynamics in the study area. Other stimuli could be considered for deep populations, for instance an increase of the organic matter flow towards the benthic system following spring phytoplanktonic blooms.

Benthic trawling impact

The IFREMER Fisheries Monitoring System provides estimates of trawling effort at the scale of ICES statistical rectangles, assuming that it is uniformly distributed over these large areas. Such an assumption is clearly a simplification. The calculation of more local trawling efforts was our answer to overcome this major difficulty. This second approach yielded results consistent with the IFREMER estimates, suggesting that the sites A and C were effectively more frequently trawled than sites B and D. Such a conclusion is also underpinned by previous studies of fishing impact in the Grande Vasière (Blanchard et al. 2004; Leloch 2004) which show more disturbed communities in the A-C area.

Despite evidence of inter-annual variability due to sampling, non ambiguous structural differences between sites B-D and A-C are visible. The two strongly trawled sites A and C exhibit lower sensitive biomass and abundance and a lower diversity of sensitive species. The removal of sensitive species at highly exploited sites has been widely reported by authors and is interpreted as an alteration of the structure of communities (Dayton et al. 1995). One may object that the domination of a few opportunistic species at the two moderately trawled sites in 2001 also supports evidence of disturbance. However, these dominant opportunistic species, namely the squat lobster *Munida rugosa*, the Norway lobster *Nephrops norvegicus* and the swimming crab *Liocarcinus depurator*, are not exclusive scavengers. They are also competitive predators that fully belong to typical undisturbed communities (Groenewold 2000). What their presence means then depends on the species composition of the communities they are embedded in. B-D communities are species rich and include organisms typically found in undisturbed environments such as *Leptometra celtica*, a fragile epibenthic sessil species.

It is worth to notice that communities do not experience any reduction of their total biomass or abundance in highly exploited sites. This result differs from what was observed at ecologically similar sites in the North Sea, where the trawling effort is considerably higher than in the Bay of Biscay (Jennings 2001). This suggests that the threshold beyond which exploitation would cause the general collapse of benthic communities has not been reached yet in the Grande Vasière.

Large species at highly trawled sites

We have shown that dominant species in disturbed conditions were large-bodied organisms. This result is surprising regarding as small-bodied species with high population growth rates should be more adapted to settle in frequently disturbed systems (MacArthur 1962).

The domination of large opportunists such as *Munida rugosa*, *Nephrops norvegicus* and *Liocarcinus depurator* at highly trawled sites could result from their higher ability to escape fishing gears. However, these three species are often caught by benthic trawlers in the North Sea (Bergmann 2001a,b; Bergmann 2002a). Lindeboom and de Groot (1998) estimate that no macrofaunal epibenthic invertebrate is mobile enough to avoid modern bottom trawls.

Another hypothesis which could explain the domination of large-bodied organisms at frequently trawled sites is linked to the production of discards by fisheries. By definition, opportunistic species are able to feed on discards and organisms killed or injured by benthic fishing gears. How such additional trophic resources influence the dynamics of opportunistic populations is not well understood (Lindeboom and de Groot 1998). However, it has been suggested that they may locally support populations of scavengers within frequently trawled communities, where the competition with sensitive species is low (Groenewold 2000; Bergmann 2002b). At frequently trawled sites, the trophic resources provided by discards could counter-balance the negative effect of trawling on large-bodied opportunistic organisms. The patchy distribution of trawling disturbance (Rijnsdorp 1998; Ragnarsson 2003) may allow large opportunists to survive in small intouched areas from which they could move into trawl tracks and feed on dead and injured individuals. This hypothesis admits a limit beyond which trawling effort is too high to allow the persistence of opportunistic populations.

Interpretation of ABC plots

In contrast with the theory that underlies the ABC method, higher trawl efforts in our study zone do not shift benthic macrofaunal communities toward increasing domination by small-bodied opportunistic species.

Within a community, the size of dominant species determines the relative position of biomass and abundance curves. Therefore, the unusual domination of large-bodied opportunistic species at highly trawled sites is likely to bias the results of the ABC method. This is confirmed by the analysis of ABC plots which yield inconsistent disturbance diagnosis. Large crustaceans *Munida rugosa*, *Nephrops norvegicus* and *Liocarcinus depurator* dominated at highly trawled sites A 2001, A 2003 and C 2003 and at moderatly trawled sites B and D 2001. Consequently, ABC plots were similar for all of these sites, with the biomass curve lying above the abundance curve. In that case, the ABC method contradictly concludes that two very different groups of communities experienced the same level of disturbance. In B and D 2003, communities were dominated by *Astropecten irregularis* and *Leptometra celtica,* two sessile epibenthic species typically found in undisturbed environments. Because *A. irregularis* and *L. celtica* are small-bodied organisms, the ABC method diagnosted a very unlikely high level of disturbance.

One may question the importance of such a result as the range of sizes (i.e. organisms captured by the 20 mm mesh sampling trawl) we considered could exclude from the study the small opportunists that are predicted to dominate in disturbed communities. The study of a wider (microfauna + macrofauna) size range of organisms could be suggested. However, the persistence of large-bodied macrobenthic organisms at high trawling effort would have altered the reliability of the ABC method in any case. On the Grande Vasière, the main commercial species belong to benthic macrofauna. It was therefore highly desirable to identify the specific pitfalls linked to the monitoring of these large organisms. The ABC method had proved to be a powerful indicator of impact of diverse kinds of disturbance on benthic communities and was then a promising tool that needed to be tested in the context of the ecosystem approach of fisheries. Our study highlights and important caveat of the method and will be useful for managers and policy makers who will have to select properly a panel of indicators to implement the sustainable exploitation of the stocks.

Conclusion

The ABC method is based on a general ecological theory which correctly describes the structural succession experienced by most communities submitted to increasing disturbance. This theory admits exceptions. Several studies actually emphasize particular situations in which the ABC method is not appropriate (Beukema 1988; Dauer 1993). The present work confirms that fishing negatively affects the state of health of benthic communities. However, the use of the ABC method is not always relevant to quantify these impacts. Above all, our study shows that synthetic tools as such indicators are “black boxes”. It underlines the need for comprehensive ecological analysis of communities before using any type of ecosystem indicators.

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Erratum

Evaluation of trawling disturbance on macrobenthic invertebrate communities in the Bay of Biscay, France: analysis of the Abundance Biomass Comparison (ABC) method.

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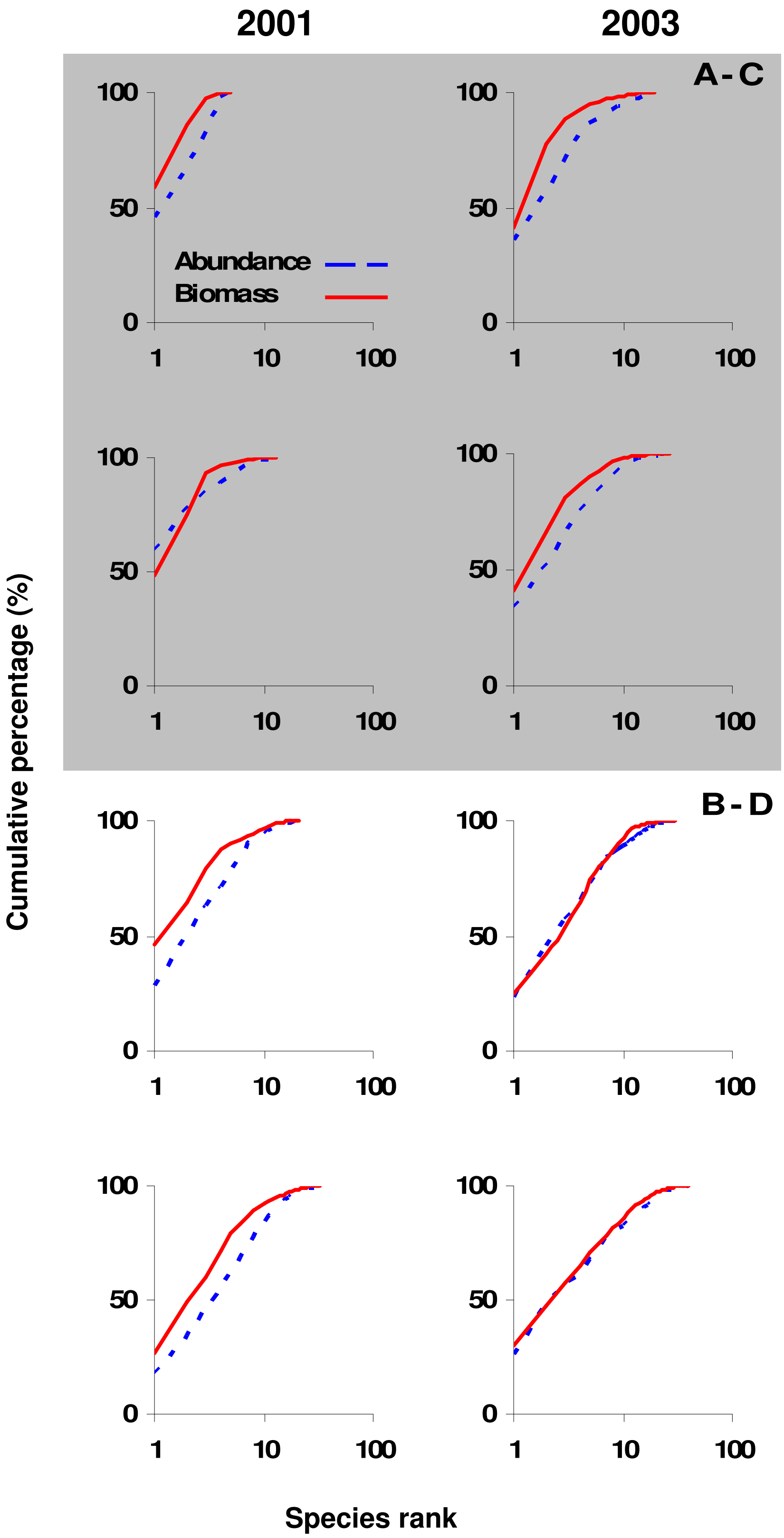

Fig. 5. ABC plots in highly (A-C) and moderately (B-D) exploited sites in 2001 and 2003. The solid line represents the ranked distribution of biomass in the community and the dashed one represents the ranked distribution of abundance.

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Outbreaks of Disease Possibly Due to a Natural Avian Herpesvirus Infection in a Colony of Young Magnificent Frigatebirds (*Fregata magnificens*) in French Guiana

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ABSTRACT: The Ile du Grand Connétable nature reserve is a rocky island off the Northern Atlantic coast of South America that hosts a unique population of Magnificent Frigatebirds (*Fregata magnificens*, Pelecaniformes). A high chick mortality, associated with nodular proliferative lesions, involving featherless areas, such as legs, neck, eyelids, and beak, was recorded during a consecutive 2 yr and affected almost half of the generation. Investigations were, therefore, conducted to determine the cause of these epidemics. Although histopathologic investigations suggested that malnutrition, because of fewer resources in the Frigates' fishing area, could be the cause of the epidemic, a novel alphaherpesvirus, tentatively called *Fregata magnificens* herpesvirus, was detected in cutaneous crusts on the diseased birds. Although in this study, we do not prove the causal link of this new virus to the symptoms observed, it can nevertheless be suggested that in debilitated hosts, a productive herpesvirus infection might accelerate, and/or be accelerated by, population declines. These results emphasize the need to take into consideration the possible role of herpesviruses in weakened populations of wild birds in conservation management plans.

Key words: Alphaherpesvirus, chick mortality, *Fregata magnificens*, Frigatebird.

Mortality outbreaks in wild bird populations are mainly related to acute or chronic pollution and infectious diseases, and these epidemic events have increasing impacts on population conservation (Daszak et al., 2001; Wellehan et al., 2003). Among viruses, herpesvirus infection has been widely reported in wild bird populations for decades; these diseases are among the most common health problems in aquatic birds, parrots, and passerines (Johnson and Tyack, 1995; Converse and Kidd, 2001; Tomaszewski et al., 2001; Newman et al., 2007). Herpesvirus infections have also been reported in vultures, falcons, wild turkeys, penguins, and ducks (Grant et al., 1975; Kincaid et al., 1988; Wojcinski et al., 1991; Forbes et al., 2000; Cardoso et al., 2005).

The Ile du Grand Connétable nature reserve (4°49′30″N, 51°56′00″W) is a rocky island located off the Northern Atlantic coast of South America that hosts a unique population of Magnificent Frigatebirds (*Fregata magnificens*, Pelecaniformes). With about 5% of the Caribbean population, this Frigatebird colony is one of the most important of the region, and the sole nesting site between the islands of Tobago and Fernando do Noronha (Dujardin and Tostain, 1990). In July 2005, after the annual hatching period, 25 dead chicks were found, and 30 live chicks among the 250 nests on the island had clinical cutaneous signs. Nodular proliferative lesions involving featherless areas, such as legs, neck, eyelids, and beaks, and keratitis and conjunctivitis were present (Fig. 1). Dead and affected birds were not geographically restricted but widespread over the entire island, in proximity to healthy animals. Clinical signs or lesions were not observed in adults or other avian species present on the island (*Sterna*

FIGURE 1. Skin lesions and cornea alteration in a Frigatebird chick.

maxima, *Sterna eurygnatha*, *Sterna fuscata*, *Anous stolidus*, and *Larus atricilla*). In the following 2 wk, 33 more dead chicks were recorded, and 27 chicks had clinical signs. After 1 mo, 41 additional dead chicks were recorded. Through intense monitoring of nests, it was confirmed that symptoms were always lethal: no animal with clinical signs recovered.

In sampled animals, we observed thickening of the skin, hyperkeratosis, bone frailty, and severe emaciation. Blood samples were collected from 11 chicks, five from healthy animals and six from animals with clinical signs. In addition, skin samples from three of six affected birds were collected and preserved in Hanks medium. One dead animal was submitted for necropsy. Clinical pathologic findings included marked hypophosphatemia (1.78 mmol/l, $n=4$, vs. 4.03 mmol/l in healthy chicks, Work 1996), whereas calcemia, hematocrit and hemoglobin measurements were within reference range values (Work, 1996). No inflammatory lesions were seen during histopathologic examination of the esophagus, intestine, and trachea. Lungs were moderately congested, and muscles had a slight interstitial edema. The liver had minor perivascular inflammatory infiltrates, and the kidneys had two foci of interstitial inflammatory cells. Bone mineralization was deficient, with a thin primary ossification area and persistent cartilage. Finally, dermal tissues had hyperkeratosis, and epidermal keratinocytes had ballooning degeneration, but no inflammatory process or intranuclear viral inclusions were observed. These findings are typical of a poor nutritional status. Bacterial cultures and microscopic evaluation of skin samples excluded the possibility of a bacterial infection and the presence of ectoparasites. The birds were negative for avian poxvirus DNA, as determined by polymerase chain reaction (PCR), using previously published procedures (Kim et al., 2003).

We attempted to amplify herpesviral sequences using a nested PCR (nPCR) approach, with degenerate consensus primers targeted to highly conserved amino acid motifs within the herpesvirus DNA polymerase gene (Rose et al., 1997). Amplification products of the expected size (about 250 base pair [bp]) were identified in one skin sample, and these products were sequenced after cloning. Database searches using the Basic Local Alignment Search Tool (BLAST) Web server revealed the presence of a new herpesvirus sequence. To extend the nucleotide sequence upstream, a specific, nondegenerate oligonucleotide was designed from the complementary sequence of the small fragment and was used in an nPCR amplification with the DFASA primer pool (Lacoste et al., 2000). The PCR products from the initial PCR were used as template DNA in the subsequent amplification reactions. The upstream nPCR products were subsequently cloned and sequenced. The resulting sequences were assembled to give a total of 476 bp (excluding primers). The obtained consensus was deposited in GenBank under accession number EU867220. BLAST searches showed that this novel sequence was most similar to the DNA polymerases of the *Alphaherpesvirinae* subfamily. Comparison of amino acid identities among alphaherpesviruses indicated that the Frigatebird herpesvirus, tentatively named FmagHV for *Fregata magnificens* herpesvirus, was most closely related to the Vulture herpesvirus (VHV), exhibiting 83.5% identity (Cardoso et al., 2005). Furthermore, within the *Alphaherpesvirinae* subfamily, our Frigatebird herpesvirus sequence was more closely related to the human herpes simplex virus types 1 and 2 (HSV-1 and HSV-2) of the simplex genus (81.4 and 79.7% amino acid identity, respectively) than to the other bird alphaherpesviruses (73% of amino acid identity with Marek's disease virus type 2 and 65% with Psittacid herpesvirus 1 and Passerine herpesvirus 1). Phylogenetic analyses were performed on 124 amino acids. The amino acid sequence was aligned using ClustalW (European Molecular Biology Laboratory, European Bioinformatics Institute, Hinxton, Cambridge, UK; Thompson et al., 1994) with other previously published sequences, and alignments were checked manually. The ProtTest program (Abascal et al., 2005) was used to determine the optimal model of amino acid evolution for the data set. A Bayesian approach was performed with the program BEAST version 1.4.7 (Drummond and Rambaut, 2007) to infer phylogenetic relationships. Analysis was performed using a WAG model of amino acid substitutions with a gamma distributed rate of variation among sites and six rate categories. We ran the analysis assuming a constant population size and a relaxed molecular clock (uncorrelated lognormal). Results from the run (10,000,000 generations with the first 1,000,000 discarded as burn-in and parameter values sampled every 100 generations) were analyzed using the program Tracer version 1.4 (Rambaut and Drummond, 2003). The phylogenetic analysis placed the Frigatebird herpesvirus (FmagHV) close to the VHV with a posterior probability value of 1. This cluster is associated with the *simplex* genus encompassing HSV-1, HSV-2, Cercopithecine herpesvirus 1 and 2 (CeHV-1 and CeHV-2), as well as bovine herpesvirus 2 (BoHV-2) with less support (0.76; Fig. 2).

In poultry or in captive avian species, symptoms of herpesviral infections are diverse. They are associated with different diseases, such as Marek's disease, duck viral enteritis, infectious laryngotracheitis, and Pacheco's disease. Pacheco's disease has no evident clinical signs in parrots, and some animals may recover (Tomaszewski et al., 2001). In passerines, clinical signs are mainly respiratory, with or without conjunctivitis (Wellehan et al., 2003). In wild bird populations, it has been suggested that herpesvirus outbreaks are often facilitated by immune suppression of

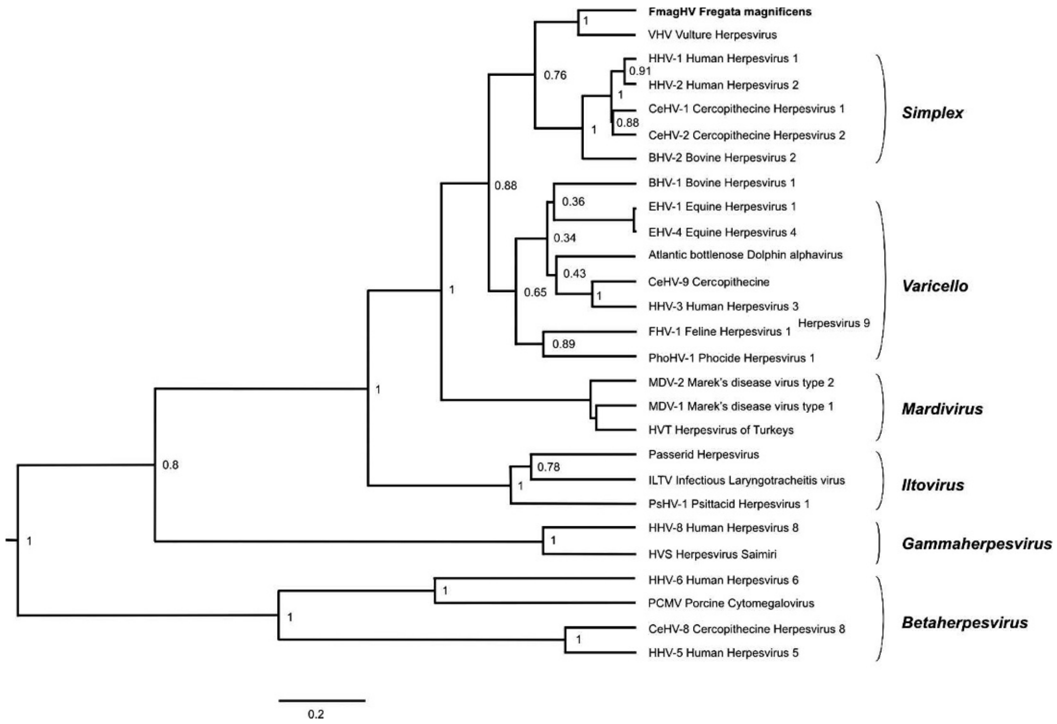

FIGURE 2. Phylogenetic tree (based on 124 amino acid sequences of the DNA polymerase gene, using a Bayesian procedure) showing relationships between *Fregata magnificens* herpesvirus and other selected herpesviruses.

animals resulting from polluted environments (Goldberg et al., 1990). Nevertheless, despite an impressive number of clinical cases recorded, molecular investigations have rarely been conducted during herpesvirus outbreaks. The particular outbreaks as well as the virus we described in this Frigatebird colony thus raised two major questions. First, concerning the immune status of the target population, there is no existing indication of immune suppression in these birds. Although there are no records of marine pollution in the nature reserve, Magnificent Frigatebirds cover an average of 223 km per foraging trip (Weimerskirch et al., 2003). It is possible that birds could be contaminated far from the site of the outbreak. Because clinical signs were restricted to juveniles, an immune deficiency due to malnutrition could also be advocated. Frigatebirds often feed on refuse from fishing ships, with more than 120 Frigatebirds frequently observed on a single trawler (Calixto-Albarran and Osorno, 2000). In French Guiana, activities associated with the industrial shrimp trawling fisheries had decreased 1 mo before the appearance of the first chick symptoms and may have resulted in malnutrition. The observed biochemistry changes and clinical signs, such as hypocalcemia, hypophosphatemia, and hyperkeratosis, support this supposition. Second, the origin of the virus is unknown. It has been suggested that migratory birds could facilitate herpesvirus dissemination (Hubalek, 2004; Newman et al., 2007), especially related to cross-species infections. The herpesvirus sequence that we isolated in Frigatebird tissues may have originated from a different avian species; however, the natural host range of most herpesviruses is highly restricted (Davison, 2002). Herpesviruses are highly adapted to their hosts, and in these hosts, severe infections are usually restricted to very young or immunosuppressed individuals.

For this reason, we believe that the virus characterized here is very likely indigenous to Frigatebirds, and the sequence reported in the present study is unique, supporting this hypothesis. In this study, we do not prove the causal link between this virus and the outbreaks; the classic herpetic viral inclusion bodies and associated dermatitis were not observed, and histologic changes were more likely related to malnutrition. The virus was only identified in skin lesions, suggesting that it might be reactivated, and that it might, therefore, interact with host fitness. Our results thus suggest that, in a context of debilitated hosts, productive herpesvirus infection might accelerate and/or be accelerated by population declines. The possible role of herpesviruses in weakened populations of wild birds, therefore, should be considered in conservation plans (Cardoso et al., 2005).

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Thermal and trophic habitats of the leatherback turtle during the nesting season in French Guiana

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ABSTRACT

Understanding environmental cues determining behaviour and habitat use of species of conservation concern is crucial if one aims at implementing sustainable management of these natural resources. In this way, here, we investigate the thermal and trophic conditions encountered by the critically endangered leatherback sea turtle *Dermochelys coriacea* during its nesting season in French Guiana where high bycatch rates have been reported.

Mean sea water temperatures obtained in situ by animal-borne recorders were 26.6 ± 0.7 °C in the water column, with all but one turtle remaining in water >25 °C during the inter-nesting interval. In terms of prey availability, regular jellyfish stranding events were recorded during the nesting season, on a 1.25-km long section of the nesting beach. The occurrence of jellyfish was supported by benthic trawls performed on the continental shelf, with a total of 45.4 kg of jellyfish collected in 3.5 h exclusively in coastal waters 10 to 20 m deep where water transparency was between 0.8 and 3 m. This is consistent with the at sea distribution area of gravid leatherbacks during their inter-nesting intervals, as they spent almost 70% of their time diving in shallow (<20 m deep) waters in front of the Maroni River estuary. In French Guiana, leatherback's gelatinous prey are thus present in very shallow water close to the nesting site and may be easily exploited by active gravid leatherbacks. This suggests that French Guiana female leatherbacks may be influenced by local trophic conditions and actively prospect productive areas overlapping with local fisheries ground.

1. Introduction

Oceanographic conditions affect marine organisms either directly through individuals' physiology or indirectly through trophic resources (e.g. Bost et al., 1997; Guinet et al., 1997; Sims and Quayle, 1998; McMahon and Hays, 2006; Witt et al., 2007). In particular, water temperature and trophic conditions during the reproductive season have been reported to have wide-ranging and significant impacts on the nesting ecology of marine turtles (e.g. Buttemer and Dawson, 1993; Sato et al., 1998; Hays et al., 2002; Southwood et al., 2005; Wallace and Jones, 2008; Schofield et al., 2009). For instance, evidence suggests that local trophic conditions may shape the activity of green turtles in their breeding grounds: when seagrass was abundant, breeding turtles spent most of their time foraging at very shallow depths while they rested at deeper depths on the seabed when food was not available (Hays et al., 2002). In the same way, water temperature on the Pacific coasts of Costa Rica has been reported to be closely linked to the diving behaviour of nesting leatherback sea turtles *Dermochelys coriacea* (Vandelli, 1761) as they spend a significant amount of their time at sea in waters <24 °C where they show low activity levels and low metabolic rates (Southwood et al., 2005; Wallace et al., 2005). In doing so, female leatherbacks may limit overheating while conserving energy for reproduction (Southwood et al., 2005; Wallace et al., 2005).

In French Guiana, where one of the world's major leatherback nesting sites occurs, gravid leatherbacks have been reported to disperse actively and extensively over the continental shelf during the nesting season while performing continuous benthic dives (Fossette et al., 2007; Georges et al., 2007) probably in order to feed on jellyfish (Fossette et al., 2008a). Importantly, this behaviour may partly explain the high rates of accidental catches of leatherbacks by coastal fisheries reported during the nesting season in this area (Fossette et al., 2008b, see also Witt et al., 2008). Indeed, interactions between leatherbacks and fisheries may result from turtles and fishermen actively searching for their respective food resources in similar areas over the Guiana continental shelf. Accordingly, understanding the mechanisms ruling both leatherbacks and fishermen behaviours is crucial if one aims at implementing

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sustainable management of natural resources while limiting interactions with species of any conservation concern such as sea turtles (e.g. Georges et al., 2007; Witt et al., 2008). However to date, leatherback's habitat off French Guiana has never been investigated so that the environmental parameters influencing sea turtles habitat use and behaviour during the nesting season still remain unknown.

Here we propose to describe the thermal and trophic (jellyfish distribution and abundance) conditions of leatherback's habitats during the nesting season in French Guiana and their potential connections with the spatial distribution and dive patterns of gravid females between two consecutive nesting events. In doing so, we aim at contributing to the implementation of more efficient protection of this critically endangered species.

2. Materials and methods

The study was carried out at Awala-Yalimapo beach (5.7 °N–53.9 °W), French Guiana, South America, and on the Guiana continental shelf.

2.1. Leatherback's habitat use

Eleven gravid leatherback turtles were tracked with Argos transmitters during their inter-nesting intervals in 2001, 2002 and 2003 (see Fossette et al., 2007 for more details). All tracks were processed as in Gaspar et al. (2006): first, Argos locations implying an apparent speed above 2.8 $m\ s^{-1}$ were discarded; tracks were then smoothed and re-sampled every 3 h. For each re-sampled track, we calculated using R© software the number of locations per 0.1°*0.1° area on the Guiana continental shelf, and then deduced the time spent in each area of 0.1°*0.1° (Georges et al., 2007).

2.2. Thermal conditions on the Guiana continental shelf

2.2.1. Remotely sensed sea surface temperatures

We estimated remotely sensed Sea Surface Temperatures (SSTs) on the Guiana continental shelf during the leatherback nesting seasons between 2001 and 2007 using monthly maps of AVHRR Oceans Pathfinder Version 5.0 SST data (4 km resolution; http://pathfinder.nodc.noaa.gov). These products are developed at RMAS and NODC and distributed in partnership with the Physical Oceanography Distributed Active Archive Center (PO.DAAC; see http://podaac.jpl.nasa.gov for details). We considered a surface area comprising the eleven inter-nesting tracks, i.e. between the French Guiana coast (approx. 5.5°N) and 7.5°N latitude, and 55–53°W longitude (see Fossette et al., 2007 for more details). In addition, we estimated SSTs along these inter-nesting tracks by bi-linear interpolation of the SST monthly fields.

2.2.2. In situ recorded temperatures

Seven leatherback turtles were fitted with electronic Time-Depth Recorders (TDRs, Little Leonardo, Tokyo, Japan) during their inter-nesting intervals in 2001, 2002 and 2003 (Table 1, see Fossette et al., 2007 for more details). Each TDR included a temperature sensor recording one measurement of in situ temperature every 10 s (range: −20 to +80 °C, ±0.1 °C). In situ temperatures recorded by the loggers were averaged between 0 and 3 m depth (hereafter called ‘in situ surface temperature’), and between 3 m and the maximum depth (hereafter called ‘in situ column temperature’). This threshold of 3 m was chosen in agreement with previous studies that reported leatherback turtles remaining, between two successive dives, between 0 and 3 m depth alternating breathing and ‘surfacing’ dives (Reina et al., 2005; Fossette et al., 2007). In situ temperatures were investigated throughout the inter-nesting interval in 12-hour intervals coinciding with local light/dark phases, as sea water temperature may vary between daytime and night time.

2.3. Trophic conditions on the Guiana continental shelf

2.3.1. Jellyfish stranding surveys

Jellyfish stranding was recorded during daily surveys of Awala-Yalimapo beach over 1.25 km of coastline from April to July 2005 ($n=76$ days of survey) and 2006 ($n=92$ days). Surveys were conducted 2 h after high tide when marine debris were left by retreating tides. Surveys lasted approximately 1 h: two persons were patrolling the beach side by side, one from the shore to the middle of the beach, and the other one from the middle of the beach to the higher water mark. Observers were switching their respective place during the backward leg for controlling the counting of each other. Genus of each stranded jellyfish was identified and the number of individuals observed in each genus was assessed. In addition, a total of 94 stranded jellyfish was randomly sampled during the 2005 nesting season, measured and weighted.

2.3.2. At sea jellyfish distribution and biomass

In May 2007, benthic trawls were performed through the “CHALOUPE” project, which aims at investigating changes in marine biodiversity structure of the Guiana continental shelf regarding impacts of the fishing activities and climate change (see http://www.projet-chaloupe.fr/). A total of 36 randomly located transects was performed between 4.7°N–6.3°N latitude and 53.7°W–51.5°W longitude, over depths ranging from 10 to 55 m. Benthic Trawls were performed by a shrimp trawler, at an average speed of 3–4 knots (5.5–7.4 $km\ h^{-1}$) during 30 min. The trawl net was 11 m long with an opening of 1 m width and a 45 mm mesh size. For each trawl, jellyfish were separated from other collected species, before being identified to the genus level, counted and weighted. The turbidity was also measured during each transect using a Secchi disk.

3. Results

3.1. Leatherback's habitat use

Based on the eleven inter-nesting tracks from Fossette et al. (2007), we calculated that turtles spent 68.3%, 20.6%, 10.1% and 1.0% of

Table 1

Summary of the in situ recorded temperatures (surface and water column) in seven TDR-equipped gravid leatherback turtles during their inter-nesting interval in French Guiana during the nesting seasons 2001, 2002, and 2003.

Turtles ID no.	Departure time	Trip duration (d)	Dive depth range (m)	Max/Min (diff.) in situ surface temp (°C)	Max/Min (diff.) in situ column temp (°C)	In situ surface temperature (°C)	In situ column temperature (°C)
200101	16 May 2001, 00:26	10.8	[0–80]	34.7/25.3 (9.4)	28.6/22.1 (6.5)	27.2 ± 0.8	25.3 ± 1.3
200102	22 May 2001, 02:58	9.9	[0–30]	30.8/25.7 (5.1)	29.2/25.4 (3.8)	27.3 ± 0.5	26.6 ± 0.6
200103	28 May 2001, 23:46	10.1	[0–20]	30.3/27.1 (3.2)	28.3/25.6 (2.7)	27.3 ± 0.6	27.0 ± 0.1
200201	30 Apr 2002, 23:30	12.1	[0–40]	29.7/26.5 (3.2)	29.3/26.0 (3.3)	27.4 ± 0.6	26.8 ± 0.3
200202	02 May 2002, 22:55	8.2	[0–30]	30.0/27.2 (2.8)	28.7/26.9 (1.8)	28.1 ± 0.6	27.4 ± 0.3
200301	05 May 2003, 22:43	9.3	[0–20]	29.2/25.9 (3.3)	27.9/25.9 (2.0)	26.9 ± 0.4	26.4 ± 0.2
200302	06 May 2003, 22:05	9.2	[0–30]	29.8/26.4 (3.4)	29.3/26.3 (3.0)	27.4 ± 0.5	26.8 ± 0.2
Mean ± s.d.				30.6 ± 1.9/26.3 ± 0.7	28.8 ± 0.5/25.5 ± 1.6	27.4 ± 0.4	26.6 ± 0.7

Values are expressed as mean ± s.d.

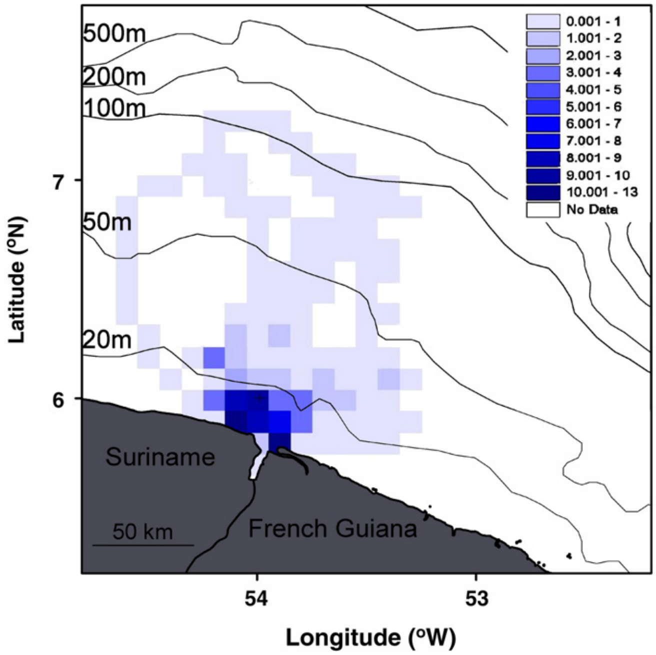

Fig. 1. Topographic representation of habitat use in terms of time spent per 0.1°*0.1° area (blue squares in days) by leatherback turtles ($n = 11$; Argos tracked leatherback turtles nesting in French Guiana between 2001 and 2003) during the inter-nesting intervals on the Guiana continental shelf.

their time in waters <20 m, 50 m, 100 m, and 200 m depth respectively, and mainly explore waters in front of the Maroni River estuary (Figs. 1, 2, and 6).

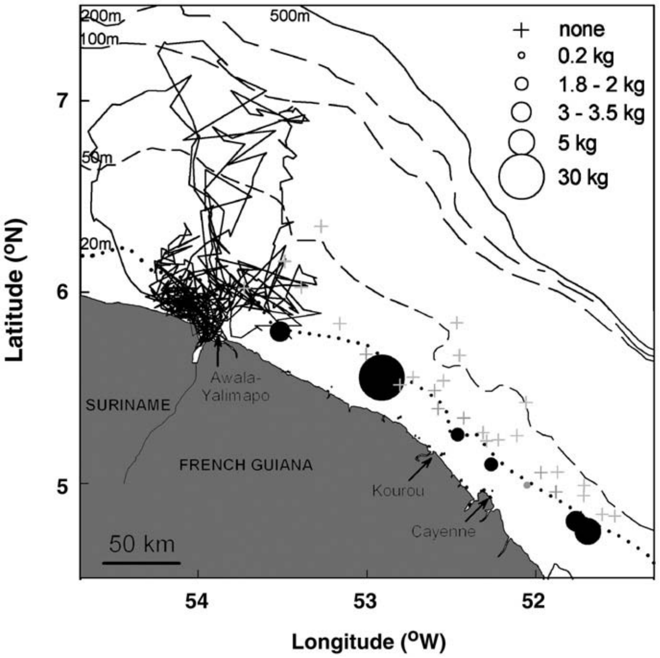

Fig. 2. Inter-nesting movements (solid black lines) of 11 Argos tracked leatherback turtles during the nesting seasons 2001, 2002 and 2003 in French Guiana and distribution of jellyfish sampled by bottom trawling on the Guiana continental shelf in May 2007. Trawling with successful and unsuccessful jellyfish sampling is represented by circles and crosses respectively. The size of each circle indicates the jellyfish biomass. Colours of the crosses and circles indicate water transparency: light grey means water transparency >3.0 m, dark grey means water transparency between 2.0 and 3.0 m, and black means water transparency between 0.8 and 2.0 m depth.

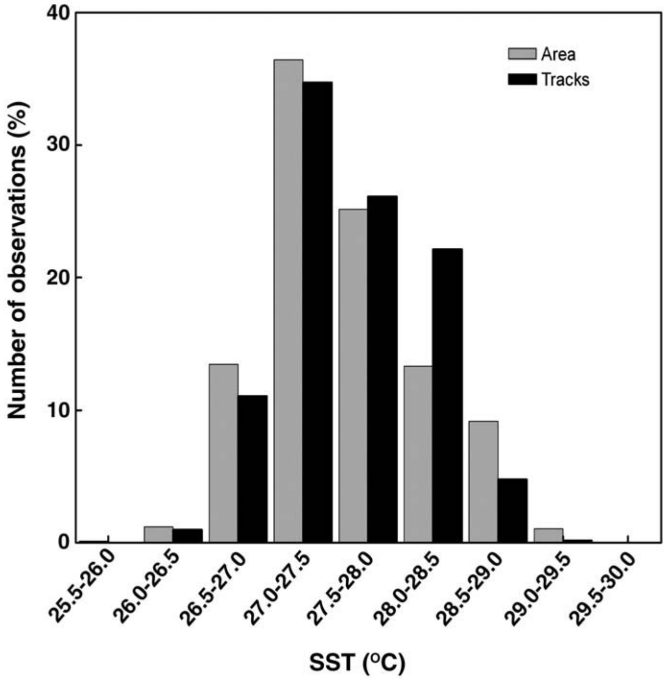

Fig. 3. Frequency distribution of remotely sensed SSTs in the area off French Guiana [coast-7.5°N/53–55°W] during the leatherback nesting season (in grey) and along the tracks of 11 leatherback turtles during their inter-nesting interval in 2001, 2002 and 2003 (from Fossette et al., 2007; in black).

3.2. Thermal conditions on the Guiana continental shelf

3.2.1. Remotely sensed sea surface temperatures

SSTs measured by satellite in the inter-nesting area (see Materials and methods) ranged from 25.5 °C to 29.5 °C (Fig. 3) and varied among years (Anova, $F_6 = 2497.23$, $P < 0.01$ followed by post-hoc Tuckey test, $P < 0.05$ in all cases; Table 2). Distributions of SST values on the continental shelf and SST values spatially interpolated along the turtles' tracks were statistically different ($\chi^2_6 = 52.2$, $P < 0.01$, Fig. 3).

3.2.2. In situ recorded temperatures

Mean (±S.D.) temperatures recorded by the TDRs were 27.4 ± 0.4 °C at the surface and 26.6 ± 0.7 °C in the water column with a minimum of 22.1 °C and a maximum of 34.7 °C, both experienced by turtle T200101 (Table 1 and Fig. 4). For each turtle in situ temperatures varied throughout the inter-nesting interval (Table 1). The maximum variations were recorded for T200101 with 9.4 °C and 6.5 °C of difference at the surface and in the water column, respectively (Table 1) while the minimum variations were recorded for T200202 with 2.8 °C and 1.8 °C of difference at the surface and in the water column, respectively (Table 1). Fig. 4 illustrates these two different temperature profiles and the corresponding dive profiles: T200101 experienced water column temperature ≤24 °C during

Table 2
Remotely sensed sea surface temperatures on the Guiana continental shelf (coast-7.5°N/55–53°W) for months of May 2001 to 2007.

		May 2001	May 2002	May 2003	May 2004	May 2005	May 2006	May 2007
SST (°C)	Mean ± s.d.	27.4 ± 0.6	27.2 ± 0.6	26.7 ± 0.4	27.3 ± 0.5	28.5 ± 0.3	27.8 ± 0.3	27.7 ± 0.4
	Min/Max	25.7/29.0	25.4/28.4	25.6/28.4	25.7/29.4	27.7/29.8	26.8/29.0	26.9/29.4

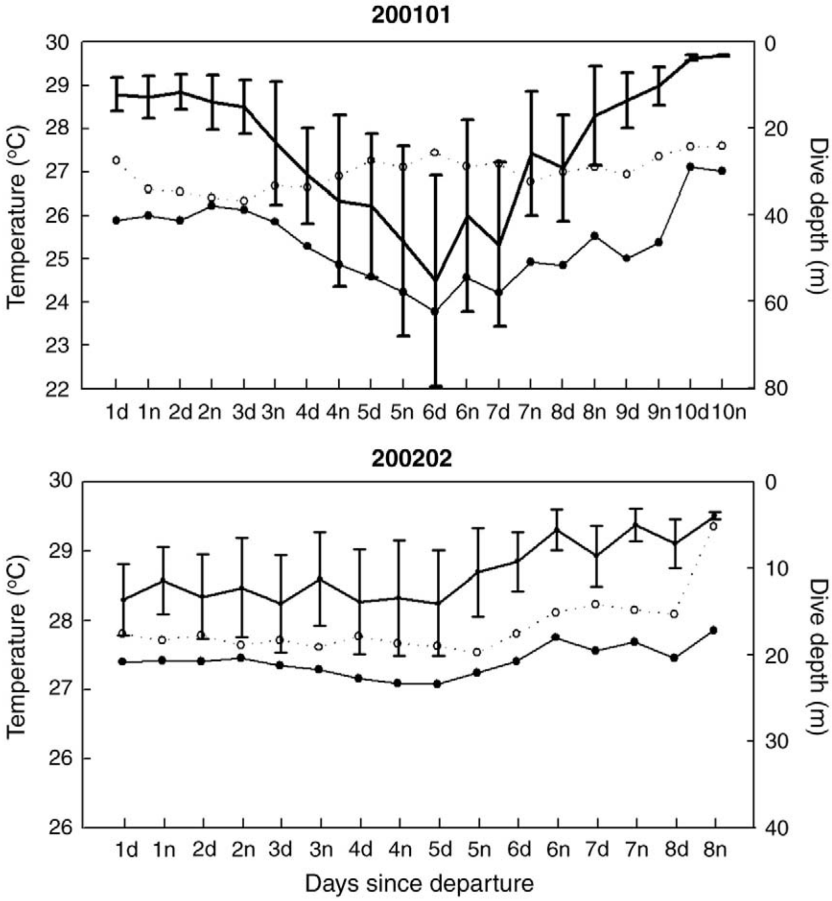

Fig. 4. Dive depth (± S.D.) (solid black line), in situ recorded temperatures (at surface: open circles, in water column: filled circles) throughout the inter-nesting interval for two TDR-equipped leatherback turtles nesting in French Guiana (one in 2001 and the second in 2002).

3.5% (9 h) of her inter-nesting interval when she reached the edge of the continental shelf and dived deeper than 60 m, while T200202 remained in shallow waters >27 °C during her entire inter-nesting interval. The other turtles did not experience water column temperature <25 °C and remained in shallow waters <30 m during their entire inter-nesting interval (Table 1).

3.3. Trophic conditions on the Guiana continental shelf

3.3.1. Jellyfish stranding surveys

A total of 1091 (14.4 ± 22.2 ind/survey) and 7095 (77.1 ± 155.1 ind/survey) jellyfish was recorded between April and July 2005 and 2006 respectively, on Awala-Yalimapo beach (Fig. 5). Daily number of

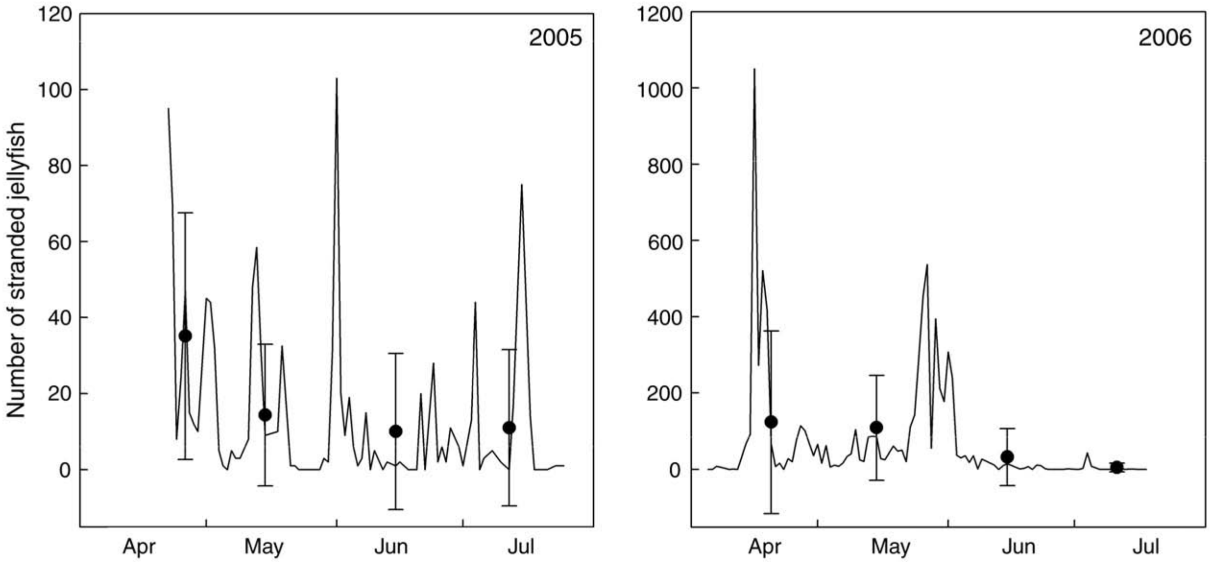

Fig. 5. Daily (solid black line) and monthly (mean ± s.d.: black dots ± error bars) number of stranded jellyfish on Awala-Yalimapo beach between April–July in 2005 ($n = 76$ daily surveys) and April–July in 2006 ($n = 92$ daily surveys).

Table 3
General characteristics of 94 stranded jellyfish randomly sampled on Awala-Yalimapo beach during the 2005–2006 leatherback's nesting season.

Genus	*N*	Size (cm)	Mass (g)
Stomolophus sp.	88	5.9 ± 2.8	32.2 ± 47.2
Aurelia sp.	6	11.2 ± 3.6	127.6 ± 58.5

stranded jellyfish was highly variable during both survey periods, the highest jellyfish stranding occurring in April every year (Kruskal–Wallis, in 2005, $H_{3,76} = 9.33$, $P < 0.05$; in 2006, $H_{3,92} = 29.66$, $P < 0.01$, Fig. 5). Conversely, very few stranding occurred in June and July 2005 and July 2006. Most of the jellyfish observed stranded on Awala-Yalimapo beach during the leatherback nesting season were *Stomolophus* sp. (Agassiz, 1862), and to a lesser extent *Aurelia* sp. (Linnaeus, 1785) and *Physalia physalis* (Linnaeus, 1758). Indeed from the 94 jellyfish randomly collected on the beach, 88 belonged to *Stomolophus* sp., and only 6 to *Aurelia* sp. (Table 3). Compared to *Aurelia* jellyfish, *Stomolophus* jellyfish were on average half the size and almost four times lighter (Table 3).

3.3.2. At sea jellyfish distribution and biomass

Stomolophus and *Aurelia* jellyfish were found in 7 out of the 36 benthic trawls, with a total biomass of 45.4 kg (range: 0.2–30 kg, Table 4, Fig. 2) for 2206 individuals (range: 33–1492 ind per haul, Table 4). Jellyfish biomass significantly increased when water depth decreased (Spearman's rank correlation, $R_s = -0.670$, $n = 36$, $P < 0.01$, Figs. 2 and 6) and turbidity increased ($R_s = 0.673$, $n = 36$, $P < 0.01$, Figs. 2 and 6). Indeed, benthic trawls collected jellyfish exclusively in waters where sea floor depth was between 10 and 20 m and water transparency between 0.8 and 3.0 m (Figs. 2 and 6).

4. Discussion

Foraging temperate habitats of the leatherback turtle have been previously described in terms of environmental temperature and prey distribution using different approaches in order to understand how the ocean environment may drive the spatiotemporal distribution of this species of conservation concern (e.g. Houghton et al., 2006; McMahon and Hays, 2006; Witt et al., 2007). Similar studies have however never been performed in leatherback's tropical nesting areas. In the present study, we described for the first time the trophic and thermal conditions over the French Guiana continental shelf during the nesting season of leatherback turtles, in order to highlight potential links between these environmental parameters and the dispersal and diving patterns of gravid females during their inter-nesting intervals.

Table 4
Jellyfish abundance and biomass in seven benthic trawls of 30 min each performed by a shrimp trawler on the Guiana continental shelf in May 2007.

Trawls	Date/time	Abundance	Total biomass (g)	Individual biomass (g)	Depth (m)
1	12 May 2007, 15:59	82	1800	22.0	14.7
2	13 May 2007, 06:29	33	200	6.1	19.1
3	13 May 2007, 15:58	71	2000	28.2	17.9
4	15 May 2007, 16:22	1492	30,000	20.1	10.7
5	16 May 2007, 10:25	160	3400	21.3	15.4
6	18 May 2007, 12:15	128	3000	23.4	16.8
7	18 May 2007, 15:36	240	5000	20.8	12.8
Total		2206	45,400		
Mean ± SD		315 ± 523	6486 ± 10475	20.3 ± 6.8	15.3 ± 2.9

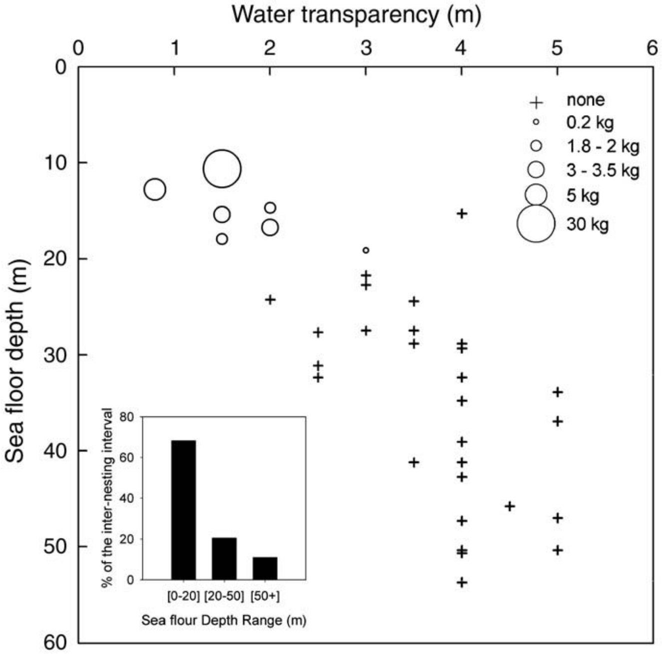

Fig. 6. Relationship between jellyfish biomass, water transparency and sea floor depth obtained from random bottom trawling between 10 m and 55 m depth on the Guiana continental shelf by a shrimp trawler in May 2007. Trawling with successful and unsuccessful jellyfish sampling is represented by circles and crosses, respectively. The size of each circle indicates the jellyfish biomass. Insert: percentage of time spent by leatherback turtles ($n = 11$; Argos tracked leatherback turtles nesting in French Guiana between 2001 and 2003) at different depths during the inter-nesting intervals on the Guiana continental shelf.

Over the inter-nesting area, remotely sensed SST was relatively warm even though slightly variable among years (2001 to 2007) during the leatherback's nesting season, as previously reported at a larger scale by in situ oceanographic study (Frouin et al., 1997). Frequency distributions of SSTs within the area and along the turtles' tracks were however different, suggesting that gravid leatherbacks preferentially explore the warmest areas on the Guiana continental shelf (i.e. with surface temperatures comprised between 27.0 °C and 28.5 °C). In situ water column temperatures obtained by animal-borne recorders were also variable among turtles. Indeed, leatherback turtles that remained during their entire inter-nesting interval in shallow waters (<30 m deep) close to the shore (this study and Fossette et al., 2007) experienced relatively warm environment (>25 °C) throughout the entire water column, while turtles that explored deeper waters at the edge of the continental shelf (this study and Fossette et al., 2007) experienced a wider range of temperatures in the water column (down to 22 °C). This suggests that, in French Guiana, during an inter-nesting interval, leatherbacks may easily reach different thermal environments. Nevertheless, this study shows that in fact most of the leatherbacks rarely experience cool waters and remain in the warmest environment close to the shore in front of the Maroni River estuary.

This contrasts with studies on the Pacific coast of Costa Rica where leatherbacks have been reported to spend relatively more time in cool waters <24 °C (on average 9.5 ± 5.8%, and up to 19.0% of their time; Wallace et al., 2005) than in French Guiana (0.5 ± 1.3%, and up to 3.5% of their time, this study). Yet, leatherback turtles experience similar average temperatures in French Guiana and Costa Rica (26.6 ± 0.7 °C this study *vs* 25.9 ± 1.4 °C Southwood et al., 2005). In Costa Rica, leatherbacks have been reported to reduce activity levels while commuting between habitats of contrasted water temperatures to potentially avoid overheating and have relatively reduced energy expenditures during the inter-nesting interval (Wallace et al., 2005). If that was the case, this suggests that there may be some physiological advantages for gravid leatherbacks to use different thermal environments when possible. In French Guiana the situation is however different since most of the leatherbacks remained in warm waters close to the shore (this study) and actively swim during their entire inter-nesting interval (Fossette et al., 2007) while they could easily shuttle to different thermal environments. In French Guiana, coastal waters are strongly influenced by enormous fresh water discharge from the adjacent rivers (Baklouti et al., 2007). By aggregating off the mouth of the Maroni river, gravid leatherbacks may thus extract the large amounts of water they need to produce eggs (Ackerman, 1997) directly from brackish water. This may be less energy consuming than drinking sea water. Females may also stay in warm waters for speeding up egg maturation as previously reported for loggerhead turtles (Schofield et al., 2009). Another possibility for gravid female turtles to actively explore warm coastal waters is that they may be able to take advantage of favourable local food resources, illustrated by the abundance of jellyfish stranded and at sea, as detailed below.

Beach stranding events have been previously used as a qualitative index of the in-water presence and seasonality of jellyfish (e.g. Doyle et al., 2007a; Houghton et al., 2007). Indeed, Houghton et al. (2007) used beach stranding data to elucidate the foraging ecology of leatherback sea turtles in temperate latitudes. In our tropical study site, three species of jellyfish commonly eaten by leatherbacks, namely *Stomolophus* sp., *Aurelia* sp. and *P. physalis* (Bjorndal, 1997; Cogger, 2000; James and Herman, 2001) stranded during the leatherback's nesting season, with the largest stranding recorded occurring in April, i.e. one month before the peak of leatherback's nesting activity. There was however large stranding also throughout the entire nesting season. These land-based observations indicate that jellyfish occur in waters immediate to the leatherback's nesting site and therefore could provide a suitable prey field to exploit during their nesting season. Consuming iso-osmotic organisms occurring in brackish waters like jellyfish in French Guiana may also help leatherbacks with their important water need during the nesting season. The hypothesis of leatherback turtles foraging during the nesting season is supported by their active, extended swimming and diving behaviours (Fossette et al., 2007, 2008a). However, it has to be noticed that in French Guiana, jellyfish species are smaller and apparently in lower densities than species usually eaten by leatherbacks at higher latitudes (Doyle et al., 2007b; Houghton et al., 2007). Therefore, even if turtles may find complementary food supply in their breeding site, local trophic conditions do not appear to be sufficient to sustain the high demands associated with reproduction (and the higher density of turtles), compared to higher prey densities leatherbacks do encounter during their migrations (Hays et al., 2004). Indeed, body mass of leatherbacks declines between high latitude foraging areas and nesting sites highlighting the absolute necessity of the migration to the foraging grounds at the end of the breeding season (James and Mrosovsky, 2004). Our observations also show important daily, monthly and annual variations in the number of stranded jellyfish on Awala-Yalimapo beach. These results, however, should be considered with caution since stranding events strongly depend on coastal currents: an absence of jellyfish stranding does not necessarily imply that they are absent from the water column (Doyle et al., 2007a; Houghton et al., 2007).

In addition to the beach stranding events of jellyfish, Continuous Plankton Recorder Survey data may be used in the NE Atlantic for constructing landscapes of gelatinous organism distribution and thus identifying probable foraging grounds for leatherback turtles in high latitudes (Witt et al., 2007). Such data are not available in leatherback's tropical nesting areas. In this study, benthic trawls conducted over the Guiana continental shelf complemented our land-based observations. Indeed, this offshore survey allowed us to detect the presence of jellyfish (mainly *Stomolophus* sp.) in the shallowest (between 10 and 20 m) and most turbid coastal waters. These waters influenced by both local rivers and Amazon river were previously refereed as productive “green” and “beige” waters (Froidefond et al., 2002). In contrast, no jellyfish were collected over deeper seabed in clearer waters. It is worth noting that the bottom trawling probably underestimated the actual jellyfish abundance on the Guiana continental shelf since the gear mainly sampled the bottom of the water column even though some jellyfish might be caught in the rest of the water column while the net is returning to the surface. Therefore, benthic trawl surveys confirm the presence of leatherback's jellyfish prey on the Guiana continental shelf, in particular in shallow and turbid waters, but abundance and distribution estimations should be taken with caution. Our results are however in accordance with previous studies reporting gelatinous plankton in coastal and estuarine waters (e.g. Arai, 1992; Cabreira et al., 2006; Houghton et al., 2006; Doyle et al., 2007a; Houghton et al., 2007), including on the bottom (e.g. Alvarez Colombo et al., 2003). For instance, high concentrations of Rhizostome jellyfish (which includes *Stomolophus* sp.) have been previously associated with brackish waters (Perez-Ruzafa et al., 2002).

In addition, no jellyfish were found during benthic trawls carried out during the dry season when the turbidity of the waters and the Amazon influence are low (F. Blanchard, unpublished). This suggests that the flow of local rivers may influence the development of jellyfish in the area, probably through modifications of turbidity and/or salinity conditions on the Guiana continental shelf during the leatherback's nesting season.

Interestingly, leatherbacks clearly focused their activity during their inter-nesting intervals off the mouth of the Maroni River (this study, Fossette et al., 2007; Georges et al., 2007) where they performed bottom dives, interpreted as foraging dives (Fossette et al., 2007, 2008a). Although our results should be interpreted with caution since trawl surveys were not conducted in the river mouth itself, nor during the same years as the turtle's tracking, they suggest that in French Guiana, the gelatinous prey are notably present in shallow waters close to the nesting site and may be easily exploited by active gravid leatherbacks. Indeed leatherbacks may locate prey even in turbid coastal waters by using buccal pumping during dive (Myers and Hays, 2006; Fossette et al., 2008a). In addition, it has been recently suggested that gravid leatherbacks may adopt an optimum search strategy, where successive dive depths follow a mathematical distribution, in order to locate prey that are patchily distributed in the water column (Sims et al., 2008). This suggests that in French Guiana female leatherbacks may actively forage in warm productive areas where coastal fisheries also operate. In comparison, the low level of activity reported for leatherbacks in Costa Rica (Wallace et al., 2005) may be related to limited food availability. Unfortunately, to date, trophic context has not been investigated there. It is worth noting that it is now possible to directly track jellyfish and precisely record their depth (Hays et al., 2008) which will allow a better understanding of the linkages between turtle diving behaviour and jellyfish depth distribution.

Given the potentially environmentally-mediated strategies leatherbacks may adopt in the different nesting sites, and given the context of accelerated climate change and overfishing resulting in major shifts in marine ecosystems toward jellyfish dominance of food web (e.g. Purcell, 2005; Lynam et al., 2006; Attrill et al., 2007), a better understanding of the trophic relationships centred on jellyfish and jellyfish predators, such as the leatherback, is crucially required for ensuring the sustainability of marine resources. Novel tracking technologies such as fastloc GPS loggers by improving accuracy in tracking marine species (Schofield et al., 2007) will surely help to manage such studies and thus to resolve the underlying patterns of movement in great detail. This may notably highlight typical searching behaviour (e.g. Sims et al., 2008) and allow a better understanding of prey–predator relationships.

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The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay

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Poulard, J-C., and Blanchard, F. 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. – ICES Journal of Marine Science, 62: 1436–1443.

Many fish species are at the southern or northern limit of their distribution range in the Bay of Biscay, where large-scale hydroclimatic changes have occurred in recent decades. We attempt here to identify the impact of these changes on the fish community of the eastern continental shelf of the Bay of Biscay. Data collected during 14 autumn groundfish surveys in 1973 and from 1987 to 2002 are used. The study area is between latitudes 48°30′N and 43°30′N while the depth ranges from 15 to 200 m. Annual abundance indices (number of individuals per km^2) of 56 fish taxa present on average in at least 5% of the tows are computed. Multivariate analysis is used to detect temporal trends in these species' abundance indices. Assuming that increased water temperature may favour subtropical species and hinder temperate ones, knowledge about the latitudinal distribution range is used to interpret time trends. Results show an increasing abundance trend with time for fish species having a wide distribution range in latitude (mainly subtropical ones), whereas the abundance of temperate and the least widely distributed species decreased steadily.

Keywords: Bay of Biscay, climate change, fish community, groundfish surveys.

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Introduction

Large-scale changes in the biogeography of calanoid copepods have been reported for the eastern North Atlantic and European shelf seas (Beaugrand *et al.*, 2002). Strong biogeographical shifts in all copepod assemblages have occurred with a northward extension of warm-water species associated with a decrease in the number of colder-water species. These biogeographical shifts were related to increasing trends in both northern hemisphere temperature and the North Atlantic Oscillation.

Northward extensions in the distribution of tropical fish species in East Atlantic waters have been recorded (Quéro, 1998). Further evidence was provided that warming of the North Atlantic is responsible for the northward extensions of the ranges of warm-water fish species, causing increasing numbers of southern immigrant species to appear off the Cornish coast of the UK (Stebbing *et al.*, 2002).

The existence of a long-term increasing trend in sea surface temperature (a mean rise of 1.4°C for the period 1972–1993) was confirmed for the southeastern part of the Bay of Biscay (Koutsikopoulos *et al.*, 1998). Reviewing the multi-decadal variations of three key regional climate and hydrological factors (sea surface temperature, windspeed, and river run-off), Planque *et al.* (2003) showed that the 1990s were characterized by warmer temperature (up to 0.6°C increase per decade from 1971 to 1998 in the southern part of the Bay) and windier conditions than the previous century. Désaunay *et al.* (in press) demonstrated that although the increase of sea temperature is lower in the northern part of the Bay of Biscay, a significant warming of winter temperatures occurred.

The eastern continental shelf of the Bay of Biscay is part of the subtropical/boreal transition subprovince of the biogeographic Lusitanian province (OSPAR Commission, 2000). The fauna in this area are mixed with groups of boreal and subtropical origin and many fish species reach the southern or northern limit of their distribution in the Bay of Biscay.

Community studies in regions of overlapping "polar" and "temperate" species base the conclusion of climate change impacts on the differential response of these two categories to warming conditions (Parmesan and Yohe, 2003). Polar species tend to be stable or decline in

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abundance, whereas temperate species at the same site increase in abundance and/or expand their distributions.

In this study, we use this approach to identify the impact on the fish community of warming in the Bay of Biscay. For this, data provided on 56 fish taxa by groundfish surveys carried out in 1973 and during the period 1987−2002 were analysed. Previous work (Poulard *et al.*, 2003) showed the relative stability through time of the spatial demersal fish community organization. Thus, we have chosen to focus the present study on temporal variations.

Material

Data were first collected during a groundfish survey carried out in November and December 1973 on the eastern continental shelf of the Bay of Biscay (Quéro *et al.*, 1989). Data were also provided by 13 groundfish surveys carried out by IFREMER since 1987 (EVHOE series with gaps in 1991, 1993, and 1996) in the same area from October to December (ICES, 1997; Souissi *et al.*, 2001; Poulard *et al.*, 2003). The sampling design was stratified according to latitude and depth. A 36/47 GOV trawl was used with a 20 mm mesh codend liner. Haul duration was 30 min at a towing speed of 4 knots. Fishing was mainly restricted to daylight. Catch weights and catch numbers were recorded for all species; all finfish were measured from 1992, while length compositions of a selection of them were recorded prior to 1992.

The study area was restricted in latitude (between 48°30′N and 43°30′N) and depth range (from 15 to 200 m) to the area sampled in 1973 (Figure 1). The number of hauls per survey varied from 56 to 154. Overall 1279 hauls were analysed. In all, 168 were caught, but only 56 fish taxa, present on average in at least 5% of the tows, were included in the analysis.

Methods

Mean catch per tow was computed per species and per year accounting for the stratified sampling design. Annual abundance indices were then normalized to maximum species-specific numerical abundance. The chosen normalization allows the same weight to be assigned to each

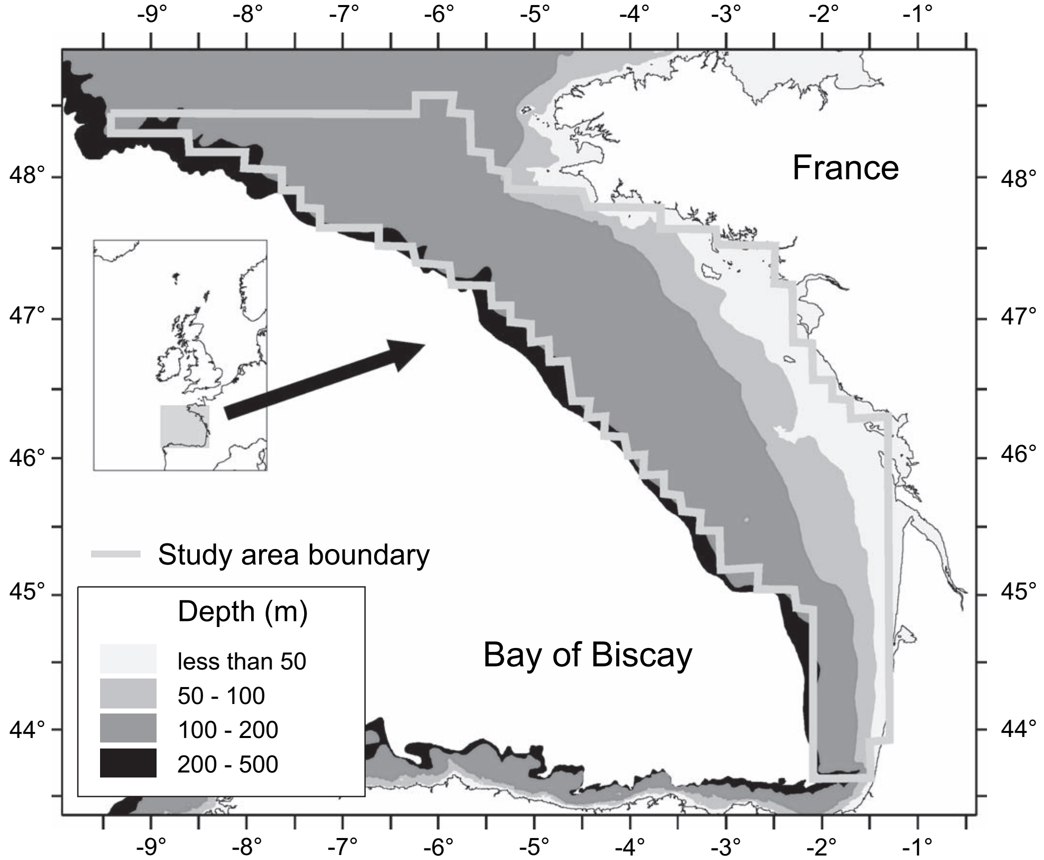

Figure 1. Area of the eastern continental shelf of the Bay of Biscay studied during the 14 groundfish surveys carried out by IFREMER from October to December, in 1973, from 1987 to 1990, in 1992, 1994, 1995 and from 1997 to 2002.

species in the following multivariate analysis. This objective is not achieved by using a log-transformation of the data. Standardized annual abundance indices were used as input in a correspondence analysis (Lebart *et al.*, 1984) to detect time trends in the fish abundance indices. The variables (columns) were the years and the profiles (rows) were the species.

Latitudinal distribution ranges of species were used to interpret the temporal trends. The latitudinal range and its midpoint have been defined for each species considering the most northern and southern latitudes reported in the literature (Whitehead *et al.*, 1986; Froese and Pauly, 2004). Latitude ranges and mean latitudes of species distributions were transformed into nominal variables by creating four equiprobable categories. This additional information is used as supplementary (or illustrative) variables that are projected into the space of the data but are not used to compute the factors of the correspondence analysis.

Overall mean length, weighted by species abundance, was computed per year from the species mean length in the survey of the year. Prior to 1992, when data on length were missing, the species mean length, computed over the available years, was used.

The species trophic levels used were those provided by Pinnegar *et al.* (2002) for the Celtic Sea, complemented by Fishbase (Froese and Pauly, 2004). The overall mean trophic level, weighted by species abundance, was computed per year.

A locally weighted regression smoother (Cleveland, 1979) was fitted to the survey species biomass for visualizing trends, and the associated 95% confidence limits were also computed. LOESS (local regression) is a method for smoothing a scatterplot ((x_i, y_i) with $i = 1, \ldots, n$). To fit a value at x_k, a window is placed about x_k; data points that lie inside the window are weighted so that nearby points get the most weight and a robust weighted regression is used to predict the value x_k (Venables and Ripley, 1994). To test for significant long-term trends in survey data, non-parametric Mann–Kendall tests were performed (Gilbert, 1987). Differences were judged significant when $p < 0.05$.

Results

The first two axes of the correspondence analysis account for 35% of the total variance. The first axis divides the study period into two parts (Figure 2): the years from 1973 to 1995 have positive coordinates on this axis, while those from 1997 to 2002 have negative ones. This contrast between years indicates that two main opposite trends can be identified in the species abundance indices. Species located on the right

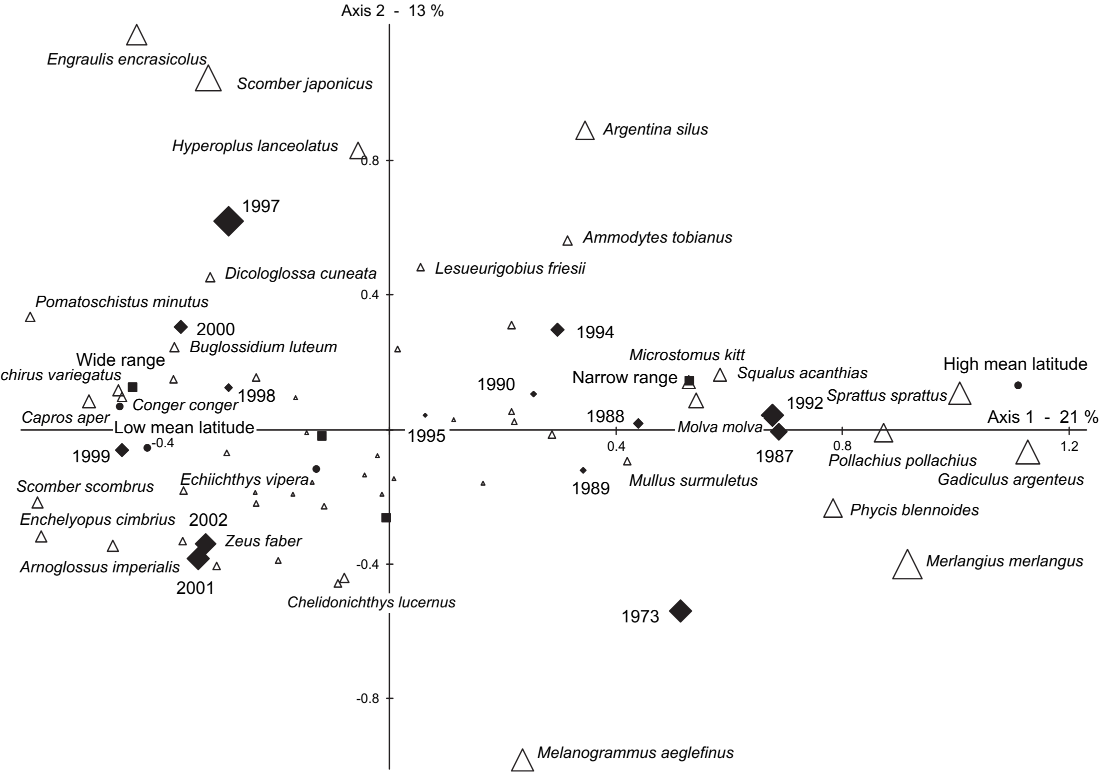

Figure 2. Correspondence analysis, projection of the 14 active variables (◆ years), two illustrative variables (● mean latitude category of species latitude distribution, ■ range category of species latitude distribution), and the 56 individuals (△ species) in the principal plane (first and second axes plane). Symbol size is proportional to the contribution of years or species to the building of axes.

side of the first axis show a declining trend over the study period, while species having negative coordinates on the first axis exhibit an increasing trend (Figure 3).

The second axis takes into account the changes in the species abundance indices occurring mainly between 1997 and 2002. The second axis is particularly explained by species like *Engraulis encrasicolus* and *Scomber japonicus,* which had high abundance indices in 1997 and low ones in 2001 and 2002.

The two extreme categories of the illustrative variable "species range" (i.e. wide range and narrow range, Figure 2) and those of the illustrative variable "mean latitude" (i.e. low mean latitude and high mean latitude, Figure 2) have significant coordinates on the first axis.

Two species groups can be identified from the species abundance trends observed over the study period. First, abundance indices declined or fluctuated for 20 species (group A). More than one-third of these species had a narrow range in latitude distribution and a high mean latitude distribution (Table 1). Second, abundance indices increased for 36 species (group B). One-third of these species had a wide range in latitude distribution and a low latitude distribution mean.

Changes in biomass over years for the two groups of species are illustrated in Figure 4. The biomass of group A is especially variable from one year to another and does not exhibit any trends over the study period. On the contrary, the biomass of group B shows an increasing trend from 1987 to 2002 (Mann–Kendall S = 52, $p < 0.0001$), even when the less precise values of the years 1999 and 2002 are not considered (Mann–Kendall S = 39, $p = 0.002$).

The biomass was computed per species range category given in Table 1. For the species of group A, the biomass of the narrowest range and the most northern species (species range category 1) declined significantly from 1987 to 2002 (Mann–Kendall S = −42, $p = 0.01$; Figure 5a). There was no significant trend for the other species range categories. The main species contributing to about 90% of the biomass of the group in 1973 and during the period 1987–2002 are listed in Table 2. Blue whiting (*Micromesistius poutassou*) replaced poor cod (*Trisopterus minutus*) as a dominant species throughout the period 1987–2002, and hake (*Merluccius merluccius*) and whiting (*Merlangius merlangus*) lost their second and fourth ranks, respectively.

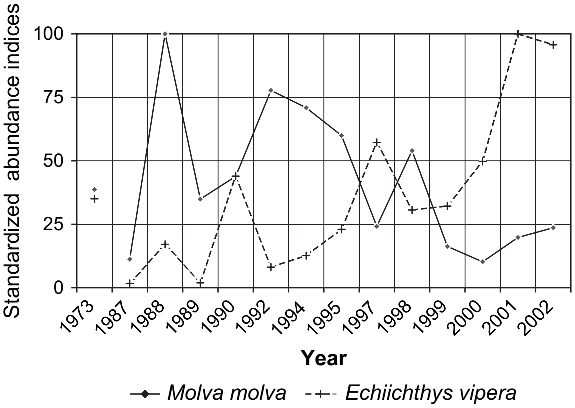

Figure 3. Examples of distribution of standardized abundance indices for species having negative (*Echiichthys vipera*) or positive (*Molva molva*) coordinates on the first axis of the correspondence analysis (see Figure 2).

Table 1. Composition of the two species groups identified from the correspondence analysis (CA) results according to the two nominal variables: mean latitude and species range. Number of species per species group, per category of latitude range and of mean latitude. The categories are those used in the CA, except that the two middle ones for each variable were pooled.

	Mean latitude (in degrees of latitude)		Species range (in degrees of latitude)			
	Category	Limits	1	2	3	
Species group			[20–40[	[40–67[	[67–127]	Total
A	1	[2.5–28[	0	0	2	2
	2	[28–47.5[	2	5	0	7
	3	[47.5–60]	7	4	0	11
		Total	9	9	2	20
B	1	[2.5–28[	0	1	12	13
	2	[28–47.5[	5	15	0	20
	3	[47.5–60]	2	1	0	3
		Total	7	17	12	36

In species group B, both species range categories 2 and 3 increased significantly from 1987 to 2002 (Mann–Kendall S = 52, $p < 0.0001$ and S = 40, $p = 0.01$, respectively; Figure 5b). Although horse mackerel (*Trachurus* spp.) remained at the first rank, there were several changes at the lower levels (Table 2). The three benthic species, red gurnard (*Chelidonichthys cuculus*), anglerfish (*Lophius piscatorius*), and cuckoo ray (*Leucoraja naevus*) present within the first five ranks in 1973, were replaced by a small demersal species, boarfish (*Capros aper*), and two pelagic species, mackerel (*Scomber scombrus*) and sardine (*Sardina pilchardus*), during the period 1987–2002.

The mean length of species group A (Figure 6) declined steadily from 1987 to 1990 and exhibited an increasing trend later (Mann–Kendall S = 20, $p = 0.044$). The mean length of species group B decreased sharply from 1990 to 1994 and, although variable, remained at a low level during the following years.

The mean trophic level of species group A (Figure 7) declined significantly from 1973 to 2002 (Mann–Kendall S = −45, $p = 0.01$). The main change occurred between 1973 and the period 1987–2002 and was caused by the relative biomass increase of the blue whiting feeding at a low

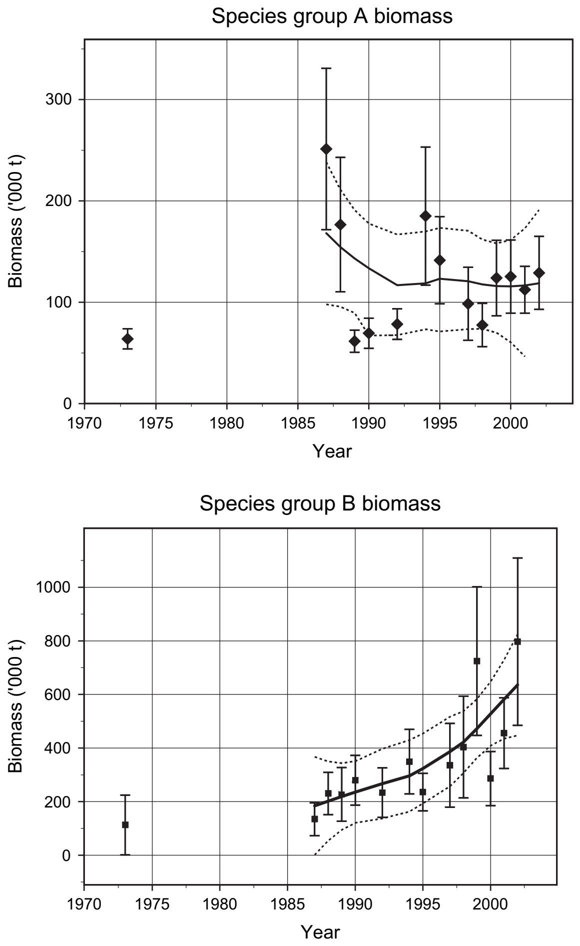

Figure 4. Evolution of the biomass of the two species groups identified from their coordinates on axis 1 of the correspondence analysis. Species group A includes a significant proportion of species with a narrow distribution range in latitude and a high mean latitude distribution. Species group B includes a significant proportion of species with a wide distribution range in latitude and a low mean latitude distribution.

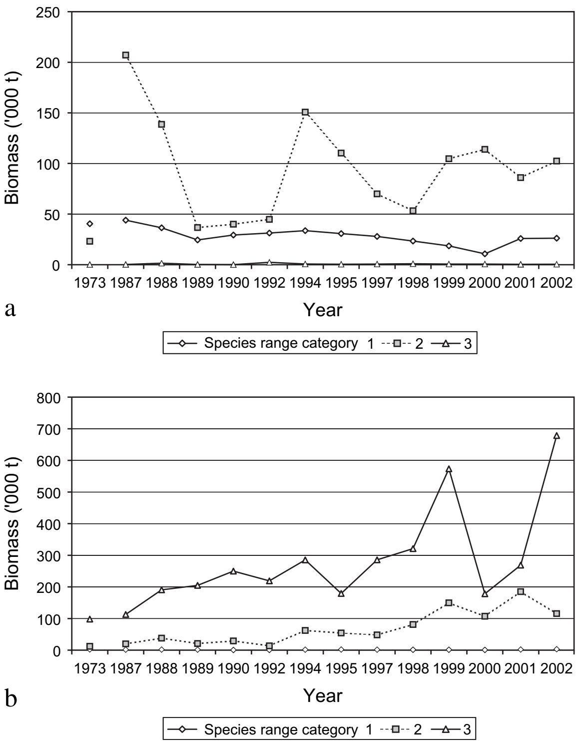

Figure 5. Biomass of the two species groups identified from their coordinates on axis 1 of the correspondence analysis (see Figure 4) broken down per species range category.

trophic level. The mean trophic level of species group B (Figure 7) was rather stable until 1992 and became especially variable afterwards. Its decline in some years was largely due to increased catches of boarfish which feeds at a lower trophic level than the other species occupying the first five ranks of the species group B (Table 2).

Discussion

In the group of species showing a declining trend of their abundance indices, seven (i.e. about one-third of the group) have a northerly distribution and a narrow latitude distribution range. The biomass of these boreal species declined during the study period, whereas the total biomass of other species (mainly transition species) varied from one year to another without trend.

Twelve species (i.e. one-third of the species) of the group exhibiting an increasing trend of their abundance indices are characterized by a southern distribution and wide species range. The biomass of these subtropical species increased from 1987 to 2002, like the biomass of transition species.

The decrease of the mean length of the "boreal" species group (A) between 1987 and 1990 was related to the decline in biomass of the transition species (range category 2; Figure 5a). Recruitment of several species (silvery pout *Gadiculus argenteus*, poor cod, bib *Trisopterus luscus*, hake, and blue whiting) increased sometimes at the same moment during the period 1990–1995, which also facilitated the lowering of the mean length of group A. Its following increase was mainly due to continuous weaker recruitment. The sharp decrease in mean length of "subtropical" species group (B) was due to an increase in the abundance of small fish species (e.g. boarfish, Mann–Kendall $S = 59$, $p < 0.0001$; imperial scaldfish *Arnoglossus imperialis*, Mann–Kendall $S = 59$, $p < 0.0001$) combined with an increase of the recruitment of some other species (e.g. wedge sole *Dicologlossa cuneata*, Mann–Kendall $S = 45$, $p = 0.01$).

Table 2. Dominant species per group during the groundfish surveys carried out in 1973 and over the period 1987−2002 on the eastern continental shelf of the Bay of Biscay. Two species of horse mackerel have been caught (*Trachurus trachurus*, the bulk of the catch, and *T. mediterraneus*) but due to mistakes in the allocation to species in the recent surveys they were pooled.

	Groundfish surveys			
	1973		1987−2002	
Group	Species	% Biomass	Species	% Biomass
A	*Trisopterus minutus*	50	*Micromesistius poutassou*	60
	Merluccius merluccius	17	*Trisopterus minutus*	17
	Trisopterus luscus	12	*Trisopterus luscus*	7
	Merlangius merlangus	9	*Merluccius merluccius*	6
B	*Trachurus* spp.	84	*Trachurus* spp.	75
	Chelidonichthys cuculus	2	*Capros aper*	8
	Lophius piscatorius	2	*Scomber scombrus*	5
	Scyliorhinus canicula	2	*Sardina pilchardus*	4
	Leucoraja naevus	2	*Scyliorhinus canicula*	1

In the absence of time-series isotope data from the study area, we obtained our trophic level values from the literature. For most of the fish species, the diet may vary according to length. Therefore, the values used were probably not the most suitable, given potential differences in length compositions between the Celtic Sea and our study area. For instance, the horse mackerel trophic level was calculated for fish having a mean length of 347 mm (Pinnegar *et al.*, 2002), while the mean length of horse mackerel in our surveys was 172 mm. We also assume that species trophic levels are stable from year to year. Nevertheless, there are some indications that trophic levels of both species groups have decreased in recent years (the lowest values of both groups were recorded in 2000). Warm-water species seem to be responsible for the decrease of individual size and trophic level in the fish community. Our results point to a causal link between the observed changes in the fish community of the eastern shelf of the Bay of Biscay and ocean warming.

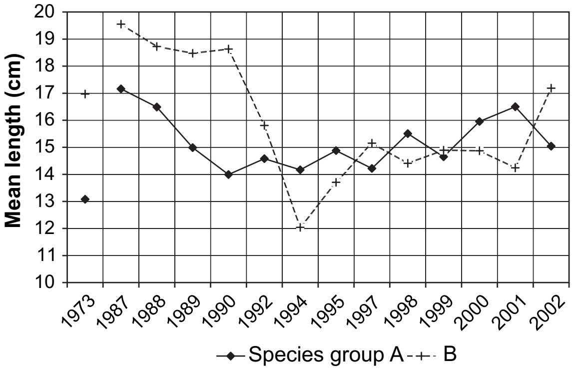

Figure 6. Mean lengths of the two species groups identified from their abundance trends in groundfish surveys over the period 1973−2002.

Records of rare tropical fish on the eastern continental shelf of the Bay of Biscay are not recent, although their number has increased since 1980, mainly in the southern part of the area (Quero *et al.*, 1998). Likewise, the climate-induced changes in the abundance of four common flatfish species were demonstrated for the Vilaine estuary and the Bay of Biscay (Désaunay *et al.*, in press).

Changes occurring in the fish community are not important enough to have had an effect on the spatial organization level of the demersal fish community (Poulard *et al.*, 2003) even if there is positive correlation between the species abundance indices and the species occurrences in the catches of the same survey (correlation equal or greater than 0.5 for nine surveys out of 14, results not shown). This means that the spatial distribution of a species usually increases when its abundance increases, and the converse is usually also true.

Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local short-term biological changes (Parmesan and Yohe, 2003). Changes which have occurred in species composition and trophic level of the "boreal" species group (A) after 1973 could be attributed to fishing (Pauly *et al.*, 2001). Indeed, hake, bib, and whiting contribute significantly to the French landings of demersal fish species coming from the eastern continental shelf of the Bay of Biscay (Poulard and Léauté, 2002). Part of their diet consists mainly of fish. Also, a release from predation may occur and account for an increase in dominance of smaller/lower trophic level species. The predation release will interact with climate warming, favour subtropical species, and is thought to have a major impact on low trophic level pelagic fish abundances (Pinnegar *et al.*, 2002).

There were changes in the sampling procedure of the groundfish surveys and, above all, trawling operations were carried out with a new research vessel from 1997 onwards

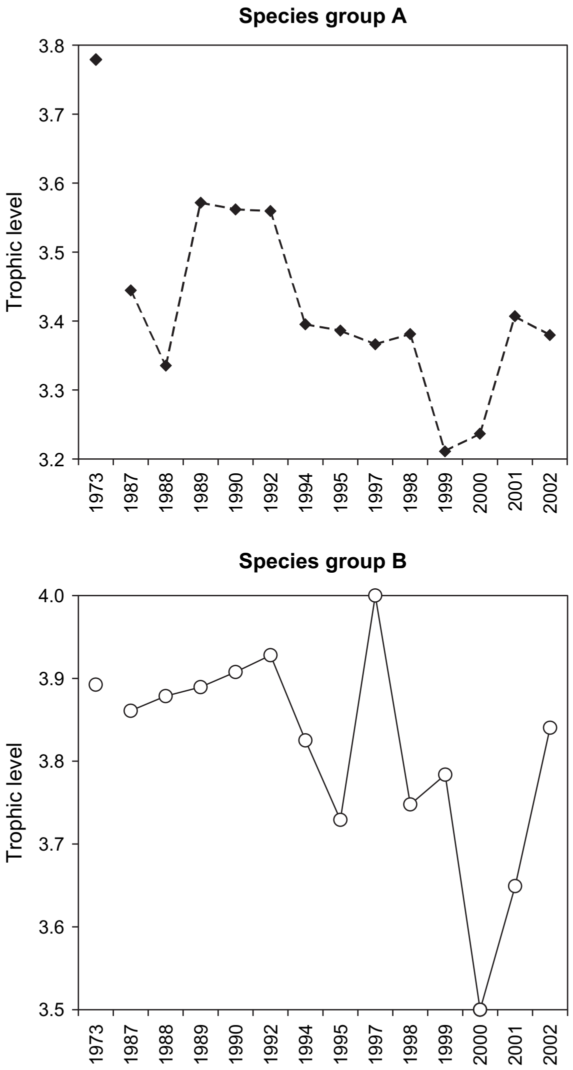

Figure 7. Patterns of change in mean trophic level for the two species groups identified from their abundance trends in groundfish surveys over the period 1973−2002.

(Poulard *et al.*, 2003). Unfortunately, there was no intercalibration experiment between the two research survey vessels in the Bay of Biscay. Conversion coefficients were available for some species from experiments carried out in the North Sea and the Celtic Sea (Pelletier, 1998). Generally, using these coefficients did not modify the observed species trends and sometimes reinforced them. In fact, most of the changes in the species abundance indices took place around 1994−1995 when the old research vessel was still being used. The position of the year 1995 on the first axis of the AFC (Figure 2) supports this interpretation.

This study does not establish a strong relationship between climate warming and changes in the fish community of the eastern continental shelf of the Bay of Biscay. However, we bring together a body of proof indicating that some climate-induced changes may have occurred, which could have been amplified by fishing.

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Ecology / Écologie

Warming and exponential abundance increase of the subtropical fish *Capros aper* in the Bay of Biscay (1973–2002)

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Abstract

The exponential abundance increase of a sub-tropical species, boarfish (*Capros aper*), as well as the sea bottom temperature increase in the continental shelf of the Bay of Biscay (France) over the three last decades are reported. This species was rare in the seventies and is now a dominant one. This is a small bathy-demersal, probably short-lived species with few predators (probably because of the presence of strong spines) and not exploited by fisheries. In the same time, a significant temperature increase in the bottom waters is observed during the breeding season of this population. The boarfish abundance increase is related to the warming, its ability to invade and the absence of predators as well as the absence of fishing. ***To cite this article: F. Blanchard, F. Vandermeirsch, C. R. Biologies 328 (2005).***

Résumé

Réchauffement et accroissement exponentiel de l'abondance du poisson subtropical *Capros aper* dans le golfe de Gascogne (1973–2002). L'abondance d'une espèce subtropicale de poisson, le sanglier (*Capros aper*) a augmentée de façon exponentielle au cours des trois dernières décennies dans le golfe de Gascogne (France). Dans les années 1970, cette espèce était rare ; elle est maintenant devenue une espèce dominante (c'est-à-dire parmi les plus abondantes). Il s'agit d'une espèce de petite taille, probablement à faible longévité, rencontrant peu de prédateurs (vraisemblablement à cause de la présence d'épines dorsales très dures) et non exploitée par les pêcheries. Dans le même temps, une augmentation significative de la température de fond est observée pendant la période de reproduction de la population. L'augmentation d'abondance est interprétée par l'effet du réchauffement, la capacité de colonisation rapide de l'espèce et l'absence de prédateurs (y compris les pêcheries). ***Pour citer cet article : F. Blanchard, F. Vandermeirsch, C. R. Biologies 328 (2005).***

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Keywords: Climate warming; Bay of Biscay; Boarfish

Mots-clés : Réchauffement climatique ; Golfe de Gascogne ; Sanglier

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1. Introduction

The temperature of the upper 300 m of the North Atlantic increased by over 0.4 °C in the two last decades [1]. Correlatively, in the eastern North Atlantic, evidences of northward shifts were brought for fish species [2–4]. At the more local scale of the Bay of Biscay (France), a warming of the sea-surface temperatures was observed [5]. The Bay of Biscay is the subtropical boreal transition subprovince between the Atlantic boreal province and the northern subtropical subprovince, so life may respond rapidly to small shifts in climate. Some first evidences of changes at the aggregate level of the demersal fish community of the continental shelf of the Bay of Biscay have been brought recently [6]. Abundance trends for flatfish species were also reported [7]. The present warming in temperate areas could increase the breeding success for subtropical species. However, the existence of such causal relationships between warming and increase of abundance remains hypothetical, because the biological changes observed concerned species living at the bottom, while bottom-temperature variations have never been analysed on the continental shelf. Hence we do not know if warming spread through the water column. Moreover, fishing effects on species abundance may be a confounding factor when analysing biological changes induced by climate.

Abundance increase of a small bathy-demersal subtropical species, the boarfish *Capros aper*, was observed from Plymouth westwards (UK) during 9 years, between 1870 and 1879, while this species was one of the rarest fish species in these waters before 1870 and after 1879 [8]. Climate events were advocated to explain this phenomenon. More recently, in the western coast of Portugal, an increase of the abundance of the boarfish between 1980 and 1990 has been reported when the warming began to be observable there [9]. Climate change may then have some impact of this fish population dynamics. Our objectives are to test whether the abundance of boarfish has increased in the Bay of Biscay during the three last decades and whether a warming may be observed also at the bottom (a warming of the sea-surface temperature is already known) during the breeding period to explain the abundance increase.

2. Materials and methods

2.1. Elements of the boarfish biology

Very few information on the biology of boarfish was available. In the Irish Sea, this species were not studied (Minchin, comm. pers.). In the Portuguese waters, some recent works on the boarfish biology were carried out, but mainly on diet [10]. Some aspects of the biology of this species were described in the fish fauna [11]. Boarfish is found in the eastern Atlantic, from western Norway, Skagerrak, Shetlands and western Scotland to Senegal and also in the western Mediterranean Sea. Characteristic morphological traits are the presence of really strong dorsal and anal spines and its deep red colour. Reported sizes are usually 5 to 13 cm up to 16 cm. Longevity and ages are unknown. This is a gregarious species that forms schools, found over rock or coral and sometimes over sandy ground mainly at 100–300-m depth. In the southwestern Ireland waters, where it reproduces in summer (June–August), boarfish feeds on crustaceans. Moreover, boarfish is rarely reported as a prey in the stomach content analyses of the main predators. Actually, boarfish is not found in the stomach contents of hake, *Merluccius merluccius*, analysed in the Bay of Biscay [12,13]. *Capros aper* is a prey of *Conger conger* and of *Phycis phycis* off the Azores [14]. Diet of these two last predators remains unknown in the Bay of Biscay. More analyses would be needed to identify the existence of potential competitors in the Bay of Biscay. This species was exploited by Portuguese fisheries in the waters of Portugal (Hill, comm. pers.) during the 1960s, but not in the Bay of Biscay.

2.2. Abundance

The data used were collected during 12 autumn groundfish surveys carried out by IFREMER from

15-m up to 450-m depth on the eastern continental shelf of the Bay of Biscay (43°30′N to 48°30′N) from 1987 to 2002 and from 15-m up to 200-m depth in 1973 and 1992. In 1973, 1987 to 1990, in 1992, 1994 and 1995 the oceanographic vessel *Thalassa 1* was used, whereas the new *Thalassa* was used from 1997 up to now. A 36/47 GVO (great vertical opening) trawl was used with a 20-mm mesh codend liner. Hauls are standardised. The common survey area (from 15 up to 200-m depth) covered within the whole time period was defined. About 60 to 150 hauls were available for each survey in this area. The mean fish number per haul was then calculated for each species as well as its rank.

2.3. Temperature

Temperature data from the World Data Center A (WDC-A) and temperature data collected by the French Research Institute for the Exploitation of the Sea (IFREMER) and the French Hydrographic and Oceanographic Service of the Navy (SHOM) were used for this study. The temperature measurements were made using a conductivity–temperature–depth (CTD), a bathythermograph (XBT, MBT) and bottle stations, over the period 1967 to 2002 in the zone of the Bay of Biscay between 43°–48°N and east of 5°. The average temperature of two water layers, at 100- and 200-m depth, was calculated for a three-month period (June, July, August), corresponding to the breeding season of *Capros aper*, using data combined from all of the stations in the zone of study. 867 stations were available for the whole period, on average 20 per year.

2.4. Temporal trends and correlations

To characterize the temporal trend of the boarfish abundance and of the temperature, three models were fitted, a linear, quadratic, and an exponential one. Non-parametric tests of correlation between abundance and temperature were performed on the log transformed datasets: Spearman rank order (R), Gamma (G) and Kendall tau correlation.

3. Results and discussion

The abundance of *Capros aper* actually significantly increased from about 7 to 1500 individuals per haul (Fig. 1). The best-fitted model is the exponential one with a r-squared value of 0.89 against 0.6 and 0.79, respectively, for the linear and quadratic models. The observed increase has really occurred in the late nineties. The relative abundance of boarfish increased from 0.27% in 1973, 15 species were then more abundant than boarfish, to 16.43% in 2000 with only two species more abundant than boarfish (Table 1). *Capros aper* is now one of the dominant species in the fish community. The main depth range of its distribution (100–300 m) encompasses the area sampled each year.

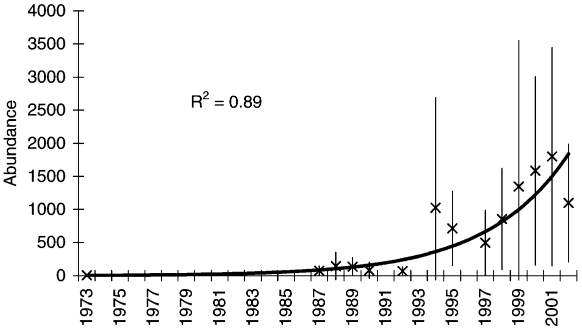

Fig. 1. Mean abundance of boarfish (*Capros aper*) per haul and confidence interval (5%) in the Bay of Biscay from 1973 to 2002 between 15-m depth up to 200-m depth and exponential trend.

Table 1
Temporal variations of the abundance rank and relative abundance (%) of the boarfish (*Capros aper*) in the fish community of the Bay of Biscay between 1973 and 2002

Year	Rank	%
1973	16	0.27
1987	6	1.17
1988	6	2.11
1989	4	2.95
1990	9	1.19
1992	8	1.16
1994	3	4.88
1995	4	6.71
1997	5	4.25
1998	4	8.41
1999	3	7.34
2000	3	16.43
2001	3	15.96
2002	3	5.9

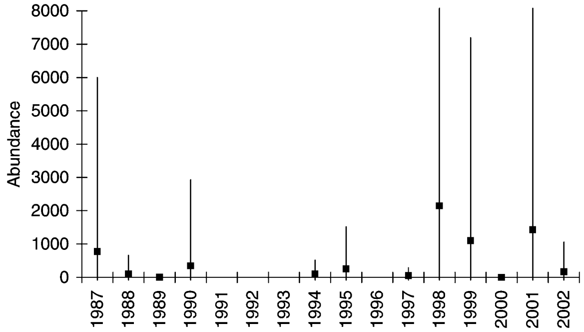

Fig. 2. Mean abundance of boarfish (*Capros aper*) per haul and confidence interval (5%) in the Bay of Biscay from 1987 to 2002 between 200-m depth up to 450-m depth.

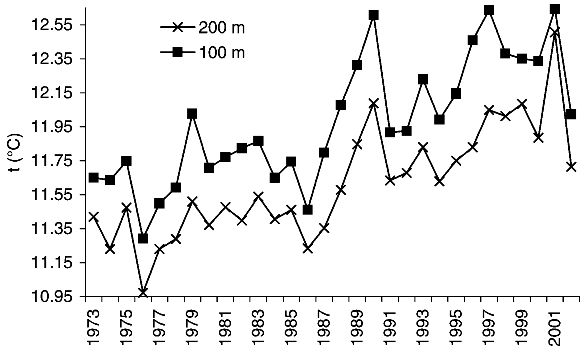

Fig. 3. Temporal variations in the average temperature during the breeding period (June to August) to a depth of 100 m (full squares) and 200 m (crosses) in the zone of the Bay of Biscay between 43°–48°N and east of 5°W from 1973 to 2002.

Table 2
Non-parametric tests of correlation between the abundance of the boarfish (*Capros aper*) and the temperature at 200 m depth during the breeding season in the Bay of Biscay between 1973 and 2002 (log transformed data). The results of the tests for temperature at 100 m depth are exactly the same as those for 200 m, they are not shown in the table

Spearman rank order correlation	
Spearman R	0.629
$t(N-2)$	2.914
p	0.012
Gamma correlation	
Gamma	0.467
Z	2.425
p	0.015
Kendall tau correlation	
Kendall	0.467
Z	2.425
p	0.015

We have then computed the mean abundance per haul from 200-m up to 450-m depth for each year except for the years 1973 and 1992. Despite highest abundances at the end of the time series in 1998, 1999 and 2001 (Fig. 2), the increasing trend is not significant on such depth according to the Spearman test ($R = 0.15$, $t(N-2) = 0.49$, $p = 0.63$).

An increase in the temperatures during the breeding season was observed (Fig. 3). This warming is coherent with the surface signal and is present over the whole column of water. This tendency was observed to be independent of the quality of the data and of the field of study as signals are coherent (data not shown) with those observed in other zones of the Bay of Biscay and also in winter. For the 200-m depth layer, the best fitted model is the quadratic one with an r-squared value of 0.67 against 0.65 and 0.66, respectively, for the linear and exponential models. For the 100-m depth layer, the r-squared value is 0.61 for the quadratic, linear and exponential models. The temperature gradient over the whole period is around 0.5 °C. As for the observed abundances, the observed temperature increase has really occurred in the late nineties. The correlation between abundance and temperature at 100 and 200 m were statistically significant for all the three tests (Table 2).

These results confirmed that in the Bay of Biscay warming occurred not only at the surface but also in the whole water column. Warming may not only favour northern immigration of subtropical species, but also may change local abundance. It has been shown for cod populations that recruitment is significantly related to temperature during the reproduction stage [15]. Experimental studies have shown that the reproductive performances of fish are closely linked to temperature [16]. One causal possible explanation is a direct physiological effect on reproduction. Temperature may actually modulate hormone action, affecting especially ovulation and spawning.

Longevity and ages of boarfish are unknown, but usually, small fish species are short-lived, fast growing and early reproducing species. Species with these biological characteristics are considered as having capacity to invade and colonize new areas (r-strategy). Colonisation may be fast if the mortality is low (no predation and no fishing). These observations are not so anecdotal in the global warming context, as it allows us to think that such changes may also concern in the near future northern species of larger size and of commercial interest for fishery and so concern the whole biodiversity and its functions in temperate ecosystems.

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An individual-based model to study the impacts of global warming and fishing activities on fish communities

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Abstract

In this article, we propose an individual-based model to study the respective impacts of global warming and fishing activities on fish communities. Understanding the roles of those two external phenomena in fish communities dynamics is necessary for a long term management of marine resources within the context of an ecosystem approach to fisheries. We studied here how global warming and fishing activities interact together in the dynamics of three indicators : the mean preferential latitude of an ecosystem, its mean trophic level and the mean length of fish in this ecosystem. We built an individual-based model to address those issues and we based our modeling on the *pattern*-oriented approach [16]. We therefore identified the *patterns* for our four simulation scenarios which confront an ecosystem to : 1° no external phenomena, 2° fishing pressure only, 3° global warming only and 4° both global warming and fishing impacts. We applied our model to the case of the Bay of Biscay, modeling nine species that represent more than 80% of the biomass of the bay as observed from trawl surveys data sets. We are able with our model to reproduce our *patterns* and, by this mean, to reproduce for the fourth scenario the long term dynamics of the indicators of the real system [25]. Studying the dynamics of fish communities, we do not reproduce the short term dynamics of any specific population : our focus scales on the Bay of Biscay's ecosystem and its dynamics from 1987 to 2004. We show that the interactions between the two studied phenomena –global warming and fishing activities– are not linear and not trivial. Thereafter, we conclude that the indicators themselves need to be used carefully.

Key words: Individual-based model, fish communities dynamics, global warming and fishing impacts, pattern-oriented modeling

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1. Introduction

Observations of fish communities in the Bay of Biscay have shown structural modifications of the ecosystem [2]. Studies of the causes of these modifications have enabled ecologists to identify global warming and fishing activities as the main processes explaining the phenomenon [25]. Yet, identifying the causes raises the question of better understanding the mutual impacts on fish communities of those two processes. Furthermore, understanding those impacts questions how species with given characteristics are favored or unfavored by such external pressures. The impact of fishing activities on ecosystems is classically described as diminishing their mean trophic level, the mean weight of individuals and favouring short-living opportunistic species. However, it is unclear if global warming has a similar impact on these indicators, an opposing impact or no impact at all. And the given indicators in the observations really reflect not only the impact of fishing activities, but also the impact of global warming [3]. Therefore, the indicators are themselves in question : what do they really describe ? What are the effects of global warming and fishing activities in their dynamics ?

Disantengling the different processes that explain the dynamics of exploited resources is a critical issue for the management of such resources [6], among

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which fish stocks are a typical example. Being able to evaluate various scenarios of the co-evolution of fish communities and fisheries economies in changing environments with different resource management options can help understand how the various processes in interaction explain the global dynamics. Thereafter, modeling such exploited ecosystems is a critical challenge in ecology and economy and one can find various studies on exploited ecosystems, among which [7, 17, 1]. Modeling enables scientists to have a *surrogative reasoning* [28], to think and interact with a theoritical or more detailled system. Hitherto, the study of such systems has been difficult because of their heterogeneity, dynamics and openess. Indeed, exploited fish communities for instance are influenced by various internal and external processes, different in nature and scale, which impacts on communities can be indirect, delayed and with unexpected consequences on the global dynamics. Exploited fish communities are therefore complex systems. Hence, envisioning the sustainability of the different components of the system requires to take into account not just the point of view of one component, but the ecological and economic points of view of the ecosystem.

Building representations – models – of exploited ecosystems should enable the experience of how the various components interact together and how the global dynamics emerge from those interactions [24]. The problem is then to choose a modeling approach and the question of the modeling tool is central as the tool creates the perspectives on which is built theory [13]. From an epistemological point of view, two modeling approaches exist in ecology : a top-down approach – the classical state variable approach – and a bottom-up approach using individual-based models (IBM). State variable modeling enables to directly describe the global dynamics of a system using a compact model. Such compactness and abstraction facilitates the model's function of mediator between reality and theory, which is a fundamental function of models [21]. One can find various works using this approach : for instance, concerning the impact of global warming on fish populations [19] or the impact of fishing activities on populations' structure [8]. Yet, top-down models are based on variables and parameters not always easy to get and that are often hard to manipulate [12, 22]. On the contrary, an individual-based approach enables to describe individual components of the system [9, 18] and therefore modeling becomes less restrictive [26]. This assertion is especiallly relevant when the system to model is complex and when its global dynamics cannot be easily formulated, as it is the case for exploited ecosystems in a changing environment. Using the IBM approach may simply be, in such a situation, a 'pragmatic' solution [13]. Nevertheless, because of the great expressivity of the approach, one must not over-complexify the model with unrelevant details in regards to the objective of the simulation activity. And even without over-complixifying the model, having the global dynamics emerging from the interactions of the components described in an IBM does not ensure that one will be able to evaluate and interpret the resulting dynamics produced by the simulations.

We noticed, as others [11], that the study of complex systems requires the use of various models and multi-modeling [13, 5]. Indeed, multi-modeling enables various experts to build models using modeling materials that were not expected to be put together. Thereafter, various models, using various modeling approaches and tools, describing various points of view of the system, may enrich modeling and ease the analyses and the understanding of the simulation results [10, 12]. In other words, several models of the same system is better than one big model from which it is hard to learn [29, 23].

We argue that we need 1° various modeling actions using multi-modeling in order to enrich the simulation experience and 2° a method to structure – and help keep the consistency of – the simulation activity and the various modeling actions. In consequence, we base our simulation activity on the *pattern* oriented modeling approach [16] that we detail in the next section. Secondly, this work is part of the Chaloupe project[1] in which various multi-modeling actions are being fulfilled. In this context, we are studying the issues developped here using top-down approaches [4], pure IBM approaches or mixted approaches using our multi-model simulation platform [5]. In this article though, we focus exclusively on the study of the continental shelf of the Bay of Biscay using an individual-based model. The question is to understand how this IBM may uncover hints of how the exploited fish community structure can react in a changing environment under anthropic pressures. The next section introduces the individual-based model and the assumptions upon which the model is built. Section 3

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[1] http ://www.projet-chaloupe.fr

than exhibits the results we obtained when executing our model. At last, section 4 is a discussion of our results.

2. Means and method

2.1. A pattern *oriented simulator*

The *pattern* oriented modeling is a method to rationalize the modeling by trying to make it more rigorous and comprehensive [14, 16]. Modeling is motivated by one(or several) issue(s) concerning a clearly identified object of study : there are questions and assumptions concerning this object that are characterized by remarquable traits in the data called *patterns*. A *pattern* is therefore the observation of a non stochastic emergent structure in the data and contains information on the internal organisation of the studied system and on the mechanisms that made it emerge [16]. The principle of this method, proposed by Grimm, is to start from the observed *patterns* to establish the structural model of the system. The model is therefore directly attached to the internal organization of the real system [15]. Thereafter, the modeling activity starts by the observation of the *patterns* characterizing the system and its dynamics. Then and only then, can the variables and processes be chosen in order to explain the emergence of the *patterns* [16].

Our simulator is based on the *pattern* oriented modeling [5] and enables to structurally build models around the *patterns*. Our approach is therefore data oriented, the data around which different modelers and experts (like ecologists or economists) can work together to build their models. Additionally, our simulator enables the coupling of heterogeneous models and therefore especially of IBMs.

2.2. Our patterns

To keep track of our system, we focus on three indicators : 1° mean individual length in the fish community, 2° the mean preferential latitude (mean latitude of the mid-domain in the fish community) and 3° the mean trophic level. Ecologists have noticed, from 1987 to 2004, a decrease of the fish mean length, the mean preferential latitude and the mean trophic level of the ecosystem of the Bay of Biscay [25]. Those three dynamics in the indicators are our three primary *patterns*.

Our approach being semi-theoretical, we also established theoretical *patterns*. Studying both the impacts of global warming and fishing activities on fish communities, we need to consider each of these two processes separately and its impact compared to the "real" case where both processes are present. Our theoretical *patterns* describe how the system would behave if simulated in three different contexts defining three out of four of our simulation scenarios : 1° fish communities are not impacted by external phenomena, 2° only global warming impacts fish communities and 3° only fishing activities impact fish communities. The first scenario is therefore the scenario of reference and will enable us to validate our assumptions on how fish communities behave without any external pressure.

Our theoretical *patterns* are described using the indicators described above. All our *patterns* are therefore described with the same indicators, as below :

Scenario 1, *theoretical* patterns*, scenario with no global warming, nor fishing activities :* when communities have no external pressure, the three indicators are stable.

Scenario 2, *theoretical* patterns*, scenario without global warming, but with fishing activities :* such pressure induces a decrease in time of the fish mean length (because of size-selective fishing mortality) and of the mean trophic level (because there is a positive relationship between length an trophic level).

Scenario 3, *theoretical* pattern*, scenario with global warming, but without fishing activities :* global warming induces a decrease in time of the mean preferential latitude (because species with affinity for warm-waters, that is to say with a low latitude mid-domain, are favoured by warming while high latitude species, with affinity for cold-water, are unfavoured).

Scenario 4, *primary* patterns*– scenario with both global warming and fishing activities :* the combined effects of global warming and fishing activities induce a decrease in time of the three identified indicators [25].

2.3. An individual-based model

In this section, we detail our individual-based model. Following the classical mean to implement individual-based models, we use a multi-agent simulation in which agents (individuals) perceive and act in a virtual environment. Figure 1 shows a schematic representation of the resulting multi-agent system. We describe, in section 2.3.1, the environment of the fish and the processes that model global warming and fishing activities. And, in section 2.3.2,

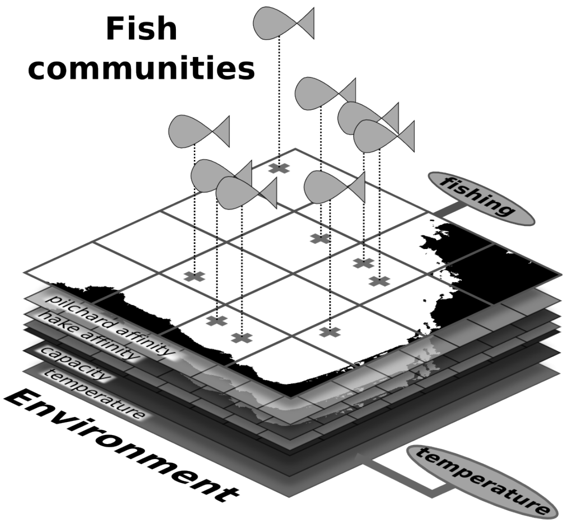

Fig. 1: A schematic representation of our individual-based model : virtual fish in a representation of the Bay of Biscay. Notice that the environment contains various information and two processes, i.e. temperature and fishing, that can modify information or perceive/act on fish (see section 2.3.1).

we describe the individuals (fish) and their various internal processes, e.g. growth or recruitment.

2.3.1. Environment's processes

General description. The environment of the fish is, first of all, topological and contains information that individuals (fish) can perceive locally or globally. Fishes are therefore spatialized and located in this environment. The information they can perceive is the temperature and the affinity. The temperature is considered as global and at any location the same. The affinity describes the habitat of the individuals and represents at a given location the affinity of individuals to their environment. The affinity is spatialized and described with a specific discretization. Finally, the environment is considered as closed.

Species habitats. Each species has its own habitat in the environment and individuals of this species are constrained in it. The habitat represents a geographic place, but also characteristics that favor the individuals. Thereby, the habitat depicts the physical environment where individuals of a given species are to be found, but also the existence of available food for this species or reproduction spots. At last, the habitat of a given species is described by a minimal and maximal latitude over and under which individuals of this species are very rarely observed. In the same way, the habitat is function of the depth, i.e. there is a minimal and maximal depth over and under which individuals of the given species are very rarely observed.

The habitats being designated in our environments by means of latitudes and depths, we model habitats using the concept of affinity. In every location of the environment, a variable affinity is defined and it represents the affinity of individuals to their environment. Outside the habitat, the affinity equals 0, while inside the habitat, its value ranges from 0 (not included) to 1. The habitat of a given species is therefore represented by the distribution in the environment of this variable affinity. Notice that depth is not explicitly modeled as it appears indirectly through the habitat and through the trophic web used to describe how species interact together (see the description of the predation process in section 2.3.2).

Temperature and global warming. To model the temperature in the environment, we assume that it is global. Yet, local variations of the temperature –spatial variations– and inter-annual variations induced by seasons –temporal variations– might be necessary in order to reproduce fish dynamics. We assume that a frequent temporal variation of the temperature is sufficient to reproduce the different temporal and spatial variations of temperature. At last, global warming induces an increase of the global temperature.

To model the temperature, we use two different scenarios for the temperature's evolution : 1° a scenario with no global warming and 2° a scenario with global warming. A process 'temperature' is then added to the environment (see figure 1). It changes the temperature with a given frequency based on the temperature scenario.

Fishing activities. This process is based on four assumptions. First, fishing activities try to catch all species and the induced pressure is the same in proportion for each species. Fishing does not impact all individuals (whatever their species) in the same manner, as there is a selectivity based on the size of fish. We also assume that the pressure induced by fishing activities on communities is constant in time, because we make the assumption that the fishing impact can be brought down to an impact on the communities' structures (structures in size in particular). Notice, by the way, that many consider that the fishing impact is relatively stable compared to the variability of individual production of the species [27, 20]. At last, we assume that the pressure induced by fishing activities on communities is sufficiently powerful to impact all locations of the environment. No niches or protected areas are therefore modeled.

Fishing activities are represented by a top-predator, which introduces a process generating fish mortality in the community. This approach has already been used in various models, like in [8]. Eventually, mortality is applied using stochastic selection of fish in each species, which is equivalent –on the long term– to a uniform distribution of the mortality in the environment. Furthermore, the same mortality *in proportion* is applied on each species separately, which is the most direct way to guarantee a uniform mortality between all species. At last, each individual has a probability to be caught, probability that depends on its length. Therefore, even if a given mortality is applied to a given species, only the fish with the proper sizes have a probability to be caught that is not null. In consequence, a given mortality might not always be fully applied to a given species if fish are too small or if fish are "hard" to catch.

2.3.2. Individual processes

Fish are composed of various processes that represent their different biological functions. Figure 2 shows a schematic view of an individual with the processes we model. Each process may use and/or modify variables like the age of the fish or its position in the environment. It may also perceive or act on other fish in the environment and the environment itself, i.e. the information contained in the environment. We now describe the different processes modeling the biological functions of fish.

Ageing. This process is based on two assumptions : 1° an individual enters the system at a given age $_{s}a_{min}$, which is its species recruitment age ; 2° an individual of a given species s has a specific lifetime $_{s}a_{max}$.

The model of this process is described by the fact that an individual grows in age every day and dies when it reaches $_{s}a_{max}$. Therefore, we have $_{s}a_{min} \leq {}^{i}_{s}a \leq_{s} a_{max}$, with ${}^{i}_{s}a$ the age of fish i of species s.

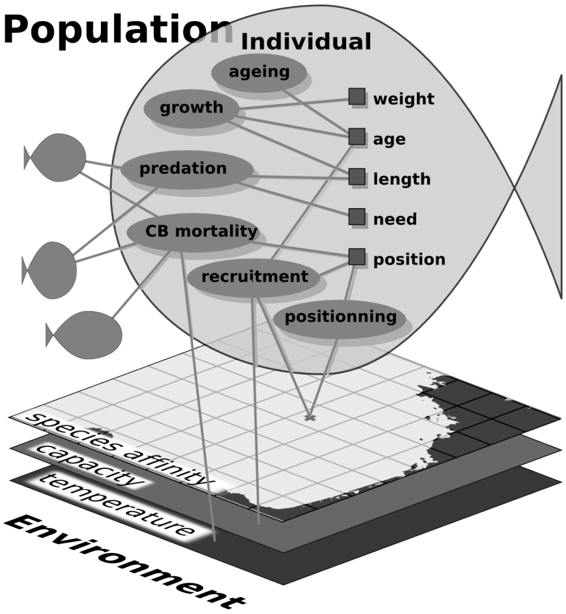

Fig. 2: A schematic representation of an individual. Notice the different biological functions –processes– that we model, e.g. ageing, growth or recruitment (see section 2.3.2). Each process may use variables, e.g. the weight or the age, and can get information on other fish or in the environment, e.g. the affinity or the environment's temperature. Notice that CB mortality means capacity based mortality.

Growth. This process is based on three assumptions : 1° the growth of individual i is only function of its age ; 2° growth is not influenced by the environment, the habitat or the temperature ; 3° growth is not linked to feeding. In consequence, there is no individual variability.

The process' model is described using von Bertalanffy's length at age relationship :

$$\ell(t) = L_\infty \times (1 - e^{-K(t-t_0)})$$

Thereafter, growth in weigth is defined by the following length-weight relationship :

$$w(t) = {}_{s}a \times \ell(t)^{{}_{s}b}$$

with $w(t)$ the weight of the fish, $_{s}a$ and $_{s}b$ parameters specified for each species s and $\ell(t)$ the length of the fish.

Recruitment. This process is based on various assumptions. First, individual fecundity is function of the individual's weight. No distinction is made between males and females, all individuals have a fecundity. An individual is mature at a given length ${}_s\ell_{mat}$, which depends on the species s of the individual. An individual's fecundity is function of its affinity to its local environment. The number of recruits depends on the number of adults, therefore there is a stock-recruitment relationship for every species. Recruitment takes place all year long. At last, temperature affects fecundity : fecundity is maximal for a given temperature ${}_s\theta*$ and is not possible (null) beyond a domain of values $[{}_s\theta_l, {}_s\theta_u]$. For species s, ${}_s\theta*$ is set to the mean sea-surface temperature of the median of its distribution area.

The fecundity ${}^i_s\phi(a)$ of an individual i of species s is given by :

$$ {}^i_s\phi(a) = {}^i_s\alpha_H \times {}_s\rho({}^i\theta) \times f(\ell_i) $$

with ${}^i_s\alpha_H$ the affinity of the individual i to its local environment, ${}_s\rho({}^i\theta)$ the component taking into account the temperature (see below) and $f(\ell_i)$ the component function of the individual's length (see below).

The component describing the impact of the temperature is described by :

$$ {}_s\rho(\theta) = -e^{(\theta - {}_s\theta_{opt})^2/(2*(({}_s\theta_{max} - {}_s\theta_{min})/6)^2)} $$

with θ the local temperature and ${}_s\theta_{opt}$, ${}_s\theta_{max}$ and ${}_s\theta_{min}$ the optimal, maximal and minimal temperatures of species s.

At last, the component that is function of the individual's length is given by :

$$ \begin{array}{ll} f(\ell_i) = \frac{1}{2} \times \gamma_\phi \times w(\ell_i) & \text{if } \ell > {}_s\ell_{mat} \\ f(\ell_i) = 0 & \text{otherwise} \end{array} $$

with γ_ϕ, $w(\ell_i)$ the weight of i and ${}_s\ell_{mat}$ its length at maturity for species s. Note that the $\frac{1}{2}$ appearing in the formula comes from the fact that only half[2] the individuals (females) can actually have a fecundity. Also note that the fecundity enables an individual i of species s to know the number ${}^i_sN_{recruits}$ of recruits to create given the following rule :

$$ {}^i_sN_{recruits} = floor({}^i_s\phi(a)) $$

with ${}^i_s\phi(a)$ the fecundity processes above and $floor(x)$ the function which to x associates its whole part.

Environment capacity based mortality. The process is based on three assumptions : 1° a species habitat can only accept a finite number of individuals, it is therefore characterized by a capacity : individual survival is function of this capacity and of the total number of individuals in the habitat ; 2° the capacity of the environment is defined for each species, there is no interspecific spatial competition ; 3° species tend to fill up their habitat.

It would be more natural for each individual to locally perceive if their habitat is full or not. But such a model requires fine mechanisms to traduce a global capacity into a local capacity. For our modeling question, we need a capacity based mortality, yet introducing a fine model would require precise assumptions and a complexification of our model. Moreover, such complexification seems unrelevant for our description scale and questioning. Therefore, to model our capacity based mortality, we propose that each individual can directly perceive the total number of individuals of the same species. Such a model, beyond being simple and relevant, is consistent with the concept of niche and all individuals of a community may still regroup in specific areas of their habitat given certain conditions (e.g. intensive predation or fishing). Thereafter, an individual dies because of too many individuals of its species in the environment given the value of Θ :

$$ \text{If } N_s > {}_sN_\infty, \text{ then } \Theta(i) = 1 \text{ otherwise } \Theta(i) = 0 $$

Predation. This process is based on quite a few assumptions. First, predation is applied by predators on preys and the consequence is the death of the preys. The length of a predator prevents it to eat any prey it meets and predation is based on the ratio ${}_s\tau$ between the predator's length and the prey's length – the predator may eat a given prey only if their length ratio is less than ${}_s\tau$. Young predators may have a different diet than adults : each species s is characterized by a length ℓ_{pred} and only individuals bigger than ℓ_{pred} may hunt preys. Predators need a given quantity of food per year that is function of their weight and of a parameter ${}_sB_r$. Predators feeding is limited. Predation is organized by a trophic network and each species has a specific trophic level ${}_s\tau_{trophic}$, which describes its position in the trophic network. Predation has no impact on predators, thus lack of preys does not induce the death of predators for instance. In consequence of all those assumptions, species with the smallest trophic levels do not practice predation, there food is

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[2] This is an approximation, which is not false given the model.

considered as a non limiting factor and is not modeled.

Only predators hunt. In order to do that, predators first process the biomass they need to eat. Given an individual i, if i's length is sufficient ($_s\ell_i \geq {}_s\ell_{pred}$), then i requires the following biomass :

$$B(dt) = w(\ell_i) \times {}_sB_r(dt)$$

with $w(\ell)$ the function that associates the length ℓ of an individual to its weight and $_sB_r(dt)$ the biomass rate required by individuals of species s per dt. With this quantity in biomass $B(dt)$, an individual randomly hunts preys in its neighborhood[3]. Finally, each hunted prey is eaten if the ratio between its length and the predator's length is less than $_s\tau$.

Spatial positioning. This process is based on the following assumptions. First, fish tend to be in their habitat. Second, fish migrations and local transportations do not affect the communities global dynamics ; such assumption is consistent with our observation and analysis scales (temporal and spatial). In the same way, seasonal migrations have no influence on communities global dynamics ; again such assumption is consistent with our observation and analysis scales (temporal). The two previous assumptions imply that fish are considered as sedentary. New individuals –i.e. freshly born– in the environment are recruits. Recruits appear in their habitat, yet there is no reason for recruits to appear next to their genitors.

To model this process, we state that all newborn individuals are placed in their habitat and their position is function of the affinity of individuals to their local environment. Thereafter, an individual has more chances to be set somewhere in the environment where the affinity is maximal and it has no chances to appear in an area where the affinity is null. To do this, we use distribution of probabilities initialized with the distribution of affinities of each species. Note that the initialization of the communities at the beginning of each simulation is done using the same technique and each species is distributed in the environment in regards to its habitat.

3. Results

3.1. Application to the Bay of Biscay

Fish populations. We focus for this case of study on the nine following species : 1° anchovies, *Engraulis encrasicolus* ; 2° anglers, *Lophius piscatorius* ; 3° atlantic horse mackerels, *Trachurus trachurus* ; 4° whitings, *Merlangius merlangus* ; 5° blue whitings, *Micromesistius poutassou* ; 6° european hakes, *Merluccius merluccius* ; 7° poor cods, *Trisopterus minutus* ; 8° european pilchards, *Sardina pilchardus* ; 9° poutings, *Trisopterus luscus.* Those species are the dominant ones and represent 80% of the fish community of the Bay of Biscay as sampled from bottom trawl surveys (EVHOE campaigns).

Table 1 summarizes most of the parameters used to model all species (data get from Fishbase). Table 2 shows the depths and latitudes used to build each species habitats (observed from the trawl survey data set) and figure 3 shows the resulting habitats. At last, the trophic network is based on the following rules (from Fishbase) : 1° hakes eat pilchards, anchovies, poor cods, blue whitings and horse mackerels ; 2° anglers eat poutings, horse mackerels, blue whitings and poor cods ; 3° horse mackerels eat poutings, poor cods and whitings ; and 4° whitings eat horse mackerels and poor cods.

Forcing global warming . Global warming is applied using a temperature scenario based on observations in the Bay of Biscay. Table 3 shows the mean temperature intervals used to build this scenario. Recall that the temperature process, at a given time step, chooses a random temperature in one of those temperature intervals, with a higher probability –twice as much– to get a temperature centered in the interval as the two seasons –spring and autumn– don't reach extreme temperatures. Note that simulations with no global warming use the temperature intervals of table 3 from 1982 to 1987. Note that global warming, following the observations, corresponds to an increase of the mean temperature of 0.5°C (consistent with [2] and [25]).

Fishing impacts. Fishing activities are induced through a mortality of 20% of the individuals of each species each year. This mortality is constant in time.

3.2. Simulations

3.2.1. Scenarios

No warming, no fishing – scenario 1 : no warming process, nor fishing process is added

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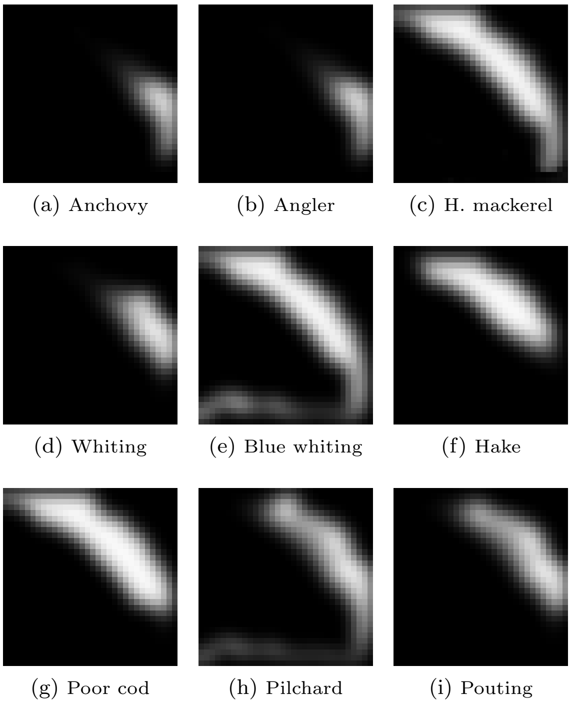
[3] The neighborhood is defined by the environment's discretization.

Species	Depths (meters)		Latitudes ($^\circ N$)	
	potential habitat	*preferential habitat*	*potential habitat*	*preferential habitat*
Anchovy	[0, 200]	[0, 50]	[43, 48.5]	[44, 46]
Angler	[0, 200]	[0, 50]	[43, 48.5]	[44, 46]
H. mackerel	[0, 200]	[100, 200]	[43, 48.5]	[43, 48.5]
Whiting				
Blue whiting	[0, 200]	[100, 200]	[43, 48.5]	[43, 48.5]
Hake	[0, 200]	[50, 200]	[43, 48.5]	[46, 48]
Poor cod	[0, 200]	[50, 200]	[43, 48.5]	[45, 48.5]
Pilchard	[0, 200]	[0, 50]	[43, 48.5]	[43, 48.5]
Pouting	[0, 200]	[0, 50]	[43, 48.5]	[45, 48]

TAB. 2: Description of the species habitats – potential and preferential depths and latitudes for the 9 species of the Bay of Biscay as inferred from the EVHOE surveys data set.

espèce	anchovy	blue whiting	poor cod	pilchard	pouting	angler	hake	horse mackerel	whiting
Environment's capacity$^{(2)}$: N	751666608	3217545919	959784585	211274564	161833832	1492375	163109946	6593621354	26380667
Preferential latitude$^{(?)}$	21.5	52.0	47	40.5	45	53	42.5	19	53.4
trophic level$^{(?)}$	2.9	3.7	3.7	2.7	3.7	4.5	4.4	3.7	4.4
maximum age : year (1)	5	10	5	10	6	22	15	15	10
$L_\infty{}^{(1)}$: cm	22.1	36	22	25.6	22	150	110	44.9	52.2
K$^{(1)}$	0.54	.28	0.39	0.42	0.5	0.088	0.12	0.2	0.45
$T_0{}^{(1)}$	-0.59	-2.48	-1.7	-1.6	-0.4	-.024	-0.5	-0.59	-0.21
a$^{(1)}$	0.002954	.0023	0.0086	0.005936	0.00738	0.02457	0.00438	0.007325	0.0004549
b$^{(1)}$	3.2579	3.499	2.98	3.0767	3.1561	2.8561	3.113	3.0254	3.1669
Reproduction min t°$^{(?)}$: C°	10.6	5.2	6.6	8.2	7.1	5.7	7.7	10.1	4.9
Reproduction optimal t°$^{(?)}$: C°	14.6	9.2	10.6	12.2	11.1	9.1	11.7	14.6	8.9
Reproduction max t°$^{(?)}$: C°	18.6	12.2	14.6	16.2	15.1	13.7	15.7	19.1	12.9
Reproduction min length$^{(1)}$: cm	10	25	14	20	18	62	53	23	33
Reproduction rate$^{(3)}$	0.025	1	1	0.025	0.2	0.15	0.025	0.025	1

TAB. 1: Details of the parameters of our IBM and of their values used to model our nine species of the Bay of Biscay. $^{(1)}$ From Fishbase. $^{(2)}$ Processed out of EVHOE surveys. $^{(3)}$ Obtained by experimenting our model through simulation. $^{(?)}$ DTC.



(a) Anchovy (b) Angler (c) H. mackerel

(d) Whiting (e) Blue whiting (f) Hake

(g) Poor cod (h) Pilchard (i) Pouting

FIG. 3: Species habitat maps – for each species, its affinity to the environment is a variable that is distributed in the environment based on the depths and latitudes ranges in which this species is to be found. A matrix of values is obtained for each species describing its affinity distribution, what is shown here using grey scale images. White corresponds to the highest affinity, black to the lowest. In between values are described by a grey gradient.

year temperatures : [min, max]			
1982 [11.98, 19.9]	1983 [11.29, 20.48]	1984 [10.98, 20.12]	1985 [11.17, 19.35]
1986 [10.84, 20.02]	1987 [10.52, 20.21]	1988 [11.33, 20.14]	1989 [12.06, 21.28]
1990 [12.9, 21.15]	1991 [11.23, 20.83]	1992 [11.5, 20.69]	1993 [12.01, 19.81]
1994 [11.23, 20.62]	1995 [11.86, 21.19]	1996 [11.98, 19.86]	1997 [11.7, 20.99]
1998 [12.51, 20.53]	1999 [11.73, 21.01]	2000 [11.63, 20.65]	2001 [12.05, 20.26]
2002 [11.6, 19.19]	2003 [11.56, 22.49]	2004 [11.33, 20.52]	2005 [11.27, 20.58]
2006 [11.11, 21.47]	2007 [12.39, 19.78]		

TAB. 3: Mean temperature intervals –minimum and maximum reached per year– observed from Reynolds data set in the Bay of Biscay from 1982 to 2007.

to the system. Therefore, the fish communities have no external pressures. The temperature scenario is based on observed temperatures from 1987 to 1991, before the observed warming.

Fishing only – scenario 2 : only the process representing the fishing activites is added to the system. The temperature scenario is the same as used for scenario 1.

Warming only – scenario 3 : only the process representing the global warming is added to the system. The temperature scenario is based on the temperatures described in table 3.

Warming and fishing – scenario 4 : both global warming and fishing activities processes are added to the system. This last scenario should produce dynamics close (in tendencies) to the one observed in the real system.

Important remark. All our simulations have a period of initialization of 25 years, which enables fish communities to stabilize themselves. During this initialization period, no global warming, nor fishing activities impact the ecosystem whatever the scenario. Moreover, all simulations are not stopped right at the end of the scenario (2004). Thereafter, the simulated dynamics virtually ends on the year 2014, but we strongly stress out the fact that we only try here to validate our simulation on the period of time going from 1987 to 2004. This work is not a prospective study and the results obtained at the end of the scenarios can only give a larger view of the dynamics, but cannot be considered as predictions.

3.2.2. Simulation outputs

Remark. Note that in any figure –i.e. figures 4 and 5–, the solid black line corresponds to scenario 1, the dashed blue line to scenario 2, the red triangles to scenario 3 and the green dots to scenario 4. Besides, the period of time given in the figures goes from 1982 to 2014. Yet again, we stress out that the period of time we tried to simulate goes from 1987 to 2004, period of time that is made visible by two vertical lines.

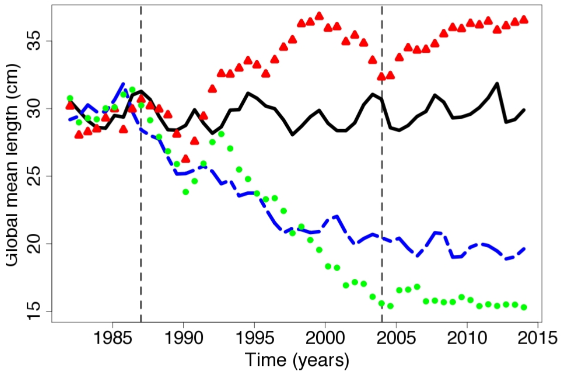
Patterns. Figure 4a shows the evolutions for the four scenarios of the fish mean length. Figure 4b shows the evolutions for the four scenarios of the mean preferential latitude. And finally, 4c shows the evolutions for the four scenarios of the mean trophic level. We notice that all *patterns* stated in section 2.2 are reproduced, whether they are theoretical or coming from observations.

Details of each population's dynamics. Figure 5 shows the evolutions in number of the different species for the four scenarios. The results show that the trajectories of each species are not absurd, structurally valid and relevant to our questioning, yet they do not correspond in details to the trajectories of the real species.

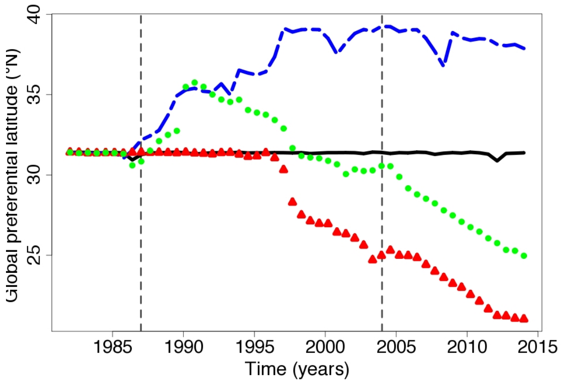
4. Discussion

Our goal was to study the dynamics of the ecosystem of the Bay of Biscay. We built an individual-based model in order to do so and experimented it based on the *pattern* oriented approach. We thus defined as a starting point the *patterns* that our model had to reproduce and upon which it was designed. We described three series of "theoretical" *patterns* and one series of "real" *patterns*. Thence, we note that our results reproduce all specified *patterns*. Moreover, the "real" *patterns*, issued from observations [25], are also reproduced by our system. In other words, the resulting trajectories of our model in simulation for the fourth scenario – i.e. with the processes of fishing and global warming – match the observations done in the Bay of Biscay for the corresponding period of time.

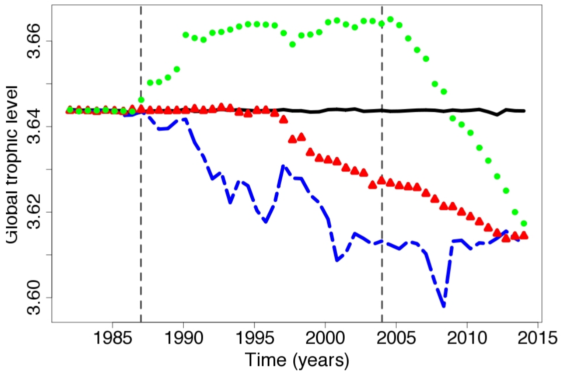
However, we would like to strongly insist on the fact that our approach is semi-theoretical. As we can see in figure 5, the results concerning the temporal trajectories of each population and showing



(a) Evolution of the fish mean length

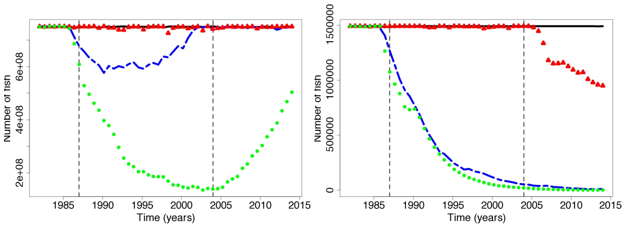


(b) Evolution of the mean preferential latitude

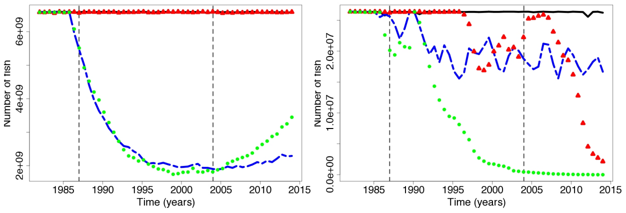


(c) Evolution of the mean trophic level

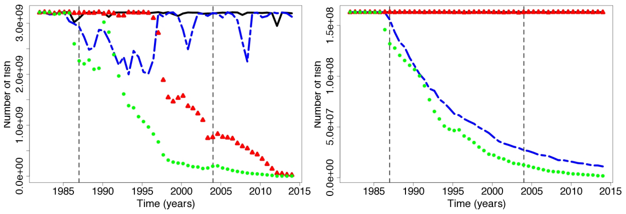
Fig. 4: Simulation results : evolution of the fish mean length, of the mean preferential latitude and of the mean trophic level. Scenario 1 corresponds to the black curves, scenario 2 to the blue curves, scenario 3 to the red curves and scenario 4 to the green ones.



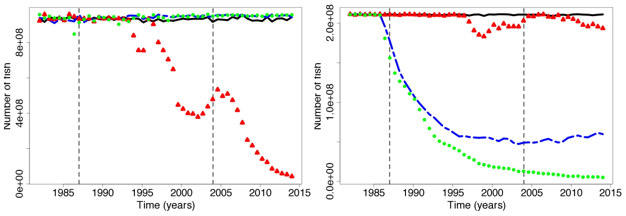
(a) Anchovy (b) Angler



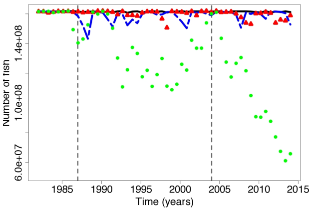
(c) Horse mackerel (d) Whiting



(e) Blue whiting (f) Hake



(g) Poor cod (h) Pilchard



(i) Pouting

Fig. 5: Species dynamics in number through time for scenario 1 in black, scenario 2 in blue, scenario 3 in red and scenario 4 in green.

their evolution in number are not completely faithful to the real ones. Yet, we argue that such dynamics are relevant for our questioning and our scale of study, that is the study of community dynamics for several decades (20∼30 years). In other words, we are not studying population dynamics and our focus is not to reproduce or explain the dynamics of any specific population. Our focus is on ecosystem and on the communities structuring it, and as so, we have not tried to model in details each population. In any case, modeling the specificities of each population of species would have been very challenging. We therefore have modeled each population as a "model" with specific parameters – e.g. a given mortality, a given reproduction rate –, which enable us to study how such specific parameters/characteristics could favor or unfavor a population on the long-term given the external processes of fishing and global warming. At last, we would like to highlight that, given our scale of focus and semi-theoretical approach, the dynamics shown in figure 5 are not absurd and help us understand and even validate the dynamics of our indicators.

Concerning the results brought here,first, as one can see in figure 4, the results are not linear and several paradox arise. For instance, concerning the third scenario (only global warming), the mean length tends to increase (fig. 4a) while the trophic level decreases (fig. 4c), which is counter-intuitive. Actually, individual size and trophic levels are positively correlated : top-predator species are mainly the largest fish species. However, such correlations are true when a complete biota is observed but may be not detectable when only a part of the biota is considered, as in the present exercise of modeling. Concerning the second scenario (only fishing activities), the mean length and trophic level dynamics behave as expected and both decrease in time (figs. 4a and 4c), nevertheless the latitude here increases (fig. 4b), which was unforeseen. It may only be an indirect consequence of fishing : the horse mackerel is a species with affinity for low latitude. As this species is the most dominant in the community, the decrease in biomass and number because of the fishing mortality will induce an increase of the mean latitude value in the community. Thereafter, we can conclude that the indicators' dynamics are not linear and can exhibit from time to time complex behaviors due to various processes.

Second, we shall now focus on discussing the respective impacts of both fishing activities and global warming on fish communities. The question is to understand those impacts and therefore the interactions of those two processes. What appears in the results is that those impacts are not trivial and can even interact in unexpected manners. Unfortunately, those interactions are not simple to interpret, especially because the various species have different life-history parameters, which result in different reproduction speeds or mortality speeds, which themselves result in different reactions from those species to external factors, and thus indirect interactions take place between the different communities, interactions that are hard to establish. Moreover, the values of the model's parameters were chosen in a semi-theoretical approach, which sets apart even more the results with the possibility to establish a deep interpretation of them. In consequence, we can only establish here the fact that those interactions are not trivial and quite rich. Those interactions are by the way different depending on the indicator that is considered.

At last, we shall now discuss the question of the indicators we have used. Indeed, relevant and well understood indicators are required for implementing the ecosystem approach to fisheries.. Our study in this article fuels us with lessons addressing this questioning. As discuss previously, interactions between fishing activities and global warming appear in non trivial manners from the indicators. Each indicator reacts to both processes, in an expected manner, or sometimes in a more unexpected manner. We are not capable here of validating or disconfirming any of the three used indicators, with the first reason being that our model is semi-theoretical and therefore our results are large-grained and would need more refinement. We can only argue, as others, that one must be cautious using those indicators and interpretating their dynamics. Yet, in conclusion, we showed the reactions of those processes to fishing activities and global warming, result that was already only partly showed for the mean length indicator [3]. Finally, apart from the question of the tools for ecosystem approach to fisheries, such as the indicators, the model has been built up, and should be used in this way, to study the ecological resilience of the systems. What is the answer of ecosystems, through fish communities, to various scenarios of fishing and environmental change ? Would the answer to environmental change be greater when the community is heavily fished (the corollary being a more resistant community if not exploited) ? Would more diverse communities, be more resistant to environmental changes under fishing pressure ? Such comparisons could be made by simulations with communities with characteristics near from real ones observed for contrasted case studies (temperate vs tropical for example).

We shall finish this article with two perspectives for this work. First, we plan in refining the fishing scenarios. Especially, we want to experiment specific fishing selectivities for each species, which might strongly enrich and sophisticate the results. Secondly, we have based our work on the assumption that the impact of global warming on communities was established through individual reproduction. Such an assumption now must be put into question and further studies should be fulfilled in order to refine our understanding of this issue.

Acknowledgements

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Fishing the food web: integrated analysis of changes and drivers of change in fisheries of the Bay of Biscay

In Coping with Change in marine social-ecological systems, R. Ommer, I. Perry, P. Cury and K. Cochrane (Eds.), Wiley-Blackwell Fisheries and Aquatic Resources Series. *In Press*

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Abstract

A growing number of studies have shown that major changes are occurring in the composition of fisheries production worldwide. Selective fishing pressure on more highly valued components of fish communities leading to their overexploitation/depletion, and the effects of such pressure within the food web, are amongst the key factors proposed to explain these changes. Under *de facto* open access conditions, it is suggested that sequential over-harvesting of higher valued fish and/or fish species leads to modifications in the structure of both fish communities and fisheries landings at various scales. A central assumption here is that large, slow-growing, late reproducing, low fecundity, predator species are more highly valued, while at the same time, they are more sensitive to fishing mortality than small, fast-growing, early-reproducing, prey species, often lesser valued. Changes in the physical environment of fish stocks, in particular in the context of global warming, can also impact population distribution areas and population dynamics (recruitment, growth, reproduction and mortality), hence the structure of fish assemblages and of landings derived from their exploitation. This has also recently been proposed as a driver of changes in fish communities, which can interact with the effects of fishing.

This chapter presents key results obtained from an integrated analysis of the role of ecological and economic drivers on long-term modifications in the structure of fisheries production, and the potential economic impacts of these changes at the scale of large marine ecosystems. The analysis focused on trends observed in the landings of French fishing fleets over the last three decades. Landings series were considered at various scales, ranging from the entire fish production derived by French vessels from the North-East Atlantic to the production of selected fish species harvested in the Bay of Biscay. Changes in the composition of landings were described, and compared to changes observed from scientific surveys carried out at sea in the same areas during the same period, and the potential drivers of these changes were analyzed.

The research showed that part of the changes observed in the composition of landings may be related to modifications of the components of marine ecosystems exploited by fishing fleets. These modifications, due to both direct and ecosystems effects of fishing, are re-enforced by climate change. Modifications of species availability, along with changes in fishing patterns under de facto "regulated open access" conditions, led to significant changes in the structure of landings. This contributed to the reduction in the value of production by French fleets, as a larger proportion of low-priced fish was landed in the later years of the study period. Other factors explaining the reduced production value in recent years include the drop in volumes landed, and increased international competition in fish marketing conditions in Europe, leading to a decrease in first sale prices.

Introduction

There has been a growing number of studies showing that major changes are occurring in fish communities and the associated landings by commercial fisheries worldwide (National Research Council, 2006).

Most studies to date have focused mainly on the ecological dimensions of these changes. Selective fishing pressure on certain components of fish communities—leading to the collapse of higher trophic level fish species, and its ecosystem effects within the food-web, small prey species being favoured because of predation release and/or their better ability to bear fishing mortality due to their life-history traits characteristics (the so-called “fishing down the food web” process)—has been one of the key factors proposed to explain the changes in landings (Pauly et al., 1998). Other researchers have argued that changes in the composition of landings can also result from the sequential addition of new species to the portfolio of species targeted and landed by fishing fleets (Essington et al., 2006), thus referring to a “fishing through the food web” process. Yet other researchers have placed emphasis on the potential contribution of climate change to the modifications observed in fish communities and associated fisheries landings (Perry et al., 2005; Dulvy et al., 2008; Hiddink and Ter Hofstede, 2008), and have stressed the complex interactions between fishing and climate which may drive changes in fish communities (Benoit and Swain, 2008; Planque et al., 2008).

Overall, although at least some of these studies imply the existence of selective harvesting as a key driver of changes, only limited research has specifically involved analyzing the human drivers underlying such spatial and/or temporal patterns. Some authors have examined the social dimensions of these modifications, such as in the case of the Newfoundland’s cod crisis (Hamilton and Butler, 2001; Hamilton et al., 2004) and the case of the West Greenland’s cod-to-shrimp transition (Hamilton et al., 2003). However, few studies have focused on the economic drivers of the sequential harvesting of different fish species in a community, and the economic consequences of changes in the composition of landings.

Sumaïla (1998) presented an analysis based on FAO marine fisheries catch data collected from all fishing nations for 1950 to 1996 for over 1000 species of fish. Based on a classification of fish into either high or low trophic level species, the author observed a shift in the proportion of total world catches towards more catch of low trophic level species relative to high trophic level species, and suggested that this entails differences in the evolution of relative prices between the two groups of species. Pinnegar et al. (2002) used this assumption to develop a model of how the relative price of species located at different trophic levels in a fish community might evolve with increasing fishing pressure. According to these authors, the increase in fishing pressure on species with high trophic levels leads to a rarefaction of these species on markets, leading to an increase in their prices, relative to those of low trophic level. This entails substitution effects with consumers increasing their demand for lower trophic level species, thus leading to increased fishing pressure on the latter and an increase in their price due to their ensuing rarefaction. Based on their analysis of long term changes in the Celtic Sea fish community and fisheries, the authors showed that there has been a decrease in the mean trophic level of catches, and an increase in the relative price index of high versus low trophic level species between the late 1970ies and 2000, thus confirming that the prices of the former have increased relative to the prices of the latter over the study period.

The focus of these studies is on the responses of markets to modifications in the portfolio of species landed, and their implications for the relative prices of species. This raises the question of the role of over-harvesting and ecosystem effects of fisheries on the one hand, and changes in harvesting behaviours on the other, in any explanation of such modifications. To date, fairly little empirical work has been carried out to describe the modifications observed in fisheries landings in economic value terms, and to confront them with independent fishery data where this is available in order to assess the potential drivers of the changes observed, including environmental, institutional and economic factors.

A set of research projects was set up by the authors of this chapter, with such an objective[i] in mind, focusing on the French Atlantic fisheries, particularly in the Bay of Biscay. The chapter provides a synthesis of the key results derived from this research regarding the joint ecological-economic analysis of changes and drivers of changes in the fish community and associated fisheries of the bay. The chapter is structured as follows. The first section recalls the results obtained regarding the descriptive account of trends in landings by the French fleets operating in the bay. The second section presents the institutional context of “regulated open access”, increased competition on fish markets and the ecological effects of exploitation and climate change as some of the key drivers of change identified in the research. The third section discusses the current research perspectives which derive from these results.

Patterns of change in fisheries landings by French fleets

Patterns of change in the landings by French fleets operating in the North-East Atlantic (NEA), between the 1970s and the 1990s were analyzed at various scales, from the entire region to the Bay of Biscay, and for the entire fisheries production to sub-sets of species.

The analysis was based on data concerning: (i) annual production in volume and average ex-vessel prices per species landed by French fleets, and (ii) descriptors of the bio-geographical and ecological characteristics of each species[ii]. Landings data was extracted from the ICES database[iii] regarding annual tonnage landed per species by French fleets in different areas of the North-East Atlantic. Statistical records published by the French Central Committee for Marine Fisheries for years 1973-1990, and by the National Office for Sea and Aquaculture Products, the French Marine Fisheries and Aquaculture Directorate and the Central Committee for Marine Fisheries for years 1990-2002, were used to extract annual average first sale prices per species. In order to assess changes in the composition of landings by species groups, information was also collected from Fishbase (http://www.fishbase.org/) and from the literature regarding the bio-geographical characteristics of species landed. Indicators used included, e.g. the trophic level of species, their maximum body length, or the limits in latitude and longitude of the distribution areas over which they are observed.

Results of this analysis are presented in Steinmetz et al. (2006) and Steinmetz et al. (2008). Overall, changes in the characteristics of landings originating from the same region observed by other authors (Pauly et al. 1998; Pinnegar et al., 2002), in particular the decrease in the average trophic level of landings, were also observed for total NEA landings by French fleets (Steinmetz et al., 2004). A more detailed analysis of landings of 57 species of finfish, representing 50% in volume of the total French landings originating from the Bay of Biscay, showed similar trends (Steinmetz et al., 2008). In particular, the evolution of the index of average maximal length of finfish species caught and landed by French fleets displayed a decreasing trend from the late 1980s at the scale of the NEA; this index also decreased with some fluctuations from the early 1980s at the scale of the Bay of Biscay, implying that the share of smaller sized fish in landings had increased. Underlying changes in the composition of landings involved temporal variations of pelagic/demersal and benthic species ratio, with a strong reduction in the share of benthic fishes caught by French fleets in the Bay of Biscay, along with a moderate decline in the proportion of demersal fishes from the early 1990s, compensated by a strong increase in the share of pelagic fishes from the 1980ies onwards.

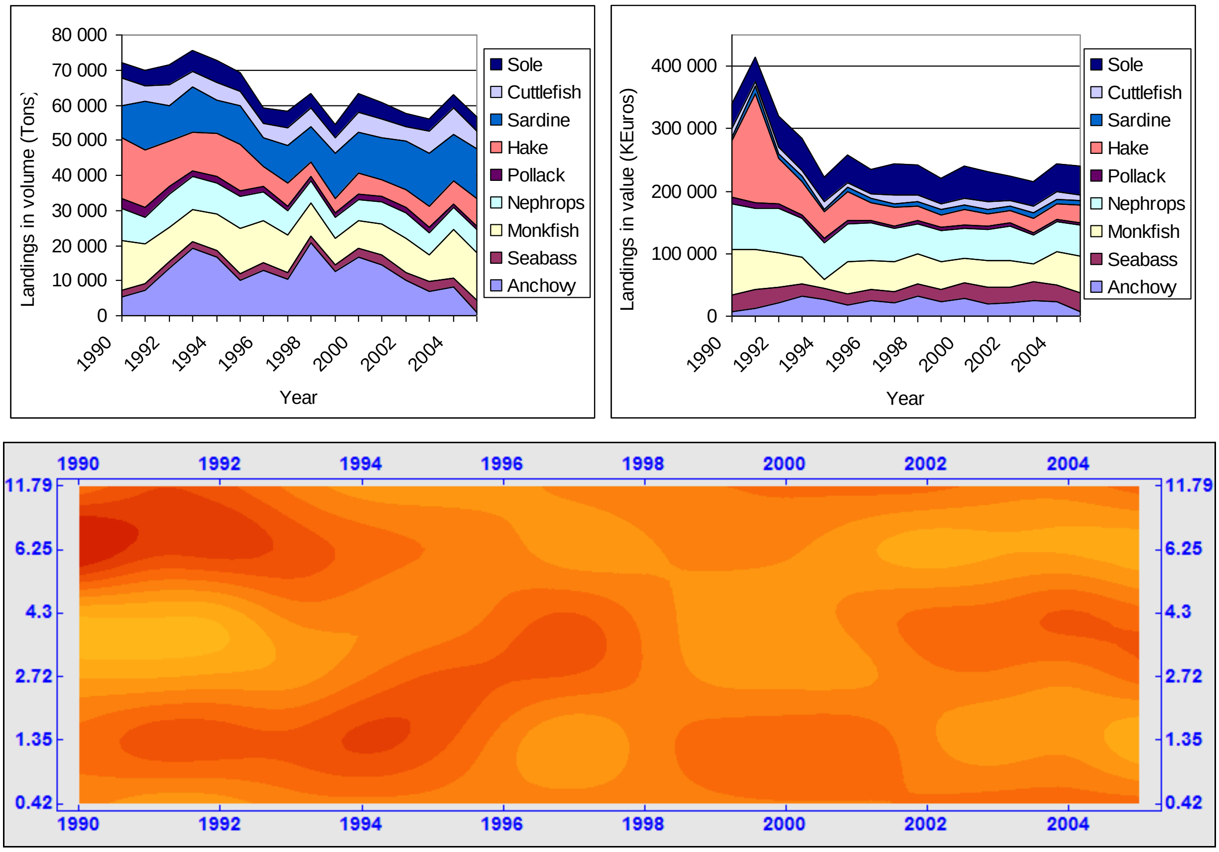

Figure 1 – Patterns of change in fisheries landings from the Bay of Biscay by French fleets for nine key commercial species, 1990-2005 (see Steinmetz et al., 2008 for a longer-term analysis including a larger set of species, and showing similar trends). Top left: total landings in volume for the major species landed by French fleets; Top right: total first sale value of landings for these species; Bottom: evolution of the composition of landings per year (x-axis) and per average first-sale price of species (y-axis, in Euro/kg); darker colour indicates a greater tonnage landed for a given year at a given annual average price. Source: data from FranceAgriMer; bottom graph by C. Mullon (see **www.projet-chaloupe.fr**, Atlas).

Trends in the quantity and value of landings by French fleets from the Bay of Biscay, were also considered. These trends are illustrated in Figure 1 for the major commercial species landed by French vessels in the more recent years of the time series[iv]. The graphs illustrate the overall decrease in the total quantity of fish landed, as well as changes in its composition. While the quantities of demersal species such as hake and pollack have tended to decrease over the study period, those of pelagic species such as sardine, cuttlefish and anchovy have tended to increase, although with some variability. In particular, the strong increase in anchovy landings of the 1990s did not last, as the Bay of Biscay stock collapsed in the mid 2000s. In value terms, there has been a sharp decline of the fleet’s landings, during the first half of the 1990s, which can partly be explained by changes in marketing conditions for fish in Europe (see infra). However, the bottom quadrant of figure 1 shows that this drop in value is at least partly due to a decrease in the proportion of the higher priced species in landings. Similar trends were observed at the scale of total fish landings by French fleets, a detailed analysis of which is given in Steinmetz et al. (2008).

Drivers of change

Beyond descriptive accounts of long-term changes in the structure of landings, the research program also sought to identify some of the major drivers of these changes, involving both economists and ecologists in this endeavour. Three areas of investigation were developed to provide complementary lines of analysis. These concerned (i) the institutional context in which fisheries operate, and the associated economic incentives driving the development of fishing capacity; (ii) the growing influence of markets in determining the evolution of first sale prices for fish landed by French fleets; and (iii) the potential influence of underlying modifications in the fish community which may result from ecosystem effects of fishing and climate change. We examine these below in this order.

Institutional context: a case of "regulated open access"

The institutional context in which French fleets operated over the study-period can largely be considered as a case of "regulated open-access", under which, despite the implementation of a limited-entry scheme in the late 1980s, and a succession of decommissioning schemes from the early 1990s, the conditions of a "race for fish" remained in place, leading to an increase in the overall catching capacity of the fleets.

By law, access to the French fishing industry was considered as free before the decision, in 1988, to create an individual operation permit ("Permis de Mise en Exploitation") for vessels in the commercial fishing fleet. Efforts to control the development of capacity in the French fleet were largely based on this permit system, associated with the definition of annual total capacity allowances measured in physical terms (initially defined based on nominal engine power in kilowatts and later, based on the gross registered tonnage of vessels), and its allocation between vessel segments (based on vessel size) and regions. Decommissioning schemes were organized nearly every year since 1991, with the aim to fulfil the targets defined under the Common Fisheries Policy regarding capacity reduction in E.U. member states (Guyader et al., 2007).

Figure 2 illustrates the evolution of an indicator of the apparent productivity of French vessels from the early 1970s to the early 2000s, taking into account the entire production that appears in the official records of landings. Apparent productivity is measured in terms of the total quantity of fish landed by the French commercial vessels operating in the North-East Atlantic (in metric tons), per ton of Gross Registered Tonnage of the vessels composing the fleet. Three distinct periods can be distinguished: (i) a period of increase in apparent productivity until the early 1980s; (ii) a period of relative stability until the early 1990s; and (iii) a new period of steady increase in the average apparent productivity of vessels from the early 1990s onwards. This latter increase occurred while limited entry and decommissioning schemes were being implemented (and was in fact partly due to the decommissioning schemes which eliminated the least performing vessels: see e.g. Thébaud et al., 2006). Overall, while the tonnage of the fleet was reduced by 44% in thirty years, the apparent productivity of vessels increased by more than 50% over the same period of time.

Under *de facto* open access conditions, the ensuing fishing pressure contributed to the development of excess harvesting of key commercial stocks which have seen their share in total landings diminish regularly over the period. Fleets were incited to reallocate their effort towards alternative species, when the relative economic attractiveness of these species became high enough due to reduced fishing opportunities on the fish stocks that were initially targeted. Hence, part of the changes observed in the composition of landings can probably be related to the incentives created by the institutional framework under which fleets operated, which led to the development of excess capacity and a sequential reallocation of fishing effort across species as these were reduced in abundance due to excess harvesting[v]. Overall, the apparent productivity of vessels increased from 1.7 tons of fish landed per ton of Gross Registered Tonnage (GRT) in 1973 to 2.7 tons in the early 2000ds.

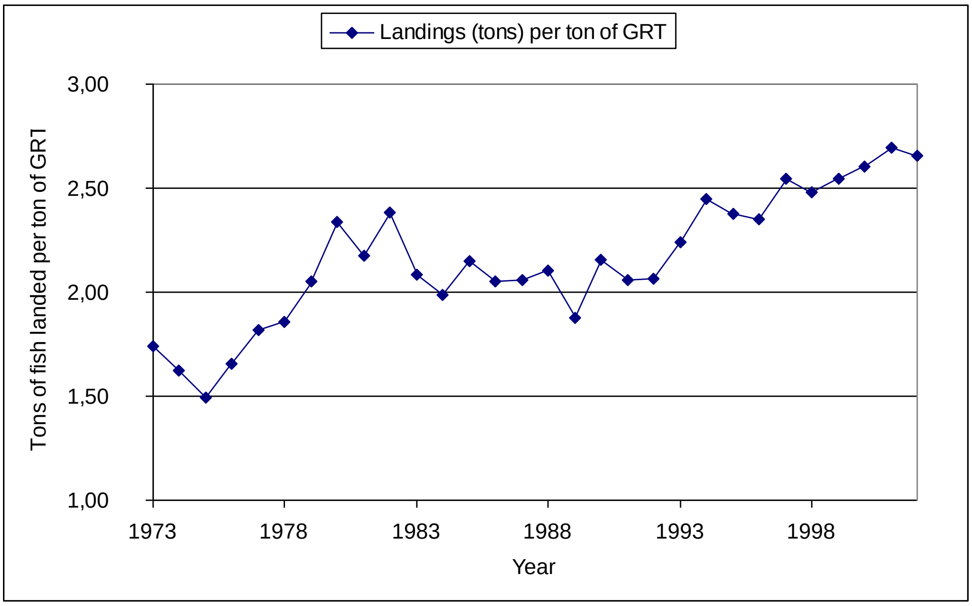

Figure 2 – Trends in the apparent productivity of French vessels operating in the North-East Atlantic, 1973-2002 (Source: Ifremer)

Increased competition in markets for fish

Analysis of the French official statistics on landings and annual average prices of fish caught in the NEA, showed that the structural modification which affected the first sale market in France in the early 1990s was another important driver of changes in the value of landings. Figure 3 illustrates this modification, by separating out changes in constant prices (in 2005 euro terms) and changes in quantities of fish landed (in tons), expressed as Fisher volume and price indices[vi].

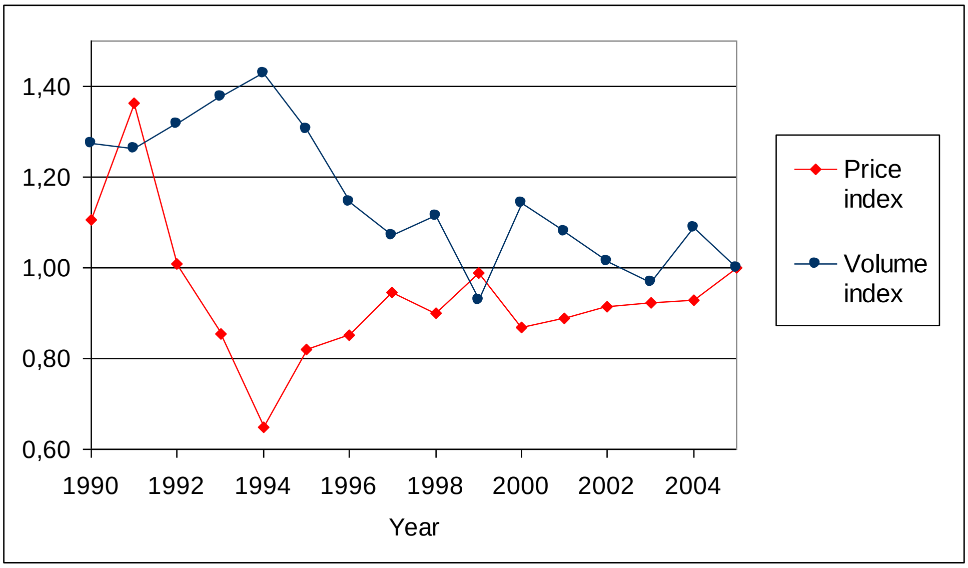

Figure 3 – Price and quantity changes in the total landings of nine major commercial species from the Bay of Biscay, 1990-2005 (Source: Ifremer, based on data from FranceAgriMer)

In the late 1980s, stagnation and then decrease in the quantities of fish landed were associated with increasing prices, which reached their highest level (in constant value terms) during years 1989-1991. This was followed by a collapse of average prices in the early 1990s, which led to a major crisis in the French fishing industry. The drop in prices was due to a set of factors, including the progressive liberalisation of trade in the markets for fish of European member states and an associated increase in market competition; the growing share of the market covered by supermarket chains which also increased this competition E.U.-wide; and modifications in the exchange rates of European currencies against the French Franc which temporarily increased the relative price of French products on both the internal and export markets. At the scale of the Bay of Biscay, the impact of the crisis was particularly strong: taking into account the nine main commercial species targeted by French fleets in the Bay, Le Floc'h *et al.* estimate that between 1991 and 1994, average prices dropped by 72% (see figure 3). During this crisis, quantities of fish landed increased. Anecdotal evidence suggests that this was a response by some fishing companies, attempting to compensate the drop in prices by an increase in volumes landed. Following this market crisis, the decrease in tonnage landed resumed, and was associated to a strong increase in prices. However, both quantities landed and prices remained lower than in the early 1990s; indeed, despite the much lower quantities landed in the later part of the period, prices remained at levels comparable to those which occurred in the early 70s, indicating that fishers now operate under new marketing conditions[vii].

This change in marketing conditions for fish landed by French fleets has contributed to the reduction, by more than 40%, of the total value of landings originating from the Bay of Biscay between the late 1980s and the early 2000s. Considering all the finfish species declared in the official landings data, Steinmetz *et al.* (2008) estimated that 42% of this decrease in the total value of landings resulted from a reduction of prices paid for fish. However, only part of this reduction (44%) was due to the drop in average prices at first sale across species resulting from the market crisis. Two thirds of this reduction were explained by the growing proportion of low price species in total landings[viii]. Indeed, when the total value index reached its maximum in the late 1980s, landings of high-priced species were also at their maximum. At the lower level of the value index in 1998, high exploitation rates were observed for low-priced species such as anchovy or pilchard, while low exploitation rates prevailed for higher-priced species such as hake or monkfish. Hence, modifications in the composition of landings, as illustrated in the previous section, contribute to explain the reduced value of fish production from the Bay of Biscay between the late 1980s and 2002.

Effects of sea warming on the fish community structure

As already stressed, changes in the composition of landings may have resulted from the sequential over-harvesting of species of higher commercial value, in a context of *de facto* open access. To some extent, these changes may also have been determined by modifications in the structure of the fish community due to sea warming. The potential role of such drivers was assessed *via* the analysis of independent fishery data regarding the status of the fish community on which French fishing fleets depend in the Bay of Biscay.

Boreal, sub-tropical and temperate species meet in the Bay of Biscay, constituting a bio-geographic ecotone (Figure 4). Species have adapted during their evolutionary history to the mean temperature conditions (among other physical conditions) that they encountered. The distribution area of the species may thus be considered as a good proxy for the thermal affinity of species, at least on a macro-ecological scale. In the Eastern Atlantic ocean, latitude and mean temperature are positively correlated, hence the latitudinal position of the distribution area of the species may be indicative of the thermal affinity of the species (Figure 4).

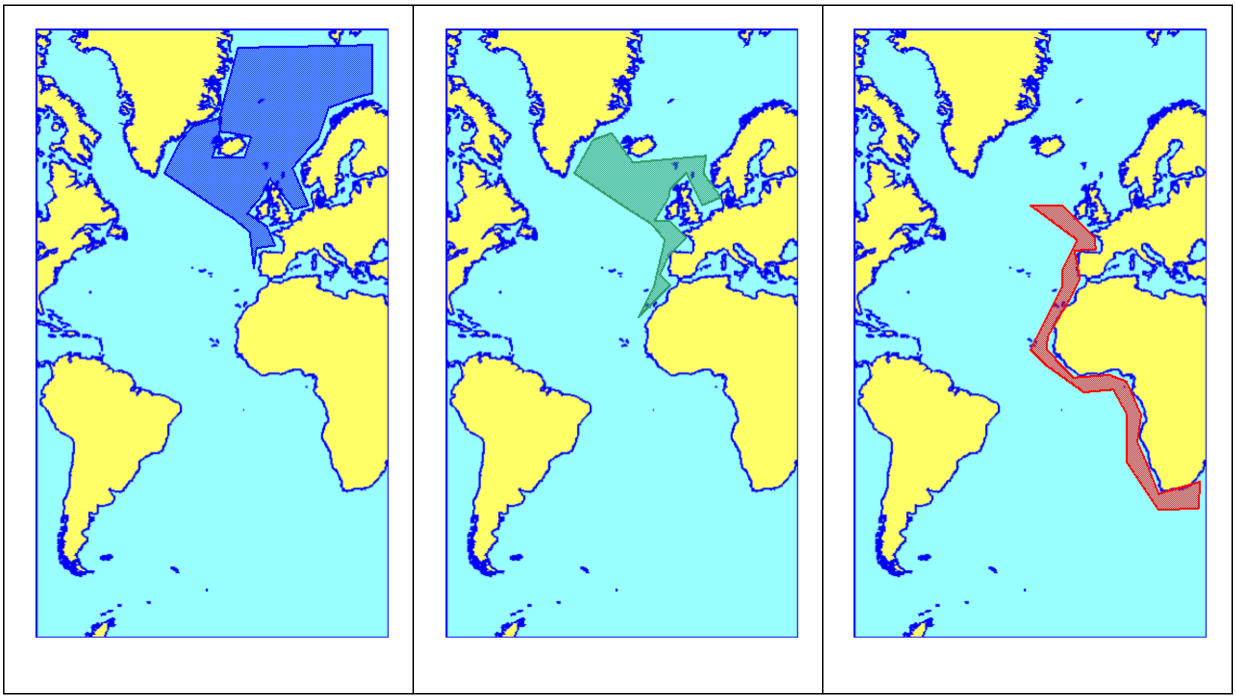

Figure 4 – Typical bio-geographic distribution area of boreal (left map), temperate (central map) and subtropical species (right map) encountered in the Bay of Biscay as sampled by the bottom-trawl surveys carried out yearly by Ifremer since 1987.

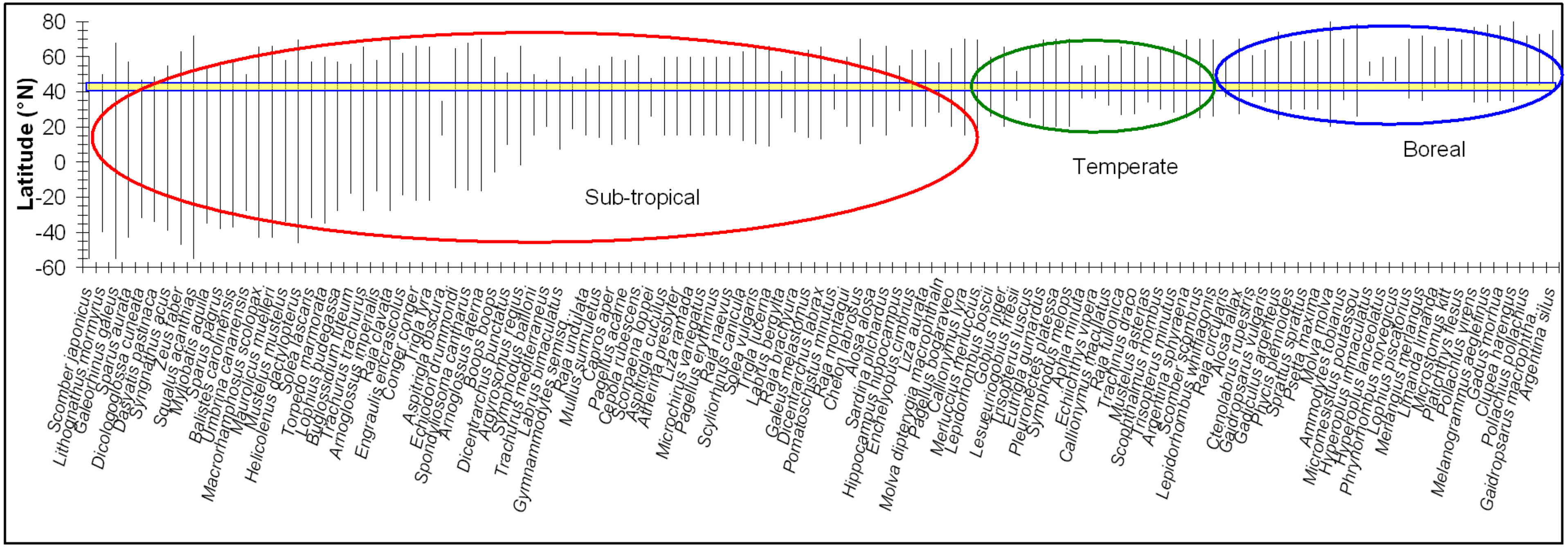

Figure 5 - Latitudinal distribution area of the boreal (right circle), temperate (middle circle) and subtropical species (left circle) encountered in the Bay of Biscay as sampled by the bottom-trawl surveys carried out yearly by Ifremer since 1987 : maximal, mean and minimal latitude values.

Based on this description of species, it is possible to classify them into three groups:

- those with affinity for waters colder than those observed in the Bay, corresponding to boreal species, with the mean latitude of the distribution area located above the northern limit of the Bay;
- those with affinity for waters warmer than those observed in the Bay, corresponding to sub-tropical species, with the mean latitude of the distribution area located below the southern limit of the Bay; and
- those with affinity for temperate waters such as those observed in the Bay, corresponding to species with the mean latitude of the distribution area located within the Bay limits.

The temporal variations of the total abundance within these groups were assessed from bottom-trawl survey data collected yearly by Ifremer since 1987 (except in 1991, 1993 and 1996) with an internationally standardised protocol. Results of this analysis showed that, while between 1987 and 1992, a relative equilibrium was observed for the three groups, the abundance of subtropical species staying within the range over which that of the two other groups varied, from 1994 onwards, the sub-tropical species group became dominant (Figure 6). In fact, after 1992, the abundance of the subtropical species was always greater than the upper bound of the range of variation in abundance of the two other groups.

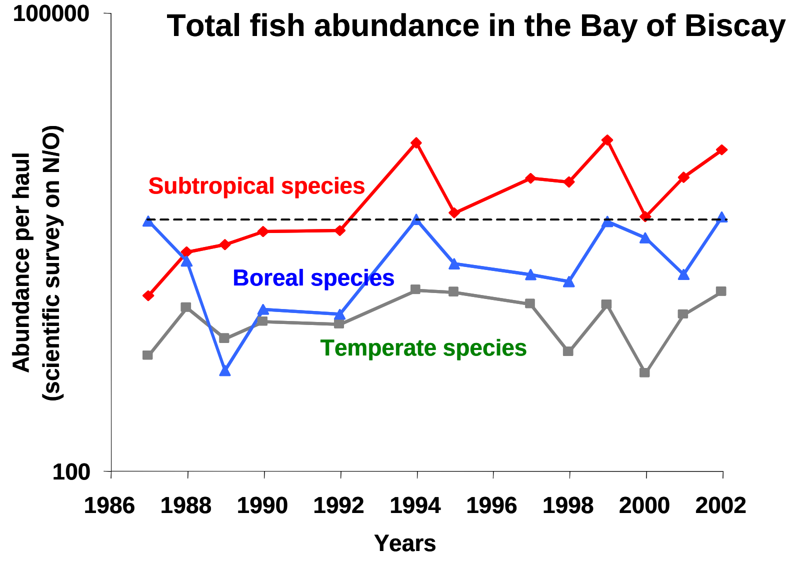

Figure 6. Temporal variations of the total abundance (log abundance per standardised trawl haul) of sub-tropical, temperate and boreal species in the Bay of Biscay, sampled from the bottom-trawl survey « EVHOE » carried out by Ifremer with the Research Oceanograhic Vessel Thalassa I. After 1992, the abundance of the subtropical species was always greater than the upper bound of the range of variation observed in abundance of the two other groups.

This change of the fish community with increasing dominance of the species with affinity for warm waters occurred simultaneously with an increase in the sea temperature, observed in the entire water column (Figure 7). Based on data compiled from different sources, the observed increase was estimated at approximately 1.5°C since 1970 in the upper 50 meters depth and approximately 0.8°C in the 50-200 m depth layer. The temperature increase was stronger in the 1990s.

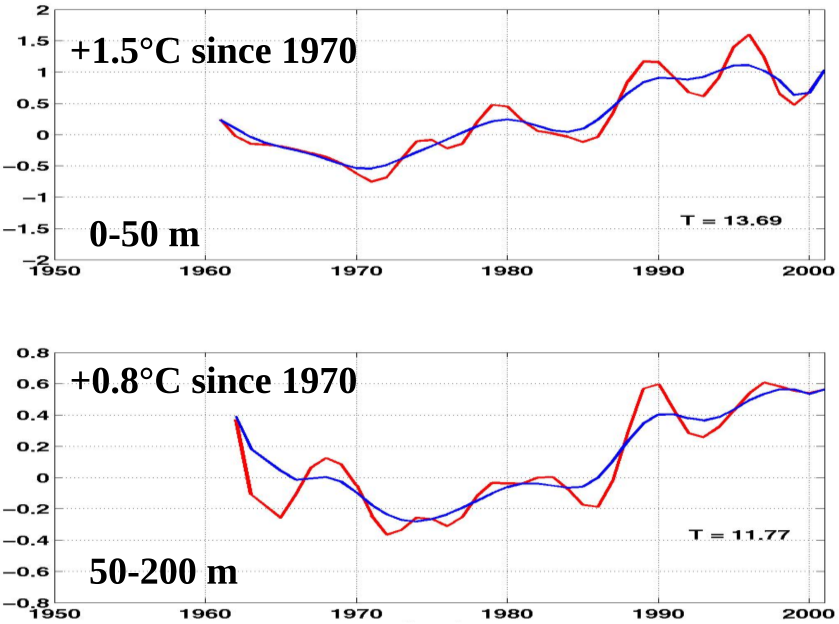

Figure 7. Temporal variations of the temperature anomalies of the water column between 0 and 50 m (upper figure) and between 50 and 200 m (bottom figure) in the Bay of Biscay (5 and 10 years smoothing); T is the mean value observed within the time series; http://www.ifremer.fr/gascogne.

In addition, analysis showed that the dominant pelagic species with low trophic levels, such as anchovy (*Engraulis encrasicolus*) and horse and common mackerels (*Trachurus* spp, *Scomber* spp), were found within the warm-water affinity group of species, while the large demersal species with high trophic levels that were historically the target species of European fisheries, such as haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*), dab (*limanda limanda*), pollack and saithe (*Pollachius pollachius* and *Pollachius virens*), and megrim (*Lepidorhombus*), were found among the species of the cold-water affinity group. This probably contributes to explain the increase in the abundance ratio of pelagic species while the trophic level of the community decreased (Figure 8).

The observed changes in the composition of the fish community could thus be interpreted as resulting not from climate change only but rather from the combined effects of fishing and warming. Changes would result, on the one hand, from the depletion by overexploitation of large predator boreal species, which are both disadvantaged by warming, and less resilient to excess harvesting, and on the other hand, from the increase in smaller sub-tropical species, of lower trophic level, that are favoured by warming, and present greater resilience than larger species to fishing mortality. Changes in the relative abundances of these species would then explain the modifications in their relative attractiveness for commercial fisheries, leading to the evolution of harvesting patterns observed over time, with a growing share of fast growing, small size, lower valued fish in the landings originating from the Bay. This would concur with the expected behaviour of a multi-species fishery where fishing firms can freely re-allocate their effort across species, even under a limited entry scheme (see Thébaud and Soulié, 2008, for a modelling approach of such behaviour). In this case, however, the dynamics could be reinforced by the role of global warming.

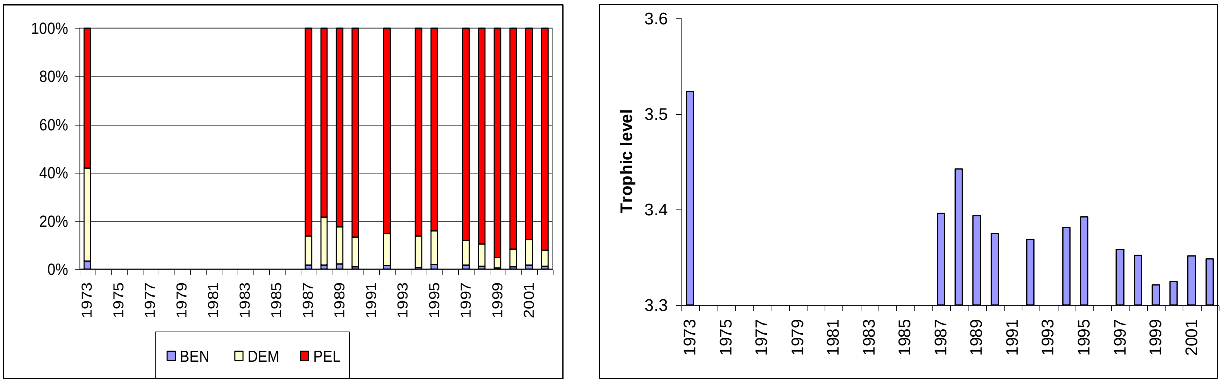

Figure 8. Patterns of change in the fish community of the Bay of Biscay as sampled by bottom-trawl surveys. Left, temporal variations of the relative abundance of groups of species benthic (BEN), demersal (DEM) and small and medium pelagic (PEL). Right, temporal variations of the mean trophic level of the fish community.

Perspectives

Landings by French fleets from the Bay of Biscay have been strongly modified over the last three decades, with an important increase in the share of pelagic species. This has entailed a reduction in the total value of landings.

The fact that the main demersal species of commercial interest in the Bay of Biscay, as well as in all the North-Eastern Atlantic waters, have been subject to excessively high levels of fishing mortality has been known for some time. These species are often boreal, hence they have probably also been disadvantaged by the warming of the waters. Effects of climate change on the fish community of the Bay of Biscay has also been observed (Blanchard and Vandermeirsch, 2005; Poulard and Blanchard, 2005), as well as for the fish community of the North Sea (Perry *et al.*, 2005). It thus seems that changes in the components of the marine ecosystems exploited by fisheries, due to both direct and ecosystems effects of fishing, may be re-enforced by climate change.

Part of the changes observed in the composition of landings may be related to these ecosystem changes. Modifications in the relative abundance of species must have led to modifications in their relative attractiveness in economic terms, leading to shifts in effort between species and to new patterns of harvesting. This would have played all the more strongly as a regulated open access situation prevailed, which most often allowed firms to shift freely between target species. The consequences of these changes in value terms have been important, as a large part of the drop in prices paid for the fish landed by French fleets can be attributed to the larger proportion of lower-priced fish in the landings. However, the evolution of gross turnover for these fleets has also been strongly affected by the changes in the marketing conditions in Europe over the past fifteen years, leading to increased competition internationally, and to lower prices paid, even though quantities landed are now lower than twenty years ago.

The fact that these observations were arrived at in a particular, temperate, ecosystem, in the economic and regulatory context of Europe and France, begs the question of the generality of this case study. The research partly confirmed results from studies carried out in the whole north Atlantic Ocean, from Canada to Norway (Hamilton, 2007). However, the study of the combined effects of various drivers on the evolution of marine ecosystems and the associated fisheries has mostly taken place in temperate or boreal systems. In systems where the ecological characteristics of species, which define their resilience to fishing and their thermal tolerance, are different, it is not clear that similar observations would be made about the respective roles of fishing and warming on fish communities. Similarly, the consequences of ecosystem changes for the economic viability of fisheries are bound to differ accross different economic and regulatory contexts. Multi-disciplinary research projects based on the comparative analysis of trends in fish communities and the associated fisheries, taking case studies from contrasted systems, would contribute to a better understanding of these issues[ix].

Acknowledgements

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Endnotes

[i] Integrated approach of economic and ecological drivers on various ecosystem components of the Bay of Biscay continental shelf as part of Ifremer's "Défi Golfe de Gascogne" (http://www.ifremer.fr/gascogne/) ; project funded under the French Biodiversity Institute's program on "Global change and biodiversity" (Compared analyses of temporal trends in fish community and landing structure in the Bay of Biscay) ; "Chaloupe" project (Ecological and economic drivers of changes in demersal communities and fisheries systems in three continental shelves : Bay of Biscay, Southern Morocco and the French Guiana, see http://www.projet-chaloupe.fr).

[ii] See Steinmetz et al., 2008 for a detailed presentation of the data used.

[iii] http://www.ices.dk/fish/statlant.asp

[iv] Anchovy (*Engraulis encrasicolus*); Cuttlefish (*Sepia officinalis*); Hake (*Merluccius merluccius*); Monkfish (*Lophius piscatorius* and *budegassa*); Nephrops (*Nephrops norvegicus*); Pollack (*Pollachius pollachius*); Sardine (*Sardina pilchardus*); Seabass (*Dicentrarchus labrax*); Sole (*Solea solea*).

[v] See Thébaud and Soulié (2008) for a formal discussion of the economic process underlying such sequential harvesting patterns.

[vi] Fisher indices are calculated as the geometric mean of Paasche and Laspeyres indices, the former using the most recent year as a base, while the latter uses the first year of the series as a base to weight the contribution of each species to the average value of the variable under consideration. For example, a Fisher index of changes in the price of landings is calculated as follows:

$$F^{p}_{t/0} = \sqrt{\frac{\sum (p_{i,t}.q_{i,0})}{\sum_{i} (p_{i,0}.q_{i,0})} \times \frac{\sum (p_{i,t}.q_{i,t})}{\sum_{i} (p_{i,0}.q_{i,t})}}$$

with $p_{i,t}$ the price of species i at time t, $q_{i,t}$ the volume landed of species i at time t, and 0 the initial time period A similar equation is used to calculate the Fisher index of quantities.

[vii] Steinmetz (2004) analyzed this structural change in detail for the different species landed by French fleets.

[viii] See Steinmetz *et al.* (2008) for more details.

[ix] This was the aim the “Chaloupe” project, funded by the French Research National Agency, which investigated these questions based on a comparative approach for three contrasted case studies: the continental shelf of the Bay of Biscay, the tropical shelf of French Guiana and the sub-tropical shelf of south Morocco.

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A bio-economic analysis of long term changes in the production of French fishing fleets operating in the Bay of Biscay

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Abstract – Selective fishing pressure on more highly valued marine living resources is one of the key factors proposed to explain changes occurring in fish communities and associated landings of commercial fisheries. The aim of this paper is to establish the nature of changes in the landings of French fishing fleets operating in the Bay of Biscay in the period 1973-2002, and whether these changes could be related to the relative economic attractiveness of different fish species. The analysis focuses on trends observed in the landings of all commercial fish species over the last three decades. It is based on data of annual quantities landed and ex-vessel prices compiled from official French landings records, and on bio-geographical descriptors of these species derived from published data. Using simple index numbers and multivariate analysis, we examined changes in total landings in terms of their volume and value, as well as changes in their composition. We show that the composition of landings significantly changed over the study period, with an increase in the proportion of pelagic species, of lower economic value. The average ex-vessel price of production by the fleets tended to decrease from the late 1980s; partly due to a cross-species drop in prices, occurring mainly after 1993, but also to the increased proportion of low-priced species in the landings. This caused a significant drop in the total gross value of production in the second half of the study period.

Key words: French fisheries production / Bio-economic analysis / Long-term changes / Bay of Biscay / North-Eastern Atlantic

Résumé – Analyse bio-économique des changements de long terme de la production des flottilles de pêche françaises opérant dans le golfe de Gascogne. La pression de pêche sélective sur les ressources marines vivantes de forte valeur est un des facteurs-clés proposés pour expliquer les changements qui surviennent dans la structure des communautés de poisson et dans les débarquements des pêcheries commerciales associés. L'objectif de cet article est d'établir la nature des changements dans les débarquements des flottilles de pêche françaises opérant dans le golfe de Gascogne, et d'examiner les relations entre ces changements et l'attractivité relative des espèces de poisson d'un point de vue économique. L'analyse se concentre sur les tendances observées au cours des trois dernières décennies dans les débarquements de toutes les espèces commerciales de poissons effectués par les flottilles de pêche opérant dans le golfe. Elle s'appuie sur des données concernant les quantités annuelles débarquées, les prix compilés à partir des enregistrements officiels des débarquements français, et les données publiées concernant les caractéristiques biogéographiques des espèces étudiées. En s'appuyant sur des indices simples et une analyse multivariée, on examine les changements des débarquements totaux en volume et en valeur, ainsi que les changements dans leur composition. On montre que la composition des débarquements a fortement changé au cours de la période étudiée, avec un accroissement important de la part des espèces pélagiques, de plus faible valeur. Le prix moyen de la production a eu tendance à décroître depuis la fin des années 1980. Ceci est en partie dû à une chute des prix de l'ensemble des espèces, après 1993, et en partie lié à l'accroissement de la part des espèces de plus faible valeur dans les débarquements. Une baisse importante de la valeur de la production en a découlé sur cette deuxième moitié de la période d'étude.

1 Introduction

In many fisheries around the world, major changes have been observed in the composition of fish landings, such as a reduction in average individual size and the mean trophic level of fish caught (Pauly 1998). These changes have been considered to be a possible consequence of modifications in biological communities due to the effects of fishing on the ecosystem (National Research Council 2006). Such modifications were

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observed in the groundfish communities of the Bay of Biscay, following trawling surveys carried out by Ifremer with oceanographic research vessels. In addition to modifications in the size and trophic level of fish, potentially due to the effects of fishing, the survey data showed that subtropical fish species seemed to be favoured compared with more boreal ones. The combined effects of fishing and global warming were advocated to explain these observations (Poulard and Blanchard 2005; Blanchard and Vandermeirsch 2005; Blanchard et al. 2006).

Most studies to date have focused mainly on the ecological dimensions of composition changes in fish communities and the landings of associated fisheries, while the economic dimensions of these modifications have not been explored, particularly from an empirical standpoint. Few studies have focused on the economic drivers behind the sequential harvesting of different fish species in a community, and the economic consequences of changes in the landing composition. Thébaud and Soulié (2008) proposed a simple bio-economic model to examine these issues, although their approach remained theoretical. Sumaïla (1998) discussed the implications of taking into account economic characteristics of the production extracted from marine communities, underlining the role of market responses in the determination of overall economic impacts of changes in landing composition. Pinnegar et al. (2002) analyzed this in the context of the Celtic Sea fisheries, showing that there had been a long-term decrease in the average trophic level of fish landings from this area. This trophic change was accompanied by changes in the relative price of species landed reflecting a modification in the relative availability of species at different trophic levels. Species of low trophic level became increasingly abundant in landings, relative to species of high trophic levels, leading to the relative price of the former decreasing, for a given demand for these species. Steinmetz et al. (2006) analyzed the long-term trends in the landings of all species caught by French commercial fishing fleets in the North-East (NE) Atlantic, looking at the ecological descriptors of landings, their economic value and the relationships between the composition of landings and their economic value. These authors concluded that a more in-depth analysis was required to assess the nature and extent of interactions between changes in landings and economic variables such as the relative prices of landed species.

We analyze these interactions on long-term changes in the composition of landings by French fleets operating in the NE Atlantic. The analysis focuses on a selection of fish species, and covers the period 1973-2002. While our analysis centred on the fisheries of the Bay of Biscay. A comparison of trends was also made with those previously observed at the larger scale of the NE Atlantic. We analyze the relationships between the ecological status of species composing the production of fishing fleets, the relative prices of these species, and the economic value of landings, at these two scales.

2 Materials and methods

The analysis was based on existing data on the evolution of landings of a selection of marine species by French fleets operating in the NE Atlantic, and more specifically in the Bay of Biscay (ICES areas VIIIa,b), over the period 1973-2002. Species selected for the analysis were restricted to marine fishes cited in landings records for French fleets operating in these two areas (see Appendix for the list of species)[1].

Table 1. Origin of the data used in the analysis.

	NE Atlantic	**Bay of Biscay (ICES[3] VIIIa,b)**
1 Landings by species (tons)	Cahiers CCPM[1], OFIMER[2], DPMA[4] coupled with FAO[5] data	ICES[3] VIII a,b landings data
2 Price per species (euros, 2002)	Cahiers CCPM[1], OFIMER[2], DPMA[4]	
3 Ecological descriptors of fish species	FishBase, Quéro and Vayne (1997)	

[1]French Central Committee of Maritime Fishing; [2]French National Interprofessional Office of Sea Products and Aquaculture; [3]International Council for the Exploration of the Sea; [4]French Maritime Fishing and Aquaculture Directorate; [5]Food and Agriculture Organization.

Table 1 lists the sources of the different data sets used in the analysis. Data used concerned: (i) annual production in volume and mean ex-vessel price per species, originating from the NE Atlantic and the Bay of Biscay and landed by French fleets and (ii) descriptors of the bio-geographic characteristics of each species.

Two sources of data were used for fisheries production. Firstly, annual reports of French landings established by the French Marine Fisheries and Aquaculture Directorate in collaboration with the agency for fisheries products (*Office des Produits de la Mer*) and the Central Committee for Maritime Fisheries, were used to construct a dataset of French production originating from the NE Atlantic over the study period. This information concerned both the volume of annual landings and average annual first sale prices of fresh fish per species. Because records were only available at the national level, other sources of information were used to exclude landings originating from other areas, particularly the Mediterranean. Such data sources included the FAO catches and landings data per area[2], and expert knowledge from French fisheries specialists. Current prices for landings from the NE Atlantic were converted to constant prices, using the French consumption price index, with 2002 as the base year.

Secondly, official data on landings by French fleets of the same species originating from the Bay of Biscay (ICES area VIII a, b) were extracted from the ICES database[3]. Information available in this database concerns annual tonnage landed per species for the production of French fisheries in the NE Atlantic, with the exclusion of year 1999 for which no official data was available. In the absence of alternative sources of information covering the same time period, average prices recorded for landings of fresh fish caught in the NE Atlantic

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[1] Analysis of trends observed in the landings of a larger selection of species, including shellfish and molluscs, by the same fleets, is presented in Steinmetz et al. (2006).

[2] http://www.fao.org/fi

[3] http://www.ices.dk/fish/statlant.asp

were used to calculate the value of landings originating from the Bay of Biscay. The assumption here, which we were not able to verify, is that both the relative ex-vessel prices of fish species and the trends registered in these prices were similar at the two scales[4].

While the data sets included all major commercial species listed in the annual reports, the data used for the present analysis concerned only 57 fish species for which information was available. Taken together over the 1973 to 2002 period, landings of these species constituted 50% of the total volume of French landings originating from the Bay of Biscay, and 78% of the total volume of French landings originating from the NE Atlantic. French landings of these species originating from the Bay of Biscay represented on average 24% in volume of the total annual landings from the bay, a proportion which remained relatively stable throughout the period, following a slight increase in the late 1970s.

In order to characterize the production of French fleets from an ecological perspective, analysis of bio-geographic characteristics of fish species was included (Table 1); these were extracted from FishBase and from Quéro and Vayne (1997).

Analysis methods

The analysis was carried out in three steps. First, trends observed in the total volume and value landed by the French fleets were analysed based on Fisher indices of changes in the volume, prices and value of production. Indices were calculated and compared at the two scales of analysis: NE Atlantic and Bay of Biscay.

Fisher indices were calculated as the geometric mean of Paasche and Laspeyres indices. The Paasche index uses the most recent year as a base while the Laspeyres index uses the first year of the series as a base in weighting the contribution of each species to the average value of the variable under consideration. For example, a Fisher index of the volume of landings is calculated as follows:

$$F^q_{t/0} = \sqrt{\frac{\sum_i (p_{i,0} \cdot q_{i,t})}{\sum_i (p_{i,0} \cdot q_{i,0})} \times \frac{\sum_i (p_{i,t} \cdot q_{i,t})}{\sum_i (p_{i,t} \cdot q_{i,0})}}$$

where $p_{i,t}$ is the price of species i at time t, $q_{i,t}$ the volume landed of species i at time t. A similar equation was used to calculate the Fisher index of prices. Using the Fisher index minimizes potential biases arising from the influence of the base chosen to weight the contributions of each species according to changes in the average price or volume of landings. Given that the analysis considered a fairly long time period, during which significant changes could be observed in the structure of production in terms of volume and/or relative prices, our use of this index allowed us to characterize the overall changes in prices and volumes landed while minimizing bias due to structural changes. We also used the property of equivalence between the product of the Fisher price and volume indices and the simple value index (Diewert 1996), to assess the relative contribution of changes in prices and volumes to the overall change in value over the time period.

The second step of the analysis was to explore the associated changes in the composition of landings underlying the modifications observed in total production. This was done by first analyzing trends in landings of species by group, distinguishing benthic, demersal and pelagic species. To test for significant long-term trends, non-parametric Mann–Kendall tests were performed (Gilbert 1987). The Mann–Kendall test is particularly useful because data need not conform to any particular distribution. Where a significant linear trend was indicated, the true slope (change per year) was estimated using the procedure developed by Sen (1968). Secondly, simple indices of the biogeographic characteristics of landings were calculated at the two scales of analysis using the following indicators: (1) maximal length of individual fish of each species, (2) trophic level of each species at the adult phase and (3) median latitude of the area over which the species is known to be distributed.

Weighted averages of these variables were calculated based on the proportion of each species in total landings of the 57 fish species considered.

The third step was to carry out a multivariate analysis of the evolution of landings. Correlations between changes in the composition of landings and the ecological characteristics of landed species were first investigated using principal component analysis (PCA). In order to capture the dynamics of exploitation, years of landings (30 for the NE Atlantic, 32 for the Bay of Biscay) were used as active variables in the analysis, with individual observations corresponding to each of the 57 species. The analysis was centred and normalized. As our objective was to study the evolution of the structure of landings, i.e. the relative contribution of each species to total landings, years of landing (variables) were uniformly weighted in the analysis, whereas species (observations) were weighted according to their respective proportions in the total volume landed over the period. Then, we used bio-geographic descriptors of the species as illustrative variables in the analysis, to establish the nature of correlations between these descriptors and the years of landings. The descriptors included for each species were: the Von Bertalanffy growth coefficient; maximum weight, length and age; trophic level; and median latitude and longitude of the area over which the species is known to be distributed.

In addition, our analysis sought to establish whether correlations existed between the position of individual species in the past record of changes in production patterns, and the economic status of these species. This was done by defining a set of three price classes for individual species for which ex-vessel prices were available (35 out of 57 species): 1) species with high average prices over the period, 2) species with medium average prices over the period, and 3) species with low average prices over the period[5] (see this classification in Table 2 and Fig. 1). The price classes were then used to characterize

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[4] In principle, there could be differences in prices between the two scales, with higher prices observed for landings of fish caught in the Bay of Biscay, a greater proportion of which are marketed fresh after shorter fishing trips and are hence of better quality than fish caught offshore and landed frozen. As our analysis was restricted to fresh fish landings, these differences are probably limited.

[5] According to our classification of species, the intermediate price group is slightly smaller than the other two groups in terms of total

Table 2. Price data class (euros 2002).

0 : No price data	21 species
1 : Low price class [0–1.75]	14 species
2 : Medium price class [1.75–4]	11 species
3 : High price class [4–12.5]	10 species

Mean price by species through the period, using 2002 constant price data.

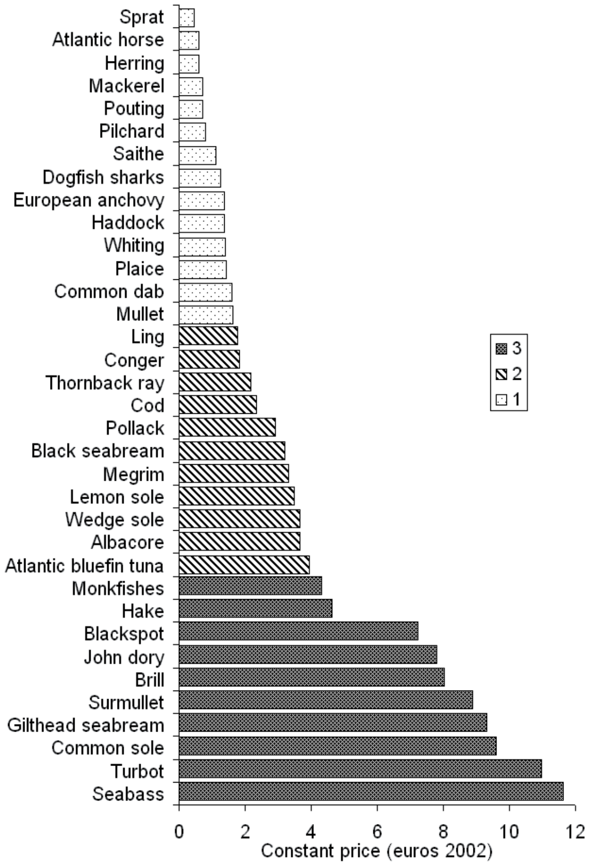

Fig. 1. Mean constant price per species, sorted by price class. Source: IFREMER, based on ICES and CCPM-OFIMER-DPMA data (see Table 1).

individual species in the first space of the PCA, and this was used to assess whether relations existed between the evolution in the structure of landings and the relative prices of the species.

3 Results

Results of the analysis are presented in the following order: first, the overall trends observed in the total volume and value of landings by French fleets at the two scales of analysis are described using the indices defined above; second, changes in the species composition of these landings are analyzed, and the nature of these changes considered, based on ecological descriptors of the species; third, the results of the multivariate analysis of modifications in landing composition, and their relations with the economic characteristics of the fish species are presented and discussed.

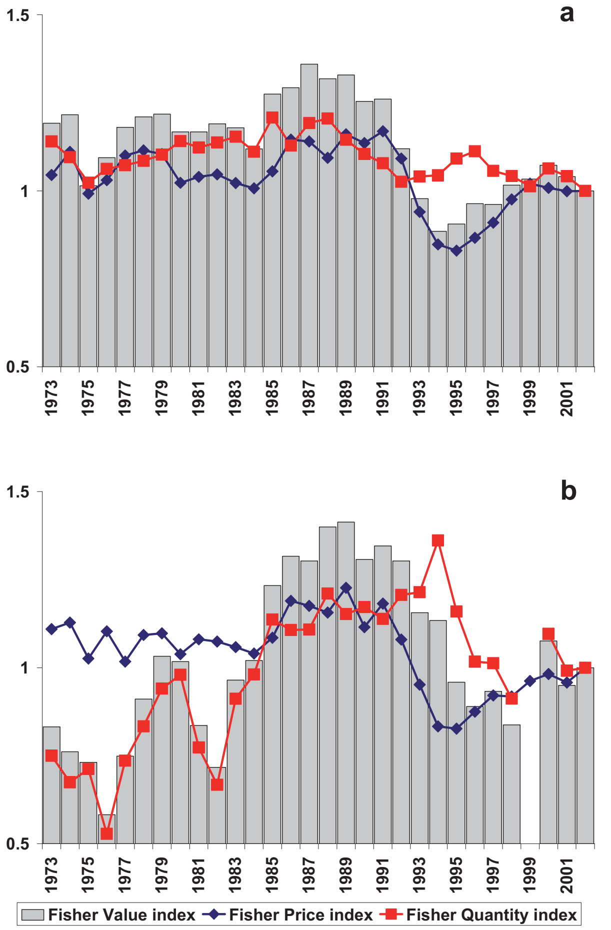

Fig. 2. Evolution of Fisher indices of the volume and value of total fish landings by French fleets fishing in (a) the NE Atlantic, 1973-2002 and (b) the Bay of Biscay, 1973-2005 (2002 fixed base and 2002 prices).

3.1 Volume and value trends in total landings of fish species

3.1.1 North-East Atlantic (Fig. 2a)

The trends observed in the volume and value indices of landings of fish species originating from the NE Atlantic by French fleets are studied over the 1973-2002 period (Fig. 2a).

The total tonnage of fish landed reached a maximum in the mid-1980s and decreased from 1988, reaching lower levels in 2002 than in 1973. Following a period of relative stability, total value tended to increase in the late 1980s, reaching a maximum in 1987. This resulted in part from a steady increase in ex-vessel fish prices. The value of landings was then severely reduced, reaching a minimum in 1995. While this was initially caused by a decrease in volumes landed, the collapse of the gross revenue of French fleets also resulted from a major drop

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weight of landings, while the high and low price groups have a similar weight throughout the period.

in prices at first sale on the French market during the early 1990s (Steinmetz et al. 2006). This crisis was due to the liberalization of trade in fish products on the European markets on which fleets operate, leading to modifications in the conditions of competition between fish products on these markets and an increased sensitivity of trade to exchange rates between European currencies (Guillotreau and Péridy 2000). From 1996 onwards, the value of landings increased again, but not enough to fully compensate for the earlier drop.

3.1.2 Bay of Biscay (Fig. 2b)

The trends observed in the volume and value indices of landings of fish species originating from the Bay of Biscay by French fleets over the 1973 to 2002 period were also considered (Fig. 2b). Total tonnage of fish landed increased strongly until the mid-1990s, after which it started to decrease. Fluctuations in the landed value were greater at the scale of the Bay of Biscay than for the NE Atlantic as a whole, and tended to increase during the period 1983-1989, reaching a maximum in 1988-89. Landed value was then severely reduced during the years of market crisis, reaching a low point in 1998. While this collapse was initially due to the drop in prices already mentioned, it was further reinforced by a strong reduction in volumes of fish landed. At the end of the period, the total value of landings originating from the Bay of Biscay was however higher than in 1973.

Comparison of the two time series shows that a greater proportion of the total value of landings by French fleets originated from the Bay of Biscay during the first part of the period: (1973-1994). The ratio of the value of landings from the Bay of Biscay to the value of landings from the NE Atlantic moved from 23% to 45% in this time period. In the second part of the study period (1995-2002) this ratio fell, so that it was only 33% in 2002. This is possibly because offshore fleets maintained and even increased their production while landings by inshore fleets, restricted to operating in the bay, declined severely. The reduction in inshore fleet size due to capacity reduction schemes (Thébaud et al. 2006) would have made a particular contribution to this effect.

3.2 Species composition of landings

Landing composition was first considered in terms of the contribution of different species groups to total production volume. The evolution of landings by French fleets are displayed at the two scales of analysis, considering three groups of species: benthic fishes (BEN), demersal fishes (DEM) and pelagic fishes (PEL). Estimated overall trends in landings for these three groups are presented (Table 3).

Overall, there was a marked decrease in the proportion of demersal fishes in landings by French fleets in the NE Atlantic over the study period, starting from the late 1980s. This was partly compensated by a slight, but temporary, increase in the proportion of benthic fishes, some of which fetch high prices. Composition of landings was mainly affected by a strong increase in the proportion of pelagic fishes, which approximately doubled over the study period.

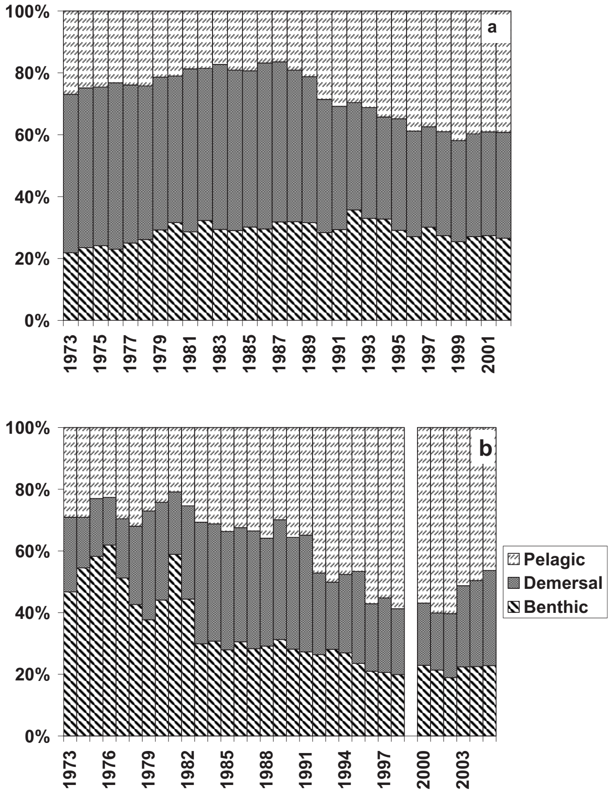

Fig. 3. Evolution of the composition of total fish landings by French fleets, originating from (a) the NE Atlantic, 1973-2002 and (b) the Bay of Biscay, 1973-2005 (the bathydemersal group, including only monkfish, has been added to the benthic group here).

A similar decline in the proportion of demersal fishes caught by French fleets in the Bay of Biscay was observed from the early 1990s (the group moved from 20% of landings in 1973, to 40% in 1990, then down to 20% in 2002). There was also a strong reduction in the proportion of benthic fishes, which moved from 45% of landings in 1973 to only 20% in 2002. There was a large increase in the proportion of pelagic fishes in the landings, starting in the 1980s: while the pelagic group represented 21% of landings in 1981, it accounted for 60% of production in 2002.

3.2.1 Bio-geographic descriptors

The evolution of the mean trophic level of landings (Fig. 4), the mean maximum length of the landed species (Fig. 5), and the average of the median latitude of areas over which the landed species are known to be distributed (Fig. 6) are described below.

Following a period of high and relatively stable mean trophic level of the species landed until the late 1980s, a marked decrease in this index was observed for both time series. The early 1990s showed a particularly significant drop in the mean trophic level of species landed, indicating a change in the composition of landings, with an increase in the proportion of species from lower trophic levels. This is possibly due to changes in fishing strategy in response to the market crisis: an attempt was made to compensate for the sharp decreases

Table 3. Trends in French landings (tons per year) of the three groups of species.

	Bay of Biscay	NE-Atlantic
Benthic fishes	↘ **(-842 tons per year)	→
Demersal fishes	→	↘ **(-3363 tons per year)
Pelagic fishes	↗ **(+982 tons per year)	↗ **(+2027 tons per year)

(*) Indicates the significance to 5% (** 1%) of the Mann-Kendall trend test; the Sen's slope is indicated in the brackets.

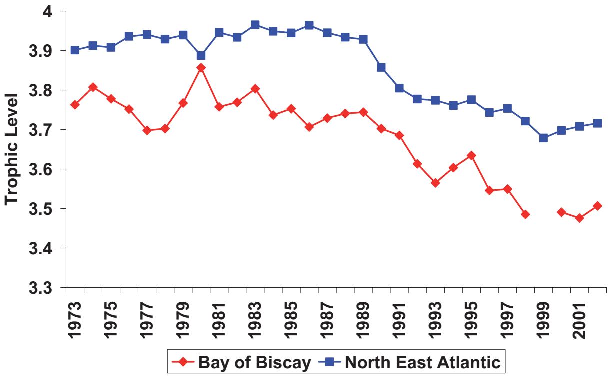

Fig. 4. Evolution of the mean trophic level of fish species landed by French fleets, originating from the Bay of Biscay and NE Atlantic areas, 1973-2002 (data for the year 1999 is missing from the ICES landings database).

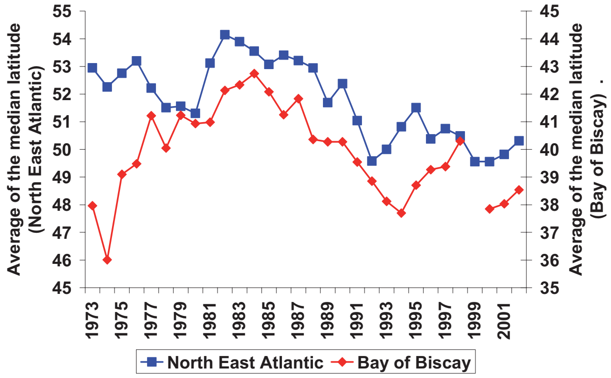

Fig. 6. Evolution of the mean latitude of distribution area of the fish species landed by French fleets, originating from (red diamonds, right axis) the Bay of Biscay and (blue squares, left axis) the NE Atlantic area, 1973-2002.

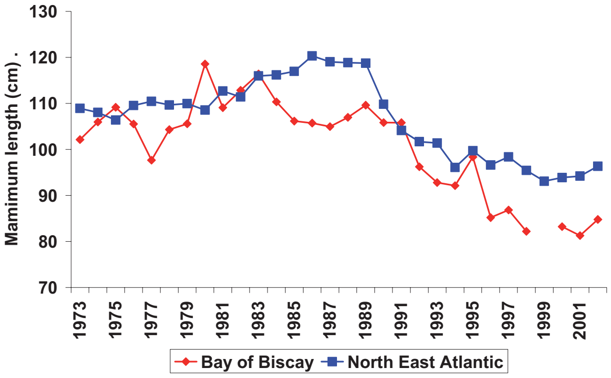

Fig. 5. Evolution of the mean maximal length of the fish species landed by French fleets, originating from the Bay of Biscay and NE Atlantic areas, 1973-2002.

in price imposed on French fleets, by an increase in volumes landed. The decline in this index continued in both areas until the end of the study period. Overall, the NE Atlantic index declined from 3.95 in the late 1980s to 3.7 in 2002. In the Bay of Biscay, there was a similar decline from 3.85 in 1980 to 3.5 in 2002.

The maximal length index (Fig. 5) also illustrates the modifications that have occurred in the composition of landings throughout the period. The evolution of this index shows a trend similar to that observed for the trophic level index: following a period of increase in the NE Atlantic and stagnation in the Bay of Biscay until the mid 1980ies, the index decreased steadily in the second half of the study period in the two areas.

The latitudinal index (Fig. 6) provides indications as to the potential influence of changes in climate and/or changes in the spatial distribution of fishing effort on modifications in the composition of landings. The index shows a declining trend starting in the mid 1980s for the two areas. In the NE Atlantic, the index reached its maximum in 1982 at 54° and fell to 50° in 2002. In the Bay of Biscay, the index reached a peak in 1984 with 42.5° and lost four degrees at the end of the study period. We are not aware of any major redistribution of fishing effort towards the South by French fleets over the study period; hence these trends probably reflect the changing composition of fish communities due to changes in the relative abundance and/or accessibility of species in the areas considered, favouring the catch of sub-tropical species. This observation concurs with those derived from fishery-independent surveys on changes in the relative abundance of fish species in the fish community of the Bay of Biscay (Poulard and Blanchard 2005).

Overall, the three indices show that modifications in the composition of landings can be related both to changes in the strategies of fishing operators in response to changes in the economic conditions under which fleets operate, and to changes in the relative availability of fish species due to ecological factors. The following section presents an analysis of correlations between these modifications, the economic status of individual fish species, and total production by French fleets.

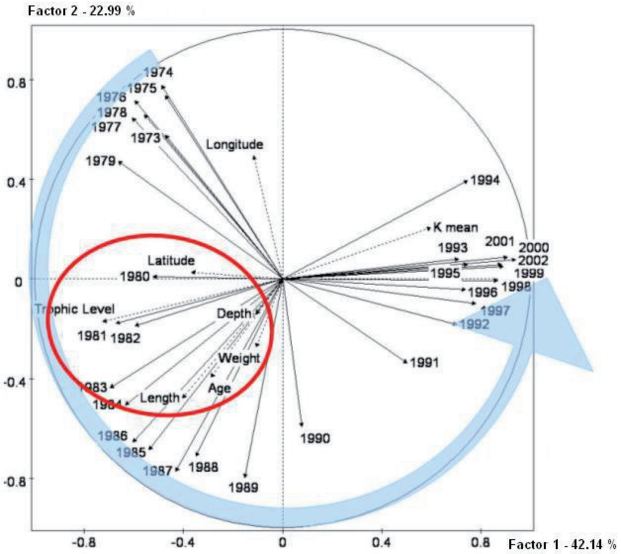

Fig. 7. Principal component analysis of the 30 active variables (years), 8 illustrative variables in the principal plane (first and second axes planes), for the NE Atlantic area.

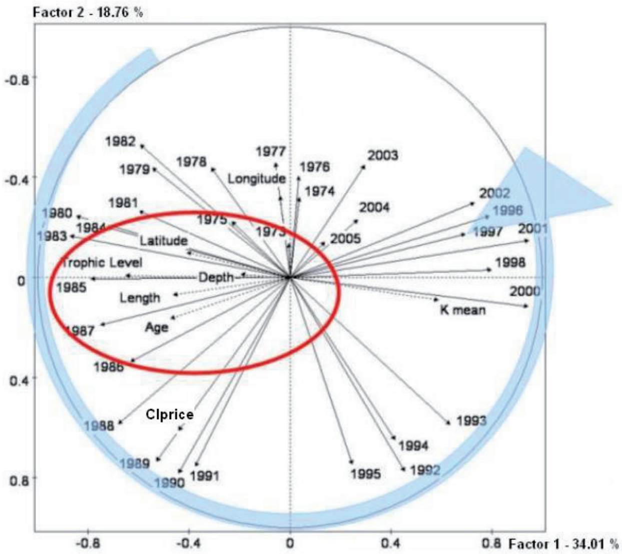

Fig. 8. Projection of the 33 active variables (years), 8 illustrative variables in the principal plane (first and second axes planes), for the Bay of Biscay area.

3.3 Multivariate analysis of changes in the structure of landings

3.3.1 NE Atlantic

The correlogram of landings-years is presented using the first two principal components resulting from the analysis representing 65% of total variance in the data for the NE Atlantic (Fig. 7). The sequence of changes in landings per year can be followed along the arrow. The beginning of the period starts in the upper-left hand part of the graph. The mid-1980s are represented in the lower-left-hand part. Years 1990-1992 are in the bottom-right-hand part of the graph and the end of the period is represented in the right-hand part (Fig. 7).

Correlations between illustrative variables (bio-geographic descriptors) and the principal components are stressed by the inner circle. Latitude appears strongly correlated with the first axis of the principal component analysis: this corresponds to the fact that exploitation of high latitude species culminated in the early 1980s, while the contribution of low-latitude species progressively increased in the years that followed it. Other descriptors such as trophic level, maximum length and maximum age are positively correlated with landings in the early 1980s, while the growth rate (K) of species is positively correlated with landings during the fisheries crisis years (1993-1994), and in the following years. The overall trends observed via descriptive analysis in the previous section are thus well summarized by the analysis presented here.

3.3.2 Bay of Biscay

The first three axes of the projection represent 34%, 18.8% and 15% of the variance in the Bay of Biscay data (Fig. 8). The sequence of changes in landings per year can be followed with the arrow. The first axis separates the mid-1980s from the 1998 to 2002 period, and the second axis isolates the 1988-1995 period.

The correlation of bio-geographic indices with the years of landings appears even stronger in this case than for the NE Atlantic. Mean latitude is positively correlated with landings at the beginning of the 1980s, and trophic level, maximum length and maximum age variables are strongly correlated with landings in the mid-1980ies.The growth coefficient variable was correlated with landings in the years around 2000. Again, changes observed in the composition of landings originating from the Bay of Biscay seem to be well synthesized by this analysis.

In this case, the price class of individual species (Fig. 1) was added as an illustrative variable (clprice) to the correlogram, in order to identify possible correlations between the years of landings and price categories of species. Highly priced species were mostly landed in the late 1980s whereas low priced species were exploited more recently (Fig. 8). Further analysis of this pattern is proposed below.

3.3.3 Correlations with the economic status of individual species in the Bay of Biscay

We examine the projection of the individuals in the first plane of the PCA for the Bay of Biscay case (Fig. 9, the size of the points is proportional to their contribution to the analysis).

This allows us to identify species such as sea bream or herring which have practically disappeared from landings over the period. The mid-1980s saw increases in the landings of pouting, followed by monkfish, a species of much higher price. The highest levels of landings of hake occurred towards the end of the 1980s. During the 1992-1995 crisis, landings of common sole reached their highest levels, and seem to have

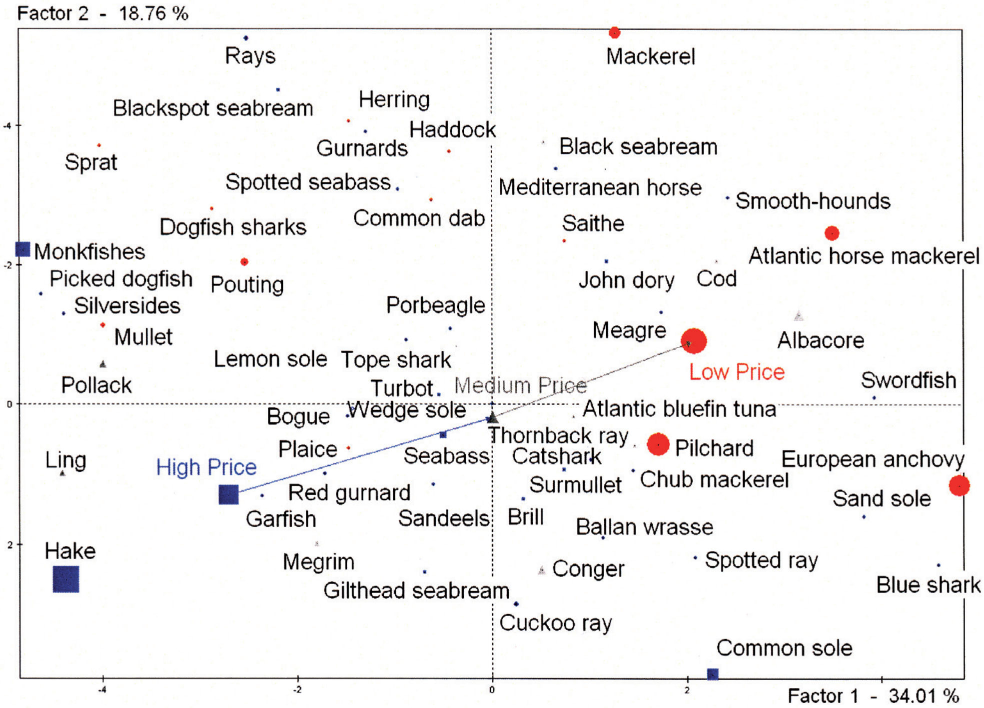

Fig. 9. Projection of the individuals (57 species) in the principal plane (first and second axes planes), for the Bay of Biscay area. Blue: high price calss, grey: medium price class; red: low price class.

played the role of a substitute species for fleets that were affected by the collapse of prices on the whitefish market. At the end of the study period, the highest exploitation levels for pelagic fish like anchovy, Atlantic horse mackerel, mackerel or albacore tuna are observed.

Using the price categories defined above, the projections of individual species in the first space of the PCA can be colour-coded, so as to assess whether correlations exist between the sequence of harvesting and the economic status of individual species. The projection including this price classification, and those from the centres of gravity of each of the three groups (low-, medium- and high-price species) are presented (Fig. 9).

While no conclusion can be derived concerning the medium-price group, the low-price group is clearly opposed to the high-price group in the projection. Largest landings of the low-price species were achieved during the later part of the time period, mainly from 1996 to 2002. On the other hand, the centre of gravity of the high-price group is located in the lower-left part of the space defined by the projection: largest landings for this group were achieved in the 1980s. In volume terms, the high-price group is mainly composed of species like hake, monkfish, sole or sea bass. John Dory (*Zeus faber*) is the main highly priced fish which appears in later years, but in small quantities.

The analysis thus lends support to the hypothesis that a correlation exists between the economic status of species caught in the Bay of Biscay and the sequence according to which they were harvested over the period 1973-2002. Overall, there appears to have been a transition during this period, from species fetching high prices on the market, to those fetching lower prices on the market.

4 Discussion

The results of this study can be used to further discuss the changes observed in the total value of production originating from the Bay of Biscay, as described by the index presented in Figure 2. Changes in the total value of landings can be explained as a consequence of three complementary factors: (i) changes in the total volumes landed; (ii) changes in the prices of the species landed; and (iii) changes in the relative weight of high/low price species in the total landings.

Total volumes landed have fluctuated significantly over the period considered. However, changes in the total value of landings have also resulted from modifications in the price index, due to changing conditions for the marketing of fish caught by French fleets rather than the fisheries themselves or their production. The relative influence of variations in price and volume of landings can be assessed using the ratio of logged Fisher indices over the logged value index. At the scale of the Bay of Biscay, the calculation for the year 2002 compared with 1989, showed that 42% of total value changes were due to price variations, and 58% to changes in quantities landed.

Modifications in the composition of landings have also played a role in the changes in value landed. Indeed, when the total value index reached its maximum in the late 1980s, landings of high-priced species were also at their maximum. At the lower level of the value index in 1998, high exploitation rates for low-priced species such as anchovy or pilchard were observed, while low exploitation rates of high-priced species such as hake or monkfish prevailed. Hence, modifications in the composition of landings, as illustrated in the previous section, contribute to explaining the reduced value of fish production from the Bay of Biscay between the late 1980s and 2002.

To quantify this structural effect, we can compare an index of the mean price of fish landed (defined as a simple average of individual species prices weighted by their annual contribution to total volumes landed), with a Laspeyres price index that weights individual species prices by their contribution to total volumes landed in 1989:

$$F^p_{t/0} = \frac{\sum (q_{i,0} \cdot p_{i,t})}{\sum_i (q_{i,0} \cdot p_{i,0})}.$$

Between 1989 and 2002, the index of mean price of fish landed by fleets operating in the Bay of Biscay moved from 1 to 0.56, while the Laspeyres price index moved from 1 to 0.80. The latter change provides an indication of what the drop in average price should have been, had the composition of landings remained the same between 1989 and 2002. From the mean price index, it is apparent that the drop in average price had indeed been much greater. This indicates that along with the overall reduction in prices across species, the growing proportion of low price species in total landings has exerted a downward pressure on the average price of fish production. The importance of this effect can be quantified by calculating the percentage of the drop in mean price, which can be explained by structural modifications in the composition of landings[6]: the part of the decrease in prices explained when the structure is kept unchanged is calculated as the log of the Laspeyres price index, with 1989 as a base, divided by the log of the mean price index. This percentage equalled 62% of the total mean price change between the two years, which in this case was a drop of 44%: two thirds of the reduction in mean prices are thus due to the increased proportion of low-priced species in the landings.

5 Conclusion

The analyses presented in this paper allow us to identify important changes in the total value of landings by French fleets operating in the NE Atlantic and Bay of Biscay during the last three decades. Three complementary factors may contribute to explaining such changes: (i) modifications of the total volumes landed; (ii) modifications of the prices of each of the species landed; and (iii) changes in the composition of the landings. The analyses presented in this paper show that all three factors have contributed to the evolution of the value of fisheries production in the case studied. Total volumes landed have fluctuated significantly over the period considered. The price index of fish landed by French fleets has also varied to a significant extent, due to external factors relating to the marketing conditions for fish in France. While these two factors seem to explain a large proportion of the variations in the total value of production, modifications in the composition of landings, probably due in part to changes in fishing strategies that have developed to face the changes in biological communities, have also contributed to the evolution of fishery production value. High priced species were mostly exploited in the early 1980s, with landings dominated by large boreal predator species such as monkfish or hake. In contrast, low-price species, such as anchovy or Atlantic horse mackerel, have dominated landings in more recent times (1996-2002). These species are characterized by lower trophic levels, smaller size and are more often sub-tropical. The lower value of landings in recent years as compared to the mid-1980s has partly resulted from this increase in the relative weight of lower valued species.

This case study of French fleets confirms that their production has been subject to species composition changes similar to those observed on wider scales. The inclusion of price data in the analysis allowed us to assess the implications of these changes in terms of the total gross value of production, and lends support to the hypothesis that the sequence of species harvesting is in part related to the relative economic attractiveness of fish species. Further work in this direction would involve quantification of the relative contributions of different factors to the overall evolution of gross fisheries production, and to the implications of these results for policy. Such work would particularly imply an analysis of the potential economic impacts of measures aiming to modify the composition of fishery landings.

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Appendix. List of species sorted by habitat and price class (average 1973-2002 ex-vessel price in constant 2002 euros). See Table 2 for the definition of price classes.

Common name	Scientific name	Price of fish (2002 euros)		
		Class 1	Class 2	Class 3
Bathydemersal				
Dogfish sharks	Squalidae	1.265		
Monkfishes	*Lophius* sp.			4.315
Benthic				
Black seabream	*Spondyliosoma cantharus*		3.198	
Blackspot seabream	*Pagellus bogaraveo*			7.218
Cod	*Gadus morhua*		2.353	
Herring	*Clupea harengus*	0.599		
John dory	*Zeus faber*			7.805
Meagre	*Argyrosomus regius*			
Picked dogfish	*Squalus acanthias*			
Pollack	*Pollachius pollachius*		2.913	
Pouting	*Trisopterus luscus*	0.725		
Tope shark	*Galeorhinus galeus*			
Whiting	*Merlangius merlangus*	1.400		
Demersal				
Bogue	*Boops boops*			
Brill	*Scophthalmus rhombus*			8.041
Common dab	*Limanda limanda*	1.593		
Common sole	*Solea solea*			9.601
Conger	*Conger conger*		1.822	
Cuckoo ray	*Leucoraja naevus*			
Gilthead seabream	*Sparus aurata*			9.322
Gurnards	*Trigla* spp.			
Haddock	*Melanogrammus aeglefinus*	1.372		
Hake	*Merluccius merluccius*			4.618
Lemon sole	*Microstomus kitt*		3.494	
Ling	*Molva molva*		1.770	
Megrim	*Lepidorhombus whiffiagonis*		3.322	
Plaice	*Pleuronectes platessa*	1.421		
Rays	Rajidae			
Red gurnard	*Aspitrigla cuculus*			
Saithe	*Pollachius virens*	1.124		

Appendix. Continued.

Common name	Scientific name	Price of fish (2002 euros)		
		Class 1	Class 2	Class 3
Sand sole	*Pegusa lascaris*			
Sandeels	Ammoditidae			
Seabass	*Dicentrarchus labrax*			11.628
Smooth-hounds	*Mustelus* sp.			
Spotted ray	*Raja montagui*			
Surmullet	*Mullus surmuletus*			8.892
Thornback ray	*Raja clavata*		2.159	
Turbot	*Scophthalmus maximus*			10.983
Wedge sole	*Dicologoglossa cuneata*		3.662	
Pelagic				
Albacore	*Thunnus alalunga*		3.668	
Atlantic bluefin tuna	*Thunnus thynnus*		3.941	
Atlantic horse mackerel	*Trachurus trachurus*	0.595		
Blue shark	*Prionace glauca*			
Chub mackerel	*Scomber japonicus*			
European anchovy	*Engraulis encrasicolus*	1.372		
Garfish	*Belone belone*			
Mackerel	*Scomber scombrus*	0.707		
Mediterranean horse mackerel	*Trachurus mediterraneus*			
Mullet	Mugilidae	1.634		
Pilchard	*Sardina pilchardus*	0.795		
Porbeagle	*Lamna nasus*			
Silversides	*Atherina* sp.			
Small-spotted catshark	*Scyliorhinus canicula*			
Spotted seabass	*Dicentrarchus punctatus*			
Sprat	*Sprattus sprattus*	0.448		
Swordfish	*Xiphias gladius*			
Recifal				
Ballan wrasse	*Labrus bergylta*			

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Analyzing the market position of fish species subject to the impact of long-term changes: a case study of French fisheries in the Bay of Biscay

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Abstract – Market position and its evolution were analysed in nine key fish and cephalopod species subject to long-term changes, using the Bay of Biscay fisheries as a case study. Although such long term changes have already been documented, and in some cases shown to be related to the impacts of fishing, changes in the physical environment, or both, relatively little work has been devoted to their potential consequences in economic terms. The nature and extent of these consequences was determined in the present study by looking at the composition of the affected fish production, and the status of different fish products on the markets. We propose a methodology to characterize market position for this set of nine species. The selected species represent a significant part of the gross turnover of French fishing fleets operating in the bay. These species were characterized in terms of their potential sensitivity to fishing and changes in environmental conditions due to global warming. We separated species potentially positively (*Engraulis encrasicolus* and *Lophius budegassa*) and negatively affected (*Pollachius pollachius* and *Lophius piscatorius*) by warming. Evolution of the value of production of the nine species was then depicted using analysis of macro-economic index (production and potential consumption) and price indices. This revealed the relatively high sensitivity of domestic production to the market crisis that occurred in France in the early 1990s, compared to imported and exported products. The relative position of individual species, with respect to the market and its evolution between 1990 and 2005, was analyzed by multi-factorial analysis. Results derived from the analysis clearly distinguish two groups of species, the first characterized by higher prices (monkfish, Nephrops, sole, seabass) and the second by larger volumes available on the French market (pollack, hake, anchovy, sardine, cuttlefish). We conclude that a major part (69 to 87%) of the gross turnover associated with catches of these fish species in the Bay of Biscay remains potentially unaffected by long-term changes related to climate.

Key words: Environmental change / Macro-economic aggregates / Fish market / Atlantic Ocean

Résumé – Suivi de la situation commerciale d'espèces marines sujettes au changement de long terme dans la communauté de poissons : cas des pêcheries du golfe de Gascogne. La situation commerciale de neuf espèces-clés, poissons et céphalopode, et leur évolution sont étudiées tenant compte des changements de long terme dans les communautés de poissons, en prenant comme cas d'étude les pêcheries du golfe de Gascogne. Si l'analyse des changements de long terme est bien renseignée, tant du point de vue de l'impact de la pêche que des modifications dans l'environnement physique, il existe peu d'études sur les effets économiques des espèces exploitées. La nature et l'étendue de ces effets sont déterminées par la composition spécifique de la production halieutique considérée, et par le statut des espèces pêchées sur les marchés. Nous proposons une méthode pour caractériser ce statut de ces neuf espèces commerciales. Les espèces sélectionnées contribuent significativement au chiffre d'affaire des flottilles françaises situées dans le golfe de Gascogne. Elles sont caractérisées selon leur sensibilité potentielle à l'impact de la pêche et aux variations des conditions environnementales, dont le changement climatique. Nous distinguons les espèces potentiellement moins vulnérables (*Engraulis encrasicolus* et *Lophius budegassa*) de celles potentiellement plus sensibles (*Pollachius pollachius* et *Lophius piscatorius*) aux effets du réchauffement climatique. L'évolution de la valeur de débarquement de

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ces neuf espèces est décrite à partir de l'analyse d'indicateurs macro-économiques (production et consommation apparente) et des indices de prix. On démontre ainsi la plus grande sensibilité de la production domestique pendant la crise de la pêche en France (1992-1994), par rapport à la production étrangère ou destinée aux marchés étrangers. La situation commerciale des espèces et son évolution temporelle est analysée sur la période 1990-2005 à partir d'une analyse multi-factorielle. Les résultats de cette analyse identifient clairement deux groupes de produits, dont l'un est marqué par des prix stables et élevés sur la période d'étude (baudroie, langoustine, sole, bar) et le second caractérisé par des prix plus bas et soumis aux effets de substitution entre espèces (lieu jaune, merlu, anchois, sardine, seiche). Il ressort de l'analyse que la majeure partie du chiffre d'affaire (69 à 87 %) , de la production de ces neuf espèces du golfe de Gascogne, est peu affectée par les changements de long terme.

1 Introduction

Long-term changes in marine fish communities are now well documented. Applied research devoted to the description and explanation of these modifications has shown that such changes can result both from the impacts of fishing, and/or changes in the physical environment. In particular, the decreasing trend in the mean trophic level of landings from world fisheries has been described as a consequence of the so-called "fishing down marine food webs" phenomenon (Pauly et al. 1998). Such trends have also been observed at a regional level and at the scale of the fisheries exploited by French fleets in the North East Atlantic (Steinmetz et al. 2006). Beyond the impacts of fishing, changes in the physical environment of fish communities are also considered to be a major source of perturbation, which may contribute to explaining changes observed in the relative abundance of fish species at local to regional scales. An example of an area presently under study is the Arctic region. The eight countries bordering this area are cooperating through an intergovernmental council to assess the impact of climate change on fisheries (Schrank 2007). The Arctic Climate Impact Assessment (ACIA) has shown that effects from climate change interact with effects of fishing to explain changes in fish communities and fishery production. Similar results have been obtained in studies of the Bay of Biscay shelf ecosystem. In this region, warming of surface waters, with an increase of up to 0.6 °C per decade from 1971 to 1998, has been observed (Planque et al. 2003; Koutsikopoulos et al. 1998; Désaunay et al. 2006), as well as an increase in sea bottom temperature (Blanchard and Vandermeirsch 2005). These changes have been shown to contribute to modifications in the fish community of this ecosystem (Blanchard and Vandermeirsch 2005; Poulard and Blanchard 2005; Désaunay et al. 2006).

While a growing number of fisheries research programs focus on these issues (Stenevik and Sundby 2007; Castro-Ortiz and Luch-Belda 2007), relatively little work has been done to address to potential economic consequences of fishing pressure and changes in the physical environment (Pinnegar et al. 2002; Steinmetz et al. 2006). The nature and extent of these consequences, particularly for local fisheries, will be determined by the resulting composition of the fish production, and by the status of fish products on the markets. Recent analysis of trends in the composition of landings by French fleets operating in the Bay of Biscay shows that the proportion of high-valued fish species has tended to decrease in the total volumes landed, to the benefit of lower-value species (Steinmetz et al. 2008; Thébaud et al. 2008). The economic implications of such changes depend on the potential responses of prices to variations in volumes landed, which may differ between species. A standard assumption in economics is that higher-valued products, with limited substitutes, display less price-flexibility than lower-valued products, with many substitutes (Samuelson and Nordhaus 2001). Hence, an assessment of the potential economic impacts of global changes affecting fish resources requires an evaluation of the market position of the species considered.

In this paper we propose a methodology to characterize this market position, based on the case of the production of French fisheries in the Bay of Biscay. The analysis is based on a selection of nine fish species landed by fishing fleets over the 1990-2005 period, representing a significant proportion of the gross turnover of French fishing fleets operating in the Bay. These species were first characterized in terms of their potential sensitivity to fishing and changes in environmental conditions due to global warming. Evolution of the production value of the nine species was then depicted using index analysis. This allowed us to show the relatively high sensitivity of domestic production to the market crisis that occurred in France in the early 1990s. Evolution of total resources of the nine species on the French market was then analyzed, putting emphasis on the part of production derived from the Bay of Biscay in the total resources/uses. The relative position of individual species with respect to the market and its evolution through time was analyzed via multi-factorial analysis. Based on this characterization of the position of each species on the French market, we discuss the economic implications of potential changes in the abundance of these nine species in the Bay of Biscay due to global warming.

2 Materials and methods

2.1 Species

Analysing the position of key species under long-term changes in marine fish communities implies describing the market structure of fish commodities in terms of domestic production, imports and exports. It was not possible for this study to include all commercial species exploited in the Bay of Biscay, particularly because different nomenclatures are used for species in production databases (ICES, FAO) and foreign trade statistics (EUROSTAT). Hence, a selection of nine major commercial species was made (Table 1), representing a significant proportion of the gross turnover for several segments of the French fleets. Two species considered in the analysis are pelagic: anchovy and sardine; four are demersal: cuttlefish, seabass, pollock, and hake; and the last three are

Table 1. List of the nine selected species, and the coverage rate of their potential consumption by Bay of Biscay production during the 1990-2005 period.

Common name	Species	%	
		Min	Max
Anchovy	*Engraulis encrasicolus*	9	266
Cuttlefish	*Sepia officinalis*	30	114
Hake	*Merluccius merluccius*	6	20
Monkfish	*Lophius piscatorius* and *L. budegassa*	14	26
Nephrops	*Nephrops norvegicus*	18	35
Pollack	*Pollachius pollachius*	1	4
Sardine	*Sardina pilchardus*	16	28
Seabass	*Dicentrarchus labrax*	55	80
Sole	*Solea solea*	29	58

benthic: *Nephrops norvegicus*, sole and monkfish (commercially speaking, monkfish is one product, although it includes two different species from a taxonomic point of view *Lophius piscatorius* and *L. budegassa*).

Information on catches and landings of the nine species was obtained from the ICES database of official landings per species per area by member states (http://www.ices.dk), and from the French Marine Fisheries and Aquaculture Directorate. Landings data were extracted from ICES statistical records in terms of volume (tons), selecting production for areas VIII a-e, except for the year 1999 (for which no information was sent to ICES by the French Authorities). In this case, we used production data for the French Atlantic coast published by the National Office for Sea and Aquaculture Products (Office National Interprofessionnel des Produits de la Mer et de l'Aquaculture).

Based on these statistics, the degree to which the selected species are representative can be assessed in terms of their contribution to total landings by fleets operating in the bay. Between 1990 and 2005, annual landings of the two pelagic species (anchovy and sardine) represented 39% to 78% of total annual landings of pelagic species by French fleets operating in the Bay of Biscay fisheries. Landings of the four demersal species (cuttlefish, seabass, pollock, and hake) represented between 48% and 68% of total landings by these fleets, while landings of monkfish, Nephrops and sole represented between 52% and 75% of their total benthic production. Taken together, the production of the selected species represented at least 52% of total French landings from the Bay of Biscay between 1990 and 2005.

2.1.1 Commercial data

As the ICES database focuses on catch statistics, no economic information was available from this source to analyse trends in the value of production by fishing area. Consequently, average annual ex-vessel prices per species recorded in the national statistical reports for landings in French Atlantic fishing harbours (from Douarnenez to Hendaye) were used to assess the value of landings per species. All prices were deflated to 2005 prices using the French retail price index (http://www.insee.fr).

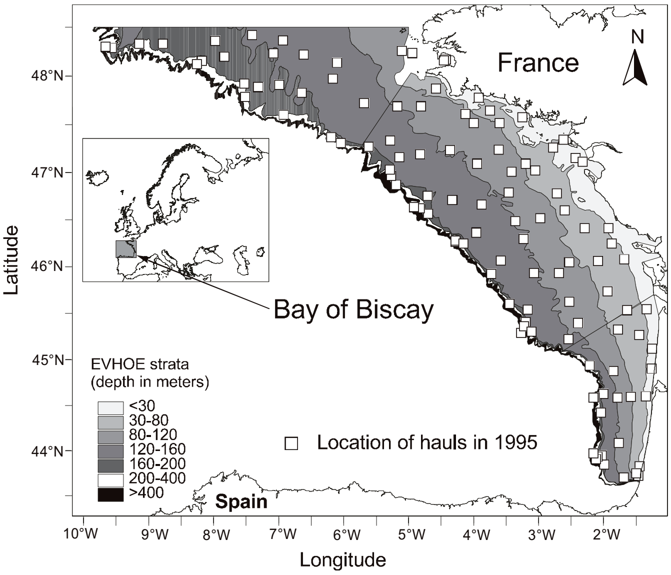

Fig. 1. Area of the eastern continental shelf of the Bay of Biscay studied during the 17 groundfish surveys carried out by IFREMER from September to December of the years 1987 to 1990, 1992, 1994, 1995 and from 1997 to 2006.

Data on foreign trade was obtained from Eurostat databases. Statistics on both annual volumes and values of imports and exports of the selected fish species were extracted for the period 1990-2005. Given that data collection and processing on imports and exports do not mention scientific species names, some aggregation of different species occurs in the trade databases. There is no straightforward approach to establishing the relative proportions of the different species included in measurements of trade flows of commonly named products: e.g. statistics for pollack include trade for Alaskan and European Pollack, and trade flows for hake include trade for European, Patagonian and South-African hake. Tests were carried out to assess the effects of excluding trade data for these species from the multi-variate analysis of the market position of individual species (see below). As no determinant impact was observed on the results, we decided to keep this information in the analysis.

2.1.2 Survey data

Biogeographic characteristics and temporal evolution of the abundance, assessed through groundfish surveys, were associated with the economic information in order to analyse the relationships between market position and biological status of the selected fish species, particularly in terms of their potential vulnerability to climate change.

Data used in the analysis was collected during 17 annual groundfish surveys carried out by IFREMER between October and December from 1987 to 2006 (EVHOE series, which has gaps in 1991, 1993 and 1996), on the eastern continental shelf of the Bay of Biscay (Poulard and Blanchard 2005; Woillez et al. 2007). The study area is located between 43°30'N and 48°30'N and its depth ranges from 15 to 600 m (Fig. 1). The sampling design was stratified according to latitude and depth.

Table 2. Biogeographic characteristics (mean latitude, latitudinal range) and species categories for the nine selected species (adapted from Poulard and Blanchard 2005).

Mean latitude (in degrees of latitude)		Species range (in degrees of latitude)		
Category		1	2	3
	Limit	[20–40[	[40–67[	[67–127]
1	[2.5–41[		*Dicentrarchus labrax* *Sardina pilchardus* *Solea solea*	*Engraulis encrasicolus* *Lophius budegassa*
2	[41–53[		*Merluccius merluccius* *Nephrops norvegicus* *Sepia officinalis*	
3	[53–60]	*Lophius piscatorius,* *Pollachius pollachius*		

A 36/47 GOV trawl was used with a 20 mm mesh codend liner. Haul duration was 30 min at a towing speed of 4 knots. Fishing was mainly restricted to daylight hours. Catch weights and catch numbers were recorded for all species.

2.2 Methods

2.2.1 Potential vulnerability of species to climate change

A growing number of studies show that climate change may significantly impact marine fish communities (Poulard and Blanchard 2005; Perry et al. 2005; Hiddink and Terhofstede 2008). We characterized the species selected for our analysis in terms of their potential sensitivity to climate change, following the classification by Poulard and Blanchard (2005). Table 2 illustrates this classification: species can be ranked according to the combination of mean latitude and range (in degrees of latitude) of the area over which they are distributed. For instance, *Lophius budegassa* is ranked in the mean latitude class "1" and the species range class "3" (with *Engraulis encrasicolus*), while *Lophius piscatorius* belongs to the mean latitude class "3" and the species range class "1" (including *Pollachius pollachius)*. The most Northern species (*Lophiusp iscatorius* and *Pollachius pollachius)* are characterized by the narrowest range. A potential index of sensitivity to climate change can be calculated as the difference between the mid-latitude of the species distribution range and the mid-latitude of the Bay of Biscay (46°48'N), weighted by species latitudinal range. Interpretation of this index is based on the assumption that increased water temperature will induce a northwards shift in species moving from southern to northern latitudes.

2.2.2 Macro-economic aggregates

Economic flows were represented through macro-economic aggregates computed according to the rules adopted by the European System of National Accounts (ESA95). Its major principles refer to a double accounting procedure (Temam 2000). Aggregates appearing on the right side of the accounts are considered as resources (output, Y; and imports, M), those included on the left side are the uses (intermediate and final consumption, C; and exports, X), such that $C + X = Y + M$. Goods available on the market are then equal to resources ($Y + M$) or uses ($C + X$). From this, the potential consumption $C = Y + M - X$ can be assessed. Here, potential consumption results from national landings adding imports and subtracting exports. All quantities included in the analysis were expressed in tons, converting all species in live weight equivalents based on transformation coefficients, which take into account the way in which traded fish are conditioned.

The Fisher price index was used to describe trends in Bay of Biscay production of the nine species, following Steinmetz et al. (2006). The Fisher price index ($FP_{t/0} = \sqrt{LP_{t/0} \times PP_{t/0}}$) measures the rate of change in landing prices, taking into account the evolution of the structure of landings in volume. It is derived from the Laspeyres price index ($LP_{t/0} = \sum_i^n p_{it}q_{i0} \Big/ \sum_i^n p_{i0}q_{i0}$) and the Paasche price index ($PP_{t/0} = \sum_i^n p_{it}q_{it} \Big/ \sum_i^n p_{i0}q_{it}$). We applied Fisher price index calculations at four levels: the fishery, French landings, exports and imports.

2.2.3 Multivariate analysis

Exploitation of the selected species in the Bay of Biscay was placed in the context of the French national market for fish, using a multi-table multivariate analysis called Multiple-Factor Analysis (MFA). The dataset was comprised of 11 indicators (Table 3) for each year and each species (Table 1), related in volume to the fishery production Y, imports M, exports X and potential consumption C for consumers (final uses) and processing plants (intermediate uses). M and X were stated for two market segments: for fresh (M_{fe},X_{fe}) and frozen (M_{fo},X_{fe}) goods. Price variables were included for production, imports and exports.

The data were organised into a 3D multi-table structure, as a collection of yearly matrices (16 years). Each matrix had nine rows, each representing a species, and 11 columns representing the indicators describing the nine species. The tables were used to run a Multiple-Factor Analysis (MFA). MFA (Escofier and Pagès 1994; Poulard and Léauté 2002; Stanimirova et al.

Table 3. List of the indicators used in the Multiple Factor Analysis (MFA) and summary of correlation between variables and the first three MFA factors. – correlation < −0.5; + correlation >0.5. The numbers in parenthesis are the number of correlated years among the 16 considered in the study. Correlations are indicated only when the number of correlated years is >9 per variable.

Variable	Code	Axis 1	2	3
Potential consumption	C	15+	16+	
Landing price (p) in the Bay of Biscay (bb)	p_Y	16–		
Import price for fresh products	p_{Mfe}	16–		
Import price for frozen products	p_{Mfo}	16–		
Export price for fresh products	p_{Xfe}	16–		
Export price for frozen products	p_{Xfo}	16–		
Landed quantities from the bay of Biscay	Y	14+	10–	9–
Imported quantities for fresh products	M_{fe}			14–
Imported quantities for frozen products	M_{fo}		16+	
Exported quantities for fresh products	X_{fe}		15–	
Exported quantities for frozen products	X_{fo}	11+		

2005; Woillez et al. 2007) extends principal component analysis (PCA) methodology to the analysis of 3D structured data. In particular, MFA is appropriate to cases where the same variables (i.e. production and economic indicators in our data matrix columns) are measured for the same individuals (i.e. species in our data matrix rows) at different times (third dimension of the data structure, i.e. the 16 years of the studied period). This method allows a single factorial space to be constructed, in which the data matrix for each time step, variable and individual is represented. This unique factorial space is a compromise that best matches those of each data matrix at each time step. It allows extensive tables of data to be represented pictorially in such a way that groupings among variables in space and time can be readily identified.

The method proceeds in two steps. First, a PCA is performed on each data matrix. Then, each variable at each time step is weighted by the inverse of the first Eigenvalue of that matrix. A general matrix is constructed that contains all the weighted variables in columns and the individuals as rows. The PCA of this general matrix constructs the MFA compromise factorial plane. Its principal axes are interpreted using the correlation of the variables with the axes. The interest of this method is the construction of a compromise factorial space in which to represent the 3D structure of the data: each individual is represented by n points (n repetitions in time) as well as by its gravity centre (average position in the compromise factorial space). In our case, results will show the mean position for each species, explained according to the nature of the markets to which products were supplied over the 1990-2005 period.

3 Results

Potential sensitivity of the nine species to warming

Table 2 presents the results of the sensitivity index that was computed. Based on the index, it appears that two species (*Pollachius pollachius* and *Lophius piscatorius*) could potentially be negatively affected by warming, while two species (*Lophius budegassa*, *Engraulis encrasicolus*) could potentially be positively affected. For five of the nine species considered in this analysis, the potential impacts of warming would appear to be undetermined. Trends observed in the scientific surveys for the nine species are presented in Table 2 so as to provide information on the changes observed in the Bay of Biscay. These reflect modifications in the abundance and characteristics of fish populations resulting from a combination of factors, including fishing pressure and environmental changes. There is hence no direct link between these trends and the sensitivity index.

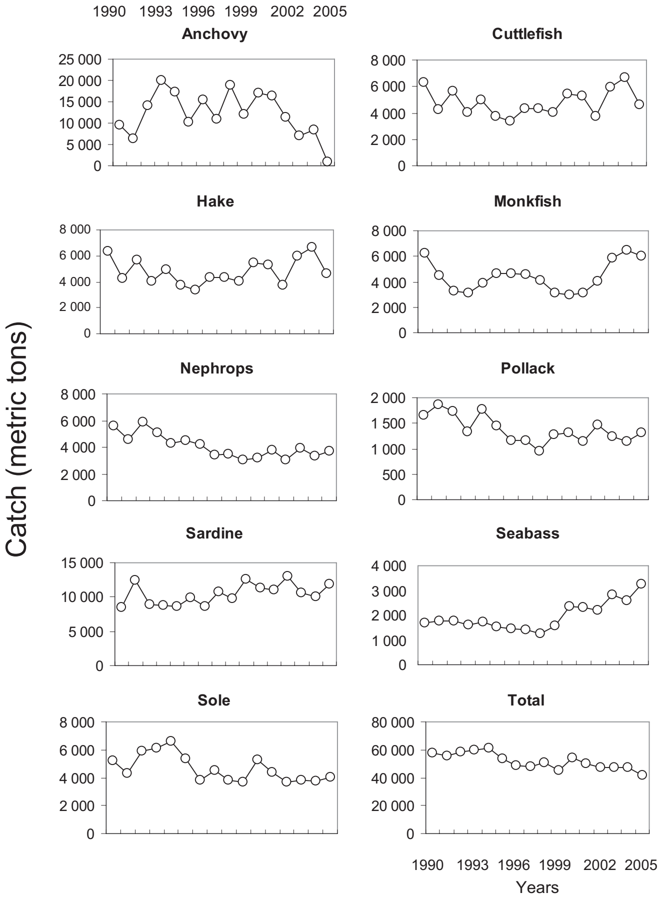

Fig. 2. French landings (in metric tons) for the nine selected species from the Bay of Biscay between 1990 and 2005. Source: ICES (1990-1998, 2000-2005) and OFIMER (1999).

Production and apparent consumption of the nine species over the 1990-2005 period

Catches of the nine selected species declined overall during the study period (Fig. 2): from 58 000 t in 1990 to 42 000 t in 2005, with a peak of 62 000 t in 1994. The highest contributions were from anchovy, hake and sardine. Although output levels for the latter species remained constant over time, hake production dropped to 6000 t from 1996 (a reduction of 50% compared with its previous levels) and anchovy decreased dramatically over the last years of the study period.

Figures 2 and 3 illustrate the evolution of French landings from the Bay of Biscay and potential consumption of the nine

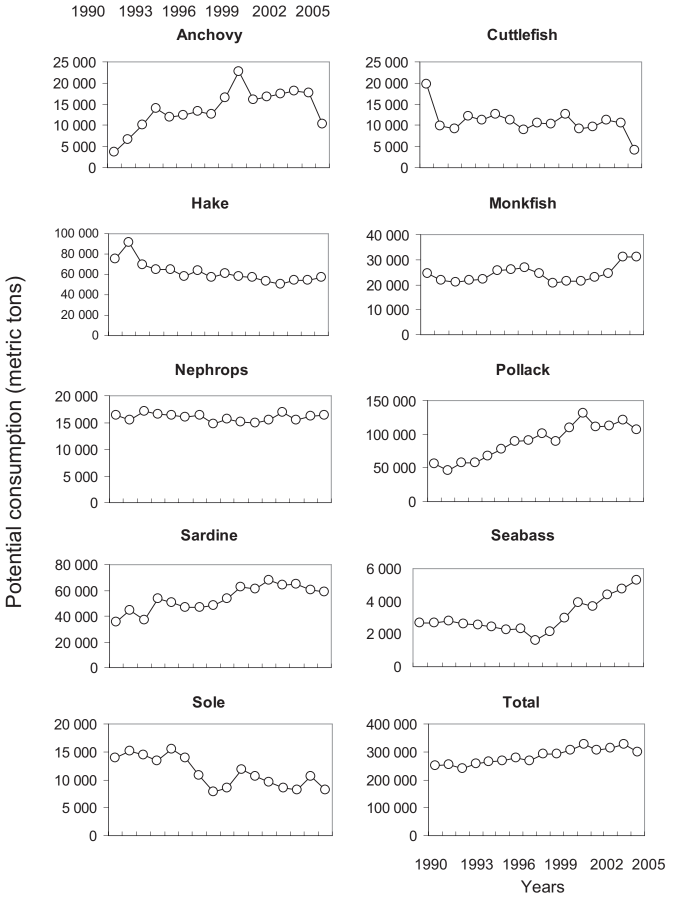

Fig. 3. Potential consumption (in metric tons) of the nine species studied on the French market during the 1990-2005 period. Source: OFIMER (landings) and EUROSTAT (exports and imports).

species on the French market, as defined in the previous section (i.e. including trade data for different species that may be labelled with the same name in the trade databases). The Bay of Biscay landings represent 38% to 56% of domestic production for the nine species as a whole, and approximately 20% of potential consumption on the French market. Relationships between fishery production and potential consumption of the French market are indicated in terms of coverage rate (Table 1). Based on this analysis, only the landings of four species derived from the Bay of Biscay can be considered as making a significant contribution to the domestic market: anchovy, cuttlefish, seabass and sole, of which more than 29% of the total consumption is covered by the Bay of Biscay production.

The case of anchovy deserves special attention, because of the emergency measures taken to close the fishery in the Bay of Biscay in 2005 (Commission of the European Communities 2005). From 2003, the production of this species was less than 50% of the potential consumption for consumers and plants; it decreased to 9% in 2005 following the implementation of fishing restrictions. In previous years, the situation was radically different, with much higher coverage rates (maximum at 266% in 1990). The Biscay production of the other species (Nephrops, sardine, monkfish, hake and particularly pollack) weighted much less on the French market. This does not mean a low dependence of the market on domestic production, because marketing channels for fish products are segmented according to conditioning techniques (in particular with a difference between fresh and frozen products). Local production is mainly conditioned fresh for final uses on the domestic market, whereas frozen goods come principally from foreign countries and are used in the fish processing sector.

Evolution of resources of the nine species on the French market

Total resources for the nine species on the French market were computed from domestic production and trade flows. The evolution of three components of total resources is presented in Figure 4: Bay of Biscay production, landings from the other French fisheries, and foreign supply. Available quantities fluctuated around 300 000 t from 1990 to 1997 and then increased to 3 000 t from 1998. At the same time, domestic contribution decreased from 40% to 30% of total resources, due exclusively to a sharp decline in landings from the Bay of Biscay fisheries (Fig. 4a). A similar trend was observed for value changes (Fig. 4b). Over the period, total resources in value maintained themselves at 800 000 constant € (2005), except during the fisheries crisis (see below) during which the total value of the resources available on the market dropped to 700 000 constant €.

Evolution of the price indices

Over the study period, changes in markets for fish did indeed have a strong impact on the evolution of price index, particularly for Bay of Biscay production. In particular, the market crisis which occurred in France in the mid-1990s, led to a particularly sharp drop in the ex-vessel prices of the selected species (Fig. 5). At the national level, prices decreased by 31% between 1991 and 1994. The decrease was dramatically higher for Bay of Biscay production, with a drop by 72% in three years. Over the same time period, changes in the price index appeared quite limited for foreign trade (–6% for exports and –14% for imports). Following the crisis, import prices tended to increase from 1996 until 2001 and then decreased over the next three years. Ex-vessel prices rose between 2000 and 2005, reaching the same level as that observed in 1990 (in constant 2005 prices) at the end of the study period.

Position of individual species in the multivariate analysis

The first three axes of the MFA accounted for 79% of the total variance in the data. The high score (15.2) of the first Eigenvalue showed that the first MFA factor represents an important direction of variance for each of the years. The correlation coefficients between the first three MFA factors and the projection of each group of indicators (years) were higher than 0.75, indicating that the structuring factors expressed by the first three principal components of the MFA were common to all years.

Table 4. Significant linear trends observed in the abundance and mean weight of the nine selected species during the period 1987 to 2006, from data collected during groundfish surveys carried out in autumn on the eastern continental shelf of the Bay of Biscay. Latitudinal categories are from Table 3.

Species	Trend in survey Abundance	Mean weight	Latitudinal category	Expected impact of climate warming on population abundance
Anchovy	⇔	⇔	13	positive
Monkfish (*L. budegassa*)	⬀	⇔	13	positive
Nephrops	⇔	⇔	23	none
Cuttlefish	⬀	⇔	22	none
Sole	⇔	⇔	22	none
Seabass	⬀	⇔	22	none
Sardine	⬀	⇔	22	none
Hake	⇔	⇔	22	none
Monkfish (*L. piscatorius*)	⬀	⬂	31	negative
Pollack	⬂	⇔	31	negative

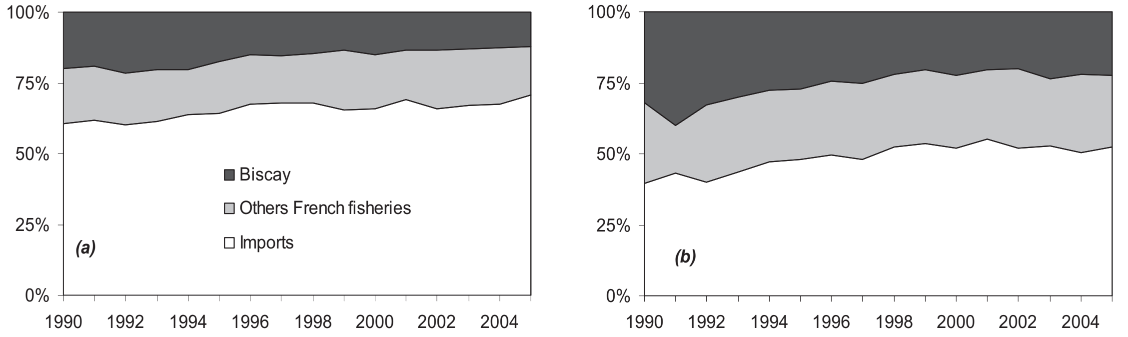

Fig. 4. Evolution of total resources of selected species on the French Market, in metric tons (a) and 2005 constant Euro (b), 1990-2005.

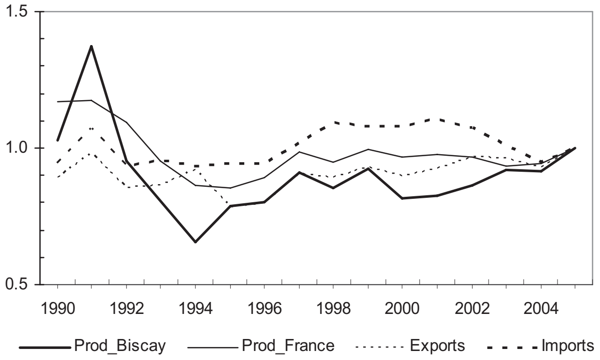

Fig. 5. Evolution of Fisher price index during the 1990-2005 period. Source: OFIMER (landings) and EUROSTAT (exports and imports).

The first three axes of the MFA provide a good representation of the main changes in the exploitation and marketing of the nine species over the studied period. The correlation between the indicators and the axes is summarized in Table 3. Potential consumption, and landings and volume of exported frozen products from the Bay of Biscay are positively correlated with axis 1, whereas all price variables are negatively correlated with this axis. Potential consumption and volume of imported frozen products are positively correlated with axis 2, while Bay of Biscay landings and volume of exported fresh products are negatively correlated with this axis. Bay of Biscay landings and volume of imported fresh products are negatively correlated with axis 3. Apart from potential consumption (correlated with axes 1 and 2) and Bay of Biscay landings (correlated with the three axes), most of the variables are more specifically correlated with just one axis.

The mean positions of species are displayed in Figure 6. The projection of individuals (species) reveals a strong inertia on the first axis. Two groups of species can be distinguished from their scores on axis 1. The first group, among which are Nephrops, monkfish, sole, and seabass, is characterized by high prices. Fresh imports of monkfish, sole and Nephrops were observed during the study period, while there was a strong increase in fresh seabass product imports. With respect to axis 1, there was a strong demand for species of the second group (pollack, hake, sardine, cuttlefish and anchovy) which were landed from the Bay of Biscay and exported in the form of frozen products in large quantities. The demand for pollack, and to a lesser extent for hake, was particularly strong and seemed to correspond to large imports of frozen products. Landings of sardine, cuttlefish and anchovy from the Bay of Biscay were relatively large and associated with exports

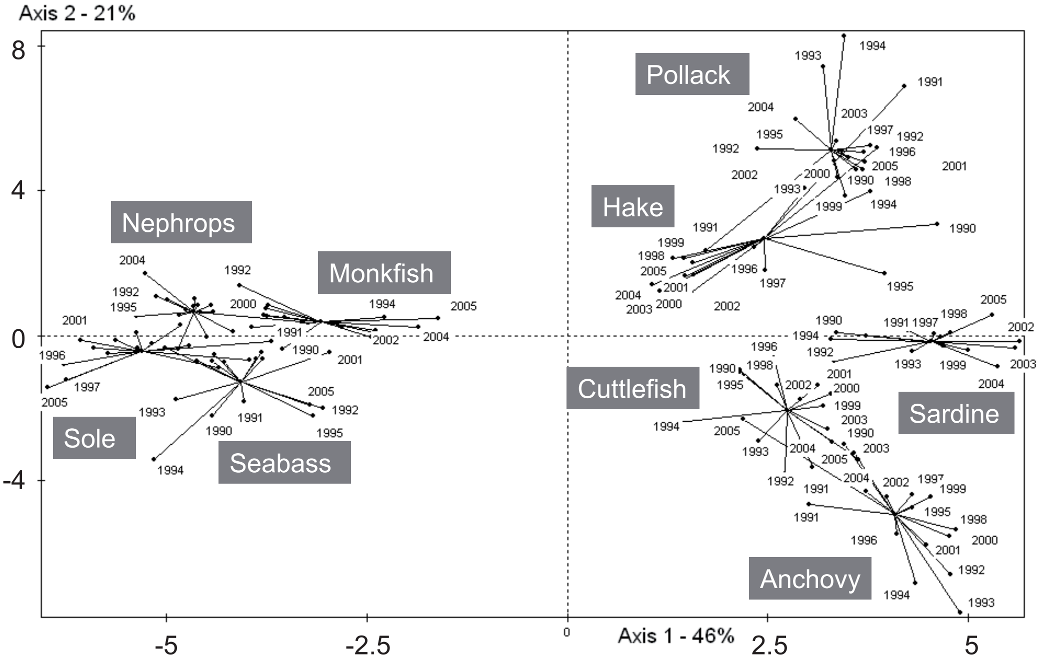

Fig. 6. Graphical depiction of the projections of the nine species on the principal multiple factor analysis plane. Diamonds represent the centres of gravity of the species observed over the 16 years. Symbol size is proportional to contribution of a species to the construction of the axes. Plus signs indicate the position of each species in the relevant year.

of fresh products. The year-to-year variability by species (i.e., the distribution of the years around each species in Fig. 6) was higher for hake, pollack, sole, anchovy and cuttlefish than for other species.

The position of the years in the principal plane of the MFA is explained by the correlation between the axes and the variables (Table 3). All years are strongly linked with the first axis (price and quantity relationships), although the two first years and the last are less well correlated. In contrast, axis 2 separated the years 1992, 1993, 1994 from others. These years displayed relatively high correlation coefficients, between 0.6 and 0.7. They were characterized by high values for potential consumption and the volume of imported frozen products, together with low landings from Bay of Biscay and low volume of exported fresh products.

4 Discussion

While a growing number of studies demonstrate the effects of global climate change on fisheries at a worldwide level (Schrank 2003) and recommend engaging similar studies at regional scales, the challenge is to include an economic perspective in this evaluation, considering both domestic and foreign production. One of the main anticipated effects of climate change is a modification in the composition of exploited fish communities. The economic implications of such changes will depend on the market position of fish production derived from these communities, and on the associated responses of prices to variations in volumes landed, which may differ between species. The results presented in the previous section provide some insights into the potential implications of climate change for fisheries, targeting the nine selected species in the Bay of Biscay.

Assessing the global economic stakes of climate-induced changes in the fish community

Climate-induced changes in the fish community of the eastern continental shelf of the Bay of Biscay were identified by Poulard and Blanchard (2005). Species having a northerly distribution and a narrow latitude distribution range exhibited declining trends of their abundance and biomass. On the other hand, species exhibiting a trend of increasing abundance indices were characterized by a southern distribution and a wide latitude range. It was not however possible to clearly separate the relative role of fishing impacts and climate-induced changes on the community. For the two Boreal species in our analysis, i.e. monkfish (*L. piscatorius*) and pollack, a negative effect of climatic warming might be expected. In this case, negative effects of fishing and climate-induced changes would be cumulative. For anchovy, a positive response to warming conditions could potentially be expected. However, in the Bay of Biscay the exploitation of anchovy depends to a large extent on yearly recruitment success. This recruitment is driven by mesoscale ocean processes (Allain et al. 2001) related to meteorological regimes. Exploitation of anchovy in the Bay of Biscay might thus be largely affected by changes in these regimes induced by global warming. In the same way, potential positive effects of warming on monkfish (*L. budegassa*) might be reduced by the high intrinsic vulnerability of this species to fishing (Cheung et al. 2007) due to its rather large body size.

Even if, based on the sensitivity index calculated above, we assume a positive potential impact of climate change on anchovy (*Engraulis encrasicolus*) and a negative potential impact on pollack (*Pollachius pollachius*) and monkfish (*Lophius piscatorius*), we come to the conclusion that a major part (69% to 87%) of the gross turnover associated with catches of the selected fish species in the Bay of Biscay remains potentially unaffected by long-term changes related to climate. Only 6 to 17% of this production could be potentially negatively affected by climate change (in relation to fisheries for *Pollachius pollachius* and *Lophius piscatorius).*

Economic implications of modifications in the composition of landings

The analysis presented in the previous section shows that the structure of fisheries production by French fleets operating in the Bay of Biscay has markedly changed over the years of this study. Based on these results, and on the typology of fish species derived from the multi-factorial analysis, we can assess the economic implications of such changes.

Results derived from the AFM clearly separate two groups of species, the first characterized by higher prices, and the second by larger volumes available on the French market. The position of the first group of species (Nephrops, monkfish, seabass and sole) on the market, as described by the multi-factorial analysis, remained relatively stable throughout the study period. Landings of these species are destined mainly for the French fresh fish market, and face limited competition from imports of fresh products. Indeed, as illustrated by the case of Nephrops, large imports of these species are mainly for frozen products with only limited potential interactions with the market for fresh products. The second group of five species (anchovy, cuttlefish, sardine, hake and pollack), characterised by lower price levels, saw greater fluctuations in the position of the individual species on the French market. Price responses to variations in landed volumes appeared to be much higher than for the first group, as is illustrated by prices of hake in 1990, pollack in 1991, cuttlefish in 1994 or anchovy in 2005. Landings of these species are destined both for the French market, on which large volumes of imported frozen products also exist (with questions as to whether these imports interact with the market for local products), and for the export market.

Species with higher prices are marketed mainly on the domestic fresh market, and appear to face a limited number of substitutes. This group of products displays less price flexibility, and demand appears to be relatively inelastic, which is characteristic of goods belonging to the luxury class. For these species, one can thus expect that even as ex-vessel prices rise, demand will not decrease, and supply may increase (Hutchinson et al. 2001), though in a "backward-bending" fashion (Copes 1970). In contrast, demand for species with lower prices, which arrive on markets where they may have many substitutes, will tend to decrease with higher prices; leading supply to stabilize or even decrease if prices remain too low compared with harvesting costs. Hence, under open access conditions, the economic implications of changes in the composition of landings by fleets operating in the Bay of Biscay, as illustrated in this article and that by Steinmetz et al. (2008), will be directly related to the position of the landed species on the market. For fishing fleets producing mainly high price products, the potential impacts of changes in landings will be related to the so-called "backward-bending supply curve" (Copes 1970), indicating that beyond the maximum sustainable yield of individual species, prices can continue to rise while output is decreasing. Changes in catch rates which may result from changes in the environmental conditions of the stocks (e.g. lower catch rates due to unfavourable environmental conditions) will accentuate this process. For fleets dependent on lower price products, changes in catch rates will be amplified via the price variations and adjustments of demand and supply, hence greater levels of variability may be expected in the gross turnover associated with the landings of these species.

The results presented here provide a basis for further exploration of the implications of the market position of fish species for the analysis of the economic consequences of composition changes in fishery landings. Future research on this issue will need to focus more specifically on the determinants of price differences and price formation for the different groups of species considered in the analysis.

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Bio-economic modelling as an integrative tool to assess the dynamics of fisheries facing global economic and environmental changes. The example of the French Guyana shrimp fishery.

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Introduction

Major changes are currently being observed in marine ecosystems and in the human activities, particularly fishing, that depend upon them. If the ecosystems are sustainable naturally, the observed changes raise growing concerns, both in terms of the loss of biodiversity, and in the capacity of the marine communities to absorb these changes without being radically transformed. These worries apply to the sustainability of fisheries, and largely also to other methods of exploitation of living aquatic resources. It seems then important to assess the adaptive ability of the fishery facing such changes and also the relevance of past and future possible public policies to improve this ability.

The French Guyana shrimp fishery is facing many dramatic changes related to the global change. On the economic side the main aspect is the globalization of the shrimp market with a decreasing trend in real prices, mainly because of the increasing production of low cost aquaculture shrimps in emerging economies. The worldwide increase of fuel prices is the second macroeconomic factor having a dramatic impact on the industry. On the environmental side, the recruitment of the two main target species seems to have decreased over the last decade, probably in relation with hydro-climatic changes.

Bio-economic modelling is a useful research way to analyse the adaptive ability of fisheries facing changes. A model of the French Guyanese trawling shrimp fishery has been produced in order to :

1) reproduce the fishery dynamics over the past ten years;
2) simulate the response of the fishery to changes in the economic context (shrimp market and fuel cost) but also to environmental perturbations or regime shifts;
3) evaluate the consequences of public policies on the economic viability of the fishery.

This communication will be organized as follows. After a short introduction about the past dynamics of the shrimp fishery in relation with its context, the model is presented and its main outcomes are discussed. Some scenarios will then be analysed. Among the array of scenarios, new orientations of public policies will be discussed.

This scientific work was developed during the last two years. This experience takes place in the “Chaloupe” program (http://www.projet-chaloupe.fr) funded by the French National Agency For Research (ANR). The objective of this program was to study the adaptation capacity of exploited marine communities and fisheries, facing environmental and economic global changes with three case studies: Bay of Biscay, Morocco and French Guyana.

1. Past dynamics of the French Guyana shrimp fishery

1.1 The development phase

The exploitation of the Guyana shrimps stocks[1] began during the 1960’s when US shrimp fishing boats, already operating in the American Gulf of Mexico Fishery, extended their

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[1] Composed mainly of two species *Farfantepenaeus subtilis* (brown shrimp) and *Farfantepenaeus brasiliensis* (pink shrimp).

fishing zones to the Guyana continental shelf, between Venezuela and Brazil (fig. 1). During nearly 20 years Cayenne (French Guyana) and Paramaribo (Surinam) were used as local landing sites by US shrimp boats for transhipment of their catches to the US market. More than 400 US shrimp boats were exploiting the Guyana shelf shrimp stock, for 20 000 t of total landings. Japanese boats did rapidly join the Guyana fishery, based in Surinam, Guyana and Brazil.

The implementation of 200 miles EEZ in 1977 had important consequences for this fishery : the Guyana continental shelf and its living resources became under control of coastal states : Surinam, Guyana, France and Brazil.

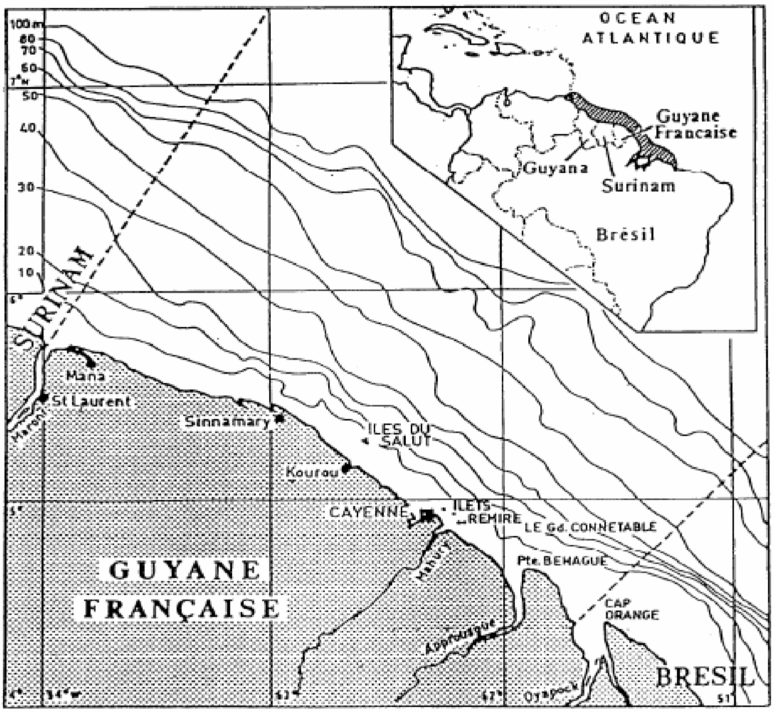
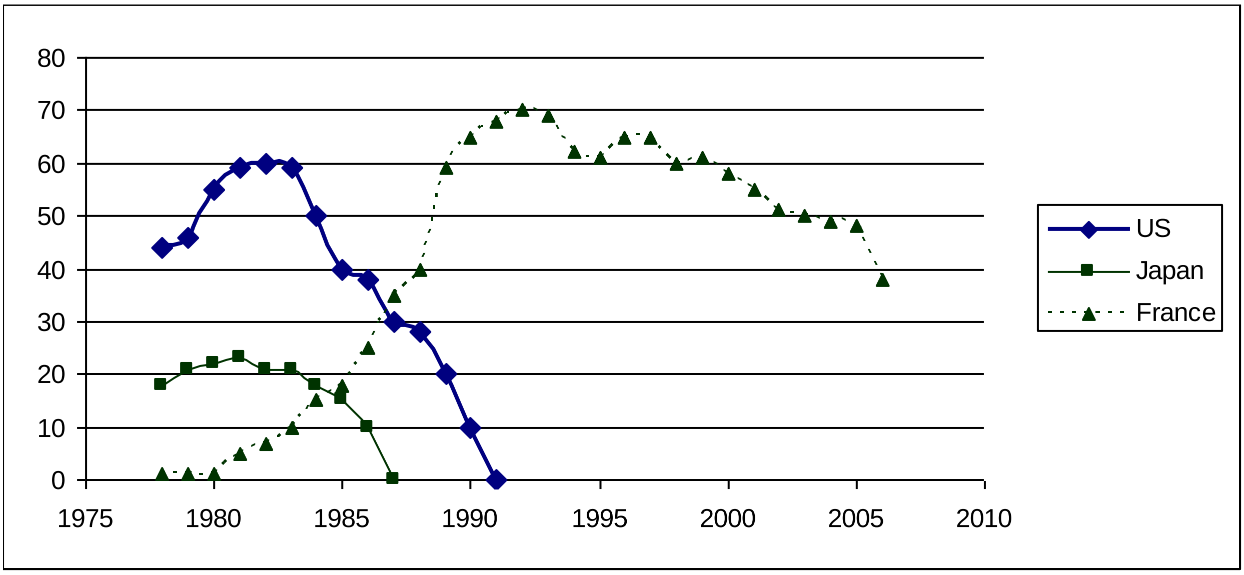


Figure 1 Geographical presentation of the fishery

In French Guyana, in the 1980’s, the objective was to promote a national fleet in substitution of the foreign one still in operation in the French Guyana ZEE. It was the so called “francisation” of the fishery. This policy was supported by a strong intervention of the state through subsidies, and infrastructure building. French “métropole” investors did take advantage of these opportunities: in 10 years the French shrimp trawlers fleet increased form zero to 70 units (fig. 2). Between 1982 and 1991 the number of US trawlers decreased from 60 to 0 ! This rapid development of the French Guyana fishery is also related to the rapid expansion of the market for warm waters peneid shrimps in United States, Japan and Europe (mainly France and Spain). During this boom period these countries had incentives to secure their supply to satisfy the increasing demand for wild tropical peneid shrimp. For instance France and Japan did compete to exploit Malagasy shrimp stock (Chaboud, 2007) and a similar situation was observed in West Africa. For France, French Guyana was considered as a domestic resource owner, and therefore offers very favourable for French investors more usually facing hard negotiations with developing countries. Another aspect did also explain the apparent and rapid success of the “francisation” policy. French Guyana, like most other french overseas territories and department did suffer from a weak economic basis: heavy external economic assistance from the mainland, few industries, high labour costs. Because of the apparent abundance of the resource, of the external promising market, the shrimp fishery was considered as a key sector for the future of French Guyana, besides the strategic spatial sector (Spatial launching in Kourou).



Source: Ifremer.

Figure 2 Number of trawlers since the EEZ creation

But the success story of the 80's didn't last. Since the beginning of the 90's the French Guyana fishing firms enter a period of economic difficulties, with a total debt up to 195 millions French francs in 1990 (Béné et Moguedet, 1996). In 1993 three fishing firms were closed. From 1993 to 2006 the fleet followed a decreasing trend, due to ecological, economic and institutional factors. We shall now concentrate our analysis on that period.

1.2. The lasting crisis of the fishery cf commentaires f2

From 1994 up today, the fishery experienced a succession of crises which have been described in scientific publications and administrative reports (Béné et Moguedet 1996, Béné 1997, Dintheer et Kalaidjian 2002). Landings show a decreasing pattern during the period (fig 3), as well as the number of trawlers (fig 2). Catch per commercial category indicate also major changes up to 1996 (fig 4). Fishing effort has concentrated in shallow waters during the "francisation" of the fleet, up to 1995, where F. subtilis biomass is high but mainly composed of small individuals, probably explaining the greater part of small commercial categories in the catches. . During the 15 past years, the catch became more increasingly dominated by small brown shrimp. It has made the fishery more vulnerable to recruitment failures and environmental variability. It is actually well known that the recruitment of tropical peneid is highly influenced par environment factors (Garcia et Lereste, 1981). On the economic and social side the fishery experienced two main crisis: 2000-2001 and 2006 onwards. The main consequences were the reduction and the concentration of the fleet: today only three fishing firms remain in the industry. One of them holds more than half of the total fishing capacity. In 2008, this main fishing firm withdrew 9 trawlers because of economic losses, and the total fleet capacity of the fishery was reduced to 23 fishing units.

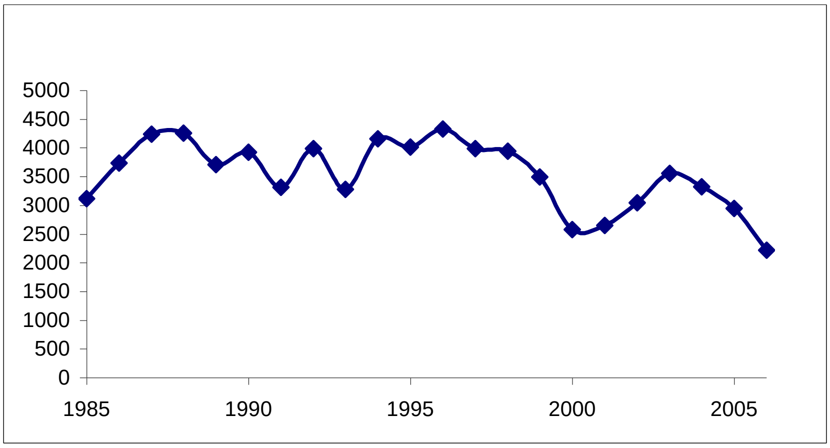


Figure 3 French Guyana total shrimp landings

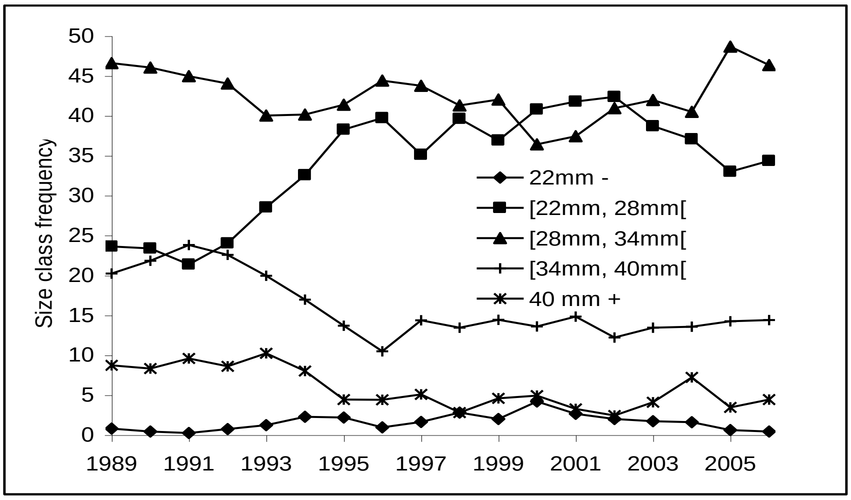


Figure 4 Size structure of the landings of *F. subtilis*

1.3. The key factors of changes

On the economic side, the main factor is the evolution of the world shrimp market since the middle of the 1990's. After the francisation of the fishery, most catches were exported to the French domestic market. Guyana shrimps did compete with imports from Madagascar or West African fishery. After 1995 the shrimp world market trends were dominated by the rise of aquaculture. In 2006 aquaculture represented 80 % of the world supply for peneid shrimp. This change had dramatic consequences for tropical shrimp fisheries which were already facing a stagnation of landings (due to full or overploitation of most shrimps stocks) and increases of fuel costs. The world unit price for shrimp, calculated from FAO international trade data has decreased since 1995. The 2003 current price (6.5 US $ / kg) is less than the price observed in 1986 (7 US $ / kg). During the last years, the rise of fuel costs heavily impacted the yet depressed economic results.

On the resource side, a general decreasing trend of shrimp biomass at the regional level is seen since 1995-96 (Dintheer et Kalidjian, 2001). In French Guyana, virtual population analysis (VPA) realised on the 1994 – 2006 period by Ifremer scientists also indicates two periods of low recruitment for the main target species (*F. subtilis*, brown shrimp): 2000-2001 and 2006. These years showed also bad economic results and social difficulties in the fishery. Bad recruitment for brown shrimp could be linked to unfavourable local and/or regional hydro-climatic conditions such as north-easterly winds and/or la Niña phenomenon

(Vendeville and Blanchard, personal communication). For the second species *F. brasiliensis*, VPA indicates also a reduction in biomass. For this species the reduction in biomass could also be explained by a higher (over)exploitation in neighbouring Surinam waters. Other environmental effects may be discussed. The increase of sea surface temperature observed over past years (Blanchard and Thébaud, 2007) could also have induced changes in growth or mortality parameters (Fig 5).

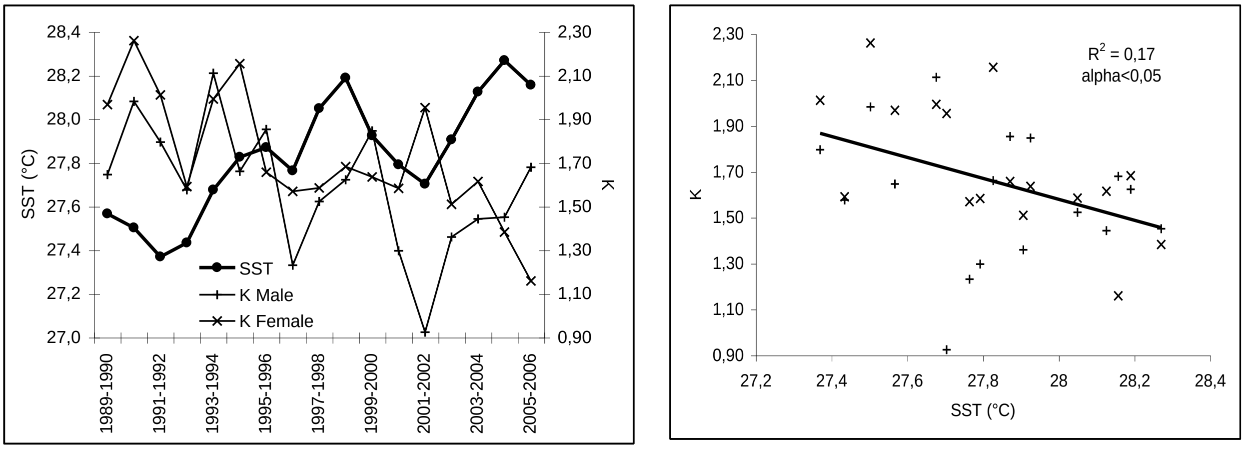


Figure 5 Temporal variations of the mean Sea Surface Temperatures (SST) on the French Guyana continental shelf (from Reynolds data set) and the growth rate k calculated for male and females (least sum of squared deviations) and the statistical relationship between k and SST (significant linear regression at 5%).

The third factor is related to institutional context and to the management of the fishery

The starting point, already discussed, was the creation of EEZ in 1977. It permitted the development of the "French" fishery, but also created favourable conditions to enhance the fishing capacity, also induced by fiscal and credit incentives for overseas investment. The French Guyana fleet was based on artificially low investment costs. This can be considered as a positive strategic element to help an emerging industry facing competition. But this argument is very misleading in the fishery industry, because the initial advantage would rapidly lead to economic overcapacity in the fishery, jeopardizing the future economic viability of the indutry.

The second point is related to the economic support accorded by the European Union (EU) to ultra peripheral regions (Azores Islands, French Antillas, Réunion) to offset the cost induced by the distance between these regions and the EU market. For the French Guyana fishery this support (Poseidom) was granted in 1993. An amount of 1,1 € was given per kg of brown or pink[2] shrimp exported to the EU market, for a maximum limit of 4 200 t per year. Since 2003, this limit was reduced to 3 300 t. It seems clear that Poseidom has contributed to maintain the fishing capacity and effort at higher levels compared to a non subsidy situation. Poseidom is also questioned as an incentive to maximise catch volume rather than value. Such an hypothesis could be supported by the same changes observed in the fishing strategies: more fishing in shallow waters for abundant small brown shrimps or less discard of small individuals…

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[2] The sea bob shrimp, very coastal, is excluded.

The management of the fishery is in compliance with European legislation. Some management rules and instruments have been reinforced or progressively implemented after the EEZ creation. But obviously their efficiency has to be questioned because of the alteration in physical and economic results.

-A total allowable catch (TAC) of 4108 t for brown and pink shrimps has been adopted in 1983, of which 108 t can be caught by neighbouring countries (Surinam, Trinidad, Barbade). Compared to the historical catch, the TAC level has never been fully achieved. This TAC level has not been changed until today, despite the decreasing trends in biomass and landings. The average catch between 2000 and 2006 was equal to 2930 t. This constant TAC can then not be considered as an active management tool, but only as the proof of the French Guyana compliance with European rules.

-In 1991 a licence system is introduced for brown and pink shrimps fishing. The main objective was initially to limit the number of boats to protect the shrimp resource. The Préfet of the Guyana region (representing the French Central state) is responsible for licence number adjustment and attribution between local fishing firms. Licences are attributed without fees. The licence system didn’t seem to be in fact an active or efficient resource management tool. The year abundance of shrimp is mainly correlated with recruitment and not with effort or number of boats. The number of licences, from 69 in 1991 was slightly reduced to 68 (1994) and 63 (1999). During this period the number of active shrimp trawlers was less than the number of licences (less than half in 2006…). Since 1991 the engine power of trawlers is limited to 500 hp (368 kW). The licence system could have been a tool to adjust the number of boats to improve economic results, but this objective was not explicitly addressed by the management system.

-Minimum Mesh size is equal to 45 mm. Mesh size regulation is considered to be an important control variable in shrimp fisheries, for both biologic and economic results.

-Spatial restriction: in order to limit the impact of trawling on juvenile shrimp and avoid conflicts with coastal small-scale fishery, trawling is forbidden in coastal waters less than 30 meters depth. This rule is more restrictive than the spatial limitation applied for trawlers in European waters.

Clearly the management system has not anticipated or even reacted efficiently to the ecological, biological and economic changes faced by the shrimp fishery. The biological and economic problems were however addressed in many scientific reports. Since the 1980’s the scientific monitoring of catch and effort is conducted par Ifremer on a regular basis. This monitoring was completed by casual economic analyses. All these analyses produced early warnings about the growing difficulties of the fishery.

2. Bioeconomic simulation model

The bio-economic model of the French Guyana shrimp fishery was developed with three main objectives:

- Represent the past dynamics of the fishery over the 1994-1996 period. This period was chosen because of the availability of good data on effort and catch collected by Ifremer scientists in charge of the scientific aspects of the fishery.
- Simulate the impact of exogenous changes on the fishery. Theses changes can be economic (mainly world shrimp prices and fuel cost), or environmental. We shall use the hypothesis that shrimp recruitment can be used as a proxy of environmental variability.
- Test the impact of changes in management or more general public policy. It concerns policy instruments already used, but we shall also simulate the impact of

some decisions, such as the adoption of selective gear to limit fish by-catch and reduce the mortality induced by shrimp fishing on endangered species like sea turtles.

2.1. General interest of shrimp fishery bio-economic modelling.

Bio-economic modelling, once not reduced to an ultra simple representation, is often costly in time and data. To build a good bio-economic simulation model, we need to have good estimation of biological (growth, natural and fishing mortality), economic (price, costs) and institutional aspects (management rules and more general public policy tools impacting the fishery sector. For most fisheries, all the data needed are not available and bio-economic modelling first impose new data collection and analysis. In the case of shrimp fisheries, such models, despite of these requirements, are of great interest, first because of high economic value of shrimp: the potential economic rent is very high. Most shrimp fisheries are in situation of dramatic overcapacity, because of the high value of the resource but also because of the existence of a “flat response” curve of shrimp catches of a wide range of fishing effort values (contrarily to many other cases where decreasing catches associated to increasing effort are considered as overexploitation indicator implying management decisions). The last argument favourable to bio-economic modelling is the very rapid response of the fishery to management decisions because of the short life cycle of the resource. For instance, biomass and total effects of changes in mesh size will be observed in the following year, but it can take years for long life fish species. For these reasons, bio-economic models have been proposed for many shrimp fisheries: Gulf of Mexico, Surinam , Bay of Carpentaria in Australia, Madagascar.

2.2. Short presentation of the French Guyana Shrimp fishery Model

This model was developed during the last two years. The Vensim® software platform was chosen as modelling tool. Some data analysis on catch and fishing effort were conducted to supply the model with updated parameters and data. Some specific surveys were necessary to obtain costs and price parameters for the year 2006.

The model is composed of different linked modules. All monetary variable are expressed in constant terms (year 2006 €) using French Guyana price index as deflator for past years. The model first intends to represent the dynamics of the fishery over the 1994 – 2006 period. Projections can be done for a ten year period following the previous period, based upon hypotheses on biological and/or economical parameters. The time step of the model is day.
The resource module used an age structured model for the two target species (brown and pink shrimps), with monthly cohorts of males and females[3]. Two types of fishing strategies have been distinguished : coast (from 30 to 50 m depth) and off shore (more than 50 m depth). The strategies are characterized by different target species catchabilities.

Computation of catch is made for each cohort per species and sex, and instantaneous total catch is obtained by summation over the different cohorts.

2.2.1. Biomass dynamics, catch and revenues

For a given cohort, the number of individuals, N_t is obtained from equation 1,

$$N_t = N_{t-1} e^{-Z_t} \qquad N_o = R \qquad (1)$$

Where Z is the total instantaneous mortality and R is recruitement.

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[3] Monthly recruitment takes place the first day of each month.

The total mortality Z is the sum of natural M and fishing mortalities F :

$$Z_t = F_t + M \qquad (2)$$

Fishing mortality per fishing strategy x is the product of catchability q_x by nominal effort E_x, number of boats at sea for each fishing strategy x.

$$F_t = \sum_x q_{xt}.E_{xt} \qquad (3)$$

The catchability coefficient is first computed from the proportion SW of the repartition surface for the species swept by a unit of effort (boat per day). The swept area per unit of effort depends on technical parameters: trawling hours per day, horizontal width of the fishing gear and average trawling speed. This proportion is multiplied by the probability of catch of a shrimp of a given length L_t “entering” in a trawl, obtained from a selectivity function S estimated by fishery technologists. The variation of the spatial repartition of shrimp, in relation with age, is represented by an accessibility function $Access_x(age)$ for the two fishing strategies and for each species. This variation of accessibility is important for the main target species *F. subtilis* : the assumption was made that all individuals under the age of 500 days are only vulnerable to the coast fishing strategy and that all others over the age of 600 days are only vulnerable to the off shore fishing strategy. We consider that *F. brasiliensis* is only vulnerable to the off shore fishing strategy.

For the main species *F. subtilis* the comparison of simulated catch with landings and of simulated biomass vs VPA estimated biomass were quite good. For the second species, the same comparison suggests an overestimation of q by the model. Different explanations seem possible: q is a function of biomass, underestimation of the surface of spatial distribution of the stock, etc …. Further analyses have to be done to improve this point. We also assume that technical progress does increase fishing power at a constant rate g (for the simulations exposed later, g = 3% per year).

$$q_{xt} = SW\ .S(L_t)Access_x(age_t).e^{gt} \qquad (4)$$

Individual growth W_t is modeled with a Von Bertalanfy growth function.

$$W_t = A.(L_\infty[1 - e^{-k(t-rt+ar)}])^B \qquad (5)$$

A and B : parameters of the length-weight relationship L_∞ : asymptotic length, k : growth rate, rt : recruitment time of the cohort, ar : age at recruitment.

Individual value V_t is computed taking into account the increase of price when W_t is increasing. Prices per commercial category are supposed to be determined by the world market conditions (the French guyanese fishermen are price – taker)

$$V_t = W_t.P_t(W_t) \qquad (6)$$

Biomass is obtained from equations (1) and (5)

$$B_t = N_t\ .W_t \qquad (7)$$

Instantaneous catch can be computed in volume y_t or in value yv_t

$$y_t = (F_t / Z_t).N_{t-1}.(1 - e^{-Z_t}).W_t \quad \text{-volume-} \quad (8)$$

$$yv_t = (F_t / Z_t).N_{t-1}.(1 - e^{-Z_t}).V_t \quad \text{-value-} \quad (9)$$

Cumulated catch (in volume or in value) for a cohort is the integral over time of equations (8) or (9). Total catch is obtained by summation over all the cohorts. Catches, like other simulations results, are also computed for year intervals.

2.2.2 Costs.

Costs parameters of fishing per boat are divided between fixed and variable costs and are supposed to be the same for the two fishing strategies. Costs are computed and cumulated within each simulation year period y.

Fixed cost FC_y are mainly composed by insurance, capital depreciation and private management costs supported by boats owners and a share of maintenance costs. FC_y is proportional to the number of boats in the fleet at the beginning of the year.

Variable cost (cv_1: fuel, main share of repair, harbour fees and maintenance at sea) are proportional to days at sea E_t and/or proportional to volume (cv_2: packaging, exports costs) or value (cv_3: labor costs) of daily catch value. The daily cost for fuel is the product of daily fuel consumption and price and can then be adjusted during simulation.

For a year period the total cost TC_y for all boats are equal to:

$$TC_y = FC_y + \int_{to\_year}^{t\max\_year} (cv_{1t} E_t + cv_{2t}\ y_t + cv_{3_t} yv_t\ )dt \quad (10)$$

These calculations can be made also for each fishing strategy.

2.2.3. Yearly economics results

It is very important to make a clear distinction between the private (ship-owners point of view) and collective economic results because of redistribution effects of taxes and subsidies.

Year y raw private profit PP_y is equal to total revenue YV_y plus European Poseidom subsidy (Sub) granted to boats owning firms, minus total costs.

$$PP_y = YV_y + Sub_y - TC_y \qquad (11)$$

Net private profit NPP is equal to PP minus taxes on profit;

$$NPP_y = PP_y(1 - pt) \qquad \textbf{s.c} \quad PP_y > 0 \qquad (12)$$

pt : profit tax rate

Economic Rent $RENT_y$, a measure of the economic wealth created by the fishery, is equal to NPP_y plus fishing fees ff_y eventually paid by the industry to get access to the resource and taxes tax_y paid on profit, less subsidies sub_y granted to boat owners. We consider here taxes on profit obtained form resource exploitation as component of economic rent.

$$RENT_y = NPP_y + ff_y + tax_y - sub_y \quad (13)$$

Other economic results are computed but not detailed here: Net Value Added (value of production less material inputs and capital depreciation), State Revenues (sum of taxes perceived on revenues from the fishery less subsidies).

2.2.4. Entry and exit in the fishery

During the first period of simulation (up to 2006) fishing activity (number of fishing days) for each strategy is forced to be equal to actual past observed values. For the projection period (after 2006) we use a year entry-exit function in the total fleet similar to the classical formulation of Smith (1969).

The relative variation of the total fleet K between year y-1 and year y, is proportional to the rate of profit $\prod_y$ multiplied by a sensitivity rate s. s may take different values for positive or negative profit rates.

The profit rate in year y is equal to net profit NPP_y divided by total cost TC_y.

$$\prod_y = NNP_y \, / TC_y \quad (14)$$

$$\begin{array}{ll} \Delta K / K_{y-1} = \Pi_{y-1}.s_1 & \Pi_{y-1} > 0 \\ \Delta K / K_{y-1} = \Pi_{y-1}.s_2 & \Pi_{y-1} > 0 \end{array} \quad (15)$$

In the following simulations, we shall use the same value (1.5) for the s_1 et s_2 parameters.

In this version of the model, the monthly distribution of total fishing effort between the two fishing strategies, for the projection period of simulations, follows the average pattern observed between 1994 and 2006, or can be modified to look at consequences of changes in the spatial repartition of effort.

3. Main results of the model

Most simulations in response of external shocks will be discussed in terms on variations and new equilibrium of biomass (natural capital) and number of boats (economic capital).

3.1. Quality of fit

The quality of fit is evaluated through the capacity of the model to reproduce the past dynamics of the fishery over the 1994-2006 period. Over this period the model gives quite good results for total shrimp catch (fig. 5) and for shrimp biomass (fig 6). On the economic side, the two main crises (2000-2001) and 2006 are also reproduced by the simulation. Because of the lack of economic data for this period we are not able to evaluate the quality of specific economic outputs of simulations.

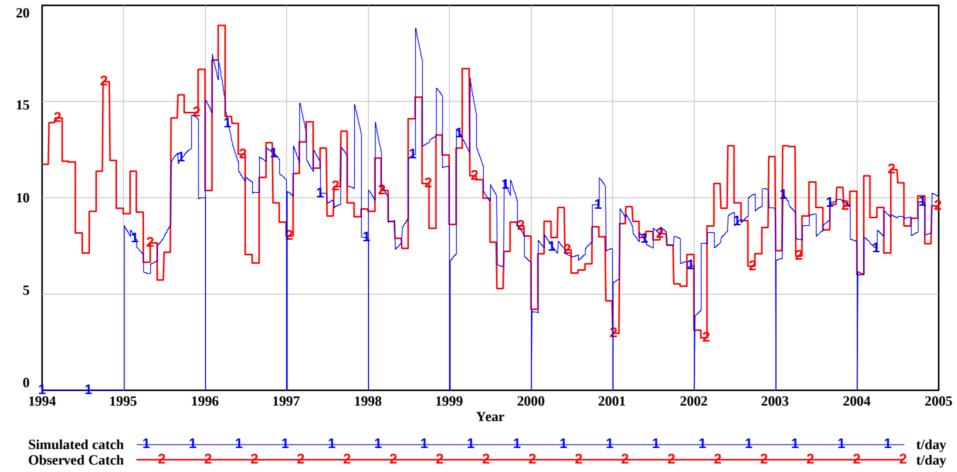

Figure 5 : Quality of fit for total shrimp catches

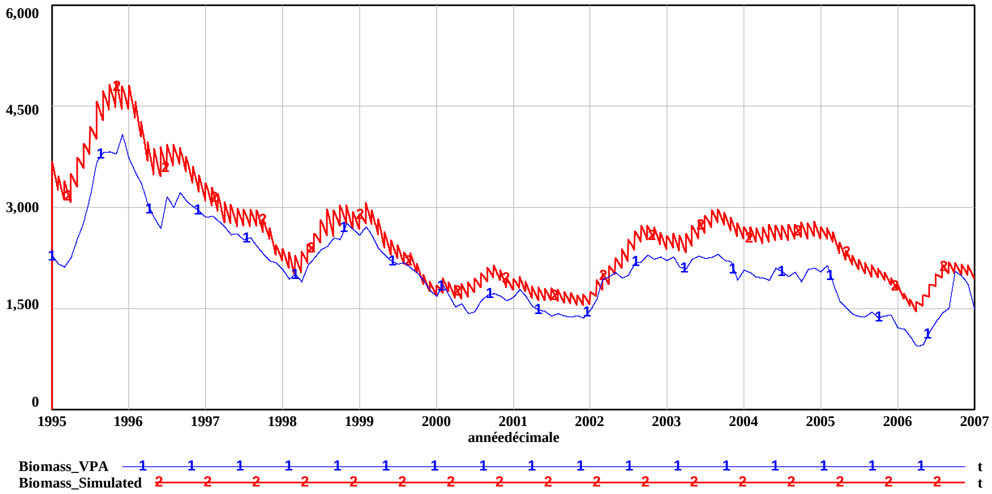

Figure 6. Quality of fit for total biomass

3.2. Responses of the fishery to exogenous shocks

Most simulations in response of external shocks will be discussed in terms of variations and new equilibrium for biomass (natural capital) and number of boats (economic capital).

3.2.1. Environmental shocks or regime changes, impact through recruitment

The recruitment of shrimp explains most of the variation of catches from year to year. No consensus seems to emerge from the literature to identify any key factor driving recruitment variations . For illustration, the climatic factors generally assumed to have impact on shrimp recruitment includes rainfall, river flow, water temperature, sea level, salinity and turbidity (Béné and Moguedet, 1998). However, biologists consider that recruitment is correlated to local environment year variability (rainfall, wind) and/or to macroclimatic events related to

ENSO[4] but these hypotheses remained to be tested (Blanchard and Vendeville, personal communication). Climate change may also affect hydro-climatic conditions necessary to success of recruitment. For instance, from year 1989 to year 2006, two different sub periods can be observed. From 1989 to 1999, with a quite high and stable recruitment. From 2000 to 2006, with more unstable recruitment (with two bad years: 2000 and 2006[5]) and a decreasing general trend.

In order to evaluate the response of the fishery to recruitment variability and shocks, we have tested different scenarios. Three different recruitment regimes were compared: the long term regime from 1989 to 2005, the last period from 2000 to 2005 (fig. 7), the last and very bad years 2004 to 2007. Projections were made using year 2006 economic conditions for prices and costs.

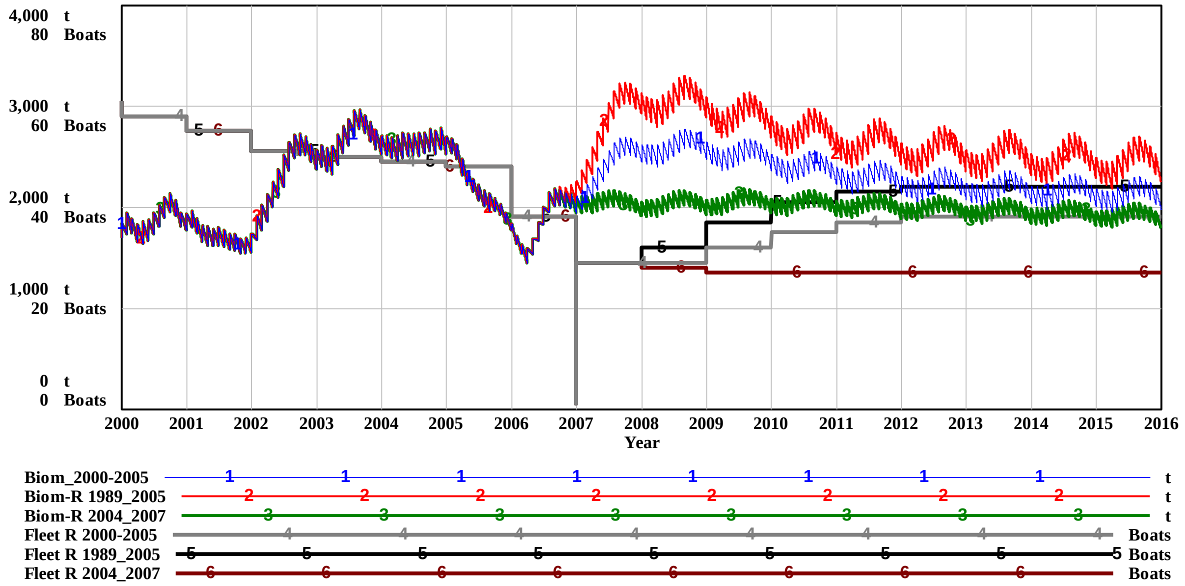

Figure 7 : Evolution of fleet and biomass in response of three different environmental regimes of recruitment.

For the three environmental regimes, the entry/exit behaviour of the boats gives three new stabilized levels of fleets (44, 38 and 27 boats). These levels cannot be seen as long term equilibria because of the increase of fishing power which may lead to further adjustments.

To simulate the impact of casual shocks for recruitment: we have multiplied the average monthly recruitment numbers observed during the 2000-2005 by 1.3 and applied it to year 2009; the original reference 2000-2005 values have been applied for other years of the 2007-2011 period.

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[4] El Niño Southern Oscillation,

[5] Year 2007 has been worse, but has not been taken into account in the model calibration.

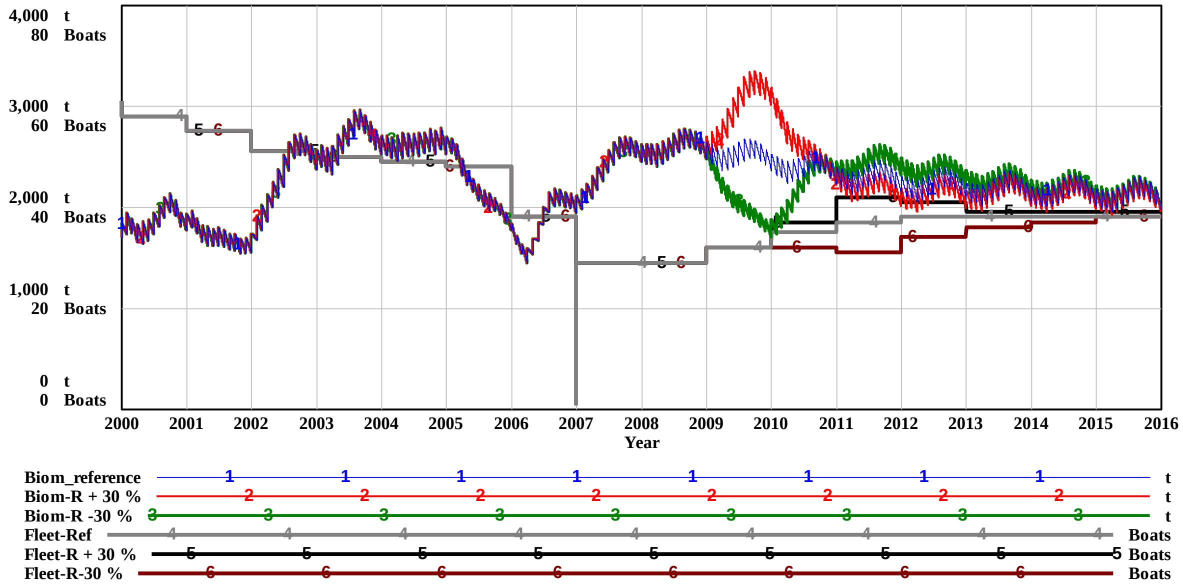

Figure 8 Biomass and fleet responses to punctual shocks on shrimp recruitment

Casual shocks in recruitment are easily and rapidly absorbed in the natural capital level (fig. 8). Numbers of boats do also got back to original levels, but it takes more time (five years).

3.2.2. Responses to economic shocks: shrimp world prices and energy prices

The main global sources of economic shocks are world markets for energy and for shrimps which have experienced rapid evolution over the past years. Another possible source of economic shocks should be an adjustment of the Poseidom subsidy. For some parameters we have use a second less pessimistic value (in brackets). Two kinds of scenarios for economic shocks were tested.

i) Decrease of the Poseidom subsidy according to commercial categories. For shrimp prices the consequences of the following changes were simulated:

- Decrease of 4 % (3%) per year for small shrimps (for 40/60 to 120Up categories[6]);
- Small decrease of 1 % (0%) per year for medium shrimp (30/40);
- Increase of 2 % per year for big size shrimp (20/30 and 10/20).

For these changes, we made the assumption of a supply increase from aquaculture, reducing the prices for small size shrimps. For medium and large size shrimp, we suppose that product differentiation for “large wild shrimp” will help to increase nominal prices.

ii) Decrease of the subsidy

- 50 % (25%) decrease of the Poseidom subsidy per metric ton

A reduction in subsidy seems to be realistic because of the international orientations through World Trade Organization to suppress trade distortions and also because of EC common fishery policy aiming at reducing public economic support to the fishery industry.

For fuel prices we used a 15% (10%) rate of increase per year. It may be quite optimistic hypothesis in comparison with the current situation on the world oil market. A trend based on

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[6] For Head-On shrimps, the standard commercial categories are defined by the number of individuals per kg.

years 2007 and 2008 variations would lead rapidly to non viable short run solutions, and we may hope it will not be the case.

The two economic scenarios were applied with the 2000-2005 period average monthly recruitment. The results are shown on figure 9 (shock1 refers to the first set of assumptions, shock2 refers to the second less pessimistic one).

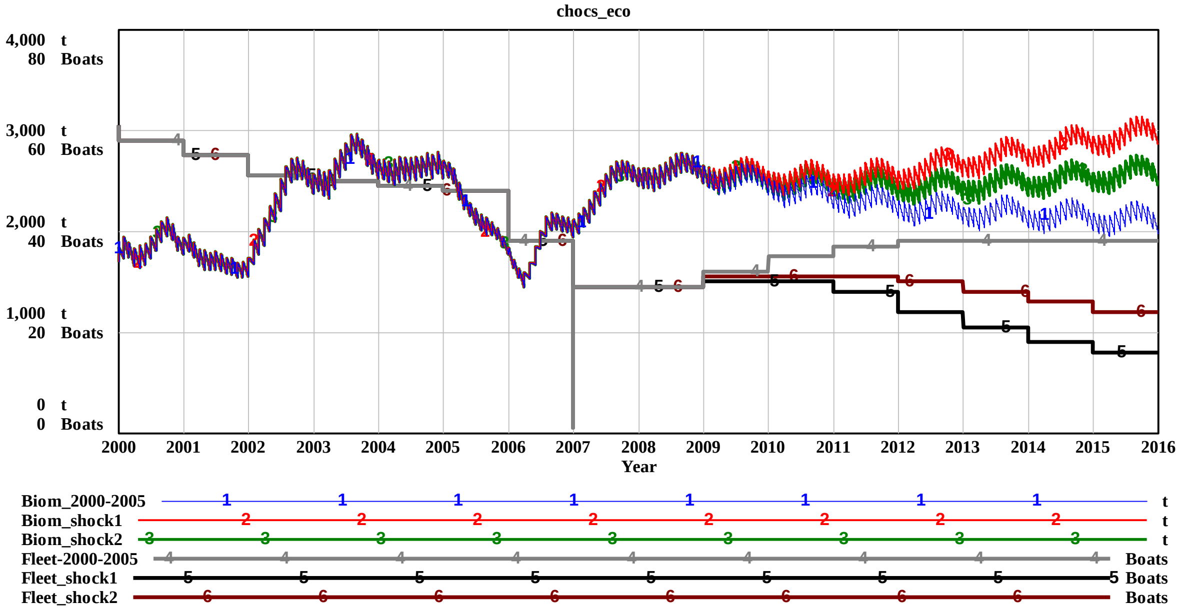

Figure 9 Impacts of economic shocks on fleet and biomass

The two scenarios lead to dramatic decreases in the number of boats of boats (-34% or -52%) compared to the reference scenario) because of the degradation of economic results. The reduction in fishing effort has a direct positive impact on biomass levels.

3.2.3. Cumulating the various type of exogenous changes

The fishery experienced simultaneous ecological and economic shocks. In the following simulation we use the last economic scenarios completed by a scenario about shrimp recruitment on the basis pattern of the 2004-2007 period. We do not use here the 2000-2005 pattern, because it was already used in the previous simulation.

Clearly, taking into account simultaneously the two types of changes will lead to a reduced fleet of 18 or 10 boats in year 2016 (fig. 10). The self regulating behaviour allows a very important recovery of the shrimp resource, despite the bad recruitment regime used in this simulation.

This result underline the possibility, for the fishery, to become not economically viable, if current trends in shrimp and fuel prices are not stabilized or inverted.

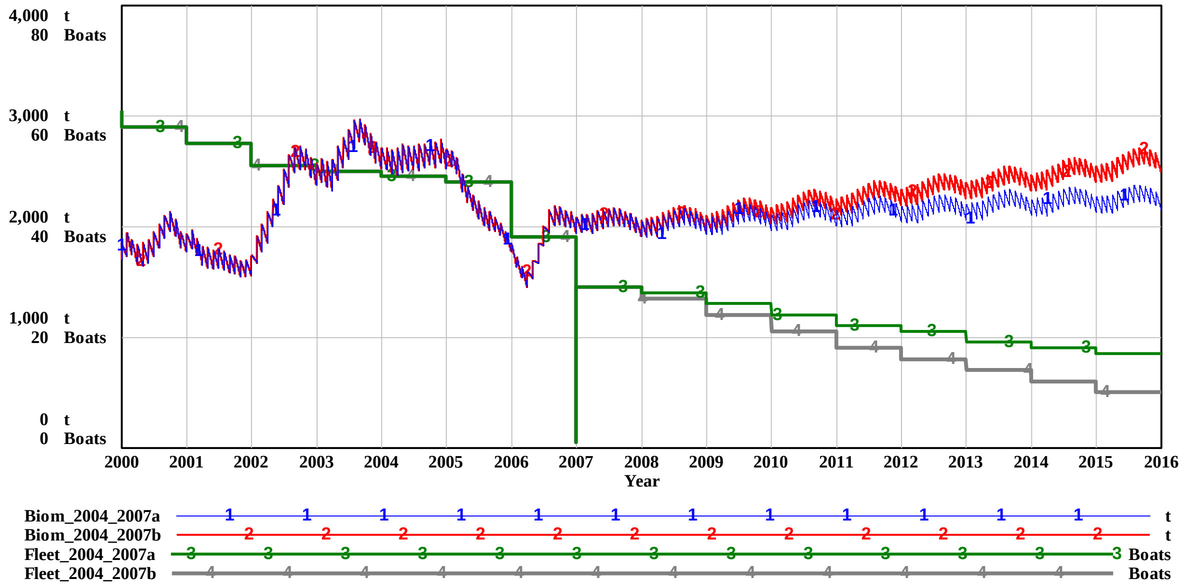

Figure 10 Impacts of economic and environmental shocks on fleet and biomass

After analysing the possible impact of the fishery to exogenous changes, we have to discuss the possibility of changes in fishery management which may improvement the adaptation capacity of the sector.

3.3. Responses to changes in public policies

3.3.1. Limiting capacity and fishing effort

Previous simulations have clearly shown that the French Guyana shrimp fishery may not be able to survive to the ongoing trends in price and fuel costs and reduced recruitment linked with environmental changes.

Limiting the overcapacity in shrimp fishery is the first public policy to simulate. Limiting the number of boats has a very important effect on fishing costs, enabling profit and rent restoration. The following simulations were based on 2000-2005 recruitment period and 2006 prices and costs. For each simulation we multiplied a reference effort (51 boats, mean fleet of the period) by a coefficient (fleet multiplier) varying from 0,1 to 1.

Table 1 : Economic impacts of effort control

Boats	Fleet Multiplier	Revenue	Net Private Profit	Rent	Net Added Value
51	1,0	20 222	-3 700	-6 797	-2 841
46	0,9	19 744	-2 104	-5 068	-1 206
41	0,8	19 097	-641	-3 452	284
36	0,7	18 240	458	-1 976	1 592
31	0,6	17 121	1 219	-675	2 673
26	0,5	15 677	1 800	405	3 471
20	0,4	13 829	2 156	1 210	3 915
15	0,3	11 478	2 233	1 671	3 916
10	0,2	8 500	1 960	1 701	3 363
5	0,1	4 739	1 253	1 190	2 116

Units : 1000 €

Erreur ! Liaison incorrecte.
Figure 11 Impact of capacity control

The results show clearly the economic overcapacity of the fishery in the reference situation. The optimum level for net private profit is obtained with 20 boats. The optimum for economic rent is obtained with 10 boats. The difference between the two optimum values is explained by the Poseidom subsidies and the taxes on profit. The estimation of optimum with increasing fuel price and decreasing shrimp prices would clearly lead to a very small optimal number of boats.

3.3.2. Closed seasons

Seasonal closures are often used in shrimp fisheries (or for other short living species like Octopus spp.), to allow the young individuals (recruits) to grow in volume and also get a higher market value. Closed seasons also allow cuts in variable costs proportional to limitation in number of days at sea.

The analysis of data recruitment for the main species *F. subtilis*, from 1989 to 2006, showed an average seasonal pattern, with higher number of recruits from April to June. We have simulated a seasonal closure for these months, from year 2007 onwards, compared to a reference simulation based on years 1989-2006 recruitment and year 2006 prices and costs.

Closed seasons improve economic results, but due to induced increases in fleet capacity, these improvements are quite dissipated at the end of the simulation.

Other important consequences are changes in catch composition per size or commercial categories (fig. 13) and improvement in the average price of landings. For instance, at the end of 2009, average price with closure is 7.6 €/kg vs. 7.16 €/kg without closure. Because also of the cut in variable cost (23 millions € vs. 26 millions €), there are significant improvements for net private profits (3.2 vs. 2.4 millions €) and for rent (1.2 vs. -0.14 millions €).

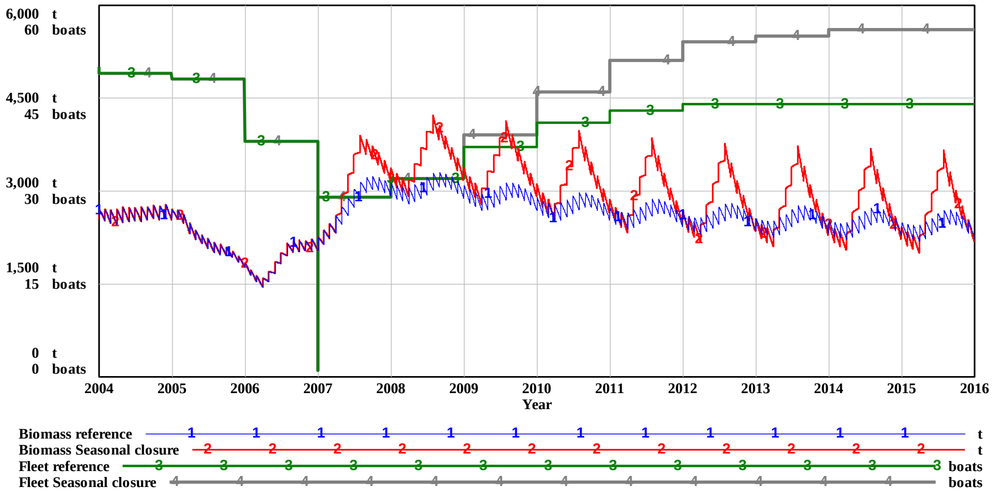

Figure 12 Impact of seasonal closure on biomass and fleet

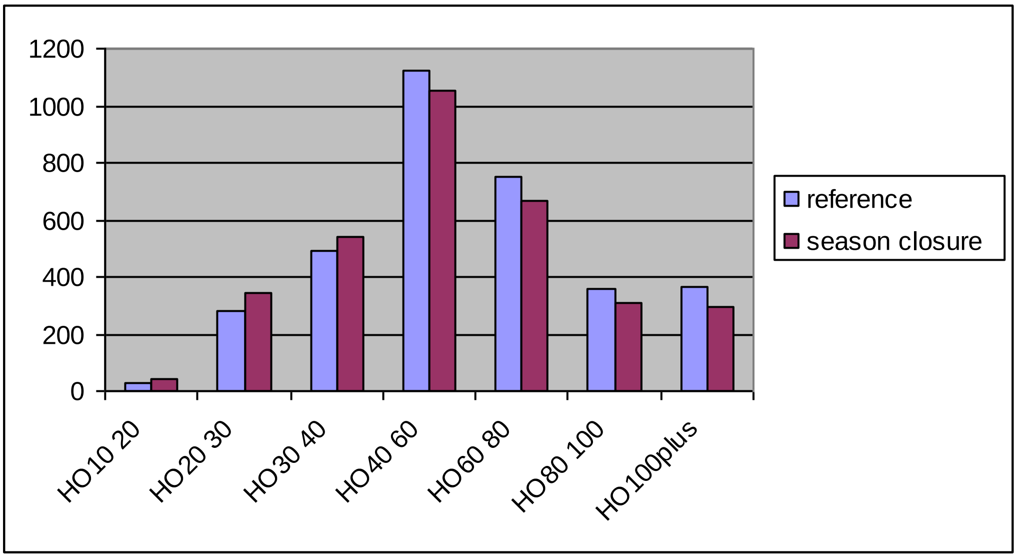

Figure 13 Impact of seasonal closure on catch structure (last simulation year)

3.3.3. Suspending European subsidies, relation with spatial distribution of effort

We first simulate the impact of a full stop of the subsidy. The reference simulation uses the 2000-2005 recruitment pattern (fig. 14). For instance, at year 2011, the suspension of subsidy leads to a reduction of fishing fleet (29 vs. 35 boats) and of catch (2577 vs. 2846 t). On the economic side we obtain an improvement for rent (1,1 vs. -0,3 millions €) and a decrease of net private profit (0.8 vs. 1.9 millions €). The improvement of economic rent is explained by the decrease of cost (18.3 vs. 21.7 millions €) due to fleet decrease.

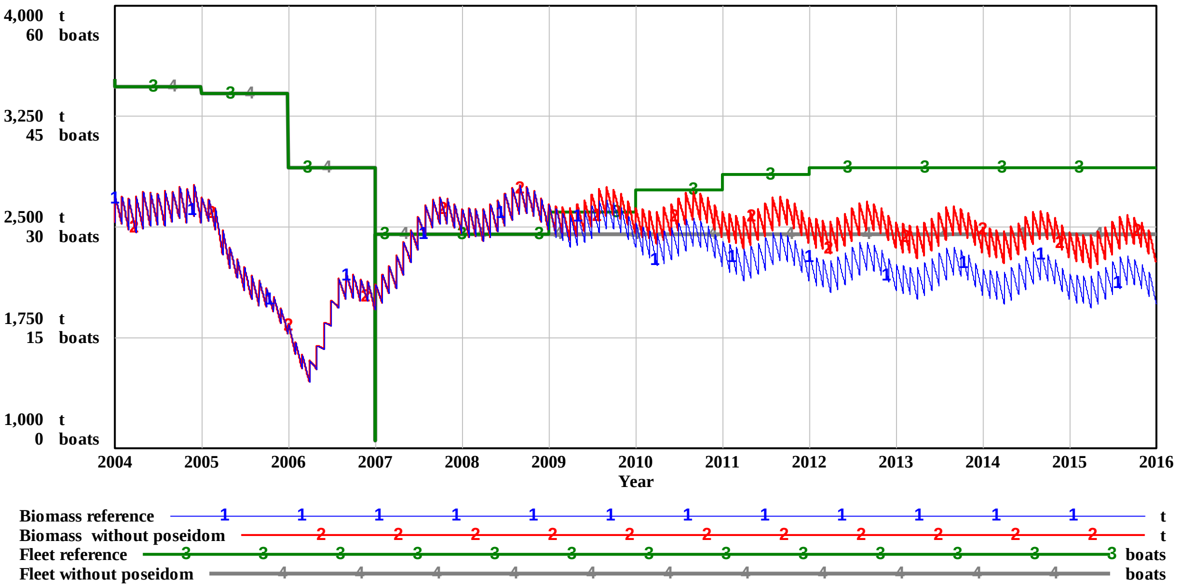

Figure 14 Impact of a full stop of the Poseidom subsidy

An often raised question is the incentive role of Poseidom subsidy for coastal fishing strategy. We have completed different simulations with proportion of coastal fishing strategy in total effort, from year 2006 up to year 2013 varying from 0 to 1. The total number of boats was hold constant (30 boats) in all simulations. The results on figure 15 show clearly that optima for rent and for net private profit are obtained for different proportions of the coastal strategy: 0.7 and 0.5 respectively. This can be compared to the proportion actually observed over the 1994-2006 period: 0.79 .The value of the observed proportion is very closed to the optimal value for NPP obtained by simulation. The Poseidom subsidy, which explains most of the difference between rent and NPP, has clearly led fishing units to concentrate their fishing effort between 30 and 50 m depth.

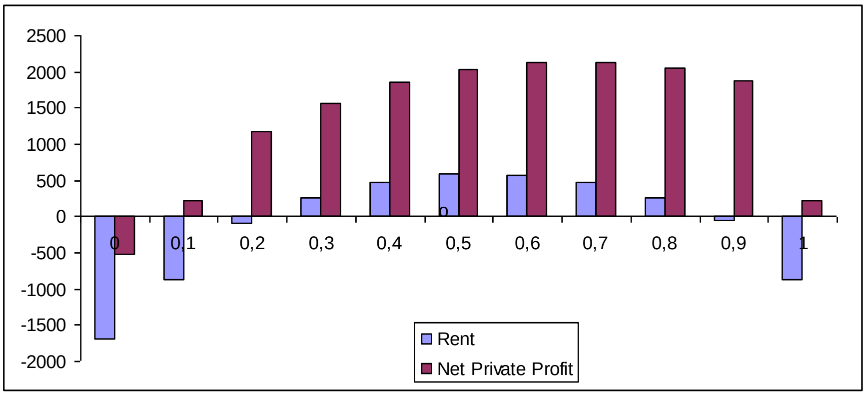

Figure 15 : Impact of coastal strategy proportion on rent and net private profit

3.3.4. Promoting selective fishing: economic consequences.

Tropical shrimp fisheries have important impacts on marine biodiversity through fish by-catch (mainly discarded) and through accidental catch of sea turtles (Environmental Justice Foundation, 2003). It has a direct environmental cost, difficult to estimate but certainly high in terms of ecosystem resilience and services but also of existence value for emblematic or endangered species. Another question is the cost of non access to markets closed for products not in compliance with conservation norms for endangered species. For instance, shrimp imports are not allowed on US market from countries where Turtle Extruder Device (TED) technology is not imposed to fishermen by law and enforced. Eco-labelling, which is a way to differentiate product on competitive markets, cannot be obtained without adoption of gear technology limiting by-catches.

In French Guyana, experiments of TED and By-catch Reducing Device (BRD) have been realised. A catchability loss of 10% for shrimp was estimated for both TED and BRD. We made the assumption of a combined simultaneous loss of 19 % for the two by-catch reducing technologies. We did not assume any change in costs or prices. The recruitment pattern of the 2000-2005 period, and year 2006 economic parameters were used for projection

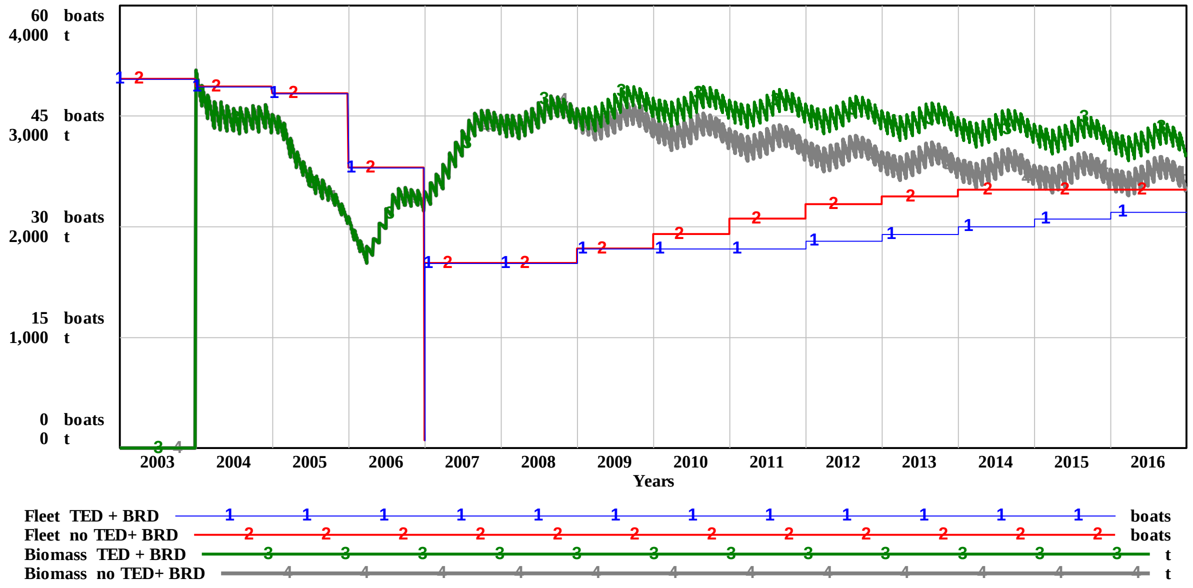

Figure 16 Impact of TED and BRD adoption

On previous figure we see the fleet and biomass responses to BRD and TED adoption in year 2009. The decrease of fishing mortality due to loss of catchability has a positive effect on biomass. In year 2016 fleet has lost 3 boats (32 vs. 35) due to temporary economic losses after new technology adoption. Four years after adoption, the global economic results are quite the same, due to fleet and costs reduction, but also due to an improvement in the catch structure per size, allowing a better average price (7.7 vs. 7.3 €/kg in 2016).

Adoption of TED and BRD looks then economically acceptable, if an adjustment of the number of boats allows to compensate the decrease in catch and revenues.

Conclusion

During the last ten years, the French Guyana shrimp fishery is characterized by poor economic results following a rapid period of expansion. This is partly because of exogenous conditions on shrimp market dominated now by low cost products from tropical aquaculture. During the last years, additional ecological changes seems to explain greater recruitment instability and negative trend, and may then also contribute to the difficulties of the sector.

The management system has been poorly reactive to adapt the fishery to new economic and ecological conditions. European subsidies sustain current private economic results but, in the absence of reactive management, also allow keeping the fishing capacity at too high levels. One of the main consequences is the succession of economic and social crisis in the fishery.

Results from bio-economic simulation show that some improvements could be achieved through more reactive management. Most of the scenarios showed that strong adaptations will be necessary if the ongoing trend in prices and fuel cost still hold in the future. A reduction of fleet capacity and closed seasons could help to restore economic efficiency. The subsidy system was not very efficient on the long term to sustain revenues. Conversely, it fostered onshore fishing strategies, maximising catch volumes rather than catch value. From the simulation results it seems that the subsidy system could be reconsidered.

In the context of international competition on shrimp markets, eco-labelling seems to be a way of differentiating French Guyana “wild shrimps” from concurrent products, particularly low cost aquaculture shrimps produced with high ecological damages. The adoption of TED and BRD are economically acceptable, but needs other management measures such as fishing capacity reduction.

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A bio-economic model for the ecosystem-based management of the coastal fishery in French Guiana

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Abstract

This paper offers a theoretical and empirical model of ecosystem-based fishery management. A multi-species and multi-fleet model integrating Lokta-Volterra trophic dynamics as well as production and profit assessments is developed and applied to the coastal fishery of French Guiana. This small-scale fishery constitutes a challenging example with high fish biodiversity, several non selective fleets and a potentially increasing local food demand due to demographic growth. The dynamic model is calibrated with thirteen species and four fleets using monthly catch and effort data from 2006 to 2009. Several contrasted fishing scenarios including status quo, total closure, economic and viable strategies are then simulated. They are compared from the viewpoints of both biodiversity preservation and socio-economic performance, assuming fixed landing prices and fixed costs. We show that fishing outputs, including food supply and fleet profitability, can be sustained on average but a loss of species cannot be avoided.

Keywords: Small-scale fishery, biodiversity, sustainability, profitability, food security, multi-species, multi-fleet, optimality, viability.

JEL Codes: Q22, Q57

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1. Introduction

Marine fishery resources are under extreme pressure worldwide. According to recent studies (Garcia and Grainger, 2005; FAO , 2010), three quarters of fish stocks are maximally exploited or over-exploited. Moreover, the proportion of marine fish stocks which are intensively exploited is growing. Hence, sustainability is nowadays a major concern raised by international agreements and guidelines to fisheries management. Standard approaches to the sustainable management of fisheries such as MSY (Maximum Sustainable Yield), MEY (Maximum Economic Yield) or ICES[1] precautionary approaches usually address each exploited species separately (Grafton *et al.*, 2007). These management approaches have not succeed in avoiding biodiversity loss, over-exploitation and fishing overcapacity worldwide (Hall and Mainprize , 2004). The Ecosystem Approach for Fisheries (EAF) or Ecosystem-Based Fisheries Management (EBFM) advocate an integrated management of marine resources to promote sustainability (FAO , 2003). Such a management policy requires first to account for the complexity of ecological mechanisms that encompass community dynamics, trophic webs, geographical processes and environmental uncertainties (habitat, climate). Furthermore, by putting emphasis on sustainability, this type of approach strives to balance ecological, economic and social objectives for present and future generations and to handle a large range of goods and services provided by marine ecosystems (Jennings , 2005), including both monetary and non-monetary values.

However, operationalizing the EBFM approach remains unclear and challenging. It requires models, indicators, reference points and adaptive management strategies. Plaganyi (2007) provides an overview of the main types of modeling approaches and analyzes their relative merits for fisheries assessment in an ecosystem context. Modeling approaches and metrics useful for planning, implementing, and evaluating EBFM are also discussed in Marasco *et al.* (2007), with particular emphasis on management strategy evaluation. The use of ecosystem indicators is analyzed by Rice (2000) and Cury and Christensen (2005). In particular, Link

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[1] International Council for the Exploration of the Sea: http://www.ices.dk.

(2005) emphasizes the need for a multi-criteria approach to achieve ecological, economic and social objectives.

This article discusses the sustainable management of a multi-species and multi-fleet fishery from an ecosystem-based perspective for the small-scale fishery of French Guiana. Taking an EBFM approach to this case study was challenging: The fishery is characterized by various complex features including a high equatorial fish biodiversity impacted by several non-selective fleets and demographic growth which could potentially affect local food demand and consequently the production of this fishery.

2. Case study

The continental shelf of French Guiana is a tropical ecosystem under the influence of the Amazon estuary, as is the entire North Brazil Shelf Large Marine Ecosystem (LME) that contains a high biodiversity (Leopold , 2004). With 350 km of coastline, French Guiana benefits from an 130,000 km^2 exclusive economic zone (EEZ) including 50,000 km^2 of continental shelf. The coastal fishery operates 16 km offshore at depths of 0-20 m. Several landing points are spread along the coastline, and this fishery currently involves about 200 wooden boats locally named *pirogues* (P), *canots créoles* (CC), *canots créoles améliorés* (CCA) and *tapouilles* (T). *Pirogues* are canoes equipped with an outboard engine, which fish for periods of a few hours essentially in estuaries using ice stored in an old refrigerator. Compared to *pirogues*, *Canots créoles* are more adapted to sea navigation. *Canots créoles améliorés* have cabins and ice tanks which make it possible to fish for several days. *Tapouilles* are wider boats with a cabin and an inboard diesel engine. The gears used are drift or fixed nets, with mesh sizes between 40 and 100 mm. The type of fleet, the length of gill nets, the number of days spent at sea and the location of fishing activities all have an influence on the quantity of fish landed and on the species composition of the total harvest. Of the numerous coastal species, 30 are exploited and about 15 species, including weakfishes, catfishes and sharks, represent more than 90% of the production. Annual landings have been estimated at approximately 2,700 tonnes for past few years, as reported in the Ifremer[2] Information System (`http://www.ifremer.fr/guyane/Chiffres-cles`).

The coastal fishery plays an important socio-economic role for all the small towns along the coastline where more than 90% of the population is located. However, assessment of this fishery only began in 2006 with data collection monitored by Ifremer. Production and fishing effort values are collected on a daily basis at the main landing points by observers from local communities. An exhaustive sampling is performed due to the small number of boats (approximately 200). 75% of the fishing activity is observed on a daily basis from January to December. Each year, some 3,600 landings are recorded. For each landing, the production by species is estimated or weighed by the observers or reported by the fishermen. Other information is also collected, such as trip duration, net length and fishing area. Since the boats are under 12 meters in length, fishermen are not obliged to provide this information. The data collection system depends significantly on the fishermen's collaboration. Economic assessment started in 2009 with a survey on production costs and selling prices carried out on the field. Coastal fishery in French Guiana remains largely informal despite 1) the founding of the French Guiana fishers' cooperative (CODEPEG) in 1982, 2) the implementation of a system of professional licenses in territorial waters by the regional fisheries committee in 1995, 3) the progressive application of national and European regulations (role of crew, safety inspections of boats, etc.). There is no quota for catches, and no limitation concerning exploited species and their size.

This coastal fishery provides an interesting case study from the perspective of EBF management. The current state of this fishery is usually postulated as safe, and the biodiversity associated with this resource does not seem to be threatened by fishing activity. Nevertheless, the sustainability of the fishery could be threatened by increasing local demand for fish linked to the demographic projections suggesting a 100% increase of the local population over the next 20 years. Consequently, this increasing demand for local fish will affect fishing

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[2] French Research Institute for Exploration of the Sea.

pressure. The question arises whether both the marine ecosystem and the fishing sector can cope with such changes and contribute to food security.

To examine these issues, this paper proposes a theoretical and empirical modeling of EBFM, using a multi-species and multi-fleet model integrating Lokta-Volterra trophic dynamics and profit functions. The dynamic model is calibrated on a monthly basis with thirteen species and four fleets (P, CC, CCA and T) using catch and effort data from 2006 to 2009 derived from the Ifremer fishery information system. Ecological and economic performance of contrasting fishing scenarios including status quo, total closure, economic and viable strategies are examined and compared.

The main contribution of this work is twofold. First, it proposes for the first time decision support tools for the management of the French Guiana coastal fishery by providing a bio-economic model, analysis and scenarios using time series on catch and fishing effort together with economic parameters. In the broader context of small-scale fisheries, such a bio-economic work relying on a perennial database is new to the best of our knowledge. It is acknowledged that small-scale fisheries are poorly managed due to a lack of tools and data adapted to their complexity, while these fisheries are crucial to sustaining many communities especially in developing or underdeveloped countries (Garcia *et al.*, 2008). The second contribution of this study is to advocate the use of co-viability approaches as a fruitful modeling framework for EBFM and sustainability issues. By accounting for complex and nonlinear dynamics in a trophic and multi-fleet context and by addressing biodiversity issues, the paper shows that viability modeling (Bene *et al.*, 2001) can be applied to high dimensional environmental systems. Moreover, this work points out that, by balancing ecological and economic goals with production and food security objectives over the next 40 years, the viability approach is well suited to coping with sustainability due to its multi-criteria perspective and the fact that it takes intergenerational equity into account, as in Péreau *et al.* (2012).

The paper is structured as follows. Section 3 is devoted to the description of the ecosystem-based model together with bio-economic indicators and scenarios. Section 4 provides the calibration results and the outputs of the different fishing scenarios with respect to biodiversity and socio-economic indicators. Results are discussed in terms of sustainability, EBFM and management tools in section 5. The final section provides a conclusion.

3. Methods

The numerical implementations of the model are carried out with the scientific software SCILAB 5.2.2 [3].

3.1. The ecosystem-based model

Among the thirty exploited species, thirteen were selected for the model as shown in table (1). These species represent 88% of the total landing from 2006 to 2009. A virtual fourteenth species which stands for all the other marine producers was added. A potential trophic web (Figure a, web appendix) was built with these selected species, according to their diet (Leopold , 2004) and their trophic level (Table 1).

The ecosystem-based model is a multi-species, multi-fleet dynamic model described in discrete time with a monthly step. The states of the species in the ecosystem-based model are supposed to be governed by a complex dynamic system based on Lotka-Volterra trophic interactions and fishing efforts from the different fleets which play the role of controls in the system. Thus, at each step t, the biomass $B_i(t+1)$ (kg) of species i at time $t+1$ depends on other stocks $B_j(t)$ and fishing efforts $e_k(t)$ of fleet k (time spent at sea, in hour) through the relation:

$$B_i(t+1) = B_i(t)\Bigg(1 + r_i + \sum_{species\ j=1}^{14} s_{i,j} B_j(t) - \sum_{fleets\ k=1}^{4} q_{i,k} e_k(t)\Bigg). \tag{1}$$

Here r_i stands for the intrinsic growth rate of the population i and $s_{i,j}$ the trophic effect of species j on species i (positive if j is a prey of i and negative if j is a predator of i). The parameter $q_{i,k}$ measures the catchability of species i by fleet k. It corresponds to the

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[3] SCILAB (`http://www.scilab.org`) is an open-source software dedicated to scientific calculus and well suited to the simulation of dynamic systems.

probability of a biomass unit of species i being caught by a boat of fleet k during one fishing effort unit. The number of the fleet k from $k = 1$ to $k = 4$ corresponds respectively to CC, CCA, P and T[4].

The catches $H_{i,k}$ of species i by fleet k at time t are thus given by the Schaefer production function:

$$H_{i,k}(t) = q_{i,k} e_k(t) B_i(t). \tag{2}$$

3.2. Model and calibration inputs

Values used to define the model parameters came from different sources. Daily observations (catches and fishing efforts) from the landing points all along the coast are available from January 2006 to December 2009. Every month during this 48-month period, for each of the four fleets, fishing effort and catches were identified for the thirteen species, for a total of 2688 observations. The literature (Leopold , 2004) and Fishbase[5] provided qualitative trophic interactions concerning the sign of the relationship between species and intrinsic growth rates to start the calibration. In particular, only prey-predator and mutual competition relationships are considered in the Lokta-Volterra model, and not symbiotic relationships between species. Initial stocks, catchabilities, trophic intensities and refined intrinsic growth rates values of this ecosystem were estimated through a least square method. This method consisted in minimizing the mean square error between the monthly observed catches $H_{i,k}^{\text{data}}$ and the catches $H_{i,k}$ simulated by the model as defined by Equations (1) and (2):

$$\min_{B_0;\ s;\ q;\ r} \sum_{t=\text{ January 2006}}^{\text{December 2009}} \sum_{i=1}^{13} \sum_{k}^{4} \left(H_{i,k}^{\text{data}}(t) - H_{i,k}(t)\right)^2 . \tag{3}$$

Here $(B_0;\ s;\ q;\ r)$ is the set of parameters to identify. $B_0 = B(t_0)$ is the vector (14×1) of initial stocks ($t_0 =$ December 2005), s the matrix (14×14) of trophic interactions, q the matrix (14×4) of catchabilities and r a vector (14×1) of intrinsic growth rates. Several simple biological and productive constraints on parameters were taken into account for the

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[4] Between 2006 and 2009, there were 71 CC, 60 CCA, 45 P and 10 T.

[5] `http://www.fishbase.org`

optimization process (Equation 3). In particular, several intra-specific interaction coefficients were set to zero (typically *B.catfish*, *F.mullet* and *P.mullet*, $i = 10, 12, 13$), prey-predator relationships (A. weakfish serve as prey for sharks $s_{5,1} > 0$ and sharks are predators of A. weakfish $s_{1,5} < 0$), common prey relationships (A. weakfish also serve as prey for G. groupers $s_{11,1} > 0$) and mutual competition (the predators shark and G. grouper prey on each other, $s_{5,11} < 0$ and $s_{11,5} < 0$) were considered (Table a, web appendix). Some catchability parameters $q_{i,k}$ were also set at zero since some species are not caught by fleets, typically fleet T (Table b, web appendix). The nonlinear optimization problem (Equation 3) was solved numerically using the Scilab routine entitled 'optim_ga' which relies on a evolutionary (or genetic) algorithm[6].

3.3. Model outputs: ecological indicators

After calibration, ecological and economic indicators were computed to assess the performance of both the ecosystem and the fishery. We first focused on biodiversity indices. Although the choice of a biodiversity metric remains controversial as pointed out in Magurran (2007), we selected the species richness, Simpson and marine trophic indicators provided by Equations (4), (5) and (6).

Species richness. Species richness $\mathrm{SR}(t)$ indicates the estimated number of species represented in the ecosystem. It is measured by an indicator function based on abundances $N_i(t)$ computed as the ratio between the biomass $B_i(t)$ and the common weight w_i of each species,

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[6] See `http://help.scilab.org/docs/5.3.3/en_US/optim_ga.html` for details on 'optim_ga'. A genetic algorithm is a search heuristic that mimics the process of natural evolution. This heuristic is routinely used to generate solutions to nonlinear optimization. Genetic algorithms belong to the larger class of evolutionary algorithms which use techniques inspired by natural evolution, such as inheritance, mutation, selection and crossover. In our case, the genetic algorithm ended up performing better than the usual optimization or calibration algorithms. This type of numerical method has already been used for bio-economic purposes in Mardle and Pascoe (2000) for instance and for other tropical fisheries in Sathianandan and J. Jayasankar (2009a, 2009b).

derived from the Fishbase information system:

$$\mathrm{SR}(t) = \sum_i \mathbf{1}_{\{]0,+\infty[\}}(N_i(t)), \quad \text{with} \;\; N_i(t) = \frac{B_i(t)}{w_i}, \tag{4}$$

where the function $\mathbf{1}_{\{]0,+\infty[\}}$ corresponds to the characteristic function[7] of positive reals. Thus, it is assumed that a species disappears whenever its abundance falls to zero (Squires *et al.*, 1994). It should be noted that rare species have a relatively huge impact on the species richness index.

Simpson's diversity. The Simpson index $\mathrm{SI}(t)$ is expressed as:

$$\mathrm{SI}(t) = 1 - \sum_i f_i^2(t), \quad \text{with} \;\; f_i(t) = \frac{N_i(t)}{N(t)}, \tag{5}$$

where $N(t) = \sum_i N_i(t)$. The index SI estimates the probability of two individuals belonging to the same species. The index varies between 0 and 1. A perfectly homogeneous community would have a Simpson diversity index score of 1. Such a metric gives more weight to the more abundant species. The addition of rare species causes only small changes in the value.

Marine trophic index. The trophic level indicates the location of a species in a food web, starting with producers (*e.g.*, phytoplankton, plants) at level 0, and moving through primary consumers that eat primary producers (level 1) and secondary consumers that eat primary consumers (level 2), and so on. In marine fishes, the trophic levels vary from two to five (top predators). The marine trophic index $\mathrm{MTI}(t)$ of the ecosystem (Pauly and Watson , 2005) is computed from the trophic level of each species T_i (Table 1) and their relative abundances f_i (see Equation 5):

$$\mathrm{MTI}(t) = \sum_{i=1} f_i(t) T_i. \tag{6}$$

3.4. Model outputs: economic indicators

We now turn to the assessment of the fishing sector through production and profitability values of the fishery provided by Equations (7) and (8).

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[7] $\mathbf{1}_{\{]0,+\infty[\}}(x) = 1$ if $x > 0$; $\quad$ 0 otherwise.

Food supply. We first considered the total catches $H(t)$ within the fishery which play the role of food supply:

$$H(t) = \sum_k \sum_i H_{i,k}(t). \tag{7}$$

This supply must be compared with local food demand, which is expected to increase at an exogenous rate provided by demographic scenarios and projections over the next 20 years.

Profits. The profit $\pi_k(t)$ of each fleet k was derived from the landings of each species $H_{i,k}$, the landing prices $p_{i,k}$, fixed costs c_k^f, variable costs c_k^v and the crew share earnings β_k as follows:

$$\pi_k(t) = (1-\beta_k)\left(\sum_i p_{i,k} H_{i,k}(t) - c_k^v e_k(t)\right) - c_k^f. \tag{8}$$

Prices, variable costs and fixed costs are those collected for 2008 (Table c, web appendix). They were assumed to remain unchanged throughout the simulations. Share contract β is the salary system commonly used in this fishery for the CCA fleet ($k = 2$) and T fleet ($k = 4$). Crews are remunerated with a share of the landing value minus the variable costs. CC fleet ($k = 1$) and P fleet ($k = 3$) crews are mostly made up of boat owners, occasionally assisted by a family member. If there is a pay system for these fleets, it differs from one owner to another. Hence, to simplify, we set $\beta_k = 0$ for CC and P fleets and $\beta_k = 0.5$ for CCA and T fleets. Variable costs c_k^v include fuel consumption, ice, food and lubricants. Equipment depreciation, maintenance and repairs are incorporated in the fixed costs c_k^f.

The total profit $\pi(t)$ is the sum of profits over all fleets:

$$\pi(t) = \sum_k \pi_k(t). \tag{9}$$

3.5. Fishing scenarios

From the calibrated model, scenarios were simulated according to different fishing efforts over forty years. We distinguished four scenarios: *closure* (CL), *status quo* (SQ), *economic* (PV) and *co-viability* (CVA). The set of ecological and economic indicators introduced previously were evaluated for these four scenarios.

The closure scenario (CL). This scenario corresponds to the implementation of a no fishing zone over the whole French Guiana coastal area:

$$e_k(t) = 0, \quad \forall\ k = 1, \ldots, 4 \quad \forall\ t = t_1, \ldots, t_f$$

where t_1 corresponds to January 2010 and t_f to December 2050.

The status quo scenario (SQ). This scenario simulates a steady fishing effort based on the mean pattern of the efforts between 2006 and 2009:

$$e_k(t) = \overline{e}_k, \quad \forall\ k = 1, \ldots, 4 \quad \forall\ t = t_1, \ldots, t_f$$

with $\overline{e}_k$ representing the mean efforts between 2006-2009 for the fleet k as follows:

$$\overline{e}_k = \frac{1}{t_1 - 1} \sum_{t=t_0}^{t_1-1} e_k(t), \tag{10}$$

where t_0 and $t_1 - 1$ correspond to January 2006 and December 2009 respectively.

The economic scenario (PV). This scenario maximizes the present value of all the future profits aggregated among the fleets $\pi(t)$ defined by Equation 9. The present value depends on fishing effort patterns as follows:

$$\mathrm{NPV}(e(.)) = \sum_{t=t_1}^{t_f} (1+\gamma)^{-t} \pi(t),$$

where γ is the discount rate set at $\gamma = 3\%$. The optimal program underlying the PV scenario is defined by

$$\max_{e_k(t)} \mathrm{NPV}(e(.)). \tag{11}$$

In this scenario, it is assumed that the fishing efforts $e_k(t)$ rely on a control strategy that can be adapted every five years[8]. In other words, eight decisions $(e_k(t_1), e_k(t_2), \cdots, e_k(t_8))$ are available for each fleet k as follows:

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[8] A refined time decomposition for fishing intensities (for instance, a one year time step) would have improved the analysis by capturing a broader intertemporal flexibility in fishing strategy. However, it would have required very demanding computation times. Steady efforts over five years as imposed here capture rigidity and inertia mechanisms in behaviors which may occur in reality. We plan to expand the time step for decisions in future models.

$$e_k(t) = \begin{cases} e_k(t_1) & \text{for } t = t_1, ..., t_1 + 60 \\ e_k(t_2) & \text{for } t = t_2, ..., t_2 + 60 \\ \vdots & \\ e_k(t_8) & \text{for } t = t_8, ..., t_8 + 60 \end{cases} \tag{12}$$

where t_1 and $t_n = t_{n-1} + 60$, for $n = 2$ to 8, are decisive months.

The optimal effort $e_k(t)$ solutions of the intertemporal program (Equation 11) were approximated numerically by again using an evolutionary algorithm, in particular the routine entitled 'optim_ga' in Scilab.

The co-viability scenario (CVA). The purpose of this scenario is to provide a satisfactory balance over time between fleet profitability, biodiversity and local food demand. Thus, viable levels of fishing effort aim at complying with the bio-economic constraints below:

- A profitability constraint: $\pi_k(t) \geq 0, \quad \forall\, t = t_1, \ldots, t_f, \ \forall\, k = 1, \ldots, 4$
- A species richness constraint: $\mathrm{SR}(t) \geq 11, \quad \forall\, t = t_1, \ldots, t_f$
- Food security constraint: $H(t) \geq H(2009) \cdot (1 + d)^t, \quad \forall\, t = t_1, \ldots, t_f$,

where d stands for the growth rate of the population. The profitability constraint holds for each fleet separately and not for the aggregated rent as in the PV scenario. Concerning the biodiversity constraint, no co-viability path maintaining the whole set of thirteen species was exhibited. This explains why the species richness required was relaxed to only eleven species. Finally, the food security constraint assumed an increase in the local fish demand at the annual rate of $d = 3\%$, according to the demographic scenario which predicts a doubling of the French Guiana's population by 2030 (INSEE , 2011). Moreover, it was assumed that fish species can be substituted, in the sense that a drop in the consumption of one species can be compensated for, by a rise in the consumption of other species.

Following DeLara and Doyen (2008) and Doyen and De Lara (2010), viable efforts for the CVA scenario were obtained by maximizing the following criterion

$$\max_{e_k(t)} \prod_{t=t_1}^{t_f} \mathbf{1}_{\{]0,+\infty[\}}\Big(\pi_k(t)\Big)\mathbf{1}_{\{]0,+\infty[\}}\Big(\mathrm{SR}(t)-11\Big)\mathbf{1}_{\{]0,+\infty[\}}\Big(H(t)-H(2009)\cdot(1+d)^t\Big), \quad (13)$$

where again, efforts $e_k(t)$ are meant to be control strategies that can change each five years as in Equation (12) and $\mathbf{1}_{\{]0,+\infty[\}}$ represents the characteristic function on positive reals. The numerical method again relies on the evolutionary optimization routine.

3.6. Sensitivity analysis and uncertainty margins

A sensitivity analysis was carried out to evaluate the role played in the bio-economic outputs by the different calibrated parameters (Tables a and b, web appendix). To achieve this, we ran additional simulations based on the SQ scenario. Given the large number of parameters, we limited the sensitivity analysis by simultaneously perturbing all the parameters of the same group *i.e.*, initial stocks B_0, catchabilities q, trophic intensities s and intrinsic growth rates r. For each group of estimated biological parameters, a noise ranging from -10% to $+10\%$ of the calibrated values was added to the parameters. The relative differences in bio-economic outputs including average catches per annum $\overline{H} = \dfrac{12}{t_f - t_1}\displaystyle\sum_{t=t_1}^{t_f} H(t)$, net present value NPV and specific richness $\mathrm{SR}(t_f)$ were computed. Leverage analysis was also carried out to examine the impact of the choice of time horizon on the outputs. Therefore, other simulations with the SQ scenario were performed increasing the simulation length t_f from December 2060 to December 2100. The corresponding bio-economic results were compared with those obtained with t_f =December 2050.

In line with this, in order to assess the reliability of the outputs for each effort scenario, simulations were replicated 400 times by introducing uncertainties in the estimated parameters (r, s, q, B_0). For each simulation, a noise ranging from -10% to $+10\%$ of the calibrated values was again randomly added to the parameters.

4. Results

4.1. Calibration and sensitivity results

Figure (1) presents the historical and simulated catches by fleet, with 95% confidence intervals. For each fleet k, confidence intervals[9] were computed from the mean relative errors Δ_k between observed and simulated catches from January 2006 to December 2009,

$$\Delta_k = \frac{1}{48} \sum_{t=t_0}^{t_1-1} \left| \frac{H_k^{data}(t) - H_k(t)}{H_k(t)} \right|, \tag{14}$$

where $H_k(t) = \sum_i H_{i,k}(t)$ stands for catches by fleet k at time t over the whole 13 species i. The mean relative errors equal[10] $\Delta_1 = 0.259$ for CC, $\Delta_2 = 0.13$ for CCA, $\Delta_3 = 0.354$ for P and $\Delta_4 = 0.176$ for T.

Figure 2 displays the sensitivity results. They stress the fact that the parameters with the greatest impact were intrinsic growth rates r_i and trophic interactions s_{ij}. The relative changes in net present value and average catch outputs appear approximatively to be linear functions of the perturbations with slopes between 0 and 1.8 highlighting bounds for the marginal effects of the parameters. In particular, the impact of initial biomasses was small since the relative changes were less than the perturbation magnitude for these biomasses. Trophic intensities and intrinsic growth rates were the inputs for which a perturbation entailed larger relative changes in the outputs. The nonlinear nature of the species richness index is captured by the staircase shape of the relative change as well as the peaks observed. Moreover, the relative changes in bio-economic outputs in comparison to the 2050 time horizon, show a reduced impact of the temporal target in the results. In particular, the net present value is not affected by a change of horizon mainly because of the discount involved. Of interest is the fact that species richness is stabilized after 2070. The average

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[9] For each month t, 95% confidence intervals are $[1 - 1.96 * \Delta_k, 1 + 1.96 * \Delta_k] * H_k^{data}(t)$.

[10] The relative errors for the Euclidean or quadratic norm, $\Delta_k^* = \sqrt{\frac{1}{48} \sum_{t=t_0}^{t_1-1} \left(\frac{(H_k^{data}(t) - H_k(t))}{H_k(t)} \right)^2}$, yields: $\Delta_1^* = 0.308$ for CC, $\Delta_2^* = 0.151$ for CCA, $\Delta_3^* = 0.414$ for P and $\Delta_4^* = 0.257$ for T.

annual catches continue to rise with the time horizon, which emphasizes the fact that overall fishery production does not collapse after year 2050 and could even be enhanced.

4.2. Scenarios effort levels

Figure 3 displays the effort multipliers $\frac{e_k(t)}{\overline{e}_k}$ by fleet for each fishing scenario. These effort multipliers are based on the comparison between effort $e(t)$ and the mean pattern of efforts $\overline{e}_k$ between 2006 and 2009 defined in Equation (10). The SQ effort multiplier is equal to one, as expected. It turns out that the PV scenario induces the largest decrease in fishing efforts to maximize the present value of aggregated rent. In particular, the PV scenario implies stopping fishing activity for the CC and CCA fleets during the entire simulation period. With regard to the T fleet, fishing effort is increased in the first two decades of the simulation and stopped in the last decade. By contrast, the fishing effort of the P fleet follows an opposite pattern. Effort is nil during the first two decades of the simulation and is increased after 2030. The multiplier for the T fleet reaches 2.4 in the first part of the simulation, while for the P fleet, multipliers range from 2.2 to 7.8 for the second part of the simulation. In contrast, the CVA scenario guarantees an activity for every fleet throughout time. On average, its effort level is lower than the baseline SQ except for the T fleet, which exhibits an effort multiplier ranging from 0.9 to 6.8. The average multiplier of the viable strategy is 0.7 for CC, 0.51 for CCA, 0.75 for P and 3.0 for T.

4.3. Ecological results

Trends in the evolution of species richness according to the scenarios are plotted in Figure 4 (Marine trophic and Simpson diversity evolutions are available in Figures b and c in the web appendix). The ‘mean’ trajectories induced by the calibrated values are plotted together with margin errors of 400 simulations derived from the perturbation of the parameters selected randomly in $[-10\%; +10\%]$. First it appears that a loss of species occurs for every scenario, as species richness decreases in every case except in the closure CL scenario, as expected (at least when the parameters are not perturbed). In other words, implementing a no fishing zone should maintain species diversity. By contrast, the baseline SQ scenario leads to the worst result in terms of diversity loss. Species richness ranges from 11 to 8 at the end of the simulation period. The mean simulation provides 9 species at the end and species like *Crucifix catfish*, *Common snook*, *Silver croaker* and *Bressou catfish* disappear. With the PV scenario, both *Crucifix catfish* and *Bressou catfish* collapse. The final state of species richness with the CVA scenario is qualitatively identical to the PV scenario since 11 species remain at the end while the same species disappear. From mean estimated parameters, two species (*Crucifix catfish* and *Bressou catfish*) become extinct in the SQ, CVA and PV scenarios, but the extinction periods are not identical: species extinctions are delayed in proportion to the reductions in effort level. Extinction periods of these two species correspond to years 2020-2032 for the SQ scenario, 2022-2040 for the CVA scenario and 2031-2047 for the PV scenario respectively.

The trajectories of the two other biodiversity indices are more complex and difficult to interpret. The species abundances change considerably in the simulation period. In particular, a major change occurs around 2015 for all ecological indicators when certain species start to decline. This decrease is illustrated by the decline in catches between 2015-2020 for the SQ scenario (Figure 5). At the start of the mean simulation, the total biomass is not equally distributed among the species with SI = 0.5, and the marine ecosystem is dominated by species with a low trophic level MTI = 2.5. At the end of the mean simulation, for all scenarios, diversity indices are better than those at the beginning (SI ranges from 0.61 to 0.77, MTI from 2.79 to 3.08, according to the scenario).

The impact of uncertainties is significant, as the ecological indices appear volatile in particular for the last years. This indicates that the results should be considered with caution.

4.4. Economic results

Catches and profits for the SQ, PV and CVA scenarios are plotted in Figures 5, 6, 7 and 8. The main biomass changes in years 2015-2020 also affect the catches and profits. The SQ scenario seems economically viable in terms of profitability, as annual profits are positive during almost the entire period for all fleets. However, exceptions occur for the CC and CCA fleets in the first years of the simulation and for the P fleet in the 2010-2011 and 2026-2034 periods. Not surprisingly, the PV scenario yields the highest cumulative discounted profit, between 1.125-2.399 billion euros, versus 123.2-203.3 million euros for the SQ scenario and 84.7-239.9 million euros for the CVA scenario. The greatest fishing activity occurs in the second part of the simulation for the P fleet. One explanation can be found in the high value of the selling prices for this fleet (Table c, web appendix). On average, the CVA scenario provides positive annual profits for each fleet throughout the simulation despite the fact that the CVA fishing effort is lower than the SQ effort. However, as the CVA scenario effort levels were computed from the mean estimated parameters, the uncertainties may alter the profitability in certain years.

Comparison of the fish demand curve with the supply curves by scenario (Figure 5) shows that yield levels may differ broadly from local fish demand projection. In particular, for a period of several years, the mean production is lower than the fish demand[11] except for the mean CVA scenario, as expected. In the same vein, the mean cumulative supply over forty years of the CVA scenario with $H = \sum_t H(t) \approx 262$ Ktons is the closest to the cumulative fish demand of 144 Ktons as compared to the SQ and PV scenarios with $H = 284$ and $H = 986$ Ktons respectively. However, it also appears that the food security constraint of the CVA scenario may be violated during some years when uncertainties are taken into account.

5. Discussion

5.1. Co-viability as a step towards sustainability

Let us first analyze our results in terms of sustainability. Obviously, a total fishery closure is not a satisfactory solution either economically or socially in terms of jobs, income and food consequences. It turns out that maintaining constant efforts through the SQ scenario is also not a suitable and sustainable strategy. In fact, aside from the fact that the CC and P fleets

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[11] It should be pointed out that prices are fixed and then do not clear the market. This assumption could be relaxed in future work.

do not realize any profit in the first years, the SQ scenario does not satisfy the constraint of local consumption from years 2028 to 2038 in the mean regime and provides the worst performance for species richness. The calibration context can partially explain the negative profits of these fleets at the beginning of the simulation. Indeed, economic data are based on year 2008 which was unusual: fuel prices reached a record and thus production costs rose considerably. More generally, the low prices at first sale and the production costs did not allow every vessel to generate profits. Not surprisingly, the largest cumulative discounted profit and the most important fish supply are obtained with the PV scenario. However, this scenario may not be socially acceptable since profits are not evenly distributed between fleets over time. This happens because this scenario imposes that the CC and CCA fleets cease their activities, inducing negative profits for these fleets due to fixed costs (Figure 7). That some fleets exhibit negative profits is consistent from the social planner point of view underlying the PV approach, since aggregated profits are optimized by favoring the most efficient fleets. A better balance between biodiversity and socio-economic performance can be reached with the CVA scenario, at least on average. Although two species disappear, this scenario appears to be the best compromise: it allows annual positive mean profits for every fleet and satisfies local consumption during the forty years of simulation. However, the variability of outputs due to noise in parameters suggests that a stochastic or robust approach would be fruitful to guarantee this viability in an uncertain context.

In addition to analysis on the case study, this work advocates an integrated and multi-criteria approach. A wide range of stakeholders are involved in fisheries, including industrial, artisanal, subsistence and recreational fishermen; suppliers and workers in allied industries; managers, environmentalists, biologists, economists; public decision makers and the general public. Each of these groups has an interest in particular outcomes from fisheries, and the outcomes that are considered desirable by one stakeholder may be undesirable for another groups (Hilborn , 2007). Considering this multi-dimensional nature of marine fisheries management is a way to guarantee the reasonable exploitation of aquatic resources, allowing the creation of conditions for sustainability from economic, environmental and social viewpoints.

The present work is fully in line with these considerations. First, of interest is the use of bio-economic models and assessments articulating ecological and socio-economic processes and goals as in Bene *et al.* (2001); Doyen *et al.* (2012); Péreau *et al.* (2012). Moreover, by focusing on sustainability and viability, the present model exhibits management strategies and scenarios that account for intergenerational equity. As emphasized in Martinet and Doyen (2007) and DeLara and Doyen (2008), viability is closely related to the maximin (Rawlsian) approach with respect to intergenerational equity. In this respect, the CVA strategy turns out to be a promising approach.

5.2. Co-viability as a step towards EBFM

Several authors have proposed the viability approach as a new, innovative and well-suited modeling framework for EBFM (Cury *et al.*, 2005; Doyen *et al.*, 2012). They argue that the viability approach, especially co-viability, is relevant in handling EBFM issues because it may simultaneously account for dynamic complexities, bio-economic risks and sustainability objectives balancing ecological, economic and social dimensions for fisheries. In particular, Cury *et al.* (2005) and Doyen *et al.* (2007) show how the approach can potentially be useful for integrating ecosystem considerations for fisheries management. Mullon *et al.* (2004), Bene and Doyen (2008) and Chapel *et al.* (2008) emphasize the ability to address complex dynamics in this framework. The computational and mathematical modeling methods proposed in this paper through the CVA strategy are motivated by a similar prospect. One major advantage of the co-viability approach is the fact that the viability framework is dynamic and thus makes it possible to capture the interactions and co-evolution of marine biodiversity and fishing. The dynamics can potentially include complex mechanisms such as trophic interactions, competition, metapopulation dynamics or economic investment processes. Here the focus is both on trophic and technical interactions through a multi-fleet and multi-species context as in Doyen *et al.* (2012).

Projections over forty years for different fishing scenarios highlight the complexity of mechanisms at play, particularly their nonlinearity. With regard to this point, the trajectories of ecological indicators are representative and should not be interpreted separately. The species richness for the CL scenario can be sustained, meaning that all species are present at the end of the mean simulation. However, the Simpson and marine trophic indices reveal that species abundances change over the simulation period, even more when uncertainties on estimated parameters are considered. Diversity index (SI, MTI) values at the end of the mean simulation lead to the following findings: 1) total biomass is better distributed among species and 2) the species with a high trophic level are better represented. Thus, the effects of fishing on the species can be deduced: fishing leads to ecosystem specialization.

5.3. Decision support for the French Guiana small-scale fishery

Small-scale fisheries remain poorly managed because of their heterogeneity, difficulties in getting consistent and perennial data and the lack of regulation tools. The problem is more acute in a tropical context with a high level informal activity and high biodiversity with low stock biomass (this is typically valid for reef ecosystems). In French Guiana, waters are very turbid and productive due to the proximity of the Amazon river. There are no reefs, but biodiversity is high, as is biomass. The bio-economic database monitored from 2006 with the help of local communities who collected time series data, offers the opportunity to go a step further towards building management tools. Since the decline of the French Guiana industrial shrimp fishery (Chaboud *et al.*, 2008), the coastal fishery has become a sector with a high potential for development. In 2008, coastal fishery production was higher than shrimp and red snapper landings. However, as previously stated, there is no quota for catches, and no limitation concerning exploited species and their size. Regulation tools are derived from commonly used national and European fisheries management systems. These standards concern the gear selectivity (mesh size) and the global size of the fleet through total engine power and total vessel capacity. However, due to the lack of studies on the stock status for the main exploited species, rules relating to overall fleet size have not been adapted to the changing level of fish stocks. The only aim of the current management strategy is to prevent fishing activity by unauthorized boats. The present bio-economic study should contribute to the design of more scientific and relevant assessments and regulations for both the marine ecosystem and this small scale fishery. At this stage, we would like to point out the methodological interest of sustaining the Fishery Information System to achieve such goals.

Fishing scenario outputs show that fishing performance, including food supply and profitability of fleets, can be increased or sustained. In particular, this suggests that the marine ecosystem and the fishing sector could cope with food demand and contribute to food security. This could have positive consequences for the development of French Guiana, since the coastal fishery plays an important socio-economic role for the small towns along the coastline where more than 90% of the population is located. However, there is a risk of losing fish biodiversity due to fishing pressure. This loss of biodiversity could potentially alter some ecosystem services (not taken into account in the current model) and the outcomes of the fishery itself in the long run. Thus, some fish stocks should be evaluated more specifically in order to anticipate their depletion (*Crucifix catfish*, *Bressou catfish*). Depending on the endangered stocks, conservation measures for the productive and reproductive capacities of these stocks should be taken. This could be achieved by banning fishing in nursery areas or providing incentives for using more selective fishing techniques. In this way, the co-viability approach could enable long term management of the French Guiana coastal fishery. The CVA scenario suggests that such a multi-functional sustainability would be maintained with a small increase in the T fleet's effort and a relative reduction for the other fleets (CC, CCA or P). This management strategy entails implementing limitations on fishing effort. Nevertheless, this scenario may remain attractive for the different stakeholders involved since the profitability constraint for each fleet, the species richness constraint and the food security constraint are all satisfied. In this sense, the CVA strategy could be potentially operationalized with the fishermen's cooperation.

6. Conclusion

This work provides a bio-economic model and analysis for the coastal fishery in French Guiana. It relies on a multi-species and multi-fleet model integrating Lokta-Volterra trophic dynamics and profit functions. The dynamic model is calibrated using data from the Ifremer fishery information system. Ecological and economic performance of contrasting fishing scenarios including status quo, total closure, economic and viable strategies are compared. The major contribution of the paper is twofold. First, it proposes for the first time decision support tools for the management of the small-scale fishery in French Guiana. Small-scale fisheries are poorly managed due to a lack of tools and data, although these fisheries are crucial to sustaining many communities especially in developing or underdeveloped countries (Garcia *et al.*, 2008). The present work emphasizes the interest of bio-economic models which rely on a perennial database in this context of small-scale fisheries. The second contribution of this study is to advocate the use of viability approaches as a relevant modeling framework for EBFM and sustainability issues. Such sustainability is known to be difficult to achieve because economic, social and ecological goals can contradict each other (Pitcher , 2001). The paper points out that, by balancing ecological and economic goals with production and food security objectives over several decades, the viability approach is well suited to address sustainability. By accounting for complex and nonlinear dynamics and by addressing biodiversity issues, the paper also shows how viability modeling can be applied to high dimensional environmental systems. More generally, the present work suggests that adopting the viability method would enable other objectives of the EBFM approach to be taken into account. For instance, fisheries are urged to transform their practices progressively, to favor eco-friendly technologies, to reinforce quality and reliability of products and services and to create jobs. New management policies integrating all these dimensions in accordance with public goals need to be defined, especially in this kind of small-scale coastal fishery (Blanchard and Maneschy , 2010).

Due to the uncertainties underlying the calibrated parameters, results of this paper should be interpreted with caution. The reliability of some parameters needs to be reinforced to obtain a more accurate model. Up to now, only shrimp and red snapper fisheries have been widely studied in French Guiana. It turns out that certain parameters are estimated from Fishbase or from the literature. Consequently, it would be fruitful to integrate more values from local field studies dedicated to this ecosystem (for instance, intrinsic growth rates and trophic levels). Stomach content data analysis would also improve trophic interaction evaluations. Similarly, as landings are computed from catchabilities and initial stocks, it would be important to obtain a refined estimation of these parameters. These uncertainties suggest that a more robust approach based on stochastic viability methods should be used (Doyen and De Lara, 2010; Doyen *et al.*, 2012). Doing so would significantly strengthen the robustness of the outcomes and assertions of this dynamic complex model. At this stage, we would like to point out the advantage to sustain the Fishery Information System with the help of local communities.

Furthermore, the ecosystem-based model is based on simplified dynamics. In fact, species in French Guiana's coastal ecosystem present different trophic levels (from 2.01 to 4.35), leading us to consider predator-prey relationships between the thirteen species selected in the model. We used a basic Lotka-Voterra model because of the high number of species considered and the lack of biological data. Indeed, other models such as an individual-based model would have required us to calibrate even more biological parameters. In future work, we plan to refine the Lotka-Volterra model by adding a predator saturation effect, such as Holling functional response (Holling, 1959), when preys are abundant.

Many other issues could be addressed in future work. From an economic and social viewpoint, taking into account the demand mechanism and endogenous prices is necessary to improve the predictions of the model. A next step would be to integrate social indicators such as employment level and job satisfaction to evaluate the scenarios with regard to social performance (Blanchard and Maneschy , 2010). From an ecological perspective, it would be interesting to extend the number of species in order to include the effects of fishing activities on the dynamics of other species (such as mammals, turtles or birds) and on plankton dynamics. In line with this, comparisons with the Ecopath (EwE) approach could be informative. Another interesting goal would be to include the effects of climatic changes, for instance sea surface temperatures (Thébaud and Blanchard , 2011). Finally, a spatial extension of this model could also be considered to integrate, for instance, the effects of protected areas.

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Table 1: The thirteen selected species representing about 90% of the catches of the fishery.

Common name	Scientific name	Trophic level T_i (Fishbase)
Acoupa weakfish	*Cynoscion acoupa*	4.05
Crucifix sea catfish	*Hexanematichtys proops*	4.35
Green weakfish	*Cynoscion virescens*	4.03
Common snooks	*Centropomus parallelus, Centropomus undecimalus*	4.2
Sharks	*Sphyrna lewini, Carcharhinus limbatus, Mustelus higmani*	4.5
Smalltooth weakfish	*Cynoscion steindachneri*	3.25
South american silver croaker	*Plagioscion squamosissimus*	4.35
Tripletail	*Lobotes surinamensis*	4.04
Gillbacker sea catfish	*Arius parkeri*	4.11
Bressou sea catfish	*Aspistor quadriscutis*	3.5
Goliath grouper	*Epinephelus itajara*	4.09
Flathead grey mullet	*Mugil cephalus*	2.13
Parassi mullet	*Mugil incilis*	2.01

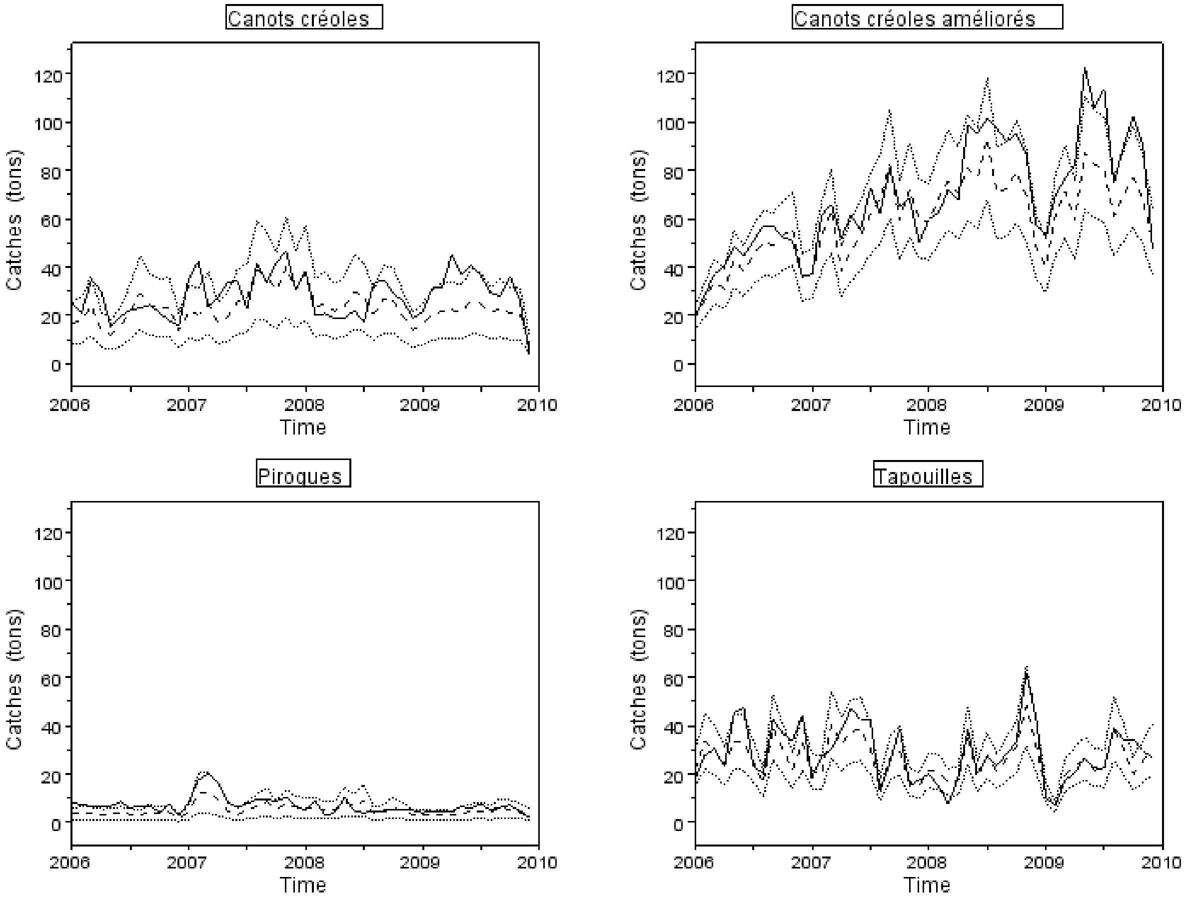


Figure 1: Comparison by fleet k between historical catches $\sum_{\text{species } i} H^{\text{data}}_{\text{species } i,k}(t)$ (solid lines) and simulated catches $\sum_{i} H_{i,k}(t)$ (dashed lines), with the confidence intervals at 95% (dotted lines).

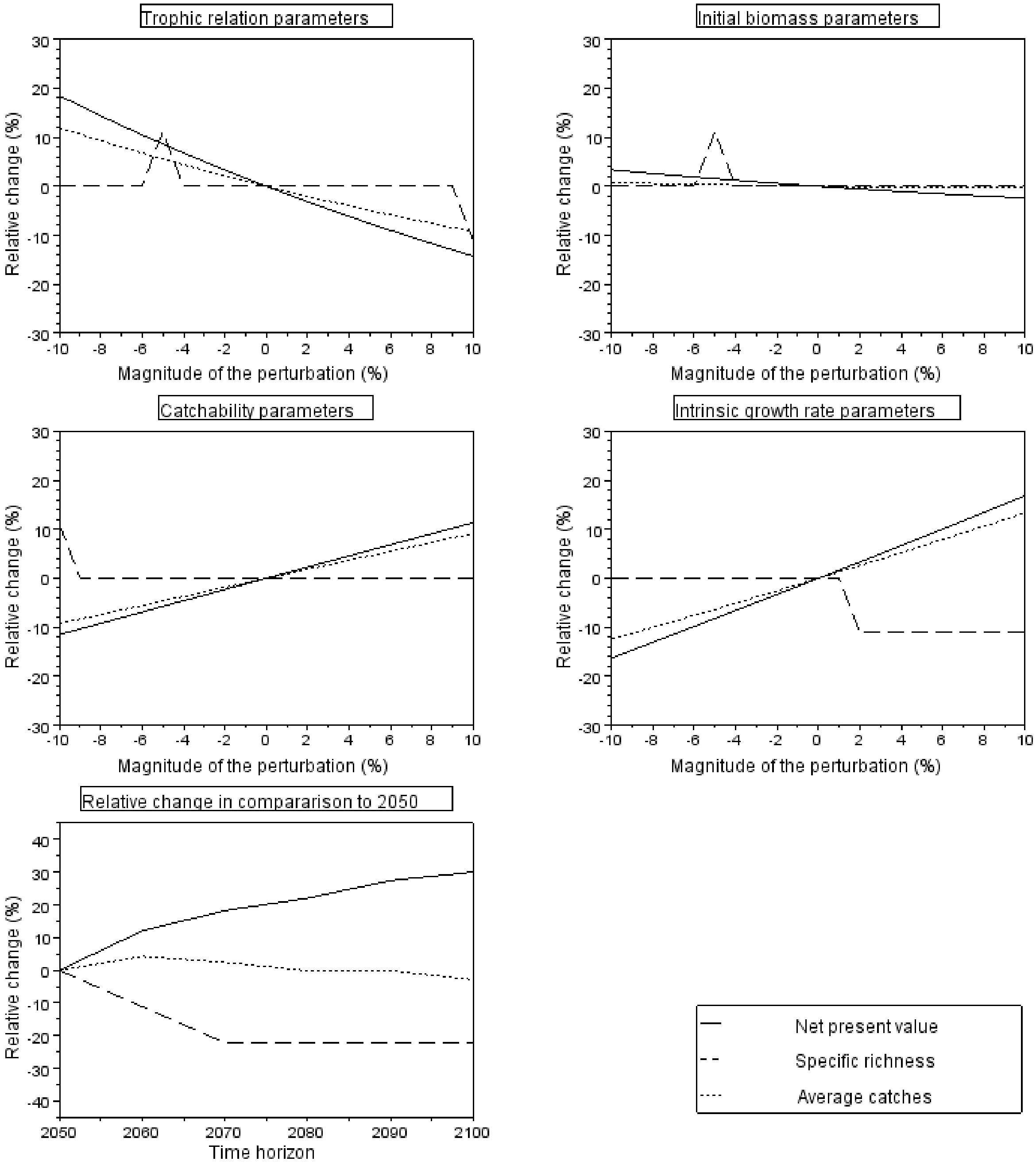


Figure 2: Relative changes of net present value NPV (solid line), average annual catches $\overline{H}$ (dotted line), species richness SR(t_f) (dashed line), according to variations in input parameters by 1% increments from -10% to +10% (a, b, c and d), and time horizon (e). The baseline is status quo scenario SQ.

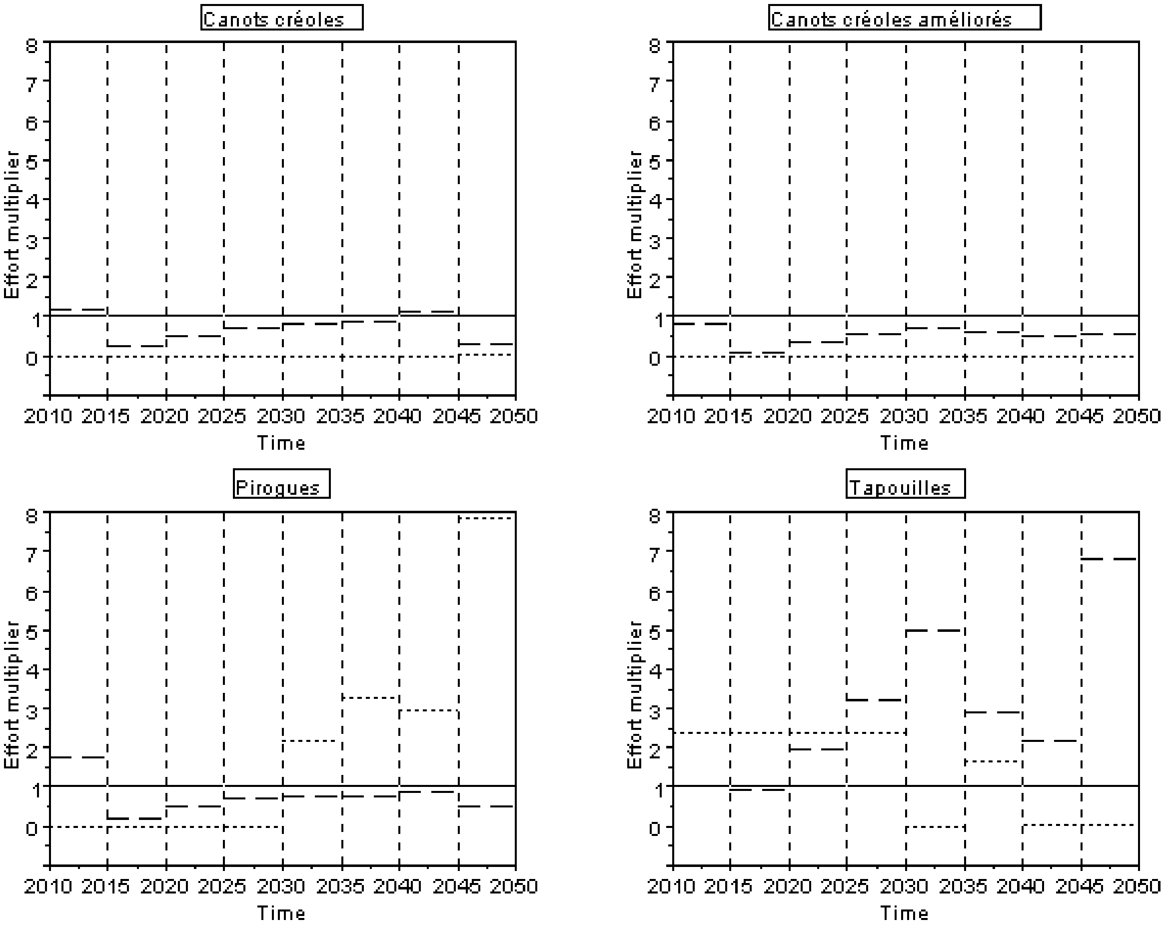
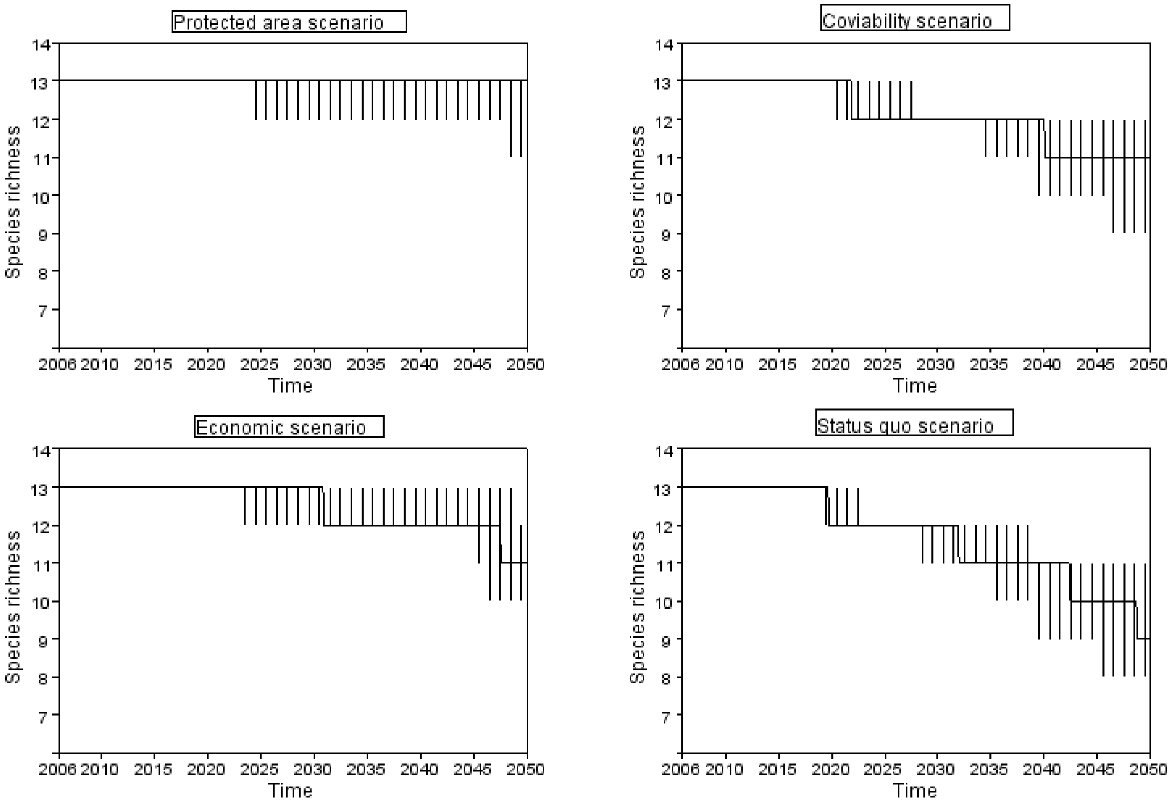


Figure 3: Fishing effort multiplier $u_k(t) = \frac{e_k(t)}{\overline{e_k}}$ by fleet and scenario, Status quo SQ (solid line), Economic PV (dotted line), Co-viability CVA (dashed line).


Protected area scenario

Coviability scenario

Economic scenario

Status quo scenario

Figure 4: Species richness SR(t) evolution by scenario (solid lines), with uncertainties (vertical lines).

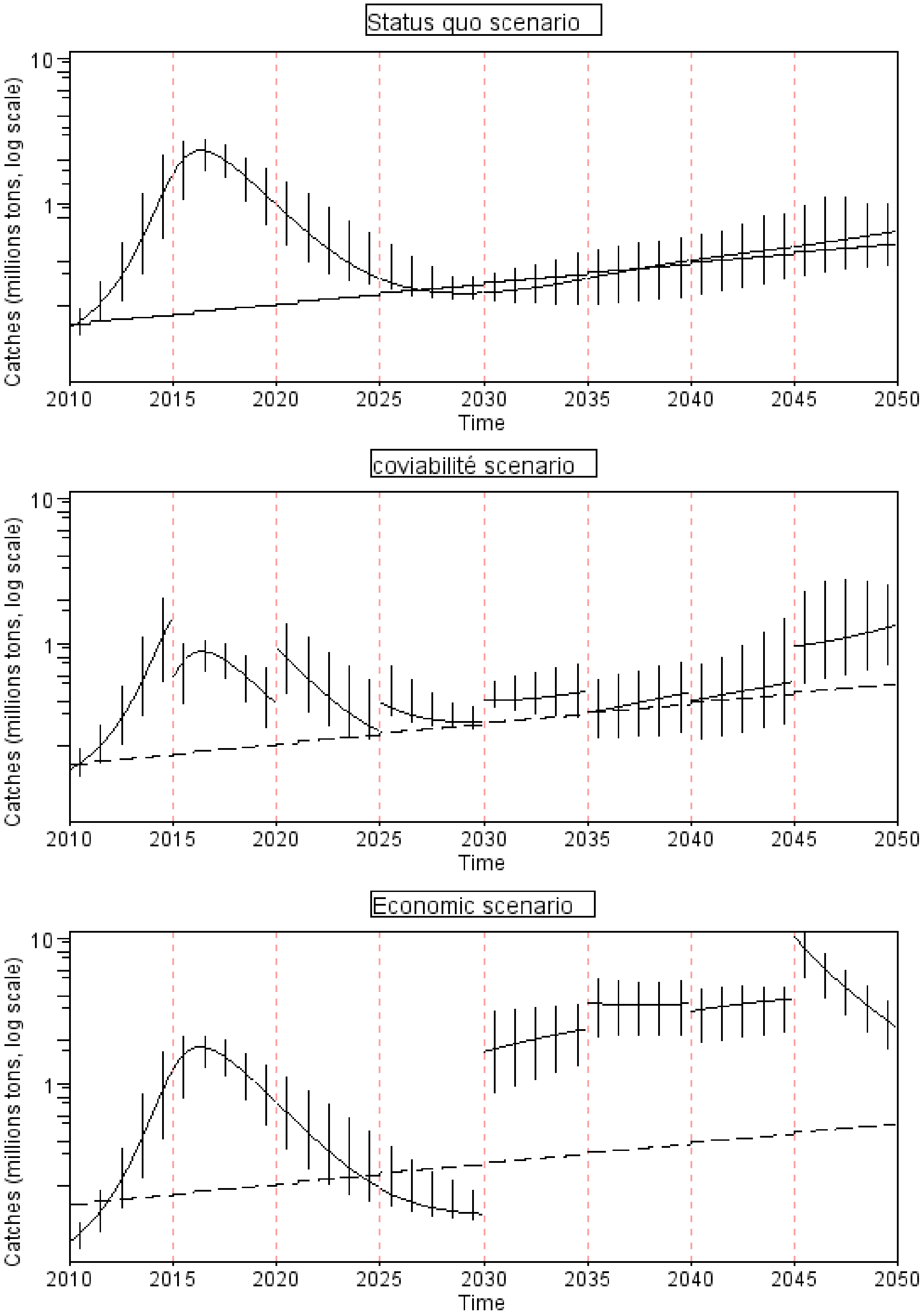


Figure 5: Total catches $H(t)$ by scenarios (solid lines) versus local fish demand (dashed line), with uncertainties (vertical lines).

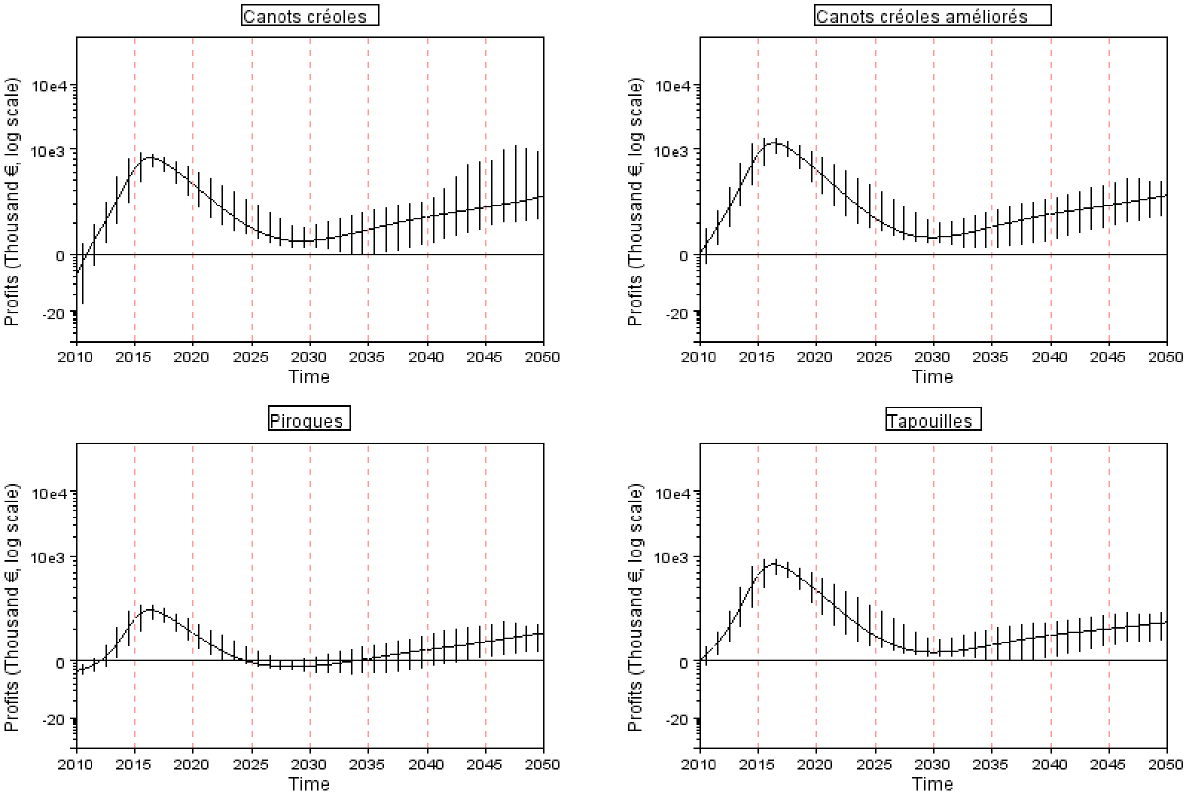


Figure 6: Profit $\pi_k(t)$ by fleet for the SQ scenario (solid lines), with uncertainties (vertical lines). The dotted line stands for profitability threshold.

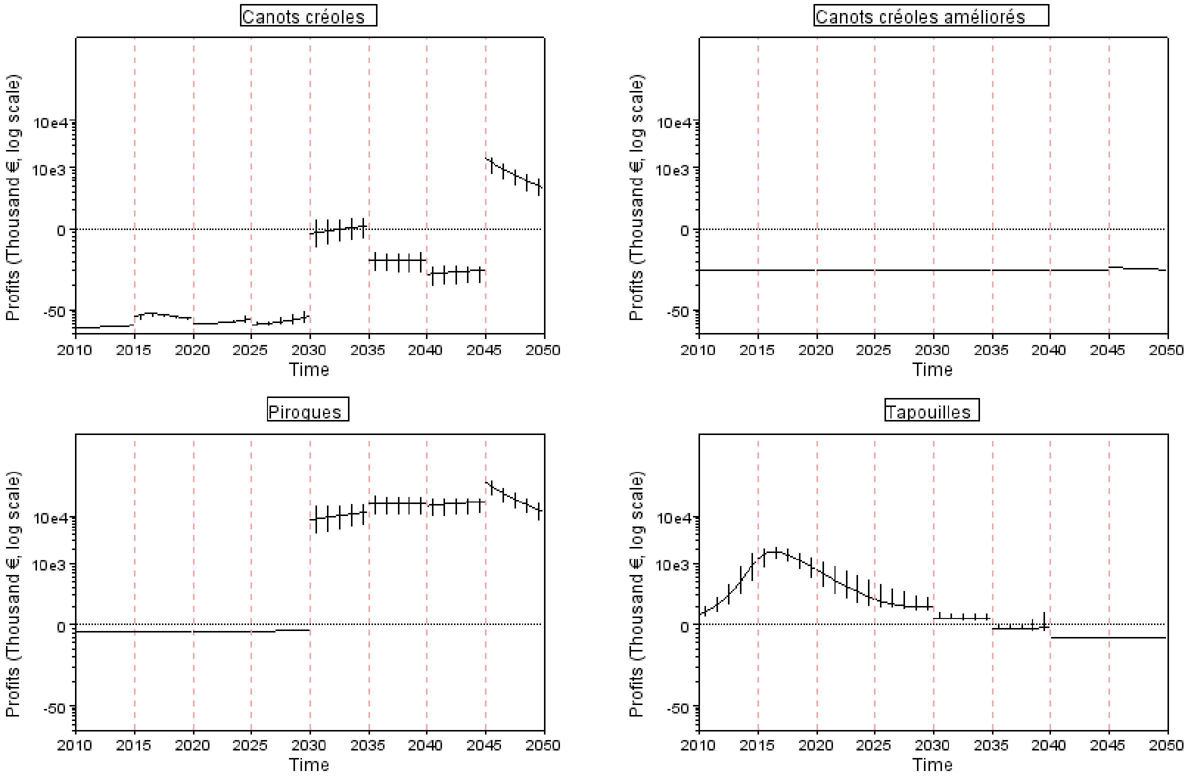


Figure 7: Profit $\pi_k(t)$ by fleet for the PV scenario (solid lines), with uncertainties (vertical lines). The dotted line stands for profitability threshold.

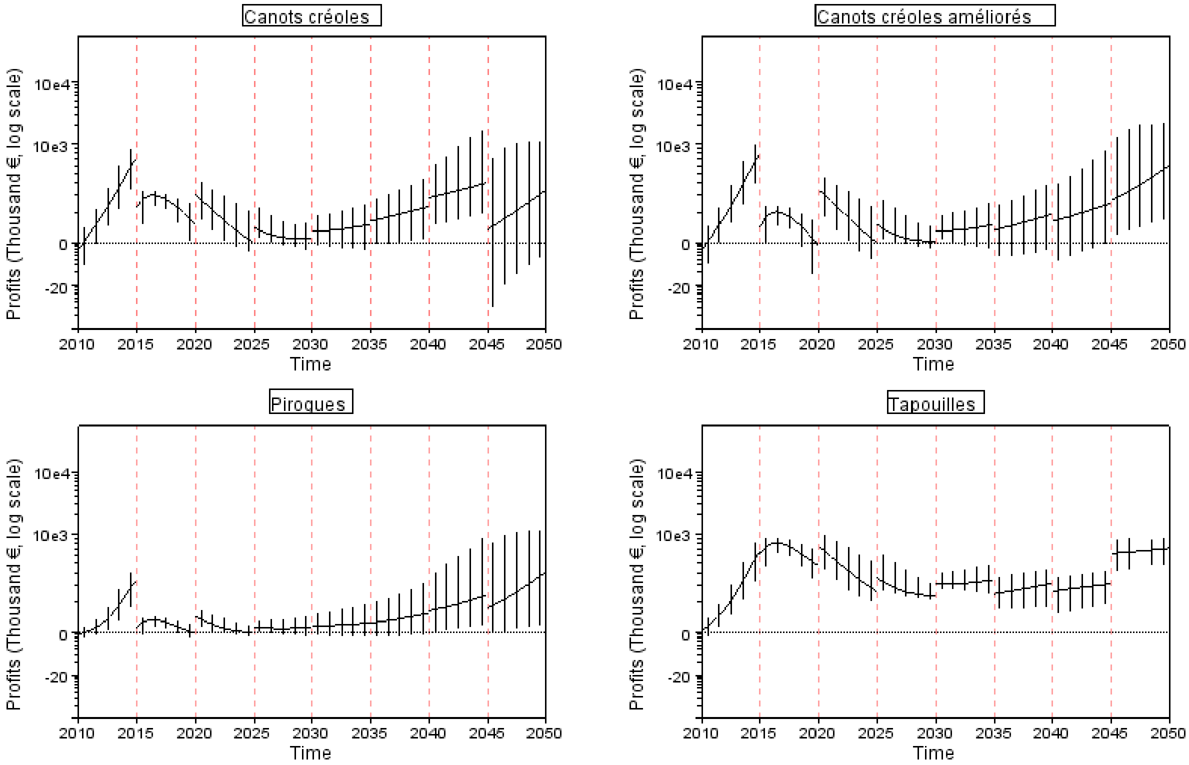


Figure 8: Profit $\pi_k(t)$ by fleet for the CVA scenario (solid lines), with uncertainties (vertical lines). The dotted line stands for profitability threshold.

Vers un développement durable des pêcheries traditionnelles côtières amazoniennes : intégrer les sciences humaines aux sciences naturelles et économiques

Fabian Blanchard
Maria-Cristina Maneschy

Résumé

La gestion actuelle de la pêche repose le plus souvent sur l'adaptation des capacités de capture à la capacité de renouvellement biologique des ressources. On intègre progressivement à la gestion, la nécessité de préservation de la biodiversité, et de l'environnement marin en général, qui subissent les impacts de la pêche. On pratique *a posteriori* des analyses économiques de l'état de la filière pêche, permettant à terme un diagnostic de viabilité économique des entreprises de pêche dans un contexte de contraintes grandissantes concernant la préservation de l'environnement : concilier préservation environnementale et développement économique. Restent que les pêcheurs ne sont pas seulement des chefs d'entreprise prédateurs de ressources. Si l'on parle d'«état de santé» écologique et économique, qu'en est-il de l'état social ? Comment concilier dans le cas de la région amazonienne, modernisation, changement de pratiques liées à la préservation des stocks et de la biodiversité avec les traditions parfois ancestrales, les cultures ? C'est notamment sur cette question que l'apport des sciences humaines est attendu dans le contexte d'un développement durable de la région.

Dans l'Etat du Pará au Brésil, les préoccupations concernant la gestion des ressources halieutiques et l'état social des communautés humaines qui les exploitent ont conduit à la création d'unités de conservation – RESEX (réserves extractivistes) – pour la protection des populations qui traditionnellement dépendent des ressources marines. Malgré les principes de base qui prônent la participation des utilisateurs traditionnels, ces unités apportent de nouvelles contraintes, règles et valeurs qui ne tiennent pas suffisamment compte i) de la diversité de situations sociales dans les populations côtières, ii) des différentes formes d'insertion sur le marché des produits de la mer par les différents catégories de pêcheurs, iii) des différents usages de l'environnement et finalement iv) de la diversité d'acteurs sociaux concernés, chercheurs et cadres de la gestion inclus. Ainsi, comment aboutir aux changements de pra-

tiques de capture et de gestion du territoire, susceptibles de promouvoir le développement durable? Risque-t-on de favoriser la protection de l'environnement au détriment des utilisateurs traditionnels et de leurs pratiques de gestion? Pour éviter cet écueil, associer l'approche biologique de la gestion au regard socio-historique autant qu'économique est un préalable.

Ce colloque offre la possibilité de combiner des expériences et questions sur deux régions différentes présentant des défis similaires en matière de gestion des ressources halieutiques exploitées par les populations côtières selon des modes traditionnels.

Introduction

Les réglementations des pêcheries pour leur gestion sont définies sur les bases de la science halieutique, fondée sur la dynamique des populations, leur biologie, isolément du milieu environnant. Le principe est de définir la capacité naturelle de renouvellement biologique des stocks de pêche, et de calibrer les prélèvements par la pêche, relativement à cette capacité, cherchant le rendement soutenable maximum. L'échec des politiques de pêche basées sur ce principe trouve selon les auteurs quatre types de causes : la qualité des données utilisées, la qualité des modèles halieutiques, le décalage entre recommandation et décision, le décalage entre décision et application sur le terrain. A ces quatre facteurs qui seront explicités dans une première partie de l'article, et qui sont souvent discutés quant à l'importance relative de l'un ou l'autre dans les échecs des politiques de gestion de la pêche, devrait être ajouté un cinquième, la complexité du système : il s'agit de règles basés sur la gestion des stocks qui sont imposées à des entreprises, mais aussi et enfin, à des hommes. Si les conditions économiques des secteurs concernés par la réglementation sont de plus en plus souvent analysées avant de faire des recommandations aux décideurs, ce n'est pas le cas de l'état social des communautés d'hommes et de femmes qui pratiquent ces pêches et de la perception qu'ils ont de leur situation. Ce dernier point, concernant la complexité du système, est développé dans la suite de l'article. Tout d'abord en reprenant le cadre conceptuel du développement durable, associant les objectifs bio-écologiques, économiques et sociaux, qui apporte un cadre théorique adapté au contexte local pour la gestion des pêcheries côtières amazoniennes et ensuite, par une illustration de la prise en compte des communautés humaines comme base de gestion, le cas des réserves extractivistes des communautés de pêcheurs au Brésil.

Des causes de l'échec de la gestion des pêches…

Des synthèses de qualité proposent une analyse des causes de l'échec des politiques des pêches (Garcia et Grainger, 2005). De manière schématique, quatre grands types de cause sont évoqués pour expliquer les échecs de la gouvernance des pêches. i) La qualité des données utilisées : les données sont de deux natures, celles collectées par les techniciens au débarquement des navires de pêche, selon un protocole bien établi, et les données issues des déclarations des pêcheurs. Par exemple, lorsque un quota de pêche pour une espèce donnée est atteint au cours de l'année, la pêcherie qui l'exploite doit s'arrêter. L'intérêt à court terme pour les pêcheurs de sous-déclarer leur capture est évidente dans ce cas. ii) la qualité des modèles : les modèles biologiques utilisés pour définir la mortalité par pêche maximale que la population peut supporter se basent sur deux hypothèses fortes et contestables. La population est en équilibre et le nombre de nouveaux juvéniles issus de la ponte est proportionnel à la quantité d'adultes. Ces deux hypothèses sont rarement vérifiées à courte échelle temporelle car le succès de la reproduction dépend fortement de facteurs écologiques tels que les conditions hydro-climatiques, très variables, les conditions de nutrition au moment de l'éclosion, de la vie larvaire, la présence de prédateurs… Il existerait autant de facteurs que de populations et d'espèces. De plus, ces modèles, s'ils permettent en théorie la préservation de la population exploitée, ne permettent pas la préservation de la biodiversité et des habitats impactés par les captures et/ou le passage des engins de pêche. Ces impacts sont parfois de nature à modifier le fonctionnement de l'écosystème, et en retour, produisent une altération de la production des espèces d'intérêt halieutiques iii) le décalage entre recommandation et décision : au niveau européen, les quotas de pêche proposés à partir des recommandations sont en effet discutés en conseil des ministres européens. Enfin, iv) le décalage entre décision et application, c'est la difficulté de contrôle sur le terrain du respect des règlements par les pêcheurs.

Le concept de développement durable

Ce concept, dont le premier énoncé reconnu le plus souvent est celui de Bruntland (1987), indique qu'une activité humaine économique, telle que la pêche, pour se développer durablement, doit être économiquement viable, ne pas altérer l'environnement, être socialement juste et respecter l'équité intergénérationnelle (Fig. 1). Dans le contexte des activités de pêche, cela signifie que les armements doivent être rentables, que les dommages causés par l'exploitation sur les populations marines, la biodiversité associée et les habitats doivent être limités de manière à ne pas modifier les équilibres écologiques et le fonctionnement des écosystèmes et enfin que le niveau de vie, les pratiques, la culture des communautés de pêcheurs doivent être respectés ; la génération suivante devant tirer de la pêche les mêmes bénéfices que leurs aînés.

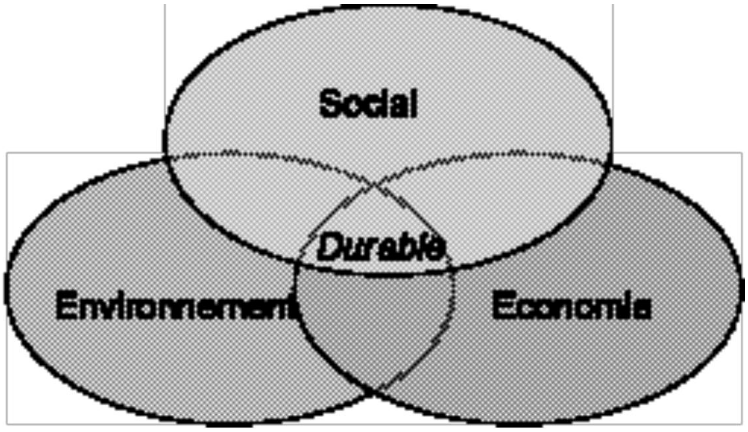


Figure 1. Une activité humaine, pour être durable selon le concept énoncé par Bruntland (1987), doit être compatible à la fois avec une rentabilité économique, le bon état de l'environnement et la justice sociale, avec de plus une dimension temporelle supplémentaire non représentée sur la figure, l'équité intergénérationnelle

On cherchera donc à évaluer l'état, ou encore le coût, bio-écologique, économique et social de la pêcherie en question et à trouver les modalités de pêche compatibles avec un bon état dans ces trois dimensions. En effet, le rendement économique maximal n'est pas toujours compatible avec le rendement biologique maximal à court terme. De même ce dernier n'est pas toujours compatible avec la préservation de la biodiversité, des habitats. Enfin, l'un et l'autre ne sont pas toujours compatibles avec le partage équitable des revenus de la pêche entre les différents acteurs et leur famille (armateur, capitaine, marins, transport, commercialisation). En revanche, il s'agit de trouver les modalités d'exploitation, sinon optimales dans les trois dimensions, du moins acceptables, trouver les compromis permettant de rendre compatible les objectifs sociaux, économiques et écologiques. La capacité de mettre en œuvre ces modalités, de trouver ces compromis, est maintenant perçue comme l'achoppement de la gestion actuelle des pêches (Boucher et Cury, 2005).

Si les méthodologies ont progressés pour qualifier et quantifier l'état bio-écologique en relation à l'exploitation, ce sont les domaines de l'halieutique et de l'écologie halieutique, et l'état économique des pêcheries, en revanche la qualification et quantification de l'état social des communautés de pêcheurs et celles qui y sont liées, reste un domaine peu avancé.

De la quantification du « bien-être social »…

La quantification du bien être social des pêcheurs, ou encore, le coût social de la pêche fait l'objet de travaux et programmes récents en sciences humaines (Bavinck et Monnereau, 2007). Dans cette orientation, le programme « ECOST » intègre dans son approche du coût sociétal des pêcheries, outre les coûts économiques et écologiques, cette dimension sociale. Les enquêtes de satisfaction au travail en tant que pêcheur représentent une méthode d'approche basée sur des indicateurs traduisant les besoins de base, les besoins sociaux, l'auto-réalisation, le management et la valeur accordée à la nature (Tableau 1).

Tableau 1. Indicateurs utilisés pour les enquêtes de satisfaction au travail dans la pêche, programme ECOST : perception des pêcheurs de leur situation.

1. Besoins de base	Sécurité physique en mer
	Prévision de revenus tirés de la pêche
	Niveau de vos revenus
	Pression mentale
	Conditions de salubrité (la propreté)
	Nombre d'heures passées quotidiennement
	Santé octroyée par le travail
	Fatigue physique causée par le travail
	Temps nécessaire pour accéder aux zones de pêche
	Capacité à nourrir sa famille
	Captures des dernières années
2 . Besoins sociaux	Temps passé en dehors du domicile pour les exigences du travail
	Opportunité de travailler à son compte
	Communauté de vie
	Temps consacré aux loisirs avec sa famille et amis
3. Auto – réalisation	Défi représenté par le travail
	"Aventure" dans le travail
	Utilité du travail
4. Management	Niveau des conflits dans la pêcherie
	Manière de résoudre les conflits
	Système de gestion
	Performance des fonctionnaires
	Types de Lois et modes de Régulations accessibles
	Influence sur la gestion de la pêcherie
5. Valeur accordée à la nature	Conditions prévalant dans le site de débarquement / port
	Conditions dans lesquelles se trouvent les stocks de pêche
	Changements intervenus au niveau des zones de pêche dans le passé et dans la période récente
	Se reconvertir dans un autre métier de pêche

Se reconvertir dans un travail, en dehors de la pêche

Relation avec l'écosystème

Avenir dans la pêche

Toutefois, sans nier l'existence du débat entre universalisme et culturalisme, il n'est pas trivial que ces approches développées récemment dans des contextes occidentaux soient transposables directement dans le contexte amazonien : la perception du bien être ou encore de la valeur accordée à la nature peut être très diverse selon les cultures. La même valeur d'un indicateur d'état est donc potentiellement interprétable comme bonne dans une culture, neutre, voire mauvaise dans une autre. Le choix d'un indicateur devrait donc être contraint par la connaissance de la perception du bien être par les populations concernées. En outre, en Amazonie, se côtoient diverses cultures, y compris dans le secteur de la pêche : amérindiennes, créoles, occidentales, avec des pratiques de pêche différentes, au moins pour le cas de la Guyane (Blanchard, 1996), ajoutant à la complexité de l'approche et du choix des indicateurs. En outre, ces cultures en Guyane sont en contact depuis plusieurs siècles, induisant des métissages pouvant parfois rendre flous les limites culturelles.

Par ailleurs, les critères de bien-être liées à la culture et aux traditions, ainsi qu'aux croyances et religions n'y sont pas pris en compte.

Enfin, la gouvernance du système basée sur concertation des acteurs de la filière (décideurs, aménageurs, scientifiques, professionnels, associations environnementalistes, associations de consommateurs…) est parfois préconisée d'une part pour parvenir à un choix de compromis entre les objectifs sociaux, écologiques et économiques et d'autre part comme un élément de mise en place des conditions d'appropriation et de réussite et des mesures préconisées pour aboutir aux compromis.

Co-viabilité des systèmes

Une fois les verrous de la quantification du bien être social levés, restera à trouver les compromis respectant objectivement les objectifs sociaux, économiques et écologiques. Pouvant être capable de modéliser le système (biodiversité-captures-profit-bien-être), il est possible de chercher mathématiquement les solutions qui satisfassent un jeu de contraintes, c'est le principe du contrôle viable, que les contraintes soient pluridisciplinaires ou non. L'ensemble des solutions constitue le « noyaux de viabilité », ou ensemble des compromis possibles garantissant la survie du système dans ses trois dimensions. De nombreux progrès ont été réalisés dans ce domaine au cours des dernières années (Doyen et al., 2008).

Les réserves extractives au Brésil : un exemple de gestion basée sur les communautés

Les préoccupations concernant la gestion des ressources halieutiques et l'état social des communautés humaines qui les exploitent ont conduit à l'institution d'unités de conservation sur les zones côtières. Ce sont les RESEX Marines (réserves extractives), qui envisagent la protection des populations qui traditionnellement dépendent des ressources marines. Il s'agit d'une catégorie d'unité de conservation inscrite au sein du Système National d'Unités de Conservation (Snuc). Sur le littoral de l'Etat du Pará, les réserves ciblent en particulier les zones des mangroves.

La modèle réserve extractive fut créée d'abord dans des domaines terriens, à la suite des mouvements sociaux de cueilleurs de caoutchouc en Amazonie Occidentale qui, durant les années 1970, avaient subi les fortes pressions de l'expansion de la frontière agricole sur les forêts dont ils prélevaient le caoutchouc depuis la fin du XIX^{e} siècle. Cette conception de territoire fut plus tard transplantée pour les zones côtières.

Les RESEX sont considérées une option pour l'utilisation durable des ressources naturelles, tout en respectant les modes de vie traditionnels et la diversité biologique (Diegues et Moreira, 2001). Leur principe de base est la gestion participative par l'ensemble d'utilisateurs traditionnels reconnus. À juste titre, le modèle souleva des expectatives positives réelles, dont on souligne l'assurance des droits d'accès aux ressources communes, ainsi qu'aux bénéfices associés aux programmes publics de support (notamment diverses formes de crédit pour des outils de travail et des fonds pour la construction de maisons). Ces expectatives stimulent plusieurs communautés locales qui revendiquent la création de réserves dans leurs communes. C'est ainsi qu'entre 2001 et 2005 on compta 9 RESEX instituées sur la côte du Pará, couvrant un territoire de 255.319,14 hectares et incluant environ 28500 «utilisateurs»[1].

La *Reserva Extrativista Marinha de Soure* (à l'est de l'Ile de Marajó située à l'embouchure de l'Amazone) fut la première de l'Etat, en 2001. Sa juridiction correspond à 274,63 km^2 d'étendues de mangroves, c'est-à-dire environ 18% du territoire de la municipalité. 12 communautés furent recensées, comprenant 400 familles vivant dans le domaine de la réserve, ou plutôt à la périphérie de la ville de Soure, siège de la municipalité, selon les chiffres de 2006 (Santos Junior, 2006).

Ces nouvelles formes de territoire apportent de nouvelles contraintes, règles et valeurs, qui réclament des procédés de concertation complexes. L'élaboration d'un plan d'utilisation et de gestion du domaine et la formation d'un conseil de gestion – des procédures inscrites dans la législation pertinente – doit pouvoir traduire les différents intérêts en cause. Ceci signifie le besoin d'organisation locale des divers groupes d'utilisateurs, moyennant des associations par exemple, et la recherche de viabilité économique de la production désormais organisée selon les directives de la conservation.

Ceci apporte également les interactions nouvelles avec la bureaucratie de l'Etat, les agences financières et de développement rural, parmi d'autres. Comme il est noté pour les familles d'agriculteurs installés sur les terres issues de la reforme agraire au Brésil, ces processus requièrent des pratiques et savoirs autres, à côté de ceux fondés sur les cultures orales locales (Neves, 2008). Cet auteur montre que ce chemin couramment s'accompagne de la dépendance d'intermédiaires politiques qui font le pont avec l'extérieur.

Il convient encore considérer les recommandations de McKean et Ostrom (2001) pour la gestion de territoires mis en commun, comme la clarté quant aux règles d'usage, aux procédés de prises de décision et leur application, quant aux critères d'appartenance aux groupes d'utilisateurs et aux frontières des ressources, ainsi que la flexibilité des règles. Celles-ci, soulignent les auteurs, doivent paraître équitables par les différents groupes.

Après une étude préliminaire à Soure (Maneschy, Prost et Moreira, 2008), on remarque que les règles ne tiennent pas toujours suffisamment compte i) de la diversité de situations sociales dans les populations côtières, ii) des différentes formes d'insertion sur le marché des produits de la mer par les différentes catégories de pêcheurs, iii) des différents usages de l'environnement et finalement iv) de la diversité d'acteurs sociaux concernés, chercheurs et cadres de la gestion inclus. Études sur des réserves marines dans d'autres régions du pays (Rebouças, Filardi e Vieira, 2006 ; Di Ciommo, 2007) mettent aussi l'accent sur la complexité sociale en cause.

À ce propos, il faut rappeler que les rapports des résidents et des pêcheurs aux mangroves et aux eaux côtières dans cette municipalité sont aussi influencés par les rapports contradictoires qu'ils entretiennent avec les grandes propriétés foncières qui côtoient ou sont en partie comprises dans le domaine de la réserve. Sources de quelques emplois et de restrictions à la mobilité spatiale des habitants, voire des conflits sur l'appropriation de terres et cours d'eau, ces fermes pratiquent depuis longtemps l'élevage extensif de bœufs et de buffles et, plus récemment, l'écotourisme tourné vers les consommateurs extérieurs.

Exemple de la diversité des rapports sociaux, l'organisation sociale des pêches aux crabes et aux crevettes, ressources qui comptent parmi les principales à valeur commerciale des mangroves à l'Etat du Pará comprennent divers rapports économiques et sociaux. Ces pêches sont pratiquées de façon individuelle et collective, par des pêcheurs plus ou moins spécialisés – les *caranguejeiros* - et pour la consommation directe et la vente éventuelle. Elles procurent aussi un revenu d'appoint à des pêcheurs attendant la saison ou une place dans un équipage de pêche côtière.

Les modalités de capture de crabe, en particulier, entraînent des déplacements saisonniers et soulèvent des critiques quant au caractère nuisible des techniques d'acquisition. D'ailleurs les déplacements de quantités considérables des pêcheurs en provenance de communes du continent vers les mangroves de l'Ile du Marajó sont signalés comme l'une des raisons à justifier la création de la réserve. Les campagnes sont fréquemment basées sur des accords préalables entre pêcheurs et « patrons » commerçants qui financent les dépenses du voyage en échange d'exclusivité à la vente. À terre, les processus de transformation du produit engagent plutôt des femmes, sous différentes formes de contrat temporaires et non formels en général. Les marchés consommateurs les plus importants sont dans les grandes villes de l'Etat et dans les États du nord-est brésilien.

Si par le passé les femmes dans les communautés littorales pouvaient pratiquer la capture des crabes, rares sont celles qui se consacrent au métier de façon continuelle à présent (Cardoso, 1999; Alves, 2002; Maneschy, 2005). L'intensité des captures qui ont éloigné les crabes des mangroves proches des agglomérations, la demande de la transformation ainsi que la perception croissante de ce travail comme dur et méprisé sont autant des facteurs qui contribuent à cette retraite des femmes.

Si les femmes dans les communautés de pêche ne sont généralement pas ou plus des pêcheurs à plein temps, il n'en reste pas moins qu'elle pratiquent des pêches pour la consommation familiale et pour suppléer aux dépenses du foyer. Elles participent aux efforts des familles pour l'entretien et l'acquisition des engins et au bien-être des équipages, ainsi que pour faire face aux fluctuations de l'halieutique. Cette position ambiguë ne leur confère pas aisément la reconnaissance d'un statut professionnel et social et donc, de parole au sein des organisations et l'éligibilité aux droits sociaux (Motta-Maués, 1998 ; Maneschy et Escallier, 2002).

La gestion participative des réserves en construction

La gestion entraîne la formation d'associations d'habitants et d'utilisateurs, associations à statut juridique. En concertation, associations, partenaires gouvernementaux, organisations d'appui, syndicats, universités et agences de recherche, doivent formuler et approuver les plans d'utilisation des ressources.

Des nouveaux concepts, pratiques, formes de coopération et de discussion publique sont ainsi mis en place par des groupes sociaux fort divers, qui ne partagent pas les mêmes sens de conservation environnementale et développement et ne disposent pas les mêmes ressources sociales.

Outre les droits d'accès aux ressources, il est question pour les locaux et les utilisateurs traditionnels d'assurer des moyens de vie durable ; ceux-ci souvent compris sous l'optique conventionnelle d'emploi d'engins plus puissants. Il faut noter encore que les politiques publiques sont très attendues par les locaux, notamment en matière de santé, éducation, sécurité sociale et emploi. Les contraintes propres à la diffusion de celles-ci font qu'elles ne vont pas de pair avec les mesures de gestion du territoire. Comment assurer la motivation des impliqués ?

À Soure, les règles de la réserve étaient perçues par les habitants interviewés comme s'appliquant à des degrés différents aux systèmes de pêche et d'acquisition d'autres ressources à intérêt commercial. Elles concernaient, d'abord, les outils permis, périodes, espèces, fréquences, volumes. Elles étaient aussi vues comme applicables aux multiples prélèvements en vue de consommation : bois pour le feu et la construction, plantes et animaux à des fins alimentaires et médicinales. Et, finalement, aux usages culturels et symboliques des composants de l'environnement, y compris l'établissement des sites permis pour les maisonnées.

On comprend donc que les règles se répercutent sur les principes de l'organisation sociale des activités: critères de groupement (parenté, voisinage ou amitié), loyautés, entraide et obligations sociales ; ceux-ci fondent en partie la flexibilité des systèmes locaux d'utilisation des ressources halieutiques. L'entrecroisement entre règles formelles et informelles reste ainsi à prendre en compte dans le processus de gestion.

Le partage de droits, responsabilités et pouvoir avec les utilisateurs locaux, le « dialogue des savoirs » et la mise en rapport des différentes échelles de gestion du territoire sont soulignés par des analystes (Berkes et Folke, 1998).

Un projet pour le développement durable des pêcheries côtières traditionnelles amazoniennes

Les échecs des systèmes de gestion occidentaux, basés sur la biologie, tenant compte de l'économie, ainsi que les limites du succès des cas de gestion basés sur des communautés humaines d'usagers, telles les réserves extractives, plaident pour une approche en région amazonienne associant réellement une gestion bio-écologique, associée à une exploitation économiquement viable et socialement acceptable dans le respect des cultures locales. Ainsi, un diagnostic bio-écologique de l'état du système littoral amazonien, un diagnostic économique de l'état des pêches traditionnelles artisanales et enfin un diagnostic de l'état socio-culturel des communautés de pêcheurs sera la première étape vers un développement nécessaire et inéluctable de la pêche dans le contexte d'une démographie forte (doublement de la population en 2030 selon le scénario intermédiaire de l'INSEE), exploitant un écosystème très productif et très diversifié. Les spécialistes des différents domaines, bio-écologie, économie et socio-anthropologie, doivent donc se mobiliser pour répondre à cet enjeu, avec une capacité de dialogue inter-disciplinaire certaine, en Guyane et au Brésil au minimum.

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Note :

1 Sources: IBAMA/CNPT; SANTOS JÚNIOR, Guilherme da Silva. Ações Políticas do Estado e da Sociedade acerca da geração de renda na Reserva Extrativista Marinha de Soure/ Marajó-PA. 2006.178f. Dissertação (Planejamento do Desenvolvimento) – Universidade Federal do Pará, Belém, 2006.