UNIVERSITÉ DE CAEN BASSE-NORMANDIE

UFR : Institut de Biologie Fondamentale et Appliquée

Ecole doctorale Biologie Intégrative Santé Environnement

THESE

Présentée par

M. Michaël GRAS

soutenue le 17 juin 2013

En vue de l'obtention du

Doctorat de l'Université de Caen Basse-Normandie

Spécialité : Physiologie, Biologie des Organismes, Populations

(Arrêté du 07 août 2006)

Sujet de la thèse :

Contribution des frayères côtières au recrutement du stock de seiche *Sepia officinalis* de Manche : lien entre le succès de la phase pré-recrutée et l'abondance de la ressource.

devant le jury composé de :

M. Eric Feunteun	Professeur MNHN	Rapporteur
M. Raymond Lae	Directeur de recherche IRD	Rapporteur
M. Didier Jouffre	Chargé de recherche IRD	Examinateur
M. Paul Marchal	Cadre de Recherche Ifremer	Examinateur
Mme. Nathalie Niquil	Directrice de Recherche CNRS	Examinatrice
M. Etienne Rivot	Maître de conférence Agrocampus-ouest	Examinateur
M. Jean-Paul Robin	Professeur UCBN	Directeur de thèse

Remerciements

Je tiens en tout premier lieu à remercier Jean-Paul Robin, Professeur à l'Université de Caen Basse-Normandie qui m'a proposé ce sujet de thèse, m'a encadré et permis de travailler dans le cadre du projet Interreg IVA Céphalopode Recrutement et Suivi des Habitats en Manche (CRESH) dont il assurait la coordination scientifique. Il m'a ainsi permis d'acquérir les connaissances et les compétences nécessaires à l'écriture de ce manuscrit de thèse.

Je tiens également à remercier M. Pascal Sourdaine pour m'avoir permis de réaliser ma thèse au sein du laboratoire UCBN-CNRS Biologie de Mollusques marins et Ecosystèmes Associées (FRE 3484 BioMEA) ainsi que Pascal Claquin qui a dirigé l'équipe d'écologie durant toute ma thèse et Pascal Favrel directeur de l'Institut de Biologie Fondamentale et Appliquée.

Mes remerciements vont également à Beatriz Roel qui m'a d'abord permis d'accéder aux données de campagne et de débarquement du Cefas mais m'a aussi prodigué les conseils nécessaires au développement du modèle utilisé pour l'évaluation du stock de seiche de Manche.

Je remercie également Eric Foucher, Jérôme Quinquis et Franck Coppin qui m'ont permis d'accéder aux données du SIH Ifremer et des campagnes scientifiques gérées par Ifremer. De plus, leur connaissance de la Manche et de ses pêcheries m'a été très utile dans la compréhension de cet écosystème et de son exploitation. L'accès aux données a été complété par Hélène Beucher qui m'a permis de remonter mes séries temporelles jusqu'à l'année 1992 et d'obtenir ainsi une vision à long terme de la dynamique et de l'exploitation de la seiche en Manche.

Je voudrais également remercier les différents collègues et partenaires du projet CRESH, Christelle Caplat, Georges Safi, Jehane Lepoittevin, Karine Grangeré, Noussithé Koueta, Nawal el Boustani, Cécile Gozlan, Hugo Lebredonchel, Fan Qin et Olivier Goetz de l'UCBN, Emma Jackson et Isobel Bloor du MBA, Paul Shaw de la Royal Holloway University of London, Véronique Legrand du Comité Régional des Pêches, André Carpentier et Yves Verin d'Ifremer Boulogne-sur-Mer dont les contributions respectives ont permis d'atteindre les objectifs du projet.

Je remercie également Jérôme Guitton dont la connaissance des données de pêche de l'Ifremer et leur valorisation grâce aux atlas en ligne qu'il développe m'ont largement aidé à avoir une vision globale des pêcheries de Manche. Je remercie également Etienne Rivot qui a accepté à plusieurs reprises de me conseiller sur les méthodes utilisées pour la standardisation des indices d'abondance et pour leur modélisation. Ces conseils m'ont été précieux et je suis heureux qu'il ait accepté d'évaluer ce travail avec les autres membres du jury de thèse.

Je remercie les membres du jury, Didier Jouffre avec qui j'ai déjà collaboré pendant 2 années à l'IRD de Dakar et qui m'avait permis de prendre un premier contact avec Jean-Paul Robin. Mais aussi Raymond Lae qui m'a encadré durant mon stage de fin d'étude et

m'a initié à l'halieutique. Et Nathalie Niquil, Eric Feunteun, Paul Marchal qui ont accepté d'évaluer ce travail.

Je tiens à remercier l'ensemble des collègues que j'ai cotoyés pendant ces années de thèse, Martin, Antoine M., Charles, Nicolas, Sébastien, Christianne, Francis, Valérie, Marie, Alexandre, Christelle, Thomas, Pauline, Camille, Stéphanie, Nadège, Maxine, Jérémie, Sami, Antoine E., Margot, Jean-Marc, Katherine, Juliette, Adrien, Anne-Flore, Juliette, Anne-Marie, Isabelle, Sandra Béatrice, Christophe et tous ceux que j'ai oubliés.

Enfin, je remercie Anne et mes parents qui tous les 3 été d'un soutien sans faille pendant les moments difficiles qu'une thèse comporte.

Acronymes

ANOVA : *ANalysis Of VAriance*
BS : *Bay of Seine* ou Baie de Seine
BTS : *Bottom Trawl Fishery*
BW : *Body Weight*
CAMANOC : CAmpagne en MANche OCcidentale
Cefas : Centre for Environment, Fisheries and Aquaculture Science
CFP : *Common Fisheries Policy*
CGFS : *Channel Ground Fish Survey*
CIAC : *Cephalopod International Advisory Council*
CIEM : Conseil International pour l'Exploration de la Mer
CRESH : Céphalopodes : Recrutement Et Suivi des Habitats en Manche ou *Cephalopods Recruitment from English Channel Spawning Habitats*
DCF : *Data Collection Framework*
DCSMM : Directive Cadre Stratégique Milieu Marin
DML : *Dorsal Mantle Length* ou Longueur Dorsale du Manteau
DPMA : Direction des Pêches Maritimes et de l'Aquaculture
EFD : *Elliptic Fourrier Descriptors* ou Descripteurs Elliptiques de Fourrier
EU : *European Union*
EVHOE : EValuation Halieutique de l'Ouest de l'Europe
EwE : *Ecopath with Ecosim*
FAO : *Food and Agriculture Organization of the United Nations*
FEDER : Fonds Européen de Développement Régional
FishDAC : *Fisheries Data Archive Centre*
GIB : *Group I Breeding*
GIIB : *Group II Breeding*
GLM : *Generalised Linear Model* ou Modèle Linéaire Généralisé
GOV : Grande Ouverture Verticale
GSI : *Gonado-Somatic Index* ou Indice Gonado-Somatique
GW : *Gonad Weight*
ICES : *International Council for the Exploration of the Sea*
Ifremer : Institut Français de Recherche pour l'Exploitation de la MER
INSEE : *French National Institute of Statistics and Economic Studies* ou Institut National des Statistiques et des Etudes Economiques
ITQ : *Individual Transferable Quotas* ou Quotas Individuels Transférables
LDA : *Linear Discriminatory Analysis*
LPUE : *Landings Per Unit Effort* ou Débarquement Par Unité d'Effort
MANOVA : *Multivariate Analysis of Variance*
MBA : *Marine Biological Association of the United Kingdom*
MEDIN : *Marine Environmental Data and Information Network*

MPA : *Marine Protected Area* ou Aire Marine Protégée
MSY : *Maximum Sustainable Yield* ou Rendement Maximum Durable
NG : *Nidamental Glands*
NO : Navire Océanographique
NOAA : *National Oceanographic and Atmospheric Administration*
OBSMER : *French National Onboard Observer Programme* ou Programme d'OBServateurs embarqués en MER
OG : *Oviducal Glands*
PCA : *Principal Component Analysis* ou Analyse en Composantes Principales
PCP : Politique Commune des Pêches
PIB : Produit Intérieur Brut
PTA : *Partial Triadic Analysis* ou Analyse Triadique Partielle
RV : *Research Vessel*
SBT : *Sea Bottom Temperature* ou Température de fond
SC : *Spermatophoric Complex*
SIH : Système d'Information Halieutique
SS : *Needham's Sac or Spermatophoric Sac*
SSB : *Spawning Stock Biomass* ou Biomasse féconde
SSR : *Sum of Squares Residuals*
SST : *Sea Surface Temperature* ou Température de Surface
STATIS : Structuration des TAbleaux à Trois Indices de la Statistique
TAC : Total Acceptable de Capture ou *Total Allowable Catch*
TB : *Torbay*
UE : Union Européenne
UK : *United Kingdom*
VHVO : *Very High Vertical Opening*
VMS : *Vessel Monitoring System*
VPA : *Virtual Population Analysis* ou Analyse de Population Virtuelle
WC : *West Cotentin* ou Ouest Cotentin
WCT : *Working Capital Turnover*
WGCEPH : *Working Group on CEPHalopods fisheries and life history*
WKMSCEPH : *Workshop on sexual Maturity Staging of CEPHalopods*

Table des matières

Table des figures

Liste des tableaux

Chapitre 1

Introduction générale

Les ressources marines mondiales ont été exploitées depuis des siècles. Depuis 1950, en raison de l'industrialisation du secteur de la pêche, les captures mondiales ont augmenté de 20 à 80 millions de tonnes jusqu'en 1990 et stagnent depuis à ce niveau malgré l'augmentation de l'effort de pêche (FAO, 2012b). La moitié des stocks mondiaux sont actuellement considérés en état de pleine exploitation et un quart en état de surexploitation (FAO, 2012a). La pêche en Atlantique N-E représente actuellement environ 11% des captures mondiales. Les mers européennes ont été exploitées très tôt et des cas de surexploitation ont même été recensés en Mer du Nord au début du XX^{ème} siècle, généralement attribués au développement des chalutiers à vapeur (Rijnsdorp, 1996; Sparholt et al., 2007). En Europe, le secteur de la pêche est actuellement confronté à une situation de crise, avec des coûts en forte augmentation et une production stagnante (Gascuel et al., 2011). Cette situation a poussé les pêcheurs à se tourner vers de nouvelles ressources pour satisfaire la demande croissante en protéines, c'est ainsi que des pêcheries de céphalopodes se sont développées à travers le monde et en Europe.

Les ressources de céphalopodes ont longtemps été considérées en Europe comme de second plan. Il est pourtant indéniable que les ressources de calmars, poulpes et seiches accessibles aux pêcheries artisanales du sud de l'Europe ont joué un rôle économique important (Shaw, 1994). En Europe du nord, l'intérêt des pêcheurs pour les stocks de céphalopodes a crû durant les années 1980 (Dunn, 1999a). L'intérêt que les pêcheurs ont porté à cette ressource a provoqué la création du *Study Group on Squid Biology* qui a par la suite donné naissance au *ICES Working Group on Cephalopod Fisheries and Life History* (WGCEPH). Cet intérêt pour les céphalopodes a également contribué à la création du *Cephalopod International Advisory Council* (CIAC) en 1983. Dans les eaux européennes, les débarquements de céphalopodes dépassent régulièrement les 100 000 tonnes annuelles (Statistiques FAO). Malgré ces captures importantes, les céphalopodes ne sont pas pris en compte dans la Politique Commune des Pêches (PCP) et seules des mesures locales ou nationales réglementent l'effort de pêche, la taille au débarquement et les périodes de pêche (Pierce et al., 2010).

La conservation ou la gestion des ressources halieutiques sont généralement réalisées par des institutions internationales (*Food and Agriculture Organization of the United Nations*, FAO, Commission Européenne), des gouvernements ou des instances régionales et ont pour objectifs de maintenir une exploitation durable de la ressource dans la zone qu'elles ont en charge. Des législations peuvent être mises en place à différents niveaux sur le maillage, la taille minimale de capture, des totaux de capture, une délimitation des zones de pêche ou une limitation de l'effort de pêche. Cependant, ces mesures de gestion ont été développées pour les poissons et ne sont pas toujours adaptées aux céphalopodes.

Les céphalopodes présentent des traits d'histoire de vie sensiblement différents des poissons et sont ainsi considérés comme des espèces atypiques (O'Dor and Webber, 1986). La forte variabilité inter-annuelle de leur abondance (Caddy, 1983) s'explique par un cycle de vie court et un taux de croissance élevé qui est fonction à la fois de la température du milieu, mais aussi de la disponibilité en nourriture (Pierce et al., 1998; Rocha and Guerra, 1999; Jackson and Moltschaniwskyj, 2002; Pierce et al., 2008).

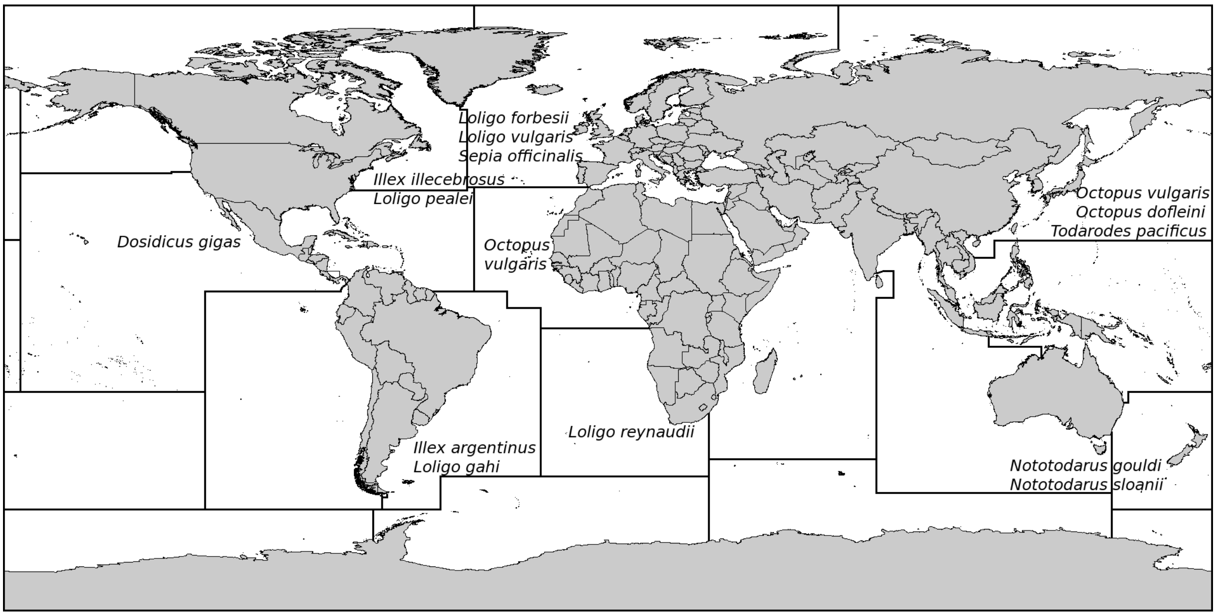

Fig. 1.1 – Stocks de céphalopodes ayant fait l'objet d'une évaluation de stock, d'après Boyle and Rodhouse (2005).

Malgré des exercices d'évaluation de stock réalisés sur différents stocks de céphalopodes dans le monde (figure 1.1), un nombre limité d'entre eux est géré dans le monde, utilisant deux grands types de méthodes de gestion. Malgré les différences observées chez les céphalopodes, la première, assez répandue pour gérer les stocks de poissons, est le Total Acceptable de Capture (TAC). Au Japon, il a d'abord été estimé en fonction de l'abondance et de la demande du marché pour *Todarodes pacificus*, méthode qui a ensuite été remplacée par un TAC couplé à des licences de pêche (Boyle and Rodhouse, 2005). En Nouvelle Zélande et en Australie, les stocks de *Nototodarus gouldi* et *Nototodarus sloanii* sont gérés depuis 1986 par des Quotas Individuels Transférables (ITQ) qui évitent une compétition entre pêcheurs pour la ressource (Gibson, 1995; Jennings et al., 2001a). En Atlantique N-W, des campagnes scientifiques sont réalisées avant l'ouverture de la saison de pêche pour évaluer les stocks d'*Illex illecebrosus* et de *Loligo pealei* afin d'estimer un TAC durable (O'Dor and Dawe, 1998; Boyle and Rodhouse, 2005). La deuxième méthode est un contrôle de l'effort de pêche qui peut être mis en œuvre sous différentes formes. Cela peut se faire par un contrôle du nombre de licences de pêche comme cela a été fait pour la gestion de *Nototodarus gouldi* et *Nototodarus sloanii* en Australie et Nouvelle Zélande jusqu'en 1983 (Boyle and Rodhouse, 2005) ou pour la gestion du stock de *Loligo reynaudii* en Afrique du sud, cette dernière étant couplée à une fermeture de la pêche (Augustyn et al., 1992; Augustyn and Roel, 1998; Lipinski, 1998). La fermeture de la pêche a aussi été utilisée pour gérer les calmars *Illex argentinus* et *Loligo gahi* des Iles Falklands (Beddington et al., 1990; Rosenberg et al., 1990; Agnew et al., 1998). En Afrique de l'ouest, la gestion du stock d'*Octopus vulgaris* se fait par fermeture annuelle de la pêche durant la saison de reproduction (Jouffre et al., 2002). Enfin, la limitation de l'effort de pêche a été mise en place au niveau national (Portugal et Espagne) ou au niveau régional pour les caseyeurs ciblant la seiche (Basse Normandie, France) avec parfois des tailles minimales au débarquement (Hastie et al., 2009).

Le choix de la méthode de gestion la plus efficace ne peut se faire qu'en s'appuyant sur une connaissance approfondie de la ressource et de sa dynamique. En Manche, les céphalopodes ont été étudiés par divers auteurs qui ont mis en évidence les fortes fluctuations du recrutement en lien probable avec les paramètres environnementaux (Robin and Denis, 1999; Denis and Robin, 2001; Denis et al., 2002). Des exercices de modélisations des stocks ont par la suite été réalisés utilisant les modèles de déplétion (Dunn, 1999b; Royer et al., 2002) ainsi que l'Analyse de Population Virtuelle (VPA ; Royer et al., 2002, 2006). Les travaux de recherche ont enfin concerné l'âge au recrutement dans la pêcherie (Challier et al., 2002) et sa variabilité spatio-temporelle (Challier et al., 2005a, 2006b) ainsi que l'effet de l'environnement et de l'abondance du stock sur le recrutement (Challier et al., 2005b) et l'intégration de cette variabilité au sein des modèles d'évaluation de stock (Challier et al., 2006a). Malgré ces travaux, les connaissances concernant la dynamique du stock de seiches de Manche restent limitées.

Le projet "Céphalopodes : Recrutement Et Suivi des Habitats en Manche" (CRESH) a été réalisé dans le cadre du programme Interreg IVA financé par le Fonds Européen de Développement Régional (FEDER) visant à promouvoir la coopération transfrontalière dans les domaines urbain, rural et côtier, du développement économique et de la gestion de l'environnement sur la période 2007-2013. Etant donné l'importance grandissante des céphalopodes pour les pêcheries de Manche, il était important d'améliorer les connaissances sur ces populations, en particulier sur : (i) les habitats nécessaires à leur reproduction, (ii) l'estimation de la contribution des aires de ponte au recrutement dans le stock exploité, (iii) la compréhension de l'effet de facteurs biotiques et abiotiques sur la croissance et la survie des juvéniles, (iv) les marqueurs génétiques d'identification des paralarves, (v) la combinaison des indices d'abondance issus des campagnes scientifiques et des statistiques de pêche pour (vi) proposer des recommandations aux pêcheurs pour une exploitation durable de la ressource de céphalopodes de Manche.

Ce travail de thèse, réalisé dans le cadre du projet CRESH, se concentre sur les points (ii) et (v).

Un premier chapitre est consacré à la présentation de la seiche, de son habitat et de son exploitation par les pêcheurs, de l'écosystème Manche et du contexte halieutique dans lequel les céphalopodes, et la seiche en particulier, tiennent une place prépondérante. Enfin une présentation des systèmes d'information français et britanniques ainsi qu'une revue des méthodes usuellement utilisées pour évaluer les stocks de céphalopodes est réalisée.

Dans un deuxième chapitre, une vérification du cycle de vie de la seiche en Manche, décrit comme durant exclusivement 2 ans (Boucaud-Camou and Boismery, 1991; Dunn, 1999a) et pouvant varier en fonction de la température du milieu (Mangold, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991; Le Goff and Daguzan, 1991; Gauvrit et al., 1997) est réalisée. Etant donné le contexte de réchauffement et de très forte exploitation de la Manche, il apparaissait utile, avant le développement d'un modèle d'évaluation de stock pour la seiche de Manche, de vérifier si ces traits d'histoire de vie avaient changé et si une partie de la population pouvait atteindre la maturité sexuelle à l'âge de un an.

Dans un troisième chapitre, étant donné que les indices d'abondance issus des pêcheries commerciales (Débarquement Par Unité d'Effort, LPUE) sont calculés à l'aide des débarquements de chalutiers de fond, il apparaissait nécessaire de vérifier la répartition de l'effort de pêche exercé par cette flotille en Manche, en particulier de mettre en évidence si elle couvrait les zones de présence et d'absence de la seiche pendant l'ensemble de son cycle de vie.

Une fois le cycle de vie vérifié et la distribution de l'effort de pêche évaluée, un modèle d'évaluation de stock a été développé. Les modèles déjà développés, modèle de déplétion (Dunn, 1999b) et VPA (Royer et al., 2006) ayant montré leurs limites, un modèle de biomasse à 2 stades est donc proposé comme nouvel outil d'évaluation du stock de seiche de Manche. Ce modèle, qui a déjà été développé pour plusieurs espèces (calmar d'Afrique du Sud ou Hareng de Mer Celtique), permet l'estimation du recrutement et le développement d'indicateurs de durabilité de l'exploitation de la seiche ainsi que la définition de points de référence.

Enfin, après avoir modélisé la dynamique du stock et évalué la variation temporelle du recrutement, une estimation de la contribution des frayères au recrutement était nécessaire. Pour cela, des individus ont été échantillonnés dans 3 frayères côtières connues pour leur importance et au sein du stock central. Le dosage d'éléments traces, les signatures isotopiques et les formes de statolithes décrites par les ellipses de Fourrier permettent de discriminer les pré-recrues puis de déterminer l'origine la plus probable des recrues. Une première approche de la contribution des différentes aires de ponte a ainsi été estimée.

Chapitre 2

Présentation de la ressource, des données et de la modélisation des stocks

2.1 Introduction

La présentation de la ressource étudiée est un préalable obligatoire à l'étude des variations de l'abondance d'un stock et des origines de ces variations. Dans un premier temps, après avoir fait une description des caractéristiques communes des céphalopodes, la biologie, l'écologie, l'aire de répartition, les traits d'histoire de vie et la position trophique de la seiche sont détaillés. Dans un deuxième temps, les particularités de la Manche et un aperçu des ressources halieutiques disponibles et de leur exploitation sont évoquées. Les systèmes d'information déployés par la France et le Royaume Uni afin de suivre l'évolution de ces ressources sont ensuite décrits. Enfin, une revue bibliographique des modèles d'évaluation de stocks les plus couramment utilisés, modèle global, Analyse de Population Virtuelle (VPA), modèles de déplétion et modèle à 2 stades, et leur application pour évaluer des stocks de céphalopodes est réalisée.

2.2 La seiche : *Sepia officinalis* Linnaeus

Les céphalopodes sont considérés comme les mollusques les plus sophistiqués des points de vues morphologique, anatomique, physiologique et comportemental (Mangold, 1989; Brusca and Brusca, 2002). Leur capacité natatoire très développée leur permettent de réaliser des cycles migratoires sur des distances importantes, une caractéristique les rapprochant du mode de vie des poissons (Boyle and Rodhouse, 2005). Leurs systèmes de défense (poche du noir et capacité de camouflage) et d'attaque (tentacules et bras préhensiles) très développés permettent de les qualifier de prédateurs avertis (Rodhouse and Nigmatullin, 1996). Cependant, les céphalopodes diffèrent des poissons sur de nombreux points. Leur cycle de vie est court (en général entre 6 mois et 2 ans et à l'exception de *Octopus chierchiae*, *Nautilus spp.* et *Argonauta argo*, tous sont semelpares (Boyle and Boletzky, 1996). Contrairement aux poissons qui passent par une phase larvaire, les céphalopodes tout juste éclos sont morphologiquement identiques aux adultes, ont déjà développé tous leurs organes et passent donc par une phase qualifiée de para-larvaire correspondant à la phase planctonique (von Boletzky, 1974). La phase para-larvaire est la période du cycle de vie durant laquelle la mortalité naturelle est la plus forte, provoquée soit par la prédation, soit par les conditions environnementales. Les céphalopodes présentent généralement une forte variabilité inter-annuelle de leur abondance (Boyle and Rodhouse, 2005).

La Manche héberge 9 espèces de céphalopodes, *Eledone cirrhosa* Lamarck 1798, *Todaropsis eblenae* Ball 1841, *Illex coindetii* Verany 1837, *Alloteuthis subulata* Lamarck 1798, *Loligo vulgaris* Lamarck 1798, *Loligo forbesii* Steenstrup 1856, *Sepia officinalis* Linnaeus 1758, *Sepiola atlantica* Orbigny 1840 et *Rossia macrosoma* Delle Chiaje, 1892. Parmi ces 9 espèces, seules 3 atteignent une taille et une abondance suffisantes pour faire l'objet d'une exploitation par les pêcheurs, 2 espèces de calmars (*Loligo vulgaris* et *Loligo forbesii* ; Royer et al., 2002) et une espèce de seiche (*Sepia officinalis* ; Royer et al., 2006). Boletzky (1983) notait déjà que la seiche était l'un des céphalopodes les plus étudiés, les seiches de Manche ayant fait l'objet de nombreuses études physiologiques (Richard, 1971, 1975), biométriques (Mattacola et al., 1984), histologiques (Medhioub, 1986; Boucaud-Camou et al., 1991), éthologique (Darmaillacq et al., 2006), écologique (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Challier et al., 2002, 2005a) et de modélisation (Dunn, 1999b; Royer et al., 2006)

2.2.1 Diagnose

La seiche *Sepia officinalis* (figure 2.1) est un mollusque céphalopode appartenant à l'ordre des Sepiida et à la famille des Sepiidae. Sa taille maximale peut atteindre 45 cm de longueur de manteau, celui-ci étant de forme ovoïde. La seiche possède 2 massues tentaculaires terminées par 5 à 6 rangées de ventouses, les centrales étant légèrement plus larges que les autres. Parmi les 8 autres bras, le 5ème en partant de la gauche est appelé bras hectocotyle. Chez le mâle mature, le bras hectocotyle est dépourvu de ventouse et sert à déposer les spermatophores sous la cavité buccale, dans un repli formé par la membrane buccale de la femelle. Deux nageoires séparées à l'extrémité postérieure permettent à la seiche de se déplacer lentement en 3 dimensions. Le siphon est utilisé pour se déplacer plus rapidement en présence d'un danger (Roper et al., 1984; Guerra, 1992; Reid et al., 2005; Pierce et al., 2010).

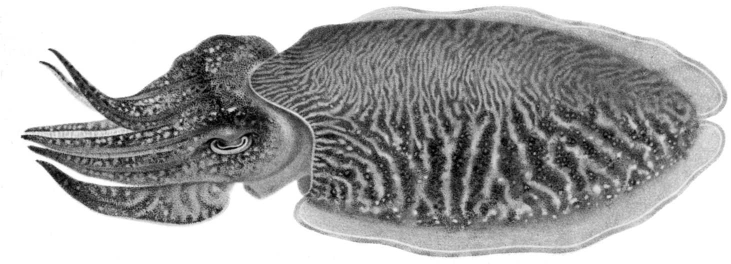

FIG. 2.1 – Représentation d'une seiche commune *Sepia officinalis* (Meyer, 1913).

2.2.2 Aire de répartition

La seiche *Sepia officinalis* est présente en Atlantique N-E (figure 2.2). La limite sud de son aire de répartition se situe aproximativement à la frontière entre le Sénégal et la Mauritanie et elle s'étend au nord jusqu'aux Iles Sheltland et au Sud de la Norvège. Il semble tout de même que les fortes abondances s'arrêtent au niveau de la Manche. La seiche est également présente en Mer Méditerranée (Reid et al., 2005). Sa distribution est fonction de la température puisqu'elle ne peut survivre à des températures inférieures à 7°C (Richard, 1971). La seiche est une espèce necto-benthique (ou démersale) et vit dans les eaux néritiques, i.e. entre la zone intertidale et 200 m de profondeur (Wells and Wells, 1991; Reid et al., 2005).

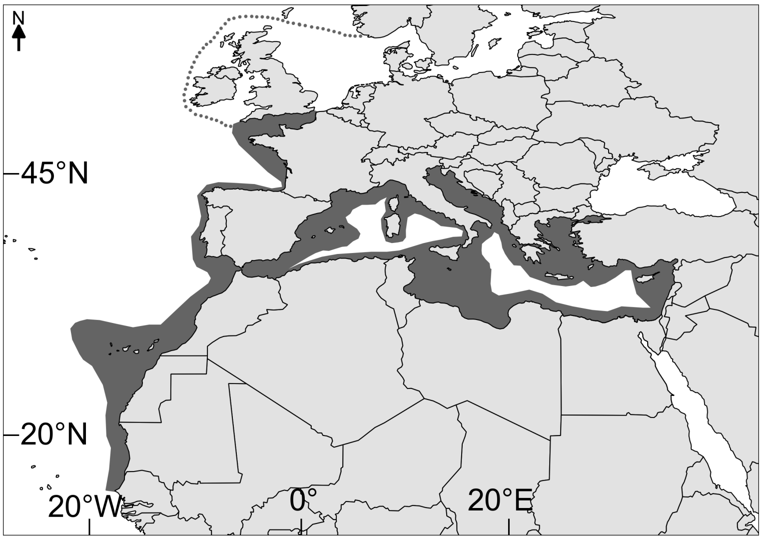

Fig. 2.2 – Aire de distribution de la Seiche *Sepia officinalis* en Atlantique N-E et en Mer Méditerranée. Les fortes abondances sont représentées en gris et les faibles abondances sont représentées en pointillés. Cette illustration est une synthèse des références citées.

2.2.3 Traits d'histoire de vie

Les seiches juvéniles éclosent à une taille variant de 6 à 9 mm (Boletzky, 1983). Le taux de croissance, très étudié en élevage (Richard, 1971, 1975; Boletzky, 1983; Palmegiano and D'Apote, 1983; Bouchaud and Daguzan, 1989; Forsythe et al., 1994; Bettencourt and Guerra, 2000) a été moins étudié en milieu naturel mais les résultats montrent une variation directement liée à la température et inversement à la taille (Medhioub, 1986; Dunn, 1999a; Challier et al., 2002, 2005a). Les seiches atteignent leur maturité sexuelle à des tailles variables en fonction de la zone dans laquelle elles vivent. L'espèce a une durée de vie qui varie de 1 à 2 ans en fonction de la température de son environnement et donc de la latitude à laquelle elle vit. Entre les côtes ouest-africaine et le Portugal, sa durée de vie est d'une année au maximum (Mangold, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991). Entre les côtes portugaises et le nord du Golfe de Gascogne, un pourcentage variable de la population se reproduit à l'âge d'un an alors que le reste se reproduit à l'âge de 2 ans (Le Goff and Daguzan, 1991; Gauvrit et al., 1997). En Manche, le cycle de vie (figure 2.3) a été jusqu'à présent décrit comme étant d'une durée exclusive de 2 ans (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991; Dunn, 1999a).

La durée de la période de reproduction est également variable en fonction de la latitute. La reproduction s'observe tout au long de l'année au sud du Portugal (Bakhayoko, 1983; Guerra and Castro, 1988) et en Mer Méditerranée (Mangold, 1966), de mars à août dans le Golfe du Morbihan (Le Goff and Daguzan, 1991) et de mai à septembre en Manche avec un pic d'éclosion en juillet (Boucaud-Camou et al., 1991; Challier et al., 2002).

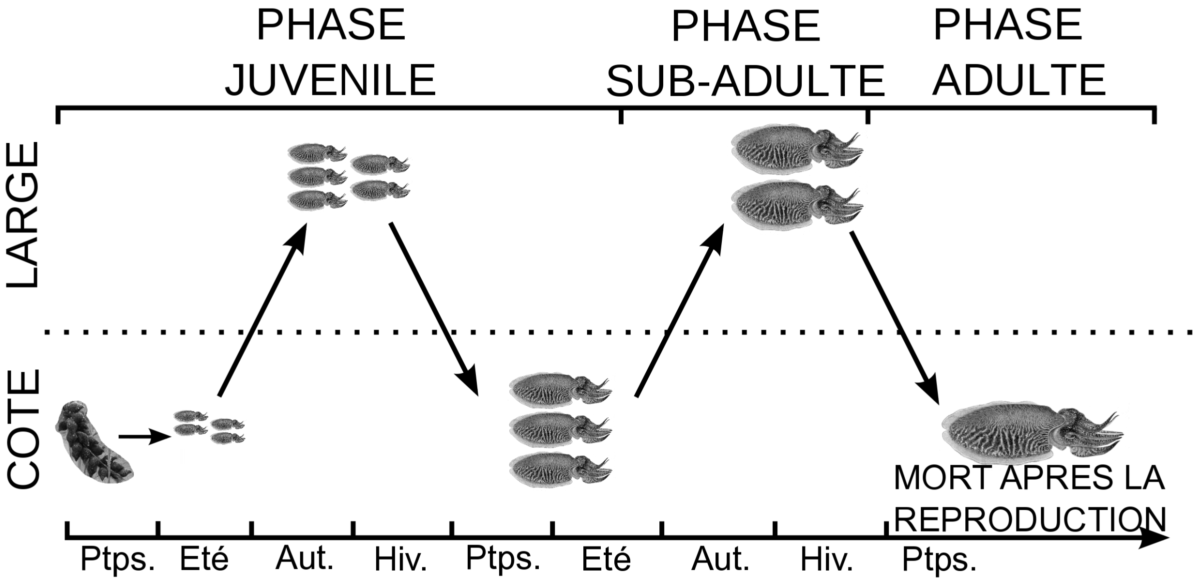

FIG. 2.3 – Cycle de vie de la seiche *Sepia officinalis* en Manche.

2.2.4 Position trophique

La seiche, comme les autres espèces de céphalopodes, est une ressource importante au sein des réseaux trophiques à la fois comme proie (prédatée par des mammifères marins et par des elasmobranches) et comme prédateur. La seiche a été retrouvée dans les contenus stomacaux de plusieurs espèces comme le phoque moine de Méditerranée, *Monachus monachus* (Salman et al., 2001), en Manche elle a été principalement retrouvée dans les contenus stomacaux du Dauphin de Risso, *Grampus griseus* (Clarke and Pascoe, 1985), de l'émissole lisse *Mustelus mustelus* (Morte et al., 1997), du requin peau bleue *Prionace glauca* (Clarke and Stevens, 1974) et de la baudroie *Lophius piscatorius* (Daly et al., 2001). Le régime alimentaire de la seiche est composé de petits crabes, de crevettes, de poissons démersaux et de polychaetes et évolue tout au long de sa vie avec sa croissance (Pinczon du Sel and Daguzan, 1997; Blanc and Daguzan, 2000; Pierce et al., 2010).

2.3 Le stock de seiche de Manche

2.3.1 Présentation de la Manche

La Manche (figure 2.4) est un bassin délimité au nord et au sud respectivement par le Royaume Uni et la France et ouvert sur l'Atlantique N-E à l'ouest et la Mer du Nord par le détroit du Pas de Calais à l'est. Sa profondeur est d'environ 40 m au niveau du détroit du Pas de Calais et de 100 m à son extrémité ouest. En Manche ouest, une fosse atteint la profondeur maximale de 150 m (Larsonneur et al., 1982). La péninsule du Cotentin se trouve à la limite entre les moitiés est et ouest respectivement dénommées par le Conseil International pour l'Exploration de la Mer (CIEM) divisions CIEM VIId et VIIe. Ces divisions CIEM sont utilisées pour gérer les différents stocks exploités en Manche par les pêcheurs français et britanniques et dans une moindre mesure par d'autres pêcheurs européens (belges et néerlandais). Les divisions CIEM VIId et VIIe sont respectivement découpées en 15 et 19 rectangles statistiques de 1° de longitude par 0,5° de latitude. En l'absence de données collectées par le *Vessel Monitoring System* (VMS), ces rectangles statististiques sont utilisés par les pêcheurs pour situer leurs captures. Cette information est ensuite collectée et archivée par les systèmes d'information de l'Ifremer et du Cefas.

En Manche, un hydrodynamisme intense est provoqué par de puissants courants de marée entrainant un courant résiduel orienté d'ouest en est et accompagné de tourbillons latéraux (Salomon, 1994). La puissance de ces courants empêche la structuration de la colonne d'eau en Manche est, zone dont la profondeur maximale atteint 50 m. La Manche ouest, plus profonde, présente quant à elle une stratification (Anonyme, 1993). La salinité est relativement constante (autour de 35‰) à l'exception de la Baie de Seine où l'estuaire crée un gradient de salinité horizontal (Guillaud and Menesguen, 1998; Videau et al., 1998)

Plusieurs rivières et fleuves se déversent dans la Manche aux niveaux du Golfe Normano-Breton, des Baies de Seine et Somme. Les apports de ces sources d'eau douce associées à l'hydrodynamisme de la Manche favorisent une forte production primaire (Brylinski et al., 1996; Maguer et al., 1998; Joint and Groom, 2000; **?**). A cela s'ajoute une importante biodiversité du plancton et des communautés macrobenthiques (Brunet et al., 1996; Dauvin, 1997; Rees et al., 1999; Desroy et al., 2003)

2.3.2 Contexte halieutique

La Manche est un écosystème riche qui permet l'exploitation d'un nombre important d'espèces (80) permettant la création de nombreux emplois directs et indirects autour de la filière pêche. Dix engins principaux sont utilisés par les pêcheurs : le casier, le chalut à perche, le chalut pélagique, le chalut à panneaux démersal, la drague, le filet, la ligne à main, la palangre, la senne coulissante et la senne démersale. Sur la période 2000-2010, en

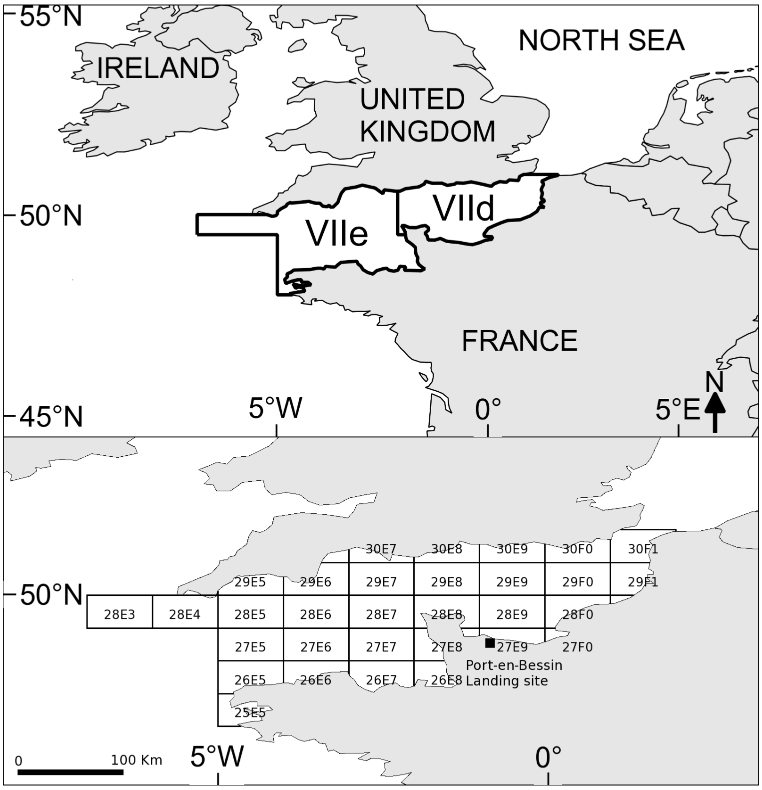

Fig. 2.4 – Situation géographique de la Manche en Antlatique N-E, limites des divisions CIEM VIId et VIIe et limites des rectangles statistiques de 1 degré de longitude par 0,5 degré de latitude découpant les divisions.

moyenne, plus de 2500 navires de pêche français et britanniques ont exploité la Manche dont plus de 80% étaient basés sur les côtes de cette mer alors que les autres proviennent des zones adjacentes. Ils ont débarqué en moyenne et par an 360 000 tonnes de produits halieutiques pour une valeur de plus de 200 millions d'€ (Tétard et al., 1995; Ulrich et al., 2002; Portail CHARM III - Interreg IV, 2012).

2.3.3 Production de céphalopodes

En Manche, les céphalopodes, calmars Loliginidés et seiche, font partie des 3 ressources démersales les plus importantes pour les pêcheurs français et britanniques opérant dans cette zone. Sur la période 2000-2010, la production annuelle de calmars est supérieure à 3200 tonnes (pour une valeur moyenne annuelle avoisinant les 18 millions d'€) et la production annuelle de seiche est supérieure à 11000 tonnes (pour une valeur supérieure à 20 millions d'€). Ces deux ressources constituent d'ailleurs respectivement les première et deuxième sources de revenu des chalutiers de fonds français et la seiche est la deuxième source de revenu des chalutiers britanniques (Portail CHARM III - Interreg IV, 2012).

2.3.4 Métiers exploitant la seiche

La seiche est une espèce migratrice exploitée tout au long de son cycle de vie par les pêcheurs français et britaniques (Denis and Robin, 2001; Royer et al., 2006). L'exploitation commence quelques semaines après l'éclosion des juvéniles, lorsque les chalutiers français sont exceptionnellement autorisés à pêcher 2 semaines durant dans la zone côtière des 3 milles nautiques sur la côte ouest du Cotentin (Pierce et al., 2010). Durant l'automne suivant l'éclosion, la seiche migre vers les profondeurs de la Manche centrale ouest, où les températures sont favorables à sa survie (Wang et al., 2003). La seiche est alors partiellement recrutée dans la pêcherie de chalutiers hauturiers français et britaniques puis entièrement recrutée à la fin du printemps (Royer et al., 2006). Cette pêcherie exploite la seiche jusqu'à la dernière migration vers les nurseries côtières pour prendre part à la reproduction à l'âge de 2 ans. Durant la période de reproduction, une dérogation permet à nouveau aux chalutiers français de pêcher dans la zone des 3 milles nautiques (Pierce et al., 2010) pour exploiter les reproducteurs qui sont également pêchés par les caseyeurs français et britanniques.

2.3.5 La collecte des données

En France, le Système d'Information Halieutique (SIH), géré par l'Ifremer, est responsable du plan d'échantillonnage, de la collecte, de l'archivage et de la diffusion des données halieutiques appartenant à la Direction des Pêches Maritimes et de l'Aquaculture (DPMA). Cette diffusion est assurée sous la forme de données à traiter pour la recherche ou d'ouvrages de synthèse destinés aux acteurs de la filière pêche (Berthou, 2012). Les données de campagne scientifiques sont quant à elles archivées et diffusées par les différents centres Ifremer (Carpentier et al., 2009).

Au Royaume Uni, la collecte de données halieutiques est organisée par le *Fisheries Data Archive Centre* (FishDAC) du *Centre for Environment, Fisheries and Aquaculture Science* (Cefas) et fait partie du *Marine Environmental Data and Information Network* (MEDIN). Le FishDAC est responsable de la collecte, de l'archivage et de la diffusion des données de campagnes scientifiques, de pêche et des statistiques halieutiques (Cefas, 2012).

Les données de campagnes scientifiques, de capture et d'effort de pêche utilisées dans ce travail de thèse ont été extraites des bases de données du SIH de l'Ifremer, de la campagne CGFS et du FishDAC du Cefas, partenaires du l'Université de Caen Basse-Normandie dans le projet CRESH.

2.4 Méthodes d'évaluation de stock

L'objectif de cette partie est de faire une revue des méthodes d'évaluation de stock couramment utilisées par les halieutes, de leurs avantages et inconvénients ainsi que de leur application pour les stocks de céphalopodes. Le modèle utilisé pour le stock de seiche de Manche est présenté en dernier et fera l'objet d'une description approfondie dans le chapitre 5.

2.4.1 Modèle global

Le modèle global (*surplus production model*) est en apparence le plus simple des modèles d'évaluation de stock. Il est généralement peu utilisé en Europe et plus particulièrement adapté pour l'évaluation de stock dans les pays en voie de développement ou lors de la phase d'expansion d'une pêcherie. En théorie, un modèle global estime que la biomasse d'une année est égale à la biomasse de l'année précédente à laquelle est ajoutée la production de la population et retranchée la capture. Cependant, le modèle global présente une vue très simplifiée de la dynamique d'une population, ne permettant pas la prise en compte des structures en âge et des structures spatiales de la population étudiée. De plus, son ajustement n'est pas évident et l'interprétation du Rendement Maximum Durable (MSY) peut s'avérer compliquée car l'estimation fait parfois l'hypothèse que le stock se trouve en état d'équilibre, ce qui est rarement le cas (Hilborn and Walters, 1992) et qui a parfois conduit à la surestimation du MSY. Enfin, ce modèle présente l'inconvénient de faire l'hypothèse que le recrutement est fortement densité dépendant, ce qui semble assez peu le cas chez les céphalopodes (Pierce and Guerra, 1994). Les modèles globaux ont l'avantage de pouvoir être appliqués rapidement (avec peu de données) mais ne fournissent que des objectifs "moyens à long terme" valables dans un environnement stable, or les céphalopodes sont connus pour leur variabilité liée à l'environnement (Pierce et al., 2008). Des modèles globaux ont été développés pour estimer les stocks de céphalopodes des côtes du Sahara Occidental (Sato and Hatanaka, 1983; Bravo de Laguna, 1989). Plus récemment, un modèle global avec effet de l'environnement a été ajusté pour évaluer le stock de poulpe au Sénégal (Laurans et al., 2002). Enfin, un modèle global de Fox (Fox, 1970) a été ajusté pour une modélisation bio-économique du stock de seiche en Manche (Ulrich et al., 2002).

2.4.2 Modèles de déplétion

Le modèle de déplétion (approche standard de Leslie-DeLury) est la méthode d'évaluation de stock la plus fréquemment utilisée pour estimer les stocks de céphalopodes et elle est considérée comme la moins onéreuse. Son principe est d'estimer les conséquences du retrait d'individus (par pêche ou mortalité naturelle) sur la population et de déterminer la taille de la population en l'absence de pêche (Hilborn and Walters, 1992). Les méthodes de déplétion peuvent d'ailleurs être appliquées à des données historiques de stocks, particulièrement au début de leur exploitation, afin d'en évaluer la biomasse en l'absence d'exploitation (Hilborn and Walters, 1992). La méthode de base (Leslie and Davis, 1939) utilise les captures cumulées et l'hypothèse d'une population fermée. Les variantes utilisent les efforts (DeLury, 1947) et ont été adaptées aux populations ouvertes avec recrutement et mortalité naturelle. Ces méthodes étant très adaptées à la modélisation des données collectées durant une période de temps réduite (en particulier si l'exploitation ne dépasse pas une année), elles sont en général priviligiées pour évaluer les stocks de céphalopodes (Boyle and Rodhouse, 2005). Sa principale limite est de poser l'hypothèse que la ressource évaluée est aléatoirement répartie, et a donc une capturabilité constante sur la zone, hypothèse forte qui est rarement vérifiée chez les céphalopodes (Pierce and Guerra, 1994). Ce type de méthode a été utilisé sur différents stocks de calmars en Atlantique N-W (Brodziak and Rosenberg, 1993), en Atlantique sud (Hatfield and Des Clers, 1998) et en Manche où elle a été adaptée pour les calmars loligindés (Royer et al., 2002) et la seiche (Dunn, 1999b).

2.4.3 Analyse de Population Virtuelle

L'Analyse de Population Virtuelle (VPA) est la méthode la plus couramment utilisée par les pays du nord pour évaluer les stocks de poissons à durée de vie longue (Hilborn and Walters, 1992). Cette méthode nécessite de discrétiser une population en plusieurs classes d'âge ce qui permet d'évaluer l'effet de la pression de pêche sur chaque âge et chaque année. Chez les céphalopodes, la VPA est généralement adaptée sur un pas de temps mensuel. Cependant, les céphalopodes présentent une forte variabilité inter-individuelle du taux de croissance et l'estimation de l'âge mensuel nécessite la collecte de pièces dures (statolithes) dont le traitement est chronophage. Malgré cette difficulté, la VPA a été développée pour plusieurs stocks de céphalpodes. Dans le cas du poulpe *Octopus vulgaris* du Sénégal, les classes d'âge ont été estimées après des opérations de marquage précisant la croissance et en utilisant les poids des catégories commerciales (Jouffre et al., 2002). La VPA a également été développée pour évaluer les stocks de calmars loliginigés (Royer et al., 2002) et de seiche en Manche (Royer et al., 2006). Dans ces deux derniers cas, les classes d'âge ont été estimées à l'aide des fréquences de longueur de manteau collectées mensuellement au débarquement. Ces deux méthodes de détermination ne sont pas considérées comme adéquates, mais l'utilisation de pièces dures n'est pas possible sans un travail conséquent de schlérochronologie (Challier et al., 2006a).

2.4.4 Modèle à deux stades

Lorsque les données de structure en âge d'une population ne sont pas assez précises pour développer une VPA mais suffisantes pour distinguer une phase pré-recrutée et une phase recrutée, il est possible d'utiliser un modèle à 2 stades. Dans le modèle à 2 stades, Collie and Sissenwine (1983) font l'hypothèse qu'une population exploitée passe par 2 stades : un stade recrutement et un stade entièrement recruté. Il est ainsi possible d'estimer la phase recrutée de la population (le stock) d'une année en ajoutant les individus complètement recrutés et les recrues de l'année précédente et en retranchant les mortalités naturelle et par pêche. Ce modèle peut être mis en œuvre soit en nombre d'individus, soit en biomasse. Contrairement aux méthodes décrites précédemment, un modèle à 2 stades peut être ajusté en utilisant simultanément plusieurs sources de données (campagnes scientifiques et indices d'abondance calculés grâce aux captures commerciales). Enfin, il permet d'obtenir des résultats équivalents à ceux des modèles structurés en âge (Mesnil, 2003). Il a souvent été utilisé pour l'évaluation des invertébrés (Conser, 1991; Conser and Idoine, 1992; Collie and Kruse, 1998; Cadrin et al., 1999; Zheng et al., 1997) et a été développé pour estimer le stock de *Loligo reynaudii*, espèce de calmar exploitée en Afrique du Sud depuis les années 1980 (Roel and Butterworth, 2000).

2.4.5 Gestion des ressources halieutiques

L'ensemble des méthodes d'évaluation de stock présentées précédemment permettent d'obtenir des indicateurs de l'état des stocks étudiés (MSY, F_{opt}, B_{PA}, relation stock-recrutement, taux d'exploitation...). Ces indicateurs servent de base aux experts d'une institution pour émettre des avis scientifiques sur l'état des stocks étudiés (CIEM). Ces avis scientifiques servent ensuite de base aux gouvernements (Union Européenne ou gouvernement national) pour la mise en place d'une politique de gestion (Total Acceptable de Capture, limitation de l'effort de pêche, limite de maillage, fermeture de zone ou de périodes de pêche). Rappelons à ce stade que, pour les céphalopodes, aucune mesure mise en œuvre en Europe ne relève d'un indicateur de l'abondance de la ressource évalué annuellement ou de l'importance de la pression de pêche.

Chapitre 3

Structure du stock de seiche (*Sepia officinalis*) de Manche en période de reproduction dans un contexte de réchauffement et de forte pression de pêche

English Channel Cuttlefish (*Sepia officinalis*) stock structure in the reproduction period under warming and high fishing pressure context

Michaël, Gras[1,2,*], Georges, Safi [1,2], Hugo, Lebredonchel[1,2], Jérôme, Quinquis[3], Eric, Foucher[3], Noussithé, Koueta[1,2], Jean-Paul, Robin[1,2]

1-Université de Caen Basse-Normandie, FRE 3484 BIOMEA, Esplanade de la paix, F-14032 Caen, France
2-CNRS INEE, FRE 3484 BIOMEA, F-14032 Caen, France
3-Ifremer, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP 32, 14520 Port-en-Bessin, France
∗ Corresponding author : michael.gras@unicaen.fr

Ce chapitre fait l'objet d'un article scientifique qui sera soumis prochainement dans une revue scientifique à comité de lecture.

Résumé

Le réchauffement global a été mis en évidence depuis des décennies dans les océans du monde et pourrait être à l'origine du changement des traits d'histoire de vie de certaines espèces marines. La forte pression de pêche est également connue pour utiliser des engins sélectionnant sur la taille. La seiche de Manche est une des ressources les plus importantes pour les pêcheurs français et britanniques. Sa durée de vie varie en fonction de la température et comme elle a été exposée à un réchauffement et à une forte pression de pêche, il apparaît nécessaire de vérifier si le cycle de vie a subi des modifications depuis ses descriptions dans les années 80 puis 90 qui ont mis en évidence une durée de vie quasi exclusive de 2 ans. Un programme d'échantillonnage sur deux ans a ainsi été réalisé sur les sites de débarquement français de Manche pendant les saisons de reproduction 2010 et 2011 pour mettre en évidence si des individus de un an étaient matures à cette période. L'estimation de l'âge a été réalisée en couplant une décomposition polymodale avec un dosage de la lipofuscine contenue dans le manteau. Les tailles à maturité pour chaque année et chaque sexe ont été estimées en ajustant un GLM à erreur binomiale. Les résultats montrent qu'un pourcentage variable de mâles et de femelles appartenant à la première cohorte sont matures et que la taille à maturité a diminué depuis la dernière étude réalisée il y a plus d'une décennie. Enfin, différents paramètres, comme la température et la pression de pêche, sont évoqués pour expliquer les changements des traits d'histoire, de vie suggérant que la seiche pourrait être un bon indicateur des modifications de l'écosystème Manche.

Mots clés

Sepia officinalis ; Manche ; Réchauffement ; Pression de pêche ; Maturité ; Traits d'histoire de vie.

Abstract

The global warming has been highlighted for decades in oceans of the world and could be at the origin of changes in marine species life history traits, such as fishing pressure which is known to use size-selective gears. The English Channel cuttlefish is one of the most important resources for French and UK fishermen. The species lifespan varies with the temperature and when exposed to a warming and a high fishing pressure, it is worth exploring if its life cycle has changed since its descriptions in the 80s and the 90s which highlighted a quasi exclusive 2 year lifespan. A two year sampling programme was thus performed in French landing sites of the English Channel during the reproduction season in 2010 and 2011 to highlight if one year old specimens were mature. Age determination was carried out by coupling polymodal decomposition and lipofuscin measurement in the mantle. Size-at-maturity for each year and each sex were estimated by fitting a binomial error GLM. Results highlight that a variable percentage of males and females belonging to the first cohort are mature and that size-at-maturity has decreased since the last study performed more than one decade ago. Finally, different parameters, such as temperature and fishing pressure are explored to explain changes in life history traits suggesting that cuttlefish could be an indicator of the regime shift in the English Channel.

Keywords

Sepia officinalis; English Channel; Warming; Fishing pressure; Maturity; Life history traits.

Présentation du chapitre 3.Structure du stock en période de reproduction[1]

Un des principaux objectifs de ce travail est d'estimer l'abondance des seiches au recrutement. Cet objectif sera réalisé en ajustant un modèle d'évaluation de stock. Un préalable indispensable à l'étude de la dynamique d'une population et à sa modélisation est la description du cycle de vie de l'espèce étudiée.

Le réchauffement global a été constaté dans les différents océans du monde et en Manche. La pression de pêche a également connu une forte augmentation durant les dernières décennies, en particulier en Atlantique N-E. Ces 2 pressions ont pour conséquences d'influencer les abondances, les distributions spatiales et le cycle de vie des espèces marines. Les céphalopodes en général, et la seiche en particulier, présentent une plasticité de leur cycle de vie qui varie en fonction de la température du milieu. Dans la littérature, le cycle de vie est décrit comme durant quasi-exclusivement 2 ans. Dans un contexte de réchauffement et de forte pression de pêche, ce travail a pour objectif de vérifier si le cycle de vie de la seiche a subi des modifications depuis ses premières descriptions dans les années 1980 et 1990.

L'étude a été réalisée en Manche, une mer épicontinentale peu profonde où la seiche constitue une ressource halieutique abondante. La seiche réalise des migrations hauturières et côtières à l'automne et au printemps respectivement jusqu'à la fin de son cycle de vie lorsqu'elle prend part à la reproduction à l'âge de 2 ans. Aux printemps 2010 et 2011, 738 et 655 individus ont été échantillonnés sur lesquels ont été collectés la taille du manteau, les poids total et de la gonade, le sexe et le stade de maturité. La taille à maturité a été déterminée à l'aide d'un GLM à erreur binomiale, des coupes histologiques des gonades ont été réalisées et un indice gonado-somatique a été calculé. Le dosage de la lipofuscine, un pigment qui s'accumule dans le manteau au cours du temps, a été effectué pour estimer l'âge des individus.

Les résultats des fréquences de taille montrent qu'une première cohorte peut être identifiée mais que la deuxième est difficilement identifiable. La taille à maturité a été déterminée à 13 cm en moyenne pour les femelles et 12,28 cm en moyenne pour les mâles, des chiffres inférieurs aux résultats présentés dans la littérature. Les dosages de lipofuscine ont permis de différencier les 2 cohortes, même si la variabilité de la mesure augmente avec le temps écoulé entre la mort de l'animal et le moment du prélèvement. Les dosages de lipofuscine réalisés sur les plus petits individus matures ont montré que leur concentration en lipofuscine n'était pas significativement différente des concentrations obtenues sur les individus de la première cohorte. Ces individus sont donc âgés de 1 an et capables de prendre part à la reproduction.

La maturation est sous le contrôle de différents paramètres environnementaux (pho-

---

[1] Les références bibliographiques se trouvent dans le corps du texte de ce chapitre

topériode, disponibilité en proies et température environnementale). La température est le paramètre qui influe le plus sur la maturation, l'augmentation de la température provoquant une accélération de la maturation. Le réchauffement de la Manche pourrait donc expliquer l'apparition d'individus matures à 1 an. A ce phénomène s'ajoute la forte pression de pêche observée en Manche. La pression de pêche est connue pour entraîner une pression de sélection qui favorise les individus maturant plus rapidement et à une taille ou un âge inférieur aux populations non exploitées. Enfin étant donné sa capacité à refléter les changements environnementaux, la seiche pourrait être considérée comme un bon indicateur des changements en Manche.

3.1 Introduction

The global warming has become unequivocal and is made of natural and anthropic components, the latter taking more and more importance during the last decades (Beaugrand, 2009). Climate variations are known to influence abundance and spatial distribution of marine species (Beaugrand and Reid, 2003; Hawkins et al., 2003; Beaugrand, 2009). According to the data collected by the Marine Biological Association of the United Kingdom (MBA), an English Channel warming has been highlighted all along the XXth century (Southward and Roberts, 1987). This warming has lead to modifications in phytoplankton assemblages, fish larval abundances and pelagic fish abundances (Southward et al., 1988). Moreover, a decline in community level, average length and length-at-maturity in demersal communities has been observed suggesting that fish assemblages become dominated by species maturing faster and taking part in the reproduction at a shorter length (Hawkins et al., 2003). Due to their short life cycle and their high metabolic rate, cephalopods are assumed to be very sensitive to an environmental warming (Pierce et al., 2010).

High fishing pressure affects directly and indirectly fish communities and populations. Among the direct effects of high fishing pressure on populations, increased mortality and size selectivity tend to reduce the proportion of old and large specimens in the population (Smith, 1994). After several years of high exploitation levels, smaller specimens maturing faster are favoured leading to a decrease in mean size and length (or age) at maturity by favouring slow growth and early maturing specimens (Bianchi et al., 2000; Shin et al., 2005; Kantoussan et al., 2009). Observations of such processes have been carried out in various stocks of the N-E Atlantic such as the North-Sea herring (Shin and Rochet, 1998; Engelhard and Heino, 2004), the North-Sea plaice (Grift et al., 2003) and the northern cod (Olsen et al., 2004). English Channel has been trawled for over 200 years and from the beginning of the XXth century to date, the fishing pressure has highly increased (Hawkins et al., 2003). As observed with the warming, a high fishing pressure might also have significant consequences on the life history traits of cephalopods.

The common cuttlefish is one of the most valuable species exploited in the English Channel. This stock, shared between French and United Kingdom (UK) fishermen, represents the third of the total catch performed in the N-E Atlantic representing an average annual landing of 11,000 tons for an average annual turnover of €20M (Royer et al., 2006; Pierce et al., 2010; Portail CHARM III - Interreg IV, 2012). *Sepia officinalis* is a short lifespan and semelparous cephalopod (Mangold, 1987) distributed from the West African coast (Senegal and Mauritania) to the English Channel and in the Mediterranean Sea. *Sepia officinalis* has a life cycle lasting between 1 and 2 years according to the latitude it lives. From West African coasts to the Portuguese coasts, the entire population has a 1 year life cycle (Mangold, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991). The Bay of Biscay is a transition zone where two different groups were identified, one, called

Group I Breeding (GIB), is able to breed at one year old (45% of male specimens and 20% of female specimens) and another one, called Group II Breeding (GIIB), breeds at two years old (Le Goff and Daguzan, 1991; Gauvrit et al., 1997). In the English Channel, cuttlefish life cycle was firstly described as lasting exclusively two years (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991). A decade later, Dunn (1999a) found that the entire female population and 96% of male specimens have a 2 year life cycle (GIIB). The remainder males (4%) were found to be mature at the age of one year old, constituting a GIB.

Previous studies describing the cuttlefish life cycle based age estimation on polymodal decomposition but growth rate in cephalopods is known to present a high inter-individual variability (Forsythe and Van Heukelem, 1987; Semmens et al., 2004; Challier et al., 2006a), this method could therefore be a source of age estimation error and should be coupled with another methodology.

During three decades, most of the scales developed to determine maturity stages in cephalopods were derived from the universal maturity scale developed by Lipinski (1979) and were based on 5 stages (Boyle and Rodhouse, 2005). The scientific community was thus in the situation of having different maturity scales for each species and sometimes for different populations of the same species. For instance, Dunn (1999a) developed his own maturity scale for the English Channel cuttlefish, derived from the universal scale of Lipinski (1979) and based on observations made by Richard (1971). In 2010, the Planning Group on Commercial Catches, Discards and Biological Sampling and the Planning Group for the Mediterranean under the Data Collection Framework (DCF) proposed a workshop to create a unique international maturity scale determination for cephalopods (Anonymous, 2010) which was used in this work.

In the context of a global warming and a high fishing pressure observed for years in the English Channel, this work aims at highlighting if modifications in the life cycle of the cuttlefish exist and, contrary to previous work published, a percentage of one year old cuttlefish can be mature and ready to spawn (part of a GIB). To achieve this goal, a two year sampling programme was carried out during the reproduction period at the English Channel French landing sites in order to highlight if a percentage of one year old English Channel cuttlefish are mature and able to breed during the reproduction period.

3.2 Material and Methods

3.2.1 Study area: the English Channel

The English Channel is situated between the N-E Atlantic and the North Sea. The International Council for the Exploration of the Sea (ICES) has divided it into two different divisions, VIId to the East and VIIe to the West. The western English Channel is characterised by a maximum depth reaching around 170 m and is strongly influenced by Atlantic waters creating favourable conditions for the wintering of the cuttlefish (Wang et al., 2003). The eastern English Channel (ICES division VIId) is characterised by shallow waters, maximum depth reaching 50 m, and an homogeneous water column. Winter sea temperature in this part of the Channel can reach 5°C, condition which is not suitable for the wintering of cuttlefish (Pingree, 1980; Boletzky, 1983).

3.2.2 Previously described migration cycle in the English Channel cuttlefish

In the English Channel, cuttlefish hatch inshore at the beginning of summer (figure 3.1). After spending the entire summer inshore to feed, it performs offshore migration to spend winter in the central western English Channel (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Royer et al., 2006) where sea bottom temperature is favourable (Wang et al., 2003). Next summer is also spent inshore to feed. At the end of second summer, male specimens finish their maturation (approximately in September). In October, cuttlefish performs its second migration to the wintering grounds where female cuttlefish complete their maturation. The last migration is performed at approximately 20 months old to reach the spawning zones. Cuttlefish die after the reproduction period (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Royer et al., 2006).

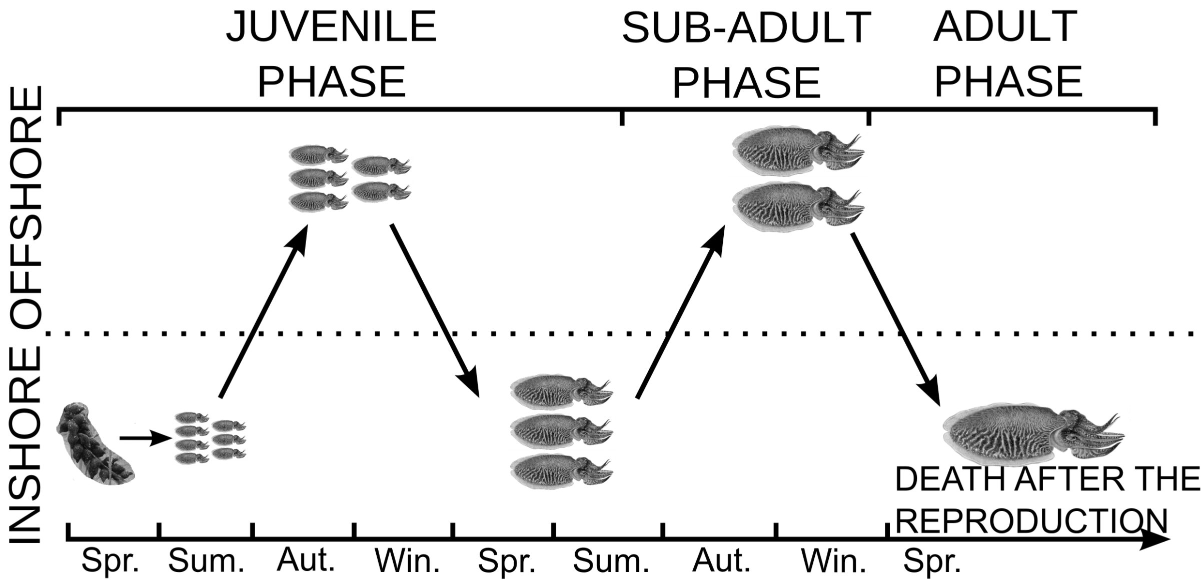

Figure 3.1: Life cycle of the English Channel cuttlefish *Sepia officinalis* as described by Boucaud-Camou and Boismery (1991), Boucaud-Camou et al. (1991) and Dunn (1999a).

3.2.3 Sample collection

Cuttlefish samples were collected in spring 2010 and 2011 in 3 different landing sites of the South English Channel coast. Specimens were caught by trawlers or trap fishermen. In 2010, from April the 12^{th} to July the 9^{th}, 738 specimens (395 males and 339 females) were collected in Erquy, Cherbourg and Port-en-Bessin landing sites. In 2011, from April the 5^{th} to June the 30^{th}, 655 specimens (444 males and 211 females) were collected in Port-en-Bessin and Cherbourg landing sites. The sex ratio was tested using a chi-square test.

3.2.4 Biometry dissection, sex determination and tissue sampling

Dorsal Mantle Length (DML) of each specimen was measured to the lesser cm and length frequencies were represented on 4 histograms, one per sex and per year. Breaks are defined every cm, immature specimens are represented in white while mature animals are represented in grey. Based on length frequencies, the threshold between the first and second cohort is defined by the less numerous length class after the first mode. Fresh total Body Weight (BW) and Gonad Weight (GW) were also measured for each specimen.

As several European countries (Spain, Portugal and Italy) are interested in cephalopod research, a Workshop on Sexual Maturity Staging of Cephalopods, WKMSCEPH (Anonymous, 2010) took place in 2010 to create a consistent international scale based on several scales developed and to suggest a conversion table for the different maturity scales existing. Mantle of the animals was opened by a ventral incision to determine the sex and maturity stage of each specimen using the macroscopic scale presented in the tables 3.1 for the females and 3.2 for the males and developed by the WKMSCEPH (Anonymous, 2010). In female specimens, maturity stages are mainly defined using the oocyte size and the Nidamental Glands (NG) development. In Male specimens, maturity stages are defined using testis size and spermatophore position in the Spermatophoric Complex (SC). Tissue samples were collected on a subsample of specimens for lipofuscin concentrations. Mantle samples were kept frozen in liquid nitrogen until analysis to avoid tissue degradation. Gonads were placed in Davidson solution (10% Glycerol, 20% Formaldehyde, 30% of 96° ethanol, 40% filtered seawater) to fix tissues for histological observations. All samples were then transported to the laboratory to be analysed.

Table 3.1: Female Cuttlefish maturity stage scale of the WKMSCEPH (Anonymous, 2010) completed with the microscopic descriptions.

Stage	Maturity state	Reproductive Apparatus Aspect	Oocyte size	Microscopic description (figure 3.2a)
0	Undetermined	Sex not distinguished with the naked eye.	Oocytes ϕ <50μm	Disordered cells without specificity.
1	Immature = Virgin	Translucent ovary, small, with granular structure. Small and translucent Nidamental Glands (NG) and Oviducal Glands (OG). Oviduct meander not visible.	Very small oocytes visible to the naked eye. Oocytes ϕ <2 mm	The oocyte nucleus is large and the chromatin is aggregated. Follicular cells wrap around the oocyte, the plasma membranes of the cells are well visible.
2a	Developing	Creamy ovary, enlarged but not reaching the posterior half of the mantle cavity. Developing and white NG/OG. NG covering some internal organs. Oviduct meander clearly visible.		Oocyte nucleus is pushed to a pole with the heterogeneous chromatin, oocyte is ovoid, without vitellus. Several strata of follicular cells, with visible membrane and numerous villosities.
2b	Maturing	Pale-yellow ovary, occupying the whole posterior half of the mantle cavity and containing only reticulated oocytes. Large NG and OG; NG covering the viscera below. Oviduct fully developed but empty.	Oocytes 2 mm< ϕ <4 mm	Nucleus not visible. The quantity of vitellus can vary from one oocyte to another. High inclusion of the follicular cells without plasma membranes progressively pushed outside the oocyte.
3a	Mature Spawning	Amber-coloured and gelatinous ovary, containing reticulated and smooth oocytes. Enlarged and turgid NG/OG. Oocytes may occur in the oviduct.	Oocytes $\phi > 4$ mm.	Vitellus is in large quantity. There is no inclusion of the follicular cells. The chorion wraps around the oocyte.
3b	Spent	Flaccid ovary with strikingly loose disorderly aspect. Few oocytes, which may be attached to the central tissue. Flaccid NG/OG.	Few oocytes which may be attached to the central tissue	Little quantity or no oocytes and follicular cells.

Table 3.2: Male Cuttlefish maturity stage scale of the WKMSCEPH (Anonymous, 2010) completed with the microscopic descriptions.

Stage	Maturity state	Reproductive Apparatus Aspect	Spermatophores development and occurrence in the Needham'sac	Microscopic description (figure 3.2b)
0	Undetermined	Sex not distinguished with the naked eye.		Disordered cells without specificity.
1	Immature = Virgin	Small, white and clearly visible testis. Semi-transparent Spermatophoric Complex (SC) with not visible vas deferens.	Absence of spermatophores	Small cysts with cluster of gonial cells.
2a	Developing	Testis increased in volume but not reaching the posterior half of the mantle cavity. SC white with visible vas deferens. Penis appears as a small prominence of SC.		Larger cysts. Numerous basis of spermatogonies and layers of spermatocytes. Presence of spermatides.
2b	Maturing	Testis filling the posterior half of the mantle cavity. Vas deferens white, meandering and enlarged. The Needham's Sac (in extenso Spermatophoric Sac, SS) may contain few spermatophores partially developed (visible as whitish particles) and/or few fully developed spermatophores.	Few spermatophores partially or fully developed	Appearance of first spermatozoa. Spermatophores are in the Needham sac.
3a	Mature Spawning	Well-developed testis with large and white vas deferens. Spermatophores packed in the Needham's Sac and sometimes present in the penis.	Plenty of well developed spermatophores	Numerous spermatozoa
3b	Spent	Testis flaccid. SS empty or with few spermatophores.	None or few spermatophores	Spermatozoa are rare or absent

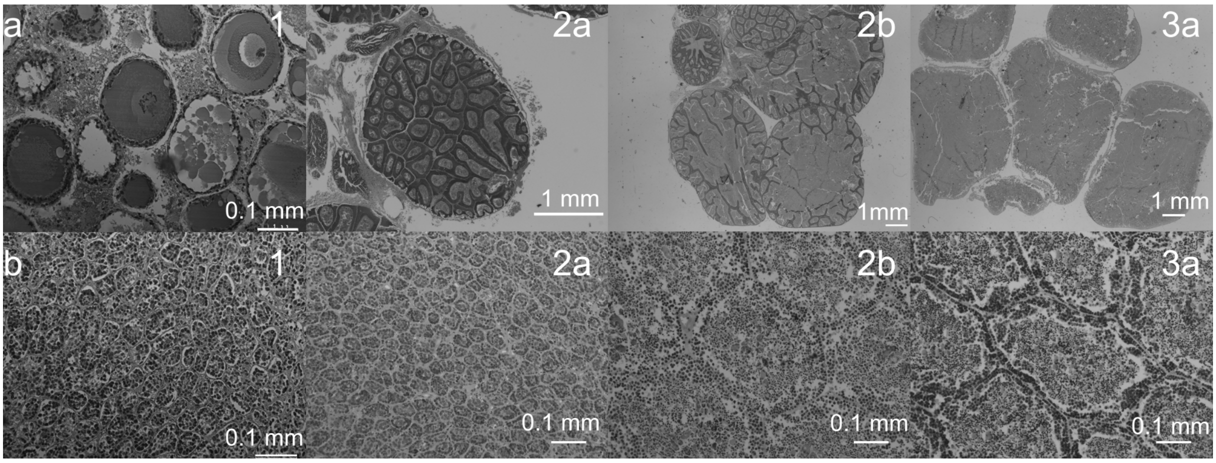

Figure 3.2: Histological cuts of the gonad tissues for females (above) and males (below).

3.2.5 Lipofuscin measurement

Different hard structures have been tested for age determination in cuttlefish (Le Goff et al., 1998) but the only consistent results were obtained from statolith daily rings during the juvenile phase (Challier et al., 2002, 2006b). But statolith rings are very difficult to read in cuttlefish and are not usable after the age of 240 days (Bettencourt and Guerra, 2001). After this threshold, some studies proposed to use the concentration of lipofuscin as a proxy of age: lipofuscin is a pigment that is accumulated during the life in tissues of some invertebrates (Sheehy et al., 1996; Ju et al., 1999; Bluhm and Brey, 2001). This methodology has been successfully used in cephalopods to have a rough estimation of the cuttlefish age (Zielinski and Pörtner, 2000; Doubleday and Semmens, 2011). Although this method does not enable an accurate age determination, it should enable the differentiation of the two annual cohorts living at the same time in the English Channel.

Lipofuscin was measured according to Zielinski and Pörtner (2000). Mantles of *Sepia officinalis* were ground under liquid nitrogen and homogenized in a chloroform-methanol mixture (1:2, v/v). After centrifugation for 10 min at 2000g, lipofuscin was found in the chloroform phase. In this phase an emission spectrum between 350 and 550 nm was obtained at an excitation wavelength of 350 nm using a Mithras LB940 fluorimeter (Berthold, Thoiry, France). The luminescence of the sample was determined at the maximum emission at 420 nm. Lipofuscin concentrations were expressed as relative fluorescence intensity according to Hill and Womersley (1991), using 0.1 μg quinine per ml 1N H_2SO_4 as a standard.

In a first step, we have tested the applicability of lipofuscin concentrations to fish market samples by measuring post-mortem variability during the next 3 days. A mantle was sampled on a living animal and lipofuscin was measured on the fresh tissue. The tissue was then kept on ice and lipofuscin concentration was measured every 24h. Differences were tested using an ANOVA. In a second step, lipofuscin concentrations were measured on 2 subsamples of 11 and 17 specimens taken from each length-modes. Assuming that each mode corresponded to an annual cohort, this experiment describes inter-cohort differences in lipofuscin concentrations. Finally, the analysis of the smallest mature specimens enabled to test (with a Student test) which cohort they belong to.

3.2.6 Histological preparation

Gonad samples were kept for a maximum period of 72 hours in Davidson solution to be fixed and then stored in 70% ethanol solution. Dehydrated fixed tissues were embedded afterwards in low melting point paraffin for sectioning. Blocks were sectioned at 5 μm and sections were mounted on slides and coloured with Prenant-Gabe trichrome.

3.2.7 Size-at-maturity estimation

Macroscopic maturity stage of each specimen observed in each length class were used to fit a binomial error Generalized Linear Model (GLM) to estimate the size-at-maturity. Specimens were considered as mature when they reach the ”Maturing stage” (2b), assuming that if they are maturing during the spring, they will become mature and able to breed and spawn before the end of the reproduction season in late summer.

3.2.8 Gonado-Somatic Index

An index of the sexual development has been computed with the Gonado-Somatic Index (GSI) such as:

$$GSI = \frac{GW}{BW - GW} \tag{3.1}$$

GSI could be considered as a proxy of the energy allocated by the specimen to reproduction to the detriment of the somatic growth. This index is a quantitative measure of sexual maturity and the relationship between GSI and DML complements the estimation of size-at-maturity.

3.3 Results

3.3.1 Samples length frequency

In female samples, collected specimens range from 6 to 27 cm in 2010 and from 7 to 26 cm in 2011. In male samples, collected specimens range from 6 to 36 cm in 2010 and from 7 to 32 cm in 2011 (figure 3.3). Length frequencies highlight that, a first cohort is identifiable and the maximum size of this first cohort can be determined at 16 cm for both sexes in 2010 and at 14 cm and 13 cm for females and males respectively in 2011. The second cohort is not easily identifiable and several modes are displayed on the histogram. In 2010, the smallest mature females were 7 cm long while the smallest mature males were 8 cm long. In 2011, smallest mature females were 11 cm long while smallest male mature specimens were 10 cm. In 2010, 17% of females and 27% of males belonging to the first cohort were found to be mature and in 2011, 3% of females and 13% of males belonging to the first cohort were found to be mature. For both years, sex ratios were significantly different from 1:1 and males were more numerous than females, particularly in 2011.

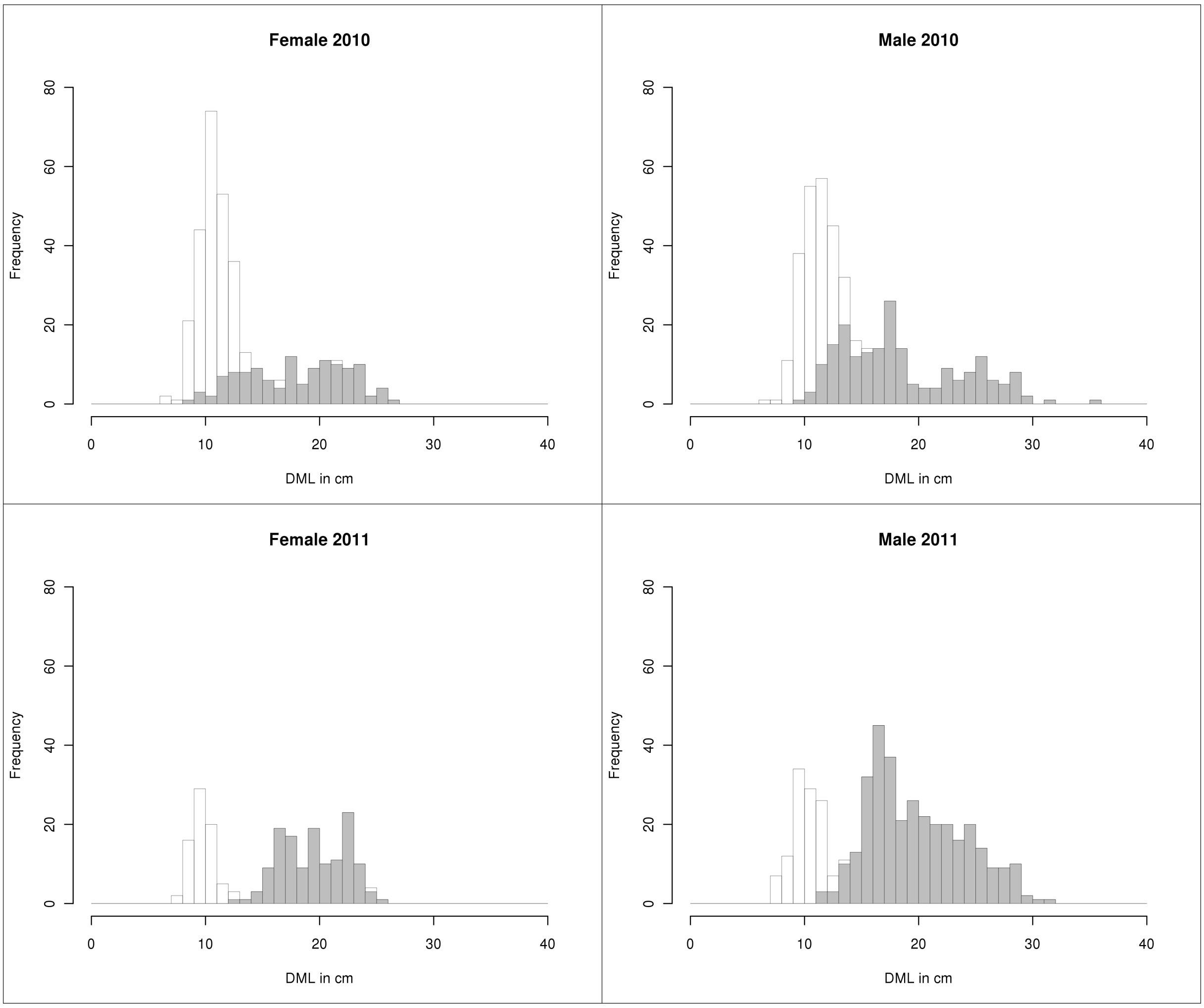

Figure 3.3: Length frequencies of the female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed in white, while mature specimens are displayed in grey.

3.3.2 Size-at-maturity determined using a binomial error GLM

For both sexes, the size-at-maturity (figure 3.4) was higher in 2010 than in 2011 and for both years, female size-at-maturity was higher than the male's. For male specimens, 100% of individuals longer than 16 cm in 2010 and 14 cm in 2011 were mature. On the opposite, for female specimens, first classes reaching 100% of mature specimens are inferior to those of males (14 cm in 2010 and 13 cm in 2011) and some female specimens longer than 14 cm in 2010 and 13 cm in 2011 can be immature.

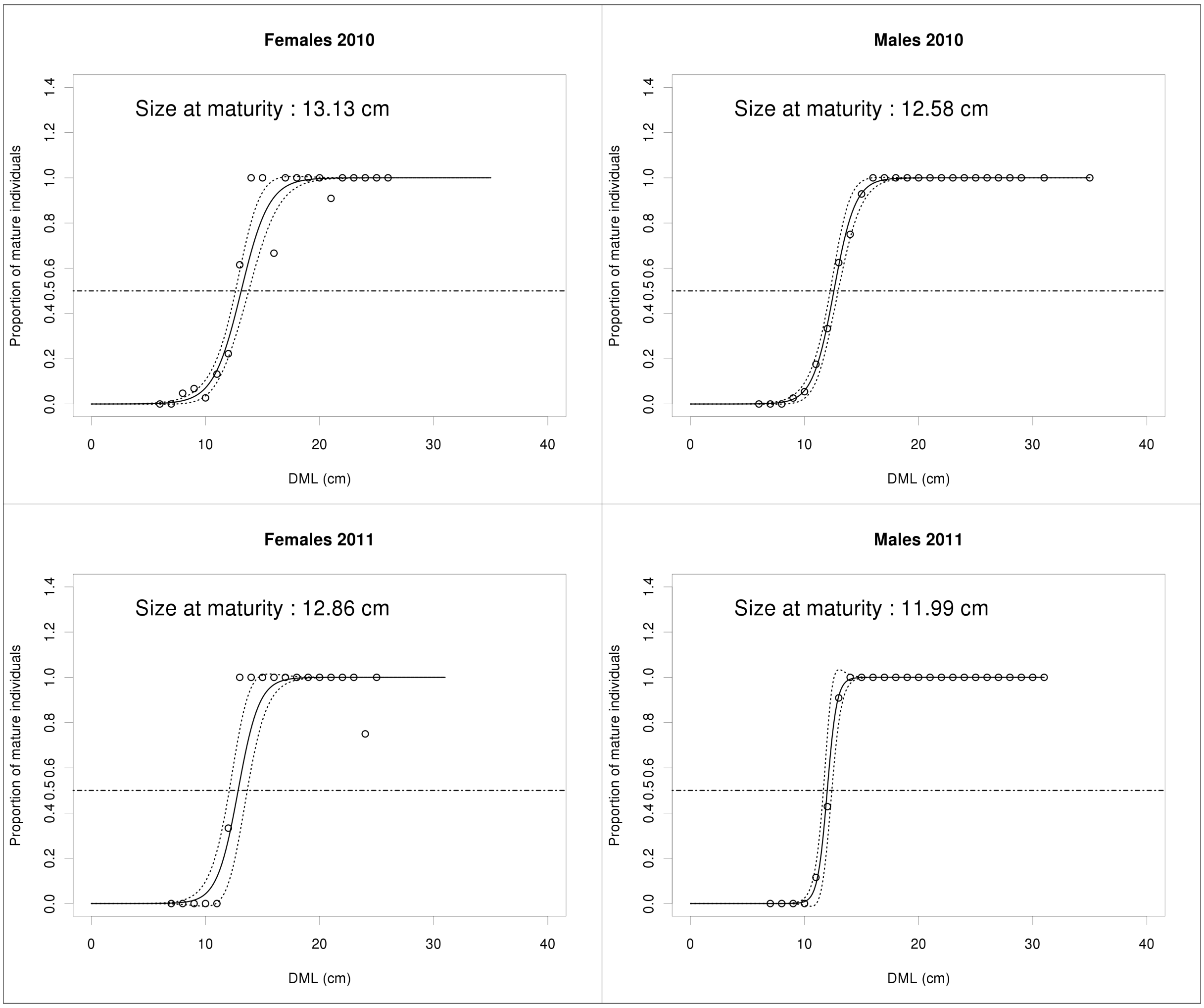

Figure 3.4: Size-at-maturity determined using a binomial error GLM for female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. The 95% confidence interval of the fitted binomial error GLM is displayed with dashed lines. Number of specimens measured per DML class is pointed out in the figure 3.3.

3.3.3 Microscopic gonad tissue description per maturity stage

For practical reasons, and in order for the future users to have tables with complete maturity stages descriptions, the descriptions have been integrated into the columns called ”microscopic description” in tables 3.1 and 3.2 and illustrated with the figure 3.2.

3.3.4 Variability in lipofuscin measurement and age estimation

The first lipofuscin measurement (figure 3.5) highlights that, during three days, no significant trend is observed in lipofuscin concentration while the standard deviation of the

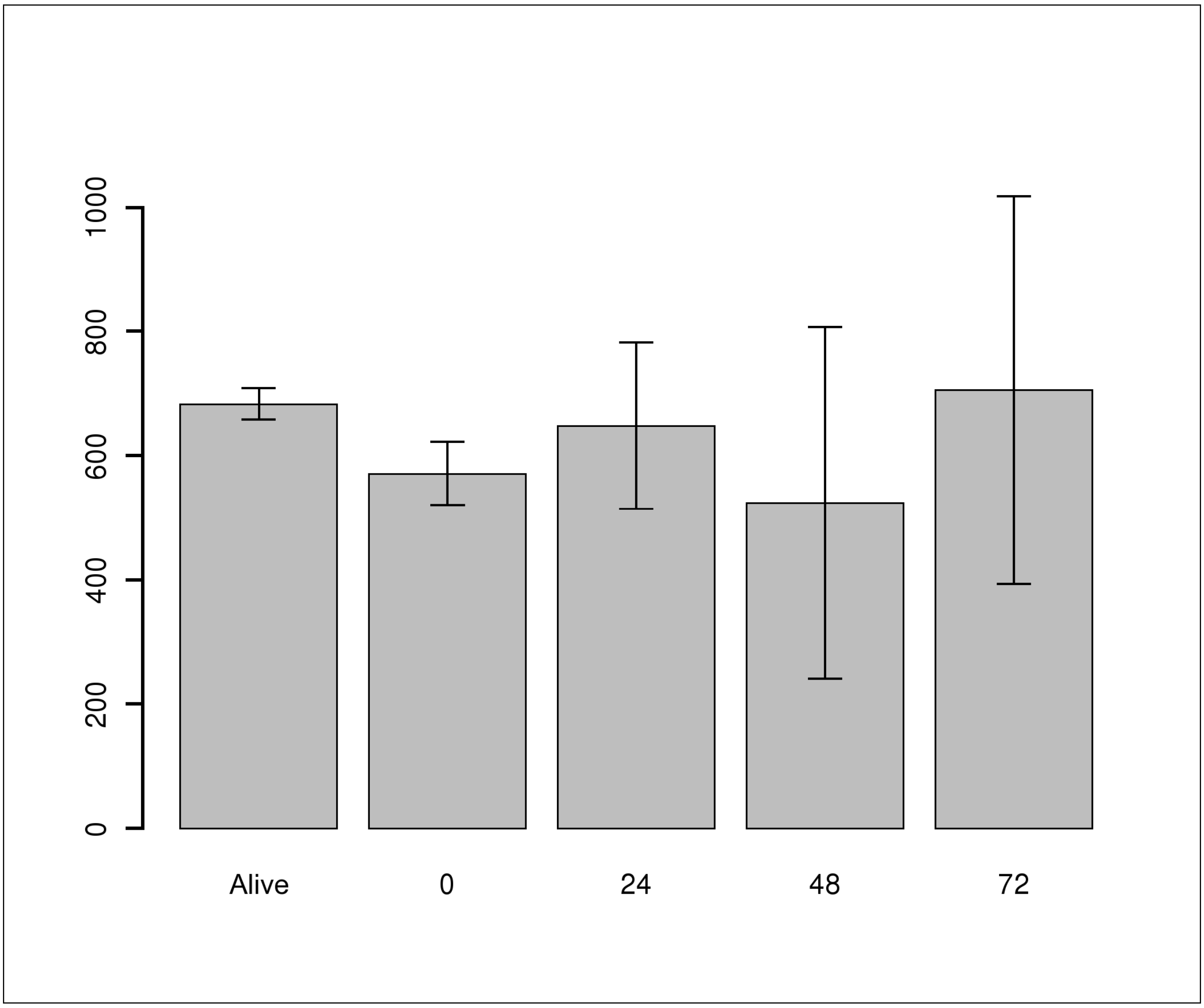

Figure 3.5: Trend in lipofuscin concentration measured in the mantle sampled on one living cuttlefish from the death to 72 hours after the death with the standard deviation of the measure.

measure increases with the time. In the second experiment, lipofuscin accumulation measured in specimens belonging to the first and second cohort are significantly different (figure 3.6). Results of the lipofuscin measurement performed on the 3 smallest mature males (figure 3.6 and table 3.3) highlight that lipofuscin accumulation of these 3 specimens is not significantly different from the first cohort while it is significantly different from the GIIB lipofuscin accumulation. These three specimens can thus be considered as part of the GIB group.

3.3.5 Gonado-Somatic Index

The GSI (figure 3.7), for each sex and each year, does not reveal inter-annual differences. For both sexes, in the reproduction period, the GSI of immature specimens is very low while the GSI of mature specimens is high. Female mature specimens are characterised by a higher GSI with a higher inter-individual variability than male mature specimens. Fi-

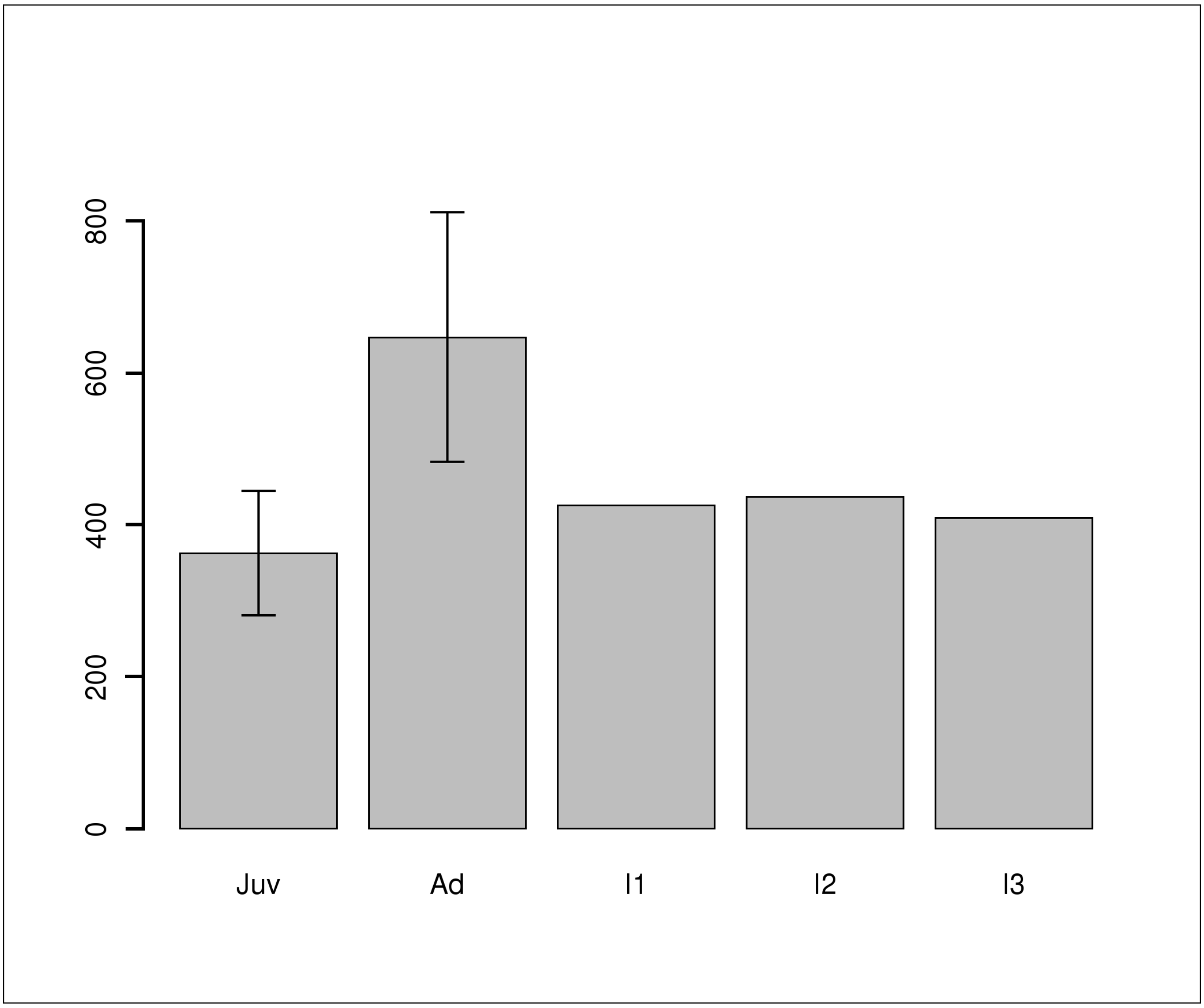

Figure 3.6: Lipofuscin concentration measured in cuttlefish mantles for juveniles (Juv, 11 specimens), Adults (Ad, 17 specimens) with the inter-individual standard deviation and lipofuscin concentration measured in 3 small mature specimens (I1, I2, I3).

Table 3.3: Probabilities of 3 small male mature specimens to be different from the GIB and GIIB cohorts.

Specimens	Length (cm)	P-value, GIB	P-value, GIIB
First cohort (immature ; 11 specimens)	10<L<13		
Second cohort (mature ; 17 specimens)	20<L<31		
Individual 1	11	0.12	0.02
Individual 2	11	0.08	0.03
Individual 3	13	0.22	0.02

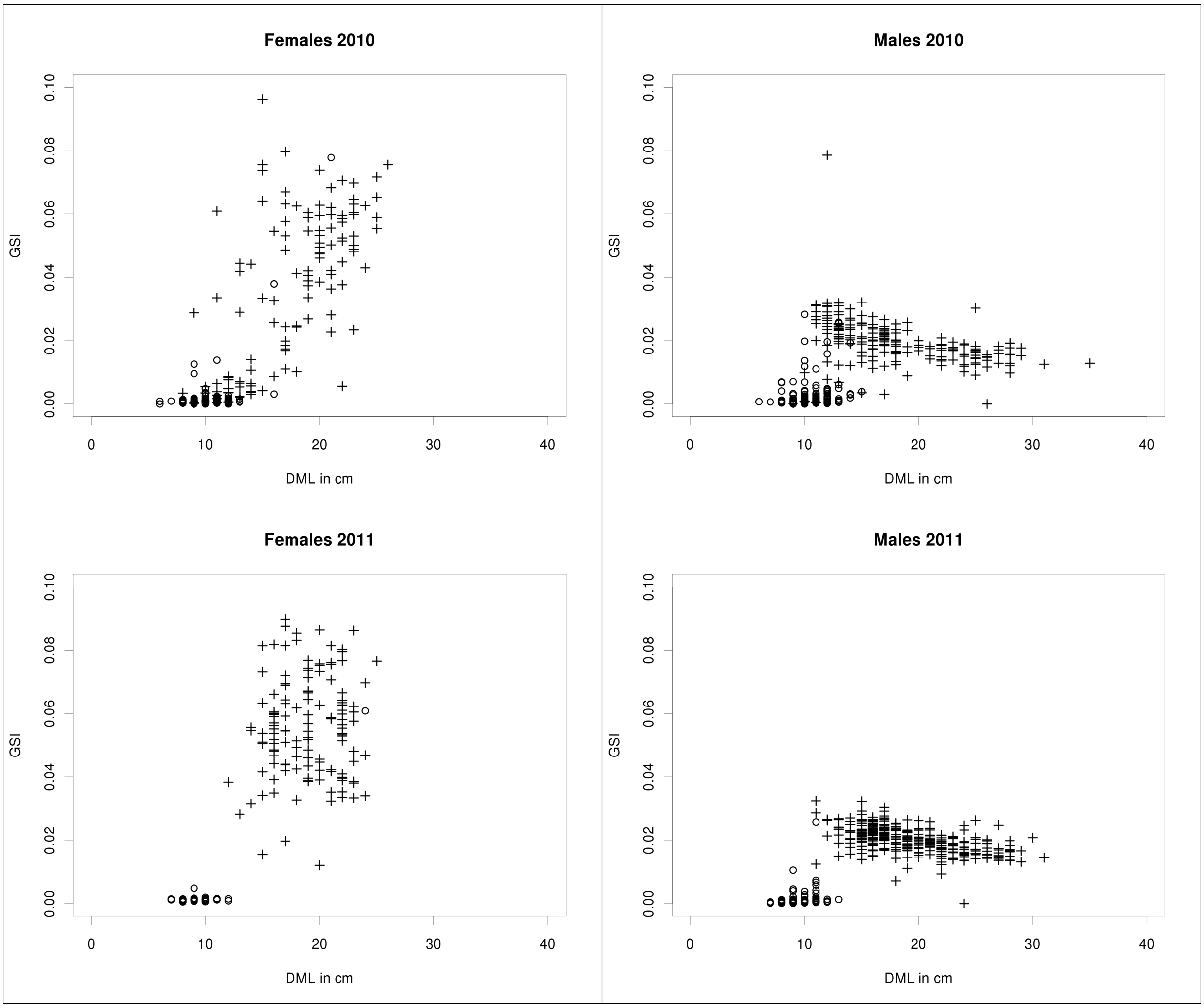

Figure 3.7: Gonado Somatic Index (GSI) vs Dorsal Mantle Length (DML) for female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed with circles while mature specimens are displayed with crosses.

nally, GSI of mature male specimens is significantly anti-correlated with the body length.

3.4 Discussion

The English Channel cuttlefish life cycle has previously been described in the 80s (Boucaud-Camou and Boismery, 1991) and in the 90s (Dunn, 1999a) as lasting quasi-exclusively 2 years. This study carried out more than a decade after the last one highlights that a percentage of mature male and female cuttlefish sampled in the English Channel population belongs to the first cohort and are part of a GIB. An inter-annual variability of this percentage has been highlighted and this work should be kept on to estimate this variability on the long term. Age determination using lipofuscin measurement (Zielinski and Pörtner, 2000; Doubleday and Semmens, 2011) was adapted and has corroborated that smallest mature animals are most likely one year old specimens and not small two years old cuttlefish. To complete and illustrate the maturity scale developed by the WKMSCEPH (Anonymous, 2010), the GSI have been calculated and show the difference between immature and mature specimens and histological samples have been photographed.

Lipofuscin measurement has helped in determining the cohort which the specimen belongs to, but this method has never been accurate enough for age estimation (Zielinski and Pörtner, 2000; Doubleday and Semmens, 2011). Moreover, accuracy decreases when time between death and sample increases and as sample is based on commercial fishery landings, this parameter is not under control. Finally, lipofuscin measurement is time and fund consuming and experiments cannot be carried out on a large number of specimens. An alternative rough age estimation can be set up using the statoliths without reading daily rings which are not accurate readable on one year old cuttlefish (Bettencourt and Guerra, 2001; Challier et al., 2002, 2006b). In several fish species, otolith length, thickness and weight have been found to grow with the age even when body growth rate is null (Reznick et al., 1989; Campana, 1990; Newman, 2002) and that otolith weights enable to display an age frequency distribution consistent with those derived from increment counts (Pilling et al., 2003; Mc Dougall, 2004). Moreover, statolith diameter has also been successfully used as a proxy of age in tunicate *Oikopleura vanhoeffeni* (Choe and Deibel, 2009). Statolith weights and dome diameters could therefore be used to help in disentangling the two annual cohorts.

In cephalopod species, based on rearing experiments, it has been shown that maturation is driven by different factors including photoperiod, food availability and temperature (Mangold, 1987). Cephalopods are known to not store ingested energy in their tissues and as it was observed in *Sepiotheuthis australis* (Ho et al., 2004) and *Loligo vulgaris* (Moreno et al., 2005), specimens, particularly females, need a regular food availability to reach maturity. Immature females belonging to the second cohort could have therefore encountered unfavourable situation. Moreover, as males need less energy to reach maturity, they have more energy available to somatic growth and can therefore reach higher average length, even if Boyle and Rodhouse (2005) suggest that differences in growth rate and length seem to have genetic origin.

It is worth noting that males size-at-maturity plots are quite homogeneous and do not reveal subgroups maturing at different sizes as described in Loliginid squid. In this situation, the smallest males, called ”sneakers” are not favoured during the mating but are able to take advantage on the larger males when their attention decreases to breed with females (Coelho et al., 1994; Moreno et al., 1994; Boyle and Rodhouse, 2005).

Temperature is known to be a key parameter influencing cephalopod life cycles, from egg development to reproduction (Rodhouse et al., 1992; Boyle and Pierce, 1994). An increase in environmental temperature generally accelerates the cephalopod somatic growth and shortens the life cycle duration by accelerating the maturation process (Moreno et al., 2007), a well known feature in cuttlefish which life cycle shortens from the north of its distribution area (English Channel) to the South (West African coasts ; Mangold, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991). The English Channel warming (Hawkins et al., 2003) could therefore explain the formation of a GIB and the observation of a lower size-at-maturity (in average 12.28 cm for the males and 13 cm for the females) than that observed by Dunn (1999a) (14.6 cm for the males and 16.4 cm for the females). Further work should investigate if GIB is actually involved in the reproduction by analysing female sperm reservoir and highlights if a cross-mating between generations exists (Gauvrit et al., 1998). English Channel warming could also lead to an increase in the reproduction season duration and let the more precocious hatchlings enough time to be mature for the next spring.

Challier et al. (2006b) have observed in their work that cuttlefish are recruited in the fishery all over the year at a constant age. One assumption to explain this observation is a continuous hatching of the cuttlefish all over the year in the English Channel which could be due to a spawning carried out all over the year or a spawning carried out at different depth (in various incubation temperatures) which could lead to a year round hatching. GIB observed in this work could thus be individuals hatched at the end of winter and which had enough time until offshore migration to start maturation and finish it before the end of next spring.

Moreover, according to Hawkins et al. (2003) work, one of the consequences of the English Channel warming is the modification in species communities in the ecosystem by increasing abundance of warm water species and decreasing abundance of cold water species. Modifications of the ecosystem could also influence the cuttlefish resource by modifying the competition and the predator-prey relationships.

English Channel has long been exploited by the French and UK fishermen. Trawling started 200 years ago and the fishing pressure has regularly increased until now (Hawkins et al., 2003). High fishing pressure largely impacts the demersal communities and can modify life history traits by favouring specimens maturing faster or getting maturity at a smaller size or a lower age (Shin et al., 2005; Kantoussan et al., 2009). This phenomenon has been observed on different N-E Atlantic stocks (Shin and Rochet, 1998; Grift et al., 2003; Engelhard and Heino, 2004; Olsen et al., 2004) and could also have influenced the English Channel cuttlefish stock to be at the origin of the appearance of a GIB and a decreasing trend in size-at-maturity. Modifications in demersal community assemblages caused by high fishing pressure could have an indirect effect on cuttlefish. Indeed, as mentioned above, cephalopods are not able to store energy in their tissue and the maturation efficiency is closely linked to the food availability in their environment (Mangold, 1987; Moreno et al., 2005). This could be the reason of the presence of female non mature specimens in the second cohort.

According to Jackson et al. (2000), an indicator of the climate change must meet 4 different criteria : (i) relevance to assessment and ecological functions, (ii) feasibility of data collection, (iii) response to the variation and (iv) interpretation and utility of data to highlight the changing environment. Cuttlefish is one of the top predators of the English Channel ecosystem. Due to its high abundance and high value on the fish markets it is one of the 3 main demersal resources exploited by French and UK fishermen. Even if it is a non quota species (Pierce et al., 2010), 2 scientific bottom trawl surveys sample it each year (Carpentier et al., 2009) and maturity stages can be easily determined using the international WKMSCEPH scale (Anonymous, 2010). This could be completed by data collected at the landing sites all over the year in the framework of the Data Collection Framework (DCF) programme. Wang et al. (2003) have shown that water temperature influences the abundance of the cuttlefish and the present work highlights consequences of a warming and a high fishing pressure on the cuttlefish life cycle and maturation, even if it is difficult to disentangle the effect of each phenomenon. Moreover, and contrary to other top predators, cuttlefish is a short lifespan species and consequences of the regime shift can be seen on the short term. Cuttlefish therefore meets the 4 criteria listed above and should be considered as an indicator of the environment shift.

Acknowledgement

This study was carried out within the EU funded project "CRESH" (under the Interreg IV A France-Manche-England programme).

Chapitre 4

Répartition de l'effort de pêche dans un contexte de hausse du prix du gasoil : le cas d'étude des chalutiers français en Manche

Fishing effort allocation under increased fuel price context : the case study of French trawlers operating in the English Channel

Michaël, Gras[1,2,*], Jérôme, Quinquis[3], Eric, Foucher[3], Jean-Paul, Robin[1,2]

1-Université de Caen Basse-Normandie, FRE 3484 BIOMEA, Esplanade de la paix, F-14032 Caen, France
2-CNRS INEE, FRE 3484 BIOMEA, F-14032 Caen, France
3-Ifremer, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP 32, 14520 Port-en-Bessin, France
∗ Corresponding author : michael.gras@unicaen.fr

Ce chapitre fait l'objet d'un article scientifique qui sera soumis prochainement dans une revue scientifique à comité de lecture.

Résumé

L'augmentation du prix du gasoil durant la période 2000-2008 a contribué à déclencher la crise économique et a créé des difficultés financières dans le secteur de la pêche, les chalutiers étant les plus vulnérables étant donné que le gasoil constitue un de leurs premiers postes de dépense. La Manche, située en Atlantique nord-est, est une importante zone de pêche exploitée par les chalutiers français et britanniques. Le chalutage est un métier multi-espèces ciblant principalement les calmars et la seiche qui sont les premières sources de revenu de ce métier dans cette zone. D'autres stocks de poissons démersaux (bar, rouget barbet...) permettent de compléter les revenus des pêcheurs. La localisation de l'effort de pêche (déclaré par les pêcheurs en utilisant la faible résolution des rectangles statistiques) et les revenus des chalutiers extraits de la base de données du Système d'Information Halieutique (SIH) géré par l'Ifremer ont été analysés à l'aide d'indicateurs, de cartes, d'Analyses en Composantes Principales (PCA) et d'une Analyse Triadique Partielle (PTA) pour mettre en évidence les tendances temporelles des revenus, les tendances spatio-temporelles de l'effort de pêche et l'influence du prix du gasoil sur l'activité de pêche. Les résultats montrent que, dans un contexte de revenus quasi constants pour les chalutiers, le prix du gasoil hors taxe a doublé. Alors que le profit diminuait, l'effort de pêche est corrélé au nombre de bateaux de pêche actifs, mais la distance parcourue par les pêcheurs pour atteindre les zones de pêche est négativement corrélée au prix du gasoil. Le léger déplacement de l'effort de pêche vers les sites de débarquement est confirmé par une augmentation de l'effort de pêche dans les rectangles statistiques côtiers. Ce phénomène a influencé l'origine spatiale des échantillonnages de céphalopodes réalisés pour collecter les fréquences de taille au site de débarquement de Port-en-Bessin, ces dernières étant utilisées dans les modèles d'évaluation de stock structurés en âge. Enfin, les limites de la méthode sont évoquées ainsi que l'influence des subventions fournies par le gouvernement pour compenser l'augmentation du prix du gasoil sur l'activité de pêche.

Mots clés

Manche ; Chalutage ; Effort de pêche ; Prix du gasoil ; Analyse Triadique Partielle.

Abstract

Fuel price increase during the 2000-2008 is one of the parameters launching the financial crisis and creating financial difficulties in the fishing sector, trawlers being the most vulnerable as fuel is one their major costs. English Channel, situated in the N-E Atlantic, is an important fishing ground exploited by French and United Kingdom (UK) trawlers. Trawling is a multi-species métier targeting mainly squids and cuttlefish which are the first sources of income in this area. Other demersal fish stocks (seabass, red mullet...) enable fishermen to complete their income. Fishing effort localisation (declared by fishermen using the coarse resolution of statistical rectangles) and trawler income data extracted from the *Système d'Information Halieutique* (SIH) database managed by the Ifremer were analysed using indicators, maps, Principal Component Analysis (PCA) and Partial Triadic Analysis (PTA) to highlight the temporal trend in revenue, spatial and temporal trends in fishing effort and the influence of the fuel price on the fishing activity. Results highlight that, in a context of quasi constant income for trawlers, the tax free fuel price has doubled. As the profit decreases, the fishing effort was correlated to the number of active fishing vessels but the distance covered by the fishermen to reach fishing grounds is negatively correlated to the fuel price. The slight movement of the fishing effort closer to the landing sites is corroborated by an increase in trawling effort displayed in inshore statistical rectangles. This phenomenon has influenced the spatial origin of cephalopod length frequency samplings made in the Port-en-Bessin landing site and used in age structured stock assessment models. Finally, limits of the methodology is mentioned as well as the influence of subsidies provided by the government to compensate the fuel price increase on the fishing activity.

Keywords

English Channel; Trawling; Fishing effort; Fuel price; Partial Triadic Analysis.

Présentation du chapitre 4.Répartition de l'effort de pêche[1]

L'ajustement d'un modèle d'évaluation de stock peut être fait à l'aide d'indices d'abondance basés sur des données de campagne scientifique mais aussi à l'aide d'indices d'abondance basés sur des débarquements de pêche commerciale. Cependant, un préalable indispensable à l'utilisation de ces données est une étude de la répartition spatiale et de la dynamique spatio-temporelle de l'effort déployé par la flotille considérée et sur la zone étudiée afin de mettre en évidence si cette dynamique permet d'obtenir des indices d'abondance fiables.

Durant le XX^{ème} siècle, le gasoil est devenu l'unique source d'énergie des pêcheurs en Europe. Le gasoil constitue une part importante des coûts des unités de pêche, particulièrement pour les chalutiers, et son prix a fortement augmenté durant la période 2000-2008. La flotille de chalutiers de fond à panneaux français en Manche constitue un tiers des navires de pêche français en Manche et peut être considérée comme principalement artisanale et multi-spécifique, les principaux stocks exploités étant les céphalopodes (calmars loliginidés et seiche). Des exercices d'évaluation de stocks à l'aide de modèles structurés en âge ont été publiés pour ces espèces et, même si elles ne sont actuellement pas gérées par la Politique Commune des Pêches, il est important de connaître l'origine des échantillons utilisés pour calibrer ces modèles. Jusqu'à présent, les études se sont concentrées sur l'impact du prix du gasoil sur la phase de pêche alors que cette étude se concentre sur les conséquences du prix du gasoil sur la répartition de l'effort de pêche

La Manche est une mer épicontinentale subissant une forte exploitation halieutique. Les chalutiers de fond à panneaux sont au nombre de 500 en Manche et sont en majorité des navires de pêche artisanale. Les données d'effort de pêche déclarés par rectangle CIEM ont été fournies par le Système d'Information Halieutique de l'Ifremer, les données de prix du gasoil ont été fournies par le Ministère de l'Ecologie, du Développement Durable et de l'Energie et les données biologiques ont été fournies par l'Université de Caen. Les données ont été analysées à l'aide de statistiques exploratoires et d'indicateurs. La dynamique spatio-temporelle a quant à elle été explorée à l'aide d'une analyse canonique, l'Analyse Triadique Partielle (PTA) qui permet de décomposer les variances annuelle, mensuelle et spatiale.

Sur la période 2000-2008, les données montrent que les revenus des pêcheurs ne varient pas significativement alors que le prix du gasoil double entre 2003 et 2008. L'effort de pêche ne présente aucune tendance et semble corrélé au nombre de bateaux actifs sur la zone d'étude. Le prix du gasoil n'est pas corrélé à l'effort de pêche total déployé sur la zone alors qu'il semble influencer la distance parcourue par les navires de pêche pour rejoindre les zones d'exploitation. Du point de vue spatial, sur la période 2000-2002, on observe un effort

---

[1] Les références bibliographiques se trouvent dans le corps du texte de ce chapitre

de pêche côtier faible et hauturier important. Sur la période 2003-2007, l'effort hauturier reste stable alors que l'effort côtier augmente en Baie de Seine et sur la côte ouest du Cotentin en même temps que le prix du gasoil. En 2008, lorsque le prix du gasoil est à son maximum, l'effort hauturier diminue fortement. L'analyse de la variance inter-annuelle à l'aide de l'ATP montre les mêmes schémas inter-annuels. L'analyse des variances mensuelle et spatiale montre que le l'effort de pêche suit un cycle saisonnier, étant plutôt important au large à l'automne et en hiver et important à la côte au printemps et en été. Les données biologiques récoltées durant la période 2000-2007 proviennent en majorité de Manche est et en minorité de Manche ouest. En 2008 les échantillons proviennent exclusivement de Manche est.

La précision géographique de l'étude est limitée par l'utilisation de la faible résolution des rectangles statistiques pour la déclaration des efforts de pêche. La faible variation de la répartition spatiale de l'effort de pêche jusqu'en 2007 s'explique par l'attribution de subventions d'Etat aux pêcheurs pour compenser l'augmentation du prix du gasoil. En 2008, la situation a fortement changé puisque les subventions d'Etat ont été attribuées pour diminuer l'effort de pêche. Les chalutiers hauturier industriels sont très dépendants de ces subventions alors que les chalutiers côtiers artisanaux capables d'exploiter des ressources alternatives en sont moins dépendants.

4.1 Introduction

During the previous century, the fuel became the only source of energy for the European fishing industry (Tyedmers et al., 2005). After the oil chocks of the 70s, the fuel price remained stable between 10 and 30$ per barrel until 2000. During the 2000-2008 period, the oil price has been multiplied per 4, being one of the parameters launching the 2008 economical crisis (Shafiee and Topal, 2010). This economical context has lead to a worrying situation for fishing fleets (Gascuel et al., 2011), particularly those which have a low energy performance (in volume of fuel consumed per ton of fish caught as defined by Tyedmers in 2001) and has lead fishermen to react in order to avoid financial difficulties (Bastardie et al., 2010).

The fuel cost can vary from 10 to 60% of the total cost according to the gear used (Priour, 2009) and bottom trawl is considered as the less efficient gear regarding the fuel consumption (Schau et al., 2009; Tyedmers et al., 2005). Compared to pelagic trawling, gill-netting and long-lining métiers, bottom trawling consumes between 1.5 times and twice more fuel. It has been estimated that, in the French trawl fishery, more than 27% of the Working Capital Turnover (WCT) is spent in fuel purchase (Leblond et al., 2010). Two periods of fuel consumption can be distinguished for a trawler, one during fishing operations and one during the route (Pelletier et al., 2009). The consumption during the fishing have recently been studied (Priour, 2009; Macdonald et al., 2007), particularly since the large increase of the fuel price in the second part of the 2000s and is considered as the most important phase regarding the fuel consumption (Schau and Fet, 2008). The second phase is the journey to the fishing grounds which is generally done at high speed. Although it is not considered as the main period of consumption for the trawlers, this phase must be taken into account (Schau and Fet, 2008). During this phase, the vessel does not consume the fuel only for the journey but also for icing, refreshing the catch and can consume more in case of bad weather conditions (Schau et al., 2009). Besides, French fishermen fishing in the English Channel declare that they have stopped travelling at full speed so as to limit the fuel costs. Although French fishermen use tax free fuel, the fuel cost is one of the main costs for vessel owners.

In the North of France, the fishing activity is dominated by small scale fishery (86% of the boats are shorter than 16 meters), a sector which is by nature sensitive to the fuel price (Pita et al., 2010), and the exploitation of natural resources plays a major part in socio-economics. Artisanal fishing boats are generally owned by the captain. In 2008, 1,415 French fishing vessels operated in the English Channel and they fished around 200,000 tons of fish and molluscs for an amount of €311 M. The fishing activity of French fishermen based on the French northern coast is mostly distributed in the English Channel and more than 90% of the vessels have declared that they work in the coastal zone (between 3 and 12 nautical miles from the shore). Among these 1,415 active vessels, approximately one third of them are equipped with a bottom trawl, 32% as full time of their activity and 68% as part time of their activity (Leblond et al., 2010; Portail CHARM III - Interreg IV, 2012). French bottom trawlers catch more than 40% of the English Channel fishery yields by France and this métier represents a major share of French fishermen's income.

The English Channel cephalopod stocks are part of the most important cephalopod stocks in the N-E Atlantic (Royer et al., 2002, 2006). During the 2000 decade, French fishermen land annually an average of 8500 tons of cuttlefish, *Sepia officinalis* (for an amount of €16 M) and more than 3000 tons of squids, *Loligo vulgaris* and *Loligo forbesii* (for an amount of €17 M). In the English Channel, cephalopods are mainly exploited by French otter bottom trawls and for cuttlefish, to a lesser extent, by trappers. The squids are more or less exploited all over the year while the cuttlefish is a seasonal resource mainly exploited by trawlers during autumn and winter. Although English Channel cephalopods are the two main resources for trawl fishermen (25% of their income according to Portail CHARM III - Interreg IV, 2012), they are not managed by the European Union (EU) but only by local measures (Pierce et al., 2010), even if stock assessment exercises have been carried out on squids (Royer et al., 2002; Young et al., 2004) and on cuttlefish (Dunn, 1999b; Royer et al., 2006). Among stock assessment models used, age structured models have been implemented for squids (Royer et al., 2002) and cuttlefish (Royer et al., 2006) in the English Channel using length frequency data collected in the Port-en-Bessin landing site. Royer (2002) showed that the species composition in squids (which is a mix between *Loligo vulgaris* and *Loligo forbesii* can vary from one zone to another and determining the origin of the biological samples is of importance in stock assessment. Moreover, otter bottom trawl is considered adequate to derive LPUE (Pierce et al., 1998) and will be used as input data in the English Channel cuttlefish stock assessment model. It is therefore important to check if the spatial distribution of the otter bottom trawl is adequate and has changed, particularly in the context of an important increase in the costs.

Understanding the spatial distribution of this fishery is of importance for understanding its dynamic in order to manage it (Hutchings and Myers, 1994; Booth, 2000; Wilen et al., 2002; Gillis, 2003; Gras et al., 2010). The EU has decided in 1998, for security purposes, to monitor the position of fishing vessels (Vermard et al., 2010). Since January 1^{st}, 2004 for boats over 18 meters, and since January 1^{st}, 2005 for boats over 15 meters, the Commission Regulation (EC 2244/2003) obliges fishermen to use the Vessel Monitoring System (VMS) to provide their geographic position every hour. VMS data give a high influx of informations enabling, using statistical methodologies, the estimation of an accurate spatialised effort (Vermard et al., 2010). Unfortunately, in the English Channel, 70% of French otter bottom trawlers are under 15 meters and fishing effort can only be estimated using declarative data which uses the coarse resolution of ICES rectangles.

To date, several works have studied the consequences of the fuel price increase on the fishing activity, particularly on the economical viability (Samples, 1983; Tidd et al., 2011), the economic capacity (Lazkano, 2008), the spatial distribution of the world fuel consumption by fishermen (Tyedmers et al., 2005) and the willingness of the fishermen to leave the fishing activity (Pita et al., 2010). The objective of this work is to highlight how the economic context might have influenced the fishing effort by studying the French otter bottom trawl fishery operating in the English Channel. Spatial and temporal trends in fishing effort and the influence of the fuel price on the fishing activity are explored. Finally, consequences of these changes on the geographic origin of fish market samples is explored with the example of cephalopod landings sampling.

4.2 Material and Methods

4.2.1 The English Channel sea

The English Channel is an open space within the N-E Atlantic (figure 4.1a) connected to the Celtic Sea at his western boundary and the North Sea at his eastern boundary. The English Channel is an important fishing ground for both bordering countries, France and the United Kingdom (UK), and is mainly exploited by fishing fleets from these two countries (Carpentier et al., 2009; Portail CHARM III - Interreg IV, 2012). The Cotentin peninsula, situated in the middle of the Channel, is the boundary between shallow, to the East, and deeper waters to the West (Pingree, 1980). As a consequence and in order to manage the different stocks encountered in these two main zones, the International Council for the Exploration of the Sea (ICES) has divided the Channel into two main zones: (i) VIId for the eastern part and (ii) VIIe for the western part which are respectively divided into 14 and 19 ICES rectangles of 1 degree per 0.5 degree (figure 4.1b). The English Channel is subjected to a large human pressure, including maritime traffic, extraction of marine aggregates and fishing activity (Ulrich et al., 2002; Carpentier et al., 2009; Portail CHARM III - Interreg IV, 2012).

4.2.2 French trawlers

The demersal trawl is among the most usual gears used in the English Channel (Portail CHARM III - Interreg IV, 2012). The French otter bottom trawl is characterized by an horizontal opening ranging between 8 and 15 meters and a vertical opening ranging between 1 and 4 meters. The trawl net is assembled with nets of a minimum of 80 mm mesh size. This gear is generally used to target mainly flatfish, seabass (*Dicentrarcus labrax*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), stripped red mullet (*Mullus surmuletus*) and cephalopods (i.e. the cuttlefish *Sepia officinalis* and the two long-finned squids *Loligo forbesii* and *Loligo vulgaris*; Carpentier et al., 2009).

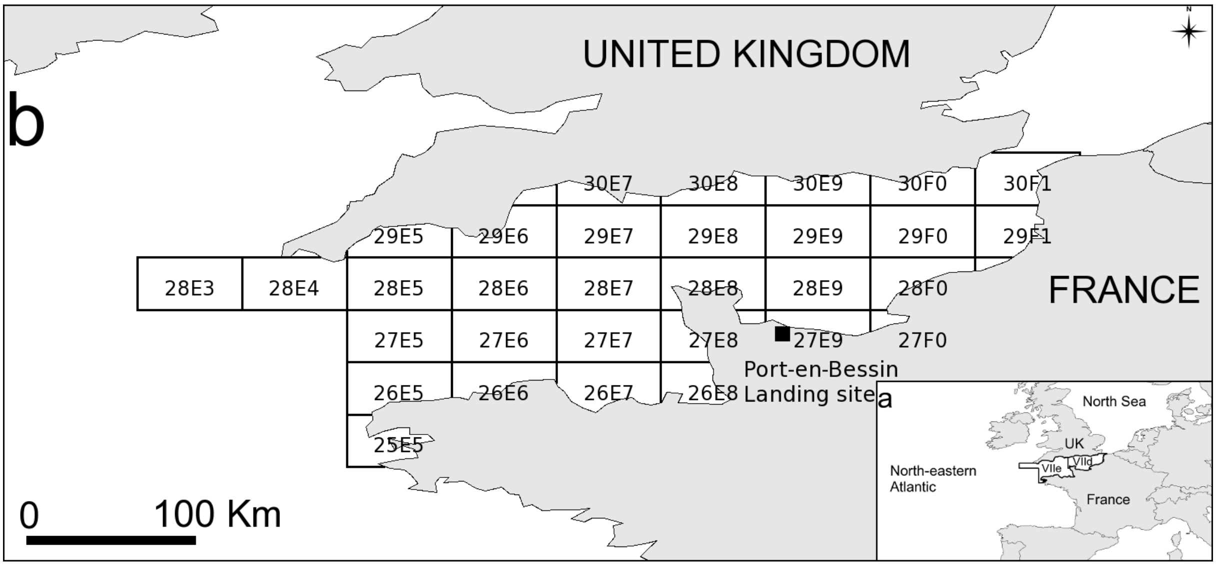

Figure 4.1: (a) English Channel localisation in the North Atlantic (b) ICES rectangles of 1 degree per 0.5 degree dividing the English Channel and Port-en-Bessin localisation on the French North coast.

4.2.3 Data

Fishing effort and production (in value) of the French otter bottom trawlers (gear code 931) were extracted from the *Système d'Information Halieutique* (SIH) of the Ifremer for the 2000-2008 period. Effort is declared by French fishermen by filling log-books for the vessels longer than 10 meters and via the fishing cards for the vessels shorter than 10 meters. Fishing effort is collected in hours of trawling for each fishing sequence and is localised using the ICES rectangles as no VMS data are available for the bulk of vessels operating in the English Channel in the studied period.

The monthly fuel price time series (free of taxes prices in Euro per hectolitre) was extracted from the database provided by the French ministry of Ecology, Sustainable Development and Energy (Ministère de l'Ecologie du Développement Durable et de L'Energie, 2009).

To avoid inflation effect, production data and fuel prices were corrected on the 2000-2008 period using the cumulated inflation (derived from the Consumer Price Index provided by the French National Institute of Statistics and Economic Studies, INSEE) in order to work in constant Euro of January 2000.

Cephalopod species composition and length frequency data in the Lower Normandy landing site, Port-en-Bessin, were collected by the University of Caen in the framework of two EU programs (Common Fisheries Policy, CFP, between 2000 and 2002 and then Data Collection Framework, DCF, until 2008). Data, collected once a month on two different otter bottom trawlers randomly chosen, enable comparisons of biological parameters (Moreno et al., 2002) and were used in stock assessment exercises (Royer et al., 2002, 2006). The sampling origin (ICES rectangle) is determined by crossing information between the University of Caen database and the SIH database.

4.2.4 Data exploration and indicator computing

Annual and seasonal differences in production per vessel (in constant Euro) are firstly explored using an ANOVA followed by a Tukey post-hoc test to highlight if the WCT coming from the fishing activity has changed during the 2000-2008 period. Annual and seasonal trends in fishing effort and fuel prices are also explored. Maps of the total annual effort and the monthly average effort exerted in each ICES rectangle are plotted to highlight inter-annual changes in spatial distribution and monthly spatial patterns of the fishing effort. Finally, annual number of cephalopod length frequency samplings carried out per ICES rectangle are represented on maps to highlight changes in the geographic origin of specimens measured.

SIH data extracted per ICES rectangle are used to estimate the distance covered by fishermen to reach fishing grounds. For each fishing trip, a proxy of the distance covered to reach fishing grounds is computed by averaging the euclidean distance between the port of departure and the centroid of the ICES rectangles explored. In some cases, fishermen have to sail around the Cotentin or even the Brittany peninsula (Finistère) to reach the fishing grounds they exploit, this distance is thus considered as a proxy of the real distance covered which is not available since no VMS data are available for these vessels. The fuel price is tested as an explaining variable of the monthly fishing effort displayed in the English Channel and the proxy of the distance covered by fishermen each month to reach fishing grounds.

4.2.5 Partial Triadic Analysis (PTA)

Principal Component Analysis (PCA) is often used in meteorology and oceanography to decompose the spatial and temporal variances of a time series of gridded map and to extract trends from a matrix time series (Woillez et al., 2010). SIH data are thus aggregated per ICES rectangle and per month to create a time series of N monthly maps divided in p rectangles (N=108 maps for the nine years of data and p=33 rectangles or columns). Data are then organised in a matrix constituted by N rows representing the data at each time step and p columns representing each rectangle of each map. The matrix is then centred and scaled to obtain a matrix of anomalies (or deviations from the mean) which is computed for each column. An eigenvalue/eigenvector decomposition on the correlation matrix is then performed to obtain the eigenvalues and the eigenvectors representing the spatial variance and the principal components representing the time amplitudes. However, in this work two time scales are used, the inter-annual and the monthly scales. So, in order to also decompose the inter-annual variance and the monthly variances, the matrix created above is divided in k=9 annual matrices of p columns and n=12 rows representing the months. It represents a 3d array or a time series of annual matrices analysed with a Partial Triadic Analysis (PTA).

PTA, part of the STATIS (*Structuration des TAbleaux à Trois Indices de la Statistique*) family, is derived from the Triadic Analysis (Tucker, 1966) and was firstly used in ecology by Thioulouse and Chessel (1987) to search the stable part in a series of matrices (Lavit, 1988). Several authors have applied this method in ecology (Dolédec, 1988; Centofanti et al., 1989; Aliaume et al., 1993; Blanc and Beaudou, 1998; Blanc et al., 1998; Jimenez et al., 2006; Carassou and Ponton, 2007; Rolland et al., 2009) to analyse a 3d array. The PTA is performed in three steps, the analysis of the inter-structure, the computation and analysis of a compromise (equivalent to a mean) and the intra-structure analysis (Thioulouse et al., 2004).

In a first step, the inter-structure analysis compares the matrix time series to highlight the correlations between the 3d array matrices and the common structure of matrix time series. Correlations between matrices are represented on a factorial plan and even if it is not the objective of this step, the coordinates of each matrix can be used to cluster the matrices. The common structure of the 3d array is then computed in a compromise matrix M_c, equivalent to an average matrix.

In a second step, the common structure represented by the compromise M_c is analysed using a PCA to disentangle the spatial and seasonal components of an average year. This step enables the representation of the correlated ICES rectangles deduced of a factorial plan describing the temporal trend in fishing exploitation.

In a third and final step, the intra-structure analysis is performed to highlight the contribution of each annual matrix to the creation of the compromise and summarize the variability of the matrix time series.

4.3 Results

4.3.1 Temporal and seasonal trends in production and fuel price

The ANOVA performed on productions highlights significant differences between years (P-value=1.10^{-4}, figure 4.2a). According to the Tukey test results, significant differences exist between year 2000 and years from 2004 to 2008. The ANOVA performed on productions between months highlights significant differences (P-value=1.10^{-11}, figure 4.2b) and the Tukey test shows that significant differences mainly come from differences in production performed during the first and second quarters on the one hand and during the third and fourth quarters on the other hand. During the 2000-2008 period, the fuel price (figure 4.2c) follows firstly a decreasing trend from €28 at the beginning of 2000 to the minimum €22 in the middle of 2003. From this year, an increasing trend period starts until the middle of the year 2008 when fuel price reached more than €60 during few months. During the 2000-2008 period, while the fuel price doubled, the production per vessel can be considered as stable. We can therefore wonder how this increase in costs have impacted the fishing activity.

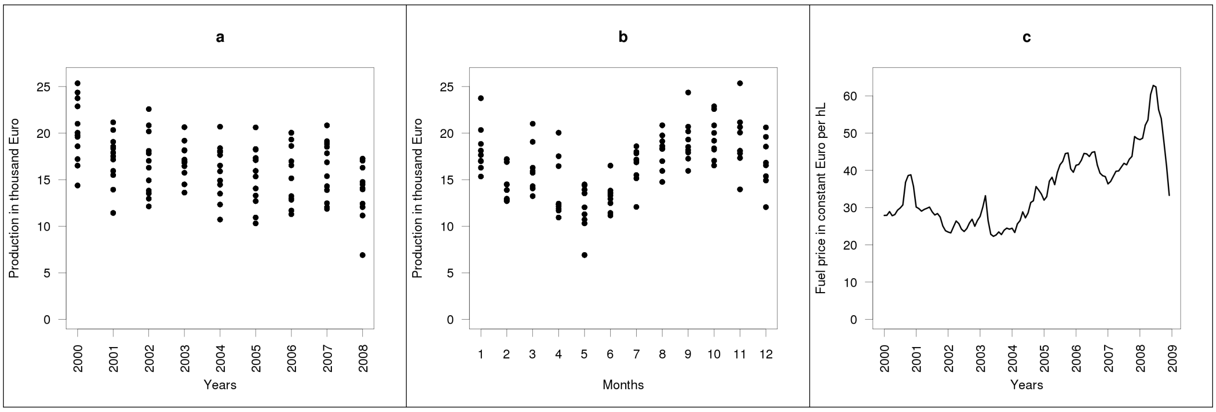

Figure 4.2: (a) French otter bottom trawl inter-annual trend in production during the 2000-2008 period. (b) French otter bottom trawl monthly trend in production during the 2000-2008 period. (c) Trend in tax free fuel price in constant Euro of January 2000 during the 2000-2008 period.

4.3.2 Temporal trend in fishing effort

Total annual fishing effort displayed in the English Channel presents no global trend during the 2000-2008 period (figure 4.3a). From 2000 to 2003, the fishing effort increases, a period followed by a slight decreasing trend before an important drop in 2008. Trend in fishing effort is significantly correlated with the number of vessels equipped with otter bottom trawls (P-value=4.10^{-3}, figure 4.3a). The seasonal trend in fishing effort (figure 4.3b) is not constant during the year and follows an increasing trend from the beginning of the year to the end of the third quarter followed by a large decrease until the end of December.

4.3.3 Fuel price as driver of the fishing activity

No significant correlation have been highlighted between the fishing effort and the fuel price (figure 4.4a) while the fuel price is negatively correlated with the proxy of the distance covered by fishermen to reach fishing grounds (figure 4.4b). These results suggest that the fuel price did not influence the fishing effort displayed but influenced its spatial distribution.

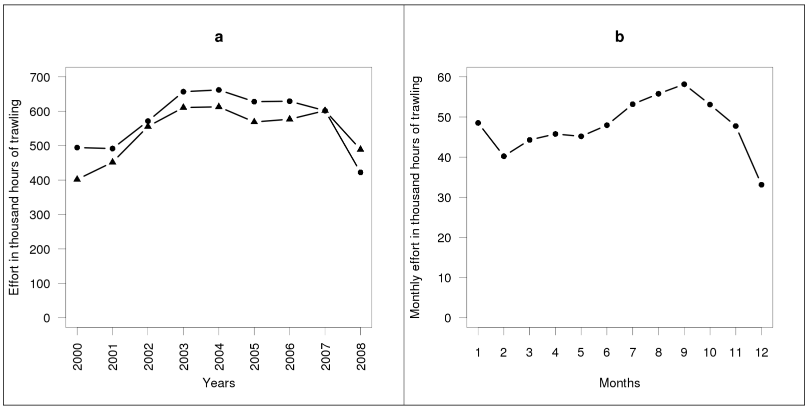

Figure 4.3: (a) Time series of the total annual fishing effort exerted in the English Channel. (b) Average monthly effort exerted in the English Channel.

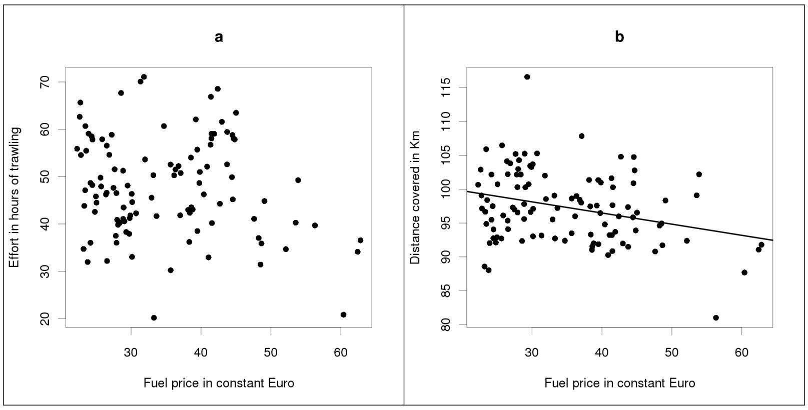

Figure 4.4: (a) Comparison of the tax free fuel price and the total monthly effort exerted in the English Channel. (b) Correlation between tax free fuel price and indicator of euclidean distance between the landing site and the explored ICES rectangle centroid.

4.3.4 Spatial distribution of the fishing effort

From the spatial point of view (figure 4.5), the trawling effort is not equally displayed in the English Channel. Some rectangles are poorly exploited all over the years from the beginning to the end of the period, the three rectangles separating the East and West English Channel (28E8, 29E8 and 30E8), the majority of English coast (from West to East, from the 29E5 to the 30E9) and three of the French inshore rectangles (25E5, 26E5 and 26E6). Among the western offshore rectangles, two patterns of exploitation can be identified. The first one is generally highly exploited during autumn and winter (28E5, 28E6, 28E7 and 29E7) while the second (27E5, 27E6 and 27E7) is exploited all over the year. In 2008, the fishing effort largely decreases in this zone. Inshore rectangles of the West English Channel (26E7, 26E8 and 27E8) are poorly exploited in 2000 and become more and more exploited until 2008, highest exploitation being generally observed in summer. In the East English Channel offshore rectangles (28E9, 29E9, 29F0 and 30F0) are generally more exploited during autumn and winter while inshore rectangles (27E9, 28F0, 29F1 and 30F1) are more exploited in spring and summer. Although 3 rectangles do not seem to present inter-annual trend in their exploitation (28F0, 29F1 and 30F1), the Bay of Seine rectangle (27E9) is more and more exploited all along the studied period.

4.3.5 Spatial and temporal correlation in effort allocation

The PTA performed explains nearly 54% of the time series variance on the first factorial plan and more than 64% on the three first axes. Years 2000-2007 are well represented on the first factorial plan (figure 4.6a) and can be split in two groups, years 2000-2002, on the one hand, and years 2003-2007 on the other hand. Vectorial correlation coefficients presented in the table 4.1 show, in the three first years, correlation coefficients varying between 0.32 and 0.42. For years 2003-2007 correlation coefficients vary between 0.31 and 0.55. Year 2008 is well represented on the third axis, independent from the two first ones, highlighting a very different pattern for this last year.

PCA performed on the compromise, which summarises the common structure of the matrix time series, explains more than 70% of the variance on the first factorial plan. Figure 4.6b highlights a seasonal cycle of the fishing effort in the English Channel. The first axis well represents the high variance observed between April and August which is negatively correlated from the winter months from December to March characterised by the lowest variance. Autumn effort is well represented on the second axis and this season seems to be a transition period, independent from the other seasons mentioned above. Clusters of ICES rectangles (figure 4.6c) highlight three different groups of ICES rectangles. Two groups well represented on the first axis are negatively correlated. The first one, well represented on the positive part of the first axis, is made of inshore rectangles exploited in summer while the second one, well represented on the negative part of the

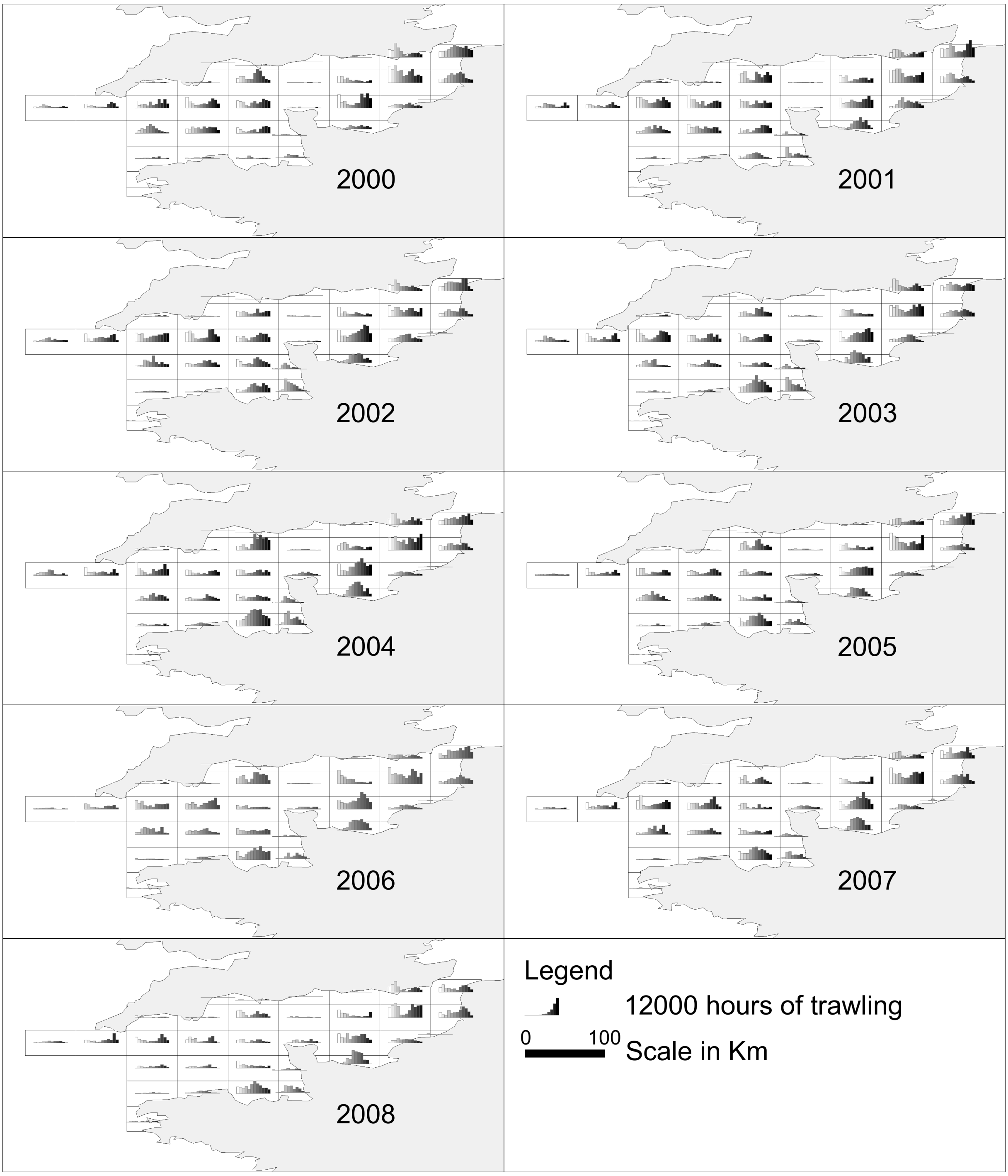

Figure 4.5: Monthly effort exerted in the English Channel per ICES rectangle for each year of the 2000-2008 period.

first axis, is made of offshore rectangles. The third group characterised by an important variance is well represented on the second axis, particularly 28E9, 29E7, 30F1 and 27E6, and is independent from the two other groups.

Contributions to the compromise computing vary with years. Years 2003 to 2007 have the highest contribution, followed by years 2000-2002. Finally, year 2008, which presents a very different pattern from other years, present the lowest contribution.

Table 4.1: Vectorial correlations computed by the PTA between the annual matrices.

Years	2000	2001	2002	2003	2004	2005	2006	2007	2008
2000	1.00								
2001	0.42	1.00							
2002	0.34	0.32	1.00						
2003	0.22	0.23	0.43	1.00					
2004	0.11	0.15	0.29	0.49	1.00				
2005	0.26	0.17	0.29	0.38	0.55	1.00			
2006	0.28	0.23	0.25	0.31	0.42	0.54	1.00		
2007	0.15	0.20	0.33	0.39	0.47	0.51	0.56	1.00	
2008	0.16	0.15	0.11	0.20	0.33	0.22	0.27	0.42	1.00

4.3.6 Changes in cephalopod length frequency sampling origin

From 2000 to 2007, the bulk of samples comes from the eastern English Channel while the western English Channel is always represented with a few samples (figure 4.7). In the eastern English Channel, the 28E9, off Port-en-bessin, is always well represented. In the West English Channel, cephalopods measured were generally caught offshore in the centre of VIIe ICES division. In 2008, and contrary to the previous years, all the samples come from a continuous zone of the East English Channel off Port-en-Bessin landing site. The 28E9 and 29E9 are the most represented (respectively 19 and 13 samples) and 27E9, 28F0 and 29F0 are less represented with respectively 6, 5 and 6 samples and a unique sample comes from the 30F0.

4.4 Discussion

This work highlights the dynamic of the French otter bottom trawl fishing effort in the English Channel during the period 2000-2008. In this period, while the vessel WCT remained stable, the fuel price has largely increased from €28 to more than €60 which is likely to impact the fishing activity. The fishing effort displayed in the English Channel is influenced by the number of active vessels and not by the fuel price which influences the distance covered by the fishermen to reach the fishing grounds. This last correlation

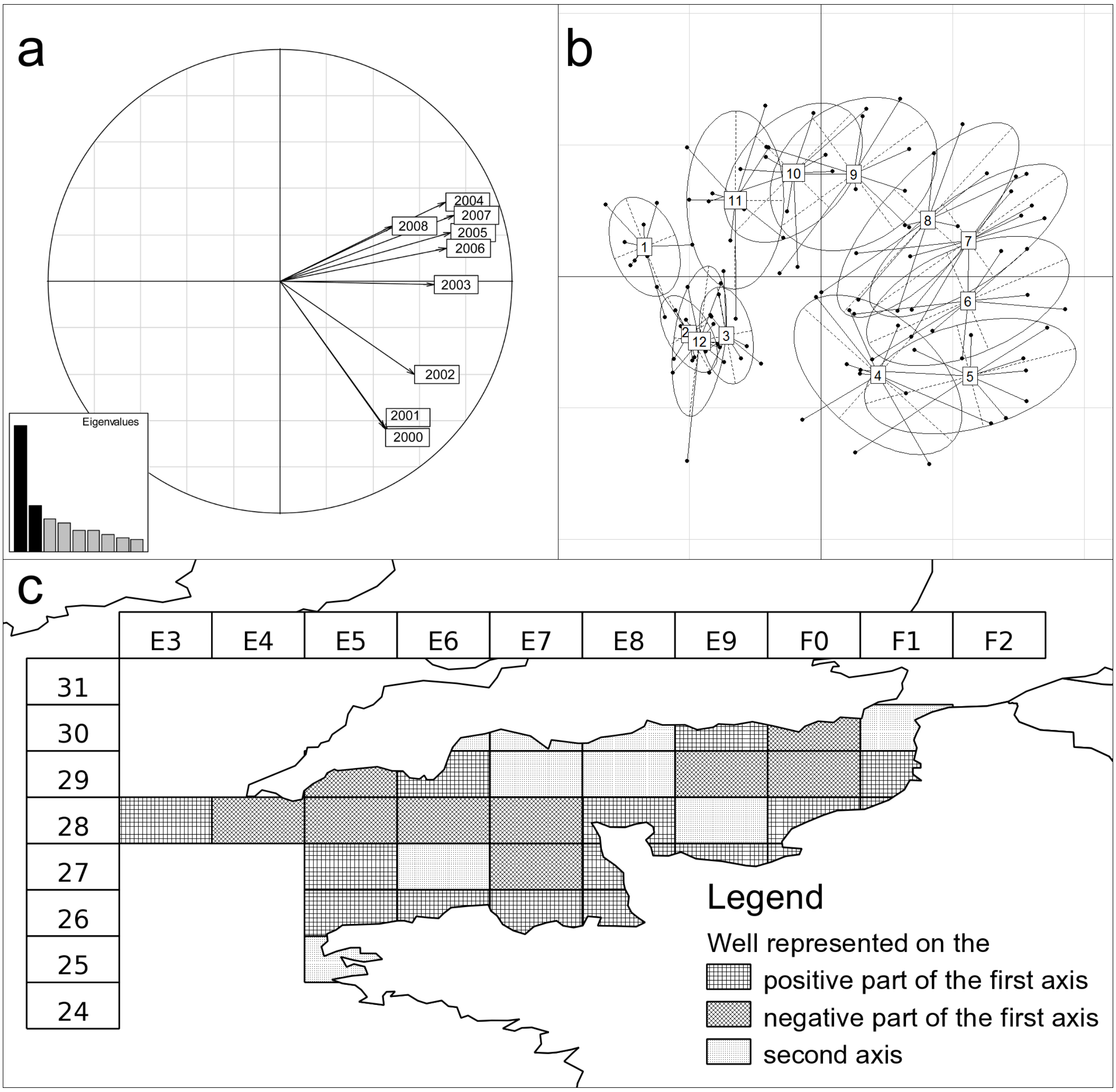

Figure 4.6: Representations of the PTA results: the inter-structure, the compromise and clusters of ICES rectangles. (a) 3d array inter-structure represented on the first factorial plan. (b) Individuals of the compromise represented with their inter-annual variance. (c) Map of the 3 clusters of correlated ICES rectangles determined by the Principal Component Analysis (PCA) performed on the compromise. Rectangles filled with vertical and horizontal lines are well represented on the positive part of the first axis, rectangles filled with the slanted lines are negatively correlated to the previous one and well represented on the negative part of the first axis and rectangles filled with the points are well represented on the second axis which is independent from the first one.

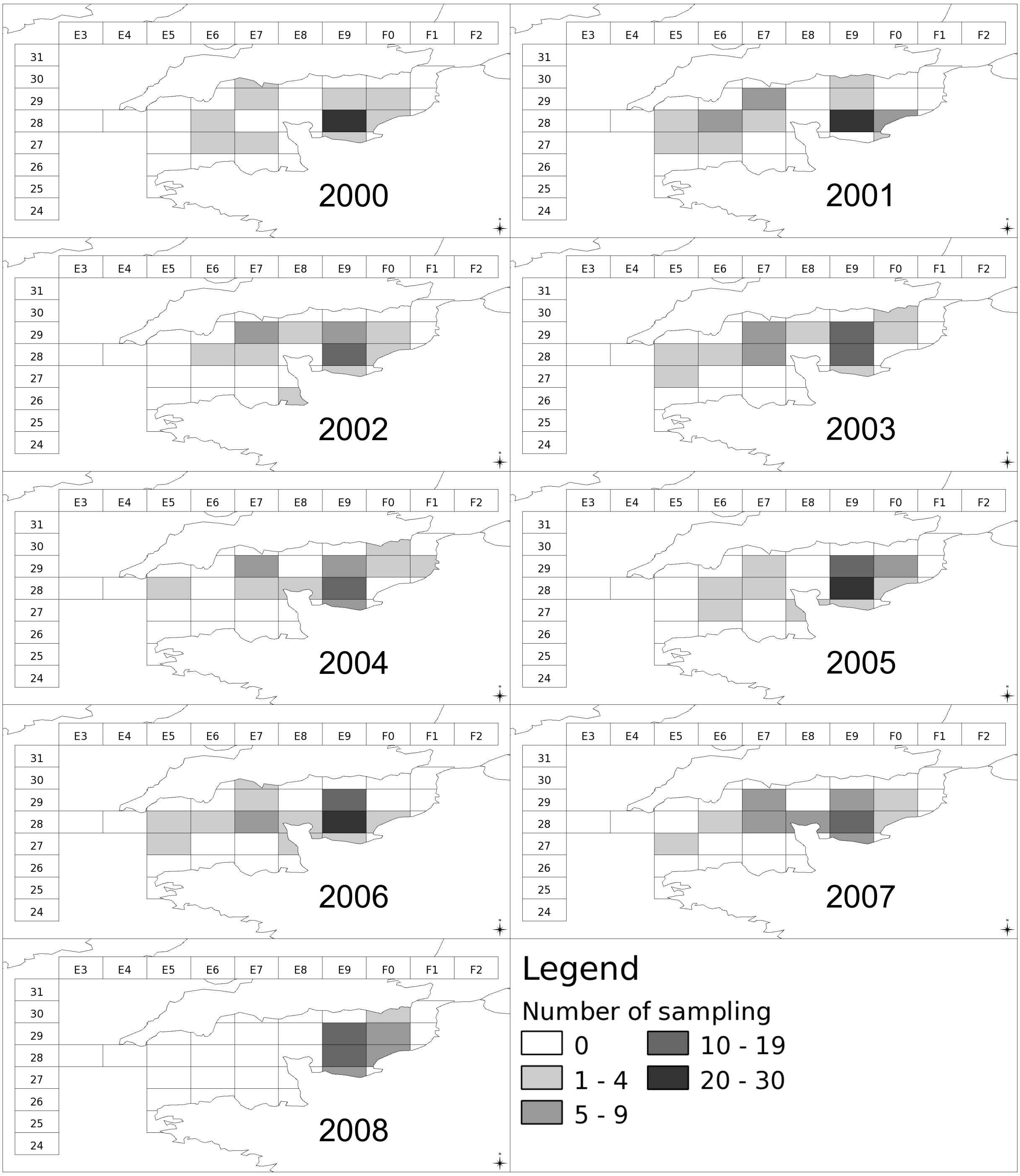

Figure 4.7: Number of cephalopod length frequency samplings carried out per ICES rectangle for each year during the data collection programme (CFP and DCF) in Port-en-Bessin landing site.

is corroborated by an increase in effort displayed in inshore ICES rectangles. In 2008, a large decrease of the fishing effort is observed, mainly in the offshore rectangles of the West English Channel and the highest fishing effort is observed inshore. Seasonal spatial distribution of the fishing effort is corroborated by the PTA results which highlight a negative correlation between offshore and inshore rectangles respectively exploited in autumn-winter and spring-summer. Modifications observed in the spatial distribution of the fishing effort has mainly impacted the origin of length frequency samples in 2008 and should be taken into account when age structured models are developed. Even if the spatial distribution of the French trawling effort have slightly changed from 2000 to 2007 and largely changed in 2008, this effort covers the whole English Channel and can be considered adequate to derive Landings Per Unit Effort (LPUE) for cephalopods. In the case of the cuttlefish, trawling covers both zones where cuttlefish concentrate and zones were they are absent giving a true image of the abundance.

As a few number of vessels were equipped with VMS, English Channel trawling effort is collected with the coarse resolution of ICES rectangles which does not enable the use of geostatistical methods. The PTA performed was thus the best tool to explore such spatio-temporal data and has the advantage to search correlations between non adjacent zones, but is not an explicative methodology. Moreover, the work was focused on the fuel cost, even if it is one of the most important one, others, such as welfare costs, exist but are not available in the SIH data. In addition, SIH stores selling data separately from landings data and it is thus difficult to link landings and direct income. Finally, alternative sources of income exist and are difficult to use such as subsidies allocated by governments.

As the fuel is a major part of the costs in trawl fisheries (Schau et al., 2009; Driscoll and Tyedmers, 2010; Sumaila et al., 2008), most of the governments managing a fisherman population allocate fuel subsidies under different forms to help them in stabilizing their costs (Sumaila et al., 2008). In France, a series of subsidies were introduced to avoid social conflicts (Mesnil, 2008). In 2000-2001, public aids were allocated to fishermen to officially compensate for the damages of the Erika oil spill but the European Commission warned the French government, considering this subsidy in nonconformity with European laws. After this period, subsidies decreased due to the decrease observed in the fuel price (figure 4.2c). When the fuel price started to increase after 2003 and to avoid the European Commission warnings, producer organisations decided to create an insurance to prevent the risks in fisheries like fuel price increase, pollution and fishery closure, the ”Fund for the prevention of risks to fishing” (Le Floc'h et al., 2007). This insurance was ready to start his activity in June 2004 when the government gave €1M to the Crédit Maritime bank. In April and July 2005, as the fuel price kept on increasing, the government added €50M to the insurance to help the fishing sector. In April 2006, another €100M was promised by the ministry to help in restructuring the sector and €22M were added a month later to compensate the fuel price increase. In the 2000-2007 period, subsidies were generally allocated to maintain or increase the fishing effort which explains the minor changes in fishing activity observed during this period. A very different situation appeared in 2008 which resulted in a drastic decrease in fishing effort in the western English Channel in this year. Even if the French government tried to help the fishing sector, EU declared the “Fund for the prevention of risks to fishing” as unauthorized government subsidies

(Ministère de l'Agriculture de l'Agroalimentaire et de la Forêt, 2009). Public aids then focused on compensation of cod fishery closure (CE No 1342/2008) and on the reduction by 10% the number of vessels (Leblond et al., 2009, 2010).

The fleet studied in this work is made of exclusive and non exclusive trawlers coming from the northern French coast (Leblond et al., 2009, 2010). Fishermen from Atlantic coast rarely exploit the English Channel and are only present on the very West part of the Channel (Portail CHARM III - Interreg IV, 2012).

Exclusive trawlers are generally large vessels (72% over 20 m) able to exploit offshore demersal resources. They always trawl and never change their gear, they are used to industrially exploit offshore grounds and seldom change their behaviour (Leblond et al., 2009, 2010). This feature explains the low variance observed in the autumn-winter offshore exploitation of the demersal resource. Offshore resources targeted in autumn and winter are generally made of cuttlefish, flatfish, seabass, squids, whiting, red mullet or cod (Carpentier et al., 2009). Exploitation of these different resources both in East and West English Channel explains the correlation observed between non adjacent offshore ICES rectangles. As exclusive trawlers generally fish far away from their home port, they consume more fuel than inshore trawlers both for the route but also for icing and costs are considered to increase with the distance covered to reach fishing grounds (Sampson, 1991). Moreover the fish is generally caught a long time before the selling and is thus less attractive for consumers (Guyader et al., 2013). As a consequence, exclusive trawlers are highly dependent from the subsidies accorded in the high fuel price context. The decrease in subsidy supporting fishing activity in 2008 is probably at the origin of the large decrease in fishing effort observed offshore in the West English Channel.

The second group is made of non exclusive trawlers which are shorter (more than 99% are shorter than 20 m) exploiting inshore resources and not equipped to fish offshore (Leblond et al., 2009, 2010). As a consequence, they adapt their fishing activity to the inshore most valuable resource available according to the season and the rules. In spring and summer, when demersal resource (for instance cuttlefish in the reproduction period) is abundant inshore, they practise the inshore trawling (Pierce et al., 2010). Due to their low storage capacity and the short distance covered, they provide very fresh fish at the landing sites (Guyader et al., 2013). Some of fishermen even have direct contracts with restaurants or fish shops to sell very fresh fish well preserved on-board. Due to their adaptability in the available resource, inshore trawling is less dependant from the subsidies (Guyader et al., 2013) and have probably been favoured as it is considered as a complementary métier to the scallop dredging. This métier replaces the trawling from the 1^{st} of October when scallop fishery is opened until the 15^{th} of May. The scallop fishery, the main English Channel resource (whatever the gear concerned ; Leblond et al., 2009, 2010 therefore leads to the seasonal decreasing trend observed in inshore trawling during fourth and first quarter.

The seasonality of the spatial allocation of trawling effort in the English Channel is thus explained by the activity of exclusive and non exclusive trawlers which respectively exploit offshore resources in autumn-winter and inshore resources. Cephalopod resources (i.e. squids and cuttlefish), which are of importance for this métier are present and exploited offshore in autumn-winter (Portail CHARM III - Interreg IV, 2012). In spring-summer, cuttlefish migrate inshore for reproduction and feeding (Boucaud-Camou and Boismery, 1991; Dunn, 1999a) and are exploited by non exclusive trawlers until the beginning autumn. Cephalopod resources thus contribute to the seasonality allocation of the fishing effort in the English Channel.

The fisheries sector in France is going through a crisis (Gascuel et al., 2011). The issues are the stagnancy of fish prices, which is due to the globalisation of seafood markets, the increasing trend in fuel price (Anderson, 2003; Sumaila et al., 2008; Abernethy et al., 2010) and the reduction of national subsidies (Mesnil, 2008). Cutting down fishing costs is thus essential to keep fishing activities within sustainable limits. Cost reduction could be achieved by using more efficient trawls (Priour, 2009), by changing fishing strategy (Parente et al., 2008; Abernethy et al., 2010) and also by decreasing fishing effort as suggested by MSY-F_{opt} reference points. This last measure implies a division of the effort by 2 or 3 which, on the mid to long term, will lead to an increase of 3 to 4 times the catch made before (Froese et al., 2008; Froese and Proelß, 2010; Gascuel et al., 2011).

Acknowledgments

We thank Monique Simier for her constructive advice in performing multivariate analysis (Partial Triadic Analysis and Principal Component Analysis) and the *Système d'Information Halieutique* (SIH) team who has provided the data used in this article. This study was carried out within the EU funded project ”CRESH” (under the Interreg IV A France-Manche-England programme).

Chapitre 5

Un modèle de biomasse à 2 stades pour évaluer le stock de seiche (*Sepia officinalis*) de Manche

A two stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis* L.) stock

Michaël, Gras[1,2,*], Beatriz A., Roel[3], Franck, Coppin[4], Eric, Foucher[5], Jean-Paul, Robin[1,2]

1-Université de Caen Basse-Normandie, FRE 3484 BIOMEA, Esplanade de la paix, F-14032 Caen, France
2-CNRS INEE, FRE 3484 BIOMEA, F-14032 Caen, France
3-Cefas, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK
4-Ifremer, Laboratoire Ressources Halieutiques, 150 Quai Gambetta, 62200 Boulogne-sur-Mer, France
5-Ifremer, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP 32, 14520 Port-en-Bessin, France
∗ Corresponding author : michael.gras@unicaen.fr

Ce chapitre fait l'objet d'un article scientifique qui a été soumis à la revue scientifique ICES Journal of Marine Science.

Résumé

Les stocks de céphalopodes sont des ressources très productives et développer un modèle d'évaluation de stock prenant en considération leurs caractéristiques biologiques particulières est un défi. La seiche de Manche (*Sepia officinalis*) est le stock de céphalopode le plus important en Atlantique N-E et parmi les 3 ressources principales pour les pêcheurs de Manche. Des exercices de modélisation utilisant les méthodes de déplétion et les modèles structurés en âge ont été publiés pour évaluer ces stocks mais ont montré leurs limites, surtout en ce qui concerne les hypothèses de modélisation ou la forte demande en données. Un modèle de biomasse à 2 stades a donc été proposé comme solution pour évaluer cette ressource. Quatre indices d'abondance basés sur des campagnes scientifiques et des données de chalutages commerciaux récoltées par l'Ifremer et le Cefas ont été calculés, standardisés et utilisés comme données pour ajuster le modèle de biomasse à 2 stades. Le modèle s'ajuste bien aux données et les résultats montrent une forte variabilité inter-annuelle sur les 17 années étudiées et une tendance négative sur les dernières années. Les indicateurs basés sur les résultats du modèle montrent que l'abondance du recrutement n'est pas corrélée à la biomasse féconde mais semble influencée par les conditions environnementales (SST) rencontrées au début du cycle de vie. Les tendances du taux d'exploitation ne montrent pas de surexploitation, néanmoins, des points de référence sont proposés et des avis de gestion sont discutés pour conserver la seiche de Manche dans les limites d'une exploitation durable.

Mots clés

Sepia officinalis ; Manche ; Indices d'abondance ; Campagne de chalutage ; Modèle de biomasse à 2 stades ; Taux d'exploitation ; Relation stock-recrutement ; SST.

Abstract

Cephalopod stocks are highly productive resources and developing a stock assessment model taking into consideration their specific biological characteristics is a challenge. The English Channel cuttlefish (*Sepia officinalis*) is the most important cephalopod resource in the N-E Atlantic and part of the 3 main resources for English Channel fishermen. Depletion methods and age structured models were applied to these stocks in trials but have shown their limits, related to the model assumptions or data demand. A two stage biomass model is therefore proposed as a solution to assess this resource. Four abundance indices derived from survey and commercial trawl data collected by Ifremer and Cefas were derived, standardized and used as input data to fit the two stage biomass model. The model fits well the abundance indices and results highlight a large inter-annual variability during the 17 year period studied and a decreasing trend during the last studied years. Indicators based on model outputs highlight that the recruitment strength is not correlated with the Spawning Stock Biomass (SSB) but rather seems to be influenced by the environmental conditions (Sea Surface Temperature, SST) encountered at the beginning of the life cycle. Trends in exploitation rate did not show evidence of over-exploitation, nevertheless reference points are proposed and management advice is discussed in order to keep the English Channel cuttlefish fishery within a sustainable range.

Keywords

Sepia officinalis; English Channel; Abundance indices; trawl survey; Two stage biomass model; Exploitation rate; Stock recruitment relationship; SST.

Présentation du chapitre 5.Modèle de biomasse à 2 stades[1]

Dans le chapitre consacré à l'étude de la structure du stock en période de reproduction, il a été mis en évidence que certains individus de chaque cohorte étaient matures et pouvaient prendre part à la reproduction à l'âge de 1 an. Cependant, comme ce pourcentage est faible, le cycle de vie défini pour la modélisation considérera que la seiche a une durée de vie exclusive de 2 ans. De plus, le chapitre traitant de la répartition de l'effort de pêche a permis de montrer que la dynamique spatio-temporelle de l'effort des chalutiers de fond à panneaux était suffisamment stable et couvrait l'ensemble de la zone étudiée sur la période 2000-2008 pour que des indices d'abondance fiables soient utilisés pour ajuster un modèle d'évaluation de stock.

En raison de la diminution des stocks de poissons durant les dernières décennies, les cépahlopodes sont devenues des ressources de plus en plus importantes pour les pêcheurs. En Atlantique N-E, la seiche de Manche (*Sepia officinalis*) est le plus important stock de céphalopode. Il est principalement exploité par les pêcheurs français et britanniques qui ont débarqué annuellement une moyenne de 11 000 tonnes de seiche sur la période 2000-2010 pour un chiffre d'affaire annuel moyen de 20 millions d'Euros. Malgré la publication de différents exercices d'évaluation de stock, la seiche de Manche n'est gérée que par des mesures locales et aucune mesure européenne n'est actuellement en vigueur. La méthode de décroissance des indices d'abondance (Leslie-DeLury) est la méthode d'évaluation de stock couramment utilisée pour évaluer les stocks de céphalopodes. Elle a été appliquée au stock de seiche de Manche mais ne se basait que sur les débarquements britanniques qui représentent seulement le tiers des débarquements totaux. L'Analyse de Population Virtuelle, la méthode d'évaluation de stock la plus utilisée pour évaluer les stocks de poissons à durée de vie longue, a été appliquée à la seiche sur une base mensuelle. Cependant, les difficultés d'estimation de l'âge mensuel n'ont pas permis de mettre en place une évaluation de stock en routine. Il est donc proposé d'utiliser un modèle de biomasse à 2 stades, un modèle adapté pour estimer l'abondance de stock dont la composition en âge est difficile et qui peut donner des résultats équivalents à ceux d'une VPA pour ces stocks. Le modèle de biomasse à 2 stades a déjà permis d'évaluer les stocks de Calmars d'Afrique du Sud (*Loligo reynaudii*) et de Hareng de Mer Celtique (*Clupea harengus*).

Des données de débarquement (débarquements des chalutiers de fond et débarquements totaux) ainsi que des données de campagne scientifique (campagnes BTS et CGFS) ont été extraites des bases de données du Cefas et de l'Ifremer pour la période 1992-2008 pour estimer des indices d'abondance (indices de campagne scientifique et Débarquements Par Unité d'Effort, LPUE). Les LPUE ont ensuite été standardisés en utilisant un Delta-GLM qui combine un GLM à erreur binomiale pour modéliser la présence/absence et un GLM à

---

[1] Les références bibliographiques se trouvent dans le corps du texte de ce chapitre

erreur normale pour modéliser l'abondance log-transformée de la ressource. Le modèle de biomasse à 2 stades pour évaluer le stock de seiche de Manche est constitué de 4 équations décrivant l'abondance de la seiche au cours de son exploitation. Le cycle de vie simplifié considère que le recrutement a lieu à l'âge de 1 an au 1^{er} juillet d'une année Y pour les individus nés au 1^{er} juillet de l'année Y-1, le cycle de vie se terminant au 30 juin de l'année Y+1. La capture est supposée avoir lieu en une seule fois au milieu de la saison de pêche. L'indice d'abondance de la campagne BTS décrit l'abondance au recrutement en juillet alors que celui de la campagne CGFS décrit l'abondance un trimestre plus tard. Les LPUE standardisés sont utilisés pour décrire la dynamique de population tout au long de la saison de pêche. Le modèle est ensuite ajusté en utilisant les 4 indices d'abondance et la méthode des moindres carrés. Enfin, les résultats du modèle ont permis de développer 2 indicateurs de l'état du stock, la relation stock-recrutement et l'estimation du taux d'exploitation de chaque cohorte de la série temporelle.

Les résultats mettent en évidence que le modèle s'ajuste bien aux données observées (les résidus ne présentent pas de tendance). Les indices d'abondance ainsi que la série temporelle de biomasse indiquent que, sur la période 1992-2000, l'abondance du stock de seiche présente une forte variabilité inter-annuelle sans tendance significative jusqu'à la forte baisse observée en 2001. En 2002, l'abondance atteint un maximum mais suit ensuite une tendance négative jusqu'en 2008. Malgré cette tendance négative, aucune relation stock-recrutement ni tendance du taux d'exploitation n'a été mise en évidence. Enfin, l'abondance au recrutement semble influencée par les conditions environnementales rencontrées durant les premiers stades de vie (dont la température de surface durant l'été suivant l'éclosion est un indicateur).

Les résultats amènent à la conclusion que, sur la période 1992-2008, la ressource semble pleinement exploitée et ne présente pas de signes de sur-exploitation, une conclusion proche de celles mentionnées dans la littérature. Différents auteurs ont mis en évidence le rôle des paramètres environnementaux dans la variabilité inter-annuelle de l'abondance des céphalopodes, particulièrement les conditions environnementales rencontrées durant les premiers stades de vie, une observation en accord avec les résultats obtenus dans cette étude. De plus, en France, la pêche côtière (dans la zone des 3 milles) est autorisée par dérogation pour cibler les juvéniles de seiche. Compte tenu de la sensibilité des premiers stades de vie de cette ressource, cette pêcherie impacte sans doute fortement l'abondance au recrutement. Au vu des résultats, une application logicielle de ce modèle de biomasse à 2 stades permettra de réaliser une évaluation en routine de cette ressource durant les années à venir.

5.1 Introduction

Cephalopods are highly productive species which represent large fishery resources but which are also a challenge for fisheries managers because of their biological characteristics (short lifespan, variable growth and recruitment). Interest of fishermen in cephalopod stocks has grown during the last decades of the XXth century due to the increasing demand in high quality protein for the human consumption and the depletion observed in finfish stocks all over the world (Caddy, 1983; Roper et al., 1984; Boyle and Rodhouse, 2005; Royer et al., 2006). At the European, scale cephalopod resources were traditionally exploited by Mediterranean and Portuguese fisheries and since the 1980s, interest of other European countries led to an increase in landings from 30,000 tons in 1950 to 120,000 tons in 2010 (Pierce et al., 2010). In the English Channel, fishermen started to fish the 3 different cephalopod species (*Sepia officinalis*, *Loligo forbesii* and *Loligo vulgaris*) during the 1980s (Dunn, 1999a; Royer et al., 2002, 2006).

The English Channel cuttlefish stock is the most important cephalopod stock exploited in the North-East Atlantic (Pierce et al., 2010). In the list of all English Channel fishery resources, cuttlefish is the third species both in weight and value. Annual landings (11,000 tons on average during the 2000-2010 decade) are caught mostly by French and United Kingdom (UK) fishermen. French fishermen catch between 56 and 75% of the resource while the rest is caught by UK fishermen. Belgian and Netherlands fishermen can also exploit cuttlefish in the English Channel but this fishing activity can be considered minor. Cuttlefish is an important source of income for fishermen considering that, in average on the 2000-2010 decade, the declared turnover varies around €15 millions for French fishermen and €5 millions for UK fishermen (Portail CHARM III - Interreg IV, 2012).

The most common model used to assess cephalopod stocks is the depletion method (Hilborn and Walters, 1992; Pierce and Guerra, 1994; Payne et al., 2006; Pierce et al., 2010) which was applied to different cephalopod stocks in the world (Rosenberg et al., 1990; Brodziak and Rosenberg, 1993; Basson et al., 1996; Agnew et al., 1998; Dunn, 1999b; Royer et al., 2002; Young et al., 2004). In the Falkland Islands, the depletion model was developed to assess two different species, *Illex argentinus* and *Loligo gahi*. Economical importance of these fisheries and results obtained have lead to use this model to manage the two stocks (Rosenberg et al., 1990; Basson et al., 1996; Agnew et al., 1998). This model was also applied in North-East Atlantic to the veined squid *Loligo forbesii* (Royer et al., 2002; Young et al., 2004) and the English Channel cuttlefish (Dunn, 1999b). However, the depletion model developed by Dunn (1999b) was only based on UK landings while they only represent one third of the total landings (Portail CHARM III - Interreg IV, 2012). Besides, recruitment estimates derived from depletion models can hardly be related to management reference points and for instance escapement objectives (Basson et al., 1996) appear somewhat arbitrary.

Age structured model is the most common method used to assess finfish stocks, particularly species which have a long lifespan (several years; Hilborn and Walters, 1992). It has been adapted on various cephalopod stocks such as *Illex illecebrosus* in the North-West Atlantic (Hendrickson and Hart, 2006) and *Octopus vulgaris* (Jouffre et al., 2002) off Mauritanian coasts. In the English Channel, Virtual Population Analysis (VPA) was firstly adapted by Royer et al. (2002) on a monthly time step to assess the loliginids squids *Loligo forbesii* and *Loligo vulgaris.* Royer et al. (2006) have then adapted the same methodology on the English Channel cuttlefish stock. VPA is a very powerful way to assess long lifespan species but it is time and data demanding (Mesnil, 2003; Trenkel, 2008), particularly when it is developed on a monthly basis adaptation. In addition, contrary to the loliginid squids, the age determination in English Channel cuttlefish is very difficult, length frequencies being unsuitable. Statoliths are the only hard structure which give the actual age of specimens but reading the daily rings is very difficult and they are not readable after the age of 240 days (Bettencourt and Guerra, 2001; Challier et al., 2002, 2006b). Although interesting results were obtained, no routine assessment was implemented due to difficulties associated with data collection.

In spite of local management measures and the publication of stock assessment exercises based on historical data (Dunn, 1999b; Royer et al., 2006), no routine assessment has been implemented to manage the English Channel cuttlefish stock. Currently, in the trawling fishery, cuttlefish benefits from more general laws which regulate the trawling, such as the ban of using mesh size smaller than 80 mm in otter trawl nets or the ban of trawling inshore (inside the 3 nautical mile inshore zone). Concerning this last law, there are two exemptions, one in spring and one in summer to respectively exploit spawners (during 6 weeks) and hatchlings (during 2 weeks). Finally, fishermen are not allowed to land specimens lighter than 100g (Council Regulation No 2406/96). Local management measures concern effort limitations and spatial segregation in the coastal zone which is for instance implemented in Lower Normandy for both trap fishing and inshore trawling (Pierce et al., 2010).

Because of their short life cycle and their specific features, cephalopod stocks are difficult to assess with classical stock assessment methods or adaptation of such classical tools. An alternative method exists with the two stage model (Roel and Butterworth, 2000; Mesnil, 2003; Trenkel, 2008; Roel et al., 2009) which is less data demanding but takes into account the recruitment strength (Ibaibarriaga et al., 2008) and gives consistent results compared with the VPA (Mesnil, 2003). It is also able to take into account more than one time series of abundance indices (Roel and Butterworth, 2000) and uses weight data rather than number of specimens. The two stage biomass model assumes observation error, which means that errors are associated with the survey and commercial fishery indices and that process error is ignored (Ibaibarriaga et al., 2008).

This work proposes a two stage biomass model for the assessment of the English

Channel cuttlefish stock. In a first step, survey and commercial data are used to derive cuttlefish abundance indices which are then standardized. In a second step, the standardized abundance indices are used as input data to fit the two stage biomass model. Finally, outputs of the model are used to highlight trends in cuttlefish abundance and to derive indicators to help managers in following the fishing impact on the stock.

5.2 Material and methods

5.2.1 The English Channel area and cuttlefish stock boundaries

The English Channel is connected to the Celtic Sea and the North Sea (figure 5.1). The English Channel is an important fishing ground for both bordering countries, France and the UK. The Cotentin peninsula, situated in the middle of the Channel is the boundary between shallower waters, to the East, and deeper waters to the West that host different benthic communities (Pingree, 1980; Dauvin, 2012) and fish stocks. As a consequence, the International Council for the Exploration of the Sea (ICES) has divided the Channel into two main zones: (i) VIId for the eastern part and (ii) VIIe for the western part which are respectively divided into 14 and 19 ICES rectangles of 1 degree per 0.5 degree. The English Channel is subjected to a large anthropic activity, including maritime traffic, extraction of marine aggregates and fishing activity (Ulrich et al., 2002; Carpentier et al., 2009).

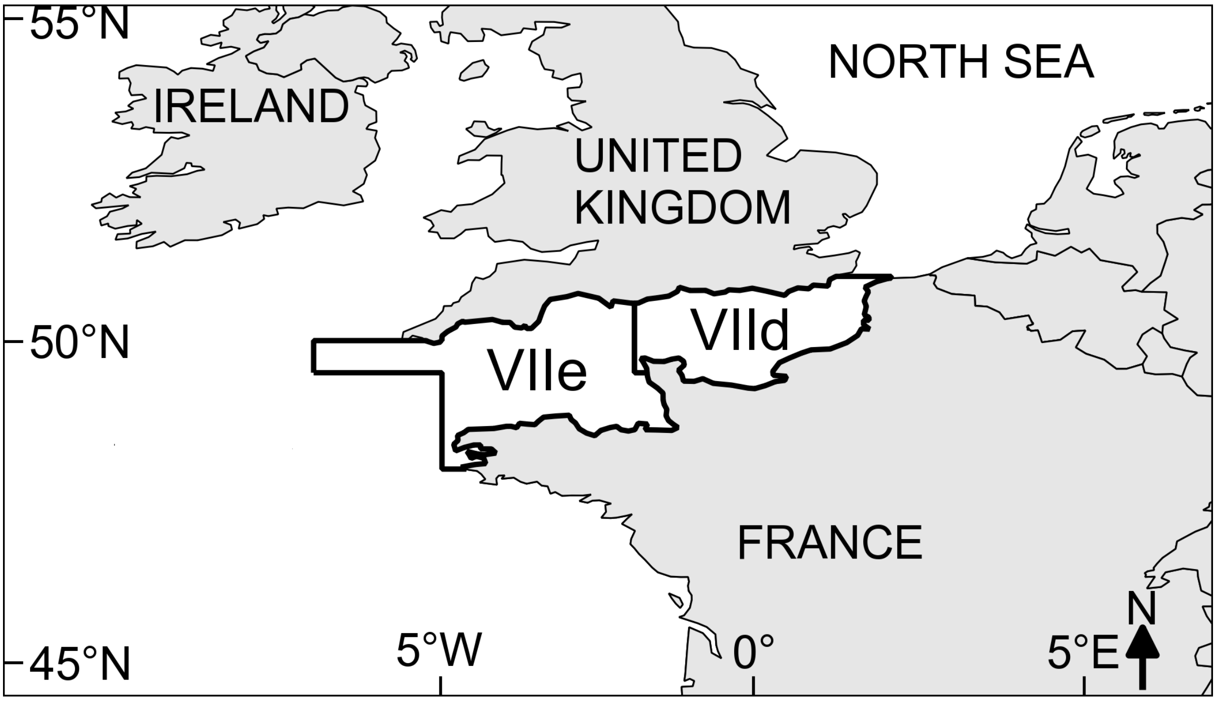

Figure 5.1: English Channel, N-E Atlantic. ICES division VIId and VIIe shown.

The English Channel cuttlefish is distributed throughout the Channel where its entire life cycle takes place, while abundance in the adjacent seas (North Sea and Celtic Sea) is very low. The English Channel cuttlefish has been considered as a single stock (Le Goff and Daguzan, 1991; Dunn, 1999a; Wang et al., 2003; Royer et al., 2006). Cuttlefish inshore/offshore migrations illustrate seasonal connections between East and West parts of the Channel (Boucaud-Camou and Boismery, 1991). Population genetic studies performed carried out by the European Project Cephalopod Recruitment from English Channel Spawning Habitats (CRESH) used microsatellites to identify population structure based on samples collected from different spawning areas situated in the English Channel. Preliminary results indicate that the English Channel cuttlefish consists of one stock (Shaw, personal communication). On these bases the assumption of a single stock is made throughout this study.

5.2.2 Métiers exploiting the English Channel cuttlefish

The English Channel cuttlefish stock is exploited by a series of métiers occurring in sequence at almost all stages of the life cycle (Denis and Robin, 2001). Exploitation starts a few weeks after hatching, during a limited period of 2 weeks at the end of August when trawlers targeting juveniles within the 3 nautical mile inshore zone are allowed by way of exemption from the law protecting the coastal zone. After the migration to the offshore wintering grounds, juveniles are partially recruited in the offshore French trawling fishery. The annual cohort is totally recruited in French and UK bottom trawl fisheries by the end of its first year of age when it comes back inshore to feed in summer. Multi-species trawlers are mainly otter bottom trawl in France and beam trawl in the UK. During the reproduction period, at the end of the 2 year life cycle, which occurs inshore on the French and UK coasts, fishermen exploit spawners using traps (Dunn, 1999a; Denis and Robin, 2001; Royer, 2002; Royer et al., 2006). Another exemption from the law allows French bottom trawlers to exploit spawners in spring during 6 weeks in the 3 nautical mile inshore zone.

5.2.3 Database extractions and abundance time series

Commercial and survey data were extracted from Cefas and Ifremer databases from 1992 to 2008. In the eastern English Channel (ICES division VIId), Cefas carries out the Bottom Trawl Survey (BTS) in July each year with Research Vessel (RV) Endeavour equipped with a 4 meter wide beam trawl. Ifremer also carries out a survey in the eastern English Channel every October, the Channel Ground Fish Survey (CGFS) with RV Gwen Drez equipped with a Very High Vertical Opening (VHVO) otter bottom trawl (10 m wide and 3 m high). Both surveys sample demersal species every year by trawling 30 minutes each station as it is defined in the survey protocols (Carpentier et al., 2009). In the BTS survey protocol, 75 stations are identified in the ICES division VIId and more than 100 are explored by the CGFS in the same area. These two fishery independent series of data give two time series of abundance indices, one during the recruitment and one a quarter after the recruitment. Both research institutes also collect landings (by all gears) and trawler landings with effort data. These last data are considered adequate to derive abundance indices from commercial fishing activity, Landings Per Unit Effort (LPUE) variations and their spatial/temporal components (Pierce et al., 1998). These fishery dependent data are used to estimate the cuttlefish abundance all over the year when fishery independent data are not available.

The two stage biomass model requires abundance indices of one year old specimens as input data. Examination of the length composition data collected on the BTS survey indicated that the cuttlefish caught consisted predominantly of one year olds. On this basis, a BTS index of abundance for that age group was constructed. In October, during the CGFS survey, juveniles are 3-4 months old and represent less than 5% of the catch weight. Records of the CGFS survey are also assumed to be estimations of one year old specimen abundance. The UK fishery is considered to catch only one year old specimens. French fishermen catch first year and second year specimens. In French landing sites, cuttlefish is landed per commercial category (Royer, 2002), which weight limits are described in the table 5.1. In this work, cuttlefish from commercial categories 1 and 2 were considered as one year old specimens and the two other ones were considered as first year of age. In the landings data, one year old specimens represent in average more than 80% of the total annual landings. As the Ifremer *Sytème d'Information Halieutique* (SIH) does not provide landings per commercial category, we have estimated a percentage of one year old specimens in the sale data and have used it to estimate the weight of one year old cuttlefish caught in the English Channel.

Table 5.1: Weight classes of French commercial categories (N.B.: The European regulation 2406/96 about marketing standards describes commercial categories 1 to 3. A fourth category appears irregularly since there is no minimal landing size in the cuttlefish).

Commercial category	Weight class (g)
1	>500
2	300-500
3	100-300
4	<100

Dunn (1999a) and Denis et al. (2002) have shown that English Channel fishermen did not discard cuttlefish in the 1990s. The French National Onboard Observer Programme, as part of the European Union Data Collection Framework, currently collect discard data (Protocol available on http://sih.ifremer.fr/Acquisition-des-donnees/Observations-a-la-mer/Documentation/Manuels-et-protocoles; European Union, 2008). Data were extracted from 2004 to 2008. Finally, a series of Sea Surface Temperature (SST) was extracted from the National Oceanographic and Atmospheric Administration (NOAA) database from 1991 to 2008 and averaged on a quarterly basis to test the effect of the SST (as a proxy of the environmental conditions) on the recruitment strength.

Scientific and commercial data, extracted from the Cefas and Ifremer databases, were computed to obtain abundance indices in Kg of cuttlefish per hour of trawling.

$$S^{obs} = \frac{C_n}{E_n} \tag{5.1}$$

or

$$U^{obs} = \frac{C_n}{E_n} \tag{5.2}$$

Where S^{obs} and U^{obs} are respectively the survey and the LPUE abundance indices, C_n and E_n are respectively the catch in Kg of cuttlefish and the effort in hour of trawling for the trip n. Survey abundance indices were estimated per ICES rectangle and then averaged on the whole western English Channel. As Hilborn and Walters (1992) suggest, fitting a GLM is the most powerful way to derive abundance indices from commercial LPUE. This method is currently used to standardize fish stock abundance indices and was already successfully used in estimating cephalopod abundance indices (Diallo and Ortiz, 2002; Royer et al., 2002, 2006). In addition, the numerous null values observed in the dataset were taken into account using a Delta-GLM method (Stefansson, 1996; Syrjala, 2000; Le Pape et al., 2003; Fletcher et al., 2005; Martin et al., 2005; Le Pape et al., 2007; Rochette et al., 2010; Acou et al., 2011) which consists in combining a binomial error GLM and a Gaussian error GLM to explain firstly the presence-absence and secondly the abundance of the resource. LPUE variability is thus explained by 4 variables (the year y, the month m, the ICES rectangle r and the engine power of the vessel p) which are introduced in both models:

$$logit(U^{obs}_{y,m,r,p})_{0/1} = \alpha_y + \beta_m + \gamma_r + \delta_p + \omega_{y,m,r,p} \tag{5.3}$$

and

$$Ln(U^{obs}_{y,m,r,p})_{>0} = Ln(\alpha_y) + Ln(\beta_m) + Ln(\gamma_r) + Ln(\delta_p) + \varepsilon_{y,m,r,p} \tag{5.4}$$

Where $\omega_{y,m,r,p}$ and $\varepsilon_{y,m,r,p}$ are the observation errors for the year y, month m, ICES rectangle r and vessel power p. Standardized LPUE (U) are then estimated using the formula.

$$U_{y,m,r,p} = \frac{e^{logit(U^{obs}_{y,m,r,p})_{0/1}}}{1 + e^{logit(U^{obs}_{y,m,r,p})_{0/1}}} \times e^{Ln(U^{obs}_{y,m,r,p})_{>0}} \times e^{\frac{\sigma^2 . Ln(U^{obs}_{y,m,r,p})_{>0}}{2}} \tag{5.5}$$

Survey abundance indices and standardized LPUE give the average spatial distribution and the trend observed in the resource abundance. Maps of the standardized abundance indices can thus be used to illustrate the inshore/offshore movements of the cuttlefish during the fishing season. The 4 time series of abundance indices are then used as input data to fit the two stage biomass model.

5.2.4 Cuttlefish life cycle and its simplification to model its biomass

English Channel cuttlefish (*Sepia officinalis*) is a semelparous species, it hatches inshore in summer and performs offshore/inshore migrations to wintering grounds in the centre of the western English Channel and to coastal feeding and spawning grounds (spring and summer). The lifespan in this population is 2-year spawners dying at the end of the reproduction period. Recruitment into the fishery begins in October of the first year and the annual cohort is fully recruited at the beginning of their second summer (at the age 1 year; Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991; Dunn, 1999a).

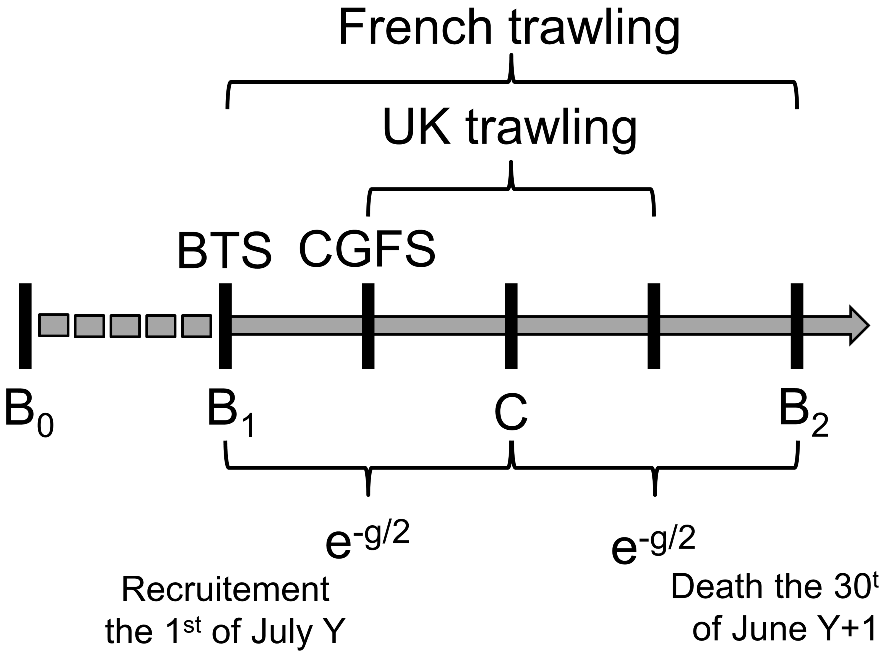

Figure 5.2: English Channel cuttlefish life cycle simplified to model the dynamic of the biomass from recruitment at the age one to the end of the cycle on the second year of life.

In a simplified version of cuttlefish life cycle (figure 5.2), fishing seasons start on the 1^{st} of July of year y and end on 30^{th} of June of year $y+1$ (when spawners die). In a cohort born on 1^{st} of July of the year $y-1$, the model describes the population dynamic of 1 year old specimens from July of the year y to the end of June of the year $y+1$. During the second year of life, initial biomass of the year y ($B_{1,y}$) is influenced by catch and by a growth and natural mortality parameter g. Just like Pope's simplified procedure in cohort analysis (Pope, 1972), the catch of one year old specimens, $C_{1+,y}$, is assumed to happen as a pulse in the middle of the fishing season (i.e. in January the 1^{st}). Considering that the recruitment is assumed to take place in July of every year, the biomass $B_{2,y}$ of the year y at the end of the life cycle can be modelled as:

$$B_{2,y} = [(B_{1,y}).e^{-g/2} - C_{1+,y}].e^{-g/2} \tag{5.6}$$

Abundance indices can then be used to fit the model. BTS index is used to estimate abundance at the beginning of the fishing season as:

$$S_y^1 = k_1.B_{1,y}.e^{\xi_y} \tag{5.7}$$

Where S_y^1 is the BTS survey index for the year y, k_1 is the BTS survey catchability and ξ_y is the observation error for the year y. CGFS survey which occurs one quarter after the recruitment can also be used to estimate B_1 as:

$$S_y^2 = k_2.B_{1,y}.e^{-g/4}.e^{\delta_y} \tag{5.8}$$

Where S_y^2 is the CGFS survey index for the year y, k_2 the CGFS survey catchability and δ_y is the observation error for the year y. Abundance indices derived from commercial trawling were also fitted. Assuming that the catch occurs as a pulse in the middle of the year, the abundance indices are modelled based on the mean biomass in the fishing season. The UK standardized LPUE (U_y^{uk}) can thus be modelled by the following equation:

$$U_y^{uk} = \frac{1}{2}q_{uk}.[B_1.e^{-g/4} + (B_1.e^{-g/2} - C'_{1+,y}).e^{-g/4}] \tag{5.9}$$

where q_{uk} is the catchability of the UK fleet. French otter bottom trawlers exploit cuttlefish resource all over the year and its standardised abundance index (U_y^{fr}) can thus be modelled by the following:

$$U_y^{fr} = \frac{1}{2}q_{fr}.[B_1 + (B_1.e^{-g/2} - C_{1+,y}).e^{-g/2}] \tag{5.10}$$

The model is finally fitted by minimizing the Sum of Squares Residuals (SSR) as:

$$SSR = \sum_{y=1992}^{y=2008} Ln\left(\frac{S_y^1}{\hat{S}_y^1}\right)^2 + \sum_{y=1992}^{y=2008} Ln\left(\frac{S_y^2}{\hat{S}_y^2}\right)^2 + \sum_{y=1992}^{y=2008} Ln\left(\frac{U_y^{uk}}{\hat{U}_y^{uk}}\right)^2 + \sum_{y=1992}^{y=2008} Ln\left(\frac{U_y^{fr}}{\hat{U}_y^{fr}}\right)^2 \tag{5.11}$$

5.2.5 Estimation of the biomass growth parameter

The parameter g is fixed externally to avoid over-parametrisation. It is composed by the natural mortality rate M (which is assumed to be known and equal to 1.2, the same assumption as Royer et al., 2006) and growth rate G (both estimated on annual basis) as

$$g = M - G \tag{5.12}$$

The g parameter is derived from the numbers at age and mean weight at age using historical data collected by the University of Caen every month in the landing site Port-en-Bessin. If $N_{a,y}$ is the number of cuttlefish at age a (a taking values from 1 to A) during the year y (y taking values from 1 to Y), and $\omega_{a,y}$ the mean weight of cuttlefish at age a during the year y, the average weight of cuttlefish at age a is computed using

$$\omega_a = \frac{1}{Y} \sum_y \omega_{a,y} \tag{5.13}$$

and G, the growth parameter, is computed as

$$G = \sum_{a=1}^{A-1} P_a.ln\left(\frac{\omega_{a+1}}{\omega_a}\right) \tag{5.14}$$

where $ln\left(\frac{\omega_{a+1}}{\omega_a}\right)$ is the log increase in weight by ages and P_a is the percentage of age a. P_a is estimated using formula

$$P_a = \frac{\sum_y N_{a,y}}{\sum_a \sum_y N_{a,y}} \tag{5.15}$$

The g parameter is the only parameter of the two stage biomass model which is defined externally. A sensitive analysis was therefore performed to understand the influence of this growth and mortality parameter on the model outputs. Model was firstly fitted using a g parameter equal to -1.01 and then by using two g parameters equal to -0.5 and -1.5.

5.2.6 Statistical error estimation using bootstrap methodology

The model variability was estimated using a bootstrap method. Using the original dataset (a table with 4 abundance indices on 17 years), a sampling with replacement on the years was carried out to re-create 1000 tables of 4 abundance index time series on 17 years. The model was then fitted using each of the 1000 generated datasets and outputs were used to compute averages and confidence intervals for the estimated biomass and abundance indices (B_1,B_2, S^1,S^2,U^{uk} and U^{fr}).

5.2.7 Indicators of the cuttlefish stock status

The biomass model provides estimates of initial and final biomass which correspond to the recruitment at the start and at the end of the second year of life. This enables to explore stock-recruitment relationships with the aim to test if recruitment overfishing occured in the studied period. In the lack of information about density-dependent phenomenons in the cuttlefish, the Hockey stick model was considered as a general framework (Barrowman and Myers, 2000; Mesnil and Rochet, 2010). The fit to the hockey stick model is considered in this exploration. It is a piecewise formulation i.e., the equation is divided into two equations describing, on the one hand, the relationship under the B$_{lim}$ and on the other hand over the B$_{lim}$ such as

$$B_1 = \begin{cases} \alpha.B_2 & if\ B_2 < B_{lim} \\ \alpha.B_{lim} & if\ B_2 > B_{lim} \end{cases} \tag{5.16}$$

If no stock-recruitment relationship is identified, B_{lim} is defined as the minimum Spawning Stock Biomass (SSB or B_2) observed on the series. The effect of the SST during the 4 quarters preceding the recruitment was also tested using a linear model.

In order to follow the fishing pressure trends, an exploitation rate (E_y) has been estimated for the year y by dividing the total landings $C_{1+,y}$ of the year y by the biomass estimated with the two stage model on January the 1st of the year y.

$$E_y = \frac{C_{1+,y}}{B_{1,y}.e^{-g/2}} \tag{5.17}$$

5.3 Results

5.3.1 Trends in cuttlefish landings

Trends in cuttlefish landings during the period 1992-2008 can be split into two sub-periods (figure 5.3), before and after 2004 when the maximum total landings were reached. During the first period (1992-2004), French and UK landings have largely increased from 4350 tons to 17400 tons. During the second period, the decreasing trend in total landings to 8650 tons was mainly due to the decrease in French landings. During the same period, UK landings remained stable.

5.3.2 Discards

Discarding observed in the framework of the OBSMER program are presented in the table 5.2. From 2004, when the validated data start, discards do not exceed 5% of the total catch. In the English Channel, cuttlefish landings can therefore be considered equivalent to the catch.

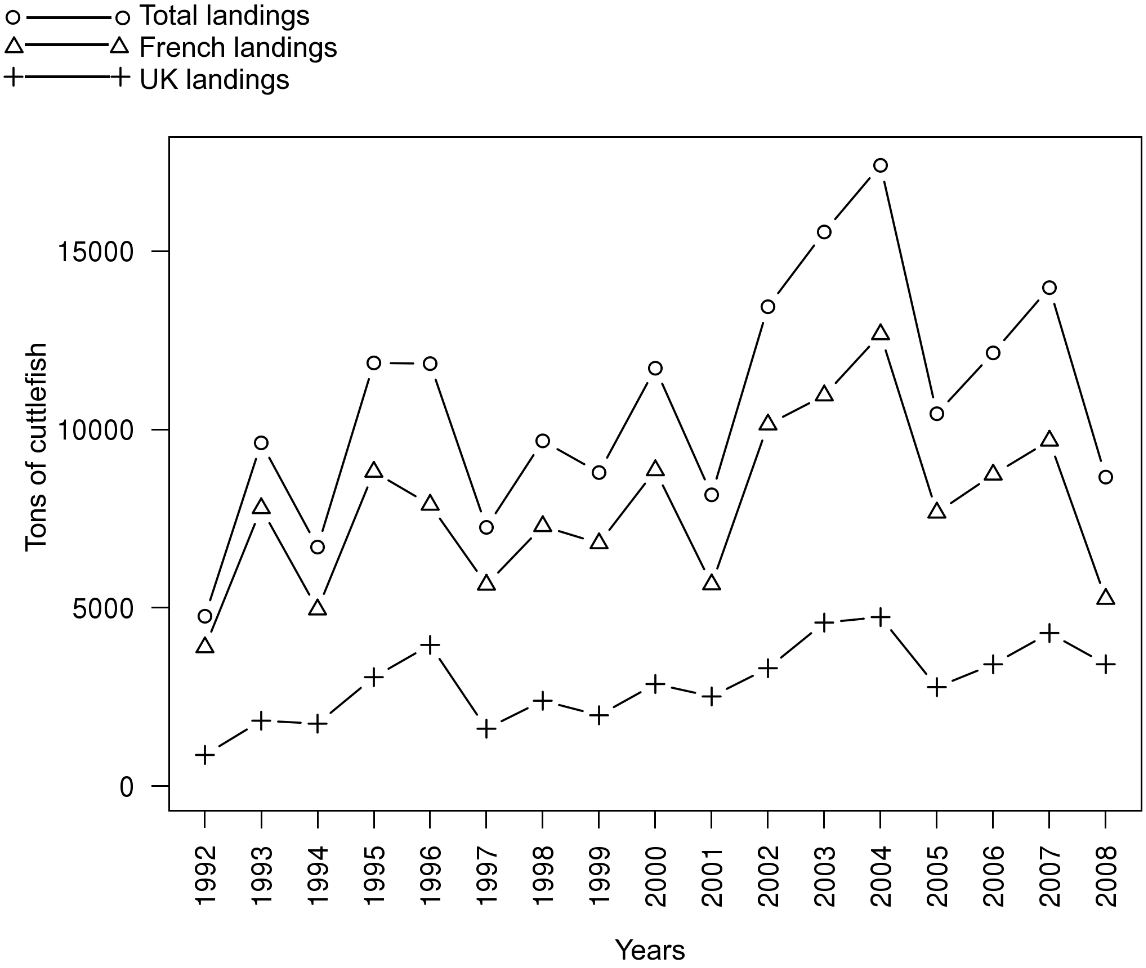

Figure 5.3: Annual total, French and UK cuttlefish landings in the English Channel from 1992 to 2008.

5.3.3 Abundance indices

The two stage biomass model fits well the survey abundance indices and commercial LPUE (residuals do not show any particular pattern) and thus seems to be suitable to estimate the English Channel cuttlefish biomass (figure 5.4). The 4 abundance indices used in this work show a high inter-annual variability in cuttlefish abundance over the whole studied period. It can also be noticed that abundance indices derived from UK data are higher than indices derived from French data. From the beginning of the time series in 1992 to 2001, abundance indices show a high inter-annual variability without any trend before dropping in 2001. From 2002 to the end of the time series in 2008, abundance indices follow a decreasing trend.

Table 5.2: Cuttlefish discards in French English Channel fishery described by the on-board observers of the OBSMER programme.

Years	Percentage discards	Kg of landings observed
2004	2%	8522
2005	4%	4187
2006	2%	4317
2007	3%	2394
2008	5%	4360

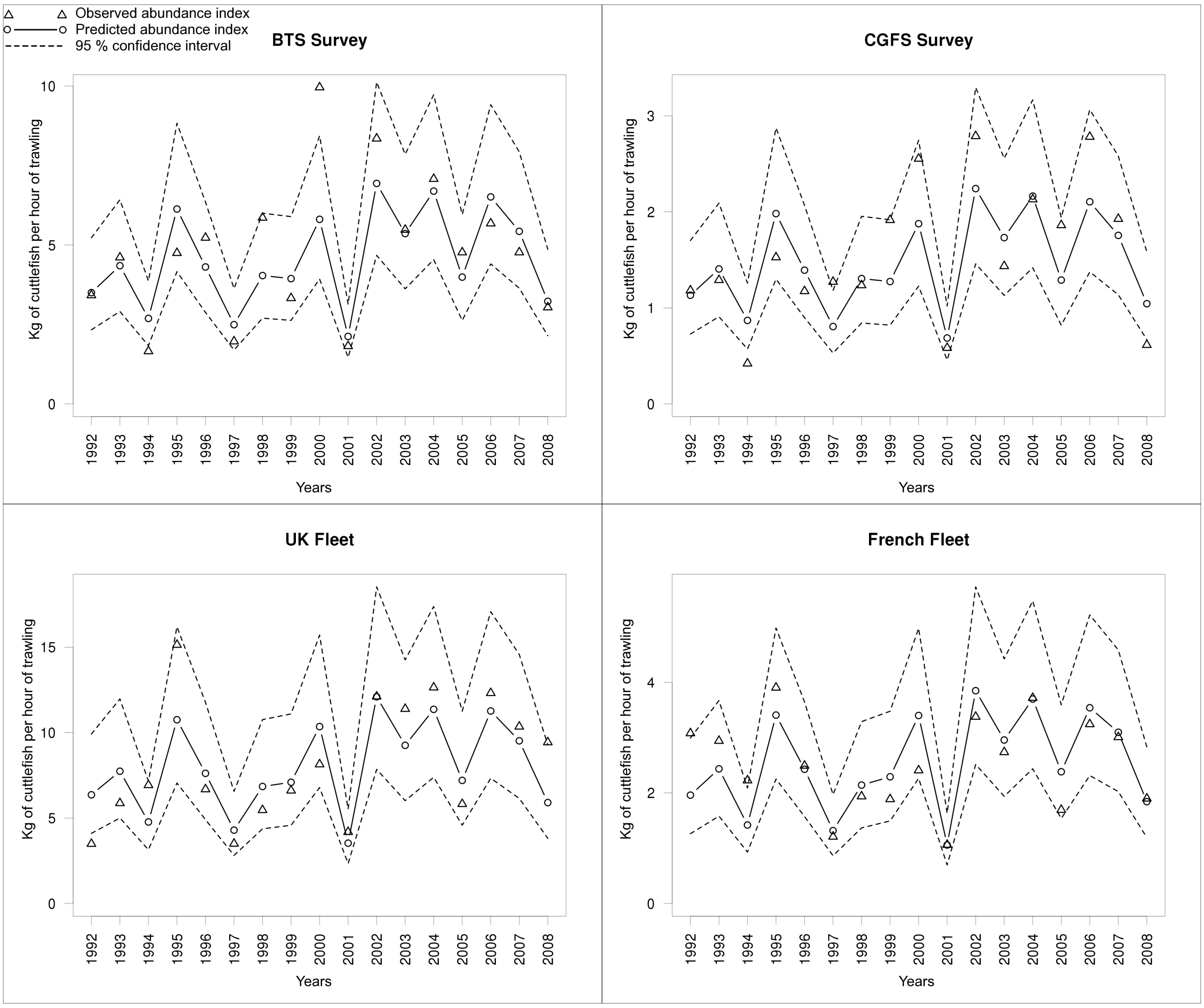

Figure 5.4: Time series of the observed and predicted abundance indices with 95% confidence interval from 1992 to 2008.

5.3.4 Spatial distribution of the cuttlefish abundance

Maps of standardized abundance indices derived from commercial fisheries are presented in the figure 5.5 by ICES rectangles, from the third quarter, when one year old juveniles are fully recruited into the fishery to the second quarter when adults take part in the reproduction. French LPUE derived from otter bottom trawl fleet are presented in the left column while UK LPUE derived from beam trawl fleet are presented in the right column. As it is observed on the abundance index time series (figure 5.4), abundance indices derived from UK fleet are higher than indices derived from the French fleet but equivalent spatial patterns are observed in the two sets of maps. Spatial variations of the cuttlefish abundance illustrate the inshore/offshore migrations described in previous studies (Boucaud-Camou and Boismery, 1991; Dunn, 1999a). Only one zone, the Norman-Breton Gulf, is characterised by high cuttlefish abundance all over the year. During the third quarter, in summer, cuttlefish abundance is more important inshore than offshore but cuttlefish are still present in the centre of the western English Channel. In autumn, during the fourth quarter when cuttlefish migrate from inshore to offshore wintering grounds, maps of LPUE show high abundances both inshore and offshore. In winter, during the first quarter, high abundances are mostly observed offshore in the ICES division VIIe in the French abundance indices while UK abundance indices highlight high abundance in the VIIe but also in the north of the VIId ICES division. Finally, in spring, during the second quarter when spring migration to inshore grounds occurs for the reproduction period, high abundances are observed inshore.

5.3.5 Biomass trends

Estimated cuttlefish biomasses at the recruitment and at the end of the life cycle during the spawning season are presented on the figure 5.6. The biomass trajectory, as estimated by the model, fluctuates widely without trend between 1992 and 2001 when the lowest biomass was estimated. A declining trend in biomass is observed between 2002 and 2008.

5.3.6 Catchabilities

Survey and commercial estimated catchabilities presented in the table 5.3 highlight that UK catchabilities (BTS survey and UK beam trawl fishery) are between 3 and 4 times higher than French catchabilities (CGFS survey and French otter bottom trawl fishery).

Table 5.3: Survey and commercial fleet catchabilites.

Survey or fleet	Catchability	95%Confidence interval
BTS	$29.71.10^{-5}$	$23.57.10^{-5}$; $37.10.10^{-5}$
CGFS	$7.47.10^{-5}$	$5.72.10^{-5}$; $9.38.10^{-5}$
UK Fleet	$35.90.10^{-5}$	$28.30.10^{-5}$; $45.75.10^{-5}$
French Fleet	$11.73.10^{-5}$	$9.55.10^{-5}$; $14.21.10^{-5}$

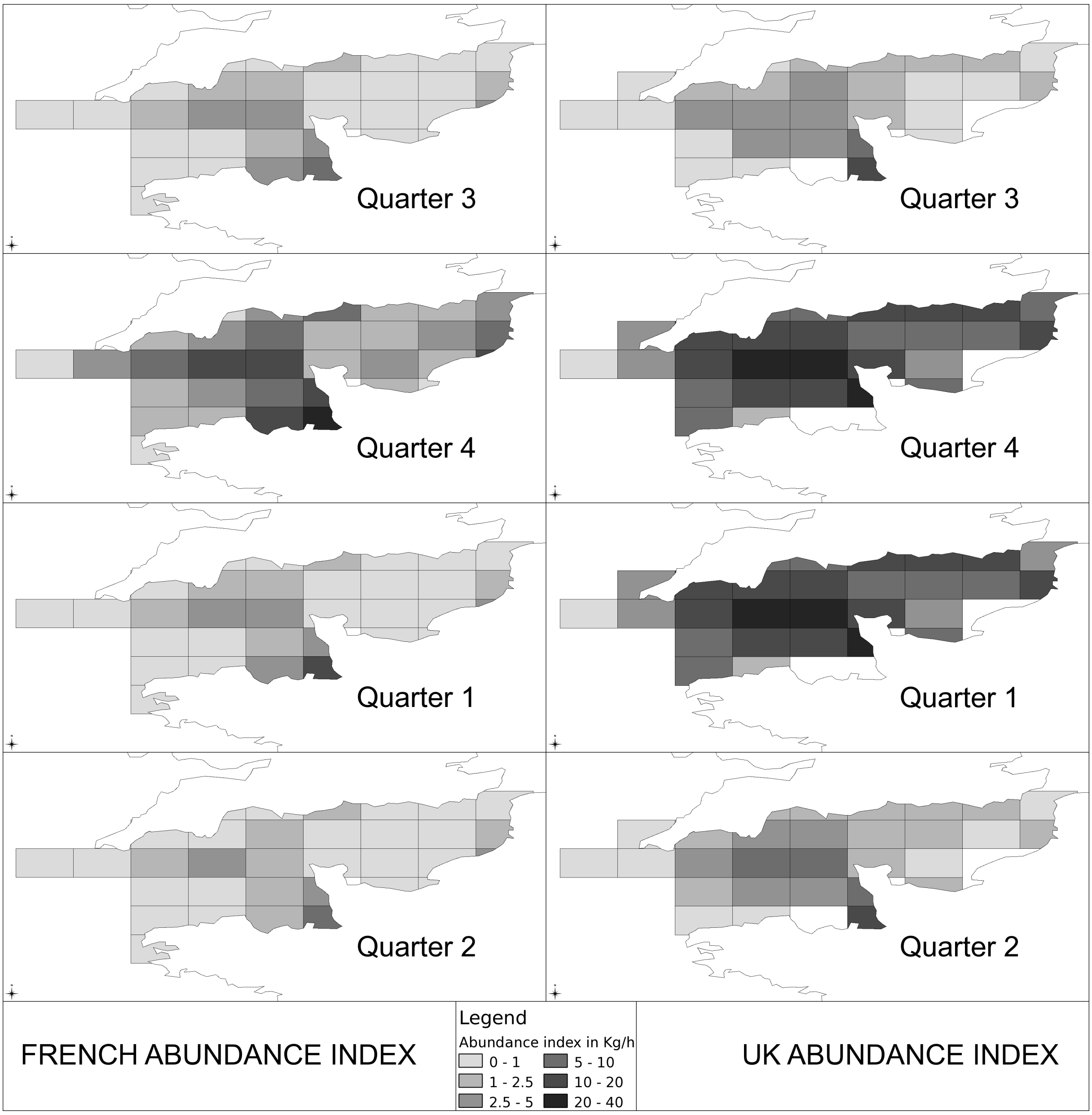

Figure 5.5: Spatial distribution of the cuttlefish abundance per ICES rectangle and per quarter computed with the French and UK LPUEs.

5.3.7 Sensitivity analysis

Results of the sensitivity analysis performed on the g parameter are presented in the table 5.4. On the one hand, they highlight that modifications of the g parameter have no consequences on the estimated recruitment (B_1) and catchabilities estimations. On the other hand, variations of the g parameter have some limited consequences on the biomass estimated in January which is used to estimate the exploitation rate and more important consequences on the estimated SSB (B_2).

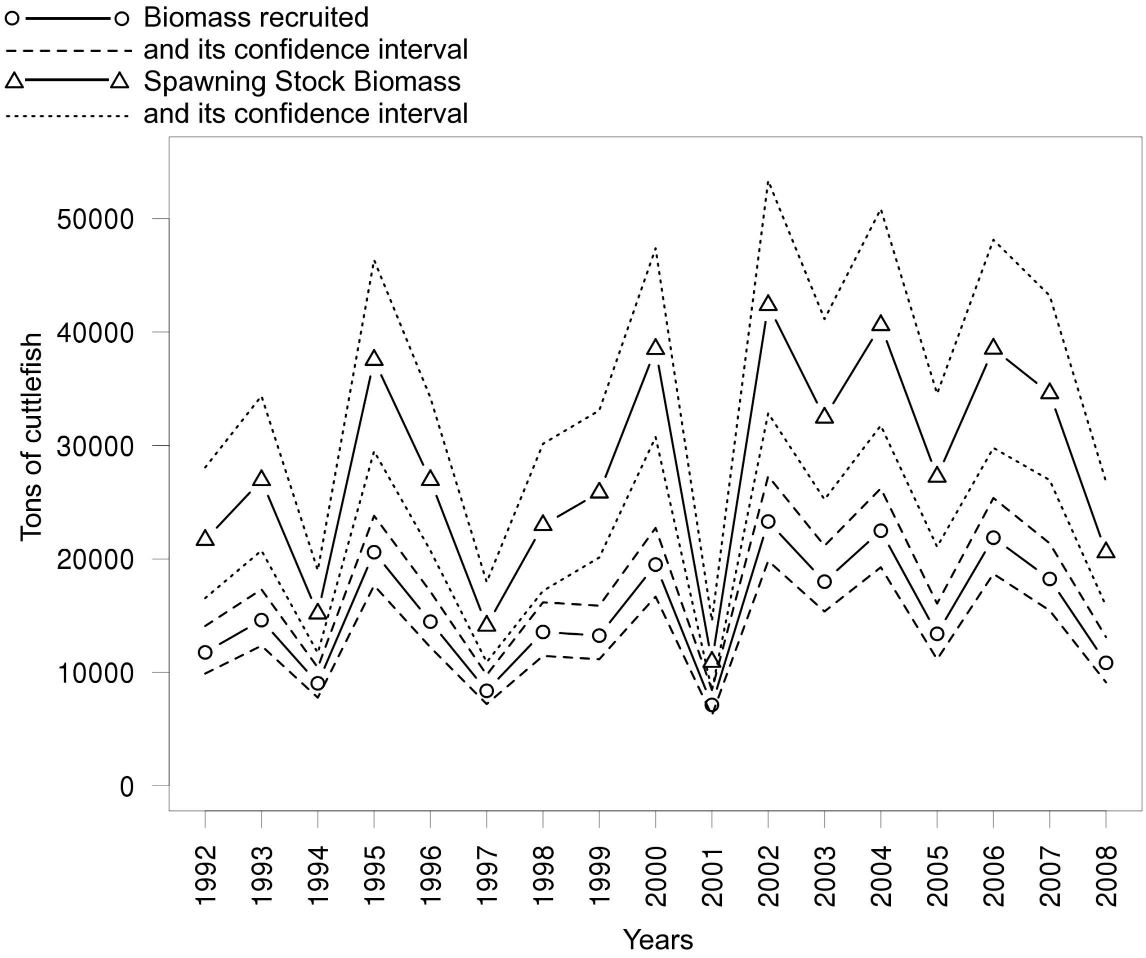

Figure 5.6: Temporal trends in biomass recruited (B_1, solid line with circles) and SSB (B_2, solid line with triangle) with their 95% confidence intervals (dashed lines).

5.3.8 Indicators of the fishing impact on the cuttlefish stock

Stock and recruitment:

In the case of the English Channel cuttlefish, we did not observe data points in the density-independent (left) part of the graph (figure 5.7). Lower SSB (B_2) are not followed by lower recruitment (B_1) the following year. We have therefore estimated an average recruitment of 15,300 tons when SSB ranges between a minimum of 11,000 tons and a maximum of 43,000 tons. The minimum estimated SSB (11,000 tons) is proposed as B_{lim} for English Channel cuttlefish based on the precautionary principle. A significant positive correlation has been identified between the SST during third quarter (summer) of the year before the recruitment and the estimated B_1. However, no correlation has been identified with the SST during the 3 other quarters before the recruitment.

Exploitation rate:

The time series of the exploitation rate computed (figure 5.8) does not highlight any significant trend during the study period. With the exception of 2001, the exploitation

Table 5.4: Percentage of variation of the outputs for a variation of 50% of g.

Output	g=-0.5	g=-1.5
B_1	$< 1\%$	$< 1\%$
Catchability	$< 1\%$	$< 1\%$
B in January	-22.8%	+28%
B_2	-49.3%	+81%

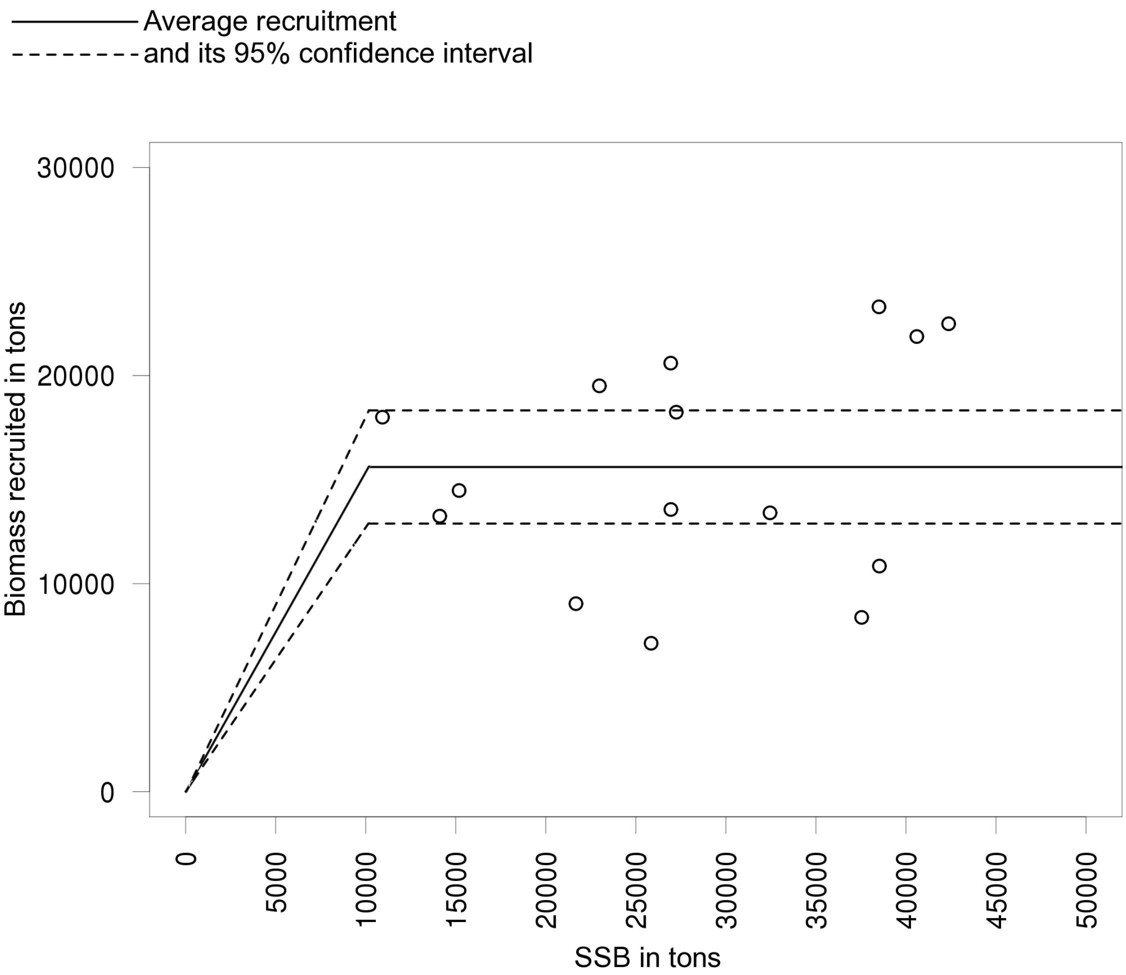

Figure 5.7: Hockey stick stock-recruitment relationship with the average annual recruitment (solid line) and its 95% confidence interval (dashed lines).

rate varies between 26% and 39% with an average at 33%. In 2001, the exploitation rate reached a maximum of 44%. It is worth noting that the peak in exploitation rate is followed (taking into account time lag) by an average-to high recruitment. Consequences in using different g values impacts the level of exploitation rate but does not impact the non signficant trend observed with the base g value (-1.01).

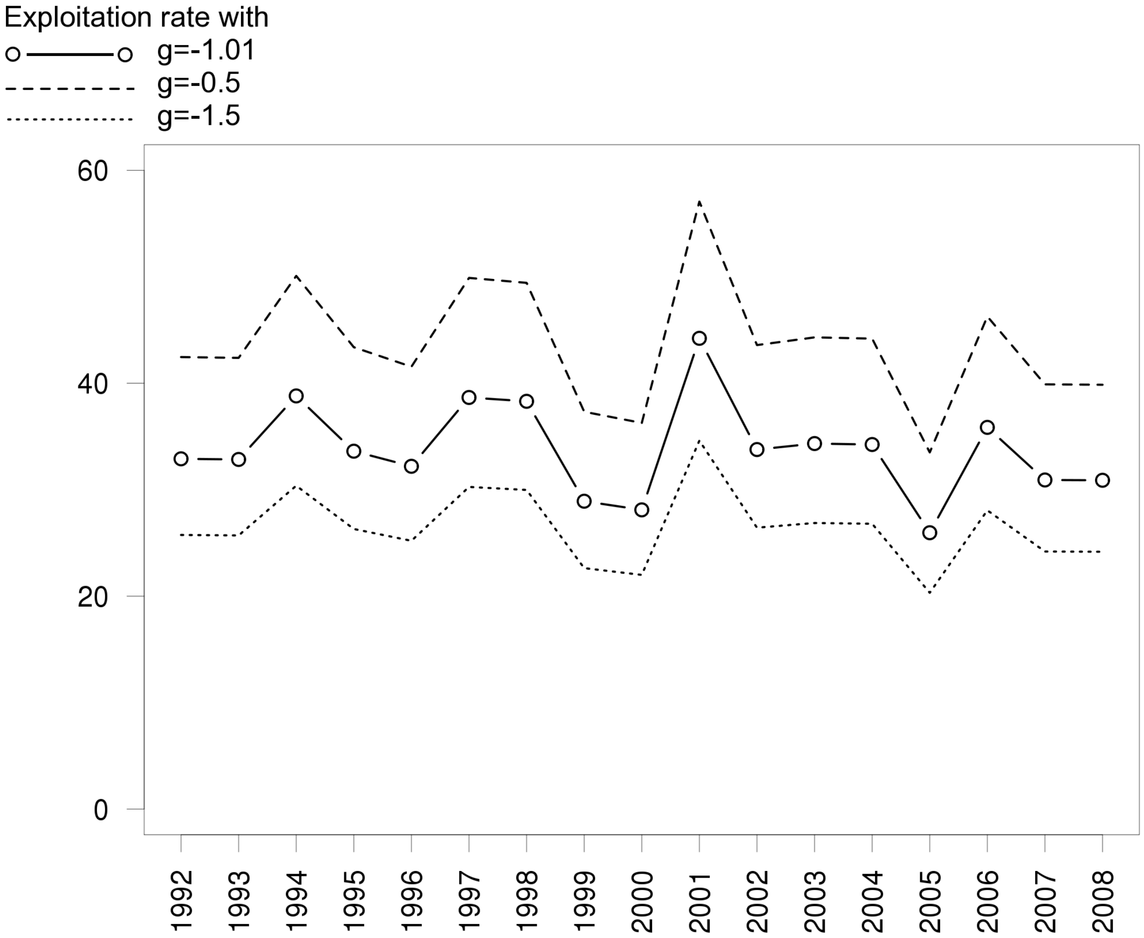

Figure 5.8: Temporal trends in exploitation rate of the cuttlefish resource from 1992 to 2008 for the model base case (g=-1.01) and two sensitivity tests, g=-0.5 and g=-1.5.

5.4 Discussion

The two stage biomass model developed here enables the assessment of the English Channel cuttlefish stock over a 17 year period while Royer et al. (2006) based their modelling over a 7 year period. The model is based on a simplified description of life-cycle and exploitation which was also the case of the depletion models (Pierce and Guerra, 1994; Young et al., 2004; Dunn, 1999b). The biomass model may be less realistic than monthly VPA (Royer et al., 2006) but is far less data demanding and could be updated routinely. This work has highlighted that cuttlefish biomass shows a high inter-annual variability, a common feature in cephalopod resources (Boletzky, 1983; Boumaaz and Dridi, 2002; Boyle and Rodhouse, 2005). The beginning of the studied period is characterised by a stable trend in abundance while the end of the period shows a decreasing trend. The maximum and minimum abundances observed in 2000 and 2001 were consistent with the results provided by the age structured model developed by Royer et al. (2006). Further comparisons of the two stage biomass results with the work of Royer et al. (2006) are not easy because VPA uses numbers at age. Despite the negative trend in observed and predicted abundances, no stock-recruitment correlation has been identified. However, a correlation between the SST during the summer preceding the recruitment and the recruitment has been identified and suggests a key role of the first summer to insure a strong recruitment. Finally, outputs of the two stage biomass model allow estimation of the exploitation rate which could be used as a management tool if a limit exploitation rate could be identified for the stock.

Both Cefas and Ifremer surveys used in this work were developed to assess demersal species in the Eastern English Channel (ICES division VIId). Unfortunately, no survey currently exists to assess the demersal communities in the western English Channel (ICES division VIIe). In addition, these surveys were not designed so as to assess the cuttlefish stock but rather to assess demersal finfish species such as flatfish. As a consequence, the timing of the CGFS surveys (which takes place in October each year) may not be ideal to derive population abundance indices. These surveys are carried out in autumn, when cuttlefish are about to leave the eastern English Channel for the wintering migration towards the western English Channel, they are likely sensitive to the onset of migration.

Differences observed in French and UK abundance indices could have different origins for survey and commercial data. In the survey abundance indices, BTS and CGFS occur in two different seasons. BTS is carried out every July after the reproduction period when one year old specimens are inshore for feeding. CGFS survey is carried out in October, during the migration season of the cuttlefish. Indeed, in October, the decrease of inshore SST triggers cuttlefish movements towards deeper and more western offshore wintering grounds (Wang et al., 2003). In addition, CGFS survey always starts in East English Channel and finishes in the centre, one month later. Cuttlefish caught during this period could thus be the latecomers which still have not left summer grounds. Differences in LPUE were also observed between UK and French bottom trawl fleets. These fleets catch the large majority of the cuttlefish landings in the English Channel and do not have the same behaviour. UK beam trawl fleet exploits mainly the western English Channel where the cuttlefish concentrate in winter, this is also the reason why equation 9 models UK abundance index from October to April, a time window that corresponds to the offshore stage in the migration cycle. On the opposite, the French otter bottom trawl fleet operates both in the western and the eastern English Channel and offshore as well as inshore. For instance trawlers based in Boulogne-sur-Mer mainly exploit the eastern English Channel where they target flatfish, seabass (*Dicentrarcus labrax*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), stripped red mullet (*Mullus surmuletus*) and the two species of squids (*Loligo vulgaris* and *Loligo forbesii*) in winter (Carpentier et al., 2009; Portail CHARM III - Interreg IV, 2012). In this area and in winter, cuttlefish is absent. These differences in fishing fleets could explain the differences observed in average abundance indices derived from UK and French commercial fleets. However, in spite of this scaling effect, both series describe similar inter-annual variations.

Boletzky (1983) has highlighted that environmental conditions have an important impact on cuttlefish spatial distribution, abundance and recruitment. In the English Channel, water column is not stratified and SST, which is positively correlated with Sea Bottom Temperature (SBT), can be assimilated as the water column temperature. From the spatial point of view, SST drives the cuttlefish seasonal migration from inshore zones to offshore wintering grounds. From the temporal point of view, Wang et al. (2003) have highlighted a positive correlation between SST and cuttlefish abundance. During the juvenile phase, low temperatures and poor nutrition reduce growth rate and increase natural mortality (Moltschaniwskyj and Martinez, 1998). This could explain the correlation identified between SST during the first months of life and the recruitment strength estimated at one year old. In the English Channel cuttlefish stock, the beginning of the life cycle is therefore a critical period during which environmental conditions largely impact the recruitment strength.

The exploitation rate is a promising indicator to monitor the stock status. Our estimates of exploitation rate varying around 33% suggest that the stock is moderately exploited. In the English Channel cuttlefish stock, the apparent lack of stock recruitment-relationship and the absence of trend in exploitation rate suggest that the fishing impact is not predominant on the renewal of this resource. Year 2001 is the only year when the exploitation rate reaches 44%, but this high exploitation rate did not seem to have short term consequences on the recruitment. Equivalent level of exploitation rates (several years over 40%) were also experienced on the Bay of Biscay anchovy without any short term consequences but a dramatic drop was observed on the long term, in 2005 (Anonymous, 2008). In the Falkland Islands, *Loligo gahi* and *Illex argentinus* supported an escapement ratio (number of animals escaped from the fishery over number of total animals which should have survived without fishing activity) above 40% (which could be considered as an exploitation rate of a maximum of 60% of the cohort; Basson et al., 1996; Agnew et al., 1998) in a series of years before two important drops in 2004 and 2010 (FAO, 2012a). By maintaining an exploitation rate below 40%, the English Channel cuttlefish resource could be considered as not showing evidence of overexploitation and seems to be fully exploited. The two stage biomass model and its exploitation rate presented here gives a global status of the cuttlefish stock. In order to better understand the stock and exploitation dynamics, further works should explore the spatial and the métiers interactions like Royer et al. (2006) did.

In European waters, finfish resources, which are generally long lifespan species, are usually managed using a Total Allowable Catch (TAC). However, the English Channel cuttlefish is a short lifespan species and, therefore, the biomass consists largely of the recruits. In addition, recruitment strength and abundance are highly variable and presumably largely influenced by the environmental conditions which are difficult to predict

(Pierce et al., 2008). As suggested by Basson et al. (1996) for *Loligo gahi* in the Falkland Islands, the best way to manage English Channel cuttlefish stock resources is most likely the control of fishing effort during the fishing season rather than by means of a TAC if this has to be agreed at the start of the calendar year.

This management is facilitated if reference points are available to provide a diagnostic on the state of the resource (Brooks, 2013; Mesnil, 2012). It was the strategy developed in the Falkland Islands to manage squid stocks using the proportional escapement ratio (Beddington et al., 1990; Rosenberg et al., 1990; Basson et al., 1996; Agnew et al., 1998). In the case of the English Channel cuttlefish stock, after fitting the two stage biomass model, its outputs can easily help in providing a diagnostic using an exploitation rate to assess the fishing impact on the current cohort. Except in 2001, it can be considered that an average exploitation rate of 33% is sustainable as SSB does not seem to have been impacted by the fishery. On the contrary, when the exploitation rate has reached 44% in 2001, the SSB seems to have been impacted by the fishery. Even if the 2003 recruitment does not seem to have been impacted, we do not know how the resource will be impacted on the long term if a high level of exploitation is maintained during several fishing seasons. As a precautionary principle, it is recommended to maintain the exploitation rate below 40%. Concerning reference points for management, a SSB of 11,000 tons is proposed as a limit because below that threshold, recruitment is unknown. In order to better monitor the stock dynamic, in season surveys are needed. This would help managers in taking real time management measures if the stock is endangered. Moreover, BTS and CGFS, could be used as an indicator of the stock status before the beginning of the fishing season (since BTS and CGFS abundance indices are positively correlated to French and UK LPUE (P-value<5%) and to total landings (P-value<1‰)).

In West Africa, in order to manage the octopus stock, two biological rests have been established to avoid a high fishing pressure during the reproduction period and the recruitment. These measures gave excellent results but had to be coupled with a limitation of the fishing effort to avoid the report of the fishing effort from one season to the next and seemed to have an effect on the long term (Boumaaz and Dridi, 2002; Jouffre et al., 2002). In France, an equivalent measure could be taken by cancelling the exemption from the law for the spring and summer inshore trawling (in the 3 nautical mile zone) which target spawners at the beginning of the reproduction period and juveniles few weeks after hatching.

Acknowledgement

This study was carried out within the EU funded project "CRESH" (under the Interreg IV A France-Manche-England programme). We thank the *Système d'Information Halieutique* (SIH) of the Ifremer which has provided French commercial landings, the

Cefas which has provided the UK survey data and UK commercial landings, the French Direction des Pêches Maritimes et de l'Aquaculture for granting permission for using the Onboard Observer data and the skippers who accepted observers onboard. We finally thank Etienne Rivot for the very constructive advices in the development of the model.

Chapitre 6

Etude de la contribution des nourriceries côtières au recrutement central par une approche multi-critères

Contribution of inshore nurseries to the cuttlefish (*Sepia officinalis*) recruitment using a multi-criteria approach

Michaël, Gras[1,2,*], Christelle, Caplat [1,2], Karine Grangeré [1,2], Fan, Qin[1,2], Isobel, Bloor[3], Emma, Jackson[3], Jean-Paul, Robin[1,2]

1-Université de Caen Basse-Normandie, FRE 3484 BIOMEA, Esplanade de la paix, F-14032 Caen, France
2-CNRS INEE, FRE 3484 BIOMEA, F-14032 Caen, France
3-Marine Biological Association of the United Kingdom - The Laboratory, Citadel Hill, Plymouth, Devon, PL1 2PB, United Kingdom
∗ Corresponding author : michael.gras@unicaen.fr

Ce chapitre fait l'objet d'un article scientifique qui sera soumis prochainement dans une revue scientifique à comité de lecture.

Résumé

De nombreuses espèces marines, comme les céphalopodes, réalisent des migrations entre les aires de reproduction et de nourrissage : comprendre ce comportement revêt une forte importance pour la gestion du stock. La seiche de Manche, l'un des stocks les plus importants pour les pêcheurs de Manche, migre vers le large après avoir éclos à la côte. Estimer la contribution de chaque aire de ponte à la formation du stock central exploité est important pour comprendre et suivre le recrutement de la seiche dans la pêcherie. Trois marqueurs de l'environnement côtier ont été analysés et utilisés à la fois chez les pré-recrues et chez les recrues : la composition en éléments traces, la signature isotopique et la forme des statolithes décrits par les Descripteurs Elliptiques de Fourrier (EFDs). Dans un premier temps, une MANOVA et une Analyse Discriminante Linéaire (LDA) descriptive ont été réalisées pour chercher les différences entre pré-recrues provenant de différentes aires de ponte. Dans un deuxième temps, une LDA prédictive a été réalisée pour attribuer les échantillons de recrues à une aire de ponte côtière. Ces estimations de la contribution de chaque aire de ponte à la formation du stock central souligne que les recrues se mélangent dans la partie centrale de la Manche. Les résultats mettent en évidence que l'aire de ponte de la Baie de Seine contribue moins que celle de l'ouest Cotentin et que la zone de ponte britannique de Torbay semble fournir la plus importante contribution au renouvellement du stock. Enfin, l'influence des facteurs environnementaux sur la contribution des zones de ponte côtières est discutée et les implications pour la gestion sont commentées.

Mots clés

Sepia officinalis ; Aire de ponte ; Recrutement ; Eléments traces ; Signature isotopique ; Forme de statolithe ; Analyse Discriminante Linéaire.

Abstract

Numerous marine species, such as cephalopods, perform migration between spawning and feeding areas and understanding this behaviour is of importance for the stock management. The English Channel cuttlefish, one of the most important stocks for English Channel fishermen, perform offshore migration after hatching inshore. Estimating the contribution of each spawning area to the formation of the central exploited stock is of importance to understand and monitor the cuttlefish recruitment into the fishery. Three different markers of the coastal environment were analysed in both pre-recruits and recruits: trace element composition, isotopic signature and statolith shape described using Elliptical Fourier Descriptors (EFDs). In a first step, a MANOVA and a descriptive Discriminant Linear Analysis (LDA) were performed to look for differences between pre-recruits coming from the different spawning areas. In a second step, a predictive LDA was performed to attribute sampled recruits to a coastal spawning area. These estimations of the contribution of each spawning area to the formation of the central exploited stock underline that recruits actually mix in the central part of the Channel. Results highlight that the Bay of Seine spawning area contributes less than West Cotentin and that the United Kingdom (UK) spawning ground of Torbay seems to provide a major contribution to the stock renewal. Finally, the influence of environmental factors on the contribution of coastal spawning grounds is discussed and management implications commented.

Keywords

Sepia officinalis; Spawning areas; Recruitment; Trace element; Stable isotope signature; Statolith shape; Linear Discriminant Analysis.

Présentation du chapitre 6.contribution des nurseries au recrutement[1]

Le modèle de biomasse à 2 stades présenté précédemment a permis d'estimer l'abondance de la seiche de Manche au recrutement et de mettre en évidence ses variations inter-annuelles. Comme cela a été montré dans le chapitre précédent, les conditions environnementales rencontrées pendant les premiers stades de vie influencent l'abondance au recrutement. Afin de mieux comprendre la dynamique de cette ressource, ce chapitre a donc pour objectif de quantifier la contribution des frayères/nurseries côtières connues et supposées principales au recrutement du stock de seiche en Manche.

De nombreuses espèces marines et les céphalopodes en particuliers sont des espèces migratrices. Comprendre l'origine spatiale des individus recrutés dans un stock est donc primordial pour la compréhension de sa dynamique. La seiche de Manche est considérée comme un stock génétiquement homogène, ses migrations hauturières et côtières sont principalement provoquées par les conditions environnementales. L'éclosion a lieu en zone côtière et la seiche est partiellement recrutée après sa première migration hauturière. Différentes méthodes de suivi des migrations existent, dans ce travail le choix a été fait d'utiliser des marqueurs influencés par les conditions environnementales rencontrées par les juvéniles dans les différentes frayères : la composition en éléments traces, la signature isotopique et la forme des statolithes. En effet, la seiche bio-accumule les métaux dont la concentration varie en fonction des écosystèmes. Les différents écosystèmes étudiés présentent des compositions en proies différentes qui influencent la signature isotopique du manteau. Les conditions variables en fonction des nurseries influencent enfin la forme des statolithes.

Les pré-recrues ont été prélevées par des pêches expérimentales dans 3 frayères/nurseries côtières de la Manche (Torbay, Ouest Cotentin et Baie de Seine) caractérisées par des conditions biotiques et abiotiques différentes. Des recrues ont également été échantillonnées au débarquement des chalutiers de fond britanniques et français. Un total de 18 éléments traces ont été dosés sur les pré-recrues et les recrues. Les signatures isotopiques ont été déterminées grâce au δ13C et au δ15N. Enfin les statolithes ont été photographiés pour réaliser une décomposition de leurs contours en ellipses de Fourrier. Ces résultats ont ensuite été traités à l'aide d'une MANOVA pour mettre en évidence les différences entre pré-recrues provenant des différentes nurseries étudiées puis par une Analyse Discriminante Linéaire (LDA) pour décrire les différences entre pré-recrues sur un plan factoriel et estimer les probabilités d'origine des recrues.

Les MANOVA réalisées sur les 3 expériences montrent que les pré-recrues d'origines différentes présentent des compositions en éléments traces, des signatures isotopiques et des formes de statolithes significativement différentes. Les résultats montrent que le

---

[1] Les références bibliographiques se trouvent dans le corps du texte de ce chapitre

stock de seiche recruté est constitué d'un mélange d'individus provenant de différentes frayères/nurseries côtières. D'après les résultats obtenus, peu de recrues présentent des similitudes avec les pré-recrues de la Baie de Seine en 2010 alors qu'aucune recrue ne présente de similitudes avec les pré-recrues de Baie de Seine en 2011-2012. En 2010 et en 2011-2012 peu de recrues présentent des similitudes avec les pré-recrues prélevées dans l'Ouest Cotentin. Un pourcentage plus important de recrues présentent des similitudes avec les pré-recrues de Torbay. Enfin, un pourcentage important de recrues ont une origine indéterminée.

Différents facteurs peuvent intervenir dans la survie des juvéniles en zone côtière parmi lesquels l'abondance des reproducteurs, la température environnementale, la salinité du milieu, la pollution, la pêche côtière ciblant les juvéniles. Afin d'approfondir la connaissance sur les migrations des seiches, l'utilisation de l'abrasion laser sur des statolithes polis permettrait de mieux comprendre les conditions environnementales rencontrées par les individus au cours de leur vie. Enfin, la forme des statolithes pourrait également être décrite en 3 dimensions alors qu'elle n'est décrite ici qu'en 2 dimensions.

6.1 Introduction

Numerous marine species perform passive or active migrations during their whole life cycle. These movements are generally driven by environmental parameters which vary both spatially and temporarily. Migrations are thus the way for the species to find the suitable habitat for each stage of their life cycle (Metcalf et al., 2002). The bulk of cephalopods have generally a short life cycle and performs migrations between breeding and feeding areas (Boyle and Rodhouse, 2005). Highlighting the spatial origin of specimens recruited in a stock is of importance for the understanding of the population dynamic and, when this population is exploited, for its management (Semmens et al., 2007).

The English Channel common cuttlefish (*Sepia officinalis*) is the most important cephalopod stock in the N-E Atlantic (Pierce et al., 2010) and is shared between French and United Kingdom (UK) fishermen. It is one of the three main demersal resources exploited in the English Channel both in term of landings (11,000 tons landed annually in the 2000 decade) and income (€20M of annual turnover for both French and UK fishermen in the 2000 decade; Portail CHARM III - Interreg IV, 2012). Cuttlefish is exploited by offshore and inshore métiers (offshore and inshore trawling respectively and trapping) according to its life cycle (Royer et al., 2006).

The English Channel cuttlefish is considered as a single stock based on population genetic studies (Shaw, personal communication). It is a migratory Sepiidae performing alternatively inshore and offshore migrations mainly driven by the environmental temperatures (Richard, 1971; Wang et al., 2003). Cuttlefish is a semelparous species, after growing and maturing during their life cycle, adults generally take part in the reproduction at the age of 2 years old every spring in several spawning/nursery grounds which are identified on both French and UK coasts (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991; Dunn, 1999a). After hatching at the end of spring, juveniles live in inshore nursery areas until their offshore migration in autumn to reach wintering grounds. Wintering grounds, in the western central English Channel, offer suitable living conditions until next spring. Cuttlefish are partially recruited when they migrate offshore and become available to the trawl fishery. In relation to commercial trawl mesh size, cohorts are considered fully recruited at one year old (average size, 12 cm Dorsal Mantle Length, DML; Royer et al., 2006).

The English Channel cuttlefish migration patterns (figure 6.1) was described by different authors using tagging methods (Boucaud-Camou and Boismery, 1991) or fishery data (Dunn, 1999a) but the contribution of different inshore spawning/nursery grounds in the formation of the central stock has not been established at the moment. Several methodologies can be used to estimate the contribution of inshore grounds, including tagging (Metcalf et al., 2002) and statistical analysis of fishery independent data (Riou et al., 2001; Le Pape et al., 2003). In this work, markers influenced by the environmental conditions have been chosen to highlight the spatial origin of recruited cuttlefish.

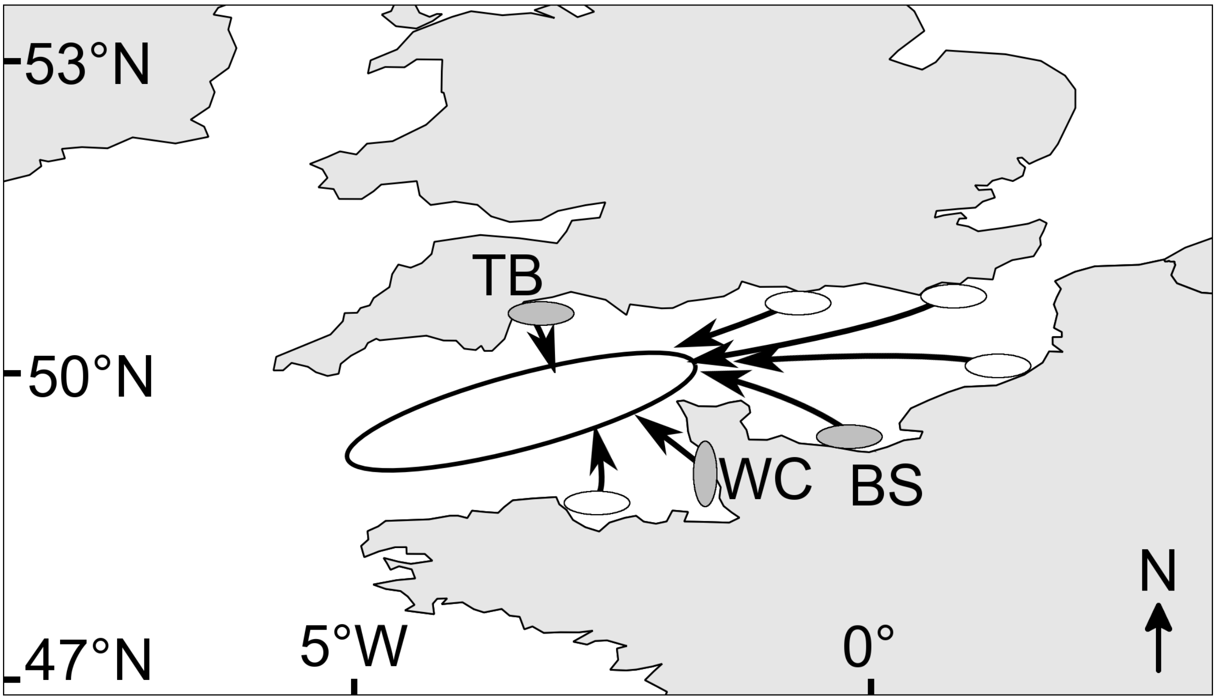

Figure 6.1: English Channel with the different known spawning areas and the three spawning/nursery grounds studied in this work. Bay of Seine (BS), West Cotentin (WC) and Torbay (TB) spawning areas are displayed in grey and unstudied spawning areas are displayed in white. The central shaded area corresponds to the cuttlefish wintering grounds.

As mentioned by Dauvin (2012), the English Channel is not an homogeneous ecosystem and each part has its own particularities. Cuttlefish spawning zones described (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Challier, 2005) are distributed from Devon to Kent coast on the UK side and from Brittany Bays to the Bay of Somme on the French coast. Distances between these coastal areas and differences in continental or anthropogenic inputs suggest that each one represent a particular environment that may influence cuttlefish juveniles. In this study, site specific influences are sought using three different markers of the environment: trace element composition, stable isotope signatures and statolith shape.

Despite its short life cycle, cuttlefish is known to bio-accumulate a list of metals in its tissues (Decleir and Vlaeminck, 1978). Trace elements have been measured in different tissues of cuttlefish sampled in the English Channel and highlight the role of different organs in the bio-accumulation (Miramand et al., 1991; Miramand and Bentley, 1992; Bustamante et al., 2002). Some of the trace elements are known to have a metabolic function (Cu, Fe, Mn, Zn) while the other ones have no known function in the metabolism and can be considered as pollutants (Ag, Cd, Co, Cr, Ni, Pb, V). Some of the trace elements are bio-accumulated in the digestive gland (V, Cu, Fe, Zn) and the other ones (Ag, Cd, Co, Cr, Mn, Ni and Pb) are bio-accumulated in the rest of the body except in the cuttlebone which presents very low concentrations in trace elements (Miramand et al., 2006). The trace element composition of a cuttlefish can thus be characteristic of each spawning area.

Stable isotopes are a useful tool to assess changes in organic matter pathways in coastal ecosystems in response to changes in environmental conditions (Fry, 1999). Stable carbon and nitrogen isotopes in animal tissues are commonly used to study trophic ecology because consumers feed on a combination of food resources whose own isotopic ratios vary in space and over time (Post, 2002). In nursery grounds, juvenile cuttlefish of each spawning area have a particular diet according to the preys available in their environment (Grangeré, personal communication). Stable isotopes can thus be used as markers of the nursery environment in order to identify the recruit origin.

The environment could influence the shape of the cuttlefish statoliths. Statoliths are paired of calcareous concretions smaller than 2 mm situated in the animal head (equivalent to the fish otoliths). They play an important role in the equilibrium of the cuttlefish and they have already been used in age estimation of juveniles since calcium settles everyday on the dome (Bettencourt and Guerra, 2001; Challier et al., 2002, 2005a). Otolith shapes are known to be sensitive to genetic and environmental factors, the latter being considered as predominant (DeVries et al., 2002; Hüssy, 2008; Capoccioni et al., 2011). In the same way as the otoliths, statoliths can therefore be used to determine the spatial origin of specimens coming from different areas and mixing after migration (Green, 2011).

The first objective of this work is to look for site-related differences between coastal juvenile cuttlefish, using three markers (trace element composition, isotopic signature and statolith shape). The second objective is to analyse offshore recruits in a similar way in order to compare them to the juveniles and to deduce the origin of recruits and the potential contribution of inshore spawning areas to the renewal of the stock.

6.2 Material and methods

6.2.1 Description of the studied spawning zones

Pre-recruits were collected in 3 different spawning zones both on the French (Bay of Seine and West Cotentin) and UK (Torbay) coasts (figure 6.1), since they are assumed to be the three most important spawning/nursery areas for the English Channel cuttlefish (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Challier, 2005).

The Bay of Seine (BS), situated in the East English Channel, is largely influenced by the Seine Estuary which carries along numerous pollutants due to the high industrial activity (Dauvin, 2008), the most important being the Cd (Chiffoleau et al., 1994). The freshwater panache created by the Seine River influences the eastern part and extends eastward along the French coast. In spite of a high level of pollution, the benthic biomass is very high, due to the absence of anoxic conditions favouring the benthic community (Dauvin, 2008).

The West Cotentin (WC) zone, in the western English Channel, is a long shore oriented North-South and facing westerly winds. Habitat is characterised by a megatidal environment (14 m). Freshwater inputs are weak and the ecosystem is largely influenced by hydrodynamic conditions. Anthropic activities are well developed with important oyster and mussel farming (Grangeré et al., 2012) as well as fishing activities (inshore trawling and trapping; Pierce et al., 2010).

Finally, Torbay (TB), in the West English Channel, situated in the Devon county in the S-W UK coast is a small bay characterized by large seagrass beds (Hirst and Attrill, 2008) and no freshwater input.

These three coastal sites offer a range of environmental conditions and their influence on early stages of cuttlefish is sought using the three studied markers

6.2.2 Sample collection

Sampling was carried out in two steps, a first one before the offshore migration to collect pre-recruits and a second one when cuttlefish are recruited in the exploited stock. The first sampling was carried out inshore using experimental trawl (mesh size of 20 mm) in the 3 spawning/nursery areas described above by experimental fishing operations carried out inshore from Ouistreham harbour (BS), Granville (WC) and Brixham (TB) in autumn 2010-2011. The second sampling was collected at commercial trawlers landing sites (Brixham and Cherbourg) and consisted of recruits of the same annual cohort fished using commercial trawl (mesh size between 80 and 100 mm) in the centre of the Channel (ICES rectangles 28E7 and 29E7) in December 2010 and January 2012.

6.2.3 Measurement of the trace element composition

Individual cuttlefish were transferred to a polyethylene bottle and were stored in a freezer (-20°C). Frozen samples were dried with a freeze-drier. Dried animals were then digested with 10 mL nitric acid (69% VWR - AnalR NORMAPUR) in a microwave digestion system (Berghof, MWS-2), under controlled phases of temperature (205°C) and oven power (1000 W). The digested solution was transferred to labeled bottles adding ultrapure water to 50 mL final volume and stored at 4°C for metal analyses. Ten cuttlefish were analysed for each sampling operation.

The total concentration of 18 trace elements (Al, As, Ba, Cd, Co, Cr, Cu, Fe, Mg, Mn, Mo, Ni, P, Pb, S, Si, Ti, Zn) was measured in each sample by Induced Coupled Plasma – Atomic Emission Spectroscopy (Varian MTX). To assess the quality of the obtained data, standard reference materials (SRM NIST-1566b oyster tissue and SRM NIST-Mussel 2976 from National Institute of Standards and Technology, Gaithersburg, MD, USA) were periodically analysed with sample series. The differences between measured and certified values for the metal concentrations were given ±9% for Cd, Co, Cu, Fe, Mg, Mn and respectively of ±50% for Al and As measured in SRM NIST-1566b oyster tissue. The differences between measured and certified values for the metal concentrations were ±10% for As, Cd, Co, Cr, Fe, Ni, Zn and ±22% for Al, Mg, Mn, Pb measured in SRM NIST-Mussel 2976.

Methodology described above enables the measurement of 18 trace elements on 53 cuttlefish sampled in autumn 2010 and 39 cuttlefish sampled in 2011-2012 (the number of pre-recruits per spawning area and number of recruits studied is detailed in the table 6.1). Results were compiled in two matrices (one for each year) of 18 columns (one per trace element) and 48 and 39 rows (one per specimen studied) respectively for the first data collection in autumn 2010 and the second data collection in 2011-2012.

Table 6.1: Number of cuttlefish pre-recruits collected in the three spawning areas studied (BS, WC and TB) and number of recruits collected in ICES rectangles 28E7 and 29E7 in autumn 2010 (left number) and in Autumn 2011-Winter 2012 (right number) to analyse the trace element composition, the stable isotope signature and the statolith shapes. In the case of the statolith shape, analysis was only performed in autumn 2010.

	Sampling sites			
Analysis performed	BS	WC	TB	Recruits
Trace element composition	10/10	9/9	15/10	19/10
Stable isotope signature	10/12	10/12	10/10	12/10
Left statolith	34	76	36	13
Right statolith	36	74	33	13

6.2.4 Stable isotope analysis

Individual cuttlefish (recruits and pre-recruits) were dissected in order to separate organs. Isotopic analysis of δ13C and δ15N were performed on the mantle. Cuttlefish samples were freeze dried and pulverized. Then 1 mg (± 0.1 mg) of each sample was weighed with a micro-analytical balance (Mettler Toledo MX5) and placed in tin capsules (3.5 x 5 mm Sercon). Analyses were performed using an elemental analyser (Eurovector) for particulate C (%C) and N (%N) and an isotope ratio mass spectrometer (IRMS GV Isoprime instrument) for C and N isotopes. The methodology for isotopic analysis will be fully described in Grangeré et al. (in prep.). Results obtained with the isotopic signature methodology enable the creation of two matrices (one per year) of 2 columns (one for the δ13C and one for the δ15N) and 42 and 44 rows (one per specimen studied, see details per collection site in the table 6.1) respectively for the samples carried out in 2010 and 2011-2012.

6.2.5 Statolith shape analysis

In finfish stocks differences in otolith outlines described by Fourrier elliptic decomposition of digitized images is one of the most powerful techniques to discriminate fish stocks (Campana and Casselman, 1993). This technique was applied to cuttlefish statolith using the SHAPE software (Iwata, 2002) for image processing.

Left and right statoliths were extracted from sampled specimens, washed in alcohol with a ultrasonic cleaner and photographed concave face up (posterior view) with a camera mounted on a stereomicroscope. Images were stored in 24-bitmap files, a format required by the SHAPE software.

Elliptic Fourrier Descriptors (EFDs) describe a complex outline with a combination of elementary ellipses. EFDs coefficient were computed using chain coded contours as described by Kuhl and Giardina (1982).

The contour of a digitized shape can be represented as a series of x and y coordinates of ordered points from an arbitrary starting point and regularly around the shape following a clockwise tour. In this procedure, the contour between two adjacent points is linearly interpolated and the length of the linear segment between the $(i-1)^{th}$ and the i^{th} point is Δt_i. The length of the contour is therefore computed from the starting point to the p^{th} as: $\Delta t_p = \sum_{i=1}^{p} \Delta t_i$ and the perimeter is computed using $T = t_K$, where K is the total number of points around the shape. The x coordinate for the p^{th} point is $x_p = \sum_{i=1}^{p} \Delta x_i$ where Δx_i is the displacement along the x axis of the contour between the $(i-1)^{th}$ point and the i^{th} point.

The elliptic Fourier expansion of the sequences of the x coordinates gives:

$$x_p = x_{cen} + \sum_{n=1}^{\infty}(a_n cos\frac{2n\pi t_p}{T} + b_n sin\frac{2n\pi t_p}{T}) \tag{6.1}$$

where x_{cen} is the coordinate of the centre point and

$$a_n = \frac{T}{2n^2\pi^2}\sum_{p=1}^{K}\frac{\Delta x_p}{\Delta t_p}(cos\frac{2n\pi t_p}{T} - cos\frac{2n\pi t_{p-1}}{T}) \tag{6.2}$$

and

$$b_n = \frac{T}{2n^2\pi^2}\sum_{p=1}^{K}\frac{\Delta x_p}{\Delta t_p}(sin\frac{2n\pi t_p}{T} - sin\frac{2n\pi t_{p-1}}{T}) \tag{6.3}$$

The elliptic decomposition provides a harmonic series of ellipses. Ellipse number n is described with coefficients a_n and b_n for x coordinates and c_n and d_n for y coordinates (c_n and d_n are computed in the same way as a_n and b_n as described by Iwata (2002)). A shape based on n ellipses is thus computed with $4n$ EFDs coefficients.

6.2.6 Statistical analysis of site related differences in juvenile and origin of recruits

The experiments presented above give 6 matrices of data describing the pre-recruits and the recruits according to the 3 sets of variables, 18 for the trace element composition, 2 for the isotopic signature and 79 for the statolith shape analysis (the first coefficient is filled with "1" and is thus cancelled in the analysed matrix). The statistical analysis is performed in three steps. In the first one, the matrices are analysed using a MANOVA to test if significant differences exist between the pre-recruits sampled in the 3 different nurseries. In a second step, a descriptive Linear Discriminatory Analysis (LDA), part of the canonical analysis family, is performed to display, on a factorial plan, the pre-recruits to visualize their differences. Two ellipses representing the 95 and 99% confidence intervals of pre-recruits data variabilities are also displayed. In a third step, a predictive LDA performed on recruits enables their representation on the factorial plan with the pre-recruits. Recruits displayed into a distinguished ellipse are considered as coming from the spawning site represented. Recruits displayed into two intersected ellipses are attributed to a spawning site according to the highest probability estimated by the predictive LDA. Finally, recruits displayed outside the ellipses are considered as either coming from one of the 3 spawning sites studied or from another undetermined spawning site.

Finally, a table summarizing the percentage of recruits per origin is computed. For each spawning site the percentage of recruits is computed as

$$P_s = \frac{n_{s,t} + n_{s,i} + \frac{n_{s,l}+n_{s,r}}{2}}{N} \tag{6.4}$$

Where P_s is the percentage of recruits attributed to spawning site s, $n_{s,t}$ is the number of recruits attributed to the spawning site s using the trace element composition, $n_{s,i}$ is the number of recruits attributed to the spawning site s using the stable isotope signature, $n_{s,l}$ is the number of recruits attributed to the spawning site s using the left statolith, $n_{r,l}$ is the number of recruits attributed to the spawning site s using the right statolith and N is the total number of studied recruits.

6.3 Results

6.3.1 Trace element composition

The MANOVA performed on the 2 matrices describing pre-recruits using trace element composition reveal that significant differences exist between pre-recruits of the different spawning zones for the studied years (P-value=3.10^{-14} in 2010 and P-value=2.10^{-9} in 2011). These significant differences are corroborated by the descriptive LDA results displayed on the figure 6.2. In 2010, the first axis of the LDA (51% of the variance between groups) represents well the differences between BS pre-recruits and the other pre-recruits while the differences between WC and TB pre-recruits are well represented on the second axis (49% of the variance). In 2011, differences between pre-recruits of the three spawning sites are well represented on the two axis (51 and 49% of the variance represented for the first and second axis respectively). The predictive LDA performed on the recruits (table 6.2) highlight that, in 2010 and 2011, no recruits have a similar trace element composition with BS pre-recruits. A minority in 2010 and no recruits in 2011 present similarities with WC pre-recruits. Finally, for both years, an equivalent number of recruits present similarities with pre-recruits from TB and unknown spawning sites.

Table 6.2: Origin of central-offshore-recruits derived from trace elements composition.

Nursery grounds sites	2010 Recruits	2012 Recruits
BS	0	0
WC	2	0
TB	8	5
Undetermined origin	9	5

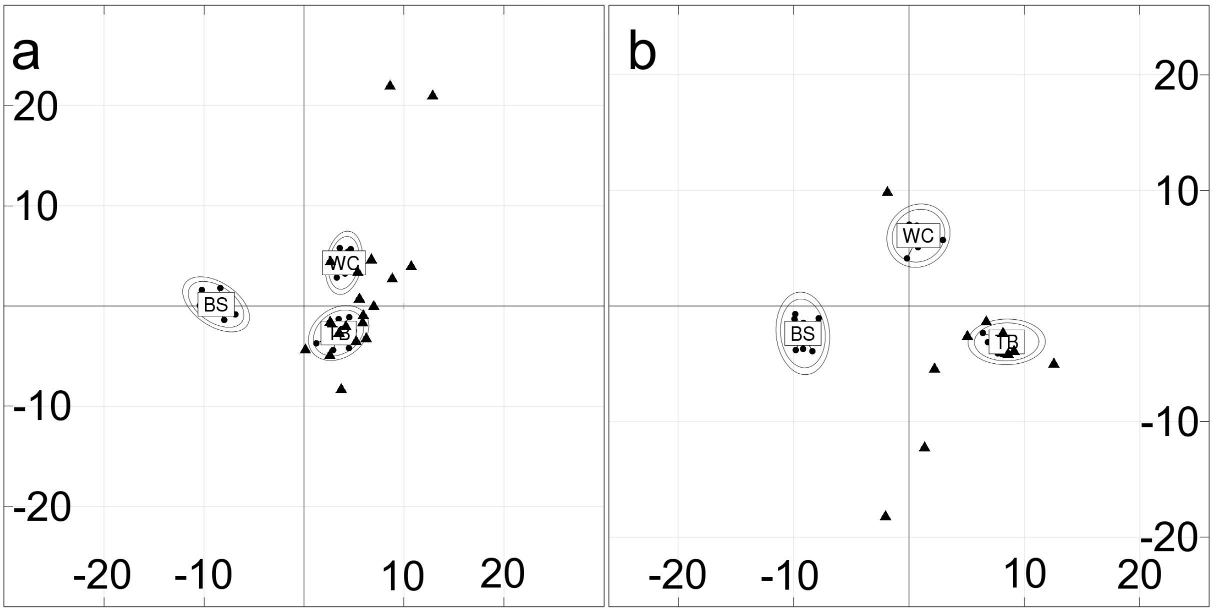

Figure 6.2: Results of the LDA performed on the pre-recruits (displayed with points) sampled in the 3 nurseries (Bay of Seine, West Cotentin and Torbay) in 2010 (left) and 2011 (right), the recruits (displayed with triangles) and characterised with the trace element composition.

6.3.2 Stable isotope signature

The MANOVA performed on the pre-recruit isotopic signatures show that pre-recruits coming from the three different nursery grounds present significant differences for both years (P-value=$3.5.10^{-10}$ in 2010 and P-value=2.10^{-16} in 2011). In 2010 and 2011, the descriptive LDA (figure 6.3) highlight on the first axis (84% and 65% of the variance represented for 2010 and 2011 respectively) the differences between BS pre-recruits on the one hand, and TB and WC pre-recruits on the other hand. A MANOVA performed between 2010 pre-recruits from TB and WC highlights no significant differences (P-value=0.15) while significant differences exist in 2011 (P-value=5.10^{-8}) and their variance is well represented on the second axis (16% and 35% of the variance represented for 2010 and 2011 respectively). The predictive LDA (table 6.3) indicates that only one recruit in 2010 and no recruit in 2011 present similarities with BS pre-recruits. For both years, a low number of recruits present similarities with WC pre-recruits. In 2010, an equivalent number of recruits present similarities with WC pre-recruits and with unknown spawning sites. In 2011, only one recruit present similarities with TB pre-recruits while a high number of recruits present similarities with unknown spawning sites.

Table 6.3: Origin of central-offshore-recruits derived from stable isotope signatures.

Nursery grounds sites	2010 Recruits	2012 Recruits
BS	1	0
WC	1	2
TB	5	1
Undetermined origin	5	7

6.3.3 Statolith shape analysis

The MANOVA performed on the matrix of EFDs coefficients show that pre-recruits coming from the three different nursery grounds present significant differences for both the left and right statoliths (P-value=$3.3.10^{-10}$ for the left statoliths and P-value=$4.8.10^{-09}$ for the right statoliths). The descriptive LDA (figure 6.4) do not highlight such clear differences as the three ellipses intersect one another and the three spawning sites are displayed regularly on the first plan. The first axis represents 53 and 55% of the variance for the left and right statolith respectively. Only one left statolith is displayed outside the ellipses suggesting that it comes from an undetermined spawning site. Similarities with pre-recruits have therefore been established based on the probabilities provided by the predictive LDA (table 6.4). A minority of recruits present similarities with BS pre-recruits while a majority present similarities with TB pre-recruits and 30% of recruits present similarities with WC pre-recruits. It must be noticed that the statolith shape

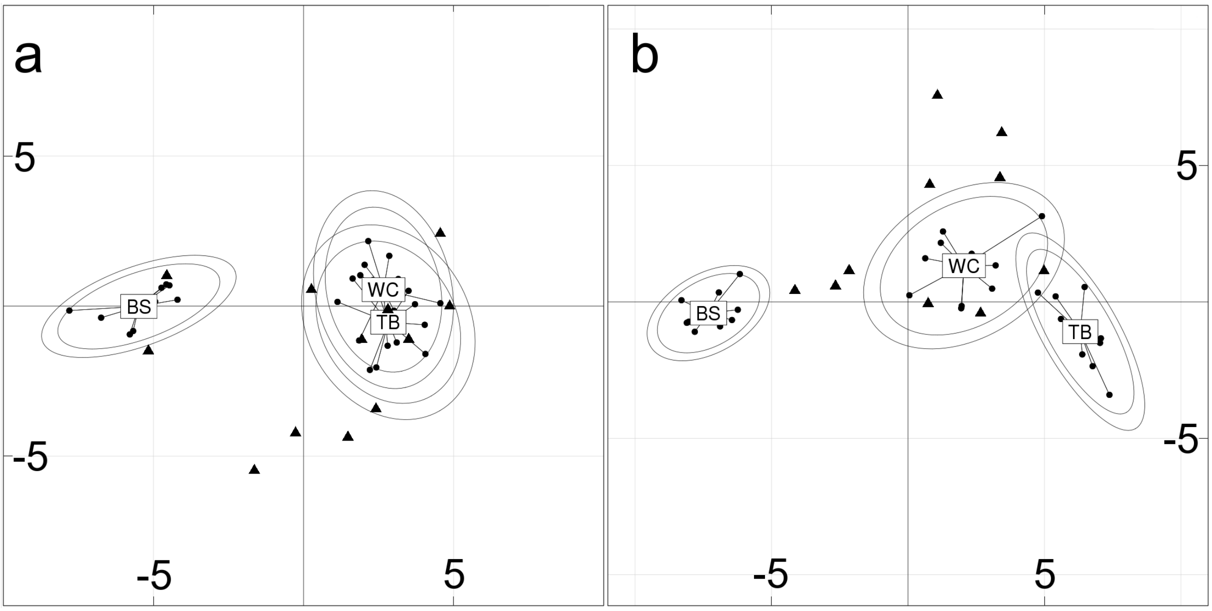

Figure 6.3: Results of the LDA performed on the pre-recruits (displayed with points) sampled in the 3 nurseries (Bay of Seine, West Cotentin and Torbay) in 2010 (left) and 2011 (right), the recruits (displayed with triangles) and characterised with the stable isotope signature.

analysis was performed on a larger sample than the previous analysis which could explain the lower variance observed.

Table 6.4: Origin of central-offshore-recruits derived from statolith shapes.

Nursery grounds sites	Left statoliths	Right statoliths
BS	1	2
WC	4	4
TB	7	7
Undermined origin	1	0

6.4 Discussion

This work is the first study describing differences among cuttlefish juveniles with a combination of 3 sets of parameters (trace element composition, stable isotope signature and statolith shape). The first objective was to look for differences between coastal areas and all techniques revealed significant differences. The samples of recruits analysed in a second step show a mixed origin whatever the technique. The three methodologies were performed on the same samples but not on the same specimens which could be a source of variability.

In marine species, recruitment depends on the Spawning Stock Biomass (SSB), its

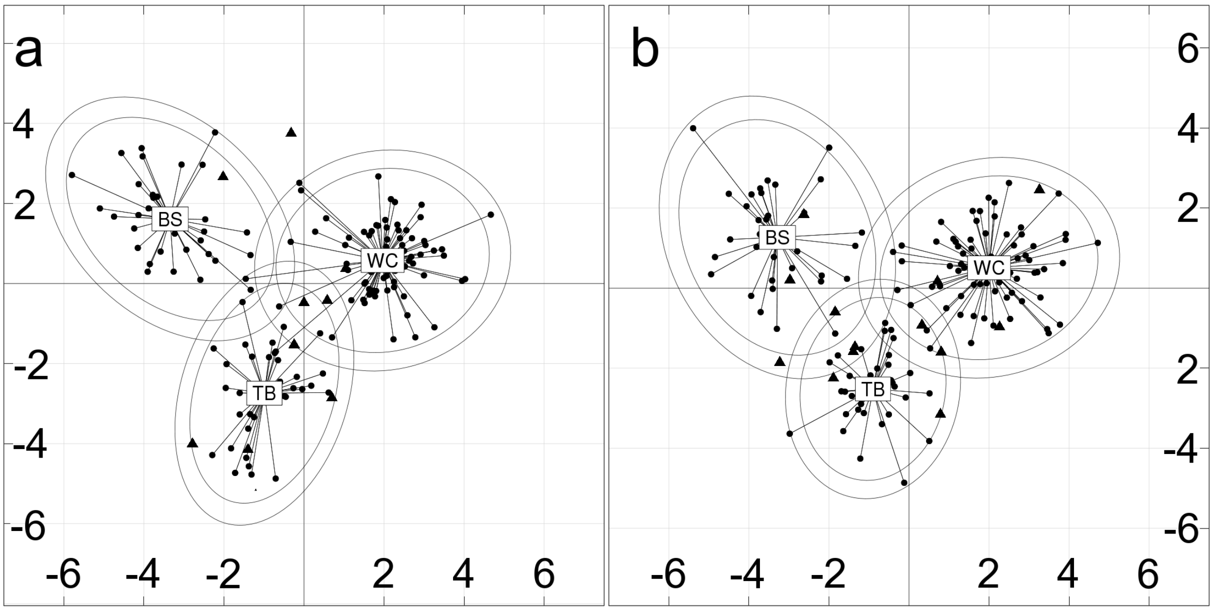

Figure 6.4: Results of the LDA performed on the pre-recruits (displayed with points) sampled in the 3 nurseries (Bay of Seine, West Cotentin and Torbay) in 2010, the recruits (displayed with triangles) and characterised with the EFDs applied to the left (left) and right (right) statoliths.

fecundity and egg abundance. Under a threshold, the recruitment is proportional to the SSB while over this threshold the recruitment generally depends on environmental conditions. However, in the English Channel cuttlefish stock, the SSB has always been estimated for the whole stock which does not enable spatial comparison in SSB between spawning grounds. Fecundity is difficult to assess (Boyle and Rodhouse, 2005) in cephalopod species and no information on English Channel cuttlefish is currently available. Egg abundances in spawning sites were estimated by performing subtidal (by scuba diving) and intertidal transects and the conclusion of the work reveals that the highest egg densities were observed in Torbay (Bloor, 2012), which could explain the highest contribution of this spawning area.

In cephalopod species, early life stages are considered as key periods for the recruitment and are sensible to various environmental parameters such as temperature, salinity, prey availability (Moltschaniwskyj and Martinez, 1998; Guerra et al., 2010) and human pressure such as pollution and fishing activities.

Temperature is a highly variable parameter in inshore waters, particularly in macrotidal inshore regime such as those observed in West Cotentin and Bay of Seine ecosystems (Grangeré et al., 2012). Temperature is the key parameter influencing the embryonic development, eggs incubating slower and juveniles hatching being larger when temperature decreases (Semmens et al., 2007). Moreover, temperature influences also the growth rate of juveniles during the weeks following the inshore hatching. Temperature can vary from one spawning/nursery ground (table 6.5) to another and juvenile growth have been found to vary geographically (Challier et al., 2005a). Size reached by the cuttlefish at the end of the summer could therefore influence their ability in surviving during the offshore migration and the first winter. Finally, the temperature influences also the cuttlefish environment, i.e. the predator and prey abundances. Temperature is thus an important parameter influencing the survival rate of cuttlefish and thus the contribution of the different spawning areas to the formation of the central stock.

Table 6.5: Sea Surface Temperatures (SST) measured in the Bay of Seine (SOMLIT), in West Cotentin (SMEL) for quarters 2, 3 and 4 for years 2010 (left) and 2011 (right) and Weymouth near Torbay (Cefas).

Nursery grounds	Q2	Q3	Q4
Bay of Seine	13.43/13.46	18.53/18.39	10.98/-
West Cotentin	13.66/15.01	18.95/18.38	10.62/12.92
Torbay	11.30/12.53	16.90/16.87	10.77/13.20

Salinity can vary from one site to another due to freshwater inputs (table 6.6). This is particularly true for the Bay of Seine and to a lesser extent in the West Cotentin areas. Lower salinities lead to a decrease in hatching rate and growth rate of juveniles (Palmegiano and D'Apote, 1983) and can influence prey availability. Freshwater inputs lead also to decreasing the visibility by increasing the turbidity. As cuttlefish is an active predator, freshwater inputs can decrease its efficiency (Hanlon and Messenger, 1996) influencing the survival rate during the juvenile phase.

Table 6.6: Salinities measured in the Bay of Seine (SOMLIT) and in West Cotentin (HYDRONOR) for quarters 2, 3 and 4 for years 2010 (left) and 2011 (right).

Nursery grounds	Q2	Q3	Q4
Bay of Seine	32.83/32.55	33.00/32.75	32.2/-
West Cotentin	35.15/34.96	35.23/35.13	34.55/34.84
Torbay	-/-	-/-	-/-

The three spawning/nursery grounds studied in this work present different levels of pollution. The Bay of Seine, largely influenced by the Seine Estuary, considered as the most polluted estuary in Europe, carries along numerous pollutants coming from the large industrial activities and urbanisation zones (Dauvin et al., 2007; Dauvin, 2008). Metals and PCBs are considered as the most important pollutants of this zone (Danis et al., 2005) and are known to have consequences both at the cell and individual levels (Kennish, 2002). These two types of pollutants are known to be bio-accumulated in the benthic community (Dauvin et al., 2007; Dauvin, 2008). Juvenile cuttlefish growing in the Bay of Seine can thus be contaminated by different ways. The metals (Ag, Cd, Co, Hg, Mn, Pb, Zn) in egg can be due to a maternal transfer (Lacoue-Labarthe et al., 2008a) or to a passive diffusion of these elements through the egg membrane (Lacoue-Labarthe et al., 2008b, 2009, 2010). Bio-accumulation of metal pollutants in the embryo could decrease the hatching rate. During the juvenile phase, invertebrate preys of the benthic community, like the brown shrimp *Crangon crangon*, among the favourite cuttlefish preys, can be also important sources of pollutants for this predator (Culshaw et al., 2002) leading to potential lower survival rates.

In France, trawling inshore (into the 3 nautical mile inshore zone) is not allowed, however an exemption from the law protecting the coastal zone allows the fishermen to trawl inshore during two periods. Fishermen are first allowed to exploit cuttlefish spawners during 6 weeks in spring and in a second period, the exploitation of juveniles is allowed during 2 weeks in August (Pierce et al., 2010). As mentioned previously (Moltschaniwskyj and Martinez, 1998; Guerra et al., 2010), early life stages are critical for the recruitment of cephalopods and the fishing mortality resulting from this exceptional fishing activity could significantly impact the recruitment of cuttlefish. On the opposite, in Torbay and all along the Lime Bay shore, inshore fishing is not allowed. This status could thus explain the high presumable contribution of this area to the formation of the central stock.

In addition, Torbay, which is known to present high abundance of seagrass beds (*Zostera marina*) and high level of biodiversity has been protected under the status of special area of conservation since August 2010. This status is favourable for the growth of the juvenile cuttlefish during the key period of the first summer. On the French coast and particularly in the Bay of Seine and in West Cotentin, no special protection areas has been implemented yet. Since June 2010, the French Marine Protected Area Agency has started a stakeholder consultation in order to implement a Marine Protected Area (MPA) in the Gulf Norman-Breton. This initiative could be favourable for the conservation and the recruitment of the English Channel cuttlefish.

The contribution of the different spawning areas is not equivalent. Biotic and abiotic parameters presented above can positively or negatively influence the surviving rate of juveniles during the first life stages. Results of this work suggest that the mix of recruits sampled in the central English Channel is made of large number of specimens coming from Torbay in 2010 and 2011 (table 6.7). A less important percentage of recruits seems to come from the West Cotentin and a few number of specimens in 2010 and none in 2011 present similarities with Bay of Seine pre-recruits suggesting a very low contribution of this last nursery ground. Finally, one third of the recruits studied in 2010 have an undetermined origin, but this proportion doubles in 2011.

Trace element composition and stable isotope signature are very expensive methodologies and statolith shape analysis was time consuming. As a consequence, the study was limited to the 3 spawning/nursery grounds (BS, WC and TB) assumed to be the most important ones with a limited number of studied specimens. A significant improvement

Table 6.7: Percentage of recruits (sampled in December 2010 and January 2012) per origin.

Nursery grounds sites	2010	2012
BS	6%	0%
WC	16%	10%
TB	45%	30%
Unknown origin	33%	60%

of the method should therefore be the characterisation of pre-recruits coming from each of the known spawning grounds and will help in determining the contribution of unstudied known spawning grounds (figure 6.1)

Methodologies used in this work has given interesting results to estimate the contribution of the different spawning areas to the formation of the central stock. Further studies should use the laser abrasion on the adult polished statoliths (Zumholz et al., 2006) to highlight environmental conditions encountered by the specimens during their whole life cycle (Semmens et al., 2007; Green, 2011). Results obtained with the EFDs did not give as information as the two other methodologies as no similarities with potential other spawning sites were identified. A further improvement of the methodology could be the use of EFDs in 3 dimensions as it was done by Godefroy et al. (2012).

Acknowledgement

This study was carried out within the EU funded project ”CRESH” (under the Interreg IV A France-Manche-England programme).

Chapitre 7

Discussion générale

Comme cela a été indiqué à plusieurs reprises, la seiche de Manche *Sepia officinalis* est le plus important stock de céphalopodes de l'Atlantique N-E. Cependant, malgré de nombreux travaux scientifiques, les connaissances nécessaires à sa gestion ne suffisaient pas à mettre en place un suivi régulier de la ressource. Les travaux réalisés durant cette thèse ont ainsi permis d'améliorer les connaissances sur le cycle de vie de la seiche en montrant que le réchauffement de la Manche et la surpêche avaient probablement modifié les traits d'histoire de vie de l'espèce, même si ces modifications n'étaient pas suffisamment importantes pour être prises en compte dans les hypothèses de modélisation. La répartition spatiale de l'effort des chalutiers de fond à panneaux et les paramètres l'influançant ont ensuite montré que ce métier permettait d'obtenir des indices d'abondance fiables pour la seiche de Manche. Un modèle de biomasse à 2 stades a ainsi été développé, permettant de mieux suivre la dynamique de la ressource et de son recrutement et d'obtenir des indicateurs de l'impact de l'exploitation sur chaque cohorte. Enfin, l'hypothèse d'un mélange des juvéniles provenant de différentes frayères et recrutés en Manche centrale a pu être confirmée et une estimation de la contribution des frayères a été faite à l'aide de 3 méthodes différentes de traçage.

Ces divers résultats sont une avancée significative dans la connaissance du stock de seiche de Manche et ils concernent différentes phases du cycle de vie de la seiche. C'est à travers ces différentes phases : reproduction, phase pré-recrutée, recrutement et phase exploitée ainsi que les liens qui existent entre elles que peut apparaître le mieux l'intérêt général des résultats acquis. Ces résultats sont ensuite synthétisés grâce à la figure 7.1. Enfin, ce travail n'est évidemment qu'une étape dans l'évaluation de cette ressource et des perspectives d'approfondissement sont présentées afin d'éclaircir les zones d'ombres qui existent encore et de montrer ce qui pourrait aider à améliorer sa gestion, c'est à dire garantir la pérennité de l'activité économique et le bon état écologique du stock.

7.1 Les phases du cycle de vie de la seiche

7.1.1 Reproduction

La seiche est une espèce semelpare, dont le cycle de vie avait été décrit comme durant 2 ans dans les années 1980 (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991) et 1990 (Dunn, 1999a). Cependant, le cycle de vie des céphalopodes est variable en fonction de la température (Rodhouse et al., 1992; Boyle and Pierce, 1994; Waluda and Pierce, 1998; Waluda et al., 1999), une augmentation de cette dernière provoquant en général une accélération de la croissance somatique et une diminution de la taille finale (Jackson et al., 1997; Forsythe et al., 2001; Jackson and Moltschaniwskyj, 2002; Forsythe, 2004; Keyl et al., 2008). En Manche, il semble que le réchauffement observé ainsi qu'un effort de pêche important (Hawkins et al., 2003) aient modifié les traits d'histoire de vie de cette espèce. Un faible pourcentage d'individus des 2 sexes dans chaque cohorte apparaît comme mature et capable de se reproduire à la fin de la première année de vie. Cette variation des traits d'histoire de vie en fonction des conditions environnementales a également été montrée chez *Loligo forbesii* (Pierce et al., 2005), *Todarodes sagittatus* (Quetglas and Morales-Nin, 2004), *Loligo reynaudii* (Olyott et al., 2006) et *Octopus vulgaris* (Moreno et al., 2005). Cependant, des analyses supplémentaires seraient nécessaires pour déterminer si ces individus matures appartenant à la première cohorte prennent réellement part à la reproduction comme cela a été montré dans le Golfe du Morbihan (Gauvrit et al., 1998). Comme le suggèrent Pierce et al. (2008), cette réponse de la population aux modifications de l'environnement doit être étudiée avant le développement d'un modèle décrivant la population.

Par ailleurs, le modèle de biomasse à 2 stades a permis d'obtenir une évaluation de la biomasse de seiche de 2 ans féconde. Sur la période étudiée, la biomasse féconde ne semble pas être impactée par une surexploitation de la pêche, il est donc probable que la ressource soit pleinenement exploitée. Cette variable calculée par le modèle a également permis de montrer qu'il n'y avait pas de relation entre la biomasse féconde et le recrutement qu'elle engendrait. Jusqu'à présent, aucune relation stock-recrutement n'a été mise en évidence chez les céphalopodes (Boyle and Rodhouse, 2005).

Enfin, les variations de l'environnement influent sur la vitesse de développement des oeufs qui augmente avec la température du milieu dans lequel ils incubent (Bouchaud and Daguzan, 1989; Dickel et al., 1997; Blanc and Daguzan, 1998) et est dépendante de la salinité (Blanc and Daguzan, 1998). En Manche, l'éclosion a lieu entre 8 et 14 semaines après la ponte donnant un pic d'éclosion au mois de juillet (Medhioub, 1986). Avec le réchauffement de la Manche, un allongement de la période de reproduction, accompagné d'une diminution de la durée d'incubation (5 à 13 semaines ; Bouchaud, 1991) pourraient être observés. La période de reproduction pourrait ainsi se rapprocher de celle observée dans le Golfe de Gascogne. Cependant, le rétro-calcul des dates d'éclosion réalisé à partir des statolithes de recrues récoltées toute l'année a montré qu'un petit nombre de seiches éclosait sans doute tout au long de l'année puisque l'âge des recrues reste assez constant (Challier et al., 2005a). Cette extension de la période de ponte ne concerne qu'un petit nombre d'individus car en dehors de la période d'août à décembre, ces recrues (correpondant à la catégorie commerciale la plus petite) sont très rares.

7.1.2 Phase pré-recrutée

La phase pré-recrutée débute juste après l'éclosion. Les premiers stades de vie sont généralement considérés chez les céphalopodes comme une période très vulnérable, la mortalité étant la plus forte à cette période (mortalité post-reproduction mise à part ; Rocha et al., 1999; Vecchione, 1999; Boyle and Rodhouse, 2005; Pierce et al., 2008; González et al., 2005; Otero, 2006). Durant la phase para-larvaire, même si les céphalopodes sont considérés comme des prédateurs compétents (von Boletzky and Hanlon, 1983; Mangold and von Boletzky, 1985; Nabhitabhata and Nilaphat, 2000; Nabhitabhata et al., 2001), leur petite taille les rend vulnérables aux prédateurs et à l'absence de proie. Les seiches ont un comportement benthique dès l'éclosion et ne présentent donc pas de paralarves mais directement des juvéniles. Cependant, leur survie dépend d'apprentissages aussi bien pour la capture des proies que pour le camouflage (Darmaillacq et al., 2006; Kelman et al., 2007; Akkaynak et al., 2013). Pour la seiche de Manche, il semble que les conditions environnementales durant les premiers stades de vie influencent de manière significative les variations du recrutement (estimé à l'aide du modèle de biomasse). Malgré la forte influence de cette phase sur l'abondance des céphalopodes, il n'existe pas de méthode d'échantillonnage adéquate pour suivre la phase para-larvaire, entraînant une faible connaissance de ce stade de vie (Boyle and Rodhouse, 2005). En Manche, il serait possible d'utiliser les pêches côtières commerciales réalisées à titre dérogatoire et durant 2 semaines en août par les chalutiers exploitant les juvéniles avant leur première migration pour améliorer les connaissances sur cette phase (Pierce et al., 2010).

Plusieurs frayères côtières ont été identifiées sur les côtes de Manche (Challier, 2005). Le dosage d'éléments traces, la signature isotopique et les formes des statolithes décrits par les ellipses de Fourrier réalisés sur les pré-recrues et les recrues montrent que les recrues proviennent de différentes frayères et se mélangent dans le stock central. Les frayères côtières ne semblent pas toutes contribuer à la même hauteur au recrutement et à l'abondance de la ressource exploitée en Manche centrale ouest. Le niveau de pollution et le chalutage côtier semblent être des paramètres influant négativement sur la contribution de la frayère alors que la protection de la zone semble favoriser l'abondance de juvéniles capables d'atteindre le recrutement. Les éléments traces et les signatures isotopiques ont déjà été utilisés pour comprendre les flux migratoires, mais en réalisant des micro-dosages à différents points de la croissance des pièces dures comme les becs ou les statolithes (Cherel and Hobson, 2005; Green, 2011). En ce qui concerne les seiches, Boucaud-Camou and Boismery (1991) avaient réalisé des études sur les migrations par marquage recapture et Dunn (1999a) avait utilisé les données de capture des pêches commerciales pour mieux comprendre les schémas migratoires. Cette connaissance devrait maintenant être complétée par un approfondissement des connaissances sur les voies migratoires. Pour cela, d'autres méthodes ont été utilisées chez les céphalopodes (marquage-recapture, utilisation de marques acoustiques, présence de parasites, utilisation de marqueurs chimiques) et ont fait l'objet d'une revue écrite par Semmens et al. (2007).

7.1.3 Recrutement

Le recrutement est théoriquement défini en halieutique comme le nombre d'invidus (ou la biomasse) qui atteignent un stade de vie (taille et/ou colonisation d'une zone) les rendant exploitables (Jennings et al., 2001b). Dans la pratique, cette phase est plus particulièrement explorée car elle permet de mesurer le succès de la reproduction d'une espèce (Boyle and Rodhouse, 2005). D'après Royer et al. (2006), le recrutement de la seiche de Manche se fait en 2 phases. La cohorte annuelle étant constituée de 2 micro-cohortes, un premier recrutement a lieu au mois d'octobre et un deuxième au printemps, la cohorte étant finalement considérée comme pleinement recrutée au début de l'été. Ce phénomène de micro-cohorte a été décrit chez les céphalopodes par Caddy (1991) et a été observé par Arkhipkin (1993) sur la population exploitée d'*Illex argentinus* qui présente 4 micro-cohortes recrutées successivement durant l'été. Le modèle à 2 stades n'utilisant que le recrutement complet, l'abondance au recrutement est donc estimée au mois de juillet de chaque année. En Manche, le recrutement de *Sepia officinalis* présente une forte variabilité inter-annuelle provenant d'une forte sensibilité des premiers stades de vie aux conditions environnementales, un phénomène déjà montré chez la seiche (Wang et al., 2003) et bien connu chez les céphalopodes (Bakun and Csirke, 1998; Dawe et al., 2000; O'Dor, 1998; Waluda et al., 1999, 2001). L'abondance au recrutement n'est pas dépendant de l'abondance des reproducteurs comme cela est généralement le cas chez les céphalopodes (Boyle and Rodhouse, 2005). Cette phase de recrutement est déterminante pour l'abondance de la phase exploitée, puisque dans le cas de la seiche comme de beaucoup d'autres céphalopodes, la population exploitée n'est constituée que d'une seule cohorte. Les variations du recrutement chez les céphalopodes impactent donc beaucoup plus l'abondance du stock que chez les poissons dont la durée de vie est généralement plus longue (Boyle and Rodhouse, 2005).

7.1.4 Phase exploitée

Les céphalopodes sont des espèces de plus en plus exploitées du fait de la diminution d'abondance des poissons constatée dans de nombreux écosystèmes (FAO, 2012b). Leur gestion est devenue un enjeu important étant donné la dépendance économique directe ou indirecte d'une partie de la population active aux revenus tirés des ressources de céphalopodes (Pierce et al., 2010). Ce travail de thèse a ainsi permis de développer un modèle de biomasse à 2 stades, considéré comme d'une mise en œuvre aussi rationelle et reproductible que les modèles structurés en âge plébiscités par les halieutes pour les poissons à cycle de vie long (Mesnil, 2003). Grâce aux sorties du modèle, il a ainsi été possible de calculer 2 indicateurs de l'état du stock : la relation stock-recrutement et le taux d'exploitation, qui permettent tous les deux d'explorer les conséquences de la pêche sur chaque cohorte exploitée mais aussi les conséquences à court et moyen termes de cette

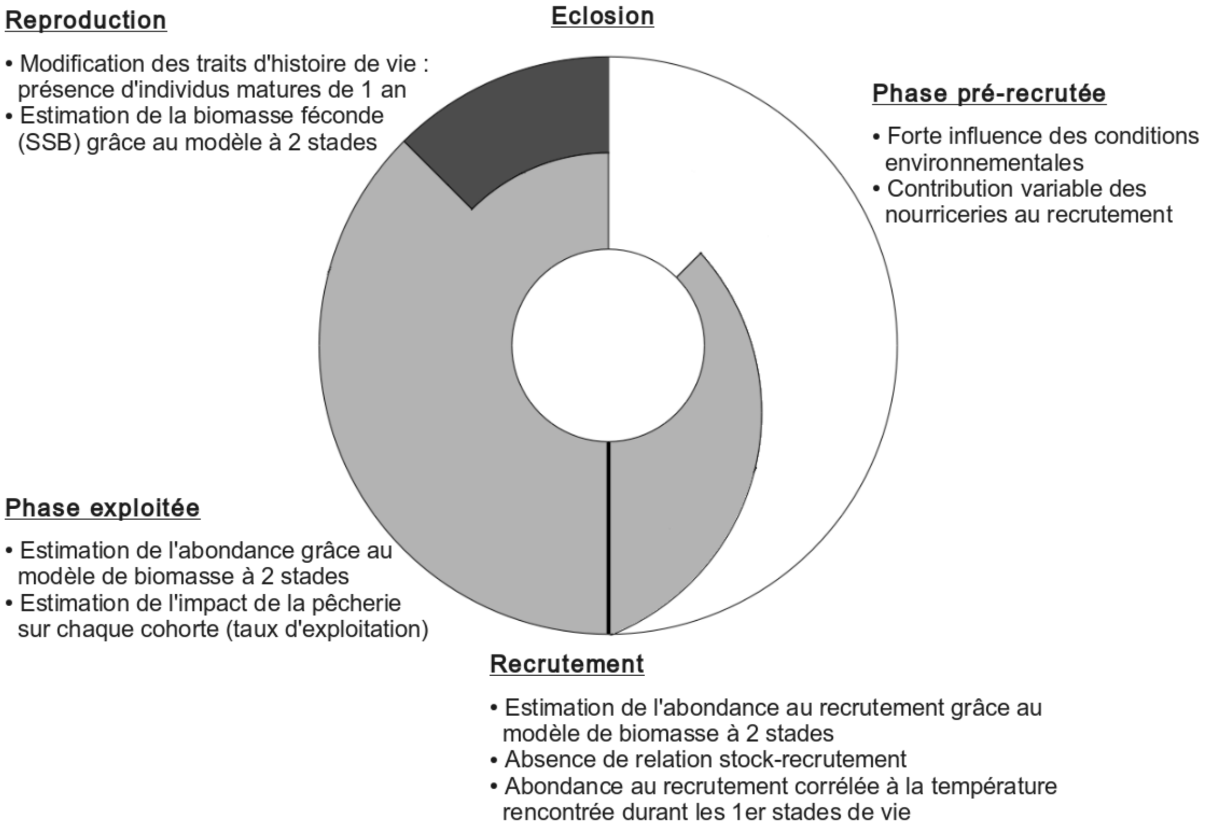

FIG. 7.1 – Cycle de vie de la seiche de Manche (2 ans) et ses différentes phases : reproduction (gris foncé), phase pré-recrutée (blanc), recrutement (noir) et phase exploitée (gris clair) et apports de ce travail de thèse pour chacune des phases.

exploitation sur la durabilité de l'activité. Comme l'ont montré Wang et al. (2003), l'abondance et la répartition de la ressource sont également fortement liées aux fluctuations environnementales qui influent directement (température favorable au développement) ou indirectement (disponibilité en proie). Malgré des avantages indéniables comme la prise en compte de plusieurs séries temporelles et le faible besoin en données de structure en âge de la population, le modèle à 2 stades a été relativement peu utilisé pour évaluer les stocks de poissons (Mesnil, 2003). Il a par contre été priviligié pour l'évaluation de stock de certains invertébrés (Conser, 1991; Conser and Idoine, 1992; Collie and Kruse, 1998; Zheng et al., 1997; Cadrin et al., 1999) ou de vertébré dont les données d'âge n'était pas suffisante pour développer un modèle structuré en âge fiable (Roel et al., 2009). Chez les céphalopodes, le seul exemple d'utilisation de ce modèle est l'évaluation du stock de *Loligo reynaudii* (Roel and Butterworth, 2000). Etant donné l'expansion attendue des pêcheries de céphalopodes, des avis ont été émis sur le besoin d'outils de gestion de ces ressources (Pierce et al., 2010). Le modèle de biomasse à 2 stades et l'indicateur d'impact des pêcheries sur le stock (taux d'exploitation) correspondent bien à cette attente et pourraient être complétés par une étude détaillée des interactions entre métiers comme celle réalisée précédemment par Royer et al. (2006). Enfin, la forte croissance et le cycle de vie court des céphalopodes leur confèrent une forte résilience face aux évènements impactant négativement leur abondance (surexploiation ou évènement climatique). Cette résilience est un atout pour ces ressources et faciliterait leur gestion afin qu'elles s'inscrivent dans une politique d'exploitaiton durable (Pierce et al., 2010).

7.2 Perspectives

Ce travail de thèse a permis d'améliorer les connaissances sur la dynamique du stock de seiche en Manche et de développer un modèle permettant de suivre les variations inter-annuelles d'abondance de la phase exploitée. Les sorties du modèle (relation stock-recrutement et taux d'exploitation) sont des outils de gestion opérationnels et facilement utilisables par un expert. Ce travail va donc faire l'objet d'un développement supplémentaire afin d'en créer une application logicielle qui sera fourni au *Working Group on CEPHalopods fisheries and life histories* (WGCEPH), afin de réaliser l'évaluation du stock de seiche de Manche annuellement et de fournir un avis scientifique sur l'état de ce stock. Cette application logicielle sera développée en langage R et utilisera comme données sources les extractions des bases de données halieutiques au format européen COST (Jansen et al., 2009) afin d'en faciliter sa diffusion et son utilisation.

Le modèle de biomasse à 2 stades, contrairement aux modèles structurés en âge, est facilement transposable d'un stock à l'autre. En effet, sa mise en place nécessite essentiellement des données d'abondance calculées à partir de campagnes scientifiques et de captures commerciales et ne nécessite pas d'autre information sur la structure en âge de la population que les deux stades entre lesquels elle est exploitée (Mesnil, 2003). La seiche du Golfe de Gascogne est exploitée par les pêcheurs espagnols et français dont les données de débarquement sont respectivement collectées par l'AZTI et l'Ifremer. Les espèces démersales du Golfe de Gascogne sont échantillonnées chaque année par le Navire Océanographique (NO) Thalassa appartenant à l'Ifremer et équipé d'un chalut à Grande Ouverture Verticale (GOV) durant la campagne EValuation Halieutique de l'Ouest de l'Europe (EVHOE) qui a lieu de mi-octobre à début décembre. Grâce à ces trois sources de données il serait ainsi possible d'adapter le modèle développé pour la Manche pour réaliser l'évaluation du stock du Golfe de Gascogne.

La seiche se répartit en fonction de la température en Manche (Wang et al., 2003) et se concentre à la côte pendant le printemps et l'été et au large à l'automne et en hiver (Boucaud-Camou and Boismery, 1991; Dunn, 1999a). Les paramètres environnementaux sont donc prépondérants dans la répartition et l'abondance de la ressource. Dans ce travail de thèse, ce phénomène n'a été mis en évidence que de manière globale, montrant la corrélation qui existe entre la température durant les premiers stades de vie et l'abondance au recrutement. Durant les campagnes scientifiques *Bottom Trawl Survey* (BTS) et *Channel Ground Fish Survey* CGFS, des paramètres environnementaux sont collectés en même temps que les abondances des espèces démersales. Une étude approfondie de ces données permettrait une meilleure compréhension de la dynamique du stock en période estivale et avant le départ en migration qui se fait généralement en octobre. Cependant, ces 2 campagnes ne couvrent que la division CIEM VIId (Manche est) et seront complétées en septembre 2014 par le lancement de la CAmpagne en MANche OCcidentale (CAMANOC) qui échantillonnera les espèces démersales de la Manche ouest avec le chalut GOV du NO Thalassa. L'étude des paramètres environnementaux pourrait être complétée à l'aide du modèle MARS 3D, développé et géré par l'Ifremer, qui est capable de calculer les paramètres environnementaux spatialisés et durant toute l'année sur l'ensemble de la Manche. Ainsi des paramètres comme la température et la salinité, connus pour influencer le cycle de vie de la seiche (Wang et al., 2003; Pierce et al., 2010), pourraient être étudiés pour mieux comprendre les tendances des abondances (LPUE) à l'échelle des rectangles CIEM ou de groupes de rectangles CIEM.

Les migrations que la seiche réalise chaque année ont été décrites depuis de nombreuses années par différents auteurs (Boucaud-Camou and Boismery, 1991; Dunn, 1999a). Cependant, le trajet exact de ces migrations n'est pour le moment pas connu. L'utilisation de marques enregistreuses (Semmens et al., 2007) permettrait d'améliorer les connaissances sur la première migration en marquant des pré-recrues durant l'été suivant leur éclosion et en les recapturant au centre de la Manche. Cela permettrait également de confirmer le mélange des recrues de différentes frayères au centre Manche montré dans cette étude. De plus, l'analyse de la composition en éléments traces des couches journalières déposées sur les statolithes (Semmens et al., 2007; Green, 2011) pourrait aider à connaître les conditions environnementales rencontrées durant les différents stades de vie de la seiche et en déduire de potentiels schémas migratoires. En particulier, les ratios Sr : Ca, Ba : Ca et parfois U : Ca peuvent renseigner sur les températures rencontrées par l'individu (Semmens et al., 2007). Enfin, l'hypothèse de capturabilité constante faite dans le modèle sur l'ensemble de la zone étudiée et durant toute l'année n'est sans doute pas réaliste. Un développement significatif du modèle pourrait donc être une spatialisation prenant en compte les mouvements migratoires de la seiche (Boucaud-Camou and Boismery, 1991; Dunn, 1999a) et les variations spatiales de capturabilité. Pour cela, les données de débarquement pourraient être agrégées par rectangle CIEM ou par groupe de rectangles CIEM (par exemple 2 groupes de rectangles côtiers au nord et au sud de la Manche, et un groupe de rectangles du large).

Les céphalopodes, en tant que prédateurs, ont été décrits comme des espèces clés dans le fonctionnement des écosystèmes (Boyle and Rodhouse, 2005; Pierce et al., 2010). Plusieurs types de modèles ont été développés durant les dernières décennies afin de modéliser les réseaux trophiques tels que *EcoPath with Ecosim* (EwE ; Christensen and Walters, 2004) ou EcoTroph (Gasche and Gascuel, 2013). Le modèle EwE a déjà été appliqué au niveau de la Manche (Araújo et al., 2005). Cependant, en l'absence d'informations sur la position trophique des céphalopodes de Manche, les positions trophiques des espèces exploitées ont été estimées à l'aide de données provenant de céphalopodes étudiés en Californie. Dans le cadre du projet CRESH, la position trophique de la seiche a été estimée à l'aide de contenus stomacaux et d'analyses isotopiques et ces résultats pourraient contribuer à améliorer la modélisation du réseau trophique de la Manche.

Les activités anthropiques marines représentent actuellement entre 3 et 5% du Produit Intérieur Brut (PIB) de l'Europe et certaines de ces activités devraient suivre une forte croissance dans les années à venir. La pêche et les ressources qu'elle exploite doivent donc être prises en compte parmi les diverses activités économiques qui se développent, afin que chacune d'entre elles se place dans une logique d'exploitation durable et que leur impact sur les écosystèmes marins en soit ainsi limité. Le descripteur 3 de la Directive Cadre Stratégique Milieu Marin (DCSMM) a pour objectif de développer les actions qui favorisent la restauration ou le maintien du bon état écologique du milieu marin. Actuellement, la majorité des outils développés pour la gestion des stocks halieutiques sont adaptés aux poissons et parfois aux mollusques bivalves (Coquille Saint Jacques). L'évaluation de ces derniers se faisant actuellement uniquement grâce à une campagne d'évaluation du recrutement pour estimer un Taux Acceptable de Capture (TAC) durable mais sans l'aide de modèle d'évaluation de stock. Avec le modèle de biomasse à 2 stades adapté pour le stock de seiche de Manche, nous proposons ici un outil adapté et facilement transposable pour gérer les stocks de céphalopodes en Europe, stocks qui ne sont généralement réglementés que par des mesures locales et non pas européennes (Pierce et al., 2010).

Bibliographie

Abernethy, K. E., Trebilcock, P., Kebede, B., Allison, E. H., and Dulvy, N. K. (2010). Fuelling the decline in UK fishing communities? *ICES Journal of Marine Science*, 67(5):1076–1085.

Acou, A., Rivot, E., Van Gils, J. A., Legault, A., Ysnel, F., and Feunteun, E. (2011). Habitat carrying capacity is reached for the European eel in a small coastal catchment: evidence and implications for managing eel stocks. *Freshwater Biology*, 56(5):952–968.

Agnew, D. J., Baranowski, R., Beddington, J. R., des Clers, S., and Nolan, C. P. (1998). Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. *Fisheries Research*, 35:155–169.

Akkaynak, D., Allen, J. J., Mäthger, L. M., Chiao, C.-C., and Hanlon, R. T. (2013). Quantification of cuttlefish (*Sepia officinalis*) camouflage: a study of color and luminance using in situ spectrometry. *Journal of comparative physiology. A, Neuroethology, sensory, neural, and behavioral physiology*, 199(3):211–25.

Aliaume, C., Monteiro, C., Louis, M., Lam, H. T., and Lasserre, G. (1993). Organisation spatio-temporelle des peuplements ichtyologiques dans deux lagunes côtières: au Portugal et en Guadeloupe. Spatial and temporal organization of lagoon fish communities (Ria Formosa in Portugal and Grand Cul-de-Sac Marin in Guadeloupe). *Oceanologica Acta*, 16(3):291–301.

Anderson, J. L. (2003). *The International Seafood Trade.* Woodhead Publishing, Cambridge, UK.

Anonyme (1993). Report of the Working Group on Cephalopod Fisheries and Life History. ICES CM 1993/G:02. Technical report, ICES, Vigo.

Anonymous (2008). Report of the Working Group on Anchovy (WGANC) International Council for the Exploration of the Sea. Technical Report June, ICES CM 2008/ACOM:04, Copenhagen.

Anonymous (2010). Report of the Workshop on Sexual Maturity Staging of Cephalopods (WKMSCEPH). Technical Report November, ICES CM 2010/ACOM:49, Livorno, Italy.

Araújo, J. N., Mackinson, S., Ellis, J. R., and Hart, P. J. B. (2005). An Ecopath model of the Western English Channel ecosystem with and exploration of its dynamic properties. *Science series technical report*, 125:45.

Arkhipkin, A. I. (1993). Age, growth, stock structure and migratory rate of pres-pawning short-finned squid, *Illex argentinus*, based on statolith ageing investigations. *Fisheries Research*, 16:313–338.

Augustyn, C. J., Lipinski, M. R., and Sauer, W. H. H. (1992). Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *South African Journal Of Marine Science*, 12:903–918.

Augustyn, C. J. and Roel, B. A. (1998). Fisheries biology, stock assessment and management of the chokka squid (*Loligo vulgaris reynaudii*) in South African waters. An overview. *California cooperative oceanic fisheries investigations reports*, 39:71–80.

Bakhayoko, M. (1983). Biology of the cuttlefish *Sepia officinalis hierreda* off Senegalese coast. In Caddy, J. F., editor, *Advances in assessment of world cephalopod resources*, pages 204–263. Rome, Italy.

Bakun, A. and Csirke, J. (1998). Environmental processes and recruitment variability. In Rodhouse, P. G., Dawe, E. G., and O'Dor, R. K., editors, *Squid recruitment dynamics.*, pages 105–124. FAO Fisheries Technical Paper No. 376.

Barrowman, N. J. and Myers, R. A. (2000). Still more spawner-recruitment curves: the hockey stick and its generalizations. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(4):665–676.

Basson, M., Beddington, J. R., Crombie, J. A., Holden, S. J., Purchase, L. V., and Tingley, G. A. (1996). Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fisheries Research*, 28(1):3–27.

Bastardie, F., Nielsen, J. R., Andersen, B. S. l., and Eigaard, O. R. (2010). Effects of fishing effort allocation scenarios on energy efficiency and profitability: An individual-based model applied to Danish fisheries. *Fisheries Research*, 106(3):501–516.

Beaugrand, G. (2009). Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(8-10):656–673.

Beaugrand, G. and Reid, P. C. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9(6):801–817.

Beddington, J. R., Rosenberg, A. A., Crombie, J. A., and Kirkwood, G. P. (1990). Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fisheries Research*, 8(4):351–365.

Berthou, P. (2012). Système d'Informations Halieutiques SIH.

Bettencourt, V. and Guerra, A. (2000). Growth increments and biomineralization process in cephalopod statoliths. *Journal of experimental marine biology and ecology*, 248(2):191–205.

Bettencourt, V. and Guerra, A. (2001). Age studies based on daily growth increments in statoliths and growth lamellae in cuttlebone of cultured *Sepia officinalis*. *Marine Biology*, 139(2):327–334.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Payá, I., Sainsbury, K., Sanchez, F., and Zwanenburg, K. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, 57(3):558–571.

Blanc, A. and Daguzan, J. (1998). Artificial surfaces for cuttlefish eggs (*Sepia officinalis* L.) in Morbihan Bay, France. *Fisheries Research*, 38(3):225–231.

Blanc, A. and Daguzan, J. (2000). Size selectivity in the diet of the young cuttlefish Sepia officinalis (Mollusca: Sepiidae). *Journal of the Marine Biological Association of the UK*, 80(06):1137–1138.

Blanc, L. and Beaudou, D. (1998). Stabilité temporelle des structures spatiales des peuplements piscicoles des régions Languedoc-Roussillon et Provence-Alpes-Côte d'Azur. *Bulletin Français de la Pêche et de la Pisciculture*, 348:23–45.

Blanc, L., Chessel, D., and Doledec, S. (1998). Etude de la stabilité temporelle des structures spatiales par analyses d'une série de tableaux de relevés faunistiques totalement appariés. *Bulletin Français de la Pêche et de la Pisciculture*, 348:1–21.

Bloor, I. (2012). *The ecology, distribution and spawning behaviour of the commercially important common cuttlefish (Sepia officinalis) in the inshore waters of the English Channel.* Ph.D., Plymouth University.

Bluhm, B. A. and Brey, T. (2001). Age determination in the Antarctic shrimp *Notocrangon antarcticus* (Crustacea: Decapoda), using the autofluorescent pigment lipofuscin. *Marine Biology*, 138(2):247–257.

Boletzky, S. (1983). *Sepia officinalis*. In Boyle, P. R., editor, *Cephalopod life cycles vol 1. Species accounts*, pages 31–52. Academic Press, London, UK.

Booth, A. J. (2000). Incorporating the spatial component of fisheries data into stock assessment models. *ICES Journal of Marine Science*, 57(4):858–865.

Boucaud-Camou, E. and Boismery, J. (1991). The migrations of the cuttlefish (*Sepia officinalis* L.) in the English Channel. In Boucaud-Camou, E., editor, *La seiche / The Cuttlefish*, pages 179–189, Caen, France. Centre de publication de l'Université de Caen.

Boucaud-Camou, E., Koueta, N., Boismery, J., and Medhioub, A. (1991). The sexual maturity of *Sepia officinalis* L. from the Bay of Seine. In Boucaud-Camou, E., editor, *La seiche / The Cuttlefish*, pages 141–151, Caen, France. Centre de publication de l'Université de Caen.

Bouchaud, O. (1991). Etude de la reproduction de seiche commune *Sepia officinalis* L. dans le Golfe du Morbihan. Premiers résultats. In Boucaud-Camou, E., editor, *La seiche / The Cuttlefish*, pages 153–166. Centre de publication de l'Université de Caen, Caen, France.

Bouchaud, O. and Daguzan, J. (1989). Etude de l'oeuf de *Sepia officinalis* en conditions experimentales. *Haliotis*, 19:189–200.

Boumaaz, A. and Dridi, A. (2002). Abondance des céphalopodes et structure démographique du poulpe commun dans le sud du Maroc. In Caverivière, A., Thiam, M., and Jouffre, D., editors, *Le poulpe Octopus vulgaris*, pages 233–246. Paris, France, IRD edition.

Boyle, P. R. and Boletzky, S. (1996). Cephalopod populations: definition and dynamics. *Philosophical Transactions: Biological Sciences*, 351(1343):985–1002.

Boyle, P. R. and Pierce, G. J. (1994). Fishery biology of the Northeast Atlantic squid. *Fisheries Research*, 21(1-2):1–314.

Boyle, P. R. and Rodhouse, P. G. (2005). *Cephalopods: Ecology and Fisheries.* John Wiley & Sons.

Bravo de Laguna, J. (1989). *Managing an international multispecies fishery: the Saharan trawl fishery for cephalopods.* Wiley-interscience publication. Wiley, illustrate edition.

Brodziak, J. K. T. and Rosenberg, A. A. (1993). A method to assess squid fisheries in the north-west Atlantic. *ICES Journal of Marine Science*, 50(2):187–194.

Brooks, E. N. (2013). Effects of variable reproductive potential on reference points for fisheries management. *Fisheries Research*, 138:152–158.

Brunet, C., Brylinski, J. M., Bodineau, L., Thoumelinb, G., Bentley, D., and Hildea, D. (1996). Phytoplankton dynamics during the spring bloom in the south-eastern English Channel. *Estuarine, Coastal and Shelf Science*, 43(4):469–483.

Brusca, R. C. and Brusca, G. J. (2002). *Invertebrates, second edition.* Sinauer Associates.

Brylinski, J. M., Brunet, C., Bentley, D., Thoumelin, G., and Hilde, H. (1996). Hydrography and phytoplancton biomass in the eastern English Channel in spring 1992. *Estuarine, Coastal shelf science*, 43:507–519.

Bustamante, P., Cosson, R. P., Gallien, I., Caurant, F., and Miramand, P. (2002). Cadmium detoxification processes in the digestive gland of cephalopods in relation to accumulated cadmium concentrations. *Marine environmental research*, 53(3):227–41.

Caddy (1991). Daily rings on squid statoliths: an opportunity to test standard population models? In Jereb, P., Raganese, S., and von Boletzky, S., editors, *Squid age determination using statoliths. Proceedings of the international workshop held in the Institute de Tecnologia de la pesca e del pescato (ITPP-CNR)*, pages 53–124, Mazara del Vallo, Italy. Special publication.

Caddy, J. F. (1983). *Advances in assessment of world cephalopod resources.* FAO Fisheries Technical Paper No. 231, Rome, fao edition.

Cadrin, S. X., Clark, S. H., Schick, D. F., Armstrong, M. P., McCarron, D., and Smith, B. (1999). Application of Catch-Survey Models to the Northern Shrimp Fishery in the Gulf of Maine. *North American Journal of Fisheries Management*, 19(2):551–568.

Campana, S. E. (1990). How Reliable are Growth Back-Calculations Based on Otoliths? *Canadian Journal of Fisheries and Aquatic Sciences*, 47(11):2219–2227.

Campana, S. E. and Casselman, J. M. (1993). Stock Discrimination Using Otolith Shape Analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(5):1062–1083.

Capoccioni, F., Costa, C., Aguzzi, J., Menesatti, P., Lombarte, A., and Ciccotti, E. (2011). Ontogenetic and environmental effects on otolith shape variability in three Mediterranean European eel (*Anguilla anguilla*, L.) local stocks. *Journal of Experimental Marine Biology and Ecology*, 397(1):1–7.

Carassou, L. and Ponton, D. (2007). Spatio-temporal structure of pelagic larval and juvenile fish assemblages in coastal areas of New Caledonia, Southwest Pacific. *Marine Biology*, 150(4):697–711.

Carpentier, A., Martin, C. S., and Vaz, S. (2009). *Channel Habitat Atlas for marine Resource Management, final report / Atlas des Habitats des Ressources Marines de la Manche Orientale CHARM II.* Boulogne-sur-Mer, France.

Cefas (2012). Cefas: FishDAC.

Centofanti, M., Chessel, D., and Dolédec, S. (1989). Stabilité d'une structure spatiale et compromis d'une analyse statistique multi-tableaux: application à la physico-chimie d'un lac réservoir. *Revue des sciences de l'eau / Journal of Water Science*, 2(1):71–93.

Challier, L. (2005). *Variabilité de la croissance des Céphalopodes juvéniles (Sepia officinalis, Loligo forbesi) et relation avec les fluctuations du recrutement, en Manche.* Phd, University of Caen.

Challier, L., Dunn, M. R., and Robin, J.-p. (2005a). Trends in age-at-recruitment and juvenile growth of cuttlefish, *Sepia officinalis*, from the English Channel. *ICES Journal of Marine Science*, 62(8):1671–1682.

Challier, L., Orr, P., and Robin, J.-P. (2006a). Introducing inter-individual growth variability in the assessment of a cephalopod population: application to the English Channel squid *Loligo forbesi*. *Oecologia*, 150(1):17–28.

Challier, L., Pierce, G. J., and Robin, J.-P. (2006b). Spatial and temporal variation in age and growth in juvenile *Loligo forbesi* and relationships with recruitment in the English Channel and Scottish waters. *Journal of Sea Research*, 55(3):217–229.

Challier, L., Royer, J., Pierce, G. J., Bailey, N., Roel, B., and Robin, J.-p. (2005b). Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. *Aquatic Living Resources*, 360(4):353–360.

Challier, L., Royer, J., and Robin, J.-P. (2002). Variability in age-at-recruitment and early growth in English Channel *Sepia officinalis* described with statolith analysis. *Aquatic Living Resources*, 15(5):303–311.

Cherel, Y. and Hobson, K. A. (2005). Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *proceedings of the royal society of London B*, 272:1601–1607.

Chiffoleau, J.-F., Cossa, D., Auger, D., and Truquet, I. (1994). Trace metal distribution, partition and fluxes in the Seine estuary (France) in low discharge regime. *Marine Chemistry*, 47(2):145–158.

Choe, N. and Deibel, D. (2009). Statolith diameter as an age indicator in the planktonic tunicate Oikopleura vanhoeffeni: Variability in age-specific growth patterns in Conception Bay, Newfoundland. *Journal of Experimental Marine Biology and Ecology*, 375(1-2):89–98.

Christensen, V. and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172(2-4):109–139.

Clarke, M. R. and Pascoe, P. L. (1985). The Stomach Contents of A Risso's Dolphin (*Grampus Griseus*) Stranded at Thurlestone, South Devon. *Journal of the Marine Biological Association of the UK*, 65(3):663–665.

Clarke, M. R. and Stevens, J. D. (1974). Cephalopods, blue sharks and migration. *Journal of the Marine Biological Association of the UK*, 54(4):949–957.

Coelho, M. L. and Marthins, M. C. (1991). Preliminary observations on the biology of *Sepia officinalis* in Ria Formosa, Portugal. In Boucaud-Camou, E., editor, *La seiche / The Cuttlefish*, pages 131–140. Centre de Publications de l'Université de Caen, Caen, France.

Coelho, M. L., Quintela, J., Bettencourt, V., Olavo, G., and Villa, H. (1994). Population structure, maturation patterns and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research*, 21(1-2):87–102.

Collie, J. S. and Kruse, G. H. (1998). Estimating king crab *Paralithodes camtschaticus* abundance from commercial catch and research survey data. In Jamieson, R. E. and Campbell, A., editors, *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management*, pages 73–83. Canadian Special Publication of Fisheries and Aquatic Sciences. 125.

Collie, J. S. and Sissenwine, M. P. (1983). Estimating population size from relative abundance data measured with error. *Canadian Journal of Fisheries and Aquatic Sciences*, 40(11):1871–1879.

Conser, R. J. (1991). A DeLury method for scallops incorporating length based selectivity of the recruiting year-class to the survey gear and partial recruitment to the commercial fishery. Research document SAW 12/2. Appendix to CRD-91-03. Technical report, North-East Regional Stock assessment Workshop report, Woods Hole, MA.

Conser, R. J. and Idoine, J. (1992). A modified DeLury model for estimating mortality rates and stocks sizes of American lobster populations. Research document SAW 14/7. Appendix to CRD-92-07. Technical report, North-East Regional Stock assessment Workshop report, Woods Hole, MA.

Culshaw, C., Newton, L. C., Weir, I., and Bird, D. J. (2002). Concentrations of Cd, Zn and Cu in sediments and brown shrimp (*Crangon crangon* L.) from the Severn Estuary and Bristol Channel, UK. *Marine environmental research*, 54(3-5):331–4.

Daly, H. I., Pierce, G. J., Santos, M. B., Royer, J., Cho, S. K., Stowasser, G., Robin, J.-P., and Henderson, S. M. (2001). Cephalopod consumption by trawl caught fish in Scottish and English Channel waters. *Fisheries Research*, 52(1-2):51–64.

Danis, B., Bustamante, P., Cotret, O., Teyssié, J. L., Fowler, S. W., and Warnau, M. (2005). Bioaccumulation of PCBs in the cuttlefish *Sepia officinalis* from seawater, sediment and food pathways. *Environmental pollution (Barking, Essex : 1987)*, 134(1):113–22.

Darmaillacq, A.-S., Chichery, R., and Dickel, L. (2006). Food imprinting, new evidence from the cuttlefish *Sepia officinalis*. *Biology letters*, 2(3):345–347.

Dauvin, J.-C. (1997). *Les biocénoses marines et littorales françaises des côtes Atlantique, Manche Mer du Nord, synthèse, menace et perspectives.* Collection Patrimoines Naturels. Laboratoire de Biologie des Invertébrés Marin et Malacologie / SPN / IEGB / MNHN, Paris, France.

Dauvin, J.-C. (2008). Effects of heavy metal contamination on the macrobenthic fauna in estuaries: the case of the Seine estuary. *Marine pollution bulletin*, 57(1-5):160–9.

Dauvin, J.-C. (2012). Are the eastern and western basins of the English Channel two separate ecosystems? *Marine pollution bulletin*, 64(3):463–71.

Dauvin, J.-C., Ruellet, T., Desroy, N., and Janson, A.-L. (2007). The ecological quality status of the Bay of Seine and the Seine estuary: use of biotic indices. *Marine pollution bulletin*, 55(1-6):241–57.

Dawe, E. G., Colbourne, E. B., and Drinkwater, K. F. (2000). Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *ICES Journal of Marine Science*, 57(4):1002–1013.

Decleir, W. and Vlaeminck, A. (1978). Determination of protein-bound copper and zinc in some organs of the cuttlefish *Sepia officinalis* L. *Comparative Biochemistry and Physiology*, 60:347–350.

DeLury (1947). On the estimation of biological populations. *bimetrics*, 3:145–167.

Denis, V., Lejeune, J., and Robin, J.-P. (2002). Spatio-temporal analysis of commercial trawler data using General Additive Models: patterns of Loliginid squid abundance in the north-east Atlantic. *ICES Journal of Marine Science*, 59(3):633–648.

Denis, V. and Robin, J.-P. (2001). Present status of the French Atlantic fishery for cuttlefish (*Sepia officinalis*). *Fisheries Research*, 52(1-2):11–22.

Desroy, N., Warembourg, C., Dewarumez, J. M., and Dauvin, J. C. (2003). Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. *ICES Journal of Marine Science*, 60(1):120–131.

DeVries, D. A., Grimes, C. B., and Prager, M. H. (2002). Using otolith shape analysis to distinguish eastern Gulf of Mexico and Atlantic Ocean stocks of king mackerel. *Fisheries Research*, 57(1):51–62.

Diallo, M. and Ortiz, M. (2002). Estimation of standardized index of abundance of octopus (*O. vulgaris*) from the senegalese's artisanal fishery (1989-1994). In Caverivière, A., Thiam, M., and Jouffre, D., editors, *Le poulpe Octopus vulgaris*, pages 223–232. Paris, France, IRD edition.

Dickel, L., Chichery, M.-P., and Chichery, R. (1997). Postembryonic maturation of the vertical lobe complex and early development of predatory behaviour in the cuttlefish *Sepia officinalis. Neurobiology of Learning and Memory*, 67:150–160.

Dolédec, S. (1988). Les analyses multi-tableaux en écologie factorielle. II Stratification de l'Ardèche à partir de descripteurs physico-chimiques. *Acta Oecologica, Oecologia generalis*, 9:119–135.

Doubleday, Z. A. and Semmens, J. M. (2011). Quantification of the age-pigment lipofuscin in known-age octopus (*Octopus pallidus*): A potential tool for age determination. *Journal of Experimental Marine Biology and Ecology*, 397(1):8–12.

Driscoll, J. and Tyedmers, P. (2010). Fuel use and greenhouse gas emission implications of fisheries management: the case of the new england atlantic herring fishery. *Marine Policy*, 34(3):353–359.

Dunn, M. R. (1999a). Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. *Fisheries Research*, 40(3):277–293.

Dunn, M. R. (1999b). *The Exploitation of Selected Non-Quota Species in the English Channel.* Phd, University of Portsmouth.

Engelhard, G. and Heino, M. (2004). Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Marine Ecology Progress Series*, 272:245–256.

European Union (2008). Council Regulation (EC) No 199/2008 of 25 February 2008 concerning the establishment of a Community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. *Official Journal of the European Union*, L 60:1–12.

FAO (2012a). FAO yearbook. Fishery and Aquaculture Statistics. Technical report, FAO, Rome.

FAO (2012b). The state of world fisheries and aquaculture. Technical report, Food and Agriculture Organization of the United Nations, Rome, Italy.

Fletcher, D., Mackenzie, D., and Villouta, E. (2005). Modelling skewed data with many zeros: A simple approach combining ordinary and logistic regression. *Environmental and Ecological Statistics*, 12(1):45–54.

Forsythe, J. and Van Heukelem, W. F. (1987). Growth. In Boyle, P. R., editor, *Cephalopod life cycles vol 2. Comparative review*, pages 135–156. Academic Press, London, UK.

Forsythe, J. W. (2004). Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. *Marine and Freshwater Research*, 55:331–339.

Forsythe, J. W., Derusha, R. H., and Hanlin, R. T. (1994). Growth, reproduction and lifespan of *Sepia officinalis* (Cephalopoda: Mollusca) cultured through seven generations. *Journal of zoological society of london*, 233:178–192.

Forsythe, J. W., Walsh, L. S., Turk, P. E., and Lee, P. G. (2001). Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. *Marine Biology*, 138:103–112.

Fox, W. W. J. (1970). An exponential surplus-yield model for optimizing exploited fish populations. *Transactions of the American Fisheries*, 99(1):80–88.

Froese, R. and Proelß, A. (2010). Rebuilding fish stocks no later than 2015: will Europe meet the deadline? *Fish and Fisheries*, 11(2):194–202.

Froese, R., Stern-Pirlot, A., Winker, H., and Gascuel, D. (2008). Size matters: How single-species management can contribute to ecosystem-based fisheries management. *Fisheries Research*, 92(2-3):231–241.

Fry, B. (1999). Using stable isotopes to monitor watershed influences on aquatic trophodynamics. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(11):2167–2171.

Gasche, L. and Gascuel, D. (2013). EcoTroph: a simple model to assess fishery interactions and their impacts on ecosystems. *ICES Journal of Marine Science*, 70(XX):XXX–XXX.

Gascuel, D., Bez, N., Forest, A., Guillotreau, P., Laloë, F., Lobry, J., Mahévas, S., Mesnil, B., Rivot, E., Rochette, S., and Trenkel, V. (2011). A future for marine fisheries in Europe (Manifesto of the Association Française d'Halieumétrie). *Fisheries Research*, 109(1):1–6.

Gauvrit, E., Le Goff, R., and Daguzan, J. (1997). Reproductive Cycle of the Cuttlefish, *Sepia Officinalis* (L.) in the Northern Part of the Bay of Biscay. *Journal of Molluscan Studies*, 63(1):19–28.

Gauvrit, E., Pinczon du Sel, G., Blanc, A., and Daguzan, J. (1998). Detection of cross-mating between two generations of the cuttlefish *Sepia officinalis* by sperm reservoir analysis. *Journal of Molluscan Studies*, 64(1):1–9.

Gibson, D. J. M. (1995). The New Zealand squid fishery. Technical report, MAF Fisheries, Wellington, New Zealand.

Gillis, D. M. (2003). Ideal free distributions in fleet dynamics : a behavioral perspective on vessel movement in fisheries analysis. *Canadian journal of zoology*, 81(2):177–187.

Godefroy, J. E., Bornert, F., Gros, C. I., and Constantinesco, A. (2012). Elliptical Fourier descriptors for contours in three dimensions: a new tool for morphometrical analysis in biology. *Comptes rendus biologies*, 335(3):205–13.

González, A. F., Otero, J., Guerra, A., Prego, R., Rocha, F., and Dale, A. W. (2005). Temporal variation of cephalopod paralarvae in a wind-driven upwelling area (Ria of Vigo, NW Spain). *Journal of Plankton Research*, 27:271–277.

Grangeré, K., Lefebvre, S., and Blin, J.-L. (2012). Spatial and temporal dynamics of biotic and abiotic features of temperate coastal ecosystems as revealed by a combination of ecological indicators. *Estuarine, Coastal and Shelf Science*, 108(null):109–118.

Gras, M., Beibou, E., Wagne, O., Bouzouma, M., Labrosse, P., and Morand, P. (2010). Survey based proxy-localisation techniques for spatial distribution assessment of small-scale fishing activity: the case study of the Banc d'Arguin National Park (Mauritania). In Nishida, T. and Caton, A. E., editors, *GIS/Spatial Analysis in Fishery and Aquatic Sciences (Vol. 4)*, pages 337–350, Saitama. International Fishery GIS Society.

Green, C. P. (2011). *Influence of environmental factors on population structure of arrow squid Nototodarus gouldi: implications for stock assessment.* Phd, University of Tasmania.

Grift, R. E., Rijnsdorp, A. D., Barot, S., Heino, M., and Dieckmann, U. (2003). Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series*, 257:247–257.

Guerra, A. (1992). Mollusca, Cephalopoda. In *Fauna Ibérica, Vol 1*, page 327. Museo Nacional de Ciencias Naturales, Madrid.

Guerra, A., Allcock, L., and Pereira, J. a. (2010). Cephalopod life history, ecology and fisheries: An introduction. *Fisheries Research*, 106(2):117–124.

Guerra, A. and Castro, B. G. (1988). On the life-cycle of *Sepia officinalis* in the Ria de Vigo. *Cahiers de biologie marine*, 29:395–405.

Guillaud, J.-F. and Menesguen, A. (1998). Modélisation sur vingt ans (1976-1995) de la production phytoplanctonique en Baie de Seine. *Oceanologica Acta*, 21(6):887–906.

Guyader, O., Berthou, P., Koutsikopoulos, C., Alban, F., Demanèche, S., Gaspar, M., Eschbaum, R., Fahy, E., Tully, O., Reynal, L., Curtil, O., Frangoudes, K., and Maynou, F. (2013). Small scale fisheries in Europe: A comparative analysis based on a selection of case studies. *Fisheries Research*, 140:1–13.

Hanlon, R. T. and Messenger, J. (1996). *Cephalopod Behavior.* Cambridge, University Press, Cambridge, UK.

Hastie, L. C., Pierce, G. J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., and Robin, J.-P. (2009). Cephalopods in the North-East Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanography and Marine Biology: An Annual Review*, 47:111–190.

Hatfield, E. and Des Clers, S. (1998). Fisheries management and research for *Loligo gahi* in the Falkand Islands. *California cooperative oceanic fisheries investigations reports*, 39:81–91.

Hawkins, S. J., Southward, A. J., and Genner, M. J. (2003). Detection of environmental change in a marine ecosystem-evidence from the western English Channel. *The Science of the total environment*, 310(1-3):245–56.

Hendrickson, L. C. and Hart, D. R. (2006). An age-based cohort model for estimating the spawning mortality of semelparous cephalopods with an application to per-recruit calculations for the northern shortfin squid, *Illex illecebrosus*. *Fisheries Research*, 78(1):4–13.

Hilborn, R. and Walters, C. J. (1992). *Quantitative fisheries stock assessment choice, dynamics & uncertainty.* Springer, har/dskt edition.

Hill, K. T. and Womersley, C. (1991). Critical aspects of fluorescent age-pigment methodologies: Modification for accurate analysis and age assessments in aquatic organisms. *Marine Biology*, 109(1):1–11.

Hirst, J. A. and Attrill, M. J. (2008). Small is beautiful: an inverted view of habitat fragmentation in seagrass beds. *Estuarine, Coastal and Shelf Science*, 78:811–818.

Ho, J. D., Moltschaniwskyj, N. A., and Carter, C. G. (2004). The effect of variability in growth on somatic condition and reproductive status in the southern calamary *Sepioteuthis australis*. *Marine and Freshwater Research*, 55(4):423.

Hüssy, K. (2008). Otolith shape in juvenile cod (*Gadus morhua*): Ontogenetic and environmental effects. *Journal of Experimental Marine Biology and Ecology*, 364(1):35–41.

Hutchings, J. A. and Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(9):2126–2146.

Ibaibarriaga, L., Fernandez, C., Uriarte, A., and Roel, B. A. (2008). A two-stage biomass dynamic model for Bay of Biscay anchovy : a Bayesian approach. *ICES Journal of Marine Science*, 65(2):191–205.

Iwata, H. (2002). SHAPE: A computer program package for quantitative evaluation of biological shapes based on Elliptic Fourier Descriptors. *Journal of Heredity*, 93(5):384–385.

Jackson, G. D., Forsythe, J. W., Hixon, R. F., and Hanlon, R. T. (1997). Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency vs. statolith age analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 54:2907–2919.

Jackson, G. D. and Moltschaniwskyj, N. A. (2002). Spatial and temporal variation in growth rates and maturity in the Indo-Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Marine Biology*, 140(4):747–754.

Jackson, L. E., Kurtz, J. C., and Fisher, W. S. (2000). Evaluation guidelines for ecological indicators. EPA/620/R-99/005. Technical Report May, U.S. Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC.

Jansen, T., Degel, H., Vigneau, J., and Jardim, E. (2009). Definition of Standard Data-exchange Format for Sampling, Landings, and Effort Data from Commercial Fisheries. Technical report, ICES Cooperative research report n° 296, Copenhagen.

Jennings, S., Kaiser, M. J., and Reynolds, J. D. (2001a). *Marine fisheries ecology.* Blackwell Science, Oxford, United Kingdom.

Jennings, S., Kaiser, M. J., and Reynolds, J. D. (2001b). *Marine fisheries ecology.* Blackwell Science, Oxford, United Kingdom.

Jimenez, J.-J., Decaëns, T., and Rossi, J.-P. (2006). Stability of the spatio-temporal distribution and niche overlap in neotropical earthworm assemblages. *Acta Œcologica*, 30(3):299–311.

Joint, I. and Groom, S. B. (2000). Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing. *Journal of experimental marine biology and ecology*, 250(1-2):233–255.

Jouffre, D., Lanco, S., Gascuel, D., and Caverivière, A. (2002). Evaluation par modélisation analytique des effets de périodes de fermeture de la pêche du poulpe au Sénégal. In Caverivière, A., Thiam, M., and Jouffre, D., editors, *Le poulpe Octopus vulgaris*, pages 297–316. Paris, France, IRD edition.

Ju, S. J., Secor, D. H., and Harvey, H. R. (1999). Use of extractable lipofuscin for age determination of blue crab *Callinectes sapidus*. *Marine Ecology Progress Series*, 185(1):171–179.

Kantoussan, J., Ecoutin, J.-M., Fontenelle, G., Thiaw, O. T., Tito de Morais, L., and Lae, R. (2009). The relevance of size parameters as indicators of fishery exploitation in two West African reservoirs. *Aquatic ecology*, 43:1167–1178.

Kelman, E. J., Baddeley, R. J., Shohet, A. J., and Osorio, D. (2007). Perception of visual texture and the expression of disruptive camouflage by the cuttlefish, *Sepia officinalis*. *Proceedings. Biological sciences / The Royal Society*, 274(1616):1369–75.

Kennish, M. J. (2002). Environmental threats and environmental future of estuaries. *Environmental Conservation*, 29(01):78–107.

Keyl, F., Argüelles, J., Mariategui, L., Tafur, R., Wolff, M., and Yamashiro, C. (2008). A hypothesis on range expansion and spatio-temporal shifts in size at maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean. *California cooperative oceanic fisheries investigations reports*, 49:119–128.

Kuhl, F. P. and Giardina, C. R. (1982). Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing*, 18(3):236–258.

Lacoue-Labarthe, T., Warnau, M., Metian, M., Oberhänsli, F., Rouleau, C., and Bustamante, P. (2009). Biokinetics of Hg and Pb accumulation in the encapsulated egg of the common cuttlefish *Sepia officinalis*: radiotracer experiments. *The Science of the total environment*, 407(24):6188–95.

Lacoue-Labarthe, T., Warnau, M., Oberhänsli, F., Teyssié, J.-L., and Bustamante, P. (2010). Contrasting accumulation biokinetics and distribution of 241Am, Co, Cs, Mn and Zn during the whole development time of the eggs of the common cuttlefish, *Sepia officinalis*. *Journal of Experimental Marine Biology and Ecology*, 382(2):131–138.

Lacoue-Labarthe, T., Warnau, M., Oberhänsli, F., Teyssié, J.-L., Jeffree, R., and Bustamante, P. (2008a). First experiments on the maternal transfer of metals in the cuttlefish *Sepia officinalis*. *Marine pollution bulletin*, 57(6-12):826–31.

Lacoue-Labarthe, T., Warnau, M., Oberhänsli, F., Teyssié, J.-L., Koueta, N., and Bustamante, P. (2008b). Differential bioaccumulation behaviour of Ag and Cd during the early development of the cuttlefish *Sepia officinalis*. *Aquatic toxicology (Amsterdam, Netherlands)*, 86(3):437–46.

Larsonneur, C., Bouysse, P., and Affret, J. P. (1982). The superficial sediments of the English Channel and its western approaches. *Sedimentology*, 19:851–864.

Laurans, M., Gascuel, D., and Caverivière, A. (2002). Application d'un modèle global avec effet de l'environnement au stock de poulpe du Sénégal. In Caverivière, A., Thiam, M., and Jouffre, D., editors, *Le poulpe Octopus vulgaris*, Colloques et Séminaires, pages 255–267. IRD.

Lavit, C. (1988). *Analyse conjointe de tableaux quantitatifs.* Paris, France, masson edition.

Lazkano, I. (2008). Cost structure and capacity utilisation in multi-product industries: an application to the Basque trawl industry. *Environmental and Resource Economics*, 41(2):189–207.

Le Floc'h, P., Boncoeur, J., Daurès, F., and Thébaud, O. (2007). Analysing fishermen behaviour face to increasing energy costs a French case study. In *ICES ASC*, page ICES CM 2007/M:09, Helsinki.

Le Goff, R. and Daguzan, J. (1991). Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in South Brittany (France). *Bulletin of Marine Science*, 49(1-2):341–348.

Le Goff, R., Gauvrit, E., Pinczon du Sel, G., and Daguzan, J. (1998). Age group determination by analysis of the cuttlebone of the cuttlefish *Sepia officinalis* L . in reproduction in the Bay of Biscay. *Journal of Molluscan Studies*, 64(2):183–193.

Le Pape, O., Baulier, L., Cloarec, A., Martin, J., Le Loch, F., Désaunay, Y., and Desaunay, Y. (2007). Habitat suitability for juvenile common sole (*Solea solea*, L.) in the Bay of Biscay (France): A quantitative description using indicators based on epibenthic fauna. *Journal of Sea Research*, 57(2-3):126–136.

Le Pape, O., Holley, J., Guérault, D., and Désaunay, Y. (2003). Quality of coastal and estuarine essential fish habitats: estimations based on the size of juvenile common sole (*Solea solea* L.). *Estuarine, Coastal and Shelf Science*, 58(4):793–803.

Leblond, E., Daures, F., Berthou, P., Merrien, C., Pitel, M., and Jezequel, M. (2009). Synthèse des flottilles de pêche 2007 Flotte de Mer du Nord - Manche - Atlantique. Technical report, Ifremer, Brest.

Leblond, E., Daures, F., Berthou, P., Merrien, C., Pitel-Roudaut, M., Brigaudeau, C., Demaneche, S., Jezequel, M., Sih, L. D. D. S. H. D., Bodere, E., and Le Blond, S. (2010). Synthèse des flottilles de pêche 2008 Flotte de Mer du Nord - Manche - Atlantique. Technical report, Ifremer, Brest.

Leslie, P. H. and Davis, D. H. S. (1939). An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology*, 8:94–113.

Lipinski, M. R. (1979). Universal maturity scale for the commercially important squids (Cephalopoda: Teuthoidea). The results of maturity classification of *Illex illecebrosus* (Le Sueur 1821) population for years 1973-1977. Technical report, ICNAF Res. Doc. 38, ser. 5364.

Lipinski, M. R. (1998). Cephalopod life cycles, patterns and exceptions. *South African Journal Of Marine Science*, 20:439–448.

Macdonald, P., Laurenson, C., and Johnson, A. (2007). Jig fishing pilot study in Shetland coastal waters. *NAFC Marine Centre, Fisheries development note N.*, 25.

Maguer, J.-F., L'Helguen, S., Madec, C., and Le Corre, P. (1998). Absorption et régénération de l'azote dans le système brassé de la Manche : productions nouvelle et régénérée. *Oceanologica Acta*, 21(6):861–870.

Mangold (1966). *Sepia officinalis* de la mer Catalane. *Vie Et Milieu - Life and Environment*, 17:961–1012.

Mangold (1987). Reproduction. In Boyle, P. R., editor, *Cephalopod life cycles vol 2. Comparative review*, pages 157–200. Academic Press, London, UK.

Mangold, K. (1989). *Céphalopodes, traité de zoologie : anatomie, systématique, biologie.* Masson, Paris, France.

Mangold, K. and von Boletzky, S. (1985). Biology and distribution of early juvenile cephalopods. *Vie Et Milieu - Life and Environment*, 35:304.

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A. J., and Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology letters*, 8(11):1235–1246.

Mattacola, A. D., Maddock, L., and Denton, E. J. (1984). Weights and lengths of *Sepia officinalis* trawled by the laboratory's boats, 1978–1983. *Journal of the Marine Biological Association of the United Kingdom*, 64(03):735–737.

Mc Dougall, A. (2004). Assessing the use of sectioned otoliths and other methods to determine the age of the centropomid fish, barramundi (*Lates calcarifer*) (Bloch), using known-age fish. *Fisheries Research*, 67(2):129–141.

Medhioub, A. (1986). *Etude de la croissance et la maturation sexuelle de la population de seiche des côtes normandes.* Phd, Université de Caen.

Mesnil, B. (2003). The Catch-Survey Analysis (CSA) method of fish stock assessment: an evaluation using simulated data. *Fisheries Research*, 63(2):193–212.

Mesnil, B. (2008). Public-aided crises in the French fishing sector. *Ocean & Coastal Management*, 51(10):689–700.

Mesnil, B. (2012). The hesitant emergence of maximum sustainable yield (MSY) in fisheries policies in Europe. *Marine Policy*, 36(2):473–480.

Mesnil, B. and Rochet, M.-J. (2010). A continuous hockey stick stock–recruit model for estimating MSY reference points. *ICES Journal of Marine Science*, 67(8):1780–1784.

Metcalf, J., Arnold, G., and Mcdowall, R. (2002). Migration. In Hart, P. J. B. and Reynolds, J. D., editors, *Handbook of Fish Biology and Fisheries Volume 1: Fish Biology*, page 413. Blackwell Publishing.

Meyer, W. T. (1913). *Tintenfische; mit besonderer Berücksichtigung von Sepia und Octopus.* Leipzig.

Ministère de l'Agriculture de l'Agroalimentaire et de la Forêt, M. (2009). Fonds de prévention des aléas à la pêche : la France engage la procédure suite à la décision de la Commission Européenne http://agriculture.gouv.fr/fonds-de-prevention-des-aleas-a-la.

Ministère de l'Ecologie du Développement Durable et de L'Enérgie, M. (2009). Les prix de vente moyens des carburants, du fioul domestique et des fiouls lourds en France, en euros. http://www.developpement-durable.gouv.fr/energie/petrole/se_cons_fr.htm.

Miramand, P. and Bentley, D. (1992). Concentration and distribution of heavy metals in tissues of two cephalopods, *Eledone cirrhosa* and *Sepia officinalis*, from the French coast of the English Channel. *Marine Biology*, 114(3):407–414.

Miramand, P., Bentley, D., and Chanu, S. (1991). Concentration et distribution dans les tissus de seiches *Sepia officinalis* prélevés en Manche de 11 éléments traces (Ag, Cd, Co, Cr, Cu, Fe, Mn, Ni, Pb, V, Zn). In Boucaud-Camou, E., editor, *La seiche / The Cuttlefish*, pages 249–262, Caen, France. Université de Caen.

Miramand, P., Bustamante, P., Bentley, D., and Kouéta, N. (2006). Variation of heavy metal concentrations (Ag, Cd, Co, Cu, Fe, Pb, V, and Zn) during the life cycle of the common cuttlefish *Sepia officinalis. The Science of the total environment*, 361(1-3):132–43.

Moltschaniwskyj, N. A. and Martinez, P. (1998). Effect of temperature and food levels on the growth and condition of juvenile *Sepia elliptica* (Hoyle 1885): an experimental approach. *Journal of Experimental Marine Biology and Ecology*, 229(2):289–302.

Moreno, A., Azevedo, M., Pereira, J. a., and Pierce, G. J. (2007). Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. *Marine Biology Research*, 3(1):49–59.

Moreno, A., Cunha, M. M., and Pereira, J. a. M. F. (1994). Population biology of veined squid (*Loligo forbesi*) and European Squid (*Loligo vulgaris*) from the Portuguese coast. *Fisheries Research*, 21(1-2):71–86.

Moreno, A., Pereira, J. a., Arvanitidis, C., Robin, J.-P., Koutsoubas, D., Perales-Raya, C., Cunha, M. M., Balguerias, E., and Denis, V. (2002). Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. *Bulletin of Marine Science*, 71(1):515–534.

Moreno, A., Pereira, J. a., and Cunha, M. (2005). Environmental influences on age and size at maturity of *Loligo vulgaris*. *Aquatic Living Resources*, 18(04):377–384.

Morte, S., Redon, M. J., and Sanz-Brau, A. (1997). Feeding habits of juvenile *Mustelus mustelus* (Carcharhiniformes, Triakidae) in the western Mediterranean. *Cahiers de biologie marine*, 38(2):103–107.

Nabhitabhata, J., Asawangkune, P., Amornjaruchit, S., and Promboon, P. (2001). Tolerance of eggs and hatchlings of neritic cephalopods to salinity changes. *Phuket marine biological center special publication*, 25:91–99.

Nabhitabhata, J. and Nilaphat, P. (2000). Behaviour of juvenile cephalopods, preference for texture and brightness of substrata. *Phuket marine biological center special publication*, 21:103–112.

Newman, S. J. (2002). Growth rate, age determination, natural mortality and production potential of the scarlet seaperch, *Lutjanus malabaricus* Schneider 1801, off the Pilbara coast of north-western Australia. *Fisheries Research*, 58(2):215–225.

O'Dor, R. K. (1998). Can understanding squid life-history strategies and recruitment improve management? *South African Journal Of Marine Science*, 20:193–206.

O'Dor, R. K. and Dawe, E. G. (1998). *Illex illecebrosus*. In Rodhouse, P. G., Dawe, E. G., and O'Dor, R. K., editors, *Squid recruitment dynamics. FAO Fisheries Technical paper 376*, pages 77–104. Food and Agriculture Organization of the United Nations, Rome, Italy.

O'Dor, R. K. and Webber, D. M. (1986). The constraints on cephalopods: why squid aren't fish. *Canadian journal of zoology*, 64(8):1591–1605.

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., and Dieckmann, U. (2004). Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428:932–935.

Olyott, L. J. H., Sauer, W. H. H., and Booth, A. J. (2006). Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. *ICES Journal of Marine Science*, 63:1649–1664.

Otero, J. (2006). *Ecologia del pulpo comun (Octopus vulgaris) en un area afloramiento costero (Galicia, NE Atlantico)*. Phd, University of Vigo, Spain.

Palmegiano, G. and D'Apote, M. (1983). Combined effects of temperature and salinity on cuttlefish (*Sepia officinalis* L.) hatching. *Aquaculture*, 35:259–264.

Parente, J., Fonseca, P., Henriques, V., and Campos, A. (2008). Strategies for improving fuel efficiency in the Portuguese trawl fishery. *Fisheries Research*, 93(1-2):117–124.

Payne, A. G., Agnew, D. J., and Pierce, G. J. (2006). Trends and assessment of cephalopod fisheries. *Fisheries Research*, 78(1):1–3.

Pelletier, D., Mahevas, S., Drouineau, H., Vermard, Y., Thebaud, O., Guyader, O., and Poussin, B. (2009). Evaluation of the bioeconomic sustainability of multi-species multi-fleet fisheries under a wide range of policy options using ISIS-Fish. *Ecological Modelling*, 220(7):1013–1033.

Pierce, G. J., Allcock, L., Bruno, I., Bustamante, P., González, A. F., Guerra, A., Jereb, P., Lefkaditou, E., Malham, S., Moreno, A., Pereira, J. a., Piatkowski, U., Rasero, M., Sánchez, P., Santos, M. B. n., Santurtún, M., Seixas, S., Sobrino, I., and Villanueva, R. (2010). Cephalopod biology and fisheries in Europe. Technical report, ICES Cooperative research report n° 303, Copenhagen.

Pierce, G. J., Bailey, N., Stratoudakis, Y., and Newton, A. (1998). Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES Journal of Marine Science*, 55(1):14–33.

Pierce, G. J. and Guerra, A. (1994). Stock assessment methods used for cephalopod fisheries. *Fisheries Research*, 21(1–2):255–285.

Pierce, G. J., Valavanis, V. D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J. M., Katara, I., Piatkowski, U., Pereira, J. a., Balguerias, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtún, M., Boyle, P. R., Hastie, L. C., MacLeod, C. D., Smith, J. M., Viana, M., González, A. F., and Zuur, A. F. (2008). A review of cephalopod–environment interactions in European Seas. *Hydrobiologia*, 612(1):49–70.

Pierce, G. J., Zuur, A. F., Smith, J. M., Begoña Santos, M., Bailey, N., Chen, C.-S., and Boyle, P. R. (2005). Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters. *Aquatic Living Resources*, 18(04):327–340.

Pilling, G., Grandcourt, E. M., and Kirkwood, G. P. (2003). The utility of otolith weight as a predictor of age in the emperor *Lethrinus mahsena* and other tropical fish species. *Fisheries Research*, 60(2-3):493–506.

Pinczon du Sel, G. and Daguzan, J. (1997). A note on sex ratio, length and diet of a population of cuttlefish Sepia officinalis L. (Mollusca: Cephalopoda) sampled by three fishing methods. *Fisheries Research*, 32(2):191–195.

Pingree, R. D. (1980). Chapter 13 Physical Oceanography of the Celtic Sea and English Channel. In F.T. Banner, M. B. C. and Massie, K. S., editors, *The North-West European Shelf Seas: The Sea Bed and the Sea in Motion II. Physical and Chemical Oceanography, and Physical Resources*, volume 24, Part B of *Elsevier Oceanography Series*, pages 415–465. Elsevier.

Pita, C., Dickey, H., Pierce, G. J., Mente, E., and Theodossiou, I. (2010). Willingness for mobility amongst European fishermen. *Journal of Rural Studies*, 26(3):308–319.

Pope, J. (1972). An investigation of the accuracy of virtual population analysis using cohort analysis. *Research Bulletin ICANF*, 9:65–74.

Portail CHARM III - Interreg IV, ©. (2012). Atlas des pêcheries de Manche, Channel fisheries Atlas. Engelhard G., Vignot C., Leblond E., Lesueur M., Guitton J. http://charm-project.org/fr/outils/atlas-des-pecheries/atlas-des-pêcheries-outils.

Post, D. M. (2002). The long and short of food-chain length. *Trends in Ecology and Evolution*, 17(6):269–277.

Priour, D. (2009). Numerical optimisation of trawls design to improve their energy efficiency. *Fisheries Research*, 98(1-3):40–50.

Quetglas, A. and Morales-Nin, B. (2004). Age and growth of the ommastrephid squid *Todarodes sagittatus* from the western Mediterranean Sea. *Journal of the Marine Biological Association of the UK*, 84(02):421–426.

Rees, H. L., Pendle, M. A., Waldock, R., Limpenny, D. S., and Boyd, S. E. (1999). A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES Journal of Marine Science*, 56(2):228–246.

Reid, A., Jereb, P., and Roper, C. F. E. (2005). Family Sepiidae. In Jereb, P. and Roper, C. F. E., editors, *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fishery Purpos*, number 1966, page 262. Food and Agriculture Organization of the United Nations, Rome, Italy, fao edition.

Reznick, D., Lindbeck, E., and Bryga, H. (1989). Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences*, 46(1):108–112.

Richard, A. (1971). *Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de Sepia officinalis L. (Mollusque Céphalopode)*. Phd, University of Lille I.

Richard, A. (1975). Corrélations biologiques chez la seiche *Sepia officinalis*. *Haliotis*, 5:186–195.

Rijnsdorp, A. (1996). Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. *ICES Journal of Marine Science*, 53(6):1170–1184.

Riou, P., Le, O., and Rogers, S. I. (2001). Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel : application of a combined method using generalized linear models and a geographic information system. *English*, 14(2):125–135.

Robin, J.-P. and Denis, V. (1999). Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *Journal of Applied Ecology*, 36(1):101–110.

Rocha, F. and Guerra, A. (1999). Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (North-West Spain). *Journal of the Marine Biological Association of the UK*, 79(04):697–707.

Rocha, F., Guerra, A., Prego, R., and Piatkowski, U. (1999). Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). *Journal of Plankton Research*, 21(1):21–33.

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., and Le Pape, O. (2010). Effect of nursery habitat degradation on flatfish population: Application to Solea solea in the Eastern Channel (Western Europe). *Journal of Sea Research*, 64(1-2):34–44.

Rodhouse, P. G. and Nigmatullin, C. M. (1996). Role as Consumers. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351(1343):1003–1022.

Rodhouse, P. G., Symon, C., and Hatfield, E. M. C. (1992). Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series*, 89:183–195.

Roel, B. A. and Butterworth, D. S. (2000). Assessment of the South African chokka squid *Loligo vulgaris reynaudii* Is disturbance of aggregations by the recent jig fishery having a negative impact on recruitment ? *Fisheries Research*, 48:213–228.

Roel, B. A., De Oliveira, J. A. A., and Beggs, S. (2009). A two-stage biomass model for Irish Sea herring allowing for additional variance in the recruitment index caused by mixing of stocks. *ICES Journal of Marine Science*, 66(8):1808–1813.

Rolland, A., Bertrand, F., Maumy, M., and Jacquet, S. (2009). Assessing phytoplankton structure and spatio-temporal dynamics in a freshwater ecosystem using a powerful multiway statistical analysis. *Water research*, 43(13):3155–3168.

Roper, C. F. E., Sweeney, M. J., and Nauen, E. (1984). FAO Species catalogue. Vol 3: Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. Technical report, FAO Fisheries Synopsis, 125(3), Rome.

Rosenberg, A. A., Kirkwood, G. P., Crombie, J. A., and Beddington, J. R. (1990). The assessment of stocks of annual squid species. *Fisheries Research*, 8(4):335–350.

Royer, J. (2002). *Modélisation des stocks de céphalopodes de Manche.* Phd, University of Caen.

Royer, J., Periès, P., and Robin, J.-P. (2002). Stock assessments of English Channel loliginid squids: updated depletion methods and new analytical methods. *ICES Journal of Marine Science*, 59(3):445–457.

Royer, J., Pierce, G. J., Foucher, E., and Robin, J.-P. (2006). The English Channel stock of *Sepia officinalis*: Modelling variability in abundance and impact of the fishery. *Fisheries Research*, 78(1):96–106.

Salman, A., Bilecenoglu, M., and Güçlüsoy, H. (2001). Stomach contents of two Mediterranean monk seals (*Monachus monachus*) from the Aegean Sea, Turkey. *Journal of the Marine Biological Association of the UK*, 81(4):719–720.

Salomon, J.-C. (1994). Quelques aspects hydrodynamiques de la Manche. *Equinoxe*, 47-48:68–73.

Samples, K. C. (1983). An Economic Appraisal of Sail-Assisted Commercial Fishing Vessels in Hawaiian Waters. *Marine fisheries review*, 45(7-9):50–55.

Sampson, D. B. (1991). Fishing tactics and fish abundance, and their influence on catch rates. *ICES Journal of Marine Science*, 48(3):291–301.

Sato, T. and Hatanaka, H. (1983). A review of assessment of Japanese distant-water fisheries for cephalopods. In Caddy, J. F., editor, *Advances in assessment of world cephalopod resources*, pages 145–203. FAO Fisheries Technical Paper No. 231, Rome, Italy.

Schau, E., Ellingsen, H., Endal, A., and Aanondsen, S. A. (2009). Energy consumption in the Norwegian fisheries. *Journal of Cleaner Production*, 17(3):325–334.

Schau, E. M. and Fet, A. M. (2008). LCA studies of food products as background for environmental product declarations. *The International Journal of Life Cycle Assessment*, 13(3):255 – 264.

Semmens, J. M., Pecl, G. T., Gillanders, B. M., Waluda, C. M., Shea, E. K., Jouffre, D., Ichii, T., Zumholz, K., Katugin, O. N., Leporati, S. C., and Shaw, P. W. (2007). Approaches to resolving cephalopod movement and migration patterns. *Reviews in Fish Biology and Fisheries*, 17(2-3):401–423.

Semmens, J. M., Pecl, G. T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J. B., and Rigby, P. R. (2004). Understanding octopus growth: patterns, variability and physiology. *Marine and Freshwater Research*, 55(4):367.

Shafiee, S. and Topal, E. (2010). A long-term view of worldwide fossil fuel prices. *Applied Energy*, 87(3):988–1000.

Shaw, R. (1994). An economic description and assessment of the squid catching industry in the UK, Portugal and Spain. *Fisheries Research*, 21(1-2):287–303.

Sheehy, M. R. J., Shelton, P. M. J., Wickins, J. F., Belchier., M., and Gaten, E. (1996). Ageing the European lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. *Marine Ecology Progress Series*, 143(1):99–111.

Shin, Y.-J. and Rochet, M.-J. (1998). A model for the phenotypic plasticity of North sea herring growth in relation to trophic conditions. *Aquatic Living Resources*, 11(05):315–324.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*, 62(3):384–396.

Smith, P. J. (1994). *Genetic diversity of marine fisheries resources. Possible impacts of fishing.* FAO Fisheries Technical Paper No. 344, Rome, Italy.

Southward, A. J., Boalch, G. T., and Maddock, L. (1988). Fluctuations in the herring and pilchard fisheries of devon and cornwall linked to change in climate since the 16^{th} century. *Journal of the Marine Biological Association of the United Kingdom*, 68(03):423–445.

Southward, A. J. and Roberts, E. K. (1987). One hundred years of marine research at Plymouth. *Journal of the Marine Biological Association of the UK*, 67(3):465–506.

Sparholt, H., Bertelsen, M., and Lassen, H. (2007). A meta-analysis of the status of ICES fish stocks during the past half century West of Scotland. *ICES Journal of Marine Science*, 64(4):707–713.

Stefansson, G. (1996). Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES Journal of Marine Science*, 53(3):577–588.

Sumaila, U. R., Teh, L., Watson, R., Tyedmers, P., and Pauly, D. (2008). Fuel price increase, subsidies, overcapacity, and resource sustainability. *ICES Journal of Marine Science*, 65(6):832–840.

Syrjala, S. E. (2000). Critique on the use of the delta distribution for the analysis of trawl survey data. *ICES Journal of Marine Science*, 57(4):831–842.

Tétard, A., Boon, M., Bennett, D., Berthou, P., Bossy, S., Casey, J., De Clerck, R., Delpech, J. P., Dintheer, C., Giret, M., Large, P., Latroulte, D., Lemoine, M., Millner, R., Morizur, Y., Ozanne, S., Palmer, D., Pawson, M., Pickett, G., and Vince, M. (1995). Catalogue international des activités des flottilles de Manche, approche des interactions techniques. Technical report, Ifremer, Brest, France.

Thioulouse, J. and Chessel, D. (1987). Les analyses multi-tableaux en écologie factorielle. I De la typologie d'état à la typologie de fonctionnement par l'analyse triadique. Acta Œcologica, Œcologia Generalis 8:463-480. http://pbil.univ-lyon1.fr/R/article. *Acta Oecologica*, 8(4):463–480.

Thioulouse, J., Simier, M., and Chessel, D. (2004). Simultaneous analysis of a sequence of paired ecological tables. *Ecology*, 85(1):272–283.

Tidd, a. N., Hutton, T., Kell, L. T., and Padda, G. (2011). Exit and entry of fishing vessels: an evaluation of factors affecting investment decisions in the North Sea English beam trawl fleet. *ICES Journal of Marine Science*, 68(5):961–971.

Trenkel, V. M. (2008). A two-stage biomass random effects model for stock assessment without catches : What can be estimated using only biomass survey indices ? *Canadian Journal of Fisheries and Aquatic Sciences*, 65(6):1024–1035.

Tucker, L. R. (1966). Some mathematical notes on three-mode factor analysis. *Psychometrika*, 31(3):279–311.

Tyedmers, P. (2001). Energy consumed by North Atlantic fisheries. In Zeller, D., Watson, R., and Pauly, D., editors, *Fisheries' Impacts on North Atlantic ecosystems: Catch, Effort and National/Regional Datasets*, pages 12–34. Vancouver, fisheries edition.

Tyedmers, P. H., Watson, R., and Pauly, D. (2005). Fueling global fishing fleets. *Ambio*, 34(8):635–8.

Ulrich, C., Le Gallic, B., Dunn, M. R., and Gascuel, D. (2002). A multi-species multi-fleet bioeconomic simulation model for the English Channel artisanal fisheries. *Fisheries Research*, 58(3):379–401.

Vecchione, M. (1999). Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during el nino of 1987. *Fishery bulletin*, 97:1025–1030.

Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., and Gascuel, D. (2010). Identifying fishing trip behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov Models. *Ecological Modelling*, 221(15):1757–1769.

Videau, C., Ryckaert, M., and L'helguen, S. (1998). Phytoplankton in the Bay of Seine (France). Influence of the river plume on primary productivity. *Oceanologica Acta*, 21(6):907–921.

von Boletzky, S. (1974). The larvae of cephalopods: a review. *Thalassia Jugoslavia*, 10:45–76.

von Boletzky, S. and Hanlon, R. T. (1983). A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Memoirs of the National Museum, Victoria*, 44:147–187.

Waluda, C. M. and Pierce, G. J. (1998). Temporal and spatial pattern in the distribution of squid *Loligo spp* in UK waters. *South African Journal Of Marine Science*, 20:323–336.

Waluda, C. M., Rodhouse, P. G., Podestá, P. G., Trathan, P. N., and Pierce, G. J. (2001). Oceanography of *Illex argentinus* (Cephalopoda: Ommastrophidae) hatching grounds and influences on recruitment variability. *Marine Biology*, 139:671–679.

Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. (1999). Influence of oceanographic variability on recruitment of *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. *Marine Ecology Progress Series*, 183:159–167.

Wang, J., Pierce, G. J., Boyle, P. R., Denis, V., Robin, J.-P., and Bellido, J. M. (2003). Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences–a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. *ICES Journal of Marine Science*, 3139(03):1149–1158.

Wells, M. J. and Wells, J. (1991). Is *Sepia* really an octopus? In Boucaud-Camou, editor, *La seiche / The Cuttlefish*, pages 79–92. Centre de publication de l'Université de Caen, Caen, France.

Wilen, J. E., Smith, M. D., Lockwood, D., and Botsford, L. W. (2002). Avoiding surprises: incorporating fisherman behavior into management models. *Bulletin of Marine Science*, 70(2):553–575.

Woillez, M., Petitgas, P., Huret, M., Struski, C., and Léger, F. (2010). Statistical monitoring of spatial patterns of environmental indices for integrated ecosystem assessment: Application to the Bay of Biscay pelagic zone. *Progress In Oceanography*, 87(1-4):83–93.

Young, I., Pierce, G. J., Daly, H. I., Santos, M. B. n., Key, L. N., Bailey, N., Robin, J.-P., Bishop, A., Stowasser, G., and Nyegaard, M. (2004). Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). *Fisheries Research*, 69(2):211–227.

Zheng, J., Murphy, M. C., and Kruse, G. H. (1997). Application of a Catch-Survey Analysis to Blue King Crab Stocks Near Pribilof and St . Matthew Islands. *Alaska Fishery Research Bulletin*, 4(1):62–74.

Zielinski, S. and Pörtner, H.-O. (2000). Oxidative stress and antioxidative defense in cephalopods : a function of metabolic rate or age? *Comparative Biochemistry and Physiology Part B*, 125:147–160.

Zumholz, K., Hansteen, T. H., Klügel, A., and Piatkowski, U. (2006). Food effects on statolith composition of the common cuttlefish (*Sepia officinalis*). *Marine Biology*, 150(2):237–244.

english

Productions scientifiques

Publications

Gras, M., Roel, B. A., Coppin, F., Foucher, E. and Robin, J.-P. (2013). A two stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis*) stock. Soumis à ICES Journal of Marine Science.

Gras, M., Safi, G., Lebredonchel, H., Quinquis, J., Lepoittevin, J., Koueta, N. and Robin, J.-P. (2013). English Channel cuttlefish (*Sepia officinalis*) stock structure in the reproduction period under warming and high fishing pressure context. En préparation.

Gras, M., Quinquis, J., Foucher, E. and Robin, J.-P. (2013). Fishing effort allocation under increased fuel price context : The case study of French trawlers operating in the English Channel. En préparation.

Gras, M., Caplat, C., Grangeré, K., Qin, F., Bloor, I., Jackson, E. and Robin J.-P. (2013). Contribution of inshore nurseries to the cuttlefish (*Sepia officinalis*) recruitment using a multi-criteria approach. En préparation.

Safi G., Bloor I., **Gras, M.**, Grangeré K., Jackson E., Robin J.P., Koueta N. (2013). Spatial and temporal variation in characteristics of cuttlefish *Sepia officinalis* L., early life history. Soumis à Journal of Sea Research.

Gras, M., Beibou, E., Wagne, O., Bouzoumah, M., Labrosse, P. and Morand, P. (2010). Survey based proxy-localisation techniques for spatial distribution assessment of small-scale fishing activity : the case study of the Banc d'Arguin National Park (Mauritanie). In Nishida, T., and Caton, A.E. (Editors). "GIS/SPATIAL ANALYSES IN FISHERY AND AQUATIC SCIENCES (VOLUME 4)" International Fishery GIS Society, Saitama, Japan : 337-350.

Communications en congrès

Gras, M., Roel, B. A., Coppin, F., Foucher, E. and Robin, J.-P. (2012). A biomass model applied to the English Channel cuttlefish stock to disentangle fishing pressure and recruitment variability. Cephalopod International Advisory Council Symposium, 2012 (Florianopolis, Brésil).

Robin, J.-P., **Gras, M.**, Grangeré, K., Caplat, C., Shaw, P., Jackson, E., Bloor, I., Roel, B., Coppin, F. (2012). Biological variation in coastal stages of the English Channel common cuttlefish (*Sepia officinalis*) and fishery implications. Cephalopod International Advisory Council Symposium, 2012 (Florianopolis, Brésil).

Safi G., **Gras, M.**, Bloor I., Robin J.P., Koueta N., (2012). Impact of major environmental variables on the physiological characteristics of cuttlefish *Sepia officinalis* L. pre-recruits in different spawning sites of the English Channel. Cephalopod International Advisory Council Symposium, 2012 (Florianopolis, Brésil).

Safi G., Bloor I., **Gras, M.**, Jackson E., Robin J.P., Koueta N., (2011). Cuttlefish *Sepia officinalis* L. early life history from different coastal areas of the English Channel : comparison between experimental hatchlings and wild pre-recruits physiological performances. ICES Annual Science Conference, 2011 (Gdansk, Pologne).

Gras, M., Quinquis, J., Foucher, E. et Robin J.-P. (2011). Tendance de l'effort de pêche des chalutiers de fond à panneaux français en Manche et conséquences sur les ressources de céphalopodes. 10ème Forum de l'Association Française d'Halieumétrie, 2011 (Boulogne-sur-Mer, France).

Safi G., Bloor I., **Gras, M.**, Jackson E., Robin J.P., Koueta N., (2011). Comparison of the physiological performances of cuttlefish juveniles *Sepia officinalis* L. pre-recruits from different coastal areas of the English Channel. Euroceph, Cephalopod Biology Research in the 21st Century – A European Perspective, 2011 (Naples, Italie).

Gras, M., Goetz, O., Lepoittevin, J. and Robin, J.-P. (2010). English Channel cuttlefish (*Sepia officinalis*) stock structure in the reproduction period. ICES Annual Science Conference, 2010 (Nantes, France).

Posters

Gras, M., Caplat, C., Bloor, I., Jackson, E. and Robin J.-P. (2012). Chemical elements in the English Channel cuttlefish (*Sepia officinalis*) : differences among coastal juveniles and origin of offshore recruits. Cephalopod International Advisory Council Symposium, 2012 (Florianopolis, Brésil).

Gras, M., Roel B. A., Foucher E., Robin J.-P., (2011). A two stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis* L.) stock. ICES Annual Science Conference, 2011 (Gdansk, Pologne).

Lebredonchel, H., **Gras, M.**, Safi, G., Quinquis, J., Lepoittevin, J., Foucher, E. and Robin, J.-P. (2010). Structure du stock de seiche (*Sepia officinalis*) en Manche en période de reproduction. 10ème Forum de l'Association Française d'Halieumétrie, 2011 (Boulogne-sur-Mer, France).

Gras, M., Quinquis, J., Foucher, E. and Robin, J.-P. (2010). Recent trends in fishing effort by French otter bottom trawl in the English Channel and consequences on cephalopod resources. ICES Annual Science Conference, 2010 (Nantes, France).

Contribution of inshore spawning areas to the recruitment of English Channel cuttlefish *Sepia officinalis* stock: relationship between pre-recruit stage success and resource abundance.

Abstract

The English Channel cuttlefish *Sepia officinalis* is the most important cephalopod stock in the N-E Atlantic but is only managed by local measures, mainly due to a lack of suitable tools. The objective of this work is therefore to improve the knowledge of its population dynamic, particularly the parameters influencing the resource abundance. After a summary of the state of the art, in a first step, the exploration of the stock structure during the reproduction period revealed that, in a warming and high fishing pressure context, the life history traits of cuttlefish have changed and a percentage of one year old cuttlefish are mature. In a second step, the influence of the fuel price on the spatial allocation of the French trawling effort was highlighted and this métier is the most suitable to derive cuttlefish abundance indices. In a third step, a two stage biomass model, a suitable model to assess exploited marine populations with poor age data, was developed and enabled the development of two indicators of the fishing impact on the exploited cohort: the stock-recruitment relationship and the exploitation rate. In a fourth and final step, the contribution of 3 spawning areas to the recruitment was explored using 3 different techniques. Results indicate that the central stock is a mix between different spawning areas and seems to be influenced by different environmental and anthropic parameters. Finally, results are discussed in the context of each life cycle phase (reproduction, pre-recruit stage, recruitment and exploitation) and perspectives are presented.

Keywords: *Sepia officinalis*; English Channel; Life cycle; Fisheries; Stock assessment model; Recruitment.

Contribution des frayères côtières au recrutement du stock de seiche *Sepia officinalis* de Manche : lien entre le succès de la phase pré-recrutée et l'abondance de la ressource.

Résumé

La seiche de Manche *Sepia officinalis*, le plus important stock de céphalopodes de l'Atlantique N-E, est uniquement géré par des mesures locales, en raison d'un manque d'outils appropriés. L'objectif de ce travail est ainsi d'améliorer les connaissances sur la dynamique de sa population, particulièrement sur les paramètres influançant l'abondance de la ressource. Après un résumé de l'état de l'art, l'exploration de la structure du stock durant la période de reproduction a dans un premier temps révélé que, dans un contexte de réchauffement et de forte pression de pêche, les traits d'histoire de vie de la seiche avaient changé et un pourcentage de seiche de un an étaient matures. Dans un second temps, l'influence du prix du gasoil sur la répartition spatiale de l'effort de pêche des chalutiers français a été mise en évidence et ce métier est le plus approprié pour calculer des indices d'abondance. Dans un troisième temps, un modèle de biomasse à 2 stades, adapté pour évaluer les populations marines exploitées avec peu de données d'âge, a été développé et a permis la mise en place de 2 indicateurs de l'impact de la pêche sur la cohorte exploitée : la relation stock-recrutement et le taux d'exploitation. Dans un quatrième et dernier temps, la contribution de 3 frayères au recrutement a été explorée à l'aide de 3 techniques différentes. Les résultats indiquent que le stock central est un mélange de différentes frayères et semble influencé par différents paramètres environnementaux et anthropiques. Enfin, les résultats sont discutés dans le cadre de chaque phase du cycle de vie (reproduction, phase pré-recrutée, recrutement, et exploitation) et des perspectives sont présentées.

Mots clés : *Sepia officinalis* ; Manche ; Cycle de vie ; Pêcheries ; Modèle d'Evaluation de stock ; Recrutement.