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par Sylvain BONHOMMEAU

Effets environnementaux sur la survie larvaire de l'Anguille (*Anguilla anguilla*) et conséquences sur le recrutement

Environmental effects on eel larval life and consequences on recruitment

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Soutenance le 16 juin 2008 devant le jury composé de :

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Introduction générale

November 6, 7, 8, 1989

Bill Watterson *Calvin & Hobbes* (Andrews McMeel Publishing)

300 MILLIONS. C'est le nombre d'œufs que peut produire le poisson lune (*Mola mola*), l'un des vertébrés les plus féconds. Le requin marteau (*Sphyrna tiburo*) est quant à lui vivipare et donne naissance à quelques individus. Deux poissons pélagiques, deux modes de reproduction et pourtant le même objectif : perpétuer l'espèce. Toutefois, les cas d'ovoviviparité et de viviparité sont rares et la dispersion des gamètes dans le milieu est le mode de reproduction majoritairement utilisé par les espèces marines. Elle permet d'atteindre des habitats propices et favorables au développement des individus, de diminuer la compétition entre eux en les disséminant sur un plus large territoire, d'échanger des individus entre populations distantes et de favoriser ainsi le brassage génétique et la colonisation de nouveaux milieux (Roughgarden *et al.*, 1985; Doherty *et al.*, 1995; Cury and Pauly, 2000). Cependant, cette stratégie comporte aussi des inconvénients : le taux de fécondation des œufs est diminué, la survie des larves dépend des conditions environne-

mentales (disponibilité en nourriture et contraintes physiques du milieu) et ces larves sont vulnérables aux prédateurs. La dispersion des gamètes dans le milieu est ainsi un mode de reproduction risqué et fortement dépendant de l'environnement. La phase larvaire est considérée comme la phase critique qui va influer sur le maintien de la population (Trippel and Chambers, 1997; Levin and Stunz, 2005).

Comprendre les fluctuations du recrutement : un enjeu majeur pour l'écologie halieutique

La compréhension des causes des fluctuations des stocks de poissons est l'un des principaux sujets d'étude de la recherche en halieutique. Du fait de l'importance des premiers stades de vie dans le déterminisme des fluctuations d'abondance des populations, ce domaine de recherche porte particulièrement sur la compréhension des variations du recrutement. Le recrutement désigne à la fois l'effectif de la classe d'âge la plus jeune accessible aux pêcheries et les processus qui aboutissent à cet effectif (Lasker, 1989). La recherche des déterminismes du recrutement date de plus d'un siècle (Cushing, 1982). Il a été très tôt identifié que les processus qui influencent le recrutement interviennent au niveau des plus jeunes stades de vie (Hjort, 1914). Ces processus relèvent de l'environnement rencontré par ces jeunes stades (ressources, prédateurs, environnement physique) et de la population des parents eux-mêmes (abondance, structure en âge et en taille, fécondité) (Trippel and Chambers, 1997). Nous présentons dans cette introduction les principaux phénomènes qui conditionnent la variabilité du recrutement.

Importance de la disponibilité en ressources pour les larves

L'influence de l'environnement sur le taux de mortalité des premiers stades de vie a été étudiée à différentes échelles fonctionnelles, spatiales et temporelles. La première hypothèse de Hjort (1914) ('*Critical period*') concerne la disponibilité en nourriture rencontrée par les jeunes poissons lors des premiers stades de leur développement. L'hypothèse de la coïncidence ('*Match-mismatch hypothesis*') met en relation des pics saisonniers de production planctonique et la présence des larves pour expliquer les variations du recrutement (Cushing, 1975). La seconde hypothèse de Hjort (1914) s'appuie sur les processus hydrodynamiques qui déterminent le transport advectif des larves. Ce transport vers des zones propices à leur survie est considéré comme déterminant pour le recrutement (Myers and Drinkwater, 1989). L'étude des écosystèmes d'upwelling a permis de montrer un lien entre les différentes échelles spatiales et temporelles des processus physiques et biotiques avec l'hypothèse de la fenêtre optimale de Cury and Roy (1989). Ainsi, à large échelle, la force de l'upwelling détermine la disponibilité en nourriture tandis qu'à une échelle plus locale, elle influence la turbulence et ainsi la probabilité de contact entre les larves et leur nourriture. La triade fondamentale de Bakun (1996) rend compte des différents processus physiques qui favorisent le recrutement : *i)* des processus d'enrichissement du milieu en nutriments permettent l'apparition d'une production primaire (upwelling, panaches des rivières) qui engendre des disponibilités en nourriture, *ii)* des processus de concentration (zones de convergences, fronts, stratification de la colonne d'eau) conditionnent la dérive des larves vers les zones enrichies qui leur sont favorables, et *iii)* des processus de rétention maintiennent ces larves au sein de ces environnements propices.

Influence de la prédation

La variabilité du recrutement est aussi conditionnée par la variabilité de la prédation. L'hypothèse "*bigger is better*" propose que les larves les plus grandes subissent une plus faible prédation de par leur capacité à échapper aux prédateurs (Bailey and Houde, 1989). Cushing (1975) formule aussi l'*hypothèse de durée du stade* qui relie les conditions trophiques avec la capacité de croissance, l'âge à la métamorphose et ainsi la capacité d'échapper à la prédation durant le stade larvaire. Le taux de prédation est lui-même fortement dépendant des conditions environnementales qui influent sur la biomasse de prédateurs (e. g. la prédation du sprat sur les jeunes stades de morues ; Nissling, 2004) ou sur l'abondance des autres proies privilégiées des prédateurs (e. g. la morue privilégie le capelan mais dans le cas de faibles abondances, se reporte sur le hareng ; De Barros *et al.*, 1998).

Les mécanismes densité-dépendant

Lorsque les taux de croissance, de survie ou de déplacement varient en fonction de la densité ou de l'abondance de la population, on parle de processus densité-dépendant (MacCall, 1990). Les mécanismes densité-dépendant sont reliés à la capacité du milieu et à la taille de la population (Myers and Cadigan, 1993). Ces processus sont notamment susceptibles d'apparaître aux différents stades de développement sous la forme d'une mortalité proportionnelle à la densité des individus ou encore d'une croissance limitée.

La relation stock - recrutement

Les processus qui conditionnent la survie larvaire sont déterminants pour le recrutement mais celui-ci est aussi relié à la biomasse féconde de la population. Le lien entre l'abondance des géniteurs et le recrutement est une question centrale pour la gestion des stocks exploités dans la mesure où cette relation doit permettre de déterminer l'effet que peut avoir l'exploitation du stock de géniteurs sur sa capacité à se renouveler. Cependant il n'existe que peu de preuves de l'existence de cette relation (Cushing, 1971; Myers and Barrowman, 1996; Gilbert, 1997). En effet, les modèles de relation stock-recrutement expliquent faiblement le recrutement étant donné le nombre d'observations limitées, le manque de précision des données (Hilborn et Walters, 1992) et la variabilité même du recrutement, indépendamment de la biomasse féconde. De plus, le potentiel reproducteur d'un stock dépend aussi du taux de maturité et de fécondité des différentes classes d'âge ainsi que de la viabilité des œufs au travers des effets maternels (Marshall *et al.*, 1998; Marteinsdottir and Steinarsson, 1998). Dans un stock à l'équilibre, la biomasse féconde influe peu sur le recrutement qui dépend principalement des effets de l'environnement, de la prédation et des mécanismes densité-dépendant décrits ci-dessus. En revanche, en dessous d'un certain seuil du stock reproducteur, le recrutement devient plus dépendant du stock. Les moyens de gestion à mettre en œuvre pour rétablir une population située dans cette phase dépensatoire sont bien plus contraignants que ceux qui permettent de maintenir une population à l'équilibre (Muradian, 2001).

Bien souvent, les observations manquent durant la phase larvaire pour comprendre et hiérarchiser les processus écologiques en jeu dans la fluctuation de la survie des jeunes stades et, donc, prédire le recrutement. Comment déterminer l'impact de ces processus écologiques sur la survie larvaire ? L'Anguille européenne (*Anguilla anguilla*) est un cas d'étude particulièrement intéressant pour aborder cette problématique générale de l'écologie halieutique. Sa phase larvaire est longue, sur des distances très importantes. Les problèmes liés à la dispersion et la survie des larves sont, dès lors, exacerbés :

- les adultes effectuent une longue migration trans-océanique avant d'arriver sur la zone de reproduction, mais les conditions de nourriture pour leur progéniture ne sont pas assurées (*hypothèse de match-mismatch*),
- la disponibilité en nourriture pour les larves fluctue à la fois durant leur premier stade de vie mais aussi durant leur migration particulièrement longue vers les côtes européennes (*hypothèse de la phase critique*),
- la longue migration augmente les probabilités de prédation (*hypothèse de la durée du stade*),
- les conditions océaniques et les processus de rétention affectent les larves sur une large échelle spatio-temporelle (*triade fondamentale*).

Ces caractéristiques du cycle de vie de l'Anguille peuvent permettre de mieux comprendre les processus écologiques impliqués mais aussi l'intérêt évolutif de la dispersion. Comment une espèce avec une phase larvaire si longue a-t-elle pu réussir à se perpétuer depuis 10 millions d'années ?

Distribution et cycle de vie

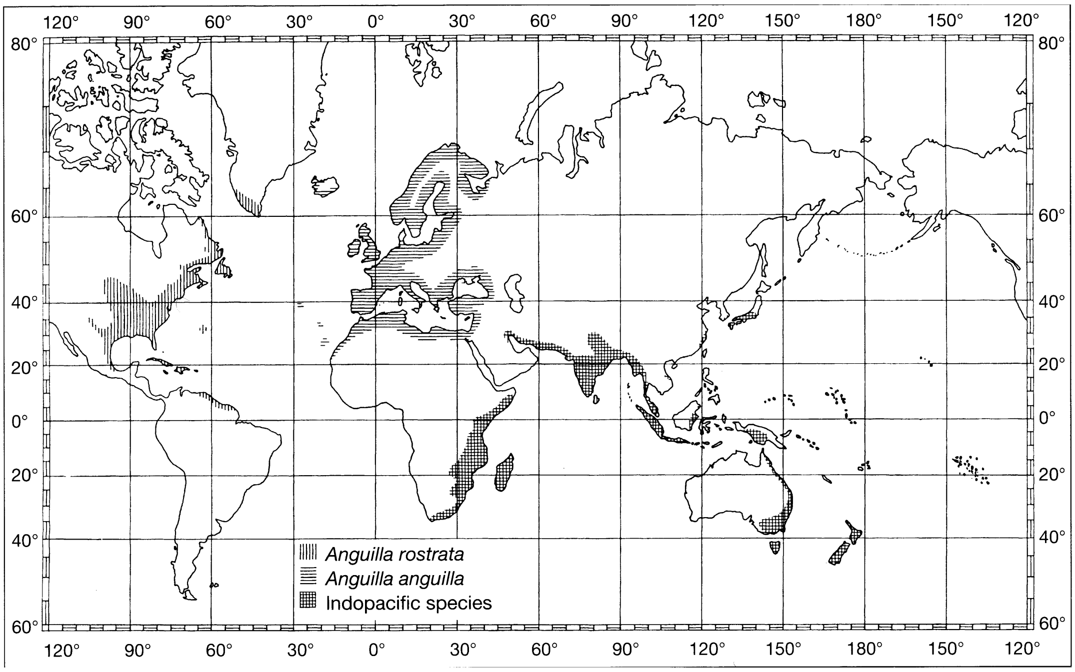

FIG. 1: Distribution géographique des différentes espèces d'Anguille (*in* Tesch, 2003).

Le genre *Anguilla* compte 15 espèces réparties sur tous les océans dans des zones tempérées ou tropicales (Fig. 1; Tesch, 2003). Dans ce travail, nous nous intéressons en particulier à l'Anguille européenne (*Anguilla anguilla*) dont l'aire de distribution s'étend du cercle polaire arctique aux côtes marocaines (Fig. 2; Schmidt, 1923).

Ce poisson migrateur vit alternativement en eau douce et en eau de mer (amphihalin) avec une phase de croissance en eau douce et une reproduction en mer (thalassotoque). Son cycle de vie (Fig. 3) est caractérisé par deux migrations transocéaniques entre l'aire de reproduction dans la mer des Sargasses et les aires de grossissement et de maturation dans les eaux littorales et dans les cours d'eau continentaux de l'Europe et de l'Afrique du Nord (Fig. 2; Schmidt, 1923). Ce cycle comporte deux métamorphoses : la première clôture la phase larvaire à l'issu de la migration océanique depuis la mer des Sargasses. Cette métamorphose intervient à la limite externe du plateau continental et voit la transformation des larves leptocéphales, transparentes et de forme aplatie (Fig. 3), en civelles de forme cylindrique qui, acquérant leur pigmentation, présentent une morphologie identique à celle des sub-adultes. La deuxième intervient peu avant la migration de reproduction et correspond à la transformation des anguilles jaunes en anguilles argentées qui vont migrer pour se reproduire dans la mer des Sargasses.

Le cycle de vie de l'Anguille européenne dans les eaux continentales est observé depuis longtemps. Environ 3 siècles avant J.-C., Aristote rapporte déjà la migration des anguilles vers la mer et suppose la remontée des alevins dans les cours d'eau. En 1684, Redi observe la migration des anguilles vers la mer, migration catadrome, puis la migration de remontée des cours d'eau des jeunes anguilles, migration anadrome, et suppose que la reproduction a lieu en pleine mer (Bertin, 1956). Jusqu'à la fin du XVII$^{\text{ème}}$, la reproduction de l'Anguille est entourée de mythes et légendes. Les anguilles se frotteraient contre les rochers et les lambeaux de peau qui se détachent de leurs corps donneraient naissance aux jeunes anguilles (*in* Bertin, 1956) ou encore d'autres modes de reproduction comme la parthénogenèse ou la scissiparité assureraient la pérennité de l'espèce (Lankester, 1872). En 1777, Mondini décrit le système de reproduction et identifie les ovaires ; puis Syrski décrit les organes reproducteurs mâles en 1874. La découverte de la métamorphose des leptocéphales en anguilles par Grassi (1896) va confirmer l'hypothèse de la phase marine de l'Anguille. L'intérêt économique de l'Anguille a très tôt généré des moyens financiers qui ont permis de mener des recherches scientifiques (Anonymous, 1882; Hjort, 1910; Schmidt, 1912; Cunningham, 1924). La semelparité de l'Anguille qui caractérise

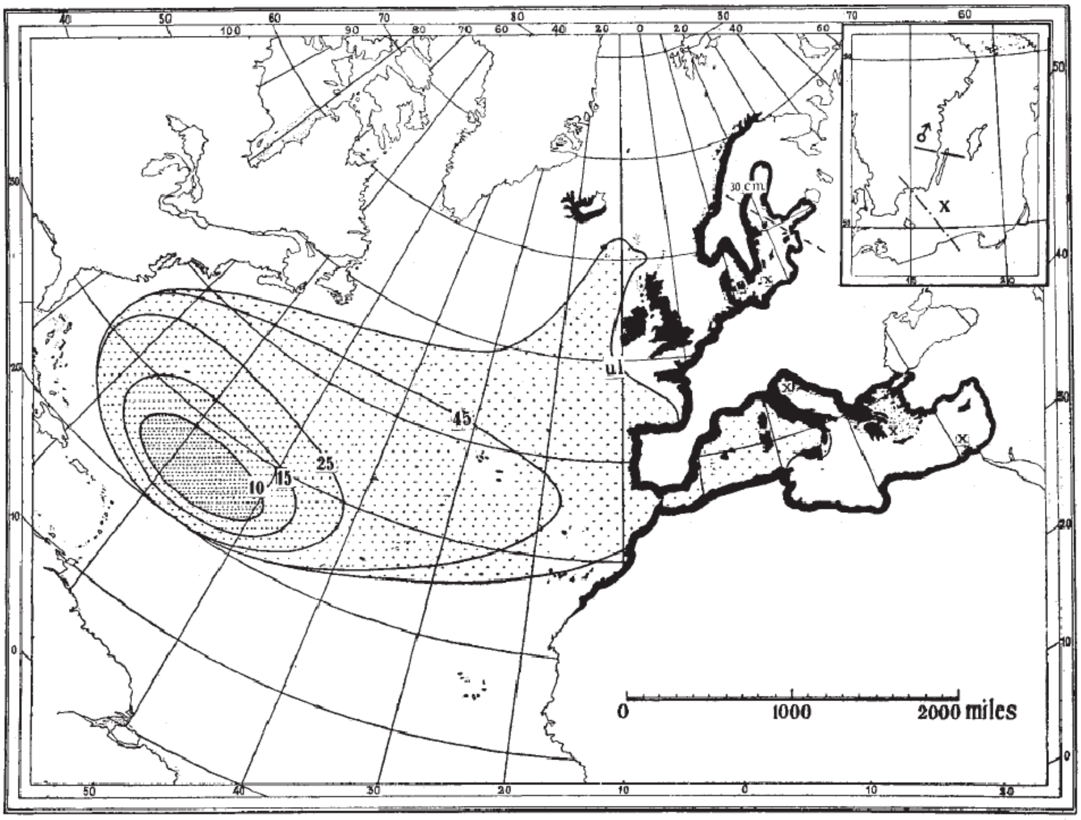

FIG. 2: Aire de ponte (à l'intérieur de la courbe 10 mm), distribution des larves (aire en pontillés) et des adultes (trait en gras) d'Anguille européenne (*in* Schmidt, 1923).

le fait que les individus meurent après l'unique reproduction, est supposé dès la fin du XIX$^{\text{ème}}$ siècle (Anonymous, 1882). Cela pose un problème de gestion important. Comment maintenir l'exploitation d'un stock qui n'a pas pu se reproduire ? Le Danemark a ainsi chargé des scientifiques d'élucider le mystère de la reproduction de l'Anguille et confié ces travaux de recherches à Johannes Schmidt. Dès lors, Schmidt va initier ses recherches pour trouver le lieu de ponte et finalement localiser l'aire de reproduction dans la mer des Sargasses en 1922.

Les fluctuations d'abondance

La remontée des civelles dans les eaux continentales est un phénomène biologique assez remarquable et de nombreuses descriptions relatent cet événement. Les fluctuations d'abondances de civelles sur les côtes sont observées depuis de nombreuses années. Chiapi (1934) reporte les variations interannuelles de remontée des civelles à Maccarese, près de Rome, à partir de données de la pêcherie civelière de 1922 à 1933 (*in* Bertin, 1956). Les

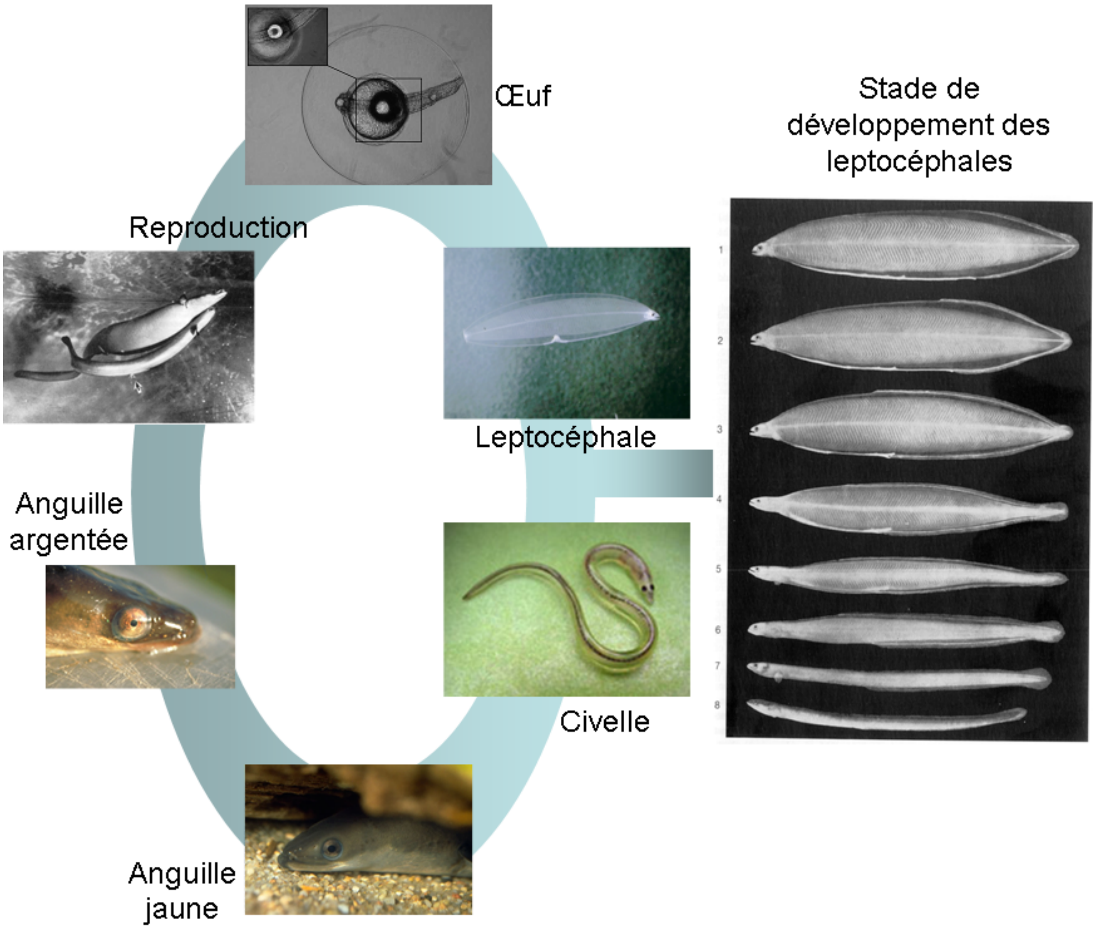

Fig. 3: Cycle de vie de l'Anguille européenne. Photos : œuf (*in* Palstra *et al.*, 2005) ; leptocéphale (http ://calphotos.berkeley.edu) ; stade de développement des leptocéphales (*in* Schmidt, 1912) ; civelle (www.ifremer.fr/delar) ; anguille jaune (www.cemagref.fr/Informations), anguille argentée (www.futura-sciences.com) et reproduction (*in* Boëtius and Boëtius, 1980).

quantités pêchées varient de moins de 500 kg à 6 500 kg d'une année à l'autre. Chiapi retrouve le même phénomène à Brême en Allemagne, à Saint Sébastien en Espagne et à Nantes (Gandolfi Hornyold, 1933, 1936; Popelin, 1971).

A l'heure actuelle, les niveaux d'abondance de civelles sont historiquement bas (Anonymous, 2003) et représentent moins de 1% de l'abondance des années 1970-80 dans certaines rivières. L'Anguille européenne a ainsi été classée à l'Annexe II B de la Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction (CITES, 2007). De plus, ce déclin très marqué de la population d'Anguille européenne se retrouve aussi chez les deux autres espèces de l'hémisphère nord principalement exploitées : l'américaine (*Anguilla rostrata*) et la japonaise (*A. japonica*).

En Basse Loire, certaines descriptions font état d'un *cordon* de plusieurs kilomètres de long pratiquement ininterrompu ayant une largeur d'1 m et 50 cm de profondeur (Bertin, 1956). Le même phénomène est décrit par Crespon en 1844 : "[...] *young eels come together at the mouth of the Rhône packing in such great quantities that I have myself seen a spherical mass of them as large as a sizeable barrel. This mass rises and falls again continually in the water and gradually in the individuals detach themselves to form a cord, like a ball of wool unwinding*" (*in* Bertin, 1956). La migration des civelles fait face à certains obstacles et le physicien Sir Humphray Davy remarque, lors de ces parties de pêche en Irlande, la ténacité des alevins : "*when I was at Ballyshannon about the end of July, the mouth of the river [...] was blackened by millions of little eels, about as long as the finger, which were constantly urging their way up the moist rocks by the side of the fall. Thousands died, but their bodies remaining moist, served as the ladder for others to make their way*" (Davy, 1831). Ces remontées en cordon ne sont plus observées aujourd'hui.

Relation environnement-recrutement chez l'Anguille ?

Cette diminution du recrutement d'Anguille au cours des dernières décennies résulte probablement de la combinaison de facteurs anthropiques comme la pêche (Dekker, 2003, 2004), les pertes et dégradations d'habitats (Castonguay *et al.*, 1994b; McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006), les pollutions (Amiard-Triquet *et al.*, 1988; Robinet and Feunteun, 2002; Belpaire and Goemans, 2007) ou les parasites et maladies (Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005) et de facteurs naturels comme les conditions environnementales lors de la phase larvaire (Castonguay *et al.*, 1994a; Knights, 2003). Le synchronisme du déclin des différentes populations d'Anguille de l'hémisphère Nord suggère des mécanismes globaux reliés à l'environnement (effet Moran ; Moran, 1953).

Ce travail se propose de comprendre l'effet de l'environnement sur le recrutement. 7 publications abordent ce lien. Ces articles font état des relations entre **disponibilité de nourriture** et survie larvaire (Castonguay *et al.*, 1994a, Désaunay and Guérault, 1997, Westerberg *in* ICES, 2001, Knights, 2003, Kettle and Haines, 2006, et Kettle *et al.*, in press), et de l'influence des **conditions physiques** du milieu sur le succès de la migration et du recrutement (Friedland *et al.*, 2007, Kettle *et al.*, in press). Cependant, dans ces articles, aucune étude quantitative n'est menée pour déterminer les relations entre la disponibilité en nourriture et le succès du recrutement. De plus, les approches concernant les conditions de transport océaniques sont menées en utilisant la North Atlantic Oscillation (NAO), un indice environnemental global qui rend difficile l'interprétation de processus écologiques sous-jacents.

Démarche

L'objectif de ce travail de thèse est de contribuer à l'étude des effets de l'environnement océanique sur le recrutement de civelles d'Anguille européenne. Cette approche se veut large en terme d'échelles spatiales et temporelles étant donné l'aire de distribution de cette espèce et l'ensemble des données disponibles depuis de nombreuses années. Nous avons adopté une approche de modélisation, et cela pour deux raisons. Tout d'abord, l'observation de la phase larvaire dans l'Océan Atlantique et la collecte de données durant cette migration sont très difficiles à mettre en œuvre. Ensuite, la démarche de modélisation permet de réduire et d'explorer la complexité du “système Anguille” en formulant et testant des hypothèses pour comprendre les processus écologiques par lesquels l'environnement agit sur le recrutement.

Deux approches de modélisation sont menées : Dans une **première partie**, une modélisation déterministe basée sur des modèles hydrodynamiques représentant les champs de courant de l'Atlantique permet d'étudier la dérive de particules relâchées dans la mer des Sargasses. L'objectif de la modélisation est double. Tout d'abord, il s'agit d'estimer le temps de migration des larves, qui est une pré-requis indispensable pour pouvoir relier temporellement les indices de recrutement de civelles sur les côtes avec les indices environnementaux lors de leur phase marine. Puis nous utilisons ces outils pour mieux comprendre la phase marine des larves d'Anguille en terme de routes et de périodes de migration.

Dans le chapitre 1, une synthèse bibliographique décrit les connaissances actuelles sur la phase larvaire marine de l'Anguille.

Dans le chapitre 2, nous estimons le temps de migration minimal pour réaliser la traversée de la mer des Sargasses aux côtes européennes sous l'hypothèse d'une dérive passive.

Dans le chapitre 3, nous prenons en compte un paramètre biologique essentiel, la mortalité, pour estimer le temps de migration moyen des larves.

Enfin, les résultats obtenus avec les modèles océaniques sont comparées aux connaissances écologiques actuelles sur les aires et dates de départ des larves ainsi que sur leurs aires d'arrivée et leur histoire de vie marine (chapitre 4).

La **deuxième partie** met en œuvre une modélisation statistique centrée sur les liens entre les conditions environnementales (disponibilité en nourriture lors des premiers stades de vie et conditions océaniques lors de la traversée) et les quantités de civelles ayant survécu à la traversée trans-océanique, en tenant compte des acquis de la première partie sur les durées de migration.

Cette analyse est faite à l'échelle de la population d'Anguille européenne (chapitre 5) puis des trois espèces d'Anguille les plus importantes commercialement, i. e. l'Anguille européenne, américaine et japonaise (chapitre 6).

Une **conclusion** sur la contribution générale de ce travail et ses perspectives est enfin présentée.

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Première partie

Les durées et les routes de migration

Introduction - Partie I

LES principaux avantages poussant les espèces à migrer sont liées à des facteurs écologiques et biogéographiques comme la saisonnalité et la répartition spatio-temporelle des ressources (Lohmann and Lohmann, 1998), des habitats (Alerstam and Enckell, 1979), de la prédation et des compétitions (Salomonsen, 1955; Alerstam *et al.*, 2003). Ces avantages sont réduits par le coût de la migration en terme de temps (c'est-à-dire entraînant une perte d'occupation du territoire), d'énergie et de mortalité. La migration trans-océanique de l'Anguille adulte n'est pas guidée par ces avantages car les individus meurent après la reproduction. Ils ne migrent donc pas pour accéder à une ressource ou un habitat qui leur serait favorable. Il s'agit donc probablement d'une migration de reproduction permettant aux larves de rencontrer les conditions environnementales favorables à leur survie. Le déplacement de l'aire de reproduction suivant la dérive des continents (hypothèse de Wegener, 1915) est un des arguments évoqués pour expliquer un si grand éloignement des habitats continentaux (Davies, 1923).

Les deux migrations qu'effectuent les anguilles sont entourées de mystères et d'incertitudes (Bertin, 1956). Pratiquement aucune anguille mature n'a été observée durant la migration catadrome vers l'aire de reproduction (Tesch, 2003). La migration des larves, quant à elle, a été l'objet de nombreuses études (par exemple Schmidt, 1922; Tesch, 1980; McCleave and Kleckner, 1987).

Connaître le temps de migration des larves est un pré-requis indispensable pour l'étude des effets de l'environnement sur le recrutement dont la mesure, en l'absence de possibilité d'estimer l'abondance des leptocéphales dans l'océan, n'est possible qu'à partir des arrivées de civelles sur les côtes.

Nous avons choisi une approche lagrangienne (dérive passive de particules dans des modèles hydrodynamiques) afin d'étudier cette durée de migration des larves, les liens possibles entre les conditions océaniques et le succès de la traversée et les routes empruntées lors de cette migration. Le chapitre 1 dresse un état de l'art des connaissances actuelles sur la phase larvaire océanique de l'Anguille. Dans le chapitre 2, sous les hypothèses des simulations lagrangiennes, nous estimons une borne inférieure de la durée de migration. L'utilisation d'une hypothèse de mortalité implémentée dans les simulations nous permet de donner, dans le chapitre 3, une estimation du temps de migration moyen des larves. Enfin, dans le chapitre 4, nous examinons les routes et les histoires de vie des individus, issues des simulations lagrangiennes, en les mettant en perspective avec d'autres approches (génétique et microchimie des otolithes).

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1

La vie océanique et les temps de migration des larves d'Anguille européenne et américaine

Résumé détaillé

Dans ce chapitre, nous dressons un état de l'art des connaissances sur la vie océanique des larves d'Anguille européenne et américaine, avec comme fil directeur, les temps de migration des larves. Le synchronisme du déclin des différentes populations d'Anguille de l'hémisphère Nord suggère en effet des mécanismes globaux reliés à l'environnement. Ainsi, la compréhension de cette phase marine n'a pas simplement un intérêt écologique mais est cruciale pour aborder les effets de l'environnement sur ces larves et ainsi sur le recrutement. Dans un premier temps, nous abordons la découverte du lieu et des dates de ponte qui ont été un mystère jusqu'au début du XX$^{\text{ème}}$ siècle. Les travaux de Johannes Schmidt ont permis de définir la mer des Sargasses comme zone de reproduction des deux espèces d'Anguille de l'Atlantique (Fig. 1.1 et 1.2) et d'établir la principale période de reproduction : de mars à juin pour l'Anguille européenne et de février à avril pour l'américaine. Ces deux espèces ont ainsi une zone et une période de ponte superposées.

La migration des larves entre cette aire de reproduction et les côtes américaines ou européennes est liée aux grands courants océaniques (Gulf Stream et Dérive Nord Atlantique) ce qui explique l'aire de distribution continentale très large pour ces espèces (Fig. 1.3).

Cette synthèse bibliographique met en exergue la grande variabilité des estimations de la durée de ce trajet. Les travaux de Schmidt sur les analyses de cohortes et de courbes de croissance de leptocéphales montrent une durée de migration supérieure à deux ans pour l'Anguille européenne et d'environ un an pour l'américaine (Fig. 1.4). Récemment, un modèle de simulations de trajectoires de particules relâchées dans la mer des Sargasses et dérivant passivement estime la durée de migration des anguilles européennes à deux ans et celle des américaines à 1 an, en cohérence avec les travaux de Schmidt. Les analyses la microstructure de l'otolithe ont remis en cause ces estimations. Le nombre d'incréments journaliers dans l'otolithe correspond à une durée de migration inférieure à un an pour l'Anguille européenne (Fig. 1.5). Les résultats de l'analyse de la microstructure de l'otolithe ont entraîné une controverse concernant la validité des estimations issues de ces lectures. La présence d'incréments journaliers non décelables par les techniques d'analyse de la microstructure nous semble être une hypothèse crédible car la croissance des leptocéphales est lente. L'hypothèse de la non-validité des résultats de lecture d'otolithe est renforcée par l'idée qu'une durée de traversée courte impliquerait un comportement de nage active, trop coûteux en énergie dans un milieu oligotrophe comme l'océan ouvert, mais reste sujette à débat.

Parmi les perspectives ouvertes par cette synthèse, l'utilisation de modèles hydrodynamiques de dérive larvaire, puis un couplage avec des modèles bioénergétiques semblent des outils prometteurs pour étudier cette migration qui reste mystérieuse à de nombreux égards.

The oceanic life and the migration duration of American and European eel larvae

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Abstract Oceanic larvae of European (*Anguilla anguilla*) and American (*A. rostrata*) eels have to cross the Atlantic Ocean from the Sargasso Sea to the European or North American coasts before entering continental habitat where they can grow. Depending on the method of analysis, the estimation of the migration durations can vary between 6 months and more than 2 years for both species. The stakes are not only to improve our knowledge about eel ecology. Eel recruitment is now less than 1 % of levels in the 1980s in some rivers. Improving knowledge of duration of oceanic migration is a prerequisite to a better understanding of the effects of the oceanic environment on eel larvae and subsequent recruitment. Here we review the different methods used to investigate the migration duration. These studies use a wide spectrum of methods, from cohort analysis to microstructure of otoliths including lagrangian modelling. The purpose of this paper is not to take sides but to review the different assumptions, results and interpretations of these different approaches. One of the great "eel challenges" in forthcoming years will be to determine the duration of the larval migration, identify larval food, and improve our knowledge of factors that determine the location of the spawning area and the environmental processes involved in the determinisms of eel recruitment during the oceanic phase. We provide some insights that may help to move these "eel mysteries" ahead.

Keywords *Anguilla*, leptocephali, migration, North Atlantic, otolith, Sargasso Sea

1.1 Introduction

In one of his letters, Johannes Schmidt described his advances in the localization of eel spawning area during his numerous expeditions in the Atlantic Ocean: "*I think I am now able after so many years' work, to chart out the spawning places of the European eel (Anguilla vulgaris)*" (*in* Smith, 1921). Nearly a century later, thanks to the investigations of scientists in the Sargasso Sea (e. g. Tesch *et al.*, 1979; McCleave *et al.*, 1987a), some aspects of the oceanic biology of Atlantic eels are more precisely established than Schmidt's findings (Schmidt, 1922, 1923). For example, key ecological issues such as spawning time and influence of oceanography in determining spawning location, vertical migrations of leptocephali, food, are better known. However, there are still many unknown aspects crucial to understanding the eel life history even if progress has been made as testified by the number of publications on eels (nearly one paper a day on eels, on average, over the last decade; 5628 papers in 16 years; ISI Web of knowledge with keywords Anguilla and eel).

A wide spectrum of academic disciplines has been involved to study the oceanic biology of eels, from genetics to oceanography. All these efforts to understand and manage eels in a sustainable way become all the more urgent in light of the current pronounced decline in eel populations worldwide (Anonymous, 2003). The European eel was listed in Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007). This decline necessitates further studies about eel and especially its oceanic phase since it is one of the major sources of mortality as it is for most fishes (Hjort, 1914). The stakes are not only pure ecology: there is also a need to improve our understanding of eel recruitment for management and conservation purposes. This can only be achieved if duration of larval migration and feeding ecology are better known.

The decline of both the European eel (*Anguilla anguilla*) and American eel (*Anguilla rostrata*) since the early 1980s is no doubt the combined effect of several, probably interacting factors: anthropogenic activities such as overfishing (Dekker, 2003, 2004), habitat loss and degradation (Castonguay *et al.*, 1994b; McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006) and unfavourable environmental conditions during the oceanic stage (Castonguay *et al.*, 1994a; Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008; Kettle *et al.*, in press) or during the freshwater stage through parasites and diseases (e. g. Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005a). To disentangle these potential causes of stock decline is a daunting task since they are often *per se* associated and occurring at the same time. For instance, changes in Sargasso Sea environment, parasites, overfishing, and pollution occurred around the same time: the early 1980s (e. g. Robinet and Feunteun, 2002; Palstra *et al.*, 2006; Bonhommeau *et al.*, 2008). Understanding factors affecting eel recruitment in a global change context is one of the most critical and challenging issue. Even if environment-recruitment relationships cannot be used for predictive models and in assessment (Myers, 1998), there are other strong justifications for studying recruitment mechanisms and its determinism. Myers (1998) emphasized: "*This information may be crucial for multispecies management and predicting the long term consequences of climate change*". Studies to understand recruitment fluctuations focus either on physical or trophic conditions that may affect eel larval survival, following hypotheses by Hjort (1914) of "*critical period*", Cushing (1975) of "*match-mismatch*", and Bakun (1996) of "*fundamental triad*". Eel recruitment data have been related to environmental factors such as large-scale oceanic and climate indices (North Atlantic Oscillation of Hurrell, 1995, Gulf Stream index of Taylor and Stephens, 1998, potential energy anomaly of Curry and McCartney, 2001), and wind trends and latitude of the 22.5°C isotherm in the Sargasso Sea supposed to be a signpost for spawning (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008; Kettle *et al.*, in press). Primary production and sea temperature fluctuations in eel spawning area are related to glass eel recruitment (Knights, 2003; Bonhommeau *et al.*, 2008). Since eel larvae abundance cannot be estimated, the available data to tackle the problem of recruitment fluctuations are often glass eel data (whether abundance or recruitment indices). Migration duration is a key issue that has strong implications to understand recruitment fluctuations. When environment factors are supposed to influence recruitment in the early life stages, time lags have to be accounted for to relate environmental series to coastal glass eel recruitment series. Friedland *et al.* (2007) used a 1-year lag but Knights (2003) and Bonhommeau *et al.* (2008) used a delay of 2.5 - 3 years. These studies did not use the same migration duration even though they were based on the same literature (e. g. Schmidt, 1923; Lecomte-Finiger, 1994a; Tesch, 2003). Such discrepancies in the estimation of migration duration remain unresolved.

In this paper, we review the available knowledge about the oceanic stage of Atlantic eel. Given the amount of mysteries remaining about the oceanic phase of eel, one might imagine that it has not been studied enough. Our review highlights that it is not as slender as one might think. Lecomte-Finiger (2003) and van Ginneken and Maes (2005) have reviewed life cycle of the eel genus but here we focus on the salient features of the oceanic life and especially on migration duration. By adopting the migration duration as the unifying thread, we review the available knowledge about (*i*) the hatching location and timing, (*ii*) the transport, and (*iii*) the metamorphosis of leptocephali into glass eels. It leads us to focus on the controversy about the methods used to determine the migration duration. Lastly, we propose perspectives to move these eel mysteries ahead.

1.2 Oceanic life cycle of Atlantic eels

In "*Historia animalum and De Partibus Animalium*" (around 350 BC), Aristotle wrote that eels were sexless and born in decaying matter: "[...] *the eels comes from what we call the entrails of the earth*" (Aristotle, translation by Thompson, D.A.W., 1918; Bertin, 1956). This quotation has been used to underscore the poor understanding of the eel life cycle and the weak consideration granted to this species. Actually, it could be a bad translation of the Greek expression "ϵντϵρα γ ῆσ" by entrails of the earth since it could rather describe vermiform animals (Bertin, 1956). Aristotle may have meant that eels come from worm-like animals such as elvers (young pigmented eels). For centuries and until the work of Grassi (1896), eels were thought to live in freshwater and the larvae were considered as another species, *Leptocephalus brevirostris* (Kaup, 1856). In his aquariums, Grassi (1896) followed step by step the metamorphosis of eel larvae (leptocephali) into glass eels and then, in eels (Lecomte-Finiger *et al.*, 2004). Actually, this observation was inspired from the description of the metamorphosis of conger eel leptocephalus made by Delage in 1886 (*in* Jordan, 1908). This discovery had far repercussions because of the economic interest in eel (already). It also had (and still does have) far implications in terms of management since eels fished in freshwater have not reproduced before. Denmark has always had a great economic interest in eels and awarded funding to the biologist Johannes Schmidt to initiate researches about eel biology. It was the beginning of travels and surveys around the Atlantic and the Mediterranean to find eel spawners and larvae. The chase was on. The fact that eels migrate back to the open ocean to reproduce is widely recognised but little is known about the way they return to the spawning area. Spawning takes place in the Sargasso Sea and eel larvae start on a transoceanic migration to reach coastal and freshwater habitat. Here we review the available knowledge on these different oceanic stages.

1.2.1 Spawning and hatching: the starting point ($t = 0$) but when and where?

1.2.1.1 Physical features as a determinism of silver eel marine migration and spawning

After undergoing a series of physiological and physical changes, adult eels initiate their seaward migration in the open ocean (Harden Jones, 1968). Excluding the eel found in the stomach of a cachalot off the Azores (Vaillant, 1898), and eels caught in the Mediterranean Sea (Bianchini *et al.*, in press), no mature eels have ever been captured in the open ocean off the continental shelf, let alone in the Sargasso Sea. However, it is commonly admitted that eels do return to their native spawning area travelling thousands of kilometres. The enigmatic phenomenon of the seaward migration of adult eels, and the factors influencing spawning in the Sargasso Sea are key elements to determine the location and timing of the early life stages of eels.

Return migration of silver eels The question is not if eels migrate back to the Sargasso Sea but "how" they do it. The review of van Ginneken and Maes (2005) emphasises several factors that might be involved in the oriented migration of mature (silver) eels. Here, we briefly review the two main hypotheses. Eels might follow scented cues using their intriguing olfactory senses that can detect chemical compounds at very low dilutions (1:2.85 $\times 10^{18}$; Teichmann, 1959; Nordeng, 1971; Sorensen and Winn, 1984). Another hypothesis is the perception of oceanic electric fields by eels. Rommel and McCleave (1972), Zimmerman and McCleave (1975) and van Ginneken *et al.* (2005b) showed that eels have sufficient sensitivity to utilize geoelectric information for orientation. Westerberg (1979) tracked migrating silver eels using ultrasonic transmitters and suggests that eels detect their orientation relative to water current by perception of an internal potential gradient induced by movement through the earth's magnetic field. Tracking experiments have been carried out to understand this behaviour (Tesch, 1979; Tesch *et al.*, 1989) but the tracking time was too short to conclude. Silver eels tracked in the North Sea showed oriented swimming and occasionally performed selective tidal stream transport (McCleave and Arnold, 1999). Monitoring European silver eels off the continental shelf into the open sea was achieved for the first time in 2007 using small pop-up tags (K. Aarestrup, National Institute of Aquatic Resources, Silkeborg, Denmark, personal communication). Future improvements in tagging technology (reduction of tag size and increase in memory capacities) should eventually make it possible to track Atlantic eels all the way to their spawning grounds. Recent pop-up tag experiments carried by Jellyman and Tsukamoto (2002) on large longfin eels (*Anguilla dieffenbachii*) should encourage this kind of approach.

Signposts for spawning The only clues to determine the spawning area are to find young larvae (<10 mm) that are found near spawning areas. One can intuitively devises that eels might use guideposts to find the spawning area and maximise the probability of successful reproduction. The determinism of the exact location was not obvious since no conspicuous factors exist in the Sargasso Sea such as seamounts for the Japanese eels (Tsukamoto, 1992, 2006). Following suggestions by Ekman (1932), Kleckner *et al.* (1983) formulated two hypotheses for identifying the spawning area by responding positively to the elevated water temperature found in the upper 300 m in this region of the Atlantic. Ekman (1932) noted that the isotherm 18-19°C at depths of 200-300 m matches the boundary estimated by Schmidt for the spawning area. McCleave *et al.* (1987a) and Kleckner and McCleave (1988) confirmed the hypothesis, initially proposed by Kleckner *et al.* (1983), that thermal fronts that split the Sargasso Sea into a northern and a southern part may act as signposts for adult eels (McCleave, 1987). Two hypotheses were investigated by Kleckner and McCleave (1988). First, a positive correlation could exist between the distribution of the Subtropical Underwater and spawning by *Anguilla*. Second, fronts along the northern edge of the warm, saline surface water mass of the southern Sargasso Sea could form the northern limit of spawning by *Anguilla*. Kleckner and McCleave (1988) carried out four main transects in the Sargasso Sea in 1983 and 1985. Using expendable bathythermographs (XBT), a conductivity-temperature-depth (CTD) probe, and a 3-m Isaacs Kidd Midwater Trawl, they sampled larvae and water properties along transects. The first hypothesis was rejected since tiny eel larvae were collected on both sides of the Subtropical Underwater. The larvae were taken in all collections south of fronts separating southern Sargasso Sea surface water from mixed Convergence Zone water to the north, confirming the second hypothesis on thermal fronts. Thus, McCleave *et al.* (1987a) and Kleckner and McCleave (1988) supported the hypothesis that physical features associated with thermal fronts might act as signposts for mature eels to stop their migration and begin spawning.

The available knowledge about the Japanese eel also reinforces the hypothesis that the differences in water masses separated by the salinity front may be used by eels as a signpost for spawning. As a genus *Anguilla* commonality, Kimura *et al.* (2001) showed a certain synchrony between Japanese eel (*Anguilla japonica*) recruitment and salinity fronts driven by El Niño Southern Oscillation (ENSO) in the Japanese eel spawning area. If eel eggs hatch south of the salinity front, larvae may be carried away by the southward Mindanao current. By contrast, hatching north of the front, leptocephali may follow the Kuroshio transporting them to their distribution area from Taiwan to Japan (Kimura *et al.*, 1994). Moreover, during the 2002 El Niño event, Kimura and Tsukamoto (2006) noticed that small larvae (<10 mm) were collected just south of the salinity front where these young larvae have never been collected in usual years.

1.2.1.2 The “true” breeding places and timing of the Eel

Location Following the work of Grassi (1896), Schmidt first focused his search in the Mediterranean Sea and found that smallest larvae (70 mm) were located in the Western part. The starting point of westward expeditions in the Atlantic came after Hjort (1910) captured 44 small eel larvae (40-60 mm) in the Central North Atlantic suggesting that the eel spawning area may lie between the Azores and Bermuda. When finding three leptocephali (40-50 mm; one American and two European eels) in old collections from the Zoological Museum, Copenhagen that came from an area near the Florida Strait, Schmidt surmised that the origin of the larvae was near this region. Collecting samples thanks to trans-oceanic trading vessels and during his numerous surveys that began in 1904, Schmidt found larvae “[...]*throughout an area of an enormous extent, stretching across the Atlantic, almost from the shore of United States, to far up in Mediterranean, and in a north-easterly direction to the Faroe-Shetland Channel*” (Schmidt, 1927). In 1920, on board the schooner ’Dana’, Schmidt succeeded to chart out the limit of occurrence of the smallest larvae (< 10 mm; both species) (Fig. 1.1; Schmidt, 1922).

The breeding places of eels were found to be located between about 22° and 30°N and about 48° and 65°W (i.e. the Sargasso Sea). The smallest larvae have been hauled from about 200 to 75 m deep. These results are consistent with later studies on vertical distribution of larvae (e. g. Castonguay and McCleave, 1987) and on tracking of artificially matured eels released in the Sargasso Sea (Fricke and Kaese, 1995). Over a period of 25 years, Schmidt collected more than 10,000 European eel larvae and 2,400 American eel larvae (Schmidt, 1925, 1935). The overlapping breeding places of the two Atlantic eel species were discovered. Nonetheless spawning adult eels have yet to be caught and the baffling quest is still on. During the 50 years following the last Schmidt's cruises, expeditions hunting small larvae and eel spawners have been carried out refining Schmidt's results. Vladykov (1964) hypothesised that the "true breeding area" of the American eel was not in the Sargasso Sea but much further south. However, using leptocephali collections gathered over the period 1933-1968, Vladykov and March (1975) later largely confirmed Schmidt's conclusions. They pointed out that the 50°W longitude was not a dividing line between American and European eels.

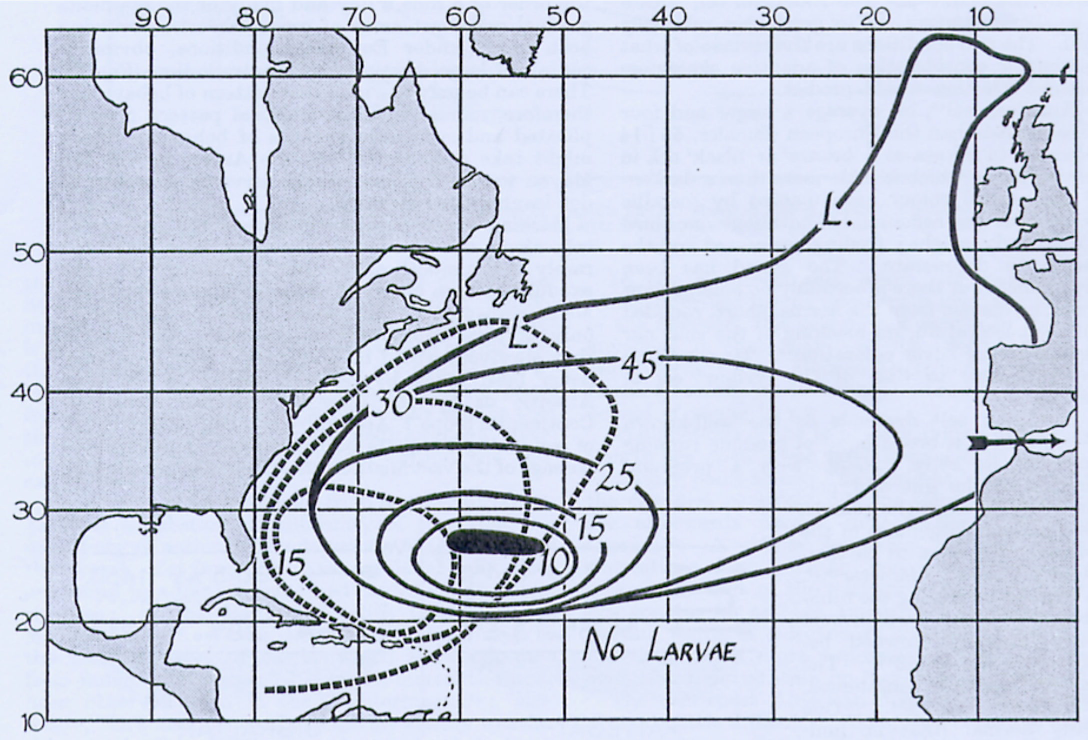

Figure 1.1: Distribution of Atlantic *Anguilla* larvae. *A. anguilla* (solid lines) and *A. rostrata* (dashed lines). The curves show the limits of occurrence of larvae of the indicated mm lengths. The black area shows the distribution of newly hatched (5-7 mm) *A. anguilla* larvae. *L* curve marks the limits for the larva distribution (*in* Tucker 1959a, after Schmidt 1922, 1935).

Timing Schmidt observed that the main spawning season begins in late winter and spreads until end of summer. Although most hauls were made during this period, Schmidt (1922) concluded that larvae were not produced uninterruptedly throughout the year because of the length distribution of eel larvae in October and no observations of tiny larvae during the autumn whether made by surveys and commercial vessels. Although Vladykov and March (1975) found leptocephali almost throughout the year, they estimated a species-specific spawning season, i.e. February to July for American eel, and May to June for European eel. Then, survey cruises to the spawning area were conducted from 1979 to 1985 (Tesch *et al.*, 1979; Schoth, 1981; Schoth and Tesch, 1981; Kracht, 1982; Schoth and Tesch, 1983; Wippelhauser *et al.*, 1985; Castonguay and McCleave, 1987; McCleave *et al.*, 1987b; Kleckner and McCleave, 1988; Tesch and Wegner, 1989). Reanalyses of Schmidt's data have been performed as well (Boëtius and Harding, 1985; McCleave and Kleckner, 1987; McCleave *et al.*, 1987a).

On the basis of this new knowledge, a more accurate timing and location of eel spawning areas have been drawn up. Estimated spawning areas of both species derived from this information are presented in Fig. 1.2 and suggest a spatial overlapping. The spawning season mainly occurs from March to June for the European eel and from February to April for the American eel (McCleave *et al.*, 1987a; McCleave and Kleckner, 1987) and suggests a temporal overlapping as well.

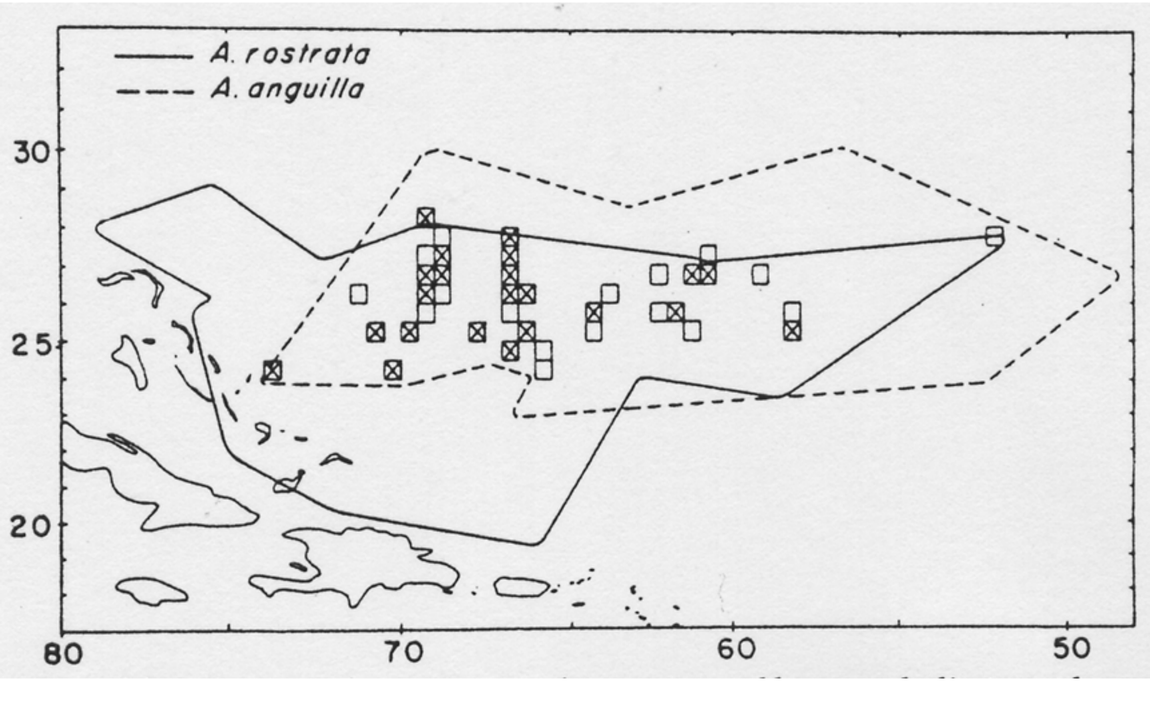

Figure 1.2: Limits of distribution of American and European eel leptocephali 10 mm long or less, and locations where leptocephali of both species 7 mm long or less (filled squares) and 10 mm long or less (all squares) were caught in the same net tow. The samples have been taken on cruises of Schmidt in 1922, of Tesch in 1979, and of McCleave in 1981, 1983, and 1985 (*in* McCleave *et al.* 1987a and McCleave 2003).

1.2.1.3 The separation of the two eel species

The overlapping spawning areas and seasons address the long-standing question of the "panmixia theory" of eels in the Sargasso Sea. Using a large body of leptocephali data, McCleave *et al.* (1987a) showed that European and American eels are partly sympatric because of both spatial and temporal partial overlapping spawning. Both species co-occur in the Sargasso Sea. Moreover, a weak proportion of American eel are found in Europe (Boëtius and Harding, 1985), as 0.16 % of 15,000 specimens examined in Europe were *A. rostrata* (Boëtius, 1980). Thus, how can one explain the continental separation of the two species? Tucker (1959b) addressed this question and generated a controversy called "*The Atlantic eel problem*". In 1959, began a succession of articles in Nature. We refer to Harden Jones (1968) for a complete discussion of this controversy. Tucker (1959a) enunciated three drastically different hypotheses from those accepted until then: "(1) [...] *the European eels need not and do not succeed in returning to the ancestral spawning-area, but perish in their own continental waters*; (2) *the American and European eels are not distinct species, but merely eco-phenotypes of Anguilla anguilla* [...] (3) *the populations of so-called 'European' eels, are therefore entirely maintained by reinforcements of larvae of American parentage*". The correspondence that ensued enlightens some of these issues. D'Ancona and Tucker (1959) emphasized the different numbers of myomeres between the two species. Jones and Tucker (1959) put forward two main relevant objections to Tucker (1959a). First, even if adult European eels have never been caught in the open ocean, neither have American eels. Second, if European eels stemmed from American eels spawning in the wrong place and were unable to migrate back to the spawning area, it would be odd that natural selection would have failed to eliminate the European eel. Deelder and Tucker (1960) adduced vehement arguments to Tucker's hypotheses. The segregation between the larvae of the two species may be explained by a difference in timing of metamorphosis. American eel larvae might complete their metamorphosis before European eel larvae, hence responding to American continental shelf conditions, and migrating as elvers in North American Rivers. The higher growth rate of *Anguilla rostrata* found by Boëtius and Harding (1985) may be interpreted in this direction as well. Tucker's hypotheses were first falsified by Comparini and Rodi (1980) who showed a genetic differentiation between leptocephali of European and American eels. From a genetics point of view, European and American eels are distinct species. The question of the distinction of Atlantic eels was solved but it raised the problem of the way by which this genetic differentiation is done. van Ginneken and Maes (2005) observed that recent molecular studies and morphological differences among European eels suggest the possibility of multiple spawning areas within and outside the Sargasso Sea. The exact mechanisms of the separation are not clear. The spatial spawning separation may lead to different pathways of migration and enable the separation of the two species (van Ginneken and Maes, 2005; Kettle and Haines, 2006). The separation of the two species may also be explained by the different growth rates between species that make the American eel respond earlier to continental shelf conditions.

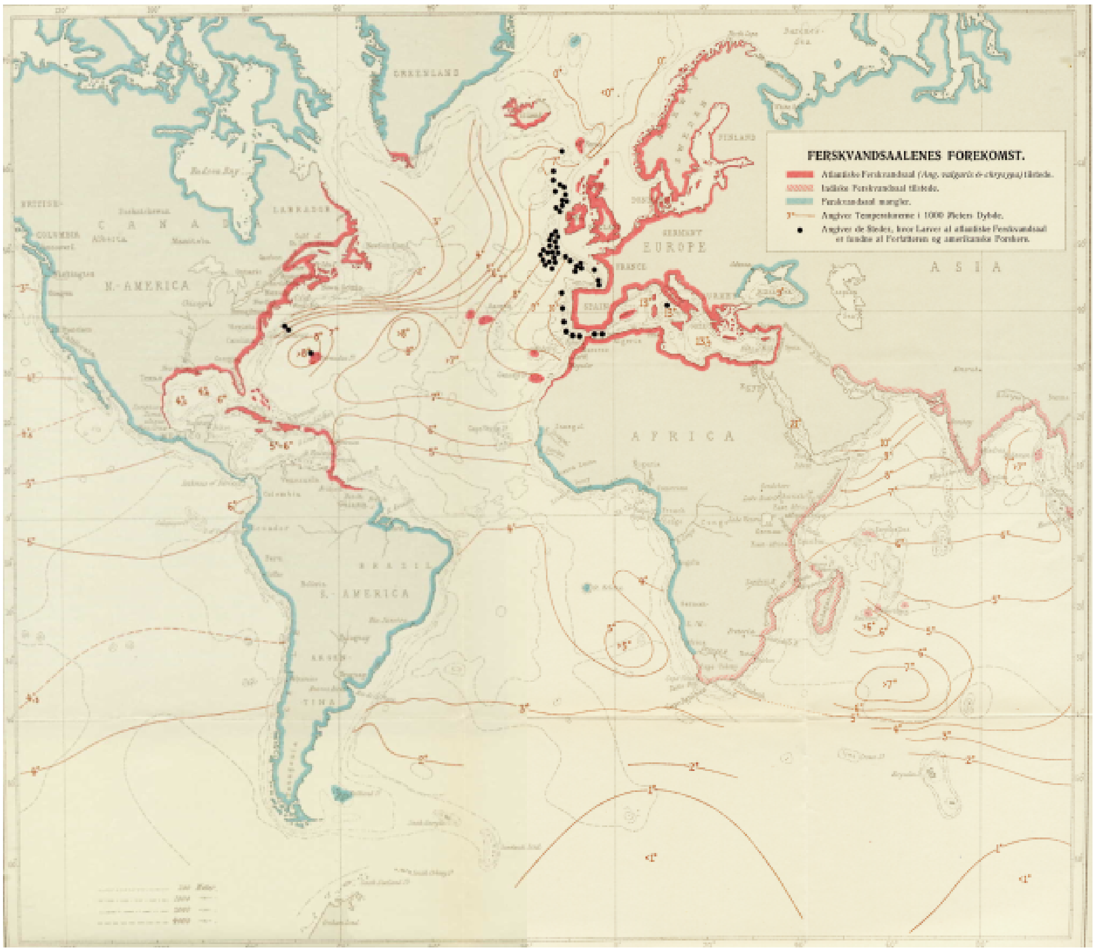

Figure 1.3: Distribution of *Anguilla anguilla*, *Anguilla rostrata*, and the Indopacific *Anguilla* species (*in* Schmidt, 1909a).

1.2.2 Leptocephalus transport: the drifting phase (t = unknown)

After hatching, eel larvae spread over the Atlantic Ocean. *Anguilla* leptocephali have been collected in the whole North Atlantic Ocean (Fig. 1.3; Schmidt, 1927, 1935) and in the Mediterranean (Strubberg, 1923). To the North, leptocephali have been sampled as far north as 61°N and 3°W in the Faroe-Shetland channel (Schmidt, 1927). No eel is present south of 20°N (Schmidt, 1922). However, American eel leptocephali have been reported from the Yucatan Channel near the mouth of the Gulf of Mexico (Smith, 1968; Miller, 2003) and in Guyana and Surinam (Schmidt, 1909a; Vladykov, 1964). The larval migration in the Atlantic still begs answers with respect to the near perfect continental separation of the two species, the migration duration, and the food source. Once again, some critical points remain uncertain.

1.2.2.1 The migration duration: still uncertain

When Grassi (1896) mentioned the migration duration of eel larvae, he wrote: "*What length of time this development requires is very difficult to establish*". This statement is still true today. Three indirect approaches were used to estimate the migration duration of European and American eels, i.e. chronologically, growth curves of leptocephali, otolithometry, and numerical models.

Cohort and growth curves (*in situ* sampling)

The spatial gradient in length observed in different locations have been charted out by Schmidt (1923) and refined by Tucker (1959a), Boëtius and Harding (1985), and McCleave *et al.* (1987a) (Fig. 1.1). Using these length gradients, Schmidt (1923) proposed migration durations for both species. Migration duration of eel larvae was first assessed plotting the larval lengths for the different months of catch of leptocephali (Fig. 1.4; Schmidt, 1922). These growth curves were grounded on the eastward change in size of *A. anguilla.* Schmidt evaluated that the European larvae takes on average two years to grow and attain the size of about 70-80 mm. Schmidt (1922) added that nearly three years elapsed before the metamorphosis into glass eel is completed. As a matter of fact, these results were reinforced by the presence in early summer of three year-classes in the Atlantic Ocean:

the youngest in the western, the next in the central, and the oldest in the eastern waters of the Atlantic (Schmidt, 1922). Regarding the American eel larvae, Schmidt (1922) concluded that the leptocephali grow more rapidly and can complete its full development from egg to elver in about one year. Schmidt separated leptocephali in age groups ('0-group' for young-of-the-year, 'I-group' for one-year-old larvae and so on). The re-analysis of Schmidt's sampling stations by Boëtius and Harding (1985) provides some insights on the migration duration. They found abundant stations where '0-groups' and 'I-groups' occur together but few where 'I-groups' and 'II-groups' can be found altogether (mainly in the western Mediterranean). The 'I-groups' seem to have a special status as they can be found all over the year and are distributed over the North Atlantic. Boëtius and Harding (1985) argued that some individuals can grow continuously from 10 mm to 60 mm or more in a single year, and can reach a length of 80 mm within 12-15 months. It is noteworthy that this estimation is likely to underestimate the migration duration since they did not account for the time of metamorphosis into glass eels. Moreover, Tesch *et al.* (1985) found a spatial gradient in length of larvae (smaller larvae in the South and larger in the North Europe) and several age-classes at the same locations indicating that the different age classes are mixed during the oceanic transport.

The extensive pioneer work of Schmidt proposed migration durations of 1 year for the American eel and 2-3 years for the European eel. Even so, as argued by Boëtius and Harding (1985) the age group classification was based on an intuition about larval age and Schmidt did not provide any validation of the age of leptocephali.

Otolith analysis

Macrostructure of eel otoliths The ability to tell the age of a fish accurately from its otoliths, scales, fin rays or other structures is one of the most useful features in fish biology and fishery science. Otoliths have long been accepted as the most suitable part for age determination in eels (Moriarty, 1973). This technique has been extensively used to investigate the duration of the larval oceanic stage. Liew (1974) found a pattern of a summer and a winter growth suggesting that American eel elvers may have spent two years at sea. van Utrecht and Holleboom (1985) compared the otoliths of eel larvae collected in the mid Atlantic and along the continental slope off the Portuguese coast to the otoliths of glass eels just before entering fresh water along the Dutch and French coasts. The majority of leptocephali caught in the mid-Atlantic had three complete growth zones

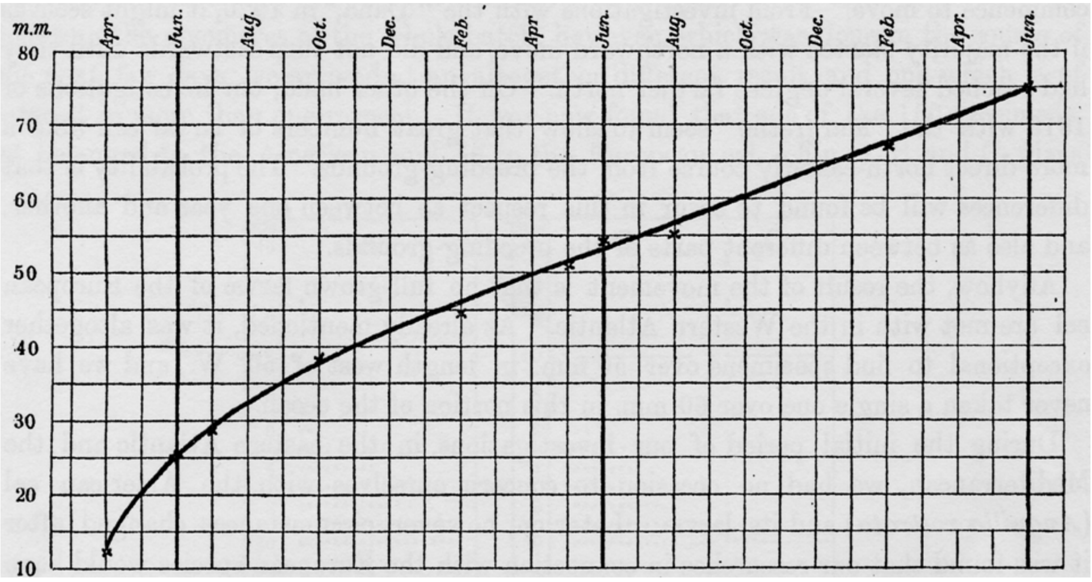

Figure 1.4: Curve of European eel larvae of growth rate (*in* Schmidt, 1922).

while those from the continental slope had four complete growth signatures. van Utrecht and Holleboom (1985) assumed that these growth zones are annual increments, implying that the glass eels arriving along the Dutch and French coasts vary between about 2 to about 6 years in age.

Microstructure of eel otoliths Pannella (1971) demonstrated the presence of daily growth increments in otoliths of marine fish and Powles *et al.* (2006) demonstrated that increment formation during metamorphosis was daily in the speckled worm eel (*Myrophis punctatus*). In the late 1980s, numerous studies concentrated on the analysis of microstructure of eel otoliths, providing a wide range of information about larval life history. Castonguay (1987) calculated a faster growth rate on the basis of otolith daily increments that what previous studies had calculated on the basis of plots of larval lengths at different collection dates (Boëtius and Harding, 1985; Wippelhauser *et al.*, 1985). For the Japanese eel, it has been shown that daily increments are deposited in sagittae at larval and elver stages and the back-calculated age of Japanese eel larvae has been determined to vary from 4 to 6 months (Tsukamoto and Umezawa, 1988; Tsukamoto, 1989; Tsukamoto *et al.*, 1988b; Umezawa and Tsukamoto, 1989). Martin (1995) and Cieri and McCleave (2001) further demonstrated that increments are deposited daily in the American eel, but at the glass eel stage.

The assumption of daily deposition of increments was used by several authors to back-calculate European eel larval migration duration (Lecomte-Finiger and Yahyaoui, 1989; Lecomte-Finiger, 1992, 1994a, b; Désaunay *et al.*, 1996b, a). These results were disconcerting because they estimated that the migration duration is less than one year. These estimates were much shorter than previous and contradicted the prevailing hypotheses. Estimates made using 423 glass eels from the Netherlands to Morocco gave a migration duration comprised between 191 and 276 days (about 6 to 9 months), for glass eels caught in Portugal and the UK, respectively (Lecomte-Finiger, 1992, 1994a). This was reconsidered by Wang and Tzeng (2000) when analyzing the microstructure of elver otoliths of American ($N = 479$) and European ($N = 440$) eels. They found that the age of American eel elvers arriving along the North American coast is comprised between 7 and 9 months (with 55 days for metamorphosis into glass eels), as previously found by Wang and Tzeng (1998), and those of European eel elvers between 14 and 16 months (98 days for metamorphosis). Arai *et al.* (2000) found intermediate migration durations, i.e. 6-8 months for *Anguilla rostrata* and 7-9 months for *A. anguilla*.

To explain the much shorter estimates of the migration duration, Lecomte-Finiger (1992) put forward an active and/or oriented migration hypothesis. According to Wang and Tzeng (2000), the dissimilarities from Lecomte-Finiger (1992) arose from the inability for leptocephali to swim faster than the current (Cheng and Tzeng, 1996). The swimming ability could not be sufficient to explain such a short migration duration found by Lecomte-Finiger (1992). Be that as it may, the study of otolith microstructure offered a totally different interpretation of the oceanic migration of larvae than the commonly-held hypothesis.

Numerical models

From the discovery of the breeding places of the eel, Schmidt (1923) noticed that "[...] *the distribution of the eels in the Atlantic area distinctly coincides with the periphery of the great anti-cyclonic circulation of water-masses in the North Atlantic*". This suggested to Schmidt that a passive drift may enhance transport of larvae to the North American and European shelves.

First estimates of migration duration were examined from several bottle experiments that have been carried out by Winge (1923), Albert, Prince de Monaco (1932), Pouchet (1939) and Hermann and Thomsen (1946). These experiments fitted with Schmidt's estimate of 2.5-3 years (Schmidt, 1922, 1923; Harden Jones, 1968). However, oceanographic evidence demonstrated that floating objects require 10 months to drift from the Florida Straits to Great Britain. It is nonetheless quite difficult to compare floating objects that are both current- and wind-driven to leptocephali that are mainly between 50-300 m (Tesch, 1980; Castonguay and McCleave, 1987). Harden Jones (1968) used observations of surface current speeds collected by British merchant and naval ships to plot the drift of leptocephali. He found that passive drift would lead larvae to arrive over the continental shelf south-west of Ireland about 2 years and 9 months after hatching in the Sargasso Sea. This simulation does not account for the deeper position of eel larvae but gives an idea of the duration of a passive drift. Brongersma (1972) used passive drifters to estimate the duration of the transatlantic migration of Loggerhead Sea Turtle (*Caretta caretta*) and stated that they can cross the Atlantic in about one year.

The first numerical model of surface currents has been developed by Power and McCleave (1983) to model the drift of particles released in the spawning areas of American and European eels. Current fields used for this model were derived from ship's drift obtained from the U.S. National Oceanographic Data Center with a 1° latitude-longitude grid. Model results suggest that larvae drift slowly and passively from the spawning area to the northwest and form a persistent accumulation northeast of the Bahamas. The gradual movement of '0-group' larvae into the Gulf Stream suggested by this model was reflected by *in situ* data described in Kleckner and McCleave (1985). This model was stopped after 270 days because it was assumed that by then, leptocephali may metamorphose and reach fresh waters by other means than passive drift. Hence, the model does not validate or invalidate the migration duration hypothesis but it does suggest that leptocephali of the American eel may be able to reach North America using only passive drift. McCleave and Kleckner (1987) examined predictions of this simulation model by determining the distribution of American and European eel larvae in the western Sargasso Sea in summer and fall. Two cruises were carried out in 1984 with transects running from the Gulf Stream southeast into the Sargasso Sea. It confirmed the general conclusion from the simulations that leptocephali are not rapidly swept from the Sargasso Sea into the Gulf Stream and that substantial concentrations of leptocephali are retained in the Sargasso Sea for several months following hatching.

Recent advances in global oceanic current simulation enabled scientists to model particle drift and provided insight in the migration of larvae. Using lagrangian models, Kimura *et al.* (1999), and Kim *et al.* (2007) explained the timing of arrival and the distribution of Japanese eel larvae in South Asia. Regarding the migration duration, they showed that the 4-6 month migration duration proposed by otolith studies (e. g. Tsukamoto *et al.*, 1989) can be confirmed by a passive drift from the seamounts near the Mariana Islands to Taiwan and Japan coasts. Using the same method, Kettle and Haines (2006) reproduced the main pattern of the migration of European eel larvae. This study concluded in a 2-year migration duration for the European eel and less than 1 year for the American eel. However, these results are debatable in two ways. First, Kettle and Haines (2006) used fixed-depth particles released in the Sargasso Sea. This assumption is shaky since leptocephali perform diel vertical migrations with 200 m amplitude (e. g. Castonguay and McCleave, 1987). Second, particles were followed for two years in the numerical simulations and stopped afterwards. If particles had been left drifting longer, their estimated mean migration duration would have been larger because many other slower particles would have eventually crossed the Atlantic. Nonetheless, this simulation of the oceanic migration of the European eel larvae showed the strong potential of this type of approach to examine hypotheses on the migration of eel larvae.

The review highlights that the estimates of migration duration remain highly uncertain and depend on the estimation method. Historical collections of surveys, otolith macrostructure, and numerical modelling tend to show that the migration is longer than 2 years for the European eel and 1 year for the American eel while otolith microstructure revisit these estimates and argue for a migration duration shorter than 1 year for both species.

1.2.3 Metamorphosis

After having attained their full term in growth, leptocephali undergo a metamorphosis into glass eels. The detrainment of glass eels along shelves mainly occurs from September to May for the European eel and from January to July for the American eel. As this metamorphosis is located in seawater and could span several weeks or months, it has to be accounted for in the migration duration.

1.2.3.1 Location

Metamorphosing leptocephali have been observed fairly close to the coasts but 'oceanic glass eels' have been found far from the shelf as well (Schmidt, 1909b; Tesch *et al.*, 1986; Antunes and Tesch, 1997) and even southwest of the Azores (Tesch *et al.*, 1979). The exact location of this transition stage is not yet eluded and both stages have been sampled during different cruises in the Bay of Biscay (e. g. Tesch, 1978). Haro and Krueger (1988) assumed that the geographic trend in elver length may come from variations in the timing of metamorphosis into glass eel. McCleave (1987) proposed that the metamorphosis might be triggered when leptocephali encounter the bottom during their diurnally vertically migration above the continental slope or shelf. This sensory contact might induce the metamorphosis of developmentally capable leptocephali (McCleave, 1993). This hypothesis would both enhance the chances of successful metamorphosis and contribute to the continental separation of the two species, but it leaves unresolved the Gulf Stream detrainment process.

How do American eels detrain from the Gulf Stream to invade the North American continental shelf while European eels remain in the Gulf Stream, keeping in mind that fish larvae have never been found to perform long-distance oriented movements (see below) and that glass eels are juvenile fish, not larvae? Is a difference in metamorphosis timing sufficient to explain why European eels have never been reported in North America? American eel leptocephali could start metamorphosing into glass eels while in the Gulf Stream after which partly or fully-metamorphosed glass eels would detrain from the Gulf Stream using directed (westward) oriented swimming. Observations by Antunes and Tesch (1997) on European eels lend support to such a hypothesis as they found that catches of glass eels are relatively common in waters deeper than 1 000 m while leptocephali have never been caught on the continental shelf. Such a mechanism (i.e. metamorphosis in the deep ocean followed by directed swimming by glass eels) could also explain how European eels invade the continental shelf. Under such a scenario, it is unlikely that contact with bottom (McCleave, 1987) would be the developmental trigger required for metamorphosis because waters in the Gulf Stream / North Atlantic Drift system are several 1 000 m deep.

1.2.3.2 Timing and duration

A great variance has been observed in timing and duration of leptocephalus metamorphosis into glass eels. Schmidt (1906) alleged that complete metamorphosis may take about a year (9-10 months from stage I to stage Va, and 2-3 months from stage Va to stage VIb). This assumption has been fully revisited using glass eel otolith. Wang and Tzeng (1998, 2000) estimated a metamorphosis starting 200 days after hatching and lasting 55 days for American eel larvae and 350 days plus 98 days for European eels. These results are quite similar to those of Lecomte-Finiger (1992) on European eels: metamorphosis starting 176-196 days after hatching and lasting 33-76 days. Arai *et al.* (2000) estimated metamorphosis to last 18 to 52 days in both species. This great variance of estimated metamorphosis duration is also observed in the Japanese eel (Cheng and Tzeng, 1996) or for the short-finned eel (*A. australis*) and the longfin eel (*A. diffenbachii*) (Marui *et al.*, 2001). It has been proposed as a life history strategy to favour the wide distribution of these species. It can also be explained by differences in temperature experienced by leptocephali during migration (Arai *et al.*, 2001).

1.3 Estimation of the migration duration from otoliths: the controversy

In the previous section, we pointed out the large discrepancies between the estimations of the migration duration obtained from different methods. Estimations are ranging from 6 months (otoliths studies) to 2-3 years (cohort analysis) or 2 years (lagrangian modelling). Much ink has been spilled on the otolith studies, especially the otolith microstructure analyses. Here we describe this controversy about the estimates of the migration duration using otolith studies.

1.3.1 Interpretation of otolith macrostructures is uncertain

In many eel otoliths, no distinct correlation exists between the occurrence or absence of growth zones and the onset of summer or winter, i.e. eel otoliths include false annuli that are difficult to distinguish from true ones, making annual age determination difficult at best (Dahl, 1967; Liew, 1974; Deelder, 1976; Moriarty, 1983). Deelder (1976) called this matter the "supernumerary zones". Different methods have been proposed to overcome the problem of ageing eels (Vøllestad *et al.*, 1987; Deelder, 1982; Berg, 1985; Véró *et al.*, 1986; Dekker, 1987) such as polishing otoliths (Wiedemann Smith, 1968) or densitometry (Deelder, 1976) but the use of otoliths for annual age determination remains to be validated and also depends on the origin of eels (Michaud *et al.*, 1988; Vøllestad and Næsje, 1988). An experiment led by Moriarty and Steinmetz (1979) compared different age assessment methods. An original aspect of this work was to distribute the same samples of eel of known-age to five experienced readers to confront their age determinations. The differences between the age determinations of the same eel by different readers were in many cases over 100 %. There was no general agreement among age readings. These results suggested that the influence of the mode of interpretation is much more important that the method itself (Charlon, 1979). Svedäng *et al.* (1998) found the same discrepancies both between readers and between eel origins, illustrating the need for training and the use of reference collections. Casselman (1982) raised another problem in reading the structure of the otolith. Analysis of the surface of sections that appeared to be uniformly translucent indicated that calcium zonation existed even though optical zonation was not apparent.

The review of the available literature on eel otolithometry points out the large uncertainties associated with age determination from the reading of the macrostructure. The next section highlights that more recent techniques of microstructure reading brought new insights on determination of eel larva age but do not bring all eel mysteries out.

1.3.2 Uncertainties regarding interpretation of otolith microstructures

Annual age determination of eels by otoliths is uncertain but gives a range of value that did not shed doubt on Schmidt's (1922) interpretation of the oceanic larval migration. By contrast, results of daily increments are in conflict with all other estimates of migration duration (e. g. Lecomte-Finiger, 1992; Wang and Tzeng, 2000). A debate on the validity of the otolith method in larval eels ensued. The debate on the validity of otolith microstructure interpretation does not limit to the eel case. Although there is no reason to doubt the apparent universality of daily increment formation in young fish under adequate growth condition (Campana and Neilson, 1985), there are a number of reported exceptions, all from temperate pelagic larvae, which indicates that other mechanisms could conceivably complicate or invalidate age interpretations derived from otolith microstructures (Campana *et al.*, 1987). Regarding the eel case, several authors pointed out that the interpretation of eel microstructure may suffer from several drawbacks, in particular the lack of validation of daily rings and the difficult interpretation of the diffusive zone (see Fig. 1.5).

Nondaily increments in eel larvae?

The microstructure of eel larva otoliths are interpreted as daily increments, but several hypotheses can be invoked to explain apparent increment formation lower than daily. The growth rate limitation hypothesis of Geffen (1982) has been cited as consistent with results of a number of studies (Bergstad, 1984; McGurk, 1984). Nondaily increment formation has been observed in a variety of fish species with slow-growing phases (Methot and Kramer, 1979; Laroche *et al.*, 1982; Bergstad, 1984; Campana, 1984). Problems of optical resolution may also prevent accurate interpretation of otolith microstructure (Geffen, 1992). Daily increment could be forming in the eel otolith, but below the resolution limit of either light or scanning electronic microscopy (SEM). The hypothesis of inadequate resolution was first presented when it was noted that narrow daily increments could only be seen after adequate otolith preparation (Campana, 1984). An extension of this hypothesis is that it is theoretically possible for daily increments to form below the resolution limit of microscopy. Apparent increment formation rate then appears to be lower than the daily true rate (Campana *et al.*, 1987). These authors proposed two criteria indicating that such bias may be present. The first one is where increment width is less than 1 μm. Lecomte-Finiger (1992) measured the mean growth rate of the otoliths in the leptocephalus growth zone was $0.605 \pm 0.060\,\mu\text{m}\cdot\text{d}^{-1}$. The second criterion concerns otoliths where increment width appears to increase in proximity to the nucleus. Lecomte-Finiger (1992, 1994b) described changes in mean increment width: the 50 first increments are wider, then decreasing to the 80th increment, and growing afterwards. Hence larval eel otoliths fit the two criteria described by Campana *et al.* (1987) where non daily increment formation may occur. Ironically, SEM is often of little help in otoliths where the increments are extremely narrow, presumably because the chemical contrast between the incremental and discontinuous zones of a given daily increment is too weak to allow etching. So it is possible that there are regions in the otolith where the daily growth is slow to the

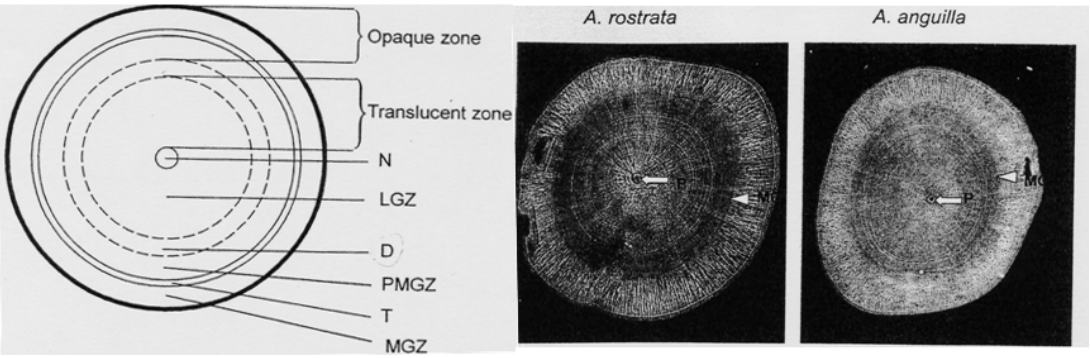

Figure 1.5: Schematic diagram of otolith of an American glass-eel (left panel). N, nucleus; LGZ, leptocephalus growth zone; D, diffuse or metamorphic zone; PMGZ, post metamorphic growth zone; T, transition ring or elver mark; MGZ, marginal zone (*in* Cieri and McCleave, 2001). Scanning electron microscope micrographs illustrating the daily growth increments in otoliths of elvers of *A. rostrata* from Nova Scotia (47.94 mm total length) and *A. anguilla* from France (68.34 mm total length; *in* Wang and Tzeng 2000)(right panel).

point where discrete increments are not visible, and that eel agers are unconsciously interpolating through that region (Steven Campana, Bedford Institute of Oceanography, Halifax, personal communication). For instance, Umezawa and Tsukamoto (1991) noted a decline in ring deposition after 5 days in unfed elvers or in elvers at low temperature. Ring deposition may depend on nutritional conditions (see below). In contrast to the nutrient-rich nearshore waters, the open ocean is much poorer, gradually becoming less productive with increasing distance from the continent (e. g. Behrenfeld *et al.*, 2006; Raven *et al.*, 2007). Hence, leptocephali may have such a low metabolic rate that increments in otoliths might not be deposited daily, or be deposited daily but be too thin to be observable in either light or scanning electronic microscopy.

Interpretation of the diffusive zone

Another contentious issue concerns the diffusive, so called 'metamorphic' zone: can growth rates from the translucent zone be extrapolated to the diffusive zone (Fig. 1.5)? The diffusive zone interpreted as the metamorphosis stage of leptocephali was seriously reconsidered by several authors (e. g. Antunes and Tesch, 1997; McCleave *et al.*, 1998) since it cannot be interpreted (i. e. counted; Fig. 1.5). Antunes and Tesch (1997) suggested that part of the diffuse zone may have been formed during a larval phase of retarded growth, during which no formation of daily rings takes place. The low metabolic rate and uncertainty in the mode of nutrition of leptocephali lend support to such an interpretation (McCleave *et al.*, 1998). The diffusive zone may therefore prevent an accurate estimation of the migration duration since no narrow circumscribed rings are visible (Correia *et al.*, 2002, 2004, 2006).

Another bias may arise due to otolith resorption during metamorphosis. Cieri and McCleave (2000) emphasized the specific remobilization of both strontium and calcium needed during metamorphosis, which may imply not only the resorption of teeth as observed in *Ariosoma balearicum* (Hulet and Robins, 1989), but also resorption of otoliths. However this possible mechanism remains highly speculative as there is no evidence of otolith resorption in any fish species (Campana and Neilson, 1985).

Age determination seems beset with great difficulties and contentions. Even if otolithometry has been shown to be accurate in some *Anguilla* species (e. g. Tsukamoto *et al.*, 1988a; Kuroki *et al.*, 2006), there remains a twilight zone that is not validated and that cannot rule out the possibility of a more than 2 years duration of migration. However, otolith microchemistry remains a useful tool to investigate life history of species. In particular, it could be used to grasp some intriguing migratory patterns of eels (e. g. Tzeng *et al.*, 1997; Tsukamoto *et al.*, 1998; Daverat *et al.*, 2005) or temperature life history of leptocephali (e. g. de Casamajor *et al.*, 2002).

1.3.3 Can *Anguilla* leptocephali swim to cross the Atlantic Ocean in 6 months?

The controversy about the migration duration lead to two different visions: (*i*) studies using ocean general circulation model and assuming a passive migration drift of eel larvae estimate the migration duration is greater than 2 years; (*ii*) otolith studies argue that the migration duration is shorter than 1 year and thus is much lower than ocean model predictions. An active and oriented migration of leptocephali has been proposed to explain these discrepencies. In this section, we address 2 questions: if we admit the hypothesis of active and oriented swimming for eel larvae, is it an exception or do other fish larvae exhibit similar capacity? Do the morphology and physiology of eel larvae enable an active and oriented swimming activity across the Atlantic Ocean? In every instance, it raises the problem of the source of energy to survive over such a long period or swim over such a long distance.

1.3.3.1 Active and oriented swimming in larval fish

Some fish larvae possess the capability to orient in the ocean, but at a much smaller scale (10s of km) than would be required for oriented swimming by Atlantic *Anguilla* (1000s of km). Leis (2006) published a literature review entitled "*Are larvae of demersal fishes plankton or nekton?*" The simple answer for eel species is that larvae are both plankton and nekton. During the early larval stage, larvae are closer to the simplifying 'passive drift with currents' assumption, although even then, they perform diel vertical migrations, thus indirectly influencing their dispersal. As larvae develop, the passive assumption becomes invalid. Larvae are capable of swimming faster than mean ambient current for long periods, travelling tens of kilometres. Most of the literature on behaviour of larval fish comes from reef ecosystems (e. g. Leis and Carson-Ewart, 2003; Leis, 2007; Paris *et al.*, 2007) where larvae have been reported to perform oriented movements as large as 10s of km using mostly reef noise or the sun as cues for orientation. Ramzi *et al.* (2001) and Fox *et al.* (2006) showed the influence of active swimming on the ability for flatfish larvae to reach their nursery area and increase the settlement success. As mentioned above, oriented swimming by partly or fully-metamorphosed glass eels could well be involved in the Gulf Stream detrainment process.

1.3.3.2 Can they physiologically swim?

Source of food

In the Pacific, the specific location of Japanese eel spawning area near seamounts may be linked to functional role of seamounts in nutrient transport. Seamounts have been shown to induce perturbations in nutrients distributions, leading to enhanced upward transport of nutrients into the euphotic zone (Furuya *et al.*, 1995) and an elevated amount of chlorophyll *a* downstream of the seamount. This ecosystem may provide eel larvae with a sufficient food supply. In the case of European eel, Kettle and Haines (2006) showed that the period where there is a maximum of chlorophyll *a* concentration in the first year of drifting matches the eel spawning season. Bonhommeau *et al.* (2008) found strong correlations between primary production in the eel spawning area and eel recruitment in Europe. These results suggest a possible match between hatching period and maximum food supply.

The exact food source for leptocephali is not clearly established due to the lack of food residues in the leptocephali gut. Schmidt (1909b) noticed that Stage Vb elvers feed on copepods. Two potential sources of nutrition have been proposed for eel larvae: dissolved organic matter and particulate organic matter in the form of zooplankton fecal pellets and appendicularian discarded houses (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler, 1999). Pfeiler (1986) first assumed that dissolved organic matter in the water is absorbed directly across the body walls. Westerberg (1990) offered then another hypothesis on the observation of the elaborate structure of leptocephalus teeth. He surmised that leptocephali feed on appendicularian discarded houses. This hypothesis was developed by Mochioka and Iwamizu (1990) and Mochioka and Iwamizu (1996) who found larvacean houses and zooplankton fecal pellets in the gut of leptocephali (from five families: Congridae, Muraenidae, Muraenesocidae, Nettastomatidae, and Ophichthidae). Marine snow has also been proposed as a potential source of nutrition (Knights, 2003). Recently, the isotope analysis (δ^{13}C) of glass eels that just entered an estuary showed that they feed primarily on an oceanic planktonic food source, marine particulate organic matter (Bardonnet and Riera, 2005). The remaining question relies upon the potentiality of these food sources to cover the energy expenditure of leptocephali.

Bioenergetics features

Eel larvae are qualified as type II larvae based upon their unique developmental strategy. After a post-hatch period during which the yolk sac is resorbed, leptocephali show a dramatic increase in size: up to 40 % of the leptocephali maximum length is reached while only 5-7 % of the maximum mass is accumulated (Bishop and Torres, 1999, 2001). Bishop and Torres (1999) found an unusual relationship between mass and metabolic rate that is related to the formation of an energy depot in the form of glycosaminoglycans that serve a skeleton function inasmuch as they are completely unossified. Because the glycoaminoglycans are metabolically inert compounds, the larvae are able to rapidly increase in size with minimal energy expenditure (Bishop *et al.*, 2000). Larvae, even very large ones, maintain low overall metabolic costs. Although the hyaluronan, the main glycosaminoglycan in the body matrix of leptocephali (Pfeiler *et al.*, 2002), is supposed to provide a source of nutrition during metamorphosis, it is never proposed as a source of possible energy for swimming (Bishop and Torres, 1999; Pfeiler, 1999; Bishop and Torres, 2001; Pfeiler *et al.*, 2002). Swimming activity has been observed in leptocephali mainly for escapement purpose (e. g. Bishop and Torres, 1999). The vertical swimming is clearly observed at different leptocephali stages (e. g. Castonguay and McCleave, 1987) but further studies should focus on energy expenditure of swimming over the thousands of kilometres of migration. Furthermore, swimming activity requires developed muscles while Leonard and Summers (1976) reported that leptocephali have only minute amounts of subcutaneous red muscle.

1.4 Conclusion

The extensive and numerous studies on eel larvae enable us to have a good overview of the main features of eel oceanic stages. The spawning season occurs from February to April for the American eel and March to June for the European eel. The spawning area is located in the Sargasso Sea and adult eels may choose physical features such as temperature to determine the location of the spawning. The different methods to determine the migration duration lead to two estimations, from less than 1 year for the otolith microstructure studies to more than 2 years for studies using cohort analyses, macrostructure of otolith, and numerical modelling. These two estimations lead to two hypotheses about the way eel larvae migrate: if it is more than 2 years, the migration could be passive, this is sustained by the validity of ocean general circulation models; if the migration lasts less than 1 year, the migration must be active and oriented.

However, in light of the different papers reviewed here, three aspects make us express reservations about the hypothesis of an active and oriented swimming ability allowing eel larvae to cross the Atlantic Ocean in 6 months. First, validation of growth increment formation in Atlantic *Anguilla* leptocephali otoliths has to be carried out. This mainly concerns the potential problem of daily increments being formed but below the resolution limit of microscopy due to slow growth rates (Campana *et al.*, 1987). Second, fish larvae have never been reported to perform large-scale active oriented migrations. Third, active large-scale oriented migration by leptocephali would require large energetic expenditure and hence they would have to rely on important food availability that is not found in the open ocean.

Several ways may be followed to investigate the migration duration question. The use of lagrangian modelling seems to be a promising approach since it enables to work not only on migration duration but on possible routes, specific location of spawning and test possible swimming speeds needed to cross the Atlantic. This kind of approach could be coupled to bioenergetics models using estimates of available food, and then, growth and necessary energy for leptocephali. It could be used to simulate otolith growth to compare it to observed patterns in leptocephali otoliths as was done by Hussy and Mosegaard (2004) for Atlantic cod (*Gadus morhua*) and Pecquerie (2007) for Bay of Biscay anchovy (*Engraulis encrasicolus*). Another promising way relies on artificial reproduction that has just been succeeded in the National Institute of Aquatic Resources of Denmark by producing viable eggs and culture larvae of captive European eel for up to 12 days (`http://www.dfu.dtu.dk`). It would therefore be possible to assess whether daily increments in otolith could be confirmed on reared leptocephali.

The well published saga of the unwieldy “eel problem” is not settled and difficult to unravel. A few bricks have been laid here. Be as it may, if the migration duration is 6 months, it would be an awesome achievement; if it is 3 years, it is an intriguing ability to survive in the nutrient-poor open ocean.

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2

Les larves d'Anguille traversent-elles l'Atlantique en 6 mois ?

Résumé détaillé

Le chapitre 1 a mis en évidence de grandes différences entre les diverses estimations de la durée de migration de l'Anguille européenne. Deux conceptions de la migration des larves s'opposent. Les résultats des analyses de cohortes et des modèles de simulation de dérive passive de particules montrent une durée de migration d'environ deux à trois ans. L'analyse de la microstructure de l'otolithe détermine un temps de migration de 6 mois et propose ainsi une durée beaucoup plus courte rendue possible par une nage active et / ou orientée des larves. Dans ce chapitre, l'objectif est d'utiliser une approche lagrangienne pour estimer le temps de migration minimal de la mer des Sargasses à une ligne fictive proche du plateau continental européen, située à 20°W.

Nous utilisons deux modèles océaniques différents de par la méthode de modélisation. Le modèle Mercator assimile des données collectées *in situ* (altimétrie, température) tandis que le modèle Drakkar utilise seulement les équations de la dynamique des fluides pour décrire l'état de l'océan. Les champs de courant de ces modèles sont utilisés à l'aide de l'outil de modélisation lagrangienne *Ariane*, qui permet de calculer les trajectoires des particules. Les larves d'Anguille sont lâchées dans la mer des Sargasses à chaque maille de ces deux modèles de circulation de l'Océan Atlantique (Drakkar et Mercator ; Fig. 2.1).

Trois hypothèses de comportement sont implémentées dans les simulations de dérive des larves. (*i*) Les particules dérivent à profondeurs fixes, comme cela est fait dans l'article de Kettle and Haines (2006). (*ii*) Les particules effectuent une migration verticale nycthémérale de -300 m le jour à -50 m la nuit, ce qui correspond aux observations lors des campagnes d'échantillonnage (e. g. Castonguay and McCleave, 1987). (*iii*) Les particules choisissent à chaque pas de temps la couche d'eau où le courant est le plus rapide. En effet, les civelles sont capables de déterminer les courants favorables à leur remontée en estuaire et nous pouvons supposer qu'il en va de même pour les leptocéphales. La période couverte par le modèle océanique Drakkar nous permet, de plus, d'étudier l'influence des fluctuations climatiques interannuelles sur la circulation océanique à grande échelle sur ces migrations.

Les simulations lagrangiennes reproduisent les principales données observées quant aux latitudes d'arrivée, aux dates de départ et à la profondeur de dérive (Fig. 2.2, 2.3 et 2.4). Ces résultats montrent que le nombre de particules réussissant à franchir le 20°W est plus grand lors des périodes où les indices océaniques grande-échelle (NAO, GSI, TI) sont forts. Inversement, la durée de migration est la plus courte quand ces indices sont élevés. Ces résultats sont cohérents dans la mesure où les fortes valeurs de ces indices sont reliées à des vents d'Ouest importants et des courants plus rapides. Pour le modèle Drakkar, la durée minimale du trajet de la mer des Sargasses au 20°W est de 10 mois et 19 jours pour un parcours de 8 447 km à profondeur fixe (-94 m). Des résultats similaires sont obtenus avec le modèle Mercator pour une particule dérivant aussi à profondeur fixe (-132 m) (Fig. 2.5). Les comportements de migration verticale et de choix du courant le plus rapide induisent une durée de migration et une distance parcourue bien plus importante (5 mois et 3 000 km de plus). Une des explications de ce résultat provient du fait que les couches d'eau supérieures sont plus rapides mais aussi plus turbulentes. La particule la plus rapide emprunte des couches d'eau à la fois plus rapides (Fig. 2.6) mais aussi moins turbulentes ce qui lui assure une trajectoire relativement linéaire et plus directe (Fig. 2.7). Le calcul de la dimension fractale des trajectoires nous permet de quantifier la linéarité des trajectoires : une dimension faible correspond à un trajet linéaire tandis qu'une valeur plus élevée indique une trajectoire plus chaotique. L'analyse confirme que les trajectoires les plus linéaires correspondent aux couches où dérivent les particules les plus rapides (Fig. 2.8. Les particules ayant un comportement de migration verticale ou de choix de courant le plus fort sont confrontées à des couches plus turbulentes, ce qui prolonge leur trajet.

La méthode utilisée dans ces simulations lagrangiennes sous-estime le temps réel de migration. En effet, la ligne d'arrivée des particules à 20°W est encore loin des côtes (1 000 à 1 500 km). De plus, la métamorphose des leptocéphales en civelle a lieu sur le plateau continental et sa durée est comprise entre 18 et 98 jours selon les études. Pour tester l'hypothèse d'une migration active des larves d'Anguille, nous calculons la vitesse nécessaire pour parcourir, en 6 mois, la même distance que la particule la plus rapide : 8 447 km / 6 mois = 54.3 cm·s^{-1}. La vitesse de cette particule en dérive passive est de 30.2 cm·s^{-1}. Ainsi, la vitesse à laquelle devrait nager une larve pour effectuer ce trajet en 6 mois devrait être de 54.3-30.2 cm·s^{-1} = 24.1 cm·s^{-1}. Cela correspond à 3.4 fois la longueur d'un leptocéphale complètement développé (70 mm). L'océan ouvert est très peu productif et ainsi les dépenses d'énergie liées à cette nage active intense sur 8 400 km paraissent difficilement recouvrables. Au vu de ces résultats, la migration des leptocéphales jusqu'aux côtes européennes en 6 mois par nage active nous semble peu probable.

Can the European eel larvae cross the Atlantic Ocean in 6 months?

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Abstract Using lagrangian simulations over three different hydroclimatic periods in the last 45 years, we estimate the fastest migration duration and the shortest distance covered by particles released in the eel spawning area and drifting passively (at fixed depths, undergoing a vertical diurnal migration, or choosing the fastest currents). This enables us to compute (*i*) a passive drift speed, and (*ii*) a hypothetic swimming speed needed for European eel larvae (leptocephali) to cross the Atlantic in 6 months (i.e. the migration duration estimated from otolith daily growth increments). Our results first show that active behaviours (vertical diurnal migration and rheotaxis) paradoxically increase the migration duration. We also find that leptocephali should continuously swim at minimum 3.4 body length per second over 8200 km to cross the Atlantic in 6 months. It does not correspond to any swimming speed of a fish larva observed over such a distance and food availability in the open ocean is not sufficient to such energy expenditure. These results provide evidence that leptocephali do not cross the Atlantic in 6 months. Once again, the migration duration of European eel larvae has to be reconsidered.

Keywords leptocephali; *Anguilla*; Gulf Stream; lagrangian modelling, fractals

Suggested running title Migration duration of European eel larvae

2.1 Introduction

The European eel is a catadromous fish that undergoes one of the longest seaward migration, more than 6,000 km across the Atlantic Ocean. Conveyed by warm currents, eel larvae (leptocephali) come from the Sargasso Sea where eels spawn, to settle to the African and European shelves, from Mauritania to the Polar Circle (Schmidt, 1923).

The current decline in eel populations worldwide is well observed (Anonymous, 2003) and the European eel has been listed in Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007) regarding its current level of abundance. The decline in European eel population since the early 1980s is no doubt the combined effect of several and probably interacting factors: direct effect of anthropogenic activities such as overfishing (Dekker, 2004), habitat loss and degradation (McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006) and increasing stress in the freshwater stage due to parasites and diseases (e. g. Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005) and in the oceanic stage due to unfavourable oceanic conditions (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008). These potential causes of stock decline are often *per se* associated and occurring at the same time and are difficult to disentangle (Anonymous, 2003).

The oceanic larval phase of European eels is of primary concerns to understand eel ecology. There has been a long history of ecological studies dealing with marine life stages of this species (Dekker, 1998). As for most fish species, the major source of mortality occurs during the larval stage (Hjort, 1914). The oceanic phase conditions the dispersion over the coastal regions and the freshwater habitats. The migration duration is certainly one of the most critical and controversial features of the oceanic larva migration. It determines eel larva oceanic trajectories and mortality, the mean generation time of eels, hence dates and areas of larva coastal arrivals. It also conditions our ability to understand how the recruitment is linked to environmental fluctuations. This is critical in a context where major changes in oceanic conditions are recorded and known to impact fish populations (Beaugrand and Reid, 2003; Lehodey *et al.*, 2006). Recruitment data have been compared to environmental factors such as large-scale oceanic and climate indices (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008; Kettle *et al.*, in press). Primary production and sea temperature fluctuations in eel spawning area have also shown to be related to glass eel recruitment (Knights, 2003; Bonhommeau *et al.*, 2008). However, all these studies used recruitment indices based on glass eel arrivals. Because oceanic environmental conditions are suspected to impact eel larvae several months earlier than glass eel arrivals, time lags have to be accounted for migration duration to link environmental descriptors to glass eel recruitment. Results still remain conditioned by the hypothesis made about migration duration, e. g. 1-year lag for Friedland *et al.* (2007) and 2.5 - 3 years for Knights (2003) and Bonhommeau *et al.* (2008).

Uncertainties about migration duration mainly arise from the difficulty to observe eels during their oceanic stage, in particular during larva emergence and migration. During the 70 years following the discovery of the breeding places of eels (Schmidt, 1922, 1923), the migration duration of the European eel was mainly speculated to be comprised between 2 and 3 years. This assumption was grounded on growth curves of eel larvae (leptocephali) and their spatial occurrence at different dates in the North Atlantic. This assertion has been reconsidered when counting daily increments in otolith microstructure. Estimations made using 423 glass eels from the Netherlands to Morocco established that the migration duration (migration + metamorphosis into glass eels) is comprised between 191 and 276 days (about 6 to 9 months), for glass eels caught in Portugal and UK respectively (Lecomte-Finiger, 1992). However, the reading accuracy of daily growth increments sparks a large debate (e. g. Antunes and Tesch, 1997; McCleave *et al.*, 1998). Several assumptions were advanced to explain such a short migration duration. Lecomte-Finiger (1992, 1994) put forward an active and / or oriented migration hypothesis. Be as it may, such a short sojourn remains difficult to explain. More recently, it has been shown how ocean general circulation models may provide insights to better grasp this trans-oceanic migration. Kettle and Haines (2006) used lagrangian simulations over a 4-year period (1993-1996) to estimate the migration duration and pathways of European eel larvae and found a 2-year migration duration.

Here we follow Kettle and Haines (2006) and attempt to learn about migration duration by performing lagrangian simulations. However, our approach differs from Kettle and Haines (2006) work in three ways.

Our approach is firstly different in its aims. In contrast to Kettle and Haines (2006), we do not investigate mean pathways and migration duration. Rather, we focus our analysis on the hypothesis testing: “Can eel larvae cross the Atlantic Ocean in 6 months?”. We then focus on the fastest particles drifting between the Sargasso Sea and the European shelves to establish a minimum bound for the migration duration.

Secondly, we used 2 different ocean general circulation configurations, Drakkar and Mercator projects that are currently the most accurate ones in the European scientific community. Simulations were possible over a period of 45 years when using Drakkar model. Thirdly, we relaxed the hypothesis of strict passive drift by testing three different behaviours of the particles. (*i*) Particles drifted at fixed-depth as in Kettle and Haines (2006). (*ii*) Particles were undergoing a vertical diurnal migration between -300m and -50m as observed *in situ* (Castonguay and McCleave, 1987). (*iii*) Particles follow the direction and depth where the speed of currents is the highest. As glass eels have a positive rheotaxis (mechanism whereby they will turn to face into an oncoming current), we assumed that leptocephali may use the same ability to drift and choose the fastest currents. In each experiment, particles are released in the Sargasso Sea every 15^th days over each year and are followed during 1.5 year.

In so doing, we calculate the passive drift speed of the fastest particles. We also address the questions: "Does active behaviour enable particles to reach European shelves faster?" and "How fast should the fastest particles swim to cross the Atlantic Ocean and cover the same distance in 6 months?"

2.2 Materials and Methods

2.2.1 Circulation models

Lagrangian simulations are performed using two different oceanic model configurations (hereafter Drakkar and Mercator). Both models are based on the NEMO/OPA numerical code (Madec *et al.*, 1998).

The Drakkar model (`http://www.ifremer.fr/lpo/drakkar`) is interesting because of the duration of the simulation (1958 to 2004), which allows us to address the interannual variability of trajectories. The model configuration is global. It uses the ORCA025 grid (a tripolar grid with a 1/4° horizontal grid resolution at the equator). The configuration is described by Barnier *et al.* (2006) who show its good performance in representing strong currents and eddy variability, even in comparison with higher resolution models. The water column is divided in 46 levels, with grid spacing ranging from 6 m near the surface to 250 m at the bottom. The simulation was run using state of the art atmospheric data (a blend of satellite products and ERA40 6-hourly winds, temperature and humidity).

Contrary to the MERCATOR (or KH2005), the Drakkar model is a so-called “fully prognostic” model, which means that it does not use assimilated ocean data (neither satellite altimetry nor *in situ* temperature or salinity), and therefore can be substantially far from observations in some areas. Indeed the model biases are similar to those of the earlier models (Treguier *et al.*, 2005). Fortunately those biases are less pronounced in the subtropical gyre, which is our region of interest, compared to the subpolar regions (Treguier *et al.*, 2005). To reduce file size and to centre on the area of our study case (i. e. the North Atlantic Ocean), we extracted an area ranging from -82 to 6°W and 10 to 60°N. Since the observed depth of leptocephali is comprised between -50 and -300 m (e. g. Castonguay and McCleave, 1987), we reduced the oceanic model to the top 24 levels (-3 to -989 m). To avoid the early spin-up phase of the model, we use the period 1960-2004 of the simulation. Circulation fields are time-means archived every 5^{th} days.

The circulation fields provided by the Mercator project (`http://www.mercator-ocean.fr`) were the $PSY1v2$ analysis over the period 1992–2002 (the whole available period of this model). Circulation fields are archived every day. The horizontal grid resolution is 1/3° at the equator. The geographical extension of this simulation is the Atlantic from 20° S to 70° N. It encompasses 43 vertical levels from surface to 5 000 m (the vertical resolution is from 12 m at the surface, to 200 m at the bottom). The model was forced by altimetry and *in situ* data that are fully described in the MERA-11 general scientific paper (Greiner *et al.*, 2006). The area covered by the model has been reduced from -98 to 20°W to 20°S - 70°N and the depth was limited to the first 16 levels (-453 m). This ocean general circulation model is equivalent to the one used by Kettle and Haines (2006) in terms of approach. However, it has a better vertical resolution and run over a longer period.

2.2.2 Lagrangian simulation designs

The aim of the study is to determine the migration duration and distance of the fastest particles drifting from the Sargassos and the European shelves. We let particles drift over a 1.5 year period, which is long enough to capture the fastest particle trajectory. We used the Ariane tool developed by B. Blanke and N. Grima, Laboratoire de Physique des Océans, CNRS-IFREMER-UBO, Brest, France and freely available at `http://www.univ-brest.fr/lpo/ariane`. It is a FORTRAN code dedicated to the computation of

3D streamlines in a given velocity field (as the output of an Ocean General Circulation Model) and subsequent water masses analyses.

In the Drakkar configuration, drifters were released at each model grid, i.e. each 1/4 degree and each 24 fixed-depth levels in an area enclosing the assumed spawning area of eels in the Sargasso Sea (Fig. 2.1). To reduce simulation time, we restrict the whole available period (1958-2004) to three NAO-contrasted periods that provide an overview of different "oceanically-speaking" periods, and analyze potential discrepancies. The Atlantic Ocean general circulation can be contrasted in terms of strength and/or latitude of the Gulf Stream (Taylor and Stephens, 1998; Curry and McCartney, 2001). Winter North Atlantic Oscillation is a good index to estimate the position and strength of the North Atlantic currents. Curry and McCartney (2001) showed that the potential energy anomaly (ı. e. the strength of the Gulf Stream) is well correlated to NAO. The same goes for the latitude of the Gulf Stream measured by the Gulf Stream index (Taylor and Stephens, 1998). Kettle *et al.* (in press) showed that the migration of eel larvae may be linked to the NAO by a larval migration failure in the Sargasso Sea due to vertical density stratification and food restrictions. The selected periods were thus 1960-1964 (mean $\text{NAO} = -1.7$), 1973-1977 (0.9), and 1986-1999 (1.6). We then tested the relationships between on the one hand arrival success and minimum migration duration and on the other hand the NAO. Particles were released every 15^{th} days throughout the year. 1 972 608 particles were thus released each year.

Regarding the Mercator configuration, drifters are released at each model grid, i.e. each 1/3 degree and each 16 depth levels over the whole period available (1992-2002) in the same area as in the Drakkar model. Particles were released every 15^{th} days throughout the year. So 691 104 particles were released each year.

Three particle behaviours were implemented in lagrangian simulations. We first assumed a fixed depth drift for all particles released at each vertical levels of the reduced model. In a second experiment, a vertical diurnal migration was implemented. Particles were able to change their vertical position every 12 hours from about -300 m to -50 m as described in Castonguay and McCleave (1987). It mimics behaviour of eel larvae in the wild. Leptocephalus collections have been showed to have a diurnal migration depending on their length (Castonguay and McCleave, 1987). Until the length of 7mm, they are uniformly distributed over the 300 m upper layers (Schmidt, 1922; Schoth and Tesch, 1983; Castonguay and McCleave, 1987). Thereafter, a diurnal vertical migration is observed from

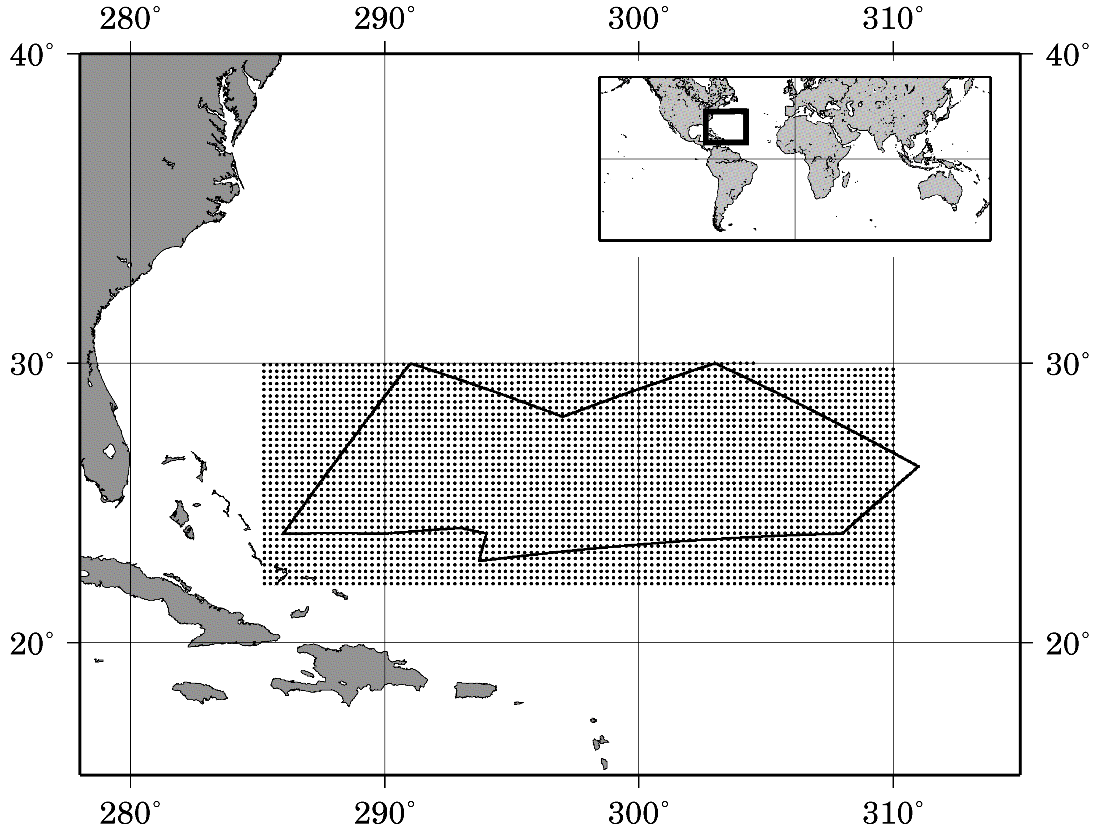

Figure 2.1: Map of the initial positions for the lagrangian simulations using the Mercator model (i.e. each 1/3°, and location of the European eel spawning area (polygon)). The initial positions using the Drakkar model has the same boundaries than Mercator but are set each 1/4°.

-300 m in daytime and -50 m at night (Schmidt, 1922; Castonguay and McCleave, 1987; McCleave, 1993; McCleave *et al.*, 1998). In a third experiment, at each time step, particles have the ability to actively select the direction where the current speed is the highest. As glass eels can feel currents and react to them (Bertin, 1956; Bolliet *et al.*, 2007), we assumed that leptocephali may have the same ability to follow the fastest currents.

Output files of lagrangian simulations include position (longitude, latitude, depth) and time for each particle. Particles are considered as having “succeeded” in their migration when crossing the 20° W whatever the latitude. This finishing line is more eastward than the 25°W chosen by Kettle and Haines (2006). Since the aim of the study is to estimate the migration duration of the fastest particle, the finishing line has to be as close as possible to the effective arrival area of eel larvae to compare to current estimates. However, 20°W is a reasonable limit since longitudes higher than 20°W correspond to continental slope that is not as well-resolved by the physical model as open ocean. Moreover, lagrangian simulations are unable to represent tidal transport of eel larvae when they reach the shelves. Knowing the position and time of each particle, we calculate the distance covered by each particle reaching the finishing line and the migration duration. The mean drift speed v_i for each particle i was estimated by the expression:

$$v_i = \frac{d_i}{t_i} \tag{2.1}$$

where d_i is the distance covered by the particle that succeeded crossing the 20°W and t_i is the corresponding time.

In order to reach the shelves the most quickly, the speed has to be the fastest and the distance has to be the shortest. We can assume that particles with the most "linear and direct" trajectory will cover the shortest distance and have the shortest migration duration. We then used a synthetic index, the fractal dimension, for each trajectory to characterise its linearity. In our study case, the fractal dimension is a measure of how successive positions of particles fill the plan where they are. It characterises the drift, from linear (lower fractal dimension) to chaotic (higher fractal dimension). The fractal dimension was calculated with the function *fdim* from the package *fdim* (de Pison Ascacibar *et al.*, 2007) of R Cran-project (R Development Core Team, 2007).

2.3 Results

2.3.1 Simulations are consistent with previous knowledge

Results of lagrangian simulations are consistent with observations and current knowledge about European eel larva migration. After 1.5 years of migration duration, the distribution area of particles at 20°W is comprised between 40 and 55°N with a peak at 50°N (Fig. 2.2a and b). Another peak appears in the North Africa area (30-35°N) as found by Kettle and Haines (2006). Most of arriving particles have their departure area located in the Western Sargasso Sea (75°- 65°W and 22°-30°N; Fig. 2.3 for the Mercator model). The same patterns are observed for the three experiments, i.e. fixed-depth, vertical migration, or faster current choice. The depth range of particles crossing the 20°W in less than 1.5 years is comprised between -400m and surface for both models (Fig. 2.4a and b). The gaussian distribution of these depths has a mode at -200 m for both models with another peak at -70 m for the Mercator model. It corresponds to the results of Kettle and Haines

(2006) and confirms the robustness of the results since ocean models used do not have the same features as those used by Kettle and Haines (2006).

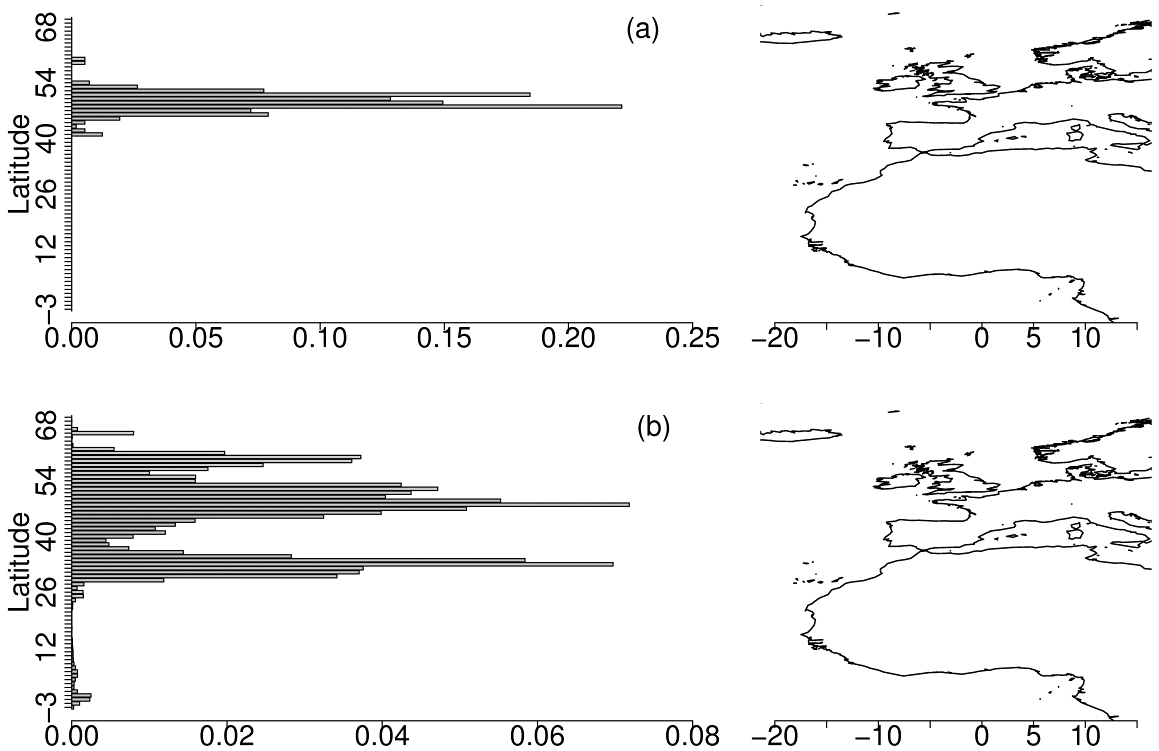

Figure 2.2: Latitude distribution of particles successfully crossing the 20°W meridian. Particles drift over 1.5 years after being released within the eel spawning area for the Drakkar (a) and Mercator (b) models. The maps on the right hand side shows the location of the latitude bins defining the histogram and is drawn up until the 20°W where particles are counted.

2.3.2 Large-scale oceanic indices influence migration success and duration

Over the whole period of simulations, 0.0025 % and 0.039 % of released particles drifting at fixed-depth succeeded in crossing the 20°W in less than 1.5 years (Drakkar and Mercator model respectively). We analyse the link between the number of particles that succeeded in reaching the 20°W and the intensity of three large-scale oceanic indices averaged over the years of drift: the winter NAO (Hurrell, 1995), the Gulf Stream Index (GSI, Taylor and Stephens, 1998), and the Potential Energy Anomalies (PEA, Curry and McCartney, 2001). For both model, when particles drift at fixed-depth, we found a significant positive relationship between winter NAO and the number of particles that succeed to arrive

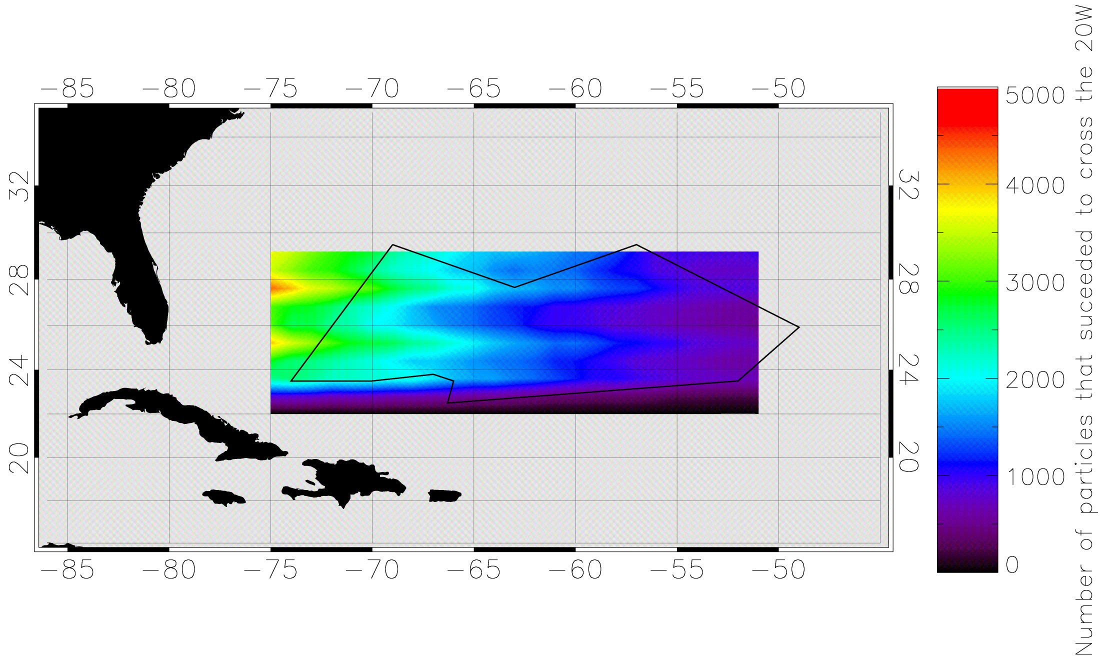

Figure 2.3: Number of successful particles as a function of starting location in the Sargasso Sea when using the Drakkar model (colour scale). The European eel spawning area is charted out by a black polygon (from Fig. 2 *in* McCleave *et al.*, 1987).

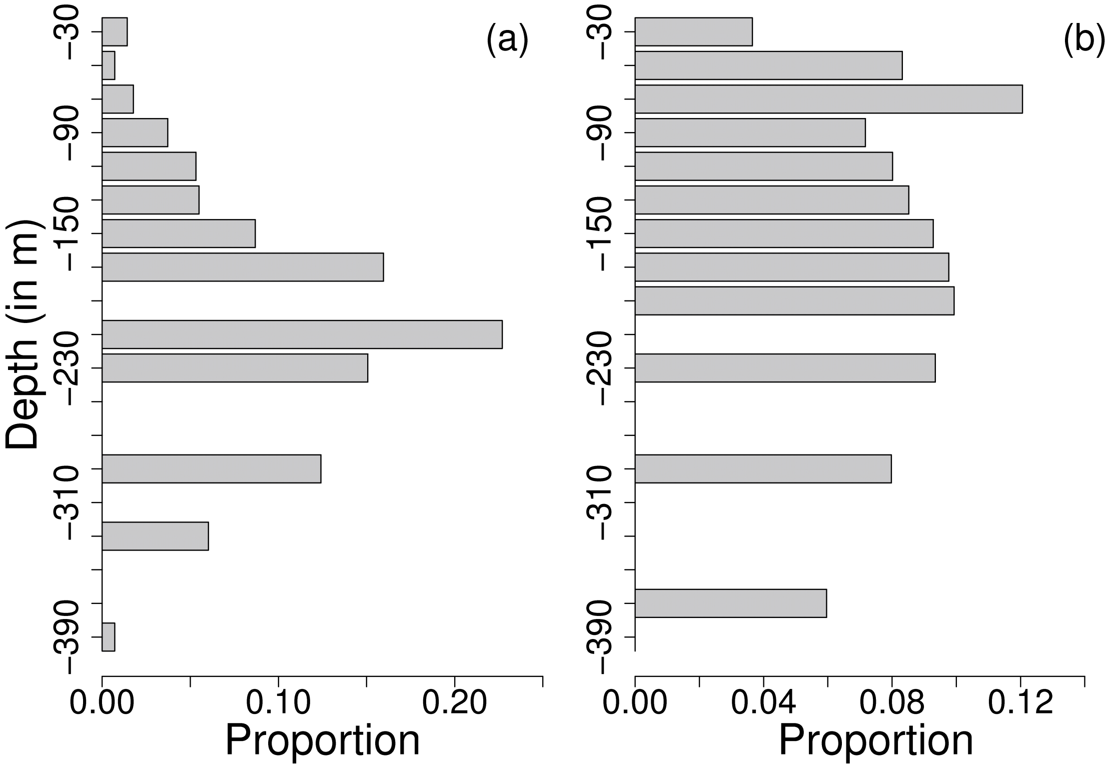

Figure 2.4: Depth distributions of the particles successfully crossing the 20°W meridian within 1.5 years after being released within the eel spawning area for the Drakkar (a) Mercator (b) model.

each year (Pearson's r = 0.50 and 0.78, p = 0.05 and 0.04, for Drakkar and Mercator respectively; autocorrelation removed following Pyper and Peterman, 1998). The same goes for the Gulf Stream index (r = 0.73 and 0.80, p = 0.01 and 0.04 for Drakkar and Mercator respectively) or the Potential Energy Anomalies (r = 0.57 and 0.47, p = 0.05 and 0.06 for Drakkar and Mercator respectively).

2.3.3 Behaviour hypotheses influence migration success estimates

For the two models, the two active behaviours of particles tend to diminish the migration success. Over the period of simulations, 0.0011 % and 0.0004 % of released particles having a vertical diurnal migration succeeded to cross the 20°W in less than 1.5 years (Drakkar and Mercator model respectively). When particles were able to select the fastest current, the arrival success is still lower than the fixed depth experiment and similar to the vertical migration hypothesis one, i. e. 0.0014 % and 0.0006 % for Drakkar and Mercator model respectively.

2.3.4 Minimum migration duration of particles

Regarding the Drakkar model, the fastest particle travelled at fixed depth from the Sargasso Sea to the "finishing" line in 10 months and 19 days, covering 8 447 km. Fig. 2.5 indicates that the migration duration of the ten, hundred and thousand next particles is much greater than the fastest one. Regarding the Mercator model, the migration duration and the distance covered are very similar to Drakkar. The fastest particle also travelled at fixed depth in 10 months and 3 days, and covered 8 498 km. The duration of the ten, hundred, and thousand fastest particles represented in Fig. 2.5 confirms results found with the Drakkar model. The fastest particle is significantly so.

Large-scale oceanic indices influence minimum migration duration The analysis of the relationships between NAO, GSI, and PEA and the minimum migration duration of particles drifting at fixed-depth reveals a negative link between NAO and minimum migration duration (r = -0.57, p = 0.04 after autocorrelation removal). The same goes for GSI (r = -0.75, p = 0.01) and PEA (r = -0.48, p = 0.05). The minimum migration duration occurs when the particle starts in 1990 (NAO over the drift equals 2.5 and

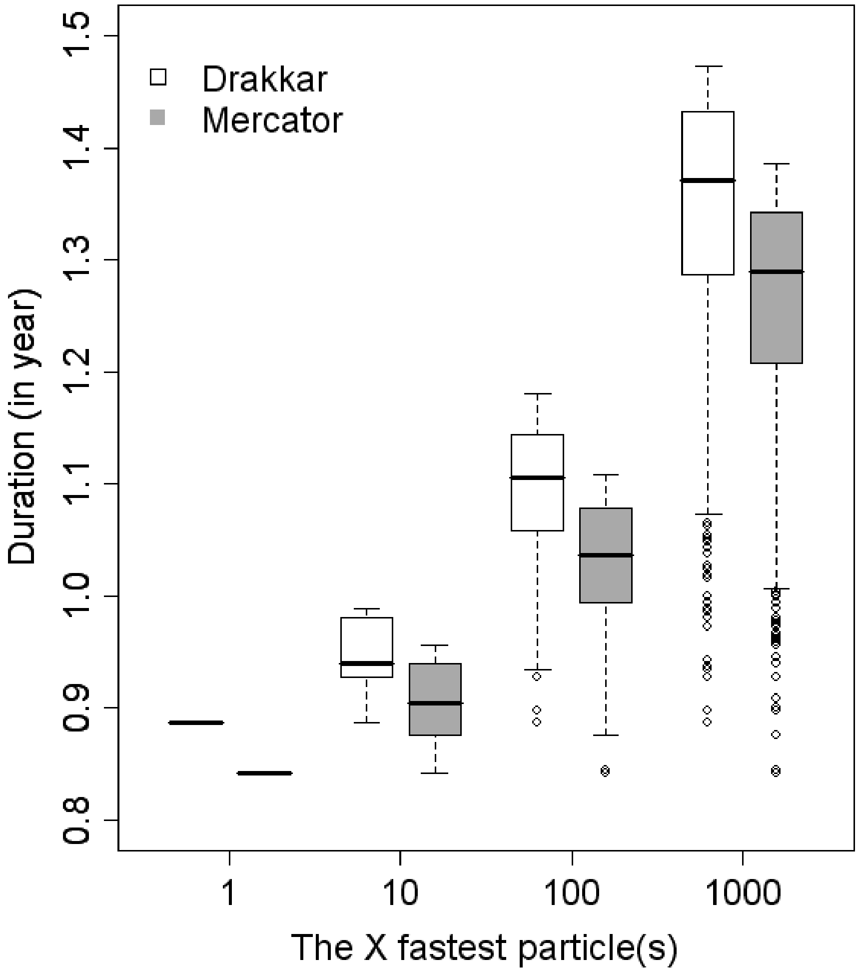

Figure 2.5: Boxplot of migration duration of the fastest particle, the ten fastest particles, the hundred fastest particles, and the thousand fastest particles for Drakkar model (white) and Mercator model (gray). Circles represent individuals outside the confidence interval.

high GSI and PEA). It indicates that when large-scale indices are high (western winds paramount and high "strength" of the Gulf Stream) the minimum migration duration is lower. We can assume that the same goes for the migration duration overall. These results are therefore consistent with the negative correlation found between larva arrival success and large-scale oceanic indices. The faster the migration, the higher the success.

Active behaviour slow down the migration and increase the distance For both models, when implementing vertical diurnal migration behaviour, the fastest particle takes more than 5 months longer compared to fixed depth experiments and the distance covered is more than 3000 km longer as well. When having a vertical diurnal migration, the fastest particle travelled from the Sargasso Sea to the "finishing" line in 1 year, 3 months and 1 day, covering 9 699 km (Drakkar model). For the Mercator model, the fastest particle

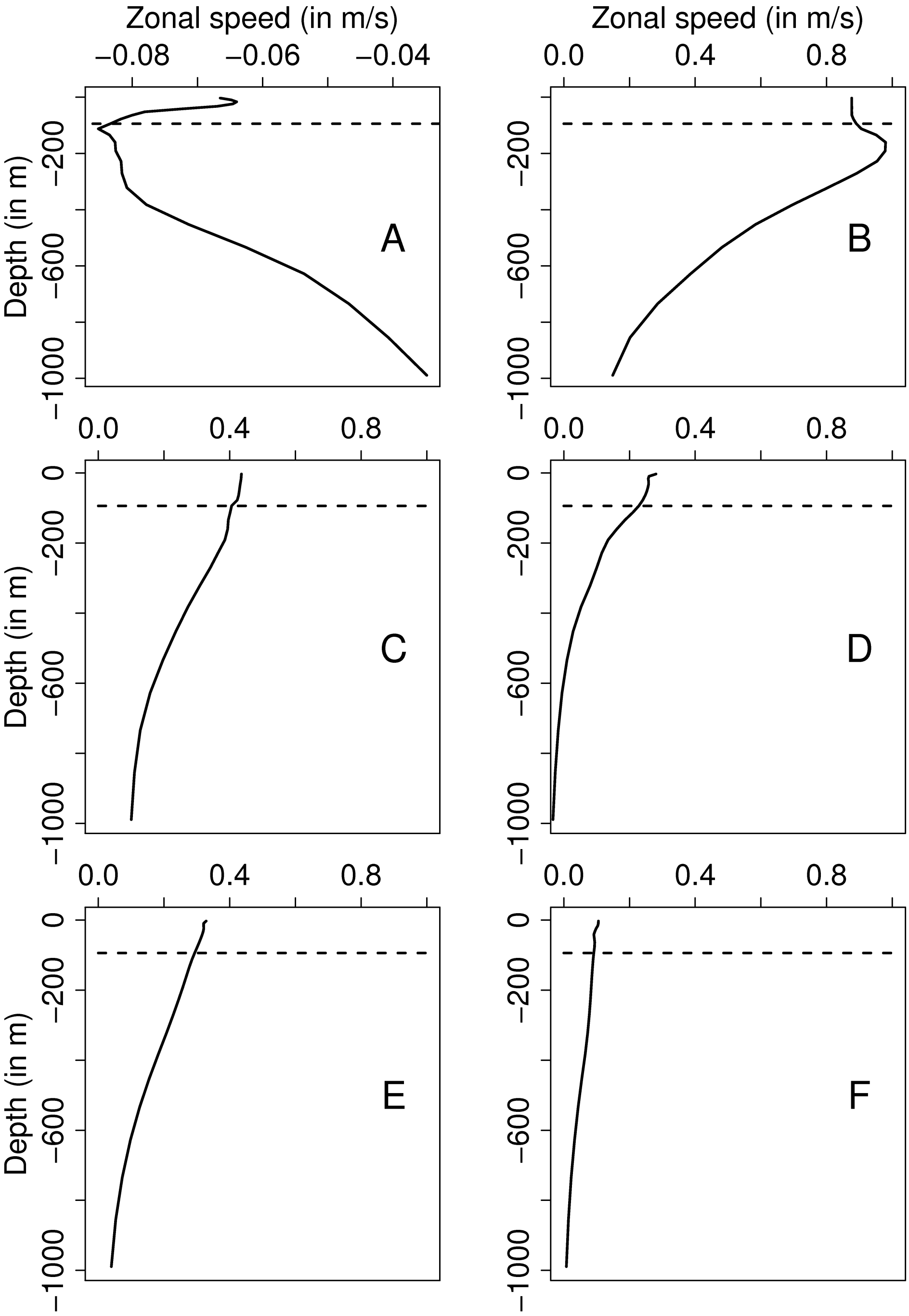

Figure 2.6: Diagrams of the zonal speed u at different depths at the positions of the fastest particle using the Drakkar model, as described in Fig. 2.7. The horizontal dashed lines represents the depth of the fastest particle (-94 m) found when running on the Drakkar model.

travelled in 1 year, 2 months and 18 days and covering 8928 km. It is the only particle that succeeded to reach the 20°W. It reaches the 20°W at a longitude too south to account for it in our study (5.8°N, off the coast of Liberia) since no eels have been reported there

(Schmidt, 1909a). The duration and distance of particles selecting the fastest current are very similar to the vertical migration experiment. The fastest particle travelled from the Sargasso Sea to the finishing line in 1 year and 28 days and covered 9 199 km (Drakkar model). When using the Mercator model, 3 particles succeeded in reaching the 20°W. The fastest particle travelled in 1 year, 2 months and 21 days over 9 748 km. We did not account for the two other trajectories since they arrived too south to be realistic (North of Senegal and South of Mauritania).

2.3.5 Current speed and fractal dimension of the trajectories

To understand possible sources that lead to such discrepancies between fixed-depth experiments and active behaviour ones, we analysed the trajectories and physical conditions that particles encounter along their drift. Fig. 2.6 shows the transects of zonal speed (West - East) carried out at different locations of the trajectory of the fastest particle in the Drakkar model (Fig. 2.7). Fig. 2.6 shows that the zonal speed is negative (i.e. from East to West) when particles leave the Sargassos and positive afterwards. Speed transects highlight that the layer where the fastest particle drifts (-94 m) is most of time either the fastest layer or almost the fastest layer (Fig. 2.6). Fractal dimension analysis confirms that migration duration is closely associated with the linearity of the trajectories. The more linear the trajectory (the lower fractal dimension D), the shorter the migration duration. For each depths, the fractal dimension of the trajectories of the fastest particle is represented in Fig. 2.8. The fractal dimension is the lowest for the depth -94 m ($D = 0.88$; Drakkar model) and -132 m ($D = 0.96$; Mercator model) (solid circles in Fig. 2.8). These depths correspond to the depths where the particles have the fastest migration duration as well. It confirms that the fastest particle have the less wiggly trajectories.

2.4 Discussion

2.4.1 Simulations fit with observations

The general results regarding departure, arrival areas and depth of drift are consistent with observations of leptocephali for both models. Most particles that succeeded in crossing the Atlantic in less than 1.5 years come from the Western Sargasso Sea. This is mainly due

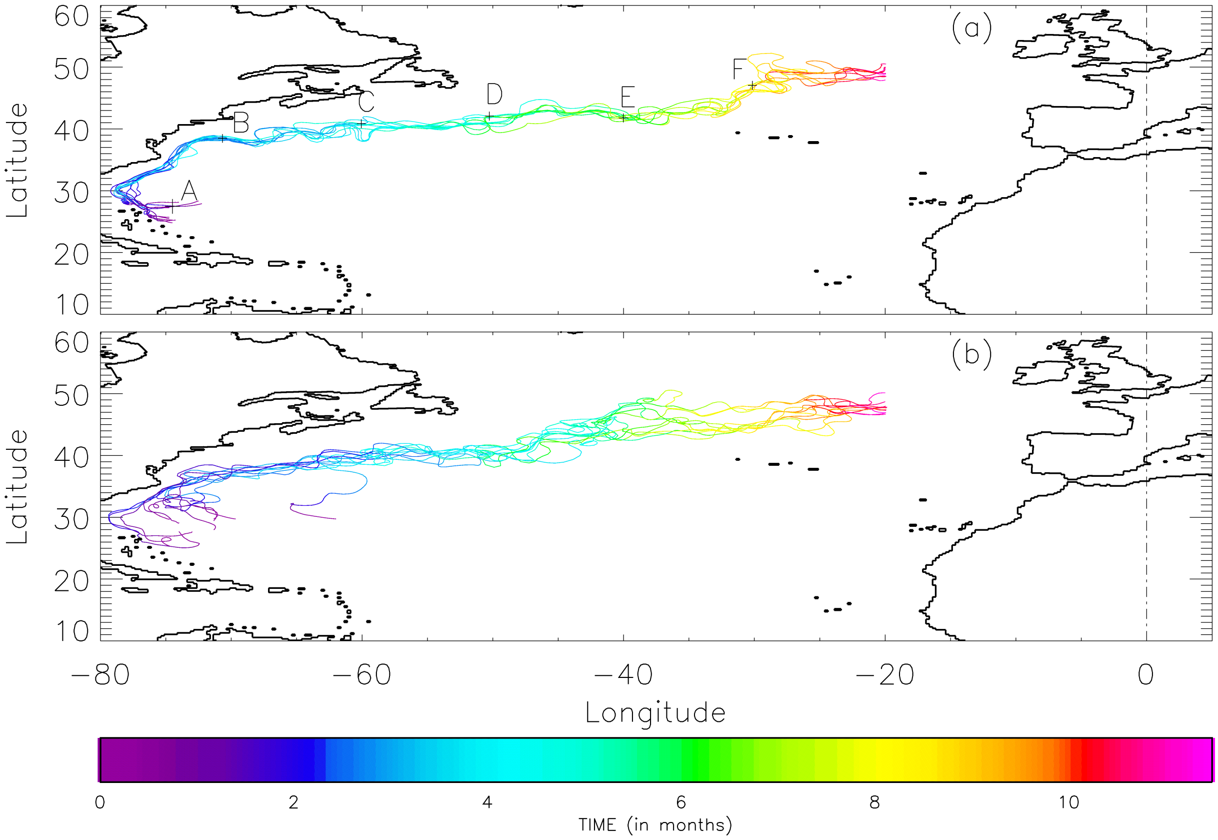

Figure 2.7: Trajectories of the ten fastest particles that succeeded to cross the 20°W using the Drakkar model (a) and Mercator model (b). The letters (A,B,C,D,E,F) represent the positions used to calculate the diagram of zonal speed at different depths (used in Fig. 2.6).

to the proximity to the Gulf Stream. It allows particles nearby to catch this current faster than more eastern particles drifting in the low currents of the Sargasso Sea before reaching the Gulf Stream (Kleckner and McCleave, 1982). The tiniest larvae found in that area are also located in the Western part of the Sargassos (see Fig. 2 *in* McCleave and Kleckner, 1987). The distribution area of particle arrivals fits well with the distribution area of the European eel (e. g. Schmidt, 1909a). This distribution is however mainly centred on West Europe at 20° and we can assume that most of them will not drift southward to Africa or do a U turn back to American coast.

Regarding the fixed depth experiment, the depth range (-400 to -50m) of particles crossing the 20° W in less than 1.5 years corresponds to the observed depths of leptocephali (e. g. Castonguay and McCleave, 1987) and to results achieved by Kettle and Haines (2006).

The positive relationships between indices of oceanic features such as the NAO, GSI (latitude of the Gulf Stream), and PEA (strength of the Gulf Stream) and the number of arrived particles per year are consistent. It indicates that a larger number of particles

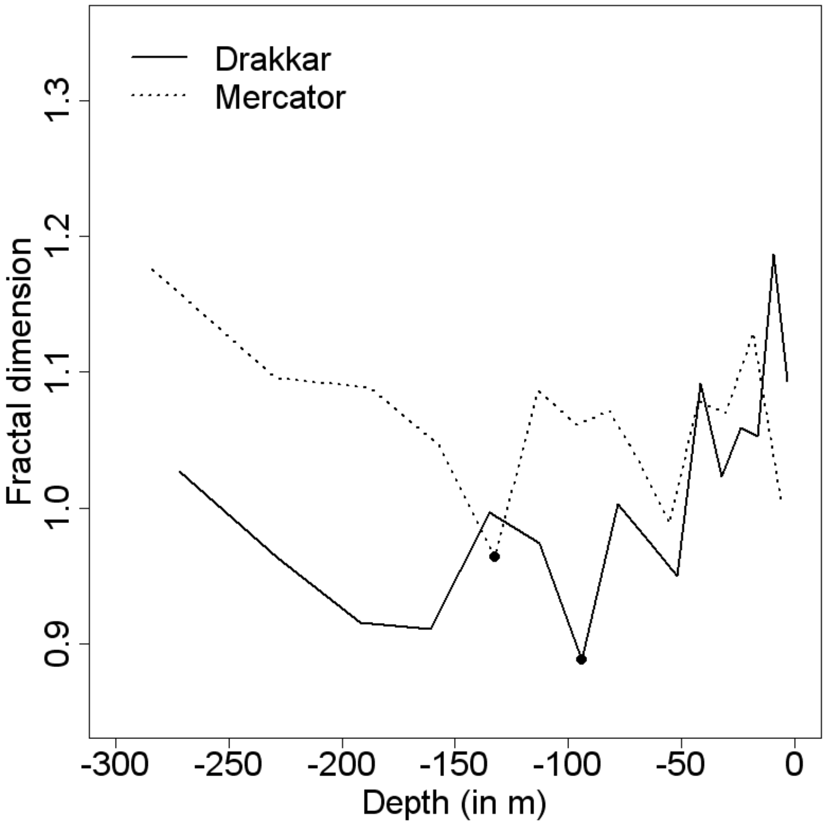

Figure 2.8: Fractal dimensions of the trajectory of the fastest particle in each depth of the Drakkar model (solid line) and the Mercator model (dashed line). The solid circle represents the depth of drift of the fastest particle in each model.

arrived during years where transport was higher. These results are nested to the negative link between large-scale oceanic indices and the minimum duration that indicates that when oceanic indices are high the minimum duration is low.

2.4.2 A minimum limit of the migration duration

The aim of this study was not to estimate the mean migration duration of eel larvae but to investigate the minimum migration duration of a passive drifter from the Sargasso Sea to the European shelves. The estimation of the mean migration duration by lagrangian model would require to account for mortality. Indeed, the histogram of the migration duration of particles can not be used to estimate mean migration duration because accounting for mortality (roughly exponential with time) will drastically change the distribution of migration durations. Particles with long migration duration have a greater chance to die relatively to particles with shorter migration duration that have a greater chance to survive and then to reach their goal. As eel larvae mortality is still unknown, we prefer not to undertake such analysis and focus on the fastest particles. It is noteworthy that accounting for mortality during the migration duration will necessarily lead to an equal or greater minimum bound for migration duration.

Drifting at fixed depth is the fastest way The fastest particle is observed when drifting at fixed depths for the two models (94 m for Drakkar and 132 m for Mercator) and cross the Atlantic Ocean in more than 10 months. Two conditions to undergo the fastest migration are gathered. It is most of time in the fastest layer and its fractal dimension is the lowest. The hypothesis of an active behaviour (vertical diurnal migration or rheotaxis) are more realistic in term of eel ecology. However, none of them could explain a faster migration. Both migration duration and distance are far higher. In particular, the vertical migration in upper layers (higher fractal dimension) make the particles drift in eddies and hence increase the migration duration. Consequently, the diel migration behaviour of leptocephali is certainly not a way to maximize the use of the current speed. Since leptocephali are planktonic feeders, the vertical migration could surely be driven by feeding needs and, overall, corresponds to the observed diurnal migration of plankton (e. g. Steinberg *et al.*, 2002). It could be a way to avoid predators as well.

Interestingly enough, active behaviours lead particules to reach West Africa coast where no eels have hitherto been found. Since the aim of this paper was to find the shortest migration duration to reach European shelves, we could not account for these "misfit" particles. It is however interesting to note that this pathway is possible and eel larvae can reach West Africa shelves. This result fits with Kettle and Haines (2006) who found the same "hypothetic" pathways.

Potential sources of underestimation of the passive drift speed We chose an arbitrary "finishing" line that is still far from the shelves (1 000km from Ireland and 1 500km from France). This distance remains to be done as well as the metamorphosis that is estimated to be running over 18 to 52 days (Arai *et al.*, 2000) or 98 days (Wang and Tzeng, 2000). Removing these two steps, we underestimate the migration duration. The migration duration from lagrangian simulations corresponds to the estimated age of leptocephali before their metamorphosis. The metamorphosis occurs on the continental slope (Schmidt, 1909b; McCleave, 1987; Antunes and Tesch, 1997). The finishing line is before the continental slope. The drift duration to reach the 20°W is hence surely lower than the age before metamorphosis estimated by otolith microstructure since a long distance remains to be covered until the continental slope.

Moreover, using ocean general circulation models that do not fully resolve mesoscale eddies, we surely underestimate the distance covered by particles and / or overestimate the drift speed. The Drakkar and Mercator models are among the most precise models currently running to model ocean circulation in the European scientific community with a resolution of 1/4° and 1/3° respectively. It would be interesting to assess the impact of the use of higher resolution models on the speed and the distance covered by particles. When using Drakkar (the best resolution of the two models), the migration duration is slightly longer than with Mercator. This phenomenon appears in Fig. 2.5. The use of higher resolution models (for instance 1/12°) would have enabled us to solve mesoscale eddies more accurately (Smith *et al.*, 2000). When improving the resolution of ocean general circulation model, two combined effects could be observed. First, the maximal speed is higher but second, particles have longer trajectories since they can be trapped in mesoscale eddies. Further studies may analyse possible consequences of the use of higher resolution model on the migration duration.

2.4.3 Do leptocephali swim to reach European shelves?

Our results clearly contrast with the analysis of otolith microstructure. When considering the migration duration inferred from otolith microstructure, eel larvae would be able to reach European coasts in 6 months. In contrast, our estimates of a minimum bound for migration duration is about 10 months. Here we try to discuss our results in regards with results of otolith analyses. First, it should be noted that results of otolith analyses remain questionable. To our knowledge, the age estimation of eel larvae from daily increment has never been validated for the European eel. Leptocephali may have such a low metabolic rate that increments in otoliths might not be deposited daily, or be deposited daily but be too thin to be observed in either light or scanning electronic microscopy. We refer to Chap. 1 for a complete description of possible source of mis-interpretation of otolith microstructure. Second, it is interesting to question the implications of such a sort migration duration (6 months) in terms of swimming speed. Using the drift distance and migration of the fastest particle in the Drakkar model, the mean passive drift speed (Eq. 2.1) is $30.2\,\mathrm{cm{\cdot}s^{-1}}$. The required speed to cover the same distance in 6 months is

8 447km / 6 months = $54.3\,\mathrm{cm\cdot s^{-1}}$ that would be possible with an active swimming speed of (54.3 - 30.2) $24.1\,\mathrm{cm\cdot s^{-1}}$. Regarding the Mercator model, the mean passive drift speed of the fastest particle is $32.0\,\mathrm{cm\cdot s^{-1}}$. Using the same calculation, the required speed to cover the 8 498 km in 6 months is $54.6\,\mathrm{cm\cdot s^{-1}}$, leading to a required active swimming speed of $22.6\,\mathrm{cm\cdot s^{-1}}$. Other results of Arai *et al.* (2000) showed that the age at metamorphosis may be higher than those found by Lecomte-Finiger (1992, 1994), that is a mean age of 198 days. In that case, the required speed would be $19.2\,\mathrm{cm\cdot s^{-1}}$ and $17.7\,\mathrm{cm\cdot s^{-1}}$ for the Drakkar and Mercator model respectively. This range of value remains too high to be realistic. We did not consider the fastest ten, hundred, and thousand particles to estimate a mean swimming speed because we figure that these particles may have wigglier trajectories. Thus, if leptocephali had the ability of an active oriented swimming they would not fall into this oceanic trap and avoid it. As showed in Fig. 2.7a and b, the ten fastest particles follow direct routes and an active oriented swimming would not have enabled them to reach the European shelves more directly. Our approach then suggests that such a short migration would require an active swimming around 23 $\mathrm{cm.s^{-1}}$. It means that leptocephali should swim at least at 3.4 body $\mathrm{lengths\cdot s^{-1}}$ of a fully-developed leptocephali near continental shelves (about 70 mm, Schmidt, 1922, 1923) over more than 8 400 km (the distance done by the fastest particle; Fig. 2.5). It is noteworthy that particles that have a longer passive drift should have a faster swimming speed.

Although such swimming speeds are observed for migrating adult fish (Blaxter, 1969), energy expenditure required seems not realistic for eel larvae since the open ocean is a low productive area (Raven *et al.*, 2007). As previously evoked, the hypothesis of active and oriented swimming has been asserted to make possible the 6-month migration duration of eel larvae. Authors used the work of Williamson (1987) indicating that leptocephali can "*swim vigorously*". However, Williamson (1987) paper reported that glass eels were seen in a vertical position during a diving session. Williamson (1987) added that: "*Glass eels do not feed, are transported by currents and have no need to swim horizontally [...]*". In another paper, Tesch *et al.* (1986) concluded large leptocephali could swim at $20\,\mathrm{cm\cdot s^{-1}}$. Actually, Tesch *et al.* (1986) suggested that the clearing of the sill in the Straits of Gibraltar would require a swimming speed of at least $20\,\mathrm{cm\cdot s^{-1}}$ to struggle against the current. This speed was compared to a study on juvenile sprat (*Sprattus sprattus* L.), and Atlantic herring (*Clupea harengus*) that may swim at 10-12 body $\mathrm{lengths.s^{-1}}$ during 45 min (Turnpenny, 1983). This comparison appears to be a bit far fetched. Moreover, swimming activity would need developed muscles that McCleave *et al.* (1998) defined by:

“*leptocephali [...] have only minute amounts of subcutaneous red muscle (Leonard and Summers, 1976)*”. The orientation ability of leptocephali is debatable (McCleave *et al.*, 1998), even if Nishi and Kawamura (2005) suggested that larvae at glass eel stage might record the earth’s magnetic fields during their original migration and use it to swim back to their spawning area.

Conclusion

Here we investigated the minimum migration duration of passive particles drifting from the Sargasso Sea to European shelves using high resolution ocean general circulation models. By contrast to Kettle and Haines (2006), we also examined the possible influences of active behaviour of particles (vertical diurnal migration and faster current choice) on migration duration. We showed that active behaviours are not a way to maximize the migration duration but on the contrary, it increases the migration duration. Using ocean general circulation models, very few particles can reach the 20°N in less than 1 year (1 over several millions) and the crossing in 6 months thanks to an active and oriented swimming would require a very fast swimming speed (more than 3.4 body length per second) over a very long distance (more than 8 000 km). Such energy expenditure is not possible in low productive areas such as open ocean. We do not reconsider the swimming ability of leptocephali that can swim for sure (e. g. Bishop and Torres, 1999), but this swimming capacity could not be used to reach European shelves faster. Further studies using higher resolution models such as Drakkar at 1/12° has to be carried out to investigate the effect of mesoscale eddies on the migration distance and duration. Given the precautionary approach we had regarding the time remaining to reach European shelves and metamorphose into glass eels and the choice of the fastest particle among several millions, we argue that the European eel leptocephali do not cross the Atlantic Ocean in 6 months. Their migration duration has to be reconsidered... again.

Acknowledgments

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3

Estimation de la durée moyenne de migration de l'Anguille européenne

Résumé détaillé

Comme cela est discuté dans le chapitre 2, l'estimation d'un temps moyen de migration des larves d'Anguille européenne par des simulations lagrangiennes est biaisée par le fait qu'aucune mortalité n'est prise en compte. Nous utilisons le modèle océanique Drakkar pour simuler la dérive passive de particules ayant trois comportements différents (profondeur fixe, migration verticale nycthémérale, choix du courant le plus rapide). La méthodologie est la même que dans le chapitre 2 mais les particules dérivent pendant 5 années. Les résultats des simulations lagrangiennes sont combinés avec une hypothèse écologique d'équilibre de la population, en tenant compte de la mortalité estimée aux différentes phases du cycle de vie. Grâce à cette hypothèse, nous pouvons restreindre les valeurs possibles de la mortalité des larves et l'appliquer aux résultats des simulations lagrangiennes. La mortalité est d'autant plus grande que la durée de migration est grande. Ainsi, appliquer une mortalité sélectionne préférentiellement les particules les plus rapides.

Cette méthode nous permet d'estimer un mode de la distribution du taux de mortalité à 3.2 par an (Fig. 3.5b) puis un mode de la distribution des temps de migration jusqu'au 20°W à 19 mois (Fig. 3.5a) pour les particules dérivant à profondeur fixe. Ces valeurs sont peu influencées par les hypothèses de comportement (migration verticale, choix du courant le plus rapide ; Fig. 3.5c-f) ou par les conditions océaniques (Fig. 3.6a et b). L'analyse de sensibilité aux paramètres de l'équation d'état d'équilibre de la population révèle que ces résultats sont aussi peu sensibles aux variations de ces paramètres, c'est-à-dire aux autres sources de mortalité au cours du cycle de vie larvaire (Tableau 3.2).

Le couplage des résultats des simulations avec une mortalité larvaire nous a permis d'estimer les temps de migration des leptocéphales jusqu'au 20°W. Il faut ajouter à ce temps la durée de migration jusqu'aux côtes européennes et la période de métamorphose. Les courants moyens dans cette zone sont d'environ $0.2\,\mathrm{m{\cdot}s^{-1}}$ pour une distance d'au moins 1 000 km, ce qui donne une durée de 58 jours environ pour atteindre les estuaires. Les estimations de la durée de la métamorphose varient entre 1 et 3 mois, ce qui porte la durée totale estimée de la migration à 22 mois. La période de ponte s'étale de mars à juin et celle d'arrivée sur les côtes de décembre à avril. La durée de migration des larves estimée par le modèle de dérive intégrant la mortalité correspond à cette saisonnalité (22 mois, d'avril de l'année n à février de l'année $n+2$).

L’estimation du taux de survie des larves est de 2.8 pour 1 000. Aucune estimation du taux de survie des leptocéphales n’est disponible dans la littérature et nous ne pouvons pas comparer ce résultat à d’autres études. Ce taux est largement supérieur aux survies supposées pour les autres espèces. Cependant, la phase marine des larves d’Anguille est beaucoup plus longue et un taux de survie larvaire très faible (comme celui d’autres espèces) induirait la mort de toutes les larves avant même leur arrivée sur les côtes. Cette estimation paraît donc réaliste.

A new estimate of migration duration of European eel larvae

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Abstract Using lagrangian simulations over three different hydroclimatic periods in the last 45 years, we simulate the passive drift of particles released in the eel spawning area with different behaviours: drifting at fixed depth, undergoing a vertical migration or choosing the fastest currents. We couple these simulations to mortality hypotheses to estimate the mean migration duration of the European eel. We estimate that the mean migration duration is 22 months and the mortality rate (M) is 3.2 per year.

Keywords *Anguilla*, lagrangian modelling, larval mortality, migration duration

Suggested running title Migration duration of European eel larvae

3.1 Introduction

The European eel is a catadromous fish that goes through one of the longest seaward migration, more than 6,000 km across the Atlantic Ocean. Conveyed by warm currents, eel larvae (leptocephali) come from the Sargasso Sea where eels spawn, to settle on the African and European shelves, from Mauritania to the Polar Circle (Schmidt, 1923).

The current decline in eel populations worldwide is well observed (Anonymous, 2003) and the European eel has been listed in Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007) regarding its current level of abundance. The decline in European eel population since the early 1980s is no doubt the combined effect of several and probably interacting factors: direct effect of anthropogenic activities such as overfishing (Dekker, 2004), habitat loss and degradation (McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006) and increasing stress in the freshwater stage due to parasites and diseases (e. g. Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005) and in the oceanic stage due to unfavourable oceanic conditions (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008). These potential causes of stock decline are often *per se* associated and occurring at the same time and are difficult to untangle (Anonymous, 2003).

The oceanic larval phase of European eels is of primary concerns to understand eel ecology. There has been a long history of ecological studies dealing with marine life stages of this species (Dekker, 1998). As for most fish species, the major source of mortality occurs during the larval stage (Hjort, 1914). The oceanic phase conditions the dispersion over the coastal regions and the freshwater habitats. The migration duration is certainly one of the most critical and controversial features of the oceanic larva migration. It determines eel larva oceanic trajectories and mortality, the mean generation time of eels, hence dates and areas of larva coastal arrivals. It also conditions our ability to understand how the recruitment is linked to environmental fluctuations. This is critical in a context where major changes in oceanic conditions are recorded and known to impact fish populations (Beaugrand and Reid, 2003; Lehodey *et al.*, 2006). Recruitment data have been compared to environmental factors such as large-scale oceanic and climate indices (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008; Kettle *et al.*, in press). Primary production and sea temperature fluctuations in eel spawning area have also shown to be related to glass eel recruitment (Knights, 2003; Bonhommeau *et al.*, 2008). However, all these studies used recruitment indices based on glass eel arrivals. Because oceanic environmental conditions are suspected to impact eel larvae several months earlier than glass eel arrivals, time lags have to be accounted for migration duration to link environmental descriptors to glass eel recruitment. Results still remain conditioned by the hypothesis made about migration duration, e. g. , 1-year lag for Friedland *et al.* (2007) and 2.5 - 3 years for Knights (2003) and Bonhommeau *et al.* (2008).

Uncertainties about migration duration mainly arise from the difficulty to observe eels during their oceanic stage, in particular during larva emergence and migration. During the 70 years following the discovery of the breeding places of eels (Schmidt, 1922, 1923), the migration duration of the European eel was mainly speculated to be comprised between 2 and 3 years. This assumption was grounded on growth curves of eel larvae (leptocephali) and their spatial occurrence at different dates in the North Atlantic. This assertion has been reconsidered when counting daily increments in otolith microstructure. Estimations made using 423 glass eels from the Netherlands to Morocco established that the migration duration (migration + metamorphosis into glass eels) ranges between 191 and 276 days (about 6 to 9 months), for glass eels caught in Portugal and in the UK respectively (Lecomte-Finiger, 1992). However, the reading accuracy of daily growth increments sparks a large debate (e. g. Antunes and Tesch, 1997; McCleave *et al.*, 1998). Several assumptions were brought forth to explain such a short migration duration. Lecomte-Finiger (1992, 1994) put forward an active and / or oriented migration hypothesis. Be as it may, such a short sojourn remains difficult to explain. More recently, it has been shown how general circulation models may provide insights to better grasp this trans-oceanic migration. Kettle and Haines (2006) used lagrangian simulations over a 4-year period (1993-1996) to estimate the migration duration and pathways of European eel larvae and found a 2-year migration duration.

However, Kettle and Haines (2006) recognized that their approach suffered from a critical caveat that hinders the direct use of the migration duration of particles to estimate the mean migration of eel larvae. Indeed, their approach did not account for the mortality of particles during their transport, although it is clear that the distribution of the arrival time of particles critically depends upon the mortality hypotheses. Roughly speaking, with no mortality, even the slowest particles will succeed in reaching the “finishing” line and the histogram of the migration duration, hence its mean, will be pushed toward greater values. With a non null instantaneous mortality, the slowest particles have a greater chance to die than fastest ones. The histogram of the migration duration, hence its mean, will be pushed downward. Hence, a strong negative correlation exist between the mean migration duration and the mortality.

In this paper, we address this issue by combining the results of lagrangian simulations with ecological knowledge gathered in the literature. Through a steady-state hypothesis of eel population accounting for other mortality over the whole life cycle, we restrict the range of credible values for the mortality during oceanic larvae stages. This, in turn, enables us to drastically restrict the range of estimated migration duration from lagragian simulations.

Another critical issue of lagrangian simulation is to relax the hypothesis of strict passive drift of the particles. We addressed this issue by contrasting the results obtained from three different behaviours of the particles: (*i*) Particles drifted at fixed-depth as in Kettle and Haines (2006). (*ii*) Particles were undergoing a vertical diurnal migration between -300m and -50m as observed *in situ* (Castonguay and McCleave, 1987). (*iii*) Particles follow the direction and depth where the speed of currents was the highest. As glass eels have a positive rheotaxis (mechanism whereby they will turn to face into an oncoming current), we assumed that leptocephali may use the same ability to drift in the fastest currents.

3.2 Materials and methods

3.2.1 Circulation models

Lagrangian simulations are performed using an ocean general circulation configuration, the Drakkar projects, that is currently one of the most accurate in the European scientific community and simulations were possible over a period of 45 years. This model is based on the NEMO/OPA numerical code (Madec *et al.*, 1998).

The Drakkar model (`http://www.ifremer.fr/lpo/drakkar`) is interesting because of the duration of the simulation (1958 to 2004), which allows us to address the interannual variability of trajectories. The model configuration is global. It uses the ORCA025 grid (a tripolar grid with a 1/4° horizontal grid resolution at the equator). Barnier *et al.* (2006) described this configuration and showed its good performance in representing strong currents and eddy variability, even in comparison with higher resolution models.

The water column is divided in 46 levels, with grid spacing ranging from 6 m near the surface to 250 m at the bottom. The simulation was run using state of the art atmospheric data (a blend of satellite products and ERA40 6-hourly winds, temperature and humidity). The Drakkar model is a so-called "fully prognostic" model, which means that it does not use assimilated ocean data (neither satellite altimetry nor in-situ temperature or salinity), and therefore can be substantially far from observations in some areas (Treguier *et al.*, 2005). Fortunately those biases are less pronounced in the subtropical gyre, which is our region of interest, compared to the subpolar regions considered by Treguier *et al.* (2005). To reduce file size and to centre on the area of our study case (i. e. the North Atlantic Ocean), we extracted an area ranging from -82 to 6°W and 10 to 60°N. Since the observed depth of leptocephali ranges between -50 and -300 m (e. g. Castonguay and McCleave, 1987), we reduced the oceanic model to the top 24 levels (-3 to -989 m). To avoid the early spin-up phase of the model, we use the period 1960-2004 of the simulation. Circulation fields are time-means archived every 5^th days.

3.2.2 Lagrangian simulation designs

We used the Ariane tool developed by B. Blanke and N. Grima and freely available at `http://www.univ-brest.fr/lpo/ariane`. It is a FORTRAN code dedicated to the computation of 3D streamlines in a given velocity field (as the output of an Ocean General Circulation Model) and subsequent water masses analyses.

Particles were released in the Sargasso sea during several years. For each simulation year, passive drifters were released at each model grid, i. e. each 1/4° degree and each 24 fixed-depth levels in an area enclosing the assumed spawning area of eels in the Sargasso Sea (Fig. 2 *in* McCleave and Kleckner, 1987, and Fig. 2.1). Particles were released every 15^th days throughout the year. Hence, 1 972 608 particles were released each year. We let particles drift over a 5-year period, which is long enough to encompass the probable migration duration of European eel larvae from the Sargassos and the European shelves.

Output files of lagrangian simulations include position (longitude, latitude, depth) and time for each particle. Particles are considered as having "succeeded" in their migration when crossing the 20°W whatever the latitude. This finish line is more eastward than the 25°W chosen by Kettle and Haines (2006). Since the aim of the study is to estimate the mean migration duration, the finish line has to be as close as possible from the effective arrival area of eel larvae to compare to current estimates. However, 20° is a reasonable limit since longitudes higher than 20°W correspond to continental slope that is not as well-resolved by the physical model as open ocean. Moreover, lagrangian simulations are unable to represent tidal transport of eel larvae when they reach the shelves.

Based on NAO-index, which is known to be related to strength (Curry and McCartney, 2001) and latitude (Taylor and Stephens, 1998) of the Gulf Stream, 3 periods were selected: 1960-1964 (mean NAO$= -1.7$), 1973-1977 (0.9), and 1986-1993 (3.2).

Three particle behaviours were implemented in lagrangian simulations. We first assumed a fixed depth drift for all particles released at each vertical levels of the reduced model (Exp. 1). In a second experiment, particles were able to change their vertical position every 12 hours from about -300m to -50m as described in Castonguay and McCleave (1987)(Exp. 2). In a third experiment, particles have the ability to actively select the direction where the current speed is the highest, at each time step (Exp. 3). As glass eels can feel currents and react to them (Bertin, 1956; Bolliet *et al.*, 2007), we assumed that leptocephali may have the same ability to follow the fastest currents.

3.2.3 Outline of the general methodology

Let us denote M the instantaneous mortality rate (per year). The cumulative mortality from 0 to time t is then $1 - e^{-M.t}$ (Peterson and Wroblewski, 1984). For each value of M, lagrangian simulations provide an histogram of particle migration duration d, interpreted here as a probability distribution :

$$\pi_L(d|M) \tag{3.1}$$

Combined with a "prior" distribution for M, that was chosen as uniform on the range [0,10], we obtained a joint distribution for (M,d) :

$$\pi_L(M,d) = \pi(M) \cdot \pi_L(d|M) \tag{3.2}$$

The key idea is to combine this joint distribution with ecological knowledge gathered in the literature to obtain a new distribution $\pi(M,d)$ confined to a more restricted range of value of (M, d). This is achieved by the multiplication of the joint distribution $\pi_L(M,d)$ by a second distribution independently derived from ecological knowledge denoted $\pi_E(M,d)$:

$$\pi(M,d) = \pi_L(M,d) \cdot \pi_E(M,d) \tag{3.3}$$

Once obtained, the marginal distribution of the migration duration d can be calculated by an integration over the possible values of M and vice versa:

$$\pi(d) = \int_d \pi(M, d)\ dd \tag{3.4}$$

$$\pi(M) = \int_M \pi(M, d)\ dM \tag{3.5}$$

Because the joint distribution will be estimated on a discrete grid, the computation of marginal distributions is straightforward.

3.2.4 Implementing mortality in lagrangian simulations

Particles are considered to "succeed" in their migration when they cross the 20°W. The histogram of the migration duration obtained from lagrangian simulations is sensitive to the value of the natural mortality M. To assess how the histogram changes with M, we used the following procedure. The frequencies of migration duration are assessed by class of 1 month for months $d_i = 1,\ldots,n$. Let $\{f_{d_i0}\}_{i=1,\ldots,n}$ denote the histogram formed by the frequencies, f_{d_i0}, of particles with migration durations d_i obtained from lagrangian simulation without any mortality (M=0). For each value of M, the new histogram of migration durations denoted $\{f_{d_iM}\}_{i=1,\ldots,n}$ is simply obtained by weighting the initial frequency by the survival rate up to d_i :

$$f_{d_iM} = f_{d_i0} \cdot e^{-M \cdot d_i} \text{ for i in } 1,\ldots,\text{n} \tag{3.6}$$

The new histogram $\{f_{d_iM}\}_{i=1,\ldots,n}$ is then interpreted as the conditional probability distribution $\pi_L(d|M)$, estimated on a 1-month interval grid.

Lagrangian simulations are deterministic: particles released at the same location and at the same time have the same trajectory. One could have implemented a stochastic mortality rule for each particle in the simulation. However, because the simulations are deterministic, the equation 3.6 provides an exact evaluation of the expected mean of the frequencies in the class d_i given the instantaneous mortality M.

3.2.5 Combining ecological knowledge

The aim of this section is to show how a joint distribution $\pi_E(M, d)$ can be constructed from the combination of knowledge gathered in the literature. We rely on a steady state hypothesis. For any species with a default sex ratio of 1:1, i. e. 50 % female and 50 % male, the rule 1 female gives 2 offspring (i. e. 1 male and 1 female) is necessary to maintain the steady state of their population (Jung *et al.*, 2008).

We apply this steady-state hypothesis to eels. We admit an equilibrium sex-ratio 1:1 for this species. Because the European eel is a semelparous species, the steady-state hypothesis implies that the product of the female eel fecundity by all the survival rates of their offspring until they spawn must result in 2 individuals (Eq. 3.7). This equation implies that, among all of the eggs produced by a female, only two individuals (1 male + 1 female) survive and reproduce. In our case study, it could be formulated as:

$$2 \approx \mathrm{Fec} \cdot \xi \cdot \alpha \cdot \beta \cdot \gamma \cdot \eta \tag{3.7}$$

where Fec is the fecundity of female eels, ξ, the hatching rate, α, the survival rate of leptocephali from hatching to glass eel stage, β, the survival rate of glass eels, γ, the survival rate of adult eels (continental stage) equal to $e^{-M_a \cdot d_a}$, where M_a is the mortality rate and d_a is the age of pre-migrating silver eels, and η is the rate of silver eels that succeeded to cross back the Atlantic Ocean and mate.

Estimation for all parameters in equation (Eq. 3.7) can be found in the literature, except for the parameter α. Equation 3.7 enables us to express α as a function of the other parameters :

$$\alpha \approx \frac{2}{\mathrm{Fec} \cdot \xi \cdot \beta \cdot \gamma \cdot \eta} \tag{3.8}$$

Regarding literature data (table 3.1), we selected: Fec= $1.5.10^6$ eggs, hatching survival rate= 20%, glass eel survival rate= 10%, $M = 0.14$, age of eels= 16 years and survival rate during backward migration= 30% (estimated from a 0.5 year migration duration to reach the Sargassos and a high mortality rate: 0.7).

To account for uncertainties about these point estimates, a probability distribution was assigned to each parameter (Fig. 3.1). Beta distributions were set for ξ, β, M_a, and γ as they range between 0 and 1. Gamma distributions were set to the fecundity (Fec) and the age of spawners (d_a) as these parameters have to be positive.

Fig. 3.2 shows the resulting probability distribution of α obtained from Monte Carlo simulations. A point estimate for α (modal value of the distribution) is found to be near 0.17%.

Table 3.1: Estimates of the different parameters given in Eq. 3.7. Fec is the fecundity of female eels, ξ the hatching rate, β the survival rate of glass eels, γ the survival rate of adult eels (continental stage) that equals to $e^{-M_a \cdot d_a}$, where M_a is the mortality rate and d_a is the age of yellow or silver eel, and η is the rate of silver eels that succeeded in crossing back the Atlantic Ocean and mate.

Parameter	Range of values	Source
Fec	$9.10^5 - 2.6.10^6$	Boëtius and Boëtius (1980)
(# of eggs)	1.10^6 (55cm), $4 - 5.10^6$ (95cm)	B. Knights (pers. comm.)
	$1.49.10^6$ $(9.10^4 - 6.10^6)$ (39-99cm)	Bark *et al.* (2007)
ξ	10-30 %[a]	Furuita *et al.* (2003)
	20-40 %[a]	Unuma *et al.* (2004)
β[b]	17.3-23.1 %	Berg and Jorgensen (1994)
	3-27 %	C. Briand (pers. comm.)
	26-32 %	Moriarty and Dekker (1997)
M_a	0.14 per year	Dekker (2000)
d_a	2-20 years	*in* Tesch (2003)
	8-18 years	Bertin (1956)
η	30 %	-

[a] estimates for Japanese eel

[b] for the stage

From the equation 3.8, it is now easy to derive an expression of the migration duration d (time for eel larvae to reach 20^{o}W) given the instantaneous mortality of eel larvae M. Indeed, α is a survival rate and can be written as $\alpha = e^{-M \cdot d + d_{rem}}$, where M is the natural mortality of leptocephali and $d + d_{rem}$ is the total duration from hatching to glass eel reaching the coast. This total duration is the sum of the migration duration to 20°W (d) and the time needed to reach the continental slope and metamorphose, d_{rem}. The metamorphosis is estimated to be comprised between 1 and 3 months (Lecomte-Finiger, 1992; Wang and Tzeng, 1998; Arai *et al.*, 2000; Wang and Tzeng, 2000). We arbitrarily choose to add 1 to 2 months to account for the time to reach the continental shelves and cover the 1 000-1 500 km remaining although it is difficult to estimate. This estimation arises from the mean speed of currents in that area that is about 0.2m.s^{-1}. To cover 1 000 km directly with a mean speed of 0.2m.s^{-1} lead to a 58 days period. Thus, d_{rem} was considered to be uniformly distributed between 2 to 5 months.

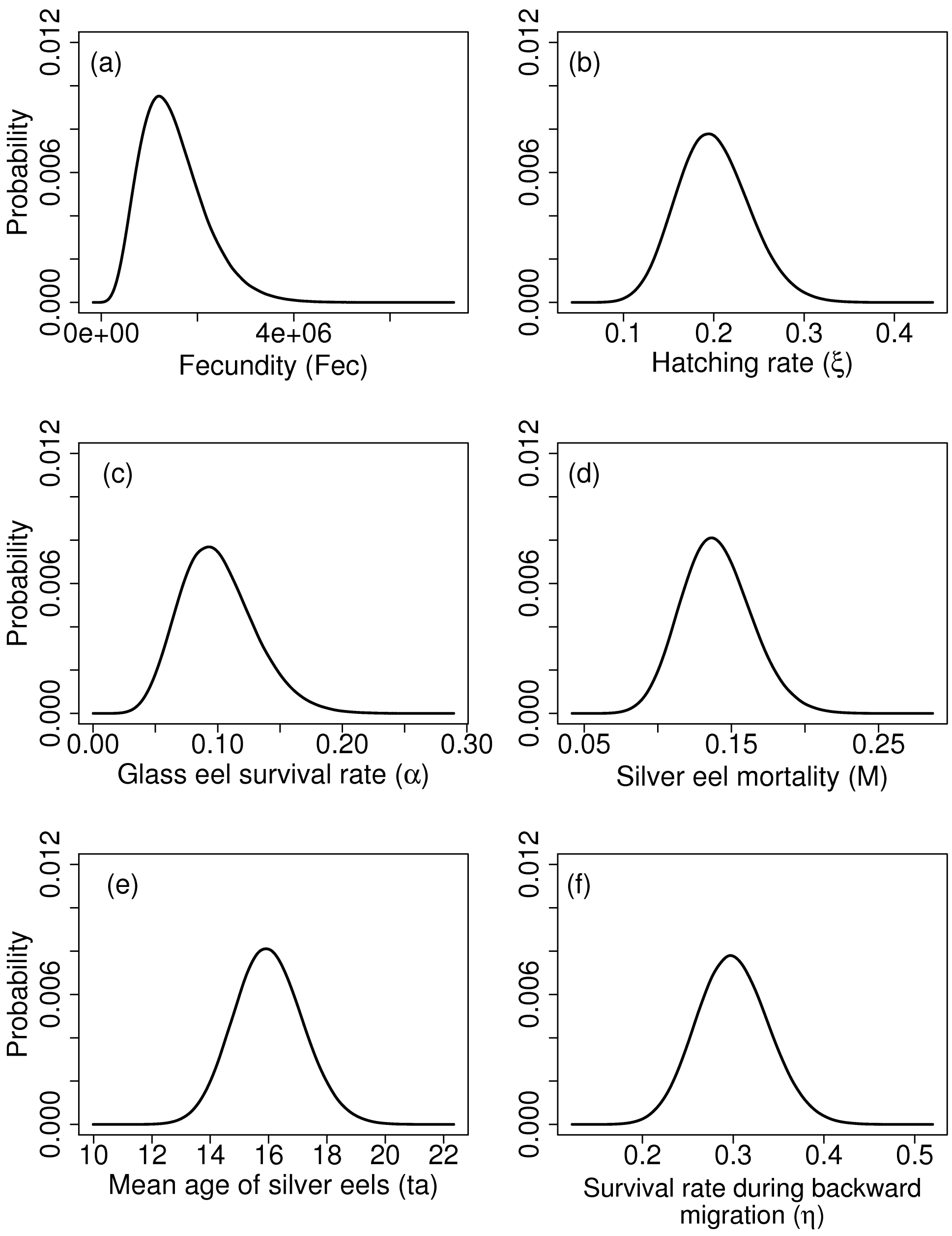

Figure 3.1: Distribution law of the different parameters used to calculate the survival rate of leptocephali.

Thus, we have the expression:

$$e^{-M\cdot(d+d_{rem})} \approx \frac{2}{Fec\cdot\xi\cdot\beta\cdot e^{-M_a\cdot d_a}\cdot\eta} \tag{3.9}$$

that gives

$$d \approx \frac{\log\dfrac{2}{Fec\cdot\xi\cdot\beta\cdot e^{-M_a\cdot d_a}\cdot\eta}}{-M} - d_{rem} \tag{3.10}$$

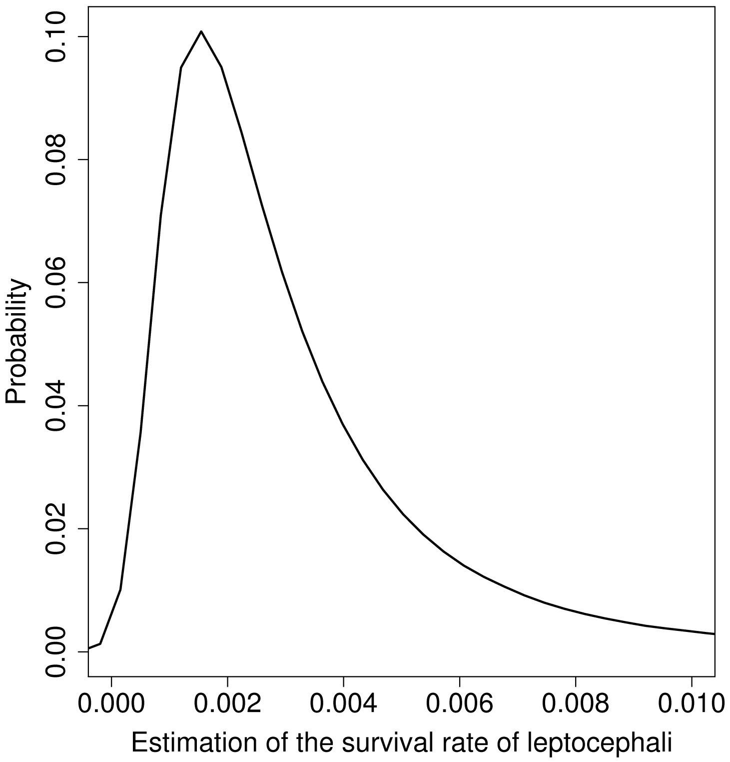

Figure 3.2: Probability of survival rate of leptocephali accounting for uncertainties on the different parameters of Eq. 3.7

By using Monte Carlo simulations, it is easy to rely on Eq. 3.10 to derive a sampling based estimation of the conditional probability of d given M, that is $\pi_E(d|M)$. Combined with a uniform distribution on M, we obtained the joint distribution $\pi_E(d, M)$ that is needed to be combined with the lagrangian distribution $\pi_L(d, M)$.

3.2.6 Sensitivity analysis

The two distributions $\pi_L(d, M)$ and $\pi_E(d, M)$ are combined to obtain our final joint estimation of the mortality M and migration duration d. To assess the sensitivity of results, the elasticity of $\bar{d}$, the mean of marginal distribution of the migration duration d, and $\overline{M}$, the mean of the marginal distribution of the annual mortality M are calculated regarding the different parameters. Elasticity is the ratio of the proportional change in one variable with respect to proportional change in another variable. It illustrates the relative change of $\bar{d}$ and $\overline{M}$ when a parameter increase by a small percentage (here, 10 %) when all other parameters are kept at their standard values.

3.3 Results

3.3.1 Lagrangian simulations are consistent with previous knowledge

The distribution area of particles at 20°W is comprised between 40 and 55°N with a peak at 50°N. Another peak appears in the North Africa area (30-35°N) (see Fig. 2.2). The main departure area of arriving particles is located in the Western Sargasso Sea (75°-65°W and 22°-30°N; see Fig. 2.3). The same patterns are observed for the three experiments, i. e. fixed-depth, vertical migration, or faster current choice. Regarding the fixed-depth experiment, the depth range of particles crossing the 20°W is between -400 m and the surface. The gaussian distribution of these depths has a mode at -200 m (see Fig. 2.4). These results fit with Kettle and Haines (2006) and observations of the eel distribution area and spawning areas (McCleave and Kleckner, 1987).

3.3.2 Estimation of migration duration and annual mortality for fixed-depth experiments

We first used the whole simulation results to assess global patterns of migration duration. Fig 3.3 a represents the histogram of migration duration for particles released every 15 days over the year 1961 and drifting over 23 years, with no mortality (M=0) and drifting at fixed depth. The distribution has a log-normal shape as it is usually the case for such analysis, with a clear mode around d = 13 years (= 156 months). Note that such a simulation over 23 years of drifting has only been carried out in 1961 for illustration purposes.

Fig. 3.3b shows the same histogram but reduced to the 0-5 years migration duration. The minimum migration duration is in the class 10-11 months but does not appear in the Fig. 3.3a since there is only one particle. The panel c illustrates how this distribution is drastically changed when applying a mortality rate. With a mortality rate of 2 per year on the distribution of Fig. 3.3b, we derive the distribution of the migration duration and a mean migration duration of 2.4 years (Fig. 3.3c). This mortality rate is equivalent to a survival rate of 14 % per year.

From the lagrangian simulations, we estimated the distribution of the migration duration

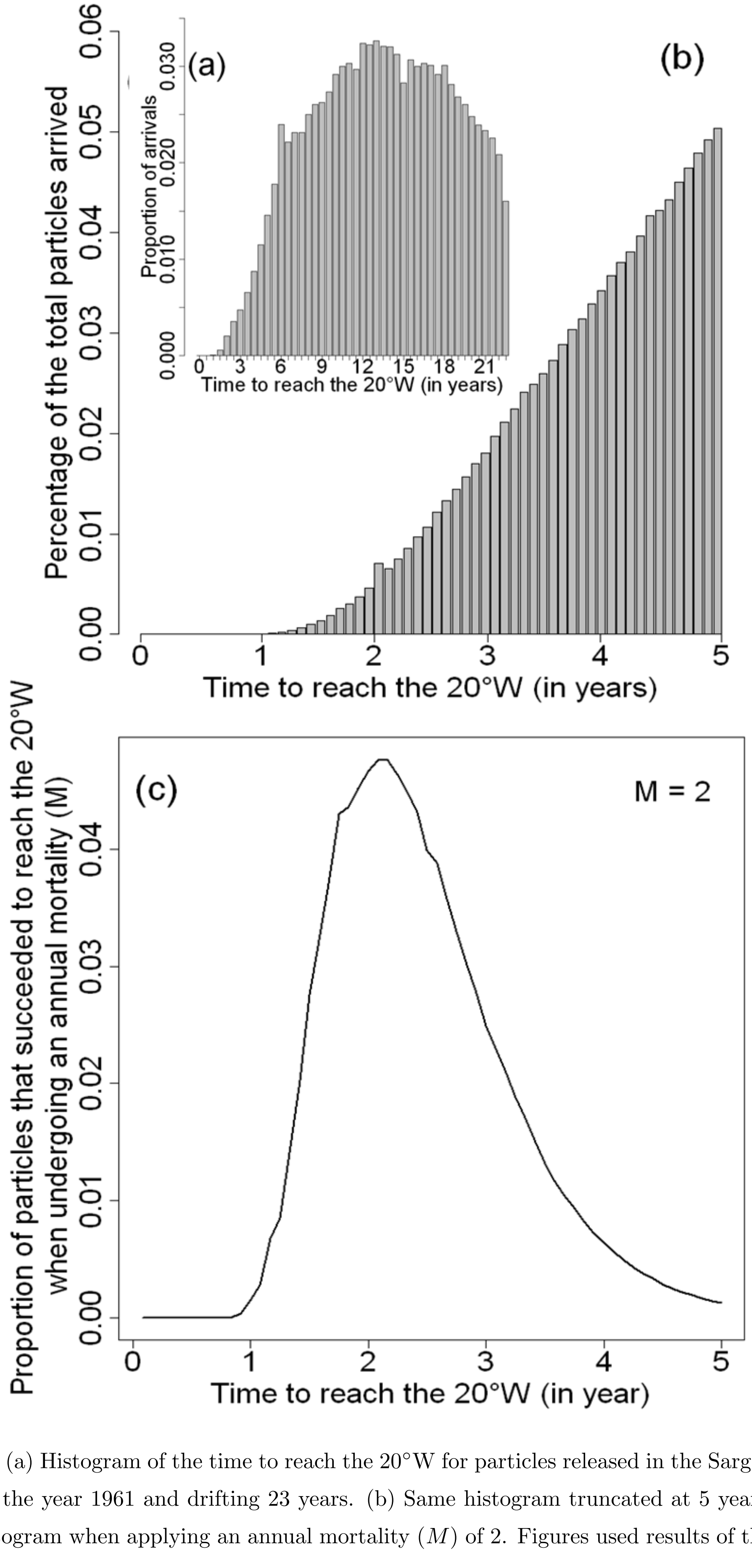

Figure 3.3: (a) Histogram of the time to reach the 20°W for particles released in the Sargasso Sea every 15 days over the year 1961 and drifting 23 years. (b) Same histogram truncated at 5 years. (c) Plot of the same histogram when applying an annual mortality (M) of 2. Figures used results of the fixed-depth experiment.

for each value of the annual mortality M comprised between 0 and 10 with a step of 0.2. By considering a uniform distribution on M, we obtained an estimation of the joint distribution $\pi_L(d, M)$ on a 51 x 60 grid. Fig. 3.4a shows the contour of the joint probability distribution $\pi_L(d, M)$. The modal value is found for a short migration duration (less than 1 year) and a high annual mortality. Fig. 3.4b shows the contour of the joint probability distribution $\pi_E(d, M)$ that is obtained from the combination of ecological knowledge following Eq. 3.10. The maximum of probability is found for migration durations close to 0 and annual mortality rate close to 10. Fig. 3.4c shows the joint probability distribution $\pi(d, M)$ that is obtained from the combination of the lagrangian probability distribution with the distribution obtained from ecological knowledge. The combination of the two sources of information drastically reduces the uncertainty about (d,M). The distribution $\pi(d, M)$ is now well shaped, with modal values around the point (d=1.5 years ; M=3.5 per year).

Marginal distributions of d and M are shown in Fig. 3.5a and Fig. 3.5b respectively. The most credible value are 1.57 years for the migration duration and 3.2 per year for the mortality rate, which correspond to a survival rate of 4.1 % per year.

3.3.3 Larva behaviour does not influence the migration duration

The behaviour of leptocephali during their transatlantic migration may impact their migration duration and mortality. Therefore, we perform the same analysis as for the fixed-depth experiment with the two other hypotheses of leptocephalus behaviour: vertical diurnal migration and faster current choice. Fig.3.5c and e show that the migration duration is not very sensitive to the hypothesis made on the larvae behaviour. Implementing an active behaviour for particles leads to sharper distributions of the migration duration. But the mean of the distributions only varies slightly. Migration duration is 1.53 years for vertical migration experiment and 1.58 for fastest current choice. It also applies for the annual mortality (Fig. 3.5d and f). The mean annual mortality is 3.26 for vertical diurnal migration and 3.18 for faster current choice.

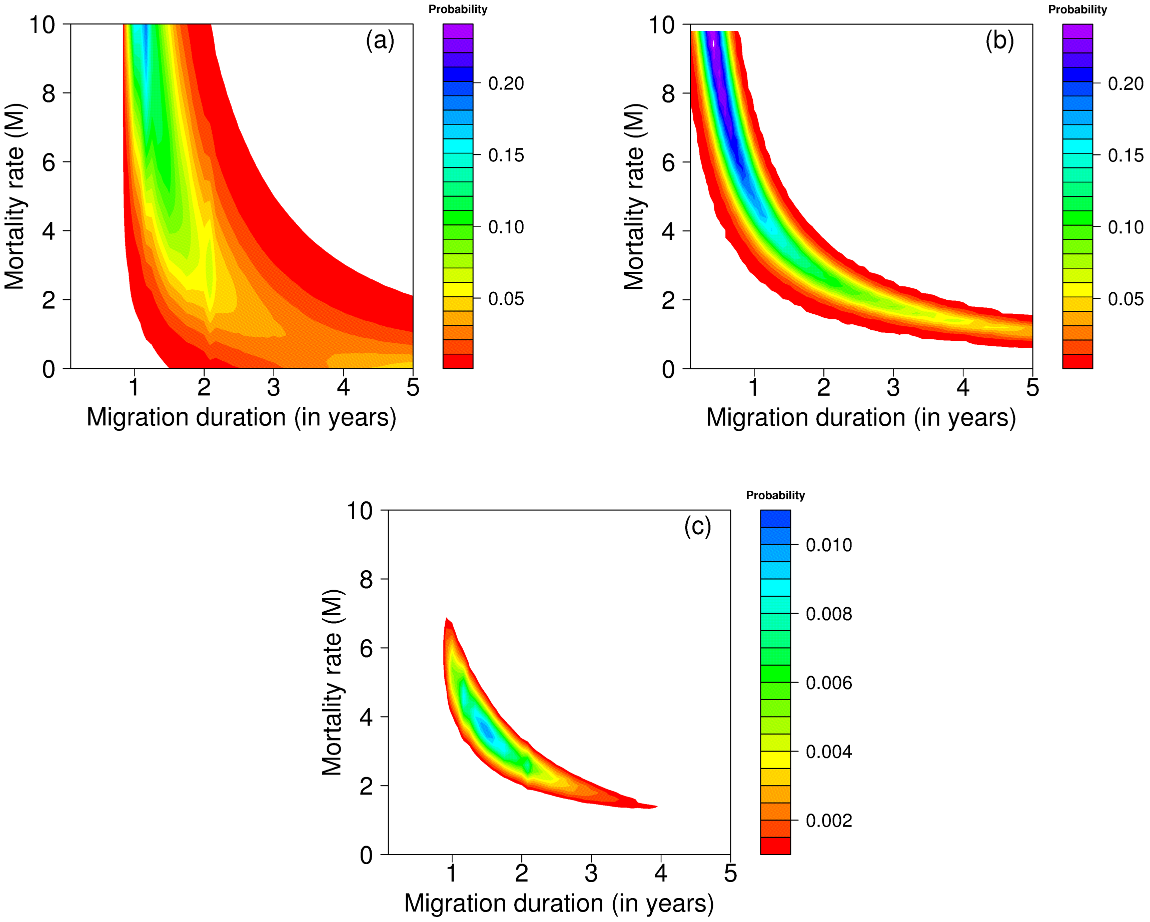

Figure 3.4: (a) Distribution of probabilities of migration durations estimated by lagrangian simulations for different annual mortalities (denoted $\pi_L(d, M)$ in the text). This figure represents the experiment at fixed-depth. (b) Distribution of probabilities of migration durations estimated by the steady state hypothesis of the population (see Eq. 3.10) for different annual mortalities (denoted $\pi_E(d, M)$ in the text). (c) Intersection of the distributions of probabilities of migration durations estimated by the steady state hypothesis of the population and by the lagrangian simulations (denoted $\pi(d, M)$ in the text).

3.3.4 Oceanic conditions do not influence estimations of migration duration and annual mortality

To assess whether oceanic conditions (strength and position of the Gulf Stream) have an impact on estimations of migration duration and annual mortality rate, we perform the same analysis as above over three NAO-contrasted periods: 1960-1964 (mean NAO $= -1.7$), 1973-1977 (0.9), and 1986-1993 (3.2). The migration duration and annual mortality are similar whatever the NAO values (Fig. 3.6a and b). Similar results are found with the two other behaviour hypotheses.

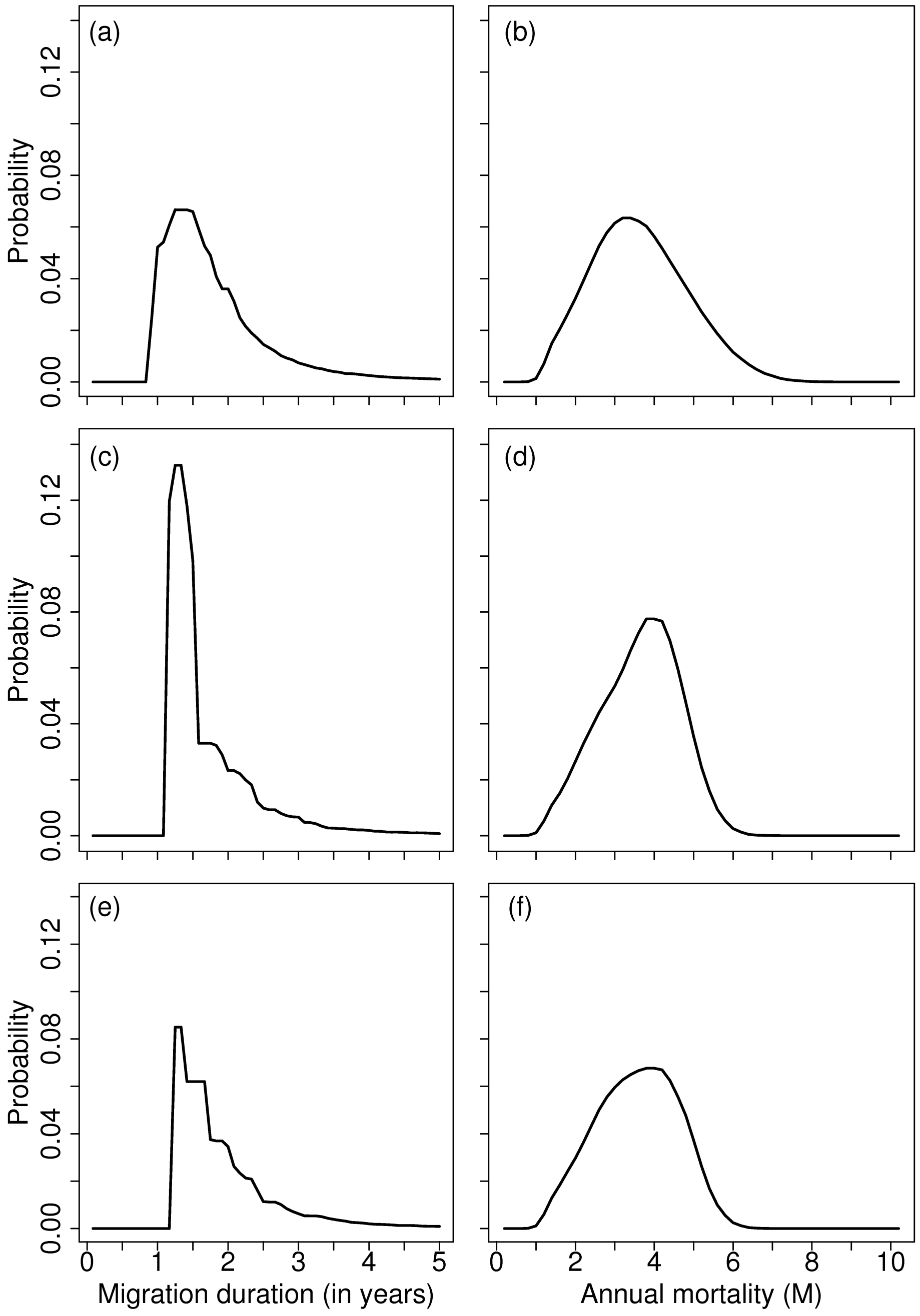

Figure 3.5: Distribution of the migration duration estimated using Eq. 3.10 for the fixed depth experiments (a), the vertical migration experiments (c), and the faster current choice (e) and the annual mortality estimated using Eq. 3.10 for the fixed depth experiments (b), the vertical migration experiments (d), and the faster current choice (f).

3.3.5 Sensitivity analysis to parameters

Elasticities of the mean migration duration and larval mortality are both low (Table 3.2). It indicates that changes in a parameter, considering the others are fixed, has a low impact on results. For instance, if ξ increases by 10 %, the mean migration duration estimated

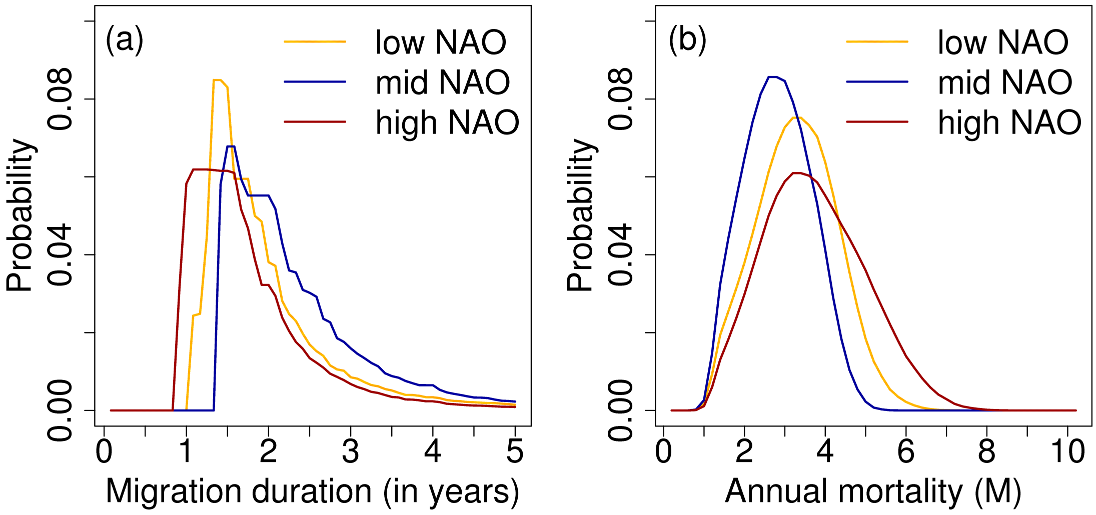

Figure 3.6: (a) Distribution of the migration duration estimated and (b) the annual mortality estimated using Eq. 3.10 for the fixed depth experiments over three NAO-contrasted periods.

in Exp. 1 will increase by 0.7 %. These results are very consistent with Eq. 3.9. If the hatching rate increases, the survival rate of leptocephali decrease to maintain the steady state of the population. The same conclusion applies for the mean migration duration. If the survival rate of glass eel increases, one solution to maintain the steady state of the population as expressed in the Eq. 3.9, is to increase the time of exposure to leptocephalus mortality. The sign of elasticity is positive and therefore consistent with our hypotheses. Furthermore, given the same experiment, elasticies should have been strictly equal for parameters that have the same role in Eq. 3.9, i. e. Fec, ξ, β, and η or M_a and d_a. The small differences stem from the re-simulations of these different parameters when adding a small variation.

3.4 Discussion

3.4.1 Estimations of migration duration are higher than those found by otolith microstructure studies

To provide accurate estimates of migration duration, the larval mortality has to be accounted for in lagrangian studies. Otherwise, as shown in Fig. 3.3a, the more we let particles drift, the more we have particles arriving to the “finish line”. Without mortality hypothesis, we would have a mean migration duration up to the 20°W encompassing 11

Table 3.2: Elasticity of the estimated mean migration duration and mortality regarding the different parameters given in Eq. 4.2 for each experiments

Fec	ξ	β	γ	M_a	d_a	η
Mean migration duration						
Exp. 1	0.07	0.07	0.07	-0.16	-0.16	0.07
Exp. 2	0.06	0.05	0.05	-0.11	-0.11	0.05
Exp. 3	0.06	0.04	0.05	-0.12	-0.12	0.05
Mortality						
Exp. 1	-0.24	-0.22	-0.22	0.49	0.49	-0.22
Exp. 2	-0.22	-0.19	-0.20	0.45	0.45	-0.20
Exp. 3	-0.23	-0.21	-0.20	0.46	0.46	-0.21

to 15 years. Here we confirm the results of Cowen *et al.* (2000) and Hare *et al.* (2002) that showed the importance of accounting for mortality in simple advection models.

When accounting for mortality, we found that the mean migration duration to reach the 20°W is about 1.58 years. We still need to account for the time it takes leptocephali to reach the continental slope and to metamorphose into glass eels. At a minimum, the distance to reach the coast is 1 000km and current speeds in that area are about 0.2m.s^{-1}. A rough estimate of the minimum time to cover this distance is 58 days. Wang and Tzeng (1998, 2000) estimated that metamorphosis of European eel leptocephali is about 98 days while Lecomte-Finiger (1992) gave a metamorphosis stage lasting 33-76 days and Arai *et al.* (2000) estimates are 18-52 days. Thus, one or two months have to be added to the migration duration to account for the metamorphosis into glass eel as well. The migration duration is therefore at least 22 months (19 months to cover the distance to the 20°W and 3 months to reach the shelves and to metamorphose). These results are obtained assuming that the eel larvae do not swim. However, as shown in Chap. 2, the swimming speed of leptocephali should be at least 3.4 body length.s^{-1} of a fully-grown leptocephalus to explain the 6-month migration duration. The swimming hypothesis seems unreliable with respect to the low food availability in open-ocean and the energy cost of swimming. Moreover, the low metabolic rate and uncertainty in the mode of nutrition of leptocephali lend support to such an interpretation (McCleave *et al.*, 1998).

Our results are not in agreement with the otolith microstructure studies. Leptocephali may have such a low metabolic rate that increments in otoliths might not be deposited daily, or may be deposited daily but too thin to be observable in either light or scanning electronic microscopy. We refer to Chap. 1 for a complete description of possible source of mis-interpretation of otolith microstructure.

Observations of leptocephali occurence in the Sargasso Sea from February to June and main arrivals on European shelves from January to April implies that the migration duration is compulsory a modulo 11 months. The 22-month migration duration proposed in this paper matches observations.

3.4.2 Estimations of natural mortality are lower than in other fish species

Reliable estimate of natural mortality, especially during the early-life stages, is critical in stock assessment, recruitment forecasting and management of marine fish species. Natural mortality rates of fish species have a wide range of estimates and even within species, estimates differ (McGurk, 1986). For instance, the natural mortality of European plaice larvae, *Pleuronectes platessa*, is estimated to 0.02 per day (Bannister *et al.*, 1974), 0.69 for the Atlantic mackerel, *Scomber scombrus*, (Ware and Lambert, 1985) and 0.16 for the cod, *Gadus morhua* (Kristiansen *et al.*, 1997).

We estimate the natural mortality of leptocephali to be 3.2 per year that is far lower than other fish larvae. Most fish have a short larval stage, from a few weeks to a few months, compared to the European eel larvae that have to cross the Atlantic Ocean. Applying a natural mortality rate to eel larvae of the same magnitude as other pelagic larvae will indisputably lead to the impossibility to cross the Atlantic. This result is therefore difficult to compare to other fish species.

To our knowledge, no study has ever provided an estimate of natural mortality of eel leptocephali, so we cannot compare to other estimates. Kettle and Haines (2006) found that of $1.6 \cdot 10^6$ drifters released, 0.66 % arrived at 25°W within 2 years. Actually, Kettle and Haines (2006) tacitly induced a mortality hypothesis since their simulations were stopped after two complete years. It is equivalent to a survival rate of 100 % up to two years and 0 % thereafter. However, the 0.66 % is not a survival rate since no realistic mortality rate is implemented in their model. The estimate of a 3.2 annual mortality over 22 months is equivalent to a survival rate of 2.8 for 1 000 larvae and is consistent with the steady-state hypothesis of the population (Eq. 3.7 and Fig.3.2). It is also consistent with observations of glass eel arrivals. The European eel spawning season is estimated to be from February to June (e. g. Schmidt, 1922; McCleave and Kleckner, 1987). If the natural mortality rate was very high, catching glass eels throughout the year would not be possible. Leptocephali that spend too much time in Atlantic Ocean would be dead. Glass eel fishery is generally concentrated between November and April depending on the location. However, catches from illegal fishing done outside the fishing season provide a substantial amount of glass eel that are to Asian market even during July and August. These observations could not be done if the mortality rate was very high.

3.4.3 Behaviour hypotheses have a weak impact on mean migration duration and mortality estimates

We found that neither the mean migration nor the mean annual mortality is influenced by behaviour. However, the distribution shape of migration duration has a more pronounced mode for experiments of vertical diurnal migration and faster current choice. This actually could be an artefact induced by lagrangian simulations. For these two experiments, we released less particles than for the fixed-depth experiment. In the fixed-depth experiment, particles were released at each vertical mesh grid (26 levels). This was not necessary for the two other behaviour hypotheses. For instance, regarding the fastest current choice behaviour, all particles starting at the same horizontal position would have chosen the same depth levels at the first time step and so on. The same applies to the vertical diurnal migration since depths are fixed at -300 m during the day and -50 m at night. Consequently, once the first particle has arrived, we have some time-classes with a low particle number for these two behaviour experiments. When applying mortality rate, the first particle was selected and has a high probability but the next ones have a very low probability.

When multiplying the two joint distributions, i. e. lagrangian results ($\pi_L(d, M)$; Fig. 3.4a) and steady-state hypothesis ($\pi_E(d, M)$; Fig. 3.4b), the joint probability ($\pi(d, M)$) of the first particle was therefore high compared to the other. It explains the pronounced mode for experiments with vertical migration and the fastest current choice. Nevertheless, the range of values between the different experiments are similar and suggest that behaviours are not a way to minimize migration duration. Vertical diurnal migration is a way to avoid predation and corresponds to feeding needs as it the case for other zooplankton species (Steinberg *et al.*, 2002).

3.4.4 Steady-state hypotheses of population and implications

Eq. 3.7 describes necessary conditions for a species to maintain its population. This equation is true when population is at steady-state, i. e. when the parameters used are those of the population at steady-state. That is why we favoured parameters given by literature when the population is supposed to be at steady-state, i. e. before the 1980's. Regarding the current decline of European eel, this equation is clearly false since one female does not produce 2 individuals able to spawn. Åström and Dekker (2007) calculate that the depletion rate is 0.1538 year^{-1}.

However, in this study, we aim at estimating the natural mortality and migration duration of leptocephali. Eq. 3.7 has to be seen as Eq. 3.9. We made the assumption that the natural mortality and migration duration are not influenced by current factors affecting the European eel such as overfishing, pollution, habitat loss, etc... Actually this assumption is also conceptually false since, for instance, fishing may select glass eels arriving in European rivers before or after the fishing season. Thus, individuals that have a shorter or longer migration duration may be genetically favoured. However, we consider that it is currently not possible to assess the evolutionary effects of fishing, pollution, etc. on eel larva migration. This assumption can be written:

$$e^{-M\cdot t} \approx \frac{2}{Fec\cdot\xi\cdot\beta\cdot e^{-M_a\cdot d_a}\cdot\eta} \approx \frac{X}{Fec\cdot\xi\cdot\beta\cdot e^{-M_a\cdot d_a}\cdot\eta\cdot\prod_i\delta_i} \tag{3.11}$$

where X is the current number of spawners produced by a female, δ_i are all other survival rate induced by the impact of overfishing, habitat loss, pollution, climate etc. on the eel. We assume that factors inducing the current decline in eel population have no effect on migration and larval mortality. When using only lagrangian simulations where eel population was assumed to be at steady-state (i. e. before the 1980's), we obtain the same mean migration duration and mortality. It reinforces the idea that using steady-state hypothesis is an accurate first assumption to estimate the mean migration duration and larval mortality. The last hypothesis we made when assuming that one female produces 2 individuals able to spawn is that the sex ratio is 1:1. This hypothesis may be wrong but currently, we have no way to estimate the sex ratio of the European eel at the European scale. To do so would require knowledge of all sex ratios and biomasses of migrating adult eels in each rivers, marsh, lagoon where European eels have settled. Sex ratios are well reported in some European rivers and depend on the carrying capacity of rivers. Density-dependent phenomena are paramount. As a first approach, we chose a sex ratio equal to 1:1.

3.5 Conclusion and perspectives

Lagrangian simulations coupled with mortality hypotheses enable us to estimate the migration duration and the natural mortality of European eel larvae. Results show the importance in accounting for mortality in lagrangian modelling of fish larvae to estimate their migration duration. In our simulations, the behaviours of leptocephali do not appear to have an influence on the mean migration duration and the mortality. These results may be influenced by the resolution of ocean general circulation models and improvements have to be considered for future works. Lagrangian simulations appears to be a promising way to understand the early life history of the eel. The use of higher resolution models of ocean general circulation may help increase the understanding of the migration of leptocephali.

Regarding our first estimations of larval mortality and migration duration using lagrangian simulations and mortality hypotheses, we find that migration duration is more than otolith microstructure estimates, i. e. more than one year and larval mortality is low compared to other fish species, i. e. 3.2 per year. It fits with the unique developmental strategy of eel larvae to achieve their migration over such a distance in a low productive open-ocean. Higher mortality rate during larval stage rather than during next ones is consistent with general considerations about the importance of this specific period (e. g. Levin and Stunz, 2005).

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4

Routes et histoires de vie des larves d'Anguille européenne

Résumé détaillé

L'objectif de ce chapitre est d'étudier l'influence des aires et des dates de départ dans la zone de reproduction des Anguilles européennes sur leurs aires d'arrivée en utilisant des simulations lagrangiennes. Le chapitre 3 nous a permis d'estimer un taux de mortalité des larves. L'influence de cette hypothèse de mortalité ainsi que trois différentes hypothèses de comportement des larves (dérive à profondeur fixe, migration verticale nycthémérale ou choix du courant le plus rapide) sur les routes de migration est examinée. Les simulations de dérive de larves utilisent deux modèles de circulation océanique (Drakkar et Mercator) qui ont des propriétés physiques différentes.

Les principaux résultats de ce chapitre sont : (*i*) Les propriétés des modèles physiques ont une influence sur l'aire d'arrivée des larves. Le modèle Drakkar offre notamment une moins bonne représentation du courant des Açores ce qui entraîne un faible succès d'arrivée dans le sud de l'aire de distribution de l'Anguille (Fig. 4.2). (*ii*) les aires de départ ont une influence sur les aires d'arrivée (Fig. 4.6). (*iii*) La prise en compte de la mortalité permet de révéler des périodes de départ favorisant certaines zones d'arrivée (Fig. 4.8). En revanche, les hypothèses de comportement ne semblent pas avoir d'influence sur les routes et le déterminisme de la migration. (*iv*) La reconstruction du passé de température des larves par les simulations de dérive montre que les passés larvaires sont différents selon les zones d'arrivée (Fig. 4.9a). Par exemple, les larves arrivant au nord ont connu des températures plus froides le long de leur trajectoire que celle du sud. Ces résultats sont confirmés par ceux de la microchimie des otolithes de civelles (Fig. 4.9b, (de Casamajor *et al.*, 2002)) et montrent que les routes et les conditions de migration sont déterminées très tôt après le départ de la mer des Sargasses (Fig. 4.10).

Par ailleurs, les études de génétique suggèrent l'existence de sous-populations d'Anguille européenne et une non-panmixie de cette espèce, avec une variabilité spatiale et temporelle de la structure génétique des sous-populations qui parviennent aux estuaires. Les modèles lagrangiens, permettant de reproduire le passé larvaire des civelles, montrent que par simple dérive, cette structure en sous-populations peut être maintenue : les futures routes de migration des larves pourraient donc être déterminées par la reproduction à certaines périodes et zones dans la mer des Sargasses et ainsi conditionner les aires d'arrivée. Ces résultats sont finalement mis en perspective par rapport aux mesures de gestion prises par la Commission Européenne afin de restaurer la population d'Anguille.

Confirmation of possible multiple spawning sites for the European eel

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Abstract We investigate the connectivity and life histories of European eel population through lagrangian simulations. We simulate the passive drift of particles released in the eel spawning area with different behaviours and couple these simulations to mortality hypotheses. We investigate temperature histories of particles and compare results to the signature of isotope temperature dependent ^{18}O in eel larva otolith. Simulation results are consistent with previous knowledge about eel larva ecology (drift depths, arrival areas). We provide evidence that eel larvae use different pathways to reach continental habitats. We show that spawning locations and timing in the Sargasso Sea determine the distribution area of arrivals. Temperature histories from simulations are consistent with otolith signature found in the wild. These results are consistent with the hypothesis of non-panmictic populations and of the existence of sub-populations maintained by specific spawning locations and timing. It may have strong implications in European eel management because it conditions the results of local restocking measures. The European eel is hitherto considered as an "open" population: one country's fisheries have the potential to impact the resources of another. One of the management measures proposed by the European Commission is the restocking of freshwater habitats of North European countries by glass eels caught in West European countries. However, it would not enhance the global stock if the European eel is not panmictic. It could even be worse if oceanic and environmental conditions are currently less favourable for offspring of North European eels.

Keywords *Anguilla*, isotope, ^{18}O, otolith, lagrangian simulations, panmixia

4.1 Introduction

The study of the connectivity and life histories of marine populations is central in the ecosystemic approach to fisheries. It conditions the population dynamics and genetics with strong bio-evolutionary consequences. It also determines how populations may interact with the whole ecosystem and provides insights on how to manage them. When marine populations are "closed", i. e. when the adults produce offspring that become members of the same population (Roughgarden *et al.*, 1985), local retention occurs and local management initiatives predicated on the appropriate population models (limited exchange) have a greater chance of producing local results (Cowen *et al.*, 2000). Conversely, when marine population are "open", one country's fisheries have the potential to impact the resources of another.

The European eel is a particularly interesting study case:

(*i*) Its life cycle includes a long oceanic larval stage and a wide dispersal that suggest an "open" population. It is a catadromous fish that undergoes one of the longest seaward migration, more than 6 000 km across the Atlantic Ocean. Conveyed by warm currents, eel larvae (leptocephali) come from the Sargasso Sea where adults spawn, to settle on the African and European shelves, from Mauritania to the Polar Circle (Schmidt, 1923). The dispersal of larvae is very extensive. *Anguilla* leptocephali have been collected in the whole North Atlantic Ocean (Schmidt, 1927, 1935, Fig. 1.1) and in the Mediterranean Sea (Strubberg, 1923). Leptocephali have been sampled as far north as 61°N and 3°W in the Faroe-Shetland channel (Schmidt, 1927). No eel specimen was found south of 20°N in the East Atlantic (Schmidt, 1922).

(*ii*) Recent advances provided by genetic studies showed that the European eel may however retain regionally distinct population structures (e. g. Daemen *et al.*, 2001; Wirth and Bernatchez, 2001; Maes and Volckaert, 2007). However, recent studies showed that temporal variance in allele frequency exceeded by far the geographic component (Maes *et al.*, 2006; Pujolar *et al.*, 2006). Possible sampling bias attributable to mixing of life stages and a lower effective population size could explain these results, which conflict with previous studies showing the spatial structure of eel sub-populations (Wirth and Bernatchez, 2003; Dannewitz *et al.*, 2005). Both hypotheses converge for a non-panmixia of the European eel in the Sargasso Sea. Either the genetic spatial differences are related to the existence of different spawning areas and timing in the Sargasso Sea, or the genetic temporal differences are related to different timing of sub-population mating in the Sargasso Sea.

(*iii*) Its current decline in abundance has led to a management plan at the European scale and management measures are based on the consideration that the stock is global. Among these measures, the restocking of glass eels caught in West Europe (France, Spain, England) towards North European countries (Sweden, Denmark, the Netherlands) is proposed to enhance the stock status. The current decline in eel populations worldwide is well observed (Anonymous, 2003) and the European eel has been listed in Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES, 2007) regarding its current level of abundance. The decline in European eel population since the early 1980s is no doubt due to the combined effect of several and probably interacting factors: direct effect of anthropogenic activities such as overfishing (Dekker, 2004), habitat loss and degradation (McCleave, 2001; Feunteun, 2002; Palstra *et al.*, 2006) and increasing stress in the freshwater stage due to parasites and diseases (e. g. Jørgensen *et al.*, 1994; Aguilar *et al.*, 2005; van Ginneken *et al.*, 2005) or in the oceanic stage due to unfavourable oceanic conditions (Knights, 2003; Friedland *et al.*, 2007; Bonhommeau *et al.*, 2008). These potential causes of stock decline are often intrinsically associated and occurring at the same time and are difficult to untangle (Anonymous, 2003).

The origin of the genetic structure of eel populations remains partially unresolved. Is the genetic structure the result of a difference in spawning location and / or timing between sub-populations? In this study, we attempt to provide further insights to this question by the use of oceanic circulation models and lagrangian simulations. In a recent analysis, Kettle and Haines (2006) investigated migration patterns of the European eel, i. e. pathways and most favourable origins and periods of departure. The ocean general circulation is turbulent and may lead to a genetic mixing before reaching the European shelves. Kettle and Haines (2006) showed that the departure area in the Sargasso Sea may be connected to the arrival area even if a genetic mixing remains. Thus, over a period of one year, different sub-populations may reach the European and North African shelves: the “scheduled” ones (as expected from Kettle and Haines, 2006) and the “random” ones (due to ocean mixing). Temporal evolution of the genetic variability all over the arrival period may provide insights on the origins of these temporal differences. It may help to determine whether temporal genetic differences stems from waves of genetically-different populations or from a main arrival mixed with "random" larvae. This type of studies still remains difficult to carry out at the European scale over an arrival season.

We follow Kettle and Haines (2006) but our approach differs in four ways.

First, we used 2 different ocean general circulation configurations, Drakkar and Mercator projects that are currently the most accurate ones in the European scientific community. Simulations were possible over a period of 45 years when using the Drakkar model.

Second, we relaxed the hypothesis of strict passive drift by testing three different behaviours of the particles: (*i*) particles drifted at fixed-depth as in Kettle and Haines (2006), (*ii*) particles undergoing a vertical diurnal migration between -300 m and -50 m as observed *in situ* (Castonguay and McCleave, 1987) and (*iii*) particles following the direction and depth where the speed of currents is the highest (see Chap. 2).

Third, we implemented a mortality hypothesis as described in Chap. 3 and better fit with ecological reality.

Fourth, to further explore the consistency of our simulations, temperature life histories of simulated particles arriving at different locations of the eel distribution were used. Results of simulations can be compared to results of the analysis of otolith isotopic signature in ^{18}O, which is a descriptor of the temperature encountered by larvae during their transoceanic migration.

We address the questions: "Do spawning areas and timing determine the arrival areas?", "Can we correctly reconstruct temperature life histories of eel larvae by lagrangian simulations?" and eventually discuss whether the European eel can be considered as an open or closed population.

4.2 Materials and methods

4.2.1 Drakkar and Mercator circulation models

Lagrangian simulations are performed using two different oceanic model configurations described in Chap. 2 (Drakkar and Mercator).

The Drakkar model (`http://www.ifremer.fr/lpo/drakkar`) is reduced in size to centre on the area of our study case (i. e. the North Atlantic Ocean), we extracted an area ranging from -82 to 6°W and 10 to 60°N. Since the observed depth of leptocephali ranges between -50 and -300 m (e. g. Castonguay and McCleave, 1987), we reduced the oceanic model to the top 24 levels (-3 to -989 m). To avoid the early spin-up phase of the model, we use the period 1960-2004 of the simulation. Circulation fields are time-means archived every 5 days.

The circulation fields provided by the Mercator project (`http://www.mercator-ocean.fr`) has been reduced from -98 to 20°W to -20 - 70°N and the depth was limited to the first 16 levels (-453 m). This ocean general circulation model is equivalent to the one used by Kettle and Haines (2006) in terms of approach. However, it has a better vertical resolution and runs over a longer time period.

4.2.2 Lagrangian simulation designs

The aim of the study is to determine the migration pathways of particles drifting from the Sargassos to the European shelves. We let the particle drift over a 5-year period. We used the Ariane tool developed by B. Blanke and N. Grima, Laboratoire de Physique des Océans, CNRS-IFREMER-UBO, Brest, France and freely available at `http://www.univ-brest.fr/lpo/ariane`. It is a FORTRAN code dedicated to the computation of 3D streamlines in a given velocity field (as the output of an Ocean General Circulation Model) and subsequent water masses analyses.

The Drakkar model provides the longest time-series available: 1960-2004, and the highest spatial resolution. Passive drifters were released at each mesh of the model grid, i. e. each 1/4° degree and each 24 fixed-depth levels in an area enclosing the assumed spawning area of eels in the Sargasso Sea (Fig. 2 *in* McCleave and Kleckner, 1987, and Fig. 2.1). We averaged patterns of migration by aggregating results obtained from three NAO-contrasted periods, which is known to be related to strength (Curry and McCartney, 2001) and latitude (Taylor and Stephens, 1998) of the Gulf Stream. The selected periods were 1960-1964 (mean $\text{NAO} = -1.7$), 1973-1977 (0.9), and 1986-1993 (3.2). Particles were released every 15 days throughout the year. Hence, 1 972 608 particles were released each year.

Regarding the Mercator configuration, passive drifters are released at each model grid, i. e. each 1/3° degree and 16 depth levels over the whole period available (1992-2002) in the same area than in the Drakkar model. Particles were released every 15 days throughout the year. Thus, 691 104 particles were released each year.

As described in Chap. 2, three particle behaviours were implemented in lagrangian simulations when using the Drakkar model: (*i*) we assumed a fixed depth drift for all particles released at each vertical levels of the reduced model, (*ii*) in a second experiment, particles were able to change their vertical position every 12 hours from about -300 m to -50 m as described in Castonguay and McCleave (1987) and (*iii*) particles have the ability to actively select the direction where the current speed is the highest. As glass eels can feel currents and react to them (Bertin, 1956; Bolliet *et al.*, 2007), we assumed that leptocephali may have the same ability to follow the fastest currents.

Output files of lagrangian simulations include position (longitude, latitude, depth), time, and temperature for each particle. Particles are considered as having succeeded in their migration when crossing the 20°W whatever the latitude. This “finish line” is more eastward than the 25°W chosen by Kettle and Haines (2006). Since we aim at studying the distribution areas of particles, the “finish line” has to be as close as possible to the real arrival area of eel larvae, i. e. estuaries. In addition, 20°W is a reasonable limit since longitudes higher than 20°W correspond to continental slope that is not as well-resolved by the physical model as open ocean. Moreover, lagrangian simulations are unable to represent tidal transport of eel larvae when they reach the shelves.

4.2.3 Mortality hypotheses

We could have implemented a stochastic mortality rule for each particle in the simulation. However, the simulations are deterministic, particles released at the same location and at the same time have the same trajectory. Therefore, as shown in Chap. 3, we apply a deterministic survival rate ($e^{-M \cdot d}$) to each particle with a migration duration d. This provides an exact value of the expected mean survival that would be obtained in a stochastic mortality model. It is interpreted as an expected mean probability of arrival for each particle and use it as a weighting parameter that preferentially select the fastest particles. As found in Chap. 3, leptocephali mortality rate is estimated to be $M = 3.2$ per year, we apply it to lagrangian simulation results.

4.2.4 Temperature histories

Using lagrangian simulation outputs that provide temperature for each position at each time step, the mean temperature for different arrival areas of particles was calculated to reconstruct the temperature life histories. These results were compared to isotopic signatures of glass eel otoliths gathered in the wild in the different estuaries. Over the season 2000/2001, sampling of glass eel otoliths have been carried out in different estuaries in Europe (from Sweden to Morocco) over the main arrival period (January-February). Isotopic signature of $\delta^{18}O$ has been measured along otolith transects to investigate the temperature histories of eel larvae (de Casamajor *et al.*, 2002). The ratio $\delta^{18}O$ is used as an indicator of temperature histories.

4.3 Results

Over the whole period of simulations, 3.1 % and 10.2 % of released particles drifting at fixed-depth succeeded in crossing the 20°W in less than 5 years (Drakkar and Mercator model respectively). Two other behaviours, i. e. vertical diurnal migration and fastest current choice, are implemented in lagrangian simulations when using the Drakkar model. The arrival success strongly decreases when particles have a vertical diurnal migration (0.15 %) or when they choose the fastest currents (0.30 %).

4.3.1 Simulations are consistent with previous knowledge

Depths of the drift For the fixed-depth drifting behaviour, the depth distribution shows that the drift has a maximum of success at a depth of -300 m (Fig. 4.1a; Drakkar model) and -200 m and another peak at -70 m (Fig. 4.1c; Mercator model). When implementing mortality in lagrangian simulations, the fastest particles are preferentially selected. The distribution of depth is not strongly impacted but is slightly skewed toward shallower layers (Fig. 4.1b and d). Results match with the observations of eel larvae in the open ocean that are mostly found at -300 m during the day and shallower at night (Castonguay and McCleave, 1987). These results also fit with Kettle and Haines (2006) who found that larvae travelled mostly between -50 and -400 m with a mode at about -200 m. Kettle and Haines (2006) used an ocean model with data assimilation and found the same range of values as the Mercator model.

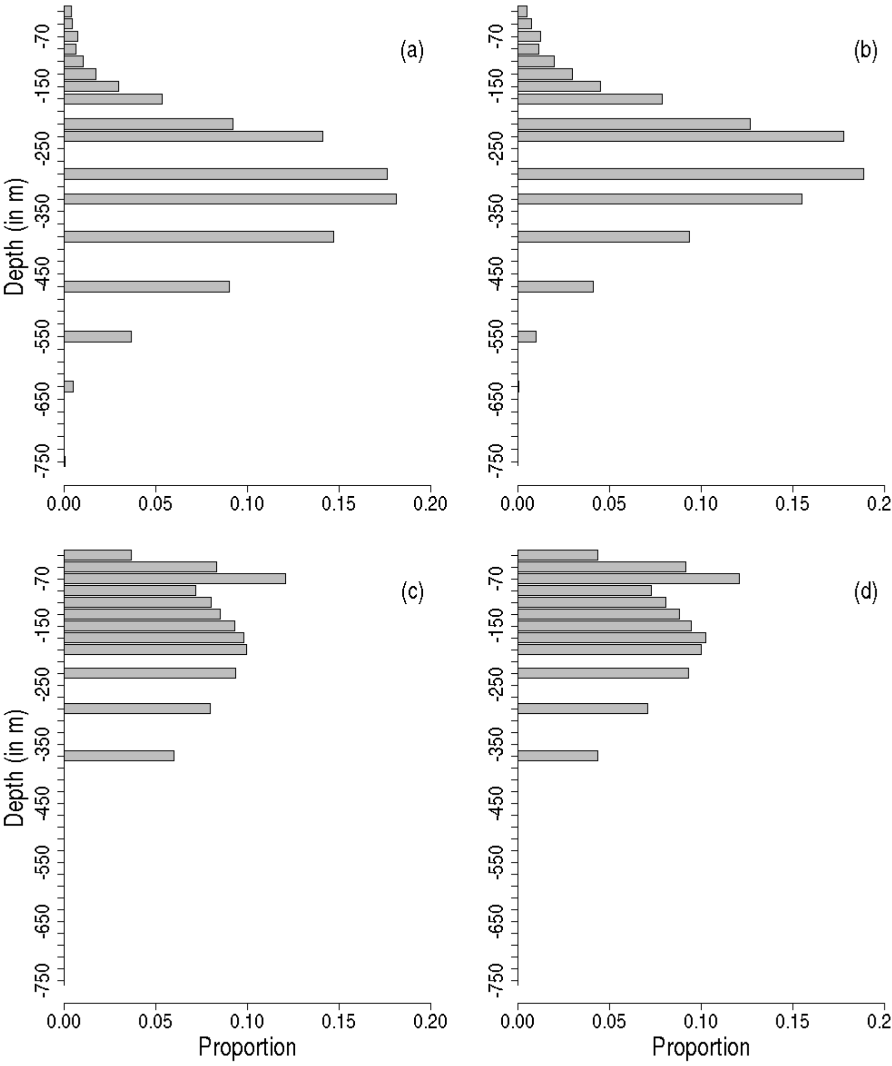

Figure 4.1: Depth distributions of the particles successfully crossing the 20°W meridian within 5 years after being released within the eel spawning area for the Drakkar model without (a) and with (b) implementation of a mortality of 3.2 per year and for the Mercator model with (c) and without (d) mortality.

Arrivals areas Regarding arrival areas, results obtained from the 2 ocean models are contrasted. While lagrangian simulations using the Drakkar model show a main peak of arrivals at 48°N and two others at 33 and 60°N (Fig. 4.2a), simulations using the Mercator model exhibit two main peaks at 48 and 33°N and one weaker at 60°N (Fig. 4.2c). Implementation of mortality hypothesis slightly narrows the distribution around the peaks (Fig. 4.2b and d). Simulations using the Mercator model are close to the results of Kettle and Haines (2006) who found a similar pattern of arrival distribution.

Interestingly enough, using the Drakkar model, the proportion of particles arriving at the extreme range of eel distribution is intensified with the two "active" behaviours and no mortality hypotheses (Fig. 4.3a and c). The implementation of mortality decreases this effect but arrivals remain higher at the extreme bins of the eel distribution (Fig. 4.3b and d) than with the Drakkar model at fixed-depth (see Fig. 4.2a and b).

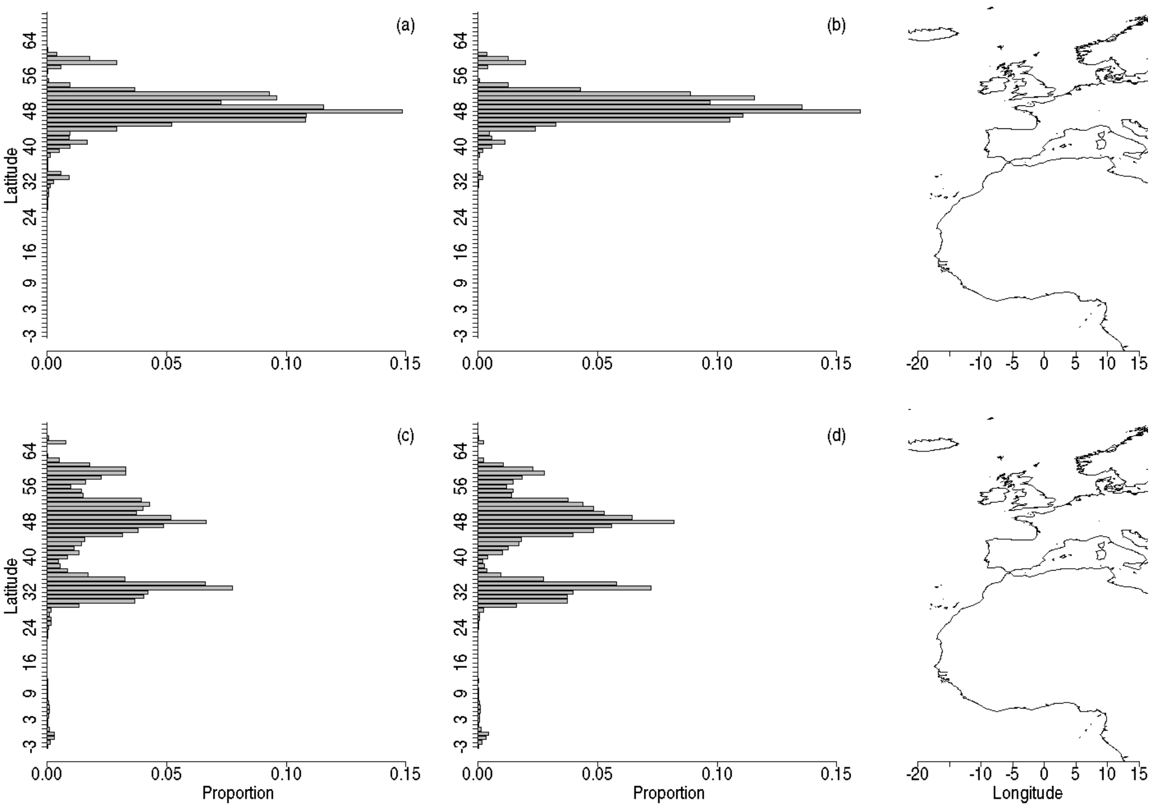

Figure 4.2: Proportion of particles successfully crossing the 20°W meridian at different latitudes arrivals. Particles drift over 5 years after being released within the eel spawning area for the Drakkar model without (a) and with (b) implementation of a mortality of 3.2 per year and for the Mercator model with (c) and without (d) mortality. The maps on the right hand side shows the location of the latitude bins defining the histogram and is drawn up until the 20°W where particles are counted.

Departure months For both ocean model, results are similar whatever the behaviour of particles. When no mortality is implemented, the monthly distribution of departure of particles that succeed in crossing the 20°W meridian is relatively uniform with a slight higher proportion at the end of the year (Fig. 4.4a and c). By contrast, the selection of the fastest particles by mortality strongly influences the monthly distribution of departure. The distribution reaches a peak during the period of March-June for the Drakkar model and December-April for the Mercator model. The variability between months is weak

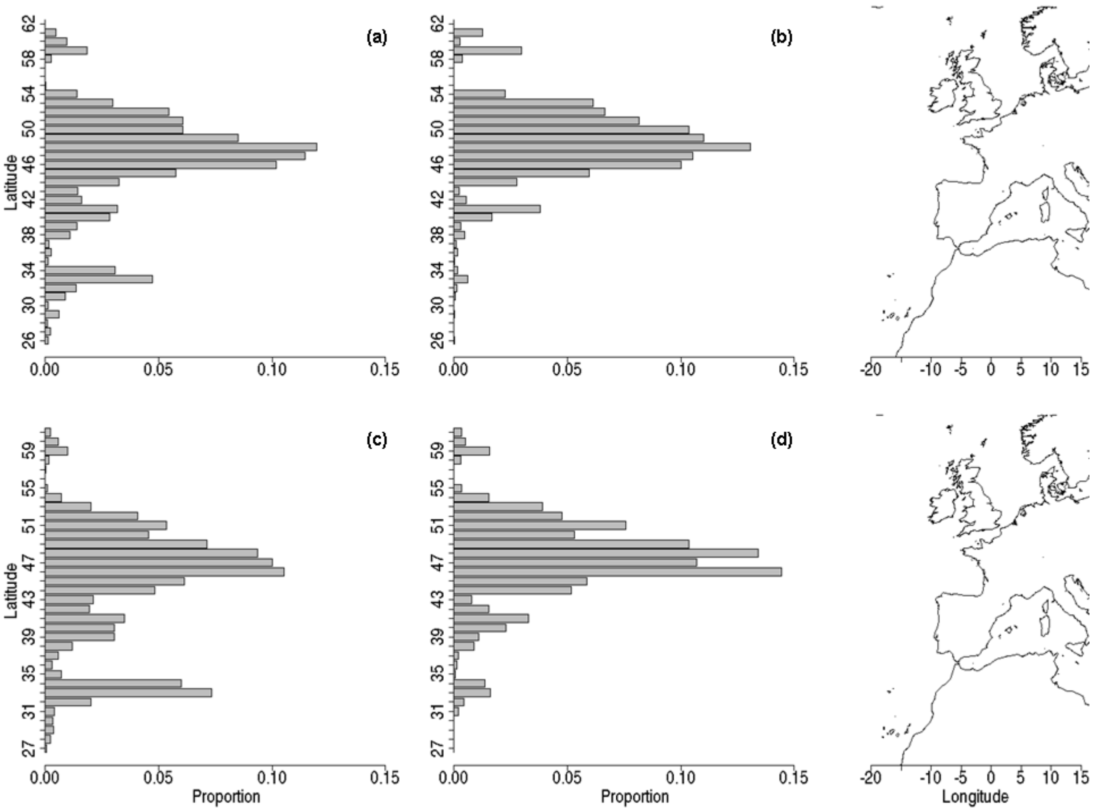

Figure 4.3: Drakkar model: Proportion of particles successfully crossing the 20°W meridian at different latitudes arrivals. Particles were released over 5 years after being released within the eel spawning area and having a vertical diurnal migration without (a) and with (b) implementation of a mortality of 3.2 per year or choosing the fastest currents with (c) and without (d) mortality. The maps on the right hand side shows the location of the latitude bins defining the histogram and is drawn up until the 20°W where particles are counted.

(maximum of difference of 0.35 % and 0.8 % for Drakkar and Mercator models respectively). The peak at the end of the year (October-December) remains in the simulation including mortality. It does not correspond to the literature about the occurrence of eel larvae in the Sargasso Sea. McCleave *et al.* (1987), for instance, found a main spawning season during the period of March-June.

4.3.2 Spawning locations and timing determine the distribution area of arrivals

The following results are not sensitive to the mortality hypothesis. Thus, only analyses performed with $M = 3.2$ are presented. In addition, we did not investigate the sensitivity of results to active behaviours because the number of arrived particles was too small.

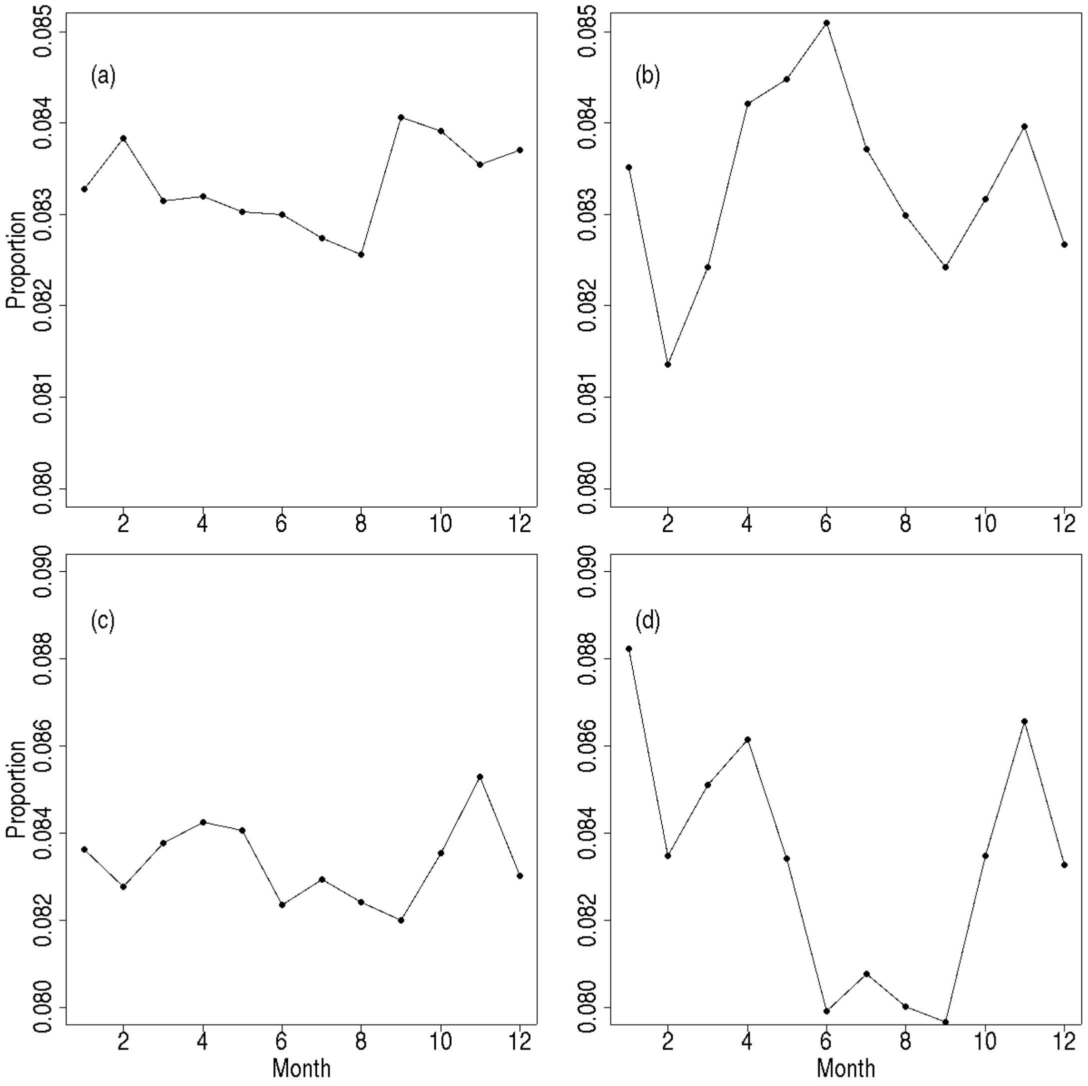

Figure 4.4: Departure monthly distribution of larvae successfully crossing the 20°W meridian within 5 years after being released within the eel spawning area for the Drakkar model without (a) and with (b) implementation of a mortality of 3.2 per year and for the Mercator model with (c) and without (d) mortality.

For both models, when no mortality is implemented, the main departure area of particles that reached the European shelves is located in the Western Sargasso Sea (75°- 65°W and 22°-30°N; Fig. 4.5 representing the Drakkar model). The same patterns are observed for the three experiments, i. e. fixed-depth, vertical migration, or faster current choice. This is mainly due to the proximity to the Gulf Stream. It allows particles nearby to come in this current faster than more eastern particles drifting in the low currents of the Sargasso Sea before reaching the Gulf Stream (Kleckner and McCleave, 1982).

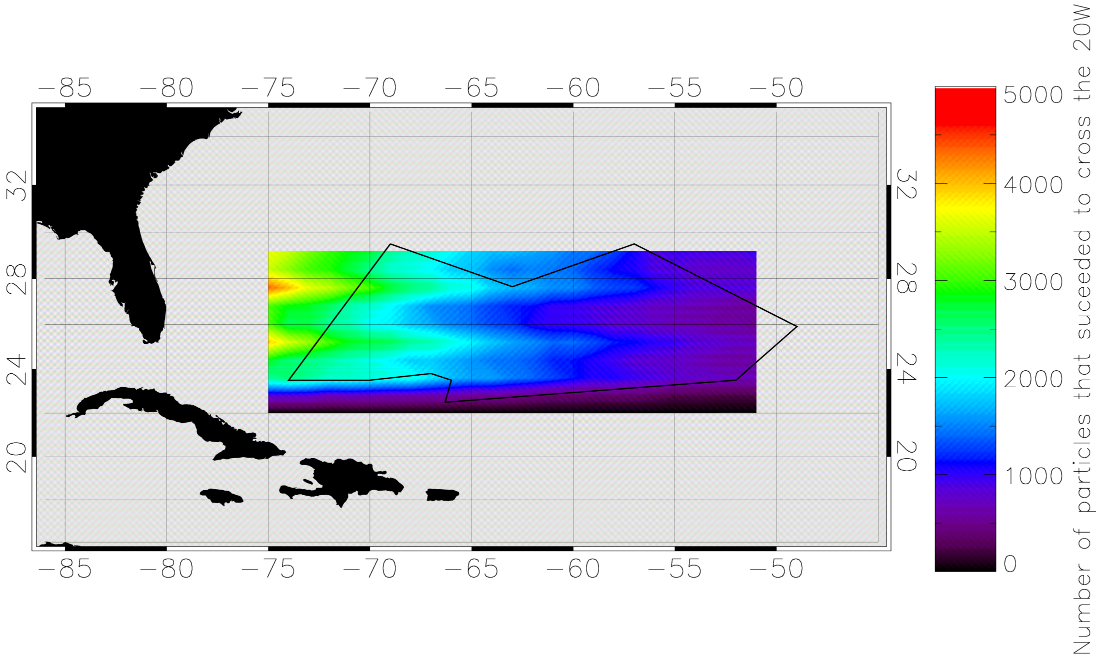

Figure 4.5: Number of successful particles as a function of starting location in the Sargasso Sea when using the Drakkar model with a 3.2 mortality (colour scale). The European eel spawning area is charted out by a black polygon (from Fig. 2 *in* McCleave *et al.*, 1987).

To investigate whether the spatial distribution of arrivals is influenced by the departure location, we focus on three arrival bins: North (>50°N), mid (≤50° and >35°N) and South Arrivals (≤35°N) and subdivide the eel spawning area in 20 bins (5° of longitude and 2° of latitude). We calculate an anomaly of arrival bins for each departure bin, i. e. the variation rate between the number of particles that arrived in one of the three arrival bins and the total number of particles arrived. A random dispersion between the 3 arrival bins would lead to an anomaly value of 0 and substantial positive deviations to 0 indicate that the corresponding departure area contributes more than expected to the arrival bin. Results are contrasted depending on the ocean model used but are not sensitive to the mortality implementation. They show that arrival areas are influenced by departure areas. It is fully consistent with results of Kettle and Haines (2006) who found the same patterns of particle origins. When using the Mercator model, particles starting from the northeast part of the Sargasso Sea arrive preferentially in the north and mid-latitude of the distribution area of European eels (Fig. 4.6a and b). Particles arriving in mid and high latitudes originate basically from the southern part of the Sargassos (Fig. 4.6a and b). Particles arriving south of the eel distribution (Morocco) preferentially come from the northeast corner of the Sargasso Sea (Fig. 4.6c).

Using the Drakkar model, we find contrasted results. Patterns between North and South arrivals bins are the opposite of those found with Mercator, i. e. particles arriving in the north of the eel distribution area mainly stem from the northeast corner of the Sargasso Sea while those arriving in the south of the eel distribution area stem from the northwest of the Sargasso Sea (Fig. 4.7a and b).

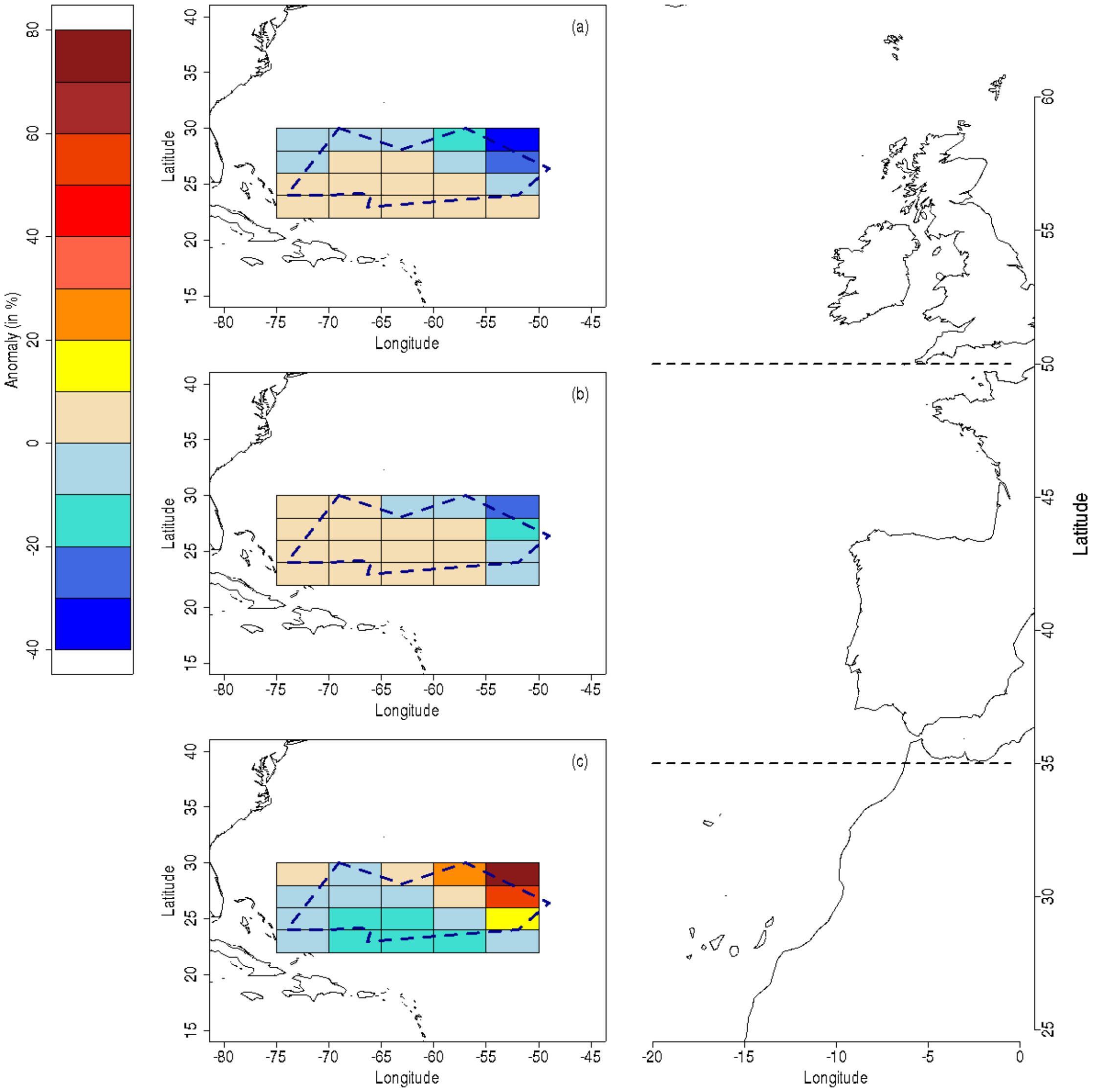

Figure 4.6: Variation rate between the number of particle that arrived in one of the three arrival bin (>50°N (a), ≤50 and >35°N (b), ≤35°N (c)) and the total number of particles arrived using the Mercator model. These anomalies of departure are analysed in 20 bins in the eel spawning area. The European eel spawning area is charted out by a black polygon (from McCleave *et al.*, 1987).

We investigate the temporal variations of departure for the three different arrival bins (North, mid-, and Southwest Europe) when mortality is implemented in lagrangian simulations. As for the spawning location, we calculate the anomaly in the monthly distribu-

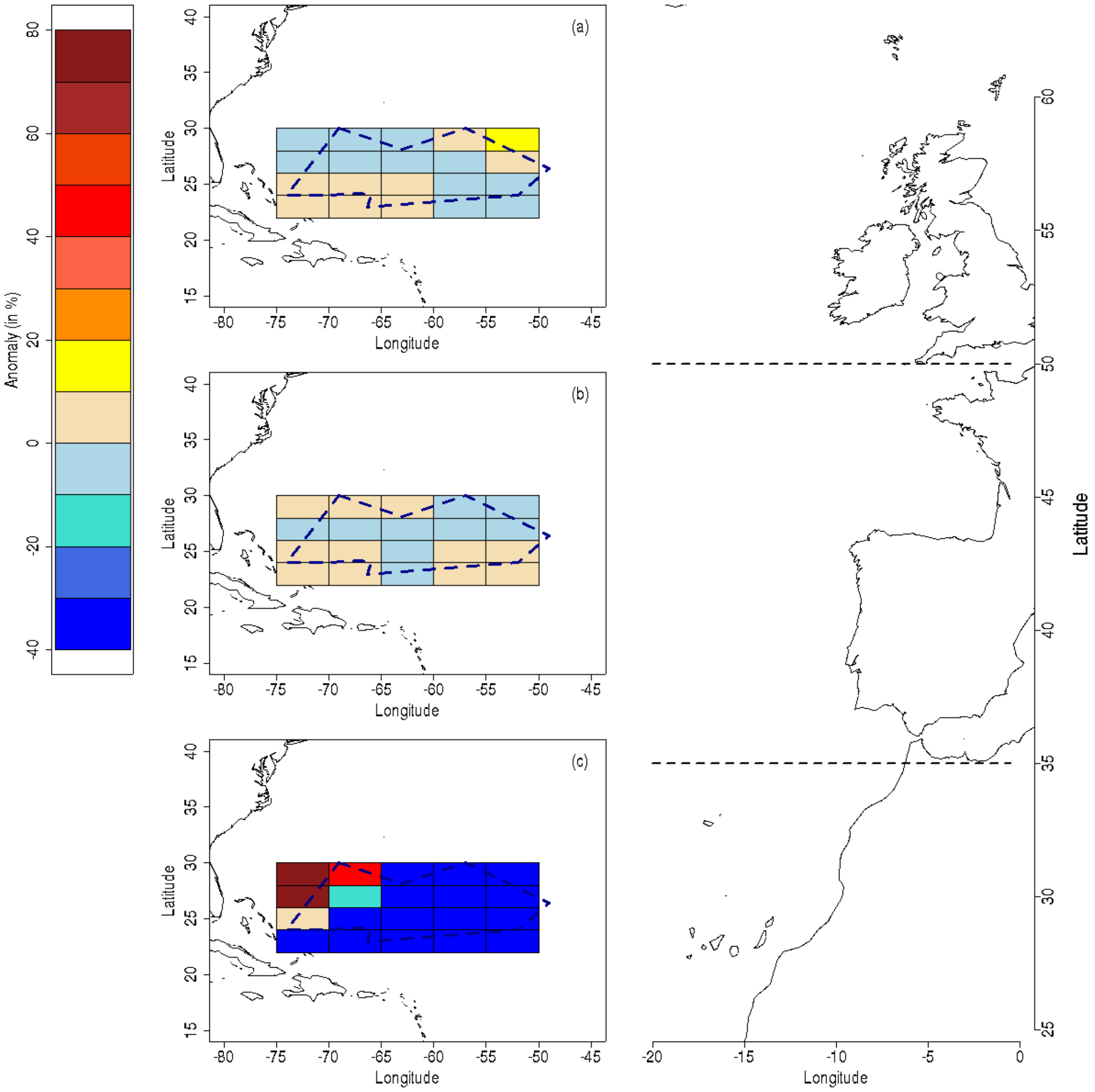

Figure 4.7: Variation rate between the number of particle that arrived in one of the three arrival bin (>50°N (a), ≤50 and >35°N (b), ≤35°N (c)) and the total number of particles arrived using the Drakkar model. These anomalies of departure are analysed in 20 bins in the eel spawning area. The European eel spawning area is charted out by a black polygon (from McCleave *et al.*, 1987).

tion of departure for the three bins. Departure month distributions differs for the 3 arrival bins (Fig. 4.8 for the Drakkar model and Fig. 4.8 for the Mercator model). Regarding the Mercator model, particles arriving north of the eel distribution mainly start during the second half of the year as well as those arriving in the mid-latitude (Fig.4.8b, d). By contrast, particles arriving south of the distribution area mainly start during the first semester of the year. Similar patterns are found when using the Drakkar model, except the monthly distribution of particles arriving north of the eel distribution, which exhibits a earlier peak in July.

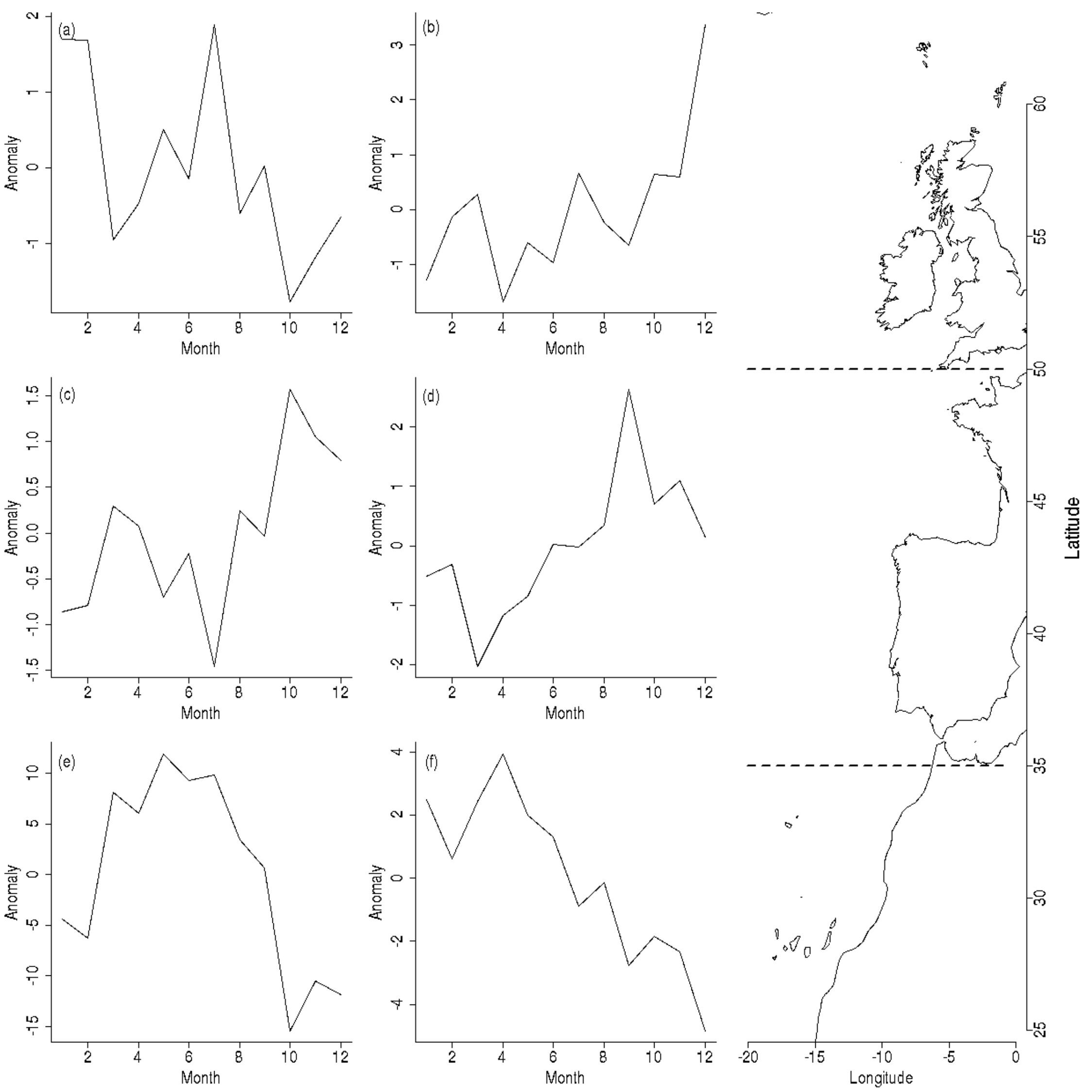

Figure 4.8: Anomaly (in%) of departure months of larvae successfully crossing the crossing the 20°W meridian at the three latitude bins within 5 years after being released within the eel spawning area model with implementation of a mortality of 3.2 per year. (a), (b), and (c): Drakkar model, and (b), (d), and (f): Mercator model. The maps on the right hand side shows the location of the latitude bins defining the distribution and is drawn up until the 20°W where particles are counted. Anomaly are not standardized and scales differ for each distribution.

4.3.3 Temperature histories of simulated particles are consistent with otolith in the wild

We compare results of lagrangian simulations to information provided by otoliths. Lagrangian simulation outputs enable us to reconstruct the temperature history of particles. We subdivided the arrival latitudes in 6 bins that fit with areas investigated by otolith study, i. e. from Sweden to Morocco, and for each bin, we calculate the mean temperature over the particle trajectories. Results were neither sensitive to the mortality hypothesis ($M = 0$ or $M = 3.2$) nor to ocean model configurations (Drakkar or Mercator) and behaviours. Only results of simulations that account for mortality with the Drakkar at fixed depth are represented. The boxplot of the temperature exhibits an decreasing trend with latitudes. The higher the latitude, the lower the temperature undergone during migration (Fig. 4.9a). Isotopic signatures of $\delta^{18}O$ measured in different estuaries in Europe and North Africa revealed a spatial gradient with a higher ratio in higher latitudes (Fig. 4.9b; de Casamajor *et al.*, 2002). As the $\delta^{18}O$ ratio is an indicator of temperature that larvae have undergone, it indicates that larvae arriving in the northern latitudes have a life history impressed by lower temperatures than those arriving in the southern latitudes.

However, these mean temperatures could be biased if particles use the same pathway during the first part of their drift (i. e. the Gulf Stream) but separate just at the end of their trajectory before crossing the 20°W. Fig. 4.10 shows the mean temperature for three arrival bins but at different longitudes along trajectories for the Mercator model. The temperature gradient observed for the latitude bins is found all over the trajectory of particles. As soon as they leave the Sargasso Sea (longitude greater than 40°W), the mean temperature is significantly different between arrival latitude bins. Similar results are found for other hypotheses and the Drakkar model. These results are consistent with observations obtained from otolith studies and reinforce the idea of an early latitudinal separation of particles.

4.4 Discussion

Early observational (Schmidt, 1922) and modelling (Harden Jones, 1968; Power and McCleave, 1983; Kettle and Haines, 2006) studies hypothesized that the Gulf Stream - North Atlantic Drift was the most important vehicle for the passive larval migration from the Sargasso Sea to Europe. Our results are in agreement with these previous studies. Furthermore, in the present work, we use (*i*) a longer period to study the drift, (*ii*) higher resolution models in 3D, and (*iii*) behaviour and mortality hypotheses, which enable us to bring further insights on the understanding of eel larva transport.

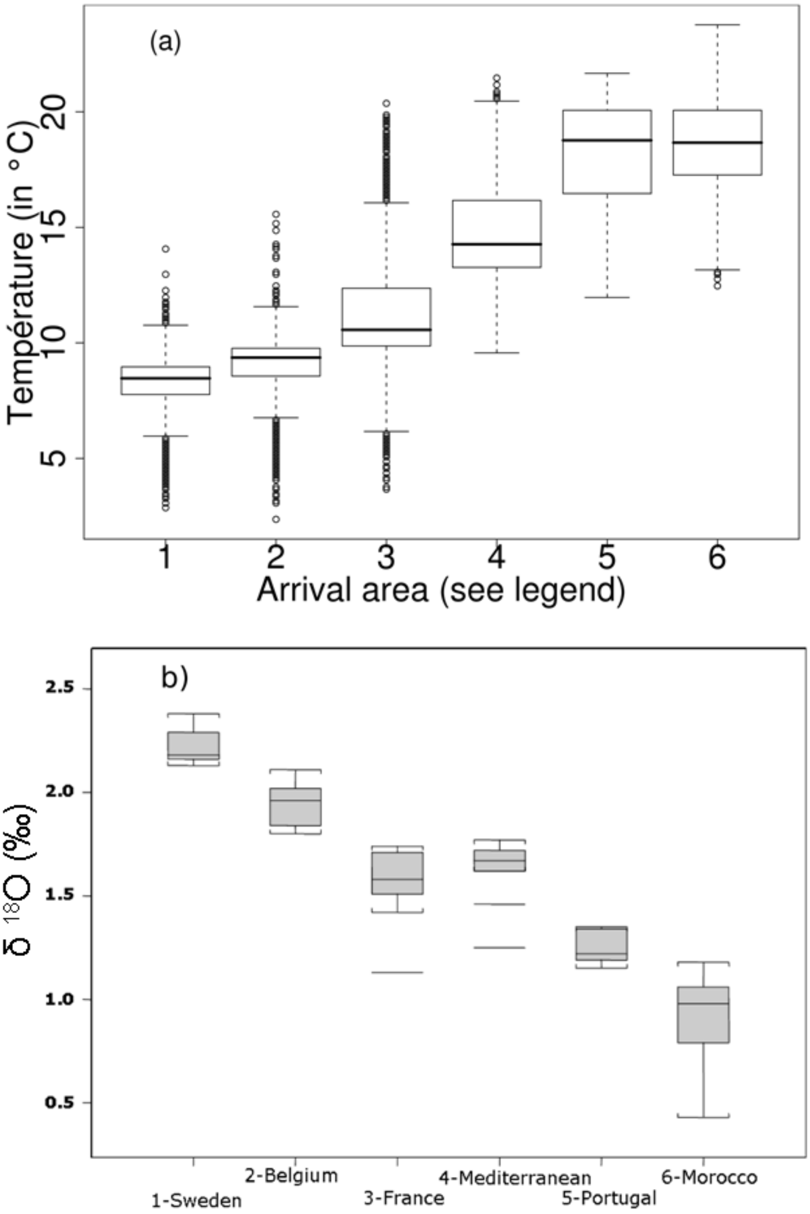

Figure 4.9: (a) Boxplot of the mean temperature over the trajectory of particles arriving at different latitude bins (1: Sweden, 2: England, 3: France, 4: Portugal, 5: Mediterannean, 6: Morocco) using the Drakkar model a mortality $M = 3.2$. Very similar results are found with Mercator model. (b) Boxplot of the isotope ratio ($\delta^{18}O$, Vienna Standard Mean Ocean Water VSMOW) of glass eel arriving at different latitude bins from Sweden to Morocco (*after* de Casamajor *et al.*, 2002).

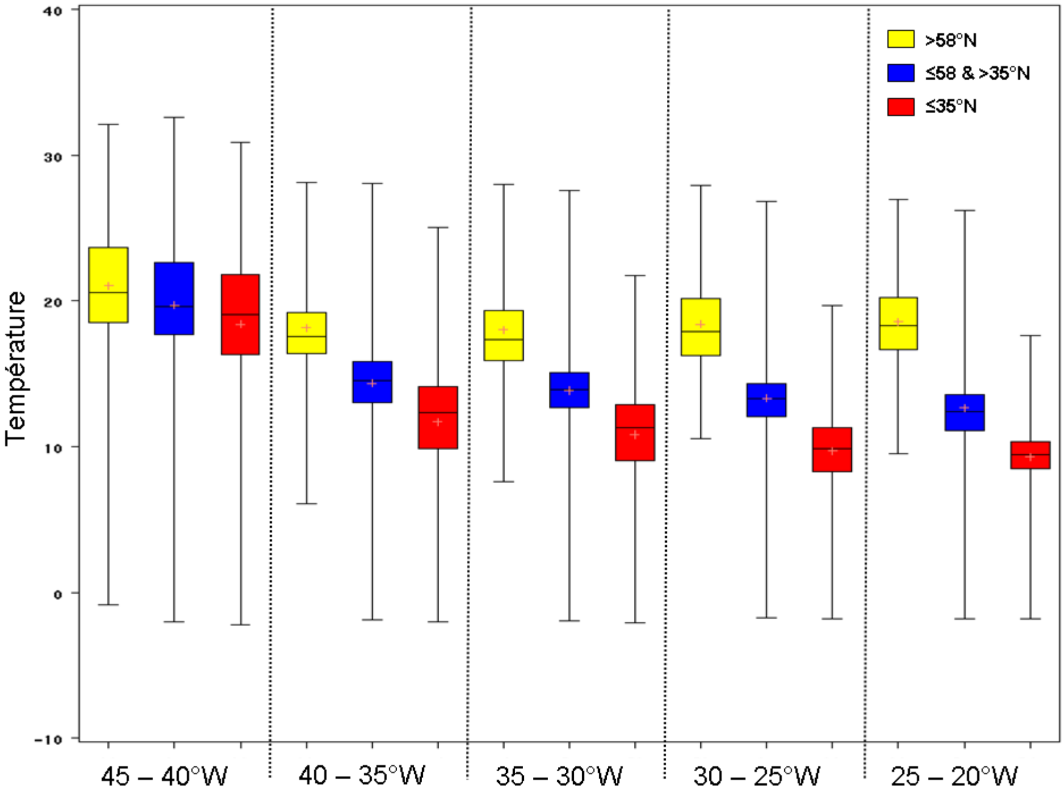

Figure 4.10: Boxplot of the mean temperature for different longitude bins over the trajectory of particles arriving at different latitude bins (colour scale) using the Mercator model with a mortality hypothesis ($M = 3.2$). Similar results were found with the Drakkar model.

4.4.1 Migration patterns are sensitive to ocean model configuration, mortality hypothesis but not to the particle behaviour

Arrival areas For both ocean models, the distribution area of arrivals is centred on Western Europe (England, France, Portugal) and the extreme latitudes of the predicted arrival area ranges between 62°N (Sweden) and 30°N (south of Morocco). However, some important differences in arrival areas are found between these 2 models. It reveals that the choice of the ocean general circulation model is crucial and special attention should be given to physical features before using lagrangian simulation.

Lagrangian simulations using the Mercator model exhibit a different proportion of arrivals along this distribution with an equivalent proportion arriving within Western European and Moroccan latitudes. By contrast, simulations using Drakkar have a weak number of particles arriving at Morocco. Active (vertical diurnal migration and fastest current choice) behaviours implemented in lagrangian simulations using the Drakkar model increase the proportion of arrivals at Morocco latitudes. The mortality hypothesis strongly reduces this proportion because migration durations of these trajectories are long. These contrasted results may arise from the fact that the Drakkar model does not assimilate data as opposed to the Mercator model. The Drakkar model is also known for its weak representation of the Azores Current (see Annexe A). Comparing two different resolutions of ocean general circulation model (0.1° and 0.28°), Smith *et al.* (2000) showed that the Azores Current is weakly represented when using lower resolution model (0.28°) but is clearly visible with a 0.1° resolution model that fits with observations. The Azores Current stems from the split of the Gulf Stream into the North Atlantic Current and into a broader flow to the south, some of which retroflects to the west as part of the recirculation south of the Gulf Stream, and the remainder turns eastward to become part of the Azores Current. The mesh grid of the ocean model has to be thin enough to discern it, otherwise this current will be weak and meanders and eddy kinetic energy will not be reproduced (see Annexe A). This is the case for the Drakkar model (0.25° resolution). In the Mercator model, the representation of the Azores current is forced by data assimilation (altimetry data). The same model without data assimilation (so-called $M069$) have the same problem as Drakkar.

Departure timing With no mortality, both models predict a fairly uniform monthly distribution of departure with a slight increase of the proportion at the end of the year (Fig. 4.4). It does not correspond to observations of the spawning period of the European eel that mainly occurs from March to June (e. g. McCleave *et al.*, 1987). According to simulation results, a March-June period for larva departure does not appear to minimize the migration duration or success. When applying mortality, the monthly distribution is not uniform and a main peak occurs from April to June with the Drakkar model and at the beginning of the year until June for the Mercator model, which fits with previous observations. Both models predict an increase of successful arrivals when starting at the end of the year. This monthly variability may be explained by the variability of the Antilles current that flows northward east of the Antilles and joins the Florida Current past the outer Bahamas. This current is dominated by short term fluctuations that may have an influence on the ability for larvae to reach the Gulf Stream. Its waters are concentrated into a strong northward jet about 80-100km wide centred at 400 m (Lee *et al.*, 1996). Moorings indicate that the Antilles current is an intensified western boundary current with mean transports of 3.2 ± 7.6 Sv northwards in the upper 800 m. Lee *et al.* (1996) found that it is not a continuous flow along the Bahamas and Antilles island chain. This conclusion is supported by the hydrographic study of Gunn and Watt (1982) who found that the Antilles current appeared more as an eddy field along the Bahamas-Antilles arc rather than as a continuous jet. A numerical model predicts that the Antilles Current would have an annual variability of around 10 Sv (Anderson and Corry, 1985).

Departure timing for different arrival areas Monthly departure distributions are different between arrival areas. For southern arrivals, the departure timing seems to be earlier in the year than northern and mid-latitude arrivals, whichever ocean model was used (Fig. 4.8). However, the patterns of monthly distribution for northern and mid-latitudes arrivals do not fit with current knowledge about European eel spawning season. Since we released particles every 15 days all throughout years, lagrangian simulations do not account for eel ecology that induce a range of month departure ranging between March and June (McCleave *et al.*, 1987). Reducing the period of release to the first part of the year may have enabled us to dissociate these patterns of departure timing.

Our results highlight that the mortality hypothesis is crucial when using lagrangian simulations. It has a strong influence and modifies the general monthly distribution of departure that matches with observations of the European eel spawning period (McCleave *et al.*, 1987). Moreover, Chap. 2 showed the necessity to account for mortality in the calculation of the migration duration. However, we found that mortality hypothesis has a weak impact on eel larva migration patterns, i. e. routes, departure and arrival areas. Further studies could focus on different mortality rates depending on the temperature where larvae drift since higher temperatures may induce higher mortality rates. In addition, different mortality hypotheses could be implemented such as decreasing mortality with time.

The influence of active behaviours such as vertical migration and fastest current choice is not as clear as the influence of mortality. Chap. 2 and 3 showed the influence of these behaviours on migration duration. Regarding the migration patterns, behaviours modify arrival areas by reinforcing the extreme latitudes of the arrival distribution. It was, however, difficult to quantify their impact on the departure dates and locations since the number of particles used was lower and no conclusion could be drawn with enough reliability.

4.4.2 Spawning locations and timing to maintain the population structure?

Spawning locations have a strong impact on arrival areas. Particles that cross the 20°W mainly start from the Western Sargasso Sea (Fig. 4.5). This is mainly due to the proximity of the Gulf Stream. The tiniest larvae found in that area are also located in the Western part of the Sargassos (see Fig. 2 *in* McCleave *et al.*, 1987). Results showed different patterns of departure areas depending on the latitude bin of arrivals. A north-south line seems to divide the eel spawning area: the southern part of the Sargassos appears to be the main departure area. It is consistent with results of Kleckner and McCleave (1988) that found a northern limit of spawning by Atlantic eels in the Sargasso Sea in relation to thermal fronts.

Nevertheless, the two ocean general circulation models do not predict the same patterns. For instance, lagrangian simulations using the Mercator model predict that particles arriving at the southern part of the eel distribution area (Morocco) mainly stem from the northeast corner of the eel spawning area. It is noteworthy that when using their model with data assimilation, Kettle and Haines (2006) found the same pattern of departure areas than the Mercator model. Conversely, when using the Drakkar model, inverse results were found: particles arriving close to the Moroccan shelves mainly stem from the northwest corner of the Sargasso Sea. These difference may arise from the weak representation of the Azores Current by the Drakkar model as it was the case for the distribution area of arrivals (see paragraph 1 of section 4.4.1). Because the Azores Current is weakly represented, a high proportion of particles reach the Morocco shelves using the Gulf Stream and North Atlantic Current and therefore start from the northwest corner of the eel spawning area.

Kettle and Haines (2006) suggest the possibility of a population selection process acting on the basis of spawning location within the Sargasso Sea. We confirm these results but also highlight the sensitivity of the results to the model configuration. The spatial repartition is combined with temporal variations and suggests possible multiple spawning areas and periods. Migrating silver eel do not have the same distance to cover in order to reach its spawning grounds and it is likely to induce a temporal differentiation during mating. Intuitively, one would say that eels from Morocco would spawn earlier than Norwegian ones since the autumnal period is the main departure period for all European silver eels with only a slight influence of the geographical area (Bertin, 1956). Kleckner and McCleave (1988) showed that eel spawning location may be determined by the position of the isotherm 22.5°C. As the position of this isotherm fluctuates during the year, both positions and timing of spawning could be different for mature eel. Here we demonstrate these fluctuations could have a strong impact on eel arrival distribution even with a simple advection model.

Differences in arrival timing of silver eels (and therefore position of isotherm 22.5°C) related to the distance they have to cover would lead to different spawning locations. It would influence subsequent arrival distribution of their larvae and fit with Wirth and Bernatchez (2003) results. Wirth and Bernatchez (2001) analysed seven microsatellite loci among 13 samples (611 glass eels) from the North Atlantic, the Baltic Sea and the Mediterranean Sea basins and found that there is a spatial genetic differentiation. They suggest a non-random mating and restricted gene flow among eels from different sampled locations, which consequently refute the hypothesis of panmixia. This spatial genetic pattern found by Wirth and Bernatchez (2001) could be explained by the spatial and temporal separation of spawning in the Sargasso Sea. However, these routes are not fixed and random pathways of eel larvae are unavoidable over such distance in the North Atlantic Ocean. Kettle and Haines (2006) demonstrated that each arrival bin is a combination of pre-determined arrivals induced by the spawning location and also random arrivals from particles that "lost their way". Arrivals of eel larvae are therefore a combination of particles originally from specific spawning areas and dispersal in the Atlantic Ocean. Temporally, it induces gradual arrivals with genetically different eel larvae: over the arrival season a continuous flux of random particles reach continental habitat and a wave of particles that are determined by specific spawning locations and timing. These patterns would induce a high temporal genetic variability. Maes *et al.* (2006) provide evidence for this temporal genetic differentiation and found that it is higher than spatial genetic differentiation. To test this hypothesis, it would be interesting to analyse the genetic variability within an arrival season and in an arrival area located at an extreme position of the eel distribution area (Morocco or Norway). If genetic variability is higher at the beginning and at the end of the season than during the peak, it could be a clue that leans towards this hypothesis.

This general hypothetic pattern may be noised by the natural variability of duration of silver eel backward migration and oceanic mixing of eel larvae. The former arises from the different migration durations of silver eel stemming from the same area. It induces mating between eels from different sub-populations. The latter is induced by eddies and current that mix eel larvae belonging to different sub-populations.

4.4.3 Temperature histories of simulated particles are consistent with microchemistry of glass eel otolith

The use of tracers such as temperature in lagrangian simulations enables us to reconstruct life histories of particles released in the eel spawning area and to compare results to information given by the analyses of otolith isotopic ratio $\delta^{18}O$. This ratio exhibits a decrease from Northern Europe to Northern Africa (Fig. 4.9b). It indicates that life histories were marked by lower temperature over the eel larva migration when arriving in the north of the distribution area and conversely. The same spatial gradient of temperature histories is found using lagrangian simulations (Fig. 4.9a) and along trajectories (Fig. 4.10).

We confirm that eel larvae take different routes to reach different areas and that the separation is determined early in the life history of eel larvae. Lagrangian simulations show that this separation can be induced only by physical features of the ocean and does not necessitate an active behaviour of eel larvae. Since it is possible to measure the isotopic signature along transects in otolith, an interesting perspective could be to reconstruct the time-series of the isotopic ratio and compare them to the time-series of temperature undergone by particles.

4.4.4 Implication in eel management: eel population may not be entirely "open"

Results show that the eel population may not be fully "open" as defined in the introduction. The existence of sub-population and non-panmixia of the European eel may have strong implications in European eel management and current decisions to restock eel in Northern European countries. Northern European silver eels may reproduce at different timing and locations than others. First, the expected results of enhancing global stock would be inefficient since it may only enhance Northern European stocks. Second, if oceanic and environmental conditions are currently less favourable for their offspring, this management decision would not enhance the global stock as expected. Conversely, removing glass eels from Western Europe to restock Northern European countries would decrease the spawner stock able to mate in the Sargasso Sea.

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Conclusion - Partie I

La synthèse bibliographique des connaissances sur la vie océanique des jeunes stades d'Anguille européenne a mis en évidence les incertitudes existant autour des estimations de la durée de migration des larves d'Anguille. Suivant les méthodes d'analyse utilisées, les estimations varient de 6 mois (analyse de la microstructure de l'otolithe) à 2 ans (analyse de cohortes et premières simulations lagrangiennes). Les estimations donnent une durée de migration courte et suggèrent une nage active des larves tandis que celles supérieures à deux ans proposent une dérive par les courants.

La difficulté d'observer la migration des leptocéphales nous a conduit à adopter une approche de modélisation lagrangienne de la dérive des larves. Pour approfondir l'analyse de cette migration océanique, deux modèles de circulation hydrodynamique de l'Atlantique Nord sont utilisés (Drakkar et Mercator). Trois hypothèses crédibles de comportement des larves dans l'océan ont été introduites dans les simulations : une dérive à profondeur fixe, une migration verticale nycthémérale ou le choix des courants les plus rapides à chaque pas de temps.

Ces différentes simulations nous ont tout d'abord permis de définir une durée minimale de dérive passive du lieu de reproduction des anguilles, la mer des Sargasses, aux côtes européennes. Parmi les trois hypothèses de comportement, la dérive à profondeur fixe donne les dérives les plus rapides et montre un temps minimum de 10 mois et 19 jours pour réaliser une migration de 8 447 km de la mer des Sargasses à l'approche du plateau continental européen (20°W). Pour parcourir la même distance en 6 mois (estimation de la durée de migration par l'analyse de la microstructure des otolithes), les leptocéphales devraient nager à $24.1\,\mathrm{cm{\cdot}s^{-1}}$ le long de cette trajectoire, soit 3.4 fois la longueur de leur corps par seconde. Une nage aussi soutenue sur plus de 8 000 km demande une dépense d'énergie que l'océan ouvert ne paraît pas capable d'alimenter. Par ailleurs, des relations sont mises en évidence entre le transport océanique et (*i*) le succès de la dérive et (*ii*) les temps de migration. Plus l'intensité du transport océanique est grande, plus le succès de la migration est important et la durée de migration courte. Les phases de transport intense depuis les vingt dernières années ne correspondent pourtant pas au recrutement faible observé sur cette même période. Il est donc peu probable que la chute récente du recrutement soit liée à une modification brutale des conditions océaniques.

Afin d'estimer une durée moyenne de migration réaliste, une hypothèse biologique de mortalité des larves est implémentée à nos simulations de dérive en se basant sur une hypothèse de population à l'équilibre tenant compte des autres sources de mortalité au cours du cycle de vie. Quelles que soient les hypothèses comportementales (dérive à profondeur fixe, migration verticale ou choix du courant le plus rapide), la durée moyenne de dérive des larves obtenue par cette approche est de 22 mois. Ces simulations suggèrent une migration longue mais aussi une survie élevée par rapport aux autres larves de poissons : 3 larves pour mille lors de la migration trans-océanique. Par ailleurs, lorsque la mortalité larvaire est prise en compte, la variabilité interannuelle du transport océanique ne modifie pas les temps moyens de migration.

Les études portant sur la génétique des larves d'Anguille suggèrent l'existence de sous-populations à l'échelle européenne et des aires et périodes de reproduction différentes dans la mer des Sargasses pour ces sous populations. Notre approche de modélisation nous permet de tester l'hypothèse d'un maintien de la structure de ces sous populations par un déterminisme des aires d'arrivée suivant les zones et dates de départ dans la mer des Sargasses. Nos simulations mettent en évidence que la position de départ des larves dans la mer des Sargasses influe sur les aires d'arrivée. L'analyse de l'influence des dates de départ révèle par ailleurs que des décalages dans les périodes de ponte entraînent aussi des différentiations spatiales de l'aire d'arrivée. Par ailleurs, nos simulations permettent de reconstruire l'histoire de température vécue par ces larves. L'analyse de ces histoires de vie montre que les routes menant aux différentes aires d'arrivée se définissent très tôt lors de la migration ; elle confirme les résultats obtenus par la microchimie de l'otolithe.

Les progrès de l'océanographie physique permettent l'utilisation des modèles physiques pour appréhender les problèmes complexes de la phase larvaire des espèces marines. La littérature croissante traitant des couplages de modèles physiques et biologiques montre l'intérêt et le potentiel de ces approches pour mieux comprendre ce stade critique qu'est la phase larvaire et ses conséquences sur le recrutement (Gallego *et al.*, 2007; Miller, 2007). L'implémentation dans les modèles physiques d'hypothèses biologiques et écologiques comme les migrations verticales (Fox *et al.*, 2006), les nages actives (Fiksen *et al.*, 2007) ou la mortalité larvaire (Hare *et al.*, 2002) permet d'appréhender des processus écologiques difficilement observables *in situ*. Dans notre cas d'étude, ce couplage physique-biologie revêt aussi un intérêt opérationnel en terme de gestion. Nous démontrons que la saisonnalité et la localisation de la reproduction favorisent certains chemins migratoires et ainsi certaines zones d'arrivée. Si la non-panmixie suggérée par les études génétiques est avérée, le maintien de sous populations d'Anguille à l'échelle européenne est rendu possible par une simple dérive passive larvaire. Une des mesures de gestions proposées par la Commission Européenne pour améliorer l'état du stock d'Anguille est le repeuplement des habitats du Nord de l'Europe en prélevant des civelles en France, en Espagne ou en Angleterre. Cette mesure a peu de chance d'être efficace pour deux raisons : (*i*) elle nécessite de prélever des civelles dans des sous-populations déjà très fragilisées et (*ii*) les conditions environnementales pourraient s'avérer être défavorables durant la phase larvaire de la sous-population du Nord.

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Deuxième partie

Effets de l'environnement sur le recrutement

Introduction - Partie II

Au vu des résultats de la partie I, les conditions de transport océanique ne semblent pas pouvoir expliquer la variabilité interannuelle du recrutement. Lorsque la mortalité est prise en compte, elles affectent peu la migration océanique des larves. D'ailleurs, les dernières décennies sont caractérisées par des transports océaniques de grande intensité dans l'Atlantique Nord. Néanmoins, c'est durant cette période que la chute du recrutement s'est amorcée. De plus, aucune modification des courants ayant pu entraîner des changements de l'aire de distribution n'est observée pendant cette période à l'échelle de l'Atlantique Nord.

Dans le cadre de l'analyse des variations du recrutement de civelle, l'incertitude sur la durée de migration pose le problème de relier des descripteurs environnementaux avec les principaux indices de recrutement dont nous disposons qui sont obtenus lors de l'arrivée sur les côtes. Les résultats de la partie I donnent un ordre de grandeur de la durée de migration et convergent vers l'idée d'une migration longue (de l'ordre de 2 ans). Nous adoptons dans cette seconde partie, une approche de modélisation statistique en utilisant ces résultats afin d'analyser les relations entre les conditions environnementales au cours de la vie larvaire (conditions trophiques en mer des Sargasses, transport océanique) et le succès du recrutement estimé à partir des abondances de civelles lors de leur arrivée en estuaire à l'issu de la migration océanique. L'objectif de cette seconde partie est de comprendre les effets de l'environnement sur les premiers stades de vie des anguilles afin d'analyser s'ils peuvent expliquer les fluctuations et tendances observées du recrutement.

Dans le Chap. 5, nous analysons les liens entre le succès du recrutement de l'Anguille européenne et la disponibilité en nourriture durant les premiers stades de vie dans la mer des Sargasses et les conditions océaniques lors de la migration des leptocéphales. Ensuite, dans le Chap. 6, nous généralisons cette analyse aux deux autres espèces de l'hémisphère nord fortement exploitées : l'Anguille américaine et japonaise.

5

Lien environnement-recrutement de l'Anguille européenne

Résumé détaillé

Dans ce chapitre, nous adoptons une approche de modélisation statistique des relations entre les conditions océaniques et trophiques durant les plus jeunes stades des larves d'Anguille européenne et le succès du recrutement. En effet, la survie lors de la traversée des larves, qui détermine en partie le recrutement, peut être influencée par les conditions physiques du milieu (transport par les courants) et/ou par la disponibilité en nourriture dans ce milieu. Les données permettant d'évaluer ce succès sont les arrivées de civelles sur les côtes.

Aucune corrélation n'est mise en évidence entre les indices de transport océanique à grande échelle (force et position du Gulf Stream) et les indices de recrutement sur les côtes européennes (Tableau 5.2 et 5.3). Les connaissances écologiques sur les larves d'Anguille sont limitées en ce qui concerne leur régime alimentaire ce qui nous a contraint à utiliser la production primaire comme un indicateur de disponibilité en nourriture. Nos analyses sur la période 1994-2004 montrent qu'une part très importante de la variabilité interannuelle d'un indice de recrutement issu de nos enquêtes auprès des pêcheurs de civelle en Loire peut être expliquée par la variabilité interannuelle de la production primaire dans la zone de reproduction, la mer des Sargasses (Fig. 5.2). Il a été démontré par ailleurs que l'augmentation de la température de l'eau entraîne une diminution de la production primaire dans les eaux chaudes comme celles de la mer des Sargasses. Cela nous permet d'utiliser la température comme un indicateur de la production primaire de cette partie de l'océan sur des séries temporelles plus longues. Les fluctuations à long terme de sept indices de recrutement de civelles le long des côtes européennes sont corrélées à celles de la température de l'eau 2,5 ans plus tôt (Fig. 5.4). De plus, la détection des principaux changements de régime de température de l'eau dans la mer des Sargasses montre un réchauffement marqué à partir de 1979. Ce changement de régime se retrouve 2,5 ans plus tard dans les séries d'indices de recrutement de civelles européennes (Fig. 5.3). Ces résultats suggèrent une forte influence de la disponibilité en nourriture lors des premiers stades de vie sur le succès du recrutement. L'altération de la production primaire, induite par le réchauffement de la température de l'eau depuis le début des années 1980, aurait affecté la survie des larves durant leurs premiers stades de vie.

Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso Sea

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Abstract European eel decline is now widely observed and involves a large number of factors such as overfishing, pollution, habitat loss, dam construction, river obstruction, parasitism and environmental changes. In the present study, we analysed the influence of environmental conditions in the Sargasso Sea and Atlantic ocean circulation on European glass eel recruitment success. Over a recent 11-year period, we showed a strong positive correlation between an original index of glass eel recruitment and primary production in eel spawning area. Moreover, primary production was negatively correlated with temperature in the Sargasso Sea. Therefore, we used sea temperature as an inverse proxy of marine production. A close negative relationship has been found over the last four decades between long-term fluctuations in recruitment and in sea temperature. These findings were reinforced by the detection of a regime shift in sea temperature that preceded the start of the decline in glass eel recruitment in the early 1980s. By contrast, variations in integrative indices measuring ocean circulation, i.e. latitude and strength of the Gulf Stream, did not seem to explain variations in glass eel recruitment. Our results support the hypothesis of a strong bottom-up control of leptocephali survival and growth by primary production in the Sargasso Sea on short and long time-scales. We argue that sea warming in the eel spawning area since the early 1980s has modified marine production and eventually affected the survival rate of European eels at early life stages.

Keywords *Anguilla anguilla*, BATS, glass eel, bottom-up, primary production, regime shift, SST, Sargasso Sea, recruitment

5.1 Introduction

European eel recruitment (*Anguilla anguilla*) has significantly dropped since the end of the 1970s and the stock is now considered in danger (ICES, 2006). This species has been listed in the red book of endangered species in several European countries (Moriarty and Dekker, 1997; Dekker, 2003b) and its inclusion in Appendix II of the Convention on International Trade in Endangered Species of wild fauna and flora (CITES) was recently proposed (CITES, 2006). A combination of factors are invoked to explain eel stock decline, including overfishing (Dekker, 2003a), anthropogenic impacts such as pollution (Amiard-Triquet *et al.*, 1988; Gony *et al.*, 1988; Feunteun, 2002; McCleave, 2001), habitat loss (Feunteun, 2002), parasites (Aguilar *et al.*, 2005), fluctuations in current speed and ocean circulation patterns (Power and McCleave, 1983; Castonguay *et al.*, 1994; Knights, 2003) and changes in climate features (Knights, 2003). So far, none of these hypotheses has been validated (Anonymous, 2003), but all are suspected to interact and push the stock downward.

In the present analysis, we investigate whether oceanographic and trophic conditions encountered by eel larvae during their early oceanic life stages may explain the patterns of variability and the decline in glass eel recruitment over several decades.

The European eel is a catadromous fish that goes through one of the longest seaward migrations, more than 6,000 km across the Atlantic Ocean. Adults spawn in the Sargasso Sea. Leptocephali larvae, conveyed by warm currents, come from the Sargasso Sea to settle on African and European shelves, from Mauritania to Polar Circle (Schmidt, 1922). There has been a long history of ecological studies dealing with marine life stages of this species (Dekker, 1998). Evidence now exists showing that oceanic conditions affect the survival of larvae during their migration in the North Atlantic. In particular, Désaunay and Guérault (1997) showed that decreases in biometric characteristics during the oceanic phase, e. g. mean length, were parallel with a decrease in recruitment. Oceanic condition may impact the condition factor of glass eels during their ingress into European estuaries. A recent study of Bureau du Colombier *et al.* (2007) showed the importance of energy state on the glass eel capacity to colonize freshwater watersheds.

It is a challenge to investigate whether major changes observed in North Atlantic marine ecosystems (Planque and Taylor, 1998; Reid and Edwards, 1998; Beaugrand *et al.*, 2002; Drinkwater *et al.*, 2003) could be responsible for fluctuation and/or regime shifts in European glass eel recruitment. This paper investigates and tests two non-exclusive hypotheses on the process by which larvae could be affected during their development and marine migration in the North Atlantic.

Firstly, the transport of eel larvae by oceanic currents may play an important part in glass eel recruitment. Leptocephali largely depend on the drift in the current for their trans-oceanic migration. Exact migration duration is still controversial (van Ginneken and Maes, 2005) and is estimated to be comprised between 9 months and 2-3 years depending on methods used to compute it (Lecomte-Finiger, 1994; Tesch, 2003). Unfavorable currents that prolong the duration of oceanic migration, and increase time of exposure to predation are suspected to impact glass eel recruitment (Désaunay and Guérault, 1997; Knights, 2003).

Secondly, food availability during the early life stages may affect eel larvae survival. Although feeding mechanisms and sources of larvae nutrition are still largely debated (Otake *et al.*, 1993; Pfeiler, 1999; Bishop and Torres, 2001), feeding is critical for survival and development of small leptocephali after hatching. Starvation and low prey availability largely affect larvae survival (Cushing, 1995; Werner *et al.*, 1997; Knights, 2003).

Assessing the relative part of these two processes, i.e. transport and food availability, in the variability of glass eel recruitment is of primary importance to improve our knowledge on eel ecology and for the management of this species. To this aim, we examined the relationships between glass eel recruitment indices and different environmental descriptors related to transport and to food availability in the Sargasso Sea. Correlations between recruitment and environmental signals were investigated on two different time-scales, i.e. short-term interannual variability and long-term fluctuations. In particular, we addressed the following questions: (1) Are the recruitment time-series related to physical indices of currents strength and latitude? (2) Can the interannual fluctuations in recruitment of European eel be explained by fluctuations in marine production in the Sargasso Sea? (3) Could long-term changes in food availability in the Sargasso Sea explain the recent decline in eel recruitment?

5.2 Materials and Methods

5.2.1 Recruitment data

Two recruitment indices were used to examine short and long-term response to marine environment. First, for long-term fluctuations analysis and detection of regime shifts, we used the seven longest time-series of glass eel recruitment available from ICES Working Group on Eel (ICES, 2006), i.e. Ems in Germany, Den Oever and IJmuiden in the Netherlands, IJzer in Belgium, Loire and Vilaine in France and Nalon in Spain (Fig. 5.1, Table 5.1). All time-series were standardized (divided by their mean over the period) to define a glass eel recruitment index. All European time-series exhibit similar long-term fluctuations (Anonymous, 2003). Despite their interest for survey at European scale, these data may suffer from heterogeneity (Dekker, 2004). The first four time-series are derived from scientific surveys while the last three are assessed by fishery-dependent surveys (see ICES, 2006). Data suffer from a certain lack of reliability because of sampling discrepancies. Thus, the decline in European eel population shown by these series may be underestimated due to difficulties in catch data collection prior the 1970s. These indices were only used to describe the general pattern and low frequency variations of European eel recruitment over the last decades but are not fully appropriate to describe recruitment interannual variability.

To investigate short-term interannual variability in glass eel recruitment, we used another original homogeneous time-series of eel recruitment derived from a precise survey of the mean annual catch of glass eel by few fishermen in the Loire river (France) between 1994 and 2004. The series was computed from the financial reports of a French glass eel trader (i.e. 3 618 daily catches of 5 fishermen over the period). This company has a long history in glass eel business and in scientific cooperation (e. g. Elie, 1979; Castelnaud *et al.*, 1994) and therefore provides reliable glass eel catch data. We selected fishermen who can be qualified as compliant and regular. “Compliant” includes fishermen who keep on fishing more than five hours per sea trip. “Regular” means that they go fishing each opening day of the season. The mean number of fishing days per fisherman per season was 107.7 with a standard deviation of 11.2 for a mean fishing season of 136 days. Our sample of fishermen fished during 79.2 % of authorized time. We averaged catches per year because monthly abundance variability depends on local factors (temperature, winds, rainfall, turbidity and flood) that influence catchability and upstream migration on a very short time-scale

Table 5.1: Summary of biological and environmental data. Gulf Stream Index (GSI), Transport Index (TI), Primary Production (PP), Temperature (T), and European sampling sites. Bermuda Atlantic Time-series Study website is http://bats.bbsr.edu.

Data	Period	Source	Proxy for:
GSI	1969-2005	scientific (Taylor and Stephens, 1998)	Latitude of Gulf Stream
TI	1958-2005	scientific (Curry and McCartney, 2001)	Intensity of Gulf Stream
PP	1988-2002	scientific (BATS website)	Eel larvae food
T	1958-2005	scientific (BATS website)	Primary Production
Ems	1960-1999	scientific (ICES, 2006)	
Den Oever	1960-2005	scientific (ICES, 2006)	
IJmuiden	1969-2005	scientific (ICES, 2006)	
IJzer	1964-2005	scientific (ICES, 2006))	
Loire	1960-2005	catch data (ICES, 2006)	
Vilaine	1971-2005	catch data (ICES, 2006)	
Nalon	1960-2005	catch data (ICES, 2006)	
Loire	1994-2004	catch data (French trader, pers. comm.)	

(White and Knights, 1997; de Casamajor *et al.*, 1999; Prouzet, 2003; Tesch, 2003; Bouvet *et al.*, 2006). Mean catches of glass eel per fisherman per year were then considered as a reliable recruitment index since fishing methods and effort remained constant during the period and since no change in fishing areas was observed.

5.2.2 Environmental data

5.2.2.1 Transport Index and Gulf Stream index

Correlation between recruitment data and (*i*) the Transport Index (TI) or (*ii*) the Gulf Stream Index (GSI) was first investigated to test the hypothesis that recruitment variability was driven by ocean currents variability. TI estimates the strength of the baroclinic gyre circulation in the North Atlantic, i.e. the strength of the Gulf Stream and North Atlantic Current system. It is calculated from the difference of the potential energy

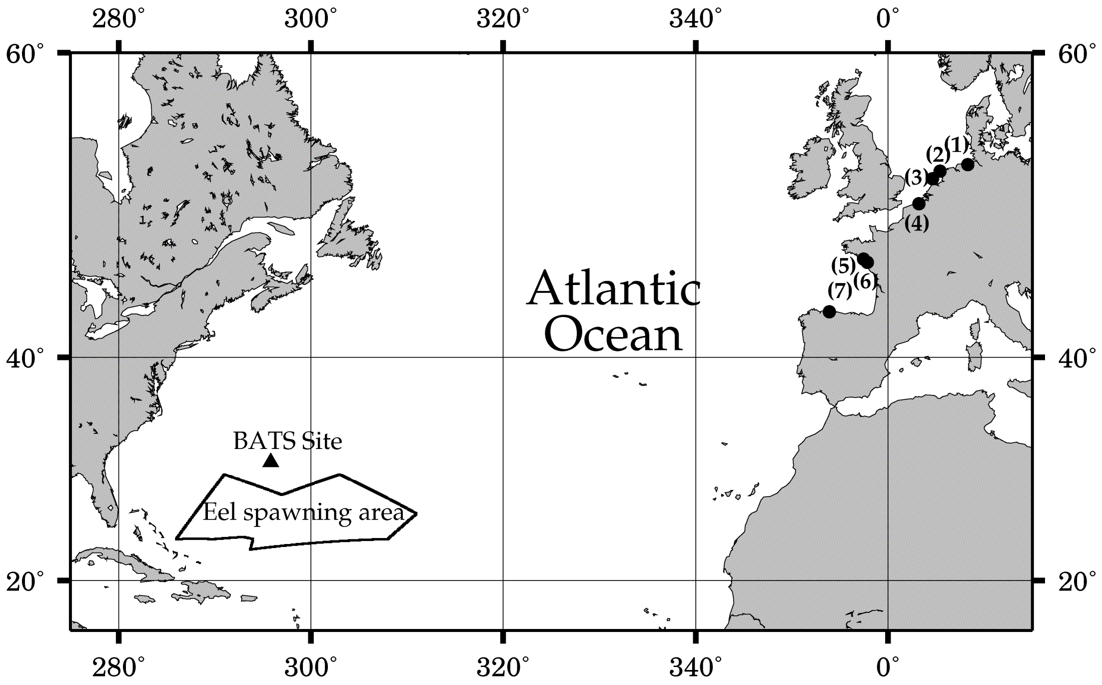

Figure 5.1: Location of the European eel spawning area (polygon; from McCleave, 1993), Bermuda Atlantic Time-series Study sampling site (black triangle, 32°50N, 64°10W) and sampling sites used to calculate recruitment indices (black dot). (1) Ems, (2) Den Oever, (3) IJmuiden, (4) IJzer, (5) Vilaine, (6) Loire, (7) Nalon.

anomalies (PEA) between Bermuda and Labrador Basin. Data from 1954 to 2005 were extracted from the website of the Ocean Observations Panel for Climate (OOPC) and with courtesy of Ruth Curry (`http://ioc3.unesco.org/oopc/state_of_the_ocean/sub/berm_lab_trans.php`).

GSI is a measure of the latitude of the Gulf Stream and is established on monthly charts of its north wall, derived from aircraft, satellite and surface observations (Taylor and Stephens, 1998). Data from 1966 to 2005 were extracted from the website `http://web.pml.ac.uk/gulfstream/data.htm`.

5.2.2.2 Primary production

We propose to use primary production (PP) as an indicator of eel larvae food. This is sustained by general considerations following Ware and Thomson (2005) and based on the available knowledge about leptocephali diet. Two potential sources of nutrition were indeed proposed for larvae: Dissolved Organic Matter (DOM) and Particulate Organic Matter (POM) in the form of zooplankton fecal pellets and larvacean houses (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler, 1999). PP was considered as a good proxy for leptocephali food as DuRand *et al.* (2001) described a strong linear relationship between phytoplankton and POM in the Sargasso Sea. Food availability in the Sargasso Sea can be critical in early life stages to determine larvae capacity to rapidly reach the size that allows them to survive during the long drift into North Atlantic currents (Knights, 2003). Eel larvae are qualified as type II larvae based upon their unique developmental strategy that allows them to increase rapidly in size while devoting the majority of their energy to metabolism, i.e. nutrition and locomotion, and not to mass increment as in most larval fish. After a post-hatched period in which the yolk-sac is resorbed, the larval fish shows a dramatic increase in size during which up to 40 % of the leptocephali maximum length is attained while only 5-7 % of the maximum mass is accumulated (Bishop and Torres, 2001).

We used data provided by the Bermuda Biological Station for Research which has been carrying out *in situ* sampling of PP by filtering the water column during cruises since 1988. PP data associated with details about methods are available on the Bermuda Biological Station website (`http://bats.bbsr.edu`). A set of 8 standard depths on 20 m intervals from 0 to 140 m is sampled in the area of eel spawning (Southeast of Bermuda, Fig. 5.1). The Bermuda Atlantic Time-series Study (BATS) station is located in the west central Sargasso Sea and can be considered as a representative of condition affecting leptocephali as they migrate and begin feeding in the entire Sargasso Sea (Nelson *et al.*, 2004). Different samplings of leptocephali in this region revealed a preferred depth of 160 m during daylight and of 60 m at night (Schoth and Tesch, 1982, 1984; Castonguay and McCleave, 1987). Most of the PP is produced over a 9-month period from November to July. PP was integrated over this period in order to derive an average estimate of the annual production in the Sargasso Sea. Averaging over this period also accounts for the time of transfer of PP in the first levels of the food chain. The hatching period that spans between March and June is included within these 9 months (McCleave, 1993; Wang and Tzeng, 2000). Using these BATS data, we calculated PP time-series over the period 1989-2002.

5.2.2.3 Sea temperature as a proxy of primary production

In order to investigate long-term regime shift and variations, temperature in the Sargasso Sea was used as an inverse proxy of PP. Indeed, plankton communities dynamics are driven by their physical environment and it has been shown that temperature can be a useful indicator of nutrient availability in thermally stratified waters (Bouman *et al.*, 2003; Behrenfeld *et al.*, 2006; Doney, 2006). The marine production increases with Sea Surface Temperature (SST) in cooler waters of the Northeast Atlantic, but it decreases as SST increases in warmer waters (Richardson and Schoeman, 2004). National Aeronautics and Space Administration (NASA) and McGillicuddy *et al.* (2001) confirmed this inverse relationship exists in the warm waters of the Sargasso Sea (`http://daac.gsfc.nasa.gov/oceancolor/locus/tutorial_6.shtml`). Warming inhibits indeed vertical mixing, reducing the upward nutrient supply and lowering marine production. Hence, in warm waters of the Sargasso Sea, when sea temperature increases, PP decreases.

5.2.2.4 Temperature data

Temperature in the Sargasso Sea has been monitored at Hydrostation S of the Bermuda Biological Station since 1955. Since PP was averaged over the 0-140 m layer and we considered that sea temperature impacts PP, we averaged sea temperature over the deepest layer where data were available, i.e. the 0-100 m layer which is above the thermocline. Temperature data were available on a monthly basis but were averaged per year to compute a mean annual time series.

5.2.3 Statistical models

Statistical analyses were performed in two ways: (i) First, the correlation between the recruitment and environmental time-series was assessed; (ii) Second, the existence of regime shifts in the time-series was investigated.

Recruitment was $\log_{10}$ transformed before each correlation analysis with environmental variables. Because migration duration of larvae is not clearly established and arouses controversy (van Ginneken and Maes, 2005), the correlation between recruitment and environmental time-series was systematically tested considering a time-lag of +1, +2 or +3 year(s). Thus, recruitment indices, X_t, were then correlated with environmental variable, Y_{t-d}, where $d = 1$, 2 or 3. When considering oceanic indices (TI, GSI) as the environmental variable Y_t, we analysed the correlation between recruitment X_t and $\overline{Y^*_{t-d}}$, where $\overline{Y^*_{t-d}}$ is the average over the years $t - d$ to t.

5.2.3.1 Testing time-series correlations

Procedures for statistical testing of the degree of correlation between the recruitment and environmental series must account for the autocorrelation in the time-series because it may result in an artificial increase in the statistically significance of the correlation test. Following Pyper and Peterman (1998), we used methods specifically designed to study long-term and short-term correlations in the case of auto-correlated time-series.

5.2.3.2 Testing short-term correlations

To assess correlations between interannual variations of recruitment index and environmental (TI, GSI, PP, sea temperature) time-series, we removed the autocorrelation by prewhitening the data series prior to statistical testing. The aim is to transform the original data to eliminate statistically significant autocorrelation whilst retaining the high frequency signal (Fox *et al.*, 2000). After the transformation, standard correlation tests can then be applied to the resultant series. Prewhitening of the recruitment and environmental time-series, both of initial length N, was performed by first-order differencing (Thompson and Page, 1989). The Pearson coefficients were used to test correlations between the first-order differenced recruitment and environmental time-series. The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with $(N-1)-2$ degrees of freedom (d.f.) where $(N-1)$ is the length of the first-differenced time-series.

5.2.3.3 Testing long-term correlations

To analyse long-term patterns between recruitment indices and environmental (GSI, TI, sea temperature) time-series, we first smoothed data with a 5-year moving average. Then we adjusted the d.f. in the statistical tests to compensate for autocorrelation in order to analyse low-frequency sources of covariation (Pyper and Peterman, 1998). To adjust d.f., we applied the equation proposed by Chelton (1984) and modified by Pyper and Peterman (1998):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_j r_{xx}(j).r_{yy}(j) \tag{5.1}$$

where N^* is the corrected sample size that interprets as the number of independent joint observations on the two time-series X (recruitment data) and Y (environmental data),

N is the length of the initial time-series and $r_{xx}(j)$, and $r_{yy}(j)$ are the autocorrelation of X and Y at lag j. Estimators of autocorrelation r are obtained using the Box-Jenkins' equation (Box and Jenkins, 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j} \frac{\sum_{j=1}^{N-j} (X_t - \overline{X})(X_{t-j} - \overline{X})}{\sum_{j=1}^{N} (X_t - \overline{X})^2} \tag{5.2}$$

where $\overline{X}$ is the overall mean. Pyper and Peterman (1998) tested a variety of d.f. adjustment methods and found Eq. 5.1 to be robust and unbiased compared to other methods. This method is also robust to the number of lags applied in the d.f.-reduction (Eq. 5.1). In the present analysis, we computed autocorrelations until the 9^{th} lag approximately equal to $N/5$, following Pyper and Peterman (1998). The correlation was then assessed using Pearson coefficients with d.f. correction for autocorrelation as described above (Eq. 5.1). The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with $N^* - 2$ degrees of freedom.

5.2.3.4 Regime shift detection

A sequential regime shift detection method was performed following Rodionov and Overland (2005) to detect major changes in trends of glass eel recruitment indices and sea temperature. Recruitment data were not $\log_{10}$ transformed prior to analysis to maintain a sufficient variance and make the regime shift detection more relevant. This method enables us to estimate the magnitude of the shift through a regime shift index (RSI). The algorithm has user-specified criteria, e. g. cut-off time-scale (l) that determines the minimum duration to qualify as a regime. The key concept is that there must be significant shifts in mean value relative to the within-regime variance in order to detect a new regime. In the present analysis, cut-off length (l) was set to 10 years and probability level at $p = 0.01$. We investigated, however, the sensitivity of the results to the parameters setting l to 15 and 20 years and $p = 0.05$.

5.3 Results

5.3.1 No correlation between recruitment and transport-related descriptors

On the short-term, no significant correlation was found between TI or GSI and recruitment time-series whatever the ICES data (not shown) or Loire recruitment index (Table 5.2) and whatever the time-lag (not shown). On the long-term, no significant correlation was found between TI or GSI and recruitment indices whatever the time-lag (not shown). Thus, this statistical analysis does not reveal any clear linear relationship between the position or the strength of the Gulf Stream and the leptocephali survival rate.

Table 5.2: Summary of relationships between Loire recruitment index and Gulf Stream Index (GSI), Transport Index (TI), Primary Production (PP) and Sargasso Sea Temperature (T) on short-term with a 3-year lag. N indicates the sample size, r the correlation coefficient, p the significance level and N^* the mean corrected sample size.

	N	r	p-value
GSI	11	-0.21	n.s.
TI	11	-0.57	n.s.
PP	10	0.81	<0.005
T	11	0.20	n.s.

5.3.2 A strong short-term correlation between recruitment in the Loire and PP in the Sargasso Sea

We only reported results of the relation between PP and the Loire recruitment index. Results obtained with other ICES recruitment indices were not significant or much less significant, except for the Loire index from ICES.

Recruitment index in Loire river and PP time-series exhibited a decreasing trend which was more outstanding for our recruitment index (Fig. 5.2a). Catches dropped from approximatively 700 kg per fisherman per year in 1994 to approximatively 200 kg in 2004 in the Loire river. Test for synchrony showed a significant positive correlation between Loire recruitment and the 3-year lagged time-series of PP ($r = 0.81$, $p < 0.005$; Table 5.3, Fig.

5.2b) whereas no significant correlations were found with 1 or 2-year lagged time series (not shown). High (resp. low) PP during first semester of year t was followed by a high (resp. low) recruitment index in Loire river in winter of year $t+3$.

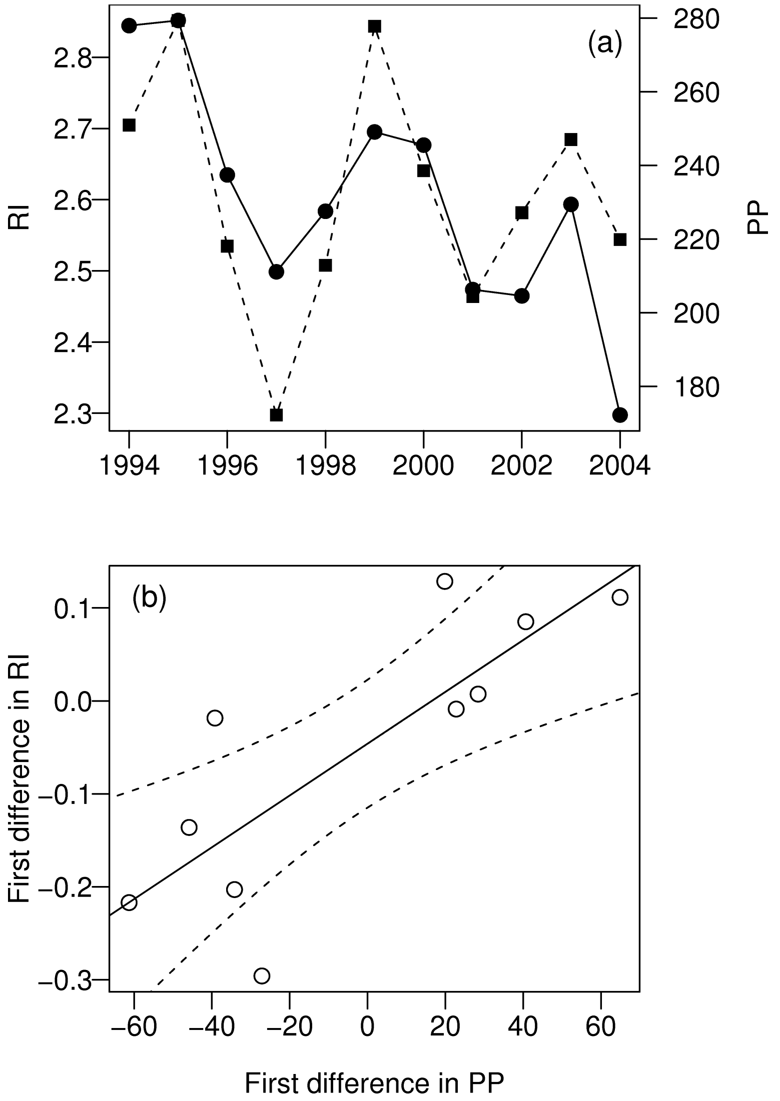

Figure 5.2: (a) Time-series of log-transformed original recruitment index (RI) (solid line with circles) from season 1994 to 2004 and integrated primary production (PP) 3-year lagged (mgC.m^{-2}; dashed line with squares) in the Sargasso Sea from 1991 to 2001 and (b) Correlation between variations in recruitment index and variations in PP lagged by 3 years expressed in first-difference form.

5.3.3 Long-term relationships between sea temperature and glass eel recruitment

Long-term variations in sea temperature were used as a proxy of PP. The negative relation between sea temperature and PP has been well established for low and mid-latitudes

(Behrenfeld *et al.*, 2006). In the Sargasso Sea, this relationship is confirmed by the significant negative relationship between monthly time-series of PP and sea temperature over the period 1989-2002 (r = -0.54, p = 0.02).

Temperature in the Sargasso Sea decreased from 1960 to the early 1970s and subsequently increased until the most recent records (Fig. 5.3). Changes in Sargasso Sea temperature resulted in a warming of the upper ocean layer (0-100 m), from less than 21.2°C in 1971 to more than 22.0°C in the 2000s, indicating strong environmental changes in the system over the last 40 years. During the colder phase, recruitment indices were high, varying around a long-term average comprised between 2 and 3, whereas it declined markedly during the warming period (after 1980) to reach a value comprised between 0 and 0.5.

Glass eel recruitment indices increased in the early 1970s to reach a peak in the beginning of the 1980s. From then on, the recruitment began to decrease. Then, glass eel recruitment indices dropped by more than 90 % in less than 25 years. A strong and significant negative relationship was found between fluctuations in sea temperature (3-year lagged) and in recruitment indices over the period 1963-2002 (Fig. 5.4). Periods of low (resp. high) sea temperature were associated with periods of high (resp. low) glass eel recruitment. Correlations were lower and less significant when using 1 and 2-year time lags between time-series (not shown).

Table 5.3: Summary of relationships between recruitment indices and Transport Index (TI) and Gulf Stream Index (GSI) on long-term with a 3-year lag. r indicates the correlation coefficient, N^* the mean corrected sample size, p the significance level with $N^* - 2$ d.f.

	Transport Index (TI)				Gulf Stream Index (GSI)			
Site	N	N^*	r	p	N	N^*	r	p
Ems	39	6.05	-0.63	0.088	29	5.17	-0.82	0.038
Den Oever	42	5.88	-0.69	>0.1	33	5.94	-0.56	>0.1
IJmuiden	33	4.98	-0.67	>0.1	33	5.90	-0.59	>0.1
IJzer	36	4.90	-0.71	0.092	33	6.00	-0.60	>0.1
Loire	42	5.26	-0.75	0.062	33	5.22	-0.69	0.091
Vilaine	31	4.77	-0.71	>0.1	31	5.15	-0.65	>0.1
Nalon	42	6.20	-0.66	0.07	33	5.92	-0.58	>0.1

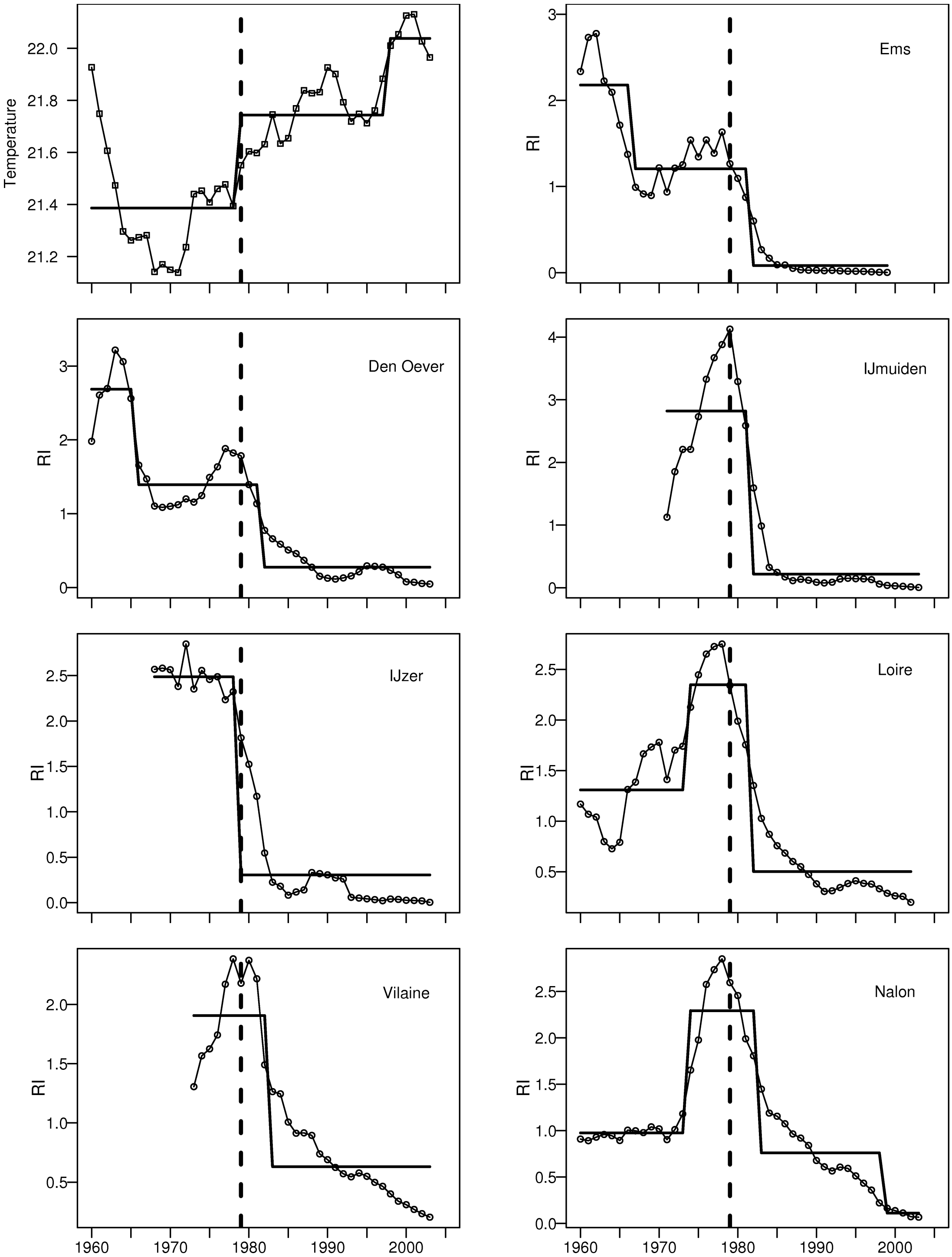

Figure 5.3: Time-series of ICES recruitment indices (5-year moving average; solid line with circles) and temperature (°C; 5-year moving average; solid line with squares) in the Sargasso Sea from 1960 to 2003. Bold lines indicate regime shift detection (Rodionov and Overland, 2005) and vertical dashed line indicates the regime shift in temperature in 1979.

5.3.4 Regime shift in glass eel recruitment indices and in sea temperature in the Sargasso Sea

The results of the regime shift detection show three main phases in the Sargasso Sea temperature, a colder phase before 1980 (mean temperature of 21.4°C), a warmer phase afterward (mean temperature of 22°C), and a third, even warmer, after 1999. The sequential regime shift detection showed a significant positive shift in temperature in 1979 ($\mathrm{RSI} = 0.98$) and a negative shift in glass eel recruitment indices in 1982 for Ems ($\mathrm{RSI} = -1.44$), Den Oever ($\mathrm{RSI} = -0.94$), IJmuiden ($\mathrm{RSI} = -1.64$) and Loire ($\mathrm{RSI} = -1.92$), in 1983 for Vilaine ($\mathrm{RSI} = -1.41$) and Nalon ($\mathrm{RSI} = -1.42$) and in 1979 for IJzer ($\mathrm{RSI} = -1.93$) (Fig. 5.3). A weaker shift occurred in 1998 for the temperature ($\mathrm{RSI} = 0.89$) but its consequences can not be detected in that analysis as recruitment time-series stopped in 2003 due to the moving average. The shift in 1979 in IJzer recruitment index could be explained by the shortness of the time-series that induced an earlier detection of the shift. Levels of recruitment have dropped again since 2001 for most European recruitment time-series (ICES, 2006) suggesting that another shift is just arising in glass eel recruitment. The main shifts described above were not sensitive to changes in the value of l and p.

5.4 Discussion

This study reinforces the hypothesis that marine production within the European eel spawning area affects its earliest life stages and subsequent glass eel recruitment on both short and long time-scales. Based on the analysis of short-term interannual variability for the most recent years (1994-2004), the negative correlation between glass eel recruitment and PP in the Sargasso Sea sustains the hypothesis that variability in glass eel recruitment may be linked to food availability and/or composition in the Sargasso Sea. As PP is negatively correlated with temperature in the Sargasso Sea (Bates, 2001; McGillicuddy *et al.*, 2001), we conjecture that the increase in temperature over the last three decades has led to a decrease in PP and hence to a significant drop in glass eel recruitment. Our findings are reinforced by the detection of a regime shift in temperature that preceded the start of the decline in glass eel recruitment in the early 1980s. By contrast, ocean

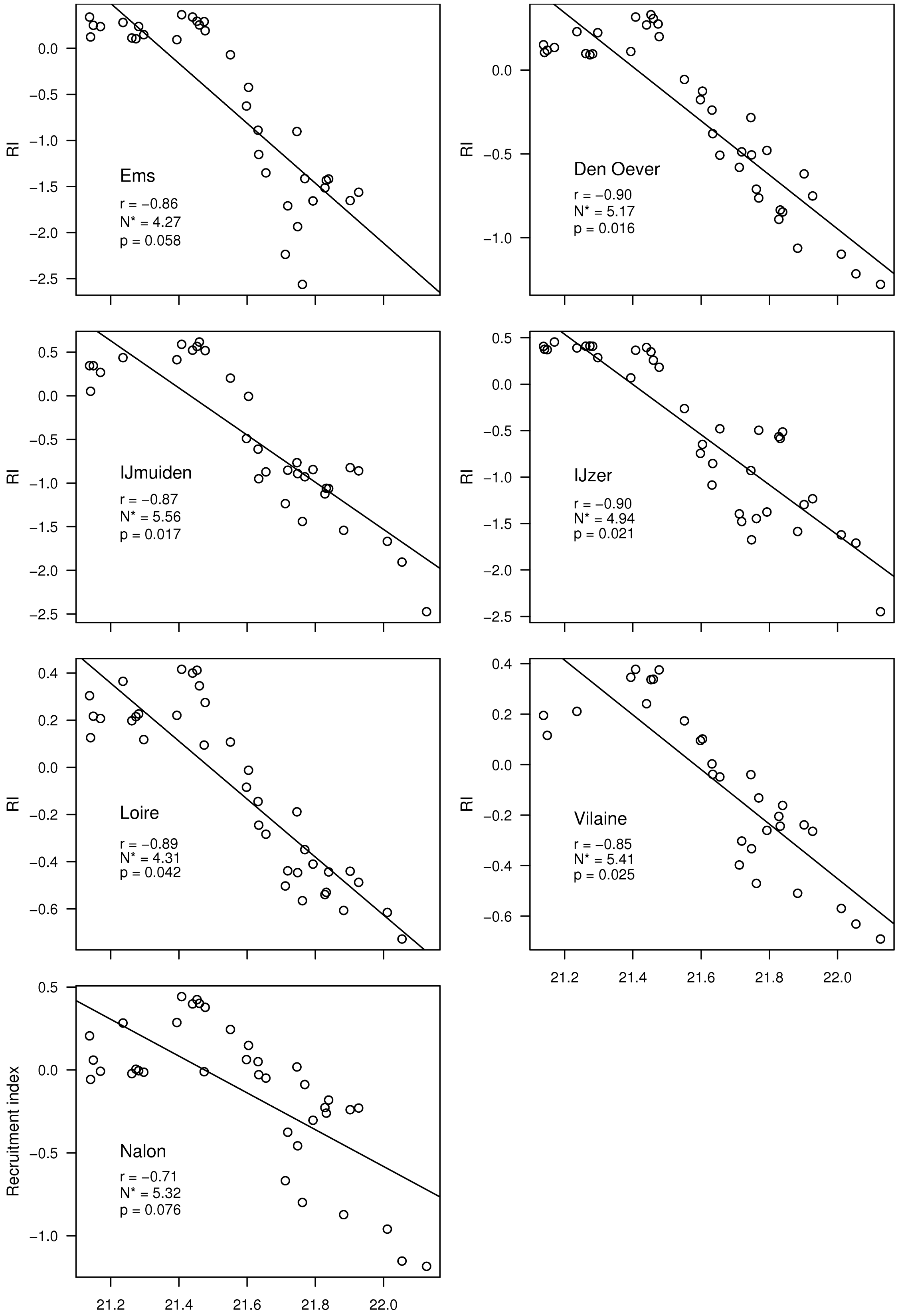

Figure 5.4: Relationships between temperature in the Sargasso Sea (°C; 5-year moving average, 3-year lagged) and the ICES recruitment indices (RI, 5-year moving average) from 1963 to 2003. *r* indicates the correlation coefficient, N^*, the number of independent joint observations, *p*, the p-value with $N^* - 2$ d.f.

circulation does not seem to be a major driver of eel larvae survival on the basis of the indices used and of linear relationships.

5.4.1 Recruitment indices

The most significant short-term correlation between recruitment and PP series was obtained using the original recruitment index series in the Loire river assessed from the French glass eel trader. This original recruitment series was particularly relevant for the analysis of interannual variability. Loire river is one of the main glass eel arrival basins in Europe. This index can be considered robust and reliable to analyse interannual variability as fishing methods, fishing wedges of fishermen, fishing date, and duration remained constant over the period 1994-2004. By contrast, other European river indices were calculated using heterogeneous data that cover different time intervals, various sources, and location (ICES, 2006) and their use to analyse interannual variations is debatable. The use of other European series produced less consistent relationships. We attribute these differences to the quality of the European series described above. However, they are of high interest for long-term analysis of recruitment fluctuations over a long period (1960-2003) and were used in several studies (e. g. Dekker, 1998; Knights, 2003).

5.4.2 Migration time

Our results contribute to the study of the migration duration of European eel larvae. Most of the significant correlations were found using a 3-year delay between recruitment and the environmental time-series. In our analysis, this time lag accounts for transatlantic migration, metamorphosis, and estuarine arrival. As PP is calculated from November to July and the fishing season is comprised between December and April, the time lag used is comprised between 2 and 3 years. The time lag of 3 years between the regime shifts in temperature and most of glass eel recruitment indices observed at the beginning of the 1980s also supports the same hypothesis about migration duration. Thus, in a context where uncertainty about migration duration between 1 and 3 years remains high, our results seem to be more consistent with a 2 to 3-year delay between hatching and glass eel recruitment. This is consistent with estimates of several authors (e. g. Schmidt, 1922; McCleave, 1993; Tesch, 2003). In particular, a migration duration longer than 2 years has been validated through Lagrangian modeling in the Atlantic ocean (Kettle and Haines, 2006, see chapter 2 and 3). Still, this hypothesis of a 2 to 3-year migration duration remains controversial since ages at recruitment back-calculated by otolithometry ranged from 7 to 15 months (Arai *et al.*, 2000; Wang and Tzeng, 2000). However, studies based on daily growth increments in glass eel otoliths have been largely criticized since it may be a period of no deposition of daily rings between hatching and migration of glass eels into estuaries (Svedäng *et al.*, 1998; Cieri and McCleave, 2000).

5.4.3 Impact of transport on glass eel recruitment success

The relationships between TI, GSI and glass eel recruitment were not clearly established. However, other studies suggest that leptocephali may be affected by oceanic features because of their long larvae oceanic phase (Knights, 2003). Recent analysis by Friedland *et al.* (2007) suggested that the influence of ocean parameters such as the shallowing of the mixed layer depth inducing a decrease in primary production, drift conditions in larval transport area, and declining trends in winds have contributed to declining recruitment as well. For instance, they show that fluctuations in Den Oever Index are related to fluctuations in North Atlantic Oscillation (NAO) which indicates recruitment may be influenced by physical and biological structure of the North Atlantic. Miller *et al.* (in prep.) suggested that the changes associated with these type of atmospheric forcing could alter the biological characteristics of the surface layer where leptocephali feed. Although NAO has been widely used to investigate response of marine ecosystems to climatic condition (e. g. Fromentin and Planque, 1996), we did not use this integrative environmental index because it does not allow direct analyses of the responses of plankton communities to their local environment as temperature does. However, large-scale atmospheric forcing by the NAO modifies winds and SST patterns that regulate mixing and stratification and hence phytoplankton abundances (Drinkwater *et al.*, 2003).

Friedland *et al.* (2007) also suggested that fluctuations in latitude of the 22.5°C isotherm which is a useful indicator of the northern limit of eel spawning area, may affect both spawning location and transport of the leptocephali out of the Sargasso Sea by increasing retention whithin the Sargasso Sea gyre. Moreover, the possibility to leave the Sargasso Sea may be altered by changes in winds in the northern Sargasso Sea, which have reduced southward Ekman transports and hence contributed to increase larval retention in the Sargasso Sea gyre. Such changes in larval retention might add up to the bottom-up control process suggested by our result and underline the various and potential combined effects of environmental changes on eel recruitment. The mysteries of oceanic life history of eel and the lack of information about eel biology and ecology (e. g. migration duration and routes, larvae diet) hinder to clear up links between eel larvae survival and these environmental changes.

Nota Bene: These results confirm those found in chap. 2 and 3 that oceanic transport have a weak impact on eel larva survival

5.4.4 Glass eel recruitment driven by environmental conditions in the Sargasso Sea

Our analysis proposed a focus on the influence of the trophic conditions in the Sargasso Sea on the subsequent recruitment of European glass eels. On the short-term, the highly significant correlation between PP and glass eel recruitment in the Loire river suggests a dynamic relationship between food availability and larvae survival rate. This indicates that a strong bottom-up control may drive the young life stage of European eel. To extend the link between PP and glass eel recruitment on a longer time-scale, we relied on the inverse relationship found between sea temperature and PP and we used variations in temperature in the Sargasso Sea as a proxy of variations in PP in that area (Bates, 2001). Sea temperature is an important manifestation of climate change and can be used as an environmental proxy associated with changes in phytoplankton community structure (Beaugrand *et al.*, 2002). Processes implied include changes in vertical mixing, changes in water mass characteristics, circulation of the subtropical gyre and distribution of mesoscale eddies (Bates, 2001). This complex response of marine production to sea temperature probably arises because temperature not only affects biota directly, but is also a proxy for other physical processes regulating the size structure, taxonomic composition, and abundance of phytoplankton communities (Li, 2002). In warmer and more stratified waters with limited nutrients, warming is likely to reduce marine production because increased heating can enhance existing stratification, thereby reducing the availability of nutrients to phytoplankton in the surface layer and leading to a microbial-dominated community (Roemmich and McGowan, 1995; Richardson and Schoeman, 2004; Behrenfeld *et al.*, 2006).

We focused on the main patterns of eel recruitment and sea temperature to investigate the synchronism of their fluctuations. The use of robust statistical test for correlation analysis accounts for autocorrelation in time-series. Using linear models allows us to point out the relationships between patterns of eel recruitment and those of sea temperature but the use of other models is beyond the scope of this paper.

The shift in sea temperature in 1979 pointed out the beginning of changes in the Sargasso Sea environment and was followed by a shift in eel recruitment detected in 1982 in most of European rivers we analysed. The drop in recruitment in northern European rivers (e. g. Göta Alv in Sweeden) was observed before that year. Our results indicate that temperature may be the main governing factor influencing eel larvae survival by decreasing food availability in the Sargasso Sea.

5.5 Conclusion

In this study, we focused on the impact of environmental conditions in the Sargasso Sea on glass eel recruitment. Our findings suggest that trophic conditions in the Sargasso Sea may affect glass eel recruitment several years later and thousands of kilometers distant. Further studies have to be engaged to improve our knowledge on the oceanic stages of eel. However, in light of the European stock decline observed for 25 years, many environmental and anthropogenic factors acting at different stages in the life cycle are involved. Moreover, the strong demand of Asian markets has maintained strong harvest pressure on eel stocks. In this context, eel management clearly needs to be integrated within an ecosystem approach in order to account for the different factors impacting eel whether ecological or economic. Further studies must be engaged concerning other eel species to confirm the trophodynamic linkages observed for *A. anguilla* during the larva drift.

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6

Lien environnement-recrutement des Anguilles de l'hémisphère nord

Résumé détaillé

Le chapitre 5 a montré que le succès du recrutement de civelles d'Anguille européenne semble fortement déterminé par la disponibilité en nourriture lors de premiers stades de vie. En revanche, ce succès n'est pas relié aux conditions océaniques de transport des larves lors de leur migration trans-océanique de la mer des Sargasses aux côtes européennes.

Dans ce chapitre, la relation trophique mise en évidence est généralisée à deux autres espèces principalement exploitées de l'hémisphère nord : les anguilles américaines et japonaises.

A court terme, les variations de la production primaire dans la mer des Sargasses (représentant la disponibilité en nourriture) sont positivement corrélées aux variations de quantités de civelles arrivant sur les côtes américaines 1,5 ans plus tard et sur les côtes européennes 2,5 ans plus tard (Fig. 6.2). A long terme, les fluctuations de la température de l'eau (en relation inverse avec la disponibilité en nourriture ; voir chapitre 5) dans les zones de reproduction des anguilles, c'est-à-dire la mer des Sargasses pour l'Anguille européenne et américaine et les montagnes sous-marines proches des Iles Mariannes pour l'Anguille japonaise, sont négativement corrélées aux fluctuations des indices de recrutement des trois espèces 2,5, 1,5 et 0,5 an(s) plus tard pour les anguilles européennes, américaines et japonaises respectivement (Fig. 6.3). Des changements de régime de températures de l'eau dans la mer des Sargasses et dans l'aire de reproduction de l'Anguille japonaise sont détectés en 1979 et 1977 respectivement. Les indices de recrutement des trois espèces montrent des changements brutaux en 1982 pour l'Anguille européenne, 1981 pour l'américaine et 1978 pour la japonaise (Fig. 6.5). Par conséquent, l'approche menée sur 2 autres populations d'Anguille de l'hémisphère nord confirment les acquis du chapitre précédent sur l'espèce européenne. Avec un décalage correspondant aux temps de migration entre la zone de fraie et la côte, il existe une corrélation forte entre la production primaire aux cours des premiers stades de vie et le recrutement. Cette relation se vérifie à trois échelles de temps : court et long terme et changement de régime. Ces résultats, observés pour les trois espèces d'Anguille de l'hémisphère nord, dans deux océans, mettent en évidence la forte dépendance du succès du recrutement à la disponibilité en nourriture durant les premiers stades de vie des larves d'Anguille. Les résultats sugèrent que le réchauffement climatique pourait être à l'origine du déclin simultané des trois espèces.

Impact of climate on eel population of the Northern Hemisphere

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Abstract Glass eel numbers are declining worldwide. This decline has mostly been attributed to direct impacts of human activities such as overfishing or habitat loss and degradation whilst the potential influence of changes in oceanic conditions has received less attention. Eel are characterized by a complex and still enigmatic life cycle that includes a trans-oceanic spawning and larval migration. The apparent synchrony in the decline of eel populations worldwide suggests that similar oceanic mechanisms are involved. We conduct an analysis of the relationships between oceanic conditions in eel spawning, larval feeding, and migration areas and glass eel recruitment success of the three most commercially important species of the genus *Anguilla*: *A. anguilla*, *A. rostrata*, and *A. japonica*. We provide evidence that the survival of eel larvae is strongly associated with food availability during their early life stages. Over the last four decades, we show that changes in the marine production related to global warming may have led to the decline of European, American and Japanese eel populations. In the Pacific and Atlantic oceans, the shifts in the temperature regime detected in the late 1970s were followed by shifts in the recruitment regime of glass eel for the three species. The decrease in primary production through climate-driven processes appears therefore to have repercussions on higher trophic levels of the food web for eels.

Keywords *Anguilla*; primary production; climate; regime shift; bottom-up

6.1 Introduction

Eel species have always excited a degree of fascination because of their complex and puzzling life cycle. As catadromous fish, they spawn in the open ocean (Fig. 6.1) - the Sargasso Sea for European and American eels (McCleave, 1993) and west of the Mariana Islands for Japanese eels (Tsukamoto, 2006). After an oceanic migration that can span thousands of kilometres and last several years (1-3 years for the European eel (Schmidt, 1923; Lecomte-Finiger, 1994; Tesch, 2003), 1-2 years for the American eel (Tesch, 2003), and 0.5-1 year for the Japanese eel (Kim *et al.*, 2007), eels colonise continental habitats where they grow before migrating back to the open ocean for spawning. The decline in eel populations of the Northern Hemisphere is alarming (Anonymous, 2003; ICES, 2006). The European eel has been listed in Appendix II of the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES) regarding its current level of abundance. In the Northern Hemisphere, the abundance of juvenile eels has dramatically decreased over the last few decades: in European waters, it is now less than 1 % of levels in the 1980s for some recruitment time series (ICES, 2006). The decline has mostly been attributed to direct impacts of anthropogenic activities especially in estuaries and continental habitats (McCleave, 2001; Feunteun, 2002; Dekker, 2003; Tatsukawa, 2003). For instance, fishing has been proposed as the major factor impacting European eel population (Dekker, 2004). However, although fishing pressure on American glass eel was lower than on European and Japanese eels before the 1980s, the population exhibited similar signs of declining trends at the same period (Casselman, 2003). Not withstanding stock-specific declining factors, the worldwide synchrony in the decline of eel abundances suggests that common factors such as ocean climate may have influenced eel population dynamics (Knights, 2003; Friedland *et al.*, 2007). As spawning, larval development, feeding, and migration take place in the open ocean, the oceanic environmental conditions are believed to be of primary importance for eel larva survival and therefore recruitment (Knights, 2003; Friedland *et al.*, 2007). Significant negative correlations were found between the North Atlantic Oscillation (NAO) and the index of catches of glass eels at Den Oever in the Netherlands over the period 1938 - 2005 (Knights, 2003; Friedland *et al.*, 2007). Negative relationships have been found between Japanese eel recruitment and El Niño Southern Oscillation (ENSO; Kimura *et al.*, 2001; Sugimoto *et al.*, 2001; Kim *et al.*, 2007). However, such integrative indices do not allow elucidation of the precise ecological processes involved and a novel aspect of our work was to focus on trophic linkage as key factors of recruitment. The surface temperature of the northern hemisphere has increased more in the 20th century than during any other century in the last thousand years, with a main warming period from 1976 onward. The estimate from the Intergovernmental Panel on Climate Change (IPCC) is that the global average surface temperature has increased by 0.6°C over the last 100 years. (IPCC, 2007). This global-scale warming has resulted in increased oceanic temperatures and has strongly affected the spatial and temporal dynamics of a broad range of marine organisms (Beaugrand *et al.*, 2002; Perry *et al.*, 2005). Although marine ecological responses to climate change have received increasing attention in recent years, the effects of increased sea temperature on the survival of fish larvae and subsequent recruitment to the fisheries remain poorly understood. Planktonic food limitation has long been considered as the dominant control for variability in fish larva survival and recruitment (Hjort, 1914). In the open ocean, remote sensing observations have revealed that the recent surface temperature increase has triggered large spatial changes in vertical structure and, consequently, a reduction in the global production of ocean phytoplankton (Behrenfeld *et al.*, 2006). The increasing temperatures since the early 1980s is believed to have resulted in a 6 % decrease in primary production (PP) at a global-ocean scale, a decline that is mostly due to a pronounced decline in net primary production in mid and low latitudes (Gregg *et al.*, 2003), including eel spawning areas. In the present work, we analysed the link between the recruitment of the European, American, and Japanese eel and the marine production in their respective spawning areas. These three temperate species represent 90 % of world eel catches over the 1950-2005 period (`www.fao.org/fi/website`). We tested the hypothesis that the recruitment of these species is determined by food availability during early life stages. Although the diet of eel larvae remains controversial, it has been suggested that they primarily feed on particulate and dissolved organic matter, i. e. at very low trophic levels (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler, 1999). Organic matter and PP are strongly correlated in the North Atlantic and North Pacific gyres (e. g. DuRand *et al.*, 2001; Bates, 2001; Pilskaln *et al.*, 2005) and PP can therefore be considered as a proxy for food availability for leptocephali. It has recently been established that a trophic link exists between marine production in the Sargasso Sea and the recruitment of glass eels in European waters: variations in food availability for eel larvae in the spawning area are shown to be strongly positively correlated with fluctuations in recruitment success in subsequent years (Bonhommeau *et al.*, 2008). We investigate whether this trophic linkage can be observed for American and Japanese eel populations as well. Using short- and long term time series and regime shift detection methods, we then analysed the effects of global warming on PP in eel spawning areas and subsequent impacts on eel recruitment.

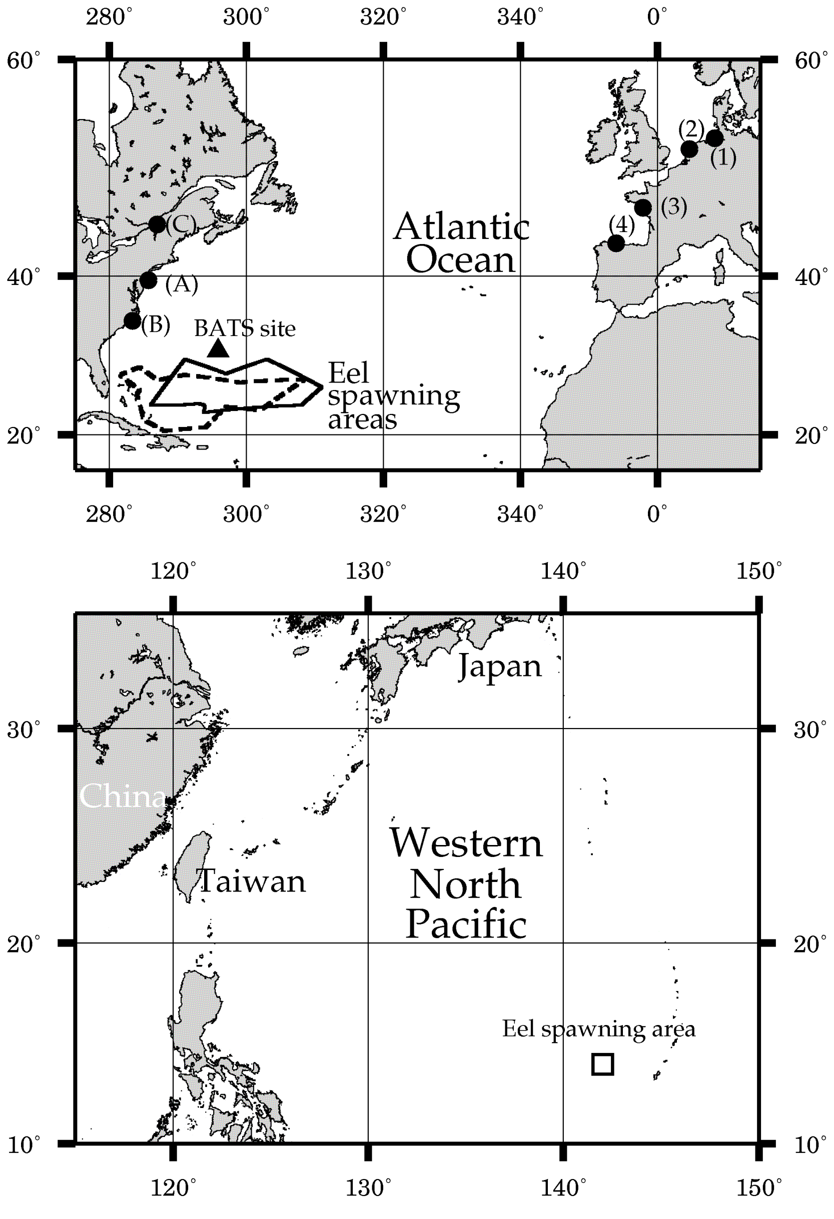

Figure 6.1: (a) Location of American (dashed polygon) and European (solid polygon) eel spawning areas (McCleave, 1993); American eel recruitment sampling sites: Little Egg Inlet (A), Beaufort Inlet (B), Moses-Saunders Dam, Ontario (C); European eel recruitment sampling sites: Ems River (1), Den Oever (2), Loire River (3), Nalon River (4); and the Bermuda Atlantic Time-series Study (BATS) site. (b) Location of Japanese eel spawning area (square; Tsukamoto, 2006).

6.2 Materials and Methods

6.2.1 Data

6.2.1.1 Eel recruitment data

For European eel, the recruitment series used for the short term analysis was the original series from the Loire River over the period 1994-2004 selected by Bonhommeau *et al.* (2008) because it provides the best picture of short term fluctuations of European glass eel recruitment. Data used for the long-term analysis were the four longest time-series of glass eel recruitment available from the ICES Working Group on eel (ICES, 2006), i. e. the Ems River (Germany), Den Oever (Netherlands), Loire River (France), and Nalon River (Spain) (Fig. 6.1). These time series were averaged after standardization (divided by their mean over the period) to define a European glass eel recruitment index over the period 1960-2005. American glass eel recruitment data used for short-term analysis are described in Sullivan *et al.* (2006). Two sampling sites are studied Sullivan *et al.* (2006): Little Egg Inlet (New Jersey) and Beaufort Inlet (North Carolina) over the period 1986-2004 (Fig. 6.1). Data used for the long-term analysis were from the index produced from the daily passage at the Moses-Saunders dam eel ladder in the upper St. Lawrence River (Ontario, Canada) over the period 1974-2001). This index is fully described in Casselman (2003). This series was 4-year lagged since eels were caught an average of 4 years after the elver stage (Castonguay *et al.*, 1994). The Japanese recruitment index was the annual catch of glass eels in Japan from 1965 to 2001 and is described in Tatsukawa (2003).

6.2.1.2 Primary production data

To our knowledge, in situ data were only available in Atlantic eel spawning areas and not in the Japanese eel spawning area. We used data provided by the Bermuda Biological Station for Research which has been carrying out in situ sampling of PP by filtering the water column during cruises since 1988 (Fig. 6.1). These data were used to analyse the relationship between biological production and Atlantic eel recruitment success. The Bermuda Atlantic Time-series Study (BATS) station is located in the west central Sargasso Sea and can be as a whole considered as a representative of eel spawning area (Nelson *et al.*, 2004). PP data associated with details about methods are available on the website of the Bermuda Biological Station (`http://bats.bbsr.edu`). A set of 8 standard depths on 20 m intervals from 0 to 140 m is sampled. Different samplings of leptocephali in this region revealed a preferred depth of 160 m during day and of 60 m at night (Schoth and Tesch, 1983, 1984; Castonguay and McCleave, 1987). PP was integrated over a 6-month period from January to July to derive an average estimate of the annual productivity in the Sargasso Sea. Most of the PP is indeed produced over this period of the year and averaging over this period also helps to account for the integration time of the PP in the first levels of the food chain. Moreover, the spawning season that span between March and July for the European eel and between February and April for the American eel are included within these 6 months (McCleave, 1993; Wang and Tzeng, 2000).

6.2.1.3 Temperature data as a proxy for primary production

We used decadal changes in SST as a proxy for PP to investigate the impact of warming on recruitment success since the 1960s. Although long term field measurements of PP are not specifically available for the Sargasso Sea or southwestern North Pacific, it has been showed that in warm stratified surface waters over decadal time scales, increasing SSTs lead to decreasing PP. A clearly identified process is that sea warming induces an inhibition in mixing that in turn, reduces the upward supply of nutrients (Behrenfeld *et al.*, 2006). In particular, the increased sea surface temperature in the western North Atlantic and North Pacific (especially at lower latitudes) has been showed to be negatively correlated with PP over decadal time scales (Sugimoto and Tadokoro, 1998; Miller and Schneider, 2000; Bates, 2001; Limsakul *et al.*, 2001; Watanabe *et al.*, 2005; Behrenfeld *et al.*, 2006; Aita *et al.*, 2007; Hashioka and Yamanaka, 2007). This complex response of PP to sea temperature probably arises because temperature not only affects biota directly - a 1°C increase in temperature is clearly not lethal -, but also acts as a proxy for other physical processes (i. e. inhibition of nutrient circulation due to enhanced stratification) regulating the size structure, taxonomic composition, and abundance of phytoplankton communities (Li, 2002). The average annual sea temperature in the Sargasso Sea over the period 1960-2005 was computed using BATS site sea temperature (`http://bats.bbsr.edu`; Fig. 6.1). Details on the computation of the Sargasso Sea temperature are provided in (Bonhommeau *et al.*, 2008). Data from the Japan Meteorological Agency (JMA) were used to estimate average annual sea temperature in the Japanese eel spawning area for the 1966-2001 period. The mean annual Sea Surface Temperature (SST) was computed using 10-day mean SSTs that are available from 1950 until present on the JMA website (`http://goos.kishou.go.jp/rrtdb/usr/pub/JMA/wnpsst/`). The 10-day mean SSTs were averaged first by month and then by year.

6.2.2 Statistical analyses

Correlation between environmental descriptors and eel recruitment indices were analysed through three different time series analysis methods. Short-term relationships were analysed between PP and recruitment indices for the two Atlantic species (over 11 years for the European eel and 13 years for the American eel). Long-term relationships were studied between temperature and eel recruitment indices for the three species (over 46 years for the European eel, 28 years for the American eel, and 36 years for the Japanese eel). Last, the regime shift detection was used to detect any synchrony between the years of transition in sea temperature and eel recruitment indices for the three species. Procedures for statistical testing of the degree of correlation between the recruitment and environmental series must account for the autocorrelation in the time series because it may result in an artificial increase in the statistical significance of the correlation test. We used methods specifically designed to study long-term and short-term correlations in the case of autocorrelated time series (Pyper and Peterman, 1998). Time lags had to be accounted for migration duration to link environmental descriptors to glass eel recruitment. Friedland *et al.* (2007) used a 1-year lag but Knights (2003) and Bonhommeau *et al.* (2008) used a delay of 2.5 - 3 years. These discrepancies arise from different estimation methods of the migration duration that are discussed below. In this study, we tested different time lags (1 to 3 years for the European and American eel, 0 to 1 year for the Japanese eel) in relation to knowledge and uncertainties about the migration duration (see Chap. 1).

6.2.2.1 Testing short-term correlations

To assess correlations between interannual variations of PP and recruitment indices, both of initial length N, we removed the autocorrelation by "prewhitening" the data series by first-order differencing prior to statistical testing (Thompson and Page, 1989; Pyper and Peterman, 1998). The aim is to transform the original data to eliminate autocorrelation whilst retaining the high frequency signal (Fox *et al.*, 2000). After the transformation, standard correlation tests can then be applied to the resultant series. The Pearson coefficients were used to test correlations between the first-order differenced recruitment and environmental time series. The p-value was assessed by comparing the Pearson coefficient against its theoretical Student distribution with $(N-1)-2$ degrees of freedom (d.f.) where $(N-1)$ is the length of the first-differenced time series. We estimated the different correlations between glass eel recruitment indices and environmental descriptors using different lags to take into account the different assumed migration duration.

6.2.2.2 Testing long-term correlations

To analyse long-term patterns between recruitment indices and sea temperature time series, we first smoothed data with a 5-year moving average to analyse low-frequency sources of covariation (Pyper and Peterman, 1998). The Pearson coefficient was used to test correlations between the smoothed time series. To compensate for autocorrelation in the smoothed time series of length N, the d.f. of the Student significance test, denoted $N*-2$, was adjusted following the equation proposed by Chelton (1984) and modified by Pyper and Peterman (1998):

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N} \sum_j r_{xx}(j).r_{yy}(j) \tag{6.1}$$

where $N*$ is the corrected sample size that is interpreted as the number of independent joint observations on the two time series X (recruitment data) and Y (sea temperature data), N is the length of the initial time series and $r_{xx}(j)$, and $r_{yy}(j)$ are the autocorrelation of X and Y at lag j. Estimators of autocorrelation r are obtained using the Box-Jenkins' equation (Box and Jenkins, 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j} \frac{\sum_{j=1}^{N-j} (X_t - \overline{X})(X_{t-j} - \overline{X})}{\sum_{j=1}^{N} (X_t - \overline{X})^2} \tag{6.2}$$

where $\overline{X}$ is the overall mean. Pyper and Peterman (1998) tested a variety of d.f. adjustment methods and found Eq. 6.1 to be robust and unbiased compared to other methods. This method is also robust to the number of lags applied in the d.f.-reduction (Eq. 6.1). In the present analysis, we computed autocorrelations until the 9^{th} lag approximately equal to $N/5$ (Pyper and Peterman, 1998).

6.2.2.3 Regime shift detection

Regime shift detection of major changes in glass eel recruitment indices and sea temperature was performed using a sequential regime shift detection (Rodionov and Overland, 2005). This method enables us to estimate the magnitude of the shift through a regime shift index (RSI). The significance level (p) is the level at which the null hypothesis that the mean values of the 2 regimes are equal is rejected by the 2-tailed Student t-test. The cut-off time scale (l) determines the minimum duration to qualify a regime. The key concept is that there must be significant shifts in mean value relative to the within-regime variance in order to detect a new regime. In the present analysis, the cut-off length (l) was set to 10 years and probability level at $p = 0.01$. We also investigated the sensitivity of the results to the parameters setting l to 15 and 20 years and $p = 0.05$.

6.3 Results

6.3.1 Short-term relationships between PP and recruitment indices

We analysed the relationship between PP in eel spawning areas and recruitment of European and American eels over 11 and 13 years respectively. For the European and American eel, only a 2.5-year lag and 1.5-year lag (respectively) exhibits a significant correlation. Highly significant positive correlations were found between PP and recruitment of European (Pearson's $r = 0.74$, $p = 0.015$) and American eels (Pearson's $r = 0.71$, $p = 0.010$), respectively (Fig. 6.2). Thus, more than 50 % of variation of coastal glass eel recruitment success can be explained by fluctuations in primary production in eel spawning area. The tight link between Sargasso Sea PP and subsequent recruitment of European and American eels suggests that food availability in the Sargasso Sea exerts a major control on eel larva survival early in its life cycle and that such bottom-up control has been driving the recruitment of European and American eels for more than a decade.

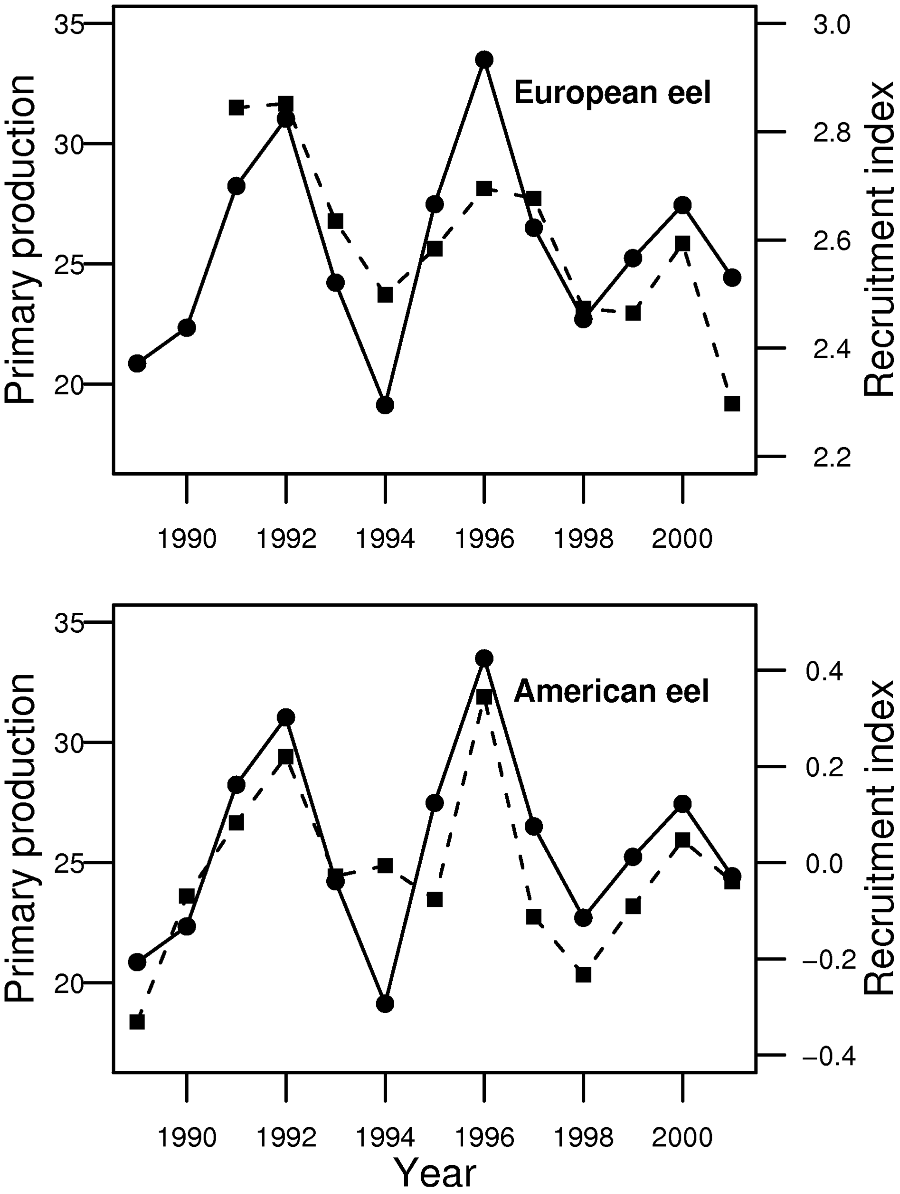

Figure 6.2: Short-term time series of European (a) and American (b) eel recruitment indices, lagged by 1.5 and 2.5 years, respectively (dashed line with squares), and integrated primary production at BATS site (mgC·m^{-3}·d^{-1}; solid line with circles).

6.3.2 Long-term relationships between fluctuations in sea temperature and eel recruitment indices

Fluctuations in Sargasso Sea surface temperature followed the same trends as the North Hemisphere Temperature anomaly, suggesting a direct link between global warming and the increase in sea temperature in these areas (Fig. 6.3). Over the past 40 years, the long-term correlations between Sargasso Sea temperature and Atlantic species recruitment indices were the most significant using a 2.5-year lag for the European eel (r = -0.88,

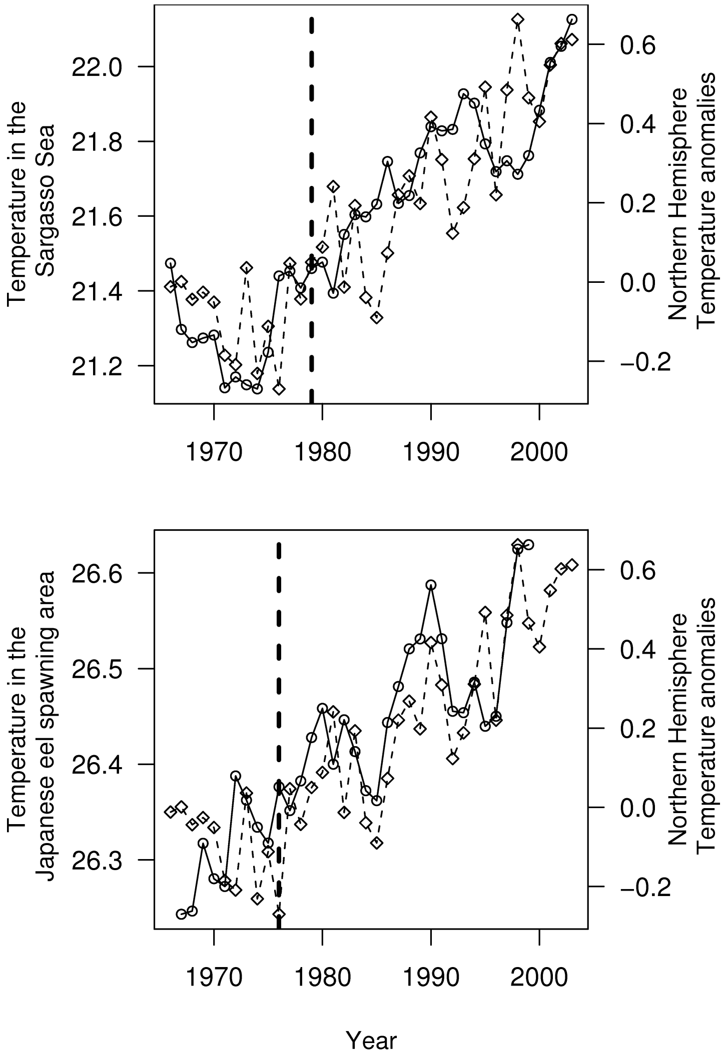

Figure 6.3: Sea temperature in (a) the Sargasso Sea (in °C, solid line with circles) and in (b) the spawning area of the Japanese eel (solid line with circles) versus North Hemisphere Temperature anomalies (www.cru.uea.ac.uk/cru/data/temperature; dashed line with diamonds). Vertical dashed lines represent the regime shift in temperature found using the regime shift detection method.

p = 0.03), a 1.5-year lag for the American eel (r = -0.90, p = 0.03). The correlation between the sea temperature in the Japanese eel spawning area and the Japanese eel recruitment index were most significant using a 0.5-year lag (r = -0.84, p = 0.01). The decrease in glass eel recruitment appears to be strongly inversely correlated with warming in eel spawning areas (Fig. 6.4).

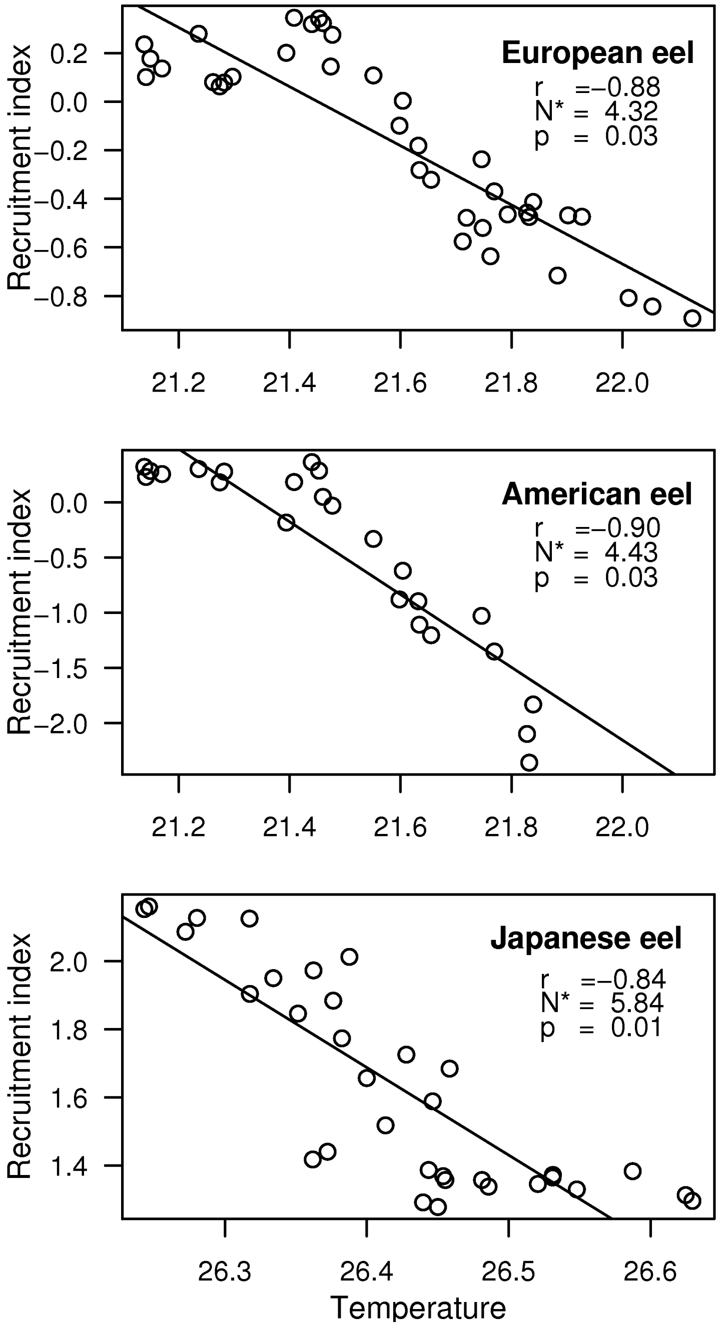

Figure 6.4: Long-term relationships (5-year moving averages) between temperature in the eel spawning areas (°C) and glass eel recruitment indices for (a) European, (b) American, and (c) Japanese eels, lagged by 2.5, 1.5, 0.5 years respectively to the sea temperature to account for different migration durations. r is the correlation coefficient, $N*$ the degrees of freedom after compensating for serial autocorrelation, and p the p-value with $N*$-2 degrees of freedom.

6.3.3 Regime shifts in eel recruitment indices, sea temperature, and North Hemisphere Temperature

The regime shift detection method applied to raw time series of recruitment and temperature revealed a negative regime shift in 1982 for the European eel and in 1981 for the American eel while a positive regime shift in Sargasso Sea temperature was shown in 1979 (Fig. 6.3 and 6.5). A negative regime shift was observed for Japanese eel recruitment one year after the shift in temperature in 1977 in the Pacific Ocean (Hare and Mantua, 2000). For each eel species, the negative shift in recruitment followed a positive shift in temperature (Fig. 6.5). In each case, time lags between temperature and recruitment shifts corresponded to lags found previously. These findings reinforce the idea of a strong link between temperature and recruitment.

6.4 Discussion

6.4.1 Primary production as a proxy for eel larvae food and importance during earliest life stages

This study used PP as an indicator of eel larval food supply. This is sustained by general considerations (Ware and Thomson, 2005) and based on the available knowledge about leptocephalus diet. Two potential sources of nutrition have been proposed for eel larvae: dissolved organic matter and particulate organic matter (POM) in the form of zooplankton fecal pellets and larvacean houses (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler, 1999). Marine snow has also been proposed as a potential source of nutrition (Knights, 2003). As a strong linear relationship between phytoplankton and POM has been described in the Sargasso Sea (DuRand *et al.*, 2001), PP was considered as a good proxy for leptocephali food (Bardonnet and Riera, 2005). Biological production may impact eel larvae because of its characteristics. Eel larvae are qualified as type II larvae based upon their unique developmental strategy. After a post-hatch period in which the yolk-sac is absorbed, the larval fish show a dramatic increase in size during which up to 40 % of the leptocephalus maximum length is attained while only 5-7 % of the maximum mass is accumulated (Bishop and Torres, 2001). This unique strategy allows them to increase rapidly in size while devoting the majority of their energy to metabolism,

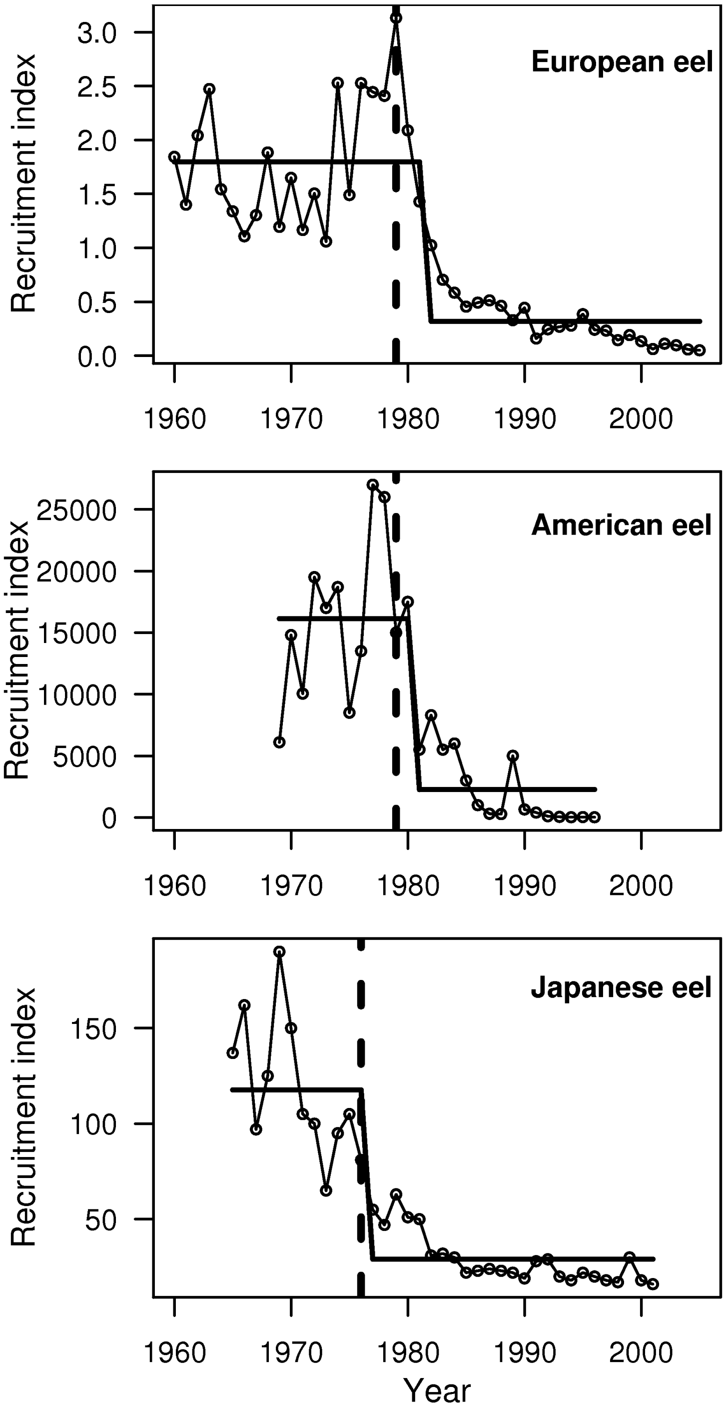

Figure 6.5: Time series of European (a), American (b), and Japanese (c) recruitment indices (solid lines with circles). Bold lines indicate regime shift detection and vertical dashed lines indicates the main regime shifts in temperature in the North Atlantic (1979) and North Pacific (1977) oceans.

i. e. nutrition and locomotion, and not to mass increment as in most larval fish. Food availability seems critical in early life stages to determine capacity of eel larvae to rapidly reach the size allowing them to survive to a long drift into currents.

The specific location of Japanese eel spawning area near seamounts may be linked to the functional role of these places in nutrient transport. Seamounts have been shown to induce perturbations in nutrients distributions, leading to enhanced upward transport of nutrients into the euphotic zone (Furuya *et al.*, 1995). This process results in an elevated amount of chlorophyll a downstream the seamount. Seamounts ecosystems may then be specific areas adequate to provide eel larvae with a sufficient food supply. The assumed locations areas relative to frontal systems (e. g. McCleave *et al.*, 1987; Kleckner and McCleave, 1988; Kimura *et al.*, 2001) are specific areas as well where mixing processes could encourage deepening of the mixed depth layers and nutrient circulation.

Food availability in spawning areas seems therefore to be an important factor for eel larva survival during the post-hatch period of these three eel species and explains the relationships found between PP and glass eel recruitment. The importance of food availability during the oceanic migration has been demonstrated as well (Désaunay and Guérault, 1997; Kettle and Haines, 2006).

6.4.2 Global warming effect on recruitment

Fluctuations in sea temperature in eel spawning areas are consistent with global changes observed for temperature, i. e. North Hemisphere Temperature. Similar orders of magnitude of sea temperature changes have been found in other studies dealing with large scale changes in water temperature and its impact on marine ecosystems (e. g. Donner *et al.*, 2007; Thresher *et al.*, 2007).

The effects of sea warming on eel recruitment seem to be indirect. Indeed, increase in sea temperature has been estimated between 0.4 and 0.8°C (Fig. 6.3) and, hence, is clearly not lethal. By contrast, temperature may have accelerated the larval development and thus reduced the exposure time to predators and / or increased the drift ability of larvae because of the increase in body surface during development. It would have however exacerbated the effects of any reductions in nutrient supply. We rather hypothesized that sea warming has an indirect effect through reinforcement of the vertical thermal stratification of the water column and decrease in marine production in warm eel spawning areas (Sugimoto and Tadokoro, 1998; Bates, 2001; Richardson and Schoeman, 2004; Watanabe *et al.*, 2005; Behrenfeld *et al.*, 2006). This is strongly supported by the high positive correlation found between primary production and glass eel recruitment lagged to account for migration duration (i. e. 2.5 years for the European eel, 1.5 years for the American eel, and 0.5

year for the Japanese eel). To analyse the relationships between recruitment and environmental conditions, we tested several lags. For the three distinct analyses (short-term relationships to PP (Atlantic species), long-term links to sea temperature, and delays between regime shifts), the most significant correlations were obtained with similar time lags: 2.5 years for the European eel, 1.5 year for the American eel and 0.5 year for the Japanese eel.

Concerning the Japanese eel, the 0.5 year delay is consistent with available and current knowledge about its migration duration (Cheng and Tzeng, 1996; Kimura *et al.*, 1999). Moreover, Wang and Tzeng (2000) and Shinoda (2004) showed that this migration duration is comprised between 98 and 227 days.

Migration durations of Atlantic eels remain controversial (see Chap. 1): ages at recruitment back-calculated by otolithometry ranged from 7 to 15 months (Lecomte-Finiger, 1994; Cheng and Tzeng, 1996; Arai *et al.*, 2000), but studies based on daily growth increments in glass eel otoliths have been criticized (McCleave *et al.*, 1998; Svedäng *et al.*, 1998; Cieri and McCleave, 2000). There is likely a period during metamorphosis into the glass eel when the oceanic eel larvae do not deposit daily rings because of low metabolic rate. It is noteworthy that there may be some resorption of otolith chemicals during the metamorphosis (Antunes and Tesch, 1997). In addition, according to McCleave *et al.* (1998), European eel leptocephali would not be able to swim cross the Atlantic Ocean in less than 1-2 years. An ocean circulation model has shown a 2.5 - 3 year migration duration of European eel larvae (Kettle and Haines, 2006). Our results appear in contradiction to approaches based on otolithometry but fit with estimates based on larval drift.

6.4.3 Other factors associated with ocean climate change

The relationships between Transport index (i. e. the strength of the Gulf Stream; Curry and McCartney, 2001), Gulf Stream Index (i. e. the latitude of the Gulf Stream; Taylor and Stephens, 1998) and European glass eel recruitment were not clearly established (Bonhommeau *et al.*, 2008). However, other studies suggest that leptocephali may be affected by oceanic features because of their long larvae oceanic phase (Knights, 2003). Recent analysis by Friedland *et al.* (2007) suggested that the influence of ocean parameters such as the shallowing of the mixed layer depth inducing a decrease in PP, drift conditions in larval transport area, and declining trends in winds have contributed to declining recruitment as well. For instance, they show that fluctuations in Den Oever Index are related to fluctuations in North Atlantic Oscillation (NAO) which indicates recruitment may be influenced by the physical and biological structure of the North Atlantic. M. Miller, S. Kimura, K.D. Friedland, D. Knights, D.J. Jellyman, K. Tsukamoto (unpubl. data) suggested that the changes associated with these types of atmospheric forcing could alter the biological characteristics of the surface layer where leptocephali feed. Friedland *et al.* (2007) also suggested that fluctuations in latitude of the 22.5°C isotherm, which is a useful indicator of the northern limit of eel spawning area, may affect both spawning location and transport of the leptocephali out of the Sargasso Sea by increasing retention within the Sargasso Sea gyre. Moreover, the possibility to leave the Sargasso Sea may be altered by changes in winds in the northern Sargasso Sea, which have reduced southward Ekman transports and hence contributed to increase larval retention in the Sargasso Sea gyre. Such changes in larval retention might add up to the bottom-up control process suggested by our result and underline the various and potential combined effects of environmental changes on eel recruitment. As a genus *Anguilla* commonality, Kimura *et al.* (2001) showed a certain synchrony between *Anguilla japonica* recruitment and salinity fronts driven by El Niño Southern Oscillation (ENSO) in the Japanese eel spawning area. If eel eggs hatch south of the salinity front, larvae may be carried away by the southward Mindanao current. By contrast, hatching north of the front, leptocephali may follow the Kuroshio transporting them to their distribution area from Taiwan to Japan (Kimura *et al.*, 1994). Moreover, in 2002 when an El Niño event occurred, Kimura and Tsukamoto (2006) noticed that small larvae (<10mm total length) were collected just south of the salinity front where these young larvae have never been collected in usual years. Kim *et al.* (2007) demonstrated that the changing oceanic conditions associated with climate change have resulted in decreased recruitment of Japanese eels as well.

Trophic conditions in eel spawning habitats appear to affect the success of eel recruitment several years later and thousands of kilometres away from the spawning site. Decadal changes in sea temperature have occurred around the Mariana Islands and in the Sargasso Sea; abrupt transitions in the temperature regimes of these regions have occurred in the late 1970s that were followed by a period of persistent warming (Hare and Mantua, 2000; Bonhommeau *et al.*, 2008). These conditions seem to have induced changes in eel larva survival through bottom-up trophic regulation. The relationships between PP and glass eel recruitment indices in the North Atlantic and North Pacific were found at different nested time scales, i. e. on the short term for interannual fluctuations, on the medium term for regime shifts and on the long-term for decadal trends. These consistent and synchronous results at multiple temporal scales provide a general explanatory mechanism for how climate-driven changes in oceanic plankton production can affect eel recruitment in the Atlantic and Pacific oceans. Nevertheless, their current status is no doubt the combined effect of several, probably interacting factors. We argue that, in conjunction with anthropogenic factors such as overfishing and habitat loss and degradation, global climate variations have resulted in a major bottom-up control that contributed to the current declining state of eel stocks.

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Conclusion - Partie II

CETTE seconde partie avait pour objectif d'analyser l'impact des conditions environnementales lors de la phase larvaire sur le succès du recrutement des civelles. Du fait de la difficulté d'estimer l'abondance des leptocéphales en milieu océanique, seules les données portant sur les civelles lors de leur arrivée en estuaire sont disponibles pour étudier le recrutement de l'Anguille. Cette partie du travail s'est ainsi appuyée sur les estimations de la durée de migration océanique des larves d'Anguille obtenues dans la partie I afin de mettre en relation les caractéristiques de l'environnement durant les premiers stades de vie et l'abondance estimée à l'issu de la migration. Deux hypothèses de processus écologiques sont tout d'abord testées pour l'Anguille européenne.

(*i*) Les conditions physiques océaniques affectent la phase de transport des larves. Les corrélations étudiées entre les indices océaniques grande échelle (force et position du Gulf Stream) et les indices de recrutement ne sont pas significatives, suggérant un faible impact des variations des conditions physiques sur le recrutement en cohérence avec la conclusion de la partie I.

(*ii*) La disponibilité en nourriture durant les premiers stades de vie influe sur la survie des larves. A court terme, une relation significative est mise en évidence entre les variations interannuelles de la disponibilité en nourriture dans la mer des Sargasses et les variations 2,5 ans plus tard d'un indice de recrutement issu de nos enquêtes auprès des pêcheurs de civelle en Loire. Il a été démontré par ailleurs que l'augmentation de la température de l'eau a un impact négatif sur la disponibilité en nourriture dans les eaux chaudes comme celles de la zone de reproduction de l'Anguille européenne, la mer des Sargasses. Cela nous a permis d'utiliser la température comme un indicateur de la production primaire de l'océan sur des séries temporelles longues. A long terme, des corrélations négatives apparaissent entre les fluctuations de la température dans la mer des Sargasses (représentant ainsi les fluctuations de disponibilité en nourriture) et celles de sept indices de recrutement de civelles le long des côtes européennes 2,5 ans plus tard. De plus, une analyse des principaux changements de régime de la température de l'eau de la mer des Sargasses montre un réchauffement à partir de 1979. Ce changement brutal se retrouve 2,5 ans plus tard dans les séries d'indices de recrutement de civelles européennes. Les fluctuations de la disponibilité en nourriture durant les premiers stades de vie dans la mer des Sargasses se répercutent donc sur le succès du recrutement des civelles européennes (voir aussi l'annexe B).

Le deuxième chapitre de cette partie généralise les relations trophiques à deux autres espèces, l'Anguille américaine et japonaise. Aux trois mêmes échelles temporelles, court et long terme et changement de régime, des relations similaires sont mises en évidence entre la disponibilité en nourriture et le succès du recrutement des civelles d'Anguille américaine et japonaise. Ce processus commun, relié au changement climatique, apparaît être l'un des facteurs ayant conduit au déclin de ces trois populations. Le synchronisme du déclin des trois espèces d'Anguille principalement exploitées (Anguille européenne, américaine, japonaise) suggère que ces variations d'abondance sont induites par des processus globaux, aussi appelés effet Moran (Moran, 1953; Ranta *et al.*, 1997; Ripa and Ranta, 2007).

Cette partie met en évidence l'impact du changement climatique sur les relations trophiques au sein d'un écosystème. L'augmentation de la température de l'hémisphère nord est de l'ordre de 0.6°C au cours des 100 dernières années (IPCC, 2007). Ce réchauffement a entraîné une diminution de la production primaire des écosystèmes marins de 6% à l'échelle mondiale (Gregg *et al.*, 2003; Behrenfeld *et al.*, 2006). Même si le recul manque pour pouvoir analyser les changements occasionnés par le réchauffement, des observations montrent déjà des effets sur certaines espèces comme le changement d'aire de distribution des poissons démersaux de la mer du Nord (Attrill and Power, 2002; Perry *et al.*, 2005) et la diminution d'abondance des bas niveaux trophiques (Fromentin and Planque, 1996) qui se répercute sur les niveaux trophiques supérieurs comme la morue (*Gadus morhua*) et le saumon (*Salmo salar*) (Beaugrand *et al.*, 2003; Beaugrand and Reid, 2003). En outre, le blanchiment des coraux lié à l'augmentation de la température (Hoegh-Guldberg, 1999) est une illustration du problème posé par le changement de climat : modification de l'habitat, baisse du succès de la reproduction et de la croissance des individus, diminution de la biodiversité et de la productivité des écosystèmes et conséquences socio-économiques de ces altérations (Walther *et al.*, 2002; Lehodey *et al.*, 2006; Stenseth *et al.*, 2002). Les résultats obtenus pour trois populations d'Anguille à l'échelle de l'hémisphère nord, viennent renforcer ce constat.

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Conclusion générale

Le principal objectif de ce travail de thèse était de comprendre les relations entre les conditions environnementales et la survie larvaire de l'Anguille européenne. En particulier, l'estimation du temps de migration des larves était un pré-requis nécessaire afin de relier des variables d'environnement lors de la migration océanique des larves avec les données de recrutement accessibles, mesurées au moment de l'arrivée des civelles sur les côtes. Nous avons adopté une démarche de modélisation permettant de formuler et de tester des hypothèses dans un contexte qui allie la complexité du "système Anguille" et la difficulté d'observer sa phase larvaire. Ce travail couple les résultats d'une modélisation déterministe de la dérive des larves, qui permet d'analyser ces migrations océaniques, avec une modélisation statistique pour quantifier les relations environnement-recrutement.

Principaux résultats et limites de l'étude

Modélisation de la dérive larvaire de l'Anguille européenne

La synthèse des connaissances biologiques et écologiques met en relief l'incertitude existant autour des durées de migration des larves d'Anguille européenne. Les estimations varient selon les méthodes utilisées de 6 mois (analyse de la microstructure de l'otolithe) à 2 ans (analyse des fréquences de taille et premières simulations lagrangiennes). Cet ordre de grandeur est trop large pour permettre de relier les conditions environnementales vécues par les larves et la variabilité du recrutement des civelles sur les côtes européennes.

La modélisation de la dérive des larves nous a tout d'abord permis d'estimer une durée minimale de migration des larves. Une des originalités de ce travail réside dans la modélisation du comportement des particules, pour représenter deux hypothèses biologiquement réalistes : migrations nycthémérales verticales et capacité de s'orienter vers les courants les plus rapides. Les résultats suggèrent une durée de migration plus longue que celle estimée par les études utilisant la microstructure de l'otolithe. Nos simulations montrent en effet que l'hypothèse de 6 mois de traversée impliquerait une nage active rapide (3,4 fois la longueur du corps). La dépense d'énergie nécessaire à cette nage active semble peu réaliste dans un environnement oligotrophe, pauvre en ressources alimentaires. Ces résultats s'avèrent de plus, très robustes au choix des hypothèses de comportement des particules.

Par la suite, nous avons introduit une hypothèse de mortalité des larves au cours de leur dérive afin d'estimer un temps de migration moyen. Les résultats indiquent que la durée de migration moyenne des leptocéphales pour atteindre les côtes européennes par dérive passive (sans nage active) est de 22 mois. La survie naturelle des larves est estimée à 2.8 pour mille lors de cette traversée.

L'analyse de la migration est développée dans la dimension spatiale afin d'appréhender l'influence des aires et dates de départ des larves sur les routes qu'elles empruntent. Selon ces simulations, la saison et le lieu de reproduction des anguilles dans la mer des Sargasses conditionnent les routes de migration des larves et ainsi leur lieu d'arrivée sur les côtes européennes. Ces résultats sont cohérents avec les approches de génétique et de microchimie des otolithes publiés par ailleurs.

Ce travail de modélisation de la dérive des larves d'Anguille s'appuie sur les connaissances actuelles en terme de modélisation océanique. Les deux modèles utilisés (Drakkar et Mercator) sont batis sur des hypothèses physiques liées à la dynamique des fluides. Ils font partie des représentations de circulation océanique les plus précises au sein de la communauté scientifique. L'utilisation de ces modèles nous a permis de formuler des hypothèses pour comprendre des phénomènes écologiques et biologiques difficiles à appréhender par l'observation. Cependant, les résultats doivent être interprétés au vu des hypothèses énoncées. Ainsi, les différences observées entre les résultats issus des deux modèles physiques (par exemple les aires d'arrivée) sont expliqués par les options de modélisation (faible représentation du courant des Açores par Drakkar) et mettent en lumière l'importance des choix des modèles hydrodynamiques pour aborder une question d'écologie.

Malgré leurs limites, la cohérence des deux modèles en ce qui concerne les temps de dérive des larves tend à favoriser l'hypothèse d'une migration longue, d'environ 2 ans. L'utilisation de modèles océaniques à résolution plus fine, développés très récemment, pourrait permettre d'affiner ces approches et d'améliorer ces estimations, en prenant en compte d'autres phénomènes comme les tourbillons à méso-échelle.

Modélisation statistique des relations environnement-recrutement de l'Anguille

Les résultats de la première partie de ce travail nous donnent une estimation de la durée de migration des larves d'Anguille européenne, donnée essentielle pour relier les conditions environnementales durant la période océanique des larves et les données de recrutement auxquelles nous avons accès : les quantités de civelles arrivant sur les côtes de l'Atlantique Nord Est.

Dans la deuxième partie de cette thèse, nous mettons en relation la disponibilité en nourriture durant les premiers stades de vie dans la mer des Sargasses et le succès du recrutement. Les connaissances écologiques sur les larves d'Anguille sont limitées en ce qui concerne leur régime alimentaire ce qui nous a contraint à utiliser la production primaire comme un indicateur de disponibilité en nourriture. (*i*) A court terme, de 1994 à 2004, les variations interannuelles de la production primaire dans la mer des Sargasses correspondent aux variations des quantités de civelles observées deux ans plus tard sur les côtes européennes. (*ii*) A long terme, les relations trophiques sont confirmées sur les 45 dernières années. Pour cela, nous avons utilisé la température de l'eau qui est un bon indicateur de la production primaire. (*iii*) L'analyse des changements de régime de la température de l'eau et des indices de recrutement de civelles montre que les ruptures dans les températures de l'eau observées dans la mer des Sargasses en 1979 se sont répercutées 2,5 ans plus tard dans les séries de recrutement de civelles européennes, ce qui correspond au temps de migration des larves. Par ailleurs, aucune relation significative n'a été décelée entre les indices des conditions océaniques physiques à large échelle (force et position du Gulf Stream) et les indices de recrutement, en conformité avec les acquis des approches par modélisation lagrangienne.

Une analyse à plus large échelle spatiale permet de généraliser la relation entre la production primaire et le recrutement à deux autres espèces d'Anguille de l'hémisphère nord (l'américaine et la japonaise) sur les trois mêmes échelles de temps. Cette étude conforte l'hypothèse selon laquelle le réchauffement global induit une baisse de la production primaire dans les zones de reproduction qui pourrait expliquer en partie la forte diminution synchrone du recrutement de ces 3 espèces d'Anguille.

Perspectives

Affiner la description des relations trophiques

Le travail de modélisation statistique repose sur des corrélations entre des variables environnementales et des variables biologiques. Les relations mises en évidence sont significatives et découlent de la formulation d'hypothèses de fonctionnement écologique. En l'absence de connaissances précises du régime alimentaire des larves, la production primaire a été utilisée comme indicateur de la disponibilité en nourriture. La détermination des proies des larves d'Anguille nous permettrait d'explorer plus en détail ces relations en utilisant par exemple le *Continuous Plankton Recorder* (SAHFOS, Plymouth, Grande Bretagne) qui dispose de données d'abondance par espèce de plancton depuis 1931 dans l'Atlantique Nord. Le même type d'approche pourrait être développé pour l'Anguille japonaise en utilisant les campagnes de collecte de données d'abondance de plancton des navires scientifiques japonais qui seront bientôt disponibles sur le site `http://www.st.nmfs.noaa.gov/plankton/`.

Vers des modèles "end-to-end"

L'approche de modélisation de la dérive des larves a mis en exergue la possibilité, au travers des modèles hydrodynamiques, de reproduire leurs grands traits de migration ainsi que leur passé, par exemple la température vécue. A partir des trajectoires obtenues, il est possible de retracer non seulement la température mais aussi la disponibilité en nourriture en utilisant les modèles de production primaire issus des données satellitaires. Ces deux paramètres pourraient être utilisées comme variables forçantes d'un modèle bioénergétique comme le Dynamic Energy Budget (DEB ; Kooijman, 2000) de l'Anguille, couplé à la dérive larvaire océanique. Cela permettrait de modéliser certaines fonctions biologiques, comme la croissance, et d'expliquer, par exemple, les différences de taille observées entre les civelles suivant leur aire d'arrivée. Un schéma conceptuel de ce couplage est donné dans la figure 1. Ce type d'approche correspond aux modèles communément

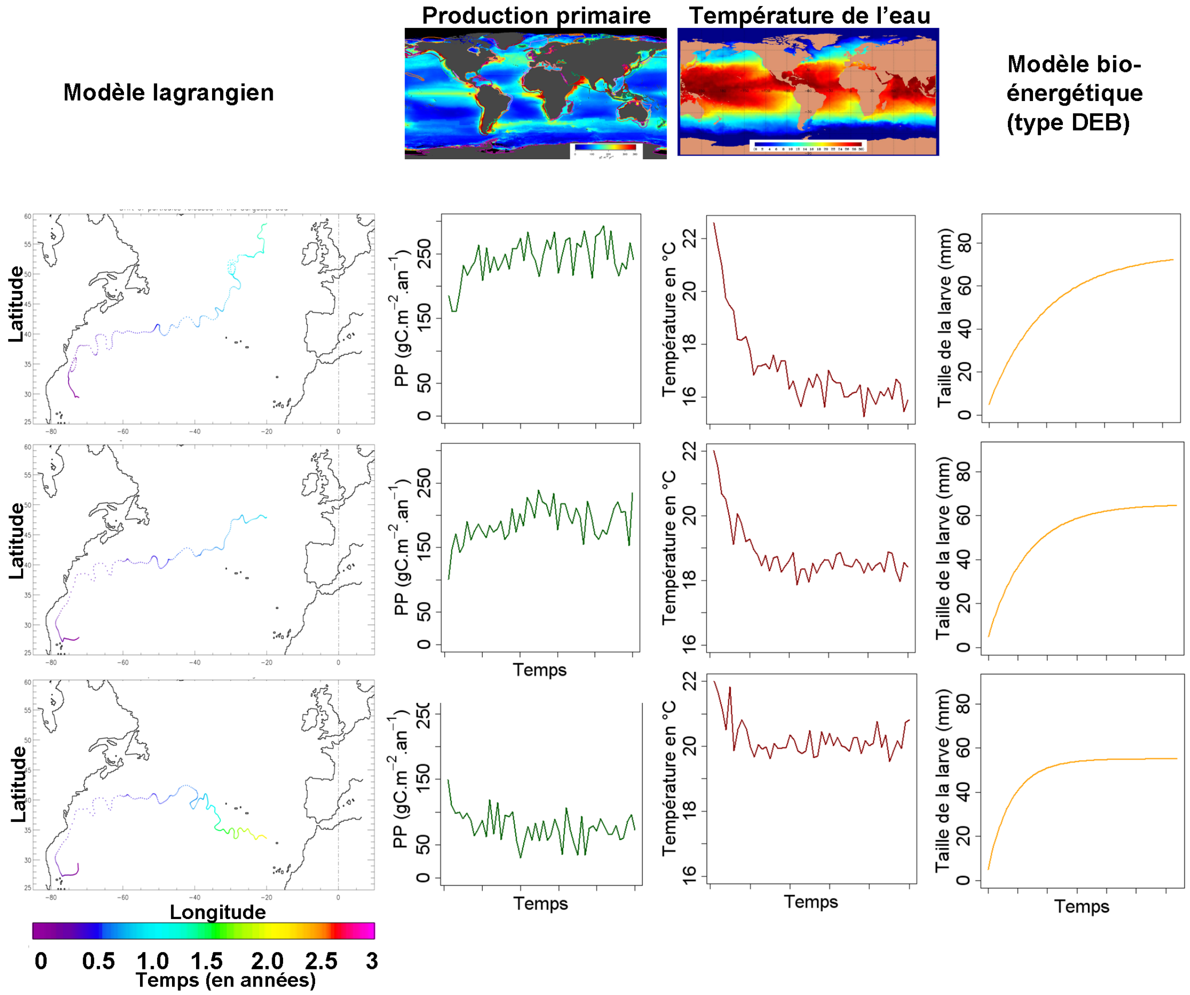

Fig. 1 Illustration du couplage possible des modèles physiques et des modèles bio-énergétiques pour déterminer les causes des différences de taille observées suivant les latitudes d'arrivée. Les données de production primaire et de température de chaque trajectoire sont collectées à partir des positions de chaque particule, obtenues par les simulations lagrangiennes (ici ces données sont factices). Le modèle bio-énergétique permet de reconstituer la taille de l'individu au cours de son trajet. Les conditions environnementales influent sur le taux de croissance et/ou sur la longueur finale au cours de la dérive océanique.

nommés "end-to-end", qui organisent le couplage déterministe de modèles physiques avec des modèles biologiques, pour comprendre la dynamique d'une population intégrée à son écosystème. Certains projets comme *Nemuro* permettent de coupler les modèles physiques du Pacific Nord avec des modèles de production primaire et secondaire (Aita *et al.*, 2007;

Hashioka and Yamanaka, 2007a, b). Ces modèles servent d'entrées à des modèles bioénergétiques d'espèces comme le hareng du Pacifique (*Clupea harengus pallasii*) ou le Balaou du Pacifique (*Cololabis saira*) pour comprendre la dynamique de population de ces espèces (Ito *et al.*, 2007; Megrey *et al.*, 2007; Werner *et al.*, 2007). Le même type d'approche, en se basant sur les travaux réalisés dans cette thèse, permettrait des avancées significatives dans la compréhension de la vie larvaire des anguilles.

Généralisation sur l'écologie et le cycle de vie de l'Anguille

Migration océanique et plasticité

Au vu des résultats de la modélisation de la dérive des larves et de la modélisation statistique des relations entre les conditions océaniques et le recrutement, la variabilité du transport des larves par les courants ne semble pas expliquer les fluctuations et la tendance du recrutement. Ceci constitue un premier élément de réponse à la question posée dans l'introduction de cette thèse : "Comment une espèce avec une phase larvaire si longue a-t-elle pu réussir à se perpétuer depuis 10 millions d'années ?" Les larves d'Anguille sont adaptées à une migration longue, environ deux ans selon nos travaux, et les variations de la durée de migration affectent peu leur capacité de survie. Le deuxième élément de réponse provient de la plasticité de l'Anguille qui lui permet de coloniser de nombreux habitats du cercle polaire arctique aux côtes marocaines (Daverat *et al.*, 2006). Ce très large spectre d'habitats colonisés permet ainsi de s'adapter aux variations majeures des courants océaniques pour maintenir l'espèce. Néanmoins, les variations de grande amplitude et à très long terme de la circulation océanique ont un impact sur le succès du recrutement. Les glaciations du Wisconsien (-20 000 ans) ou du Dryas récent (-12 000 ans) ont provoqué des ralentissements voire des arrêts du Gulf Stream (Lehman and Keigwin, 1992; Keigwin and Jones, 1994; Duplessy, 1999; Lynch-Stieglitz *et al.*, 1999; Rahmstorf, 2002). En utilisant l'ADN mitochondrial maternel d'anguilles européennes et américaines, Wirth and Bernatchez (2003) ont montré que ces périodes de faible transport ont entraîné de grandes réductions de la taille de la population d'Anguille, corrélées à une forte concentration dans quelques habitats-refuges.

Production océanique, surexploitation et raréfaction

Les travaux de la partie II mettent évidence que la disponibilité en nourriture pendant la phase larvaire des anguilles semble déterminante pour le succès du recrutement. L'augmentation de la température, liée au changement global, entraîne une diminution de la production primaire dans les aires de reproduction des anguilles. Ce contexte trophique défavorable, combiné à de fortes pressions anthropiques (surexploitation, pollution, pertes et diminutions d'habitat...), entraîne plusieurs espèces d'Anguille au bord de l'extinction et plaide en faveur d'une approche écosystémique pour préserver cette ressource (Feunteun, 2002). En effet, malgré la raréfaction des 3 espèces d'Anguille, les ressources économiques considérables engendrées par leur exploitation ont maintenue une forte pression de pêche. La théorie économique prédit qu'en dessous d'un certain seuil, les coûts d'extraction d'une ressource deviennent trop élevés pour maintenir son exploitation. Au contraire, l'annexe C de cette thèse montre que malgré cette raréfaction, la demande internationale croissante et la multiplicité des usages des civelles (consommation, élevage, alevinage) a généré une explosion des prix depuis les deux dernières décennies (effet Allee anthropique ; Courchamp *et al.*, 2006). Cela a permis de maintenir la rentabilité des pêcheries et a même conduit à augmenter la pression de pêche (légale et braconnage) sur ces ressources fortement raréfiées.

Changement de régimes, états d'équilibre et résilience

Le changement global induit une sensibilisation de l'Anguille mais aussi d'autres espèces marines qui doivent par ailleurs faire face à d'autres pressions anthropiques. La réciproque est vraie : par exemple, la pêche déstabilise les populations, les rend plus sensibles aux changements de leur environnement et augmente la variabilité de leur abondance (Anderson *et al.*, 2008; Stenseth and Rouyer, 2008). Comme l'ont révélé nos analyses, la combinaison de ces deux sources de perturbations (anthropique et climatique) a induit, pour l'Anguille, un changement de régime : d'une population stable avec des effectifs élevés vers une population proche de l'extinction. Quels sont les mécanismes qui provoquent ces changements d'équilibre et quels sont les processus écologiques et biologiques en jeu ? La réponse à ces questions est une problématique majeure en écologie dans le contexte du changement climatique. Une illustration adaptée à notre cas d'étude est donnée dans la figure 2. Lorsqu'une population est dans un état d'équilibre stable, elle fluctue autour d'une

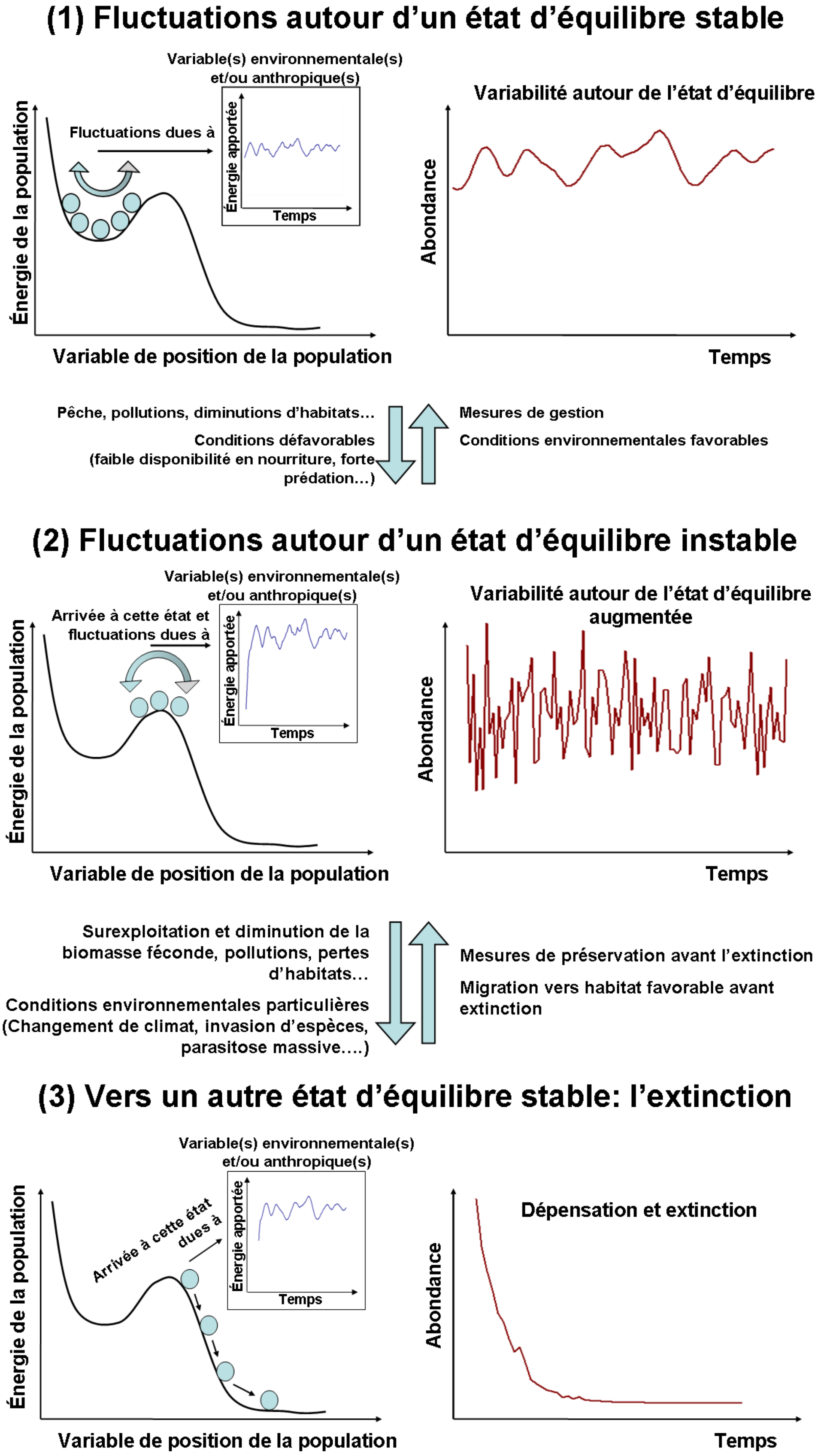

Fig. 2Illustration des changements d'équilibre pour une population. Le panel 1 représente la fluctuation d'une population autour d'une position d'équilibre stable. L'apport d'énergie à ce système déplace sa position vers un état d'équilibre instable caractérisé par des variations plus importantes de son abondance (panel 2). Cet état d'équilibre instable peut rebasculer vers l'état d'équilibre stable du panel 1 si les conditions environnementales redeviennent favorables ou si des mesures de gestion sont prises. Dans “position de repos”, c’est-à-dire, une taille moyenne dépendant des conditions environnementales (naturelles et anthropiques ; panel 1 de la figure 2) et tout particulièrement des conditions de vie au cours des premiers stades (Levin and Stunz, 2005). Si des changements sont apportés à ce système (conditions trophiques, pêche, pollutions...), la population est poussée vers un état d’équilibre instable où la variabilité de son abondance augmente : ce sont les processus décrit par Stenseth and Rouyer (2008). Les équilibres instables ne permettent pas, par définition, à la population de rester dans cette position. Deux voies sont alors possibles : soit des conditions environnementales favorables et/ou des mesures de gestion permettent à la population de retourner vers l’état d’équilibre décrit dans le panel 1 de la figure 2, soit un environnement défavorable et/ou l’absence de gestion conduisent la population vers l’état dépensatoire et finalement l’extinction (panel 3 de la figure 2). Cette représentation permet de bien comprendre l’importance de prendre des mesures de gestion assez tôt et de manière suffisamment forte pour replacer la population dans son état d’équilibre. Dans le cas contraire, l’énergie à dépenser pour rétablir la population devient de plus en plus importante (mesures de préservation) car ses capacités de résilience sont dépassées.

L’Anguille apparaît encore, cette fois-ci malgré elle, comme un bon cas d’étude pour comprendre ce qui peut conduire une espèce à l’extinction, ce qui met en avant la nécessité de prendre des mesures de gestion adaptées dès les premiers signes de déstabilisation.

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Annexes

A

Les modèles hydrodynamiques, outils d'analyse de la dérive océanique

L'objectif de cette annexe est de décrire les propriétés physiques des modèles utilisés dans ce travail. Une comparaison entre des observations et les données des modèles océaniques utilisés mais aussi entre les modèles permet de nous éclairer dans les différents résultats trouvés lors des simulations lagrangiennes.

A.1 Introduction

La phase larvaire océanique de l'Anguille est mystérieuse à de nombreux égards comme cela a été souligné dans le Chap. I. 1. Dans notre objectif général de compréhension des facteurs pouvant affecter le recrutement, il est indispensable de connaître la durée et les routes de migration pour pouvoir relier le nombre de civelles qui arrivent sur les côtes européennes (mesure du recrutement) à des descripteurs environnementaux pendant la phase larvaire. L'approche que nous avons choisie de développer pour déterminer ces durées et routes de migration est une approche lagrangienne. L'idée est d'utiliser les données d'un modèle de circulation océanique pour déterminer les trajectoires d'objets dérivants (particules) soumis aux champs de vitesse du modèle physique.

Nous disposons de deux configurations de circulation océanique qui sont parmi les plus précises actuellement disponibles au sein de la communauté scientifique européenne : les projets Drakkar et Mercator. Les caractéristiques de ces modèles seront développées par la suite. Trois différences majeures sont à noter : la période disponible, la résolution et l'"esprit" de la modélisation. Ces différences sont regroupées dans le Tableau A.1. La résolution est plus fine et la période disponible est plus longue pour Drakkar. Le modèle Mercator, quant à lui assimile des données, c'est-à-dire qu'il utilise des données d'observations telles que des températures ou des données de bouées et flotteurs pour forcer localement le modèle dans un but de réalisme et d'opérationnalité.

TAB. A.1: Principales différences entre les configurations Drakkar et Mercator

	Période	Résolution	Assimilation de données
Drakkar	1960-2004	$1/4^o$	sans
Mercator	1992-2002	$1/3^o$	avec

Deux échelles de comparaison doivent être envisagées :

– les différences entre les modèles et des données *in situ*

- les différences entre les deux modèles physiques

Nous avons choisi d'examiner quatre descripteurs qui peuvent avoir un impact sur les résultats des simulations lagrangiennes.

- la température de l'eau à la station de la Bermuda Atlantic Time-Series (BATS), *Hydrostation S*,
- le "Gulf Stream index" qui mesure la variabilité de la latitude du Gulf Stream (Taylor and Stephens, 1998),
- la vitesse des courants,
- l'"Eddy Kinetic Energy", l'énergie cinétique turbulente, c'est-à-dire la "force tourbillonnaire" des courants.

Ce chapitre décrit les caractéristiques des deux modèles physiques, leurs différences et leurs points communs mais aussi leurs "défauts" en terme de réalité physique.

A.2 Matériels et Méthodes

A.2.1 Description de l'outil lagrangien

A.2.1.1 Esprit de l'approche lagrangienne

Notre cas d'étude utilise une approche lagrangienne afin de suivre les trajectoires des larves (particules) qui dérivent dans l'océan (fluide).

Le mouvement d'un fluide est généralement décrit en variables eulériennes, c'est-à-dire par la variation au cours du temps des champs de densité, pression et vitesse mesurés en un point fixe de l'espace. La description eulérienne privilégie des points de l'espace auxquels on associe un champ de vitesse dépendant de l'espace et du temps. C'est par cette méthode que sont construites les grilles des modèles physiques océaniques. Par opposition, la description lagrangienne s'intéresse aux trajectoires individuelles des particules de fluide dans leur mouvement. La description lagrangienne privilégie les particules que l'on suit dans leur déplacement et à qui on associe un ensemble de vitesses ne dépendant que du temps.

Pour l'étude de la structure des écoulements, la description eulérienne est certainement la plus adaptée, d'autant qu'elle correspond à ce que mesure l'essentiel des capteurs. C'est également pour cette raison que les études analytiques et expérimentales en turbulence sont le plus souvent faites dans ce cadre. Par contre, les variables lagrangiennes deviennent naturelles pour traiter les propriétés de transport et de mélange des écoulements turbulents, essentielles en regard des applications pratiques.

> La description lagrangienne privilégie les particules que l'on suit dans leur déplacement et à qui on associe un ensemble de vitesses ne dépendant que du temps.

A.2.1.2 L'outil Ariane pour les simulations lagrangiennes

Ariane est un code FORTRAN dédié aux calculs de lignes de courant 3D dans un champ de vitesse comme les sorties des modèles de circulation des océans mais aussi aux transferts de masses d'eau. Ce programme a été développé par Bruno Blanke et Nicolas Grima (Laboratoire de Physique des Océans, CNRS-IFREMER-IRD-UBO, Brest, France) et est disponible gratuitement sur le site `http://www.univ-brest.fr/lpo/ariane`. Deux types d'analyse sont possibles : un mode qualitatif et un mode quantitatif. Le mode qualitatif permet de calculer les trajectoires de particules inertes dans un champ de vitesse donné. Nos simulations vont utiliser ce mode afin de déterminer les trajectoires des larves (particules) dans les champs de courant des modèles océaniques. Le mode quantitatif permet quant à lui de déterminer le transport entre une section de lâché de particules et des zones d'arrivée mais n'est pas utilisé dans ce travail. Cet outil est validé et a été utilisé dans de nombreuses applications (e. g. Blanke and Raynaud, 1997; Blanke *et al.*, 1999; Speich *et al.*, 2001; Blanke *et al.*, 2002, 2006).

A.2.2 Description des deux modèles physiques

A.2.2.1 Drakkar

La configuration océanique Drakkar (`http://www.ifremer.fr/lpo/drakkar/`) est tirée de la simulation océanique mondiale *ORCA025-G70*. Elle couvre la période 1958–2004. La résolution de la grille horizontale est de 1/4 de degré à l'équateur ce qui donne des dimensions horizontales de 1442 x 1021 mailles. La colonne d'eau est divisée en 46 niveaux avec un maillage vertical allant de 6 m près de la surface à 250 m à 5 270 m. Les principaux forçages du modèle sont les apports d'eau douce et les conditions atmosphériques fournies par une collection de données provenant de nombreuses origines qui sont décrites dans

Molines *et al.* (2006). Afin de diminuer la taille des fichiers de ce modèle et de correspondre à la zone de nos simulations lagrangiennes, nous avons réduit le champ du modèle à une aire comprise de -82 à 6°E et 10 à 60°N (Fig. A.1). Étant donné que la profondeur observée des leptocéphales est comprise entre -50 et -300 m (Castonguay and McCleave, 1987), nous avons aussi réduit le modèle océanique Drakkar à ces 24 premières couches (-3 à -989 m). Afin d'éviter certains problèmes liés à la phase d'initialisation des modèles, nous avons choisi de n'utiliser que la période 1960–2004. Les champs extraits sont composés d'une vitesse zonale (Ouest - Est), d'une vitesse méridionale (Sud - Nord), d'une vitesse verticale et de données de température à chaque maille du modèle. Ces champs sont archivés tous les cinq jours.

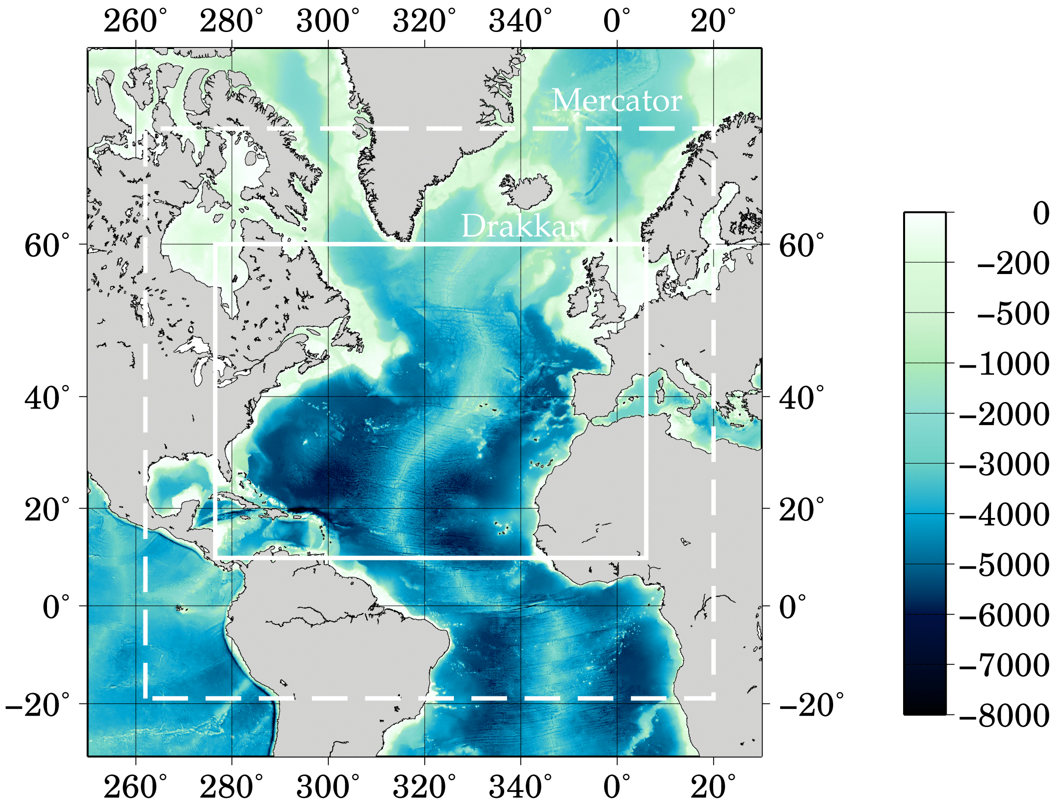

FIG. A.1: Aire géographique couverte par nos extractions des modèles Drakkar et Mercator (échelle de couleur représentant la bathymétrie en m)

A.2.2.2 Mercator

Les champs de circulation fournis par les Groupement d'Intérêt Scientifique Mercator (`http://www.mercator-ocean.fr`) proviennent de l'analyse *PSY1v2* sur la période 1992–2002. Nous avons utilisé l'intégralité de cette période lors de notre étude. La résolution de cette configuration est au 1/3 de degré à l'équateur. Elle est composée de 43 niveaux verticaux de la surface à 5 000 m (la résolution verticale est de 12 m à la surface jusqu'à 200 m au fond). Le modèle est forcé par des données d'altimétrie et *in situ* qui sont décrites dans le manuel scientifique MERA-11 (Greiner *et al.*, 2006). L'aire couverte par le modèle Mercator a été réduite à 98 - 20°W et 20°S - 70°N (Fig. A.1) et les profondeurs ont été limitées aux 16 premiers niveaux (de la surface à -453 m). Les champs conservés sont composés d'une vitesse zonale et méridionale et de données de température et de salinité. Ces champs sont archivés tous les jours.

Les principales différences entre ces deux configurations océaniques résident tout d'abord dans la période disponible : 1960–2004 pour Drakkar, 1992–2002 pour Mercator. Une autre différence majeure qui pourrait avoir des conséquences sur les simulations lagrangiennes est l'assimilation de données qui est faite dans le modèle Mercator. En effet, le modèle Mercator a un objectif opérationel et prédictif. L'assimilation contraint le modèle à correspondre à des données observées.

A.2.2.3 Comparaison avec des indices pertinents

Différents descripteurs ont été choisis pour déterminer les potentielles sources de différences entre les modèles ou avec la réalité physique. Ce choix provient du fait que ces descripteurs ont été utilisés dans la suite de ce travail. Il s'agit de la température dans la mer des Sargasses et du Gulf Stream index (cf. Partie II). D'autres indicateurs ont été déterminés par leur pertinence par rapport à l'approche lagrangienne : vitesse et énergie cinétique des courants.

Température dans la Mer des Sargasses Nous comparons la température de l'eau dans la mer des Sargasses avec les données de température des modèles physiques. La température de l'eau dans la mer des Sargasses est mesurée plusieurs fois par mois depuis 1955 à l'*Hydrostation S* (Fig. A.2) de la station biologique des Bermudes (Bermuda Institute of Ocean Sciences, BIOS). La température est disponible sur les couches d'eau allant de la surface à 4000 m. Ces températures sont disponibles sur le site du BIOS `http://bats.bios.edu`. Nous avons défini 8 classes de profondeur (0-20, 20-50, 50-100, 100-200, 200-300, 300-400, 400-500, 500-1000 m) et calculé la moyenne mensuelle de la température de l'eau mesurée *in situ* dans ces classes.

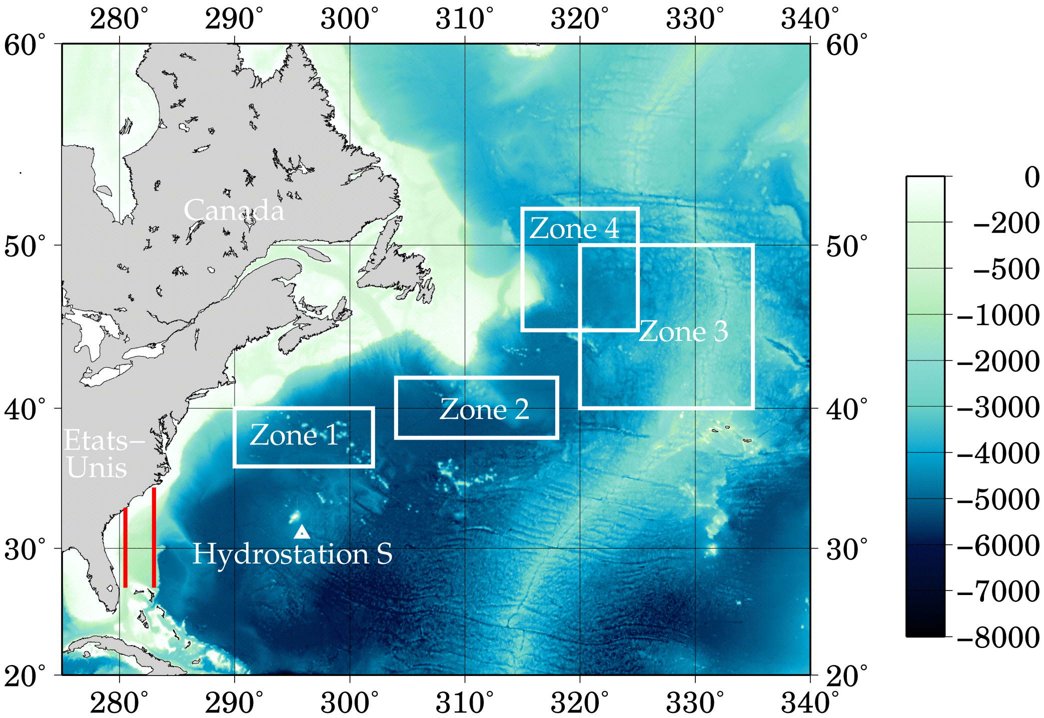

FIG. A.2: Carte de localisation des différents descripteurs utiliser pour analyser la validité des modèles (cf. A.2.2.3). La température est mesurée à l'*Hydrostation S* (triangle blanc) et les vitesses et les énergies cinétiques sont calculées dans les quatre zones décrites (échelle de couleur représentant la bathymétrie en m).

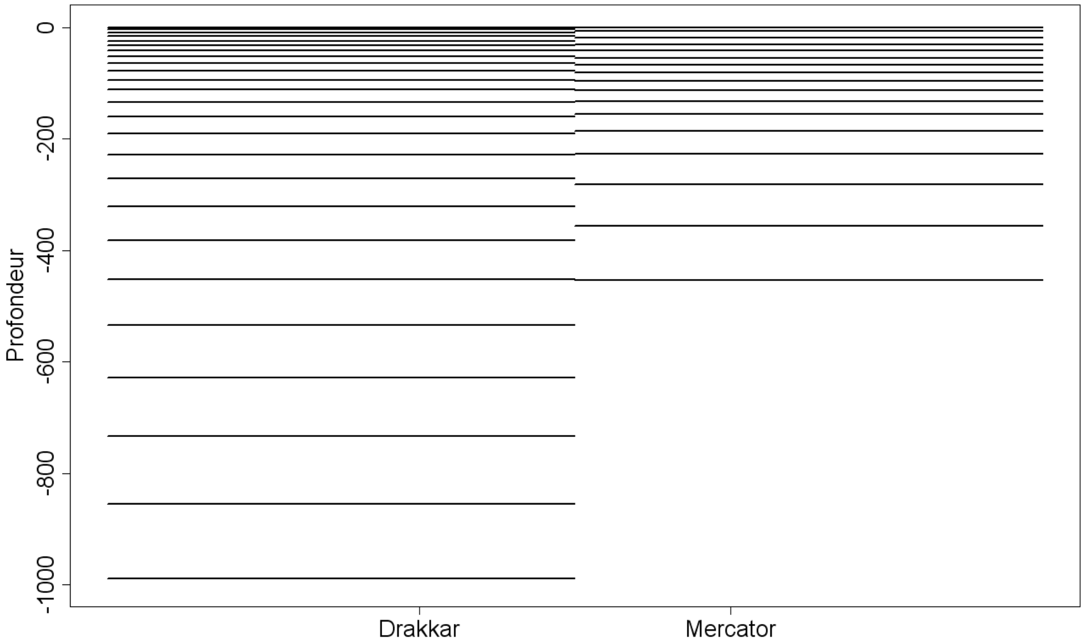

FIG. A.3: Les différentes profondeurs des couches verticales des modèles Drakkar et Mercator

Dans les modèles hydrodynamiques, les différents paramètres (vitesse, température, salinité) sont considérés constants au sein de chaque couche verticale (Fig. A.3). Lors du calcul de la température moyenne mensuelle de ces classes, nous avons pondéré la température dans chaque couche par son importance dans la classe. Par exemple, pour le modèle Drakkar, les couches 1, 2, 3, et 4 font partie de la classe 0-20 m. Cependant, elles ne représentent pas toutes la même proportion de cette classe. Sur les 20 m, la couche 1 fait 3 m, la couche 2, 6 m, la couche 3, 7 m et la couche 4, 8 m. Nous avons calculé la moyenne de température dans chaque couche pondérée par son épaisseur.

Gulf Stream Index Le “Gulf Stream index” est une mesure de la latitude du Gulf Stream issue de cartes aériennes et satellites et d’observations de surface. Il est calculé en utilisant la position du mur Nord du Gulf Stream à 6 longitudes (79, 75, 72, 70, 67 et 65°W).

La série temporelle disponible pour la configuration Mercator étant trop courte, nous ne l’avons pas utilisée pour cette partie. Afin d’estimer la position de ce mur Nord d’après les données de Drakkar, nous avons considéré que sur la même longitude, un fort gradient de température indiquait sa position. Nous avons retenu qu’une différence de 6°C entre deux latitudes distante de 1° était un bon indicateur de la position du mur Nord. Cependant, lors de la période d’été, le Gulf Stream remonte très proche de la côte du Sud des Etats-Unis. Ainsi, pendant les mois d’été, la position du mur Nord était à la côte pour les longitudes 79, 75, 72 et 70. Nous n’avons retenu que les deux longitudes les plus Est pour cette analyse, c’est-à-dire 67 et 65°W. La position du mur Nord a une variabilité différente suivant la longitude observée. Il n’est dès lors pas pertinent de faire une moyenne à ces différentes longitudes ayant des variances différentes. Pour regrouper les variations de ces positions en un indice synthétique moyen tel que le Gulf Stream index, nous avons réalisé une Analyse en Composante Principale (ACP) des positions du mur Nord du Gulf Stream pour les deux longitudes. Nous avons récupéré les valeurs de l’axe 1 de cette ACP. Cette indice calculé est ensuite comparé au Gulf Stream Index de Taylor and Stephens (1998) disponible sur le site `http://www.pml-gulfstream.org.uk` et nous a été fourni par Arnold Taylor (Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, Devon, United Kingdom).

Vitesse des courants La vitesse des courants des modèles est comparée à celle de données observées. Elles correspondent aux données issues de 1500 flotteurs dérivant à 15 m de profondeur suivis par satellite depuis 1990 dans l'Atlantique Nord. Ces données sont regroupées dans les archives publiques du "*Global Drifter Data Assembly Center*" et nous ont été fournis par David M. Fratantoni (Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA). Nous avons ainsi pu reproduire les principaux critères retenus dans l'analyse de Fratantoni (2001) avec les flotteurs. Il s'agit de la vitesse moyenne et maximale dans douze zones de l'Atlantique nord (Tableau A.2) et de profils méridionaux de vitesse à différentes longitudes (70- 65, 60, 55, 50°W) pour des latitudes allant de 33 à 45°N.

L'énergie cinétique turbulente Afin de comparer la capacité des modèles à reproduire la réalité physique, nous avons calculé l'énergie cinétique turbulente (Eddy Kinetic Energy, EKE). Il s'agit de l'énergie cinétique associée à la turbulence d'un fluide. Elle est définie par l'équation :

$$EKE = \frac{1}{2}.(u'^2 + v'^2) \tag{A.1}$$

où u' représente l'écart à la moyenne de la vitesse zonale (Ouest-Est) et v', l'écart à la moyenne de vitesse méridionale (Sud-Nord). De la même manière que pour la vitesse, nous avons comparé les critères retenus par Fratantoni (2001) avec les modèles puis les modèles entre-eux. Dans un premier temps, nous avons calculé la différence entre les données en chaque point avec les résultats des modèles, puis nous avons calculé l'EKE dans quatre zones pertinentes pour notre étude (Fig. A.2; Fratantoni, 2001).

A.3 Résultats

A.3.1 La température est bien reproduite dans la mer des Sargasses

Les températures des modèles correspondent bien aux températures observées jusqu'à 300 m (Fig. A.4). Pour des couches plus profondes, (-300 à 1000 m) le modèle Mercator reconstitue mieux la réalité des températures même s'il semble surestimer la température quelles que soient les couches.

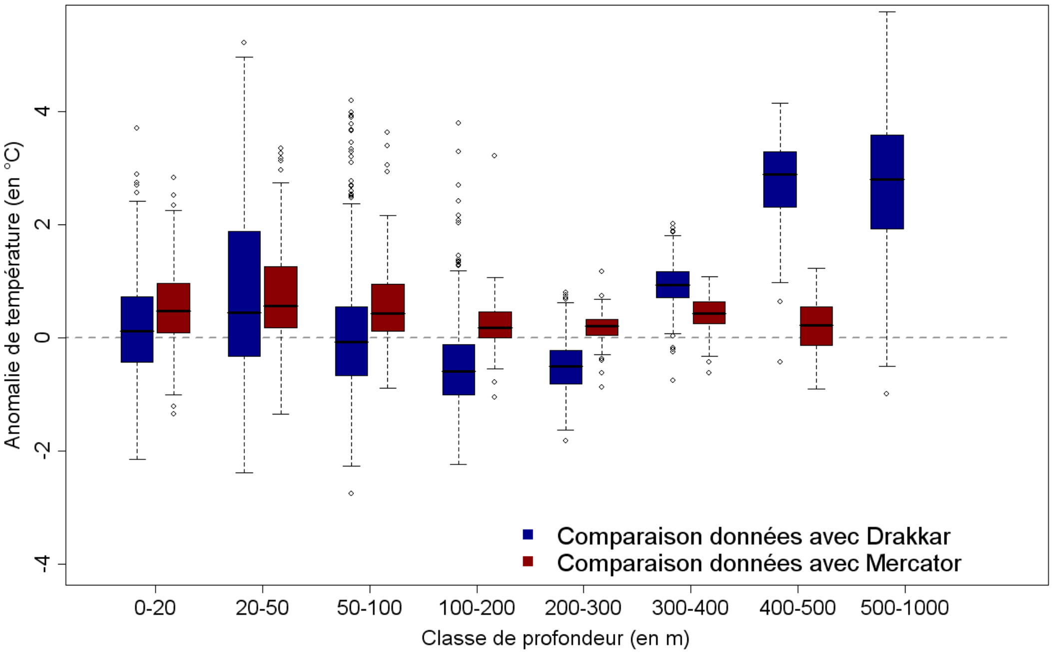

FIG. A.4: Différence entre la température observée à l'*Hydrostation S* et celle donnée par les modèles à cet endroit

La variance de l'anomalie de température est plus grande avec le modèle Drakkar qu'avec Mercator. Deux raisons peuvent expliquer ce phénomène. Le modèle Drakkar peut avoir de plus grandes différences ponctuellement avec les observations. La période sur laquelle cette anomalie est calculée est plus grande (1960-2004 pour Drakkar, 1992-2002 pour Mercator).

A.3.2 Le Gulf Stream Index est corrélé à l'indice de Taylor et Stephens (1998)

L'axe 1 de l'ACP des valeurs de latitudes trouvées explique 84,1 % de la variance. Afin d'appréhender la relation entre l'indice de Gulf Stream de Taylor and Stephens (1998) et celui calculé pour Drakkar, une moyenne mobile sur trois ans a été calculée. L'objectif est d'effacer la variabilité interannuelle afin de faire ressortir les fluctuations à long terme. Nous observons une bonne relation entre les deux courbes (Fig. A.5 ; $r = 0.75$, $p = 0.006$; après correction de l'autocorrélation, Pyper and Peterman, 1998). L'indice recalculé ne chute pas au milieu des années 1990 comme cela peut être observé pour le GSI.

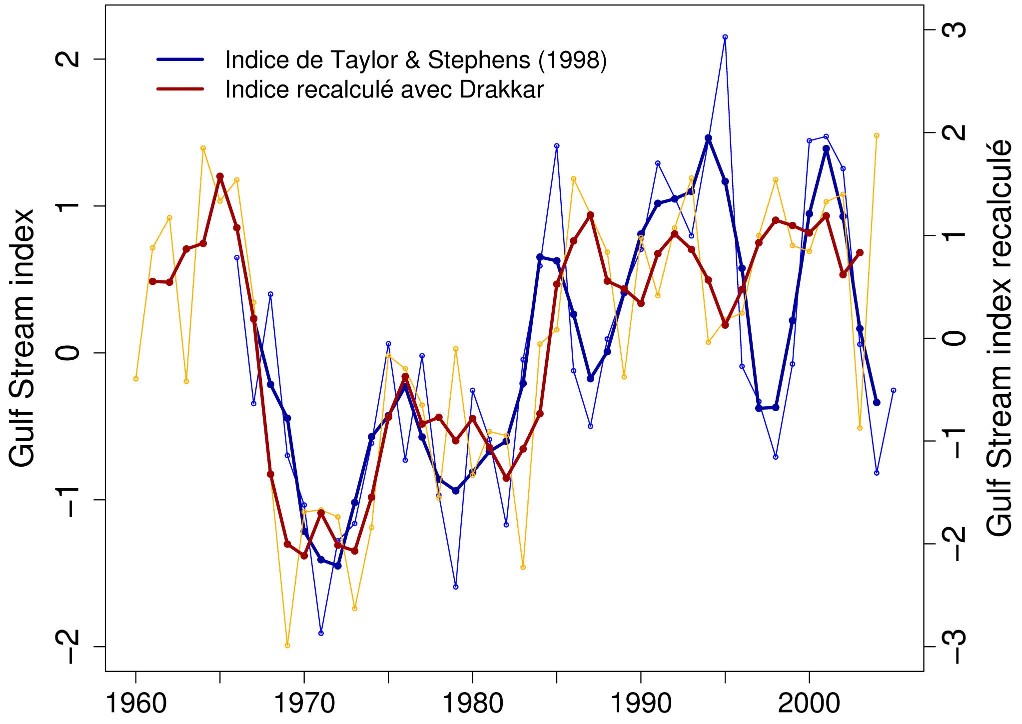

FIG. A.5: Comparaison du Gulf Stream Index de Taylor and Stephens (1998) et du Gulf Stream index recalculé en utilisant les données Drakkar. Les traits fins sont les données annuelles et les traits en gras correspondent à la moyenne mobile des données.

A.3.3 Les vitesses de courant correspondent aux données *in situ*

Dans les quatorze courants majeurs de l'Atlantique Nord définis par Fratantoni (2001), les vitesses maximales et moyennes ont été calculées dans le cas des configurations océaniques Drakkar et Mercator. Nous pouvons comparer ces valeurs aux données de flotteurs (Tableau 1 de Fratantoni, 2001).

Les vitesses maximales (Tableau A.2) observées dans les régions qui vont concerner notre étude (Courant de Floride, Gulf Stream, et Dérive Nord Atlantique) sont sous-estimées par les deux modèles par rapport aux données fournies dans Fratantoni (2001).

Les vitesses moyennes des configurations Drakkar et Mercator (Tableau A.3) sont quant à elles cohérentes avec les données observées dans les zones qui concernent *a priori* plus particulièrement notre étude.

Des profils méridionaux de la vitesse zonale (Ouest - Est) ont été réalisés à différentes longitudes dans la zone du Gulf Stream (Fig. A.6). Ces profils montrent que dans les régions où les larves d'Anguille sont censées dériver, les vitesses des courants sont similaires aux données *in situ*.

TAB. A.2: Vitesses maximales dans les principaux courants de l'Atlantique d'après Fratantoni (2001) et comparaison aves les configurations Drakkar et Mercator (n.c. = non calculable ; en rouge les zones qui concerne plus particulièrement notre étude)

	Vitesse maximale (en cm.s^{-1})					
	Fratantoni (2001) (1)	Drakkar (2)	Mercator (3)	(1)-(2)	(1)-(3)	(2)-(3)
South Equatorial (35°W-20°W, 5°S-4°N)	145	n.c.	212	n.c.	-67	n.c.
North Equatorial (40°W-20°W, 4°N-8°N)	147	n.c.	165	n.c.	-18	n.c.
North Brazil (60°W-50°W, 5°N-10°N)	171	n.c.	211	n.c.	-40	n.c.
Carribean Current (75°W-65°W, 11°N-18°N)	123	211	137	-88	-14	74
Yucatan Current (90°W-84°W, 18°N-22°N)	177	n.c.	227	n.c.	-50	n.c.
Gulf of Mexico Loop Current (90°W-80°W, 22°N-28°N)	209	n.c.	202	n.c.	7	n.c.
Florida Current (81°W-78°W, 24°N-28°N)	239	206	173	33	66	33
Gulf Stream (70°W-60°W, 37°N-39°N)	273	168	202	105	71	-34
North Atlantic Current (50°W-40°W, 40°N-50°N)	209	162	193	47	16	-31
Labrador Current (56°W-51°W, 52°N-56°N)	107	94	89	13	18	5
East Greenland Current (45°W-40°W, 58°N-64°N)	188	47	172	141	16	-125
West Greenland Current (53°W-46°W, 59°N-64°N)	179	68	118	111	61	-50
Norvegian Current (10°W-10°E, 61°N-66°N)	106	n.c.	107	n.c.	-1	n.c.
Azores Current (45°W-25°W, 32°N-36°N)	111	39	87	72	24	-48

TAB. A.3: Vitesses moyennes dans les principaux courants de l'Atlantique d'après Fratantoni (2001) et comparaison aves les configurations Drakkar et Mercator (n.c. = non calculable ; en rouge les zones qui concerne plus particulièrement notre étude)

	Vitesse moyenne (en cm.s^{-1})					
	Fratantoni (2001) (1)	Drakkar (2)	Mercator (3)	(1)-(2)	(1)-(3)	(2)-(3)
South Equatorial (35°W-20°W, 5°S-4°N)	34	n.c.	39	n.c.	-5	n.c.
North Equatorial (40°W-20°W, 4°N-8°N)	42	n.c.	39	n.c.	3	n.c.
North Brazil (60°W-50°W, 5°N-10°N)	45	n.c.	51	n.c.	-6	n.c.
Carribean Current (75°W-65°W, 11°N-18°N)	31	37	36	-6	-5	1
Yucatan Current (90°W-84°W, 18°N-22°N)	41	n.c.	40	n.c.	1	n.c.
Gulf of Mexico Loop Current (90°W-80°W, 22°N-28°N)	61	n.c.	56	n.c.	5	n.c.
Florida Current (81°W-78°W, 24°N-28°N)	97	95	79	2	18	16
Gulf Stream (70°W-60°W, 37°N-39°N)	60	57	67	3	-7	-10
North Atlantic Current (50°W-40°W, 40°N-50°N)	38	36	39	2	-1	-3
Labrador Current (56°W-51°W, 52°N-56°N)	21	35	27	-14	-6	8
East Greenland Current (45°W-40°W, 58°N-64°N)	27	14	29	13	-2	-15
West Greenland Current (53°W-46°W, 59°N-64°N)	27	26	31	1	-4	-5
Norvegian Current (10°W-10°E, 61°N-66°N)	18	n.c.	27	n.c.	-9	n.c.
Azores Current (45°W-25°W, 32°N-36°N)	18	23	28	-5	-10	-5

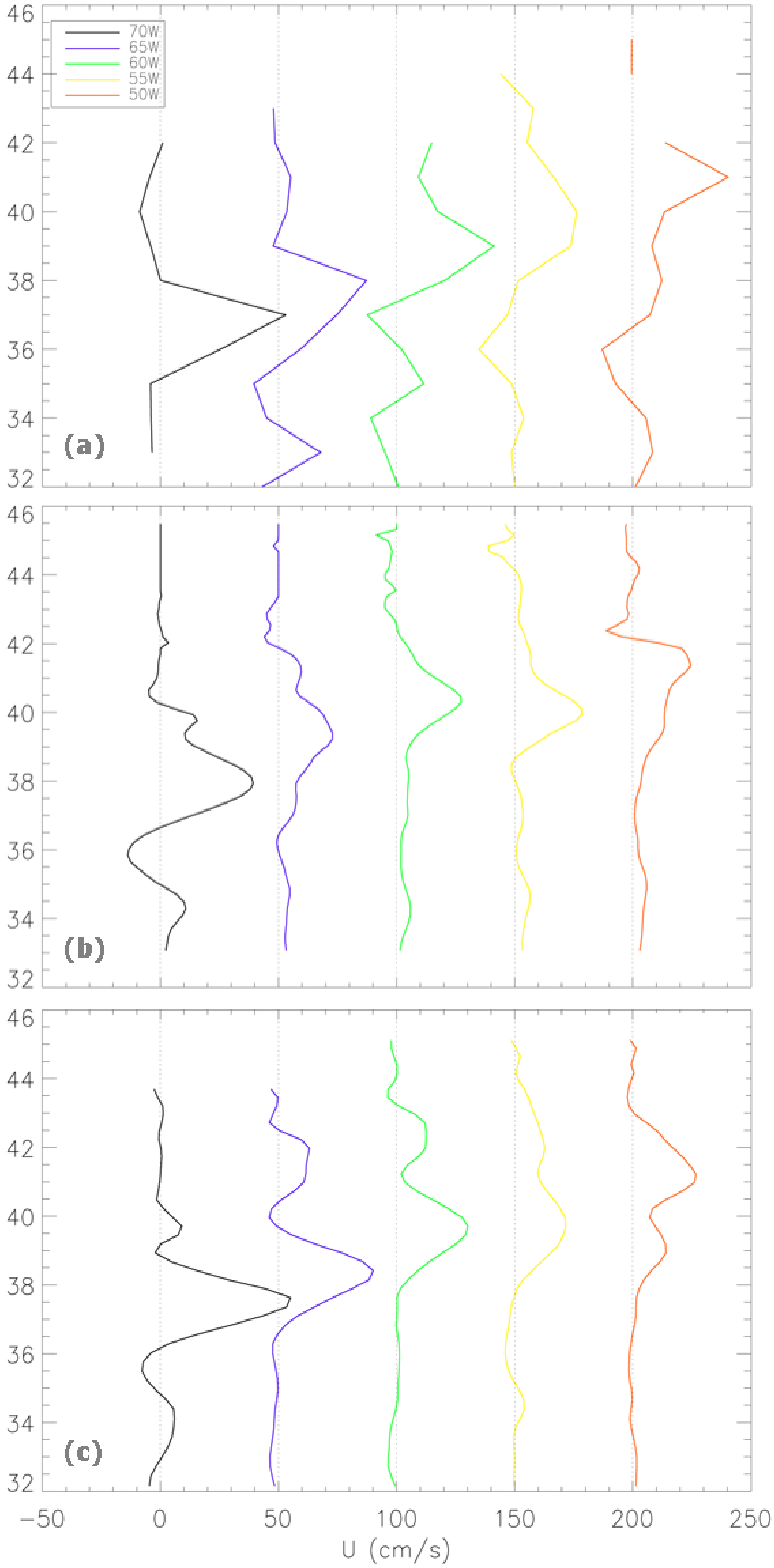

FIG. A.6: Comparaison des profils méridionaux de vitesse zonale, u, à 70, 65, 60, 55 et 50°W entre les données observées (a) de Fratantoni (2001) et le modèle Drakkar (b) et Mercator (c). Les profils

A.3.4 L'Eddy Kinetic Energy annonce quelques différences entre les deux modèles

La comparaison des énergies cinétiques des modèles par rapport aux données de Fratantoni (2001) et de Richardson (1983) montre que les modèles sous-estiment l'énergie cinétique turbulente (Fig. A.7). De plus, le modèle Mercator semble avoir une EKE supérieure au modèle Drakkar.

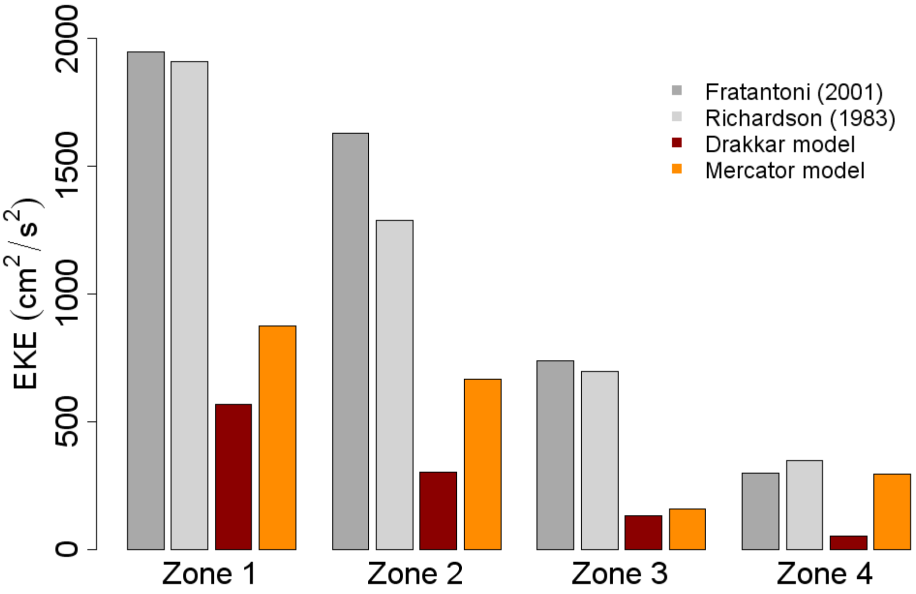

FIG. A.7: Comparaison des énergies cinétiques turbulentes dans 4 zones du Gulf Stream (cf. Fig. A.2 entre les données observées de Fratantoni (2001) et de Richardson (1983) et le modèle Drakkar et Mercator.

D'un point de vue global, les cartes des moyennes des EKEs sur la période 1990-2000 à l'échelle du bassin de l'Atlantique Nord montrent que les modèles Drakkar et Mercator (Fig. A.8a et b) représentent bien la partie du Gulf Stream et de la Dérive Nord Atlantique. Il semble que le modèle Mercator représente mieux le courant des Açores.

De la même manière que pour les champs de vitesse, des profils d'énergie cinétique turbulente ont été réalisés à différentes longitudes dans le Gulf Stream (Fig. A.9). Le modèle Drakkar a tendance à sous estimer les valeurs de l'énergie cinétique (Fig. A.9b). Le modèle Mercator quant à lui surestime la valeur d'énergie cinétique pour la longitude 70°W mais sous estime les valeurs pour les autres longitudes.

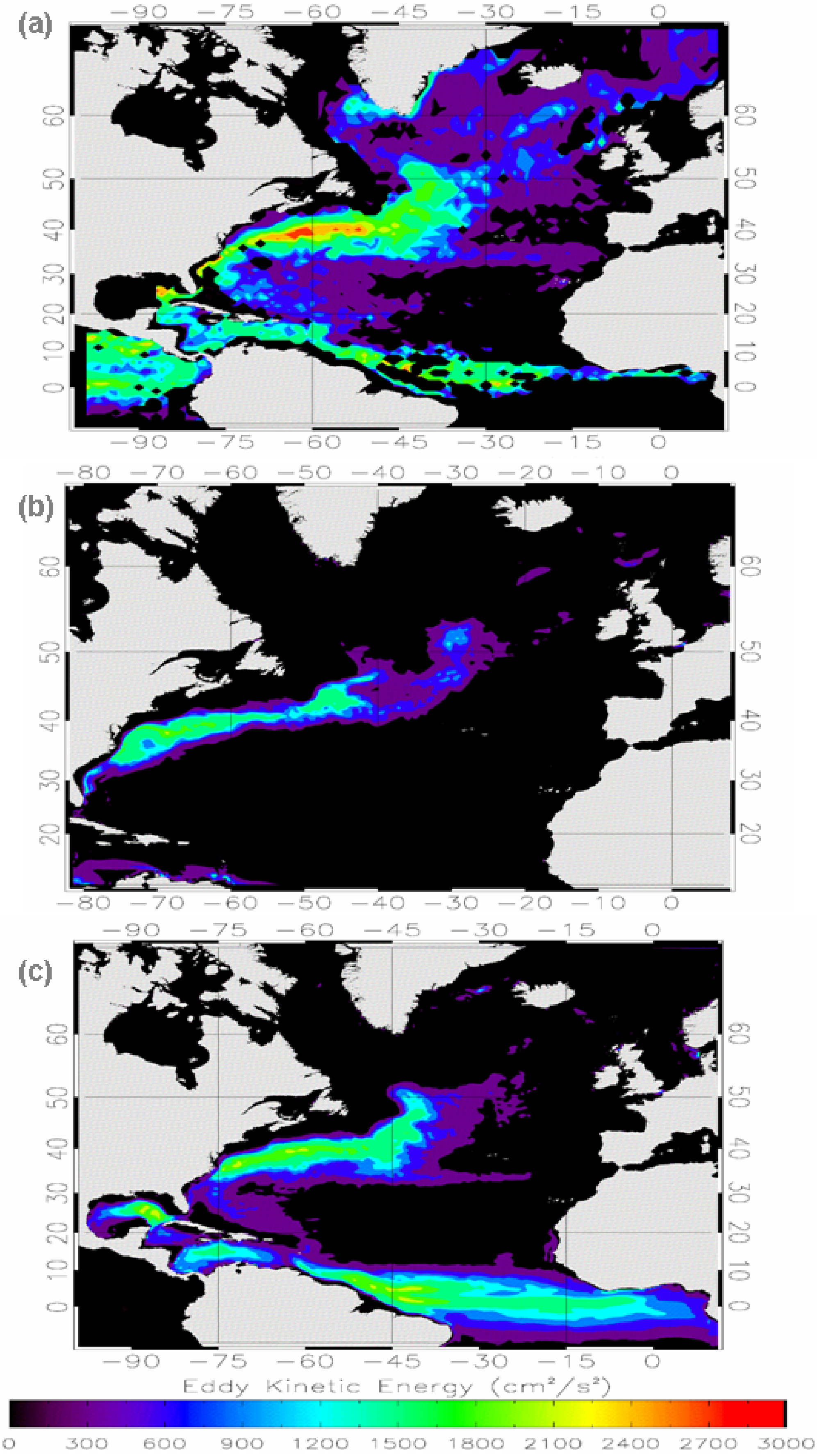

FIG. A.8: Moyenne des énergies cinétiques turbulentes sur la période de 1990 à 2000 à l'échelle de l'Atlantique Nord d'après le données de Fratantoni (2001) (a), du modèle Drakkar (b) et du modèle Mercator (c).

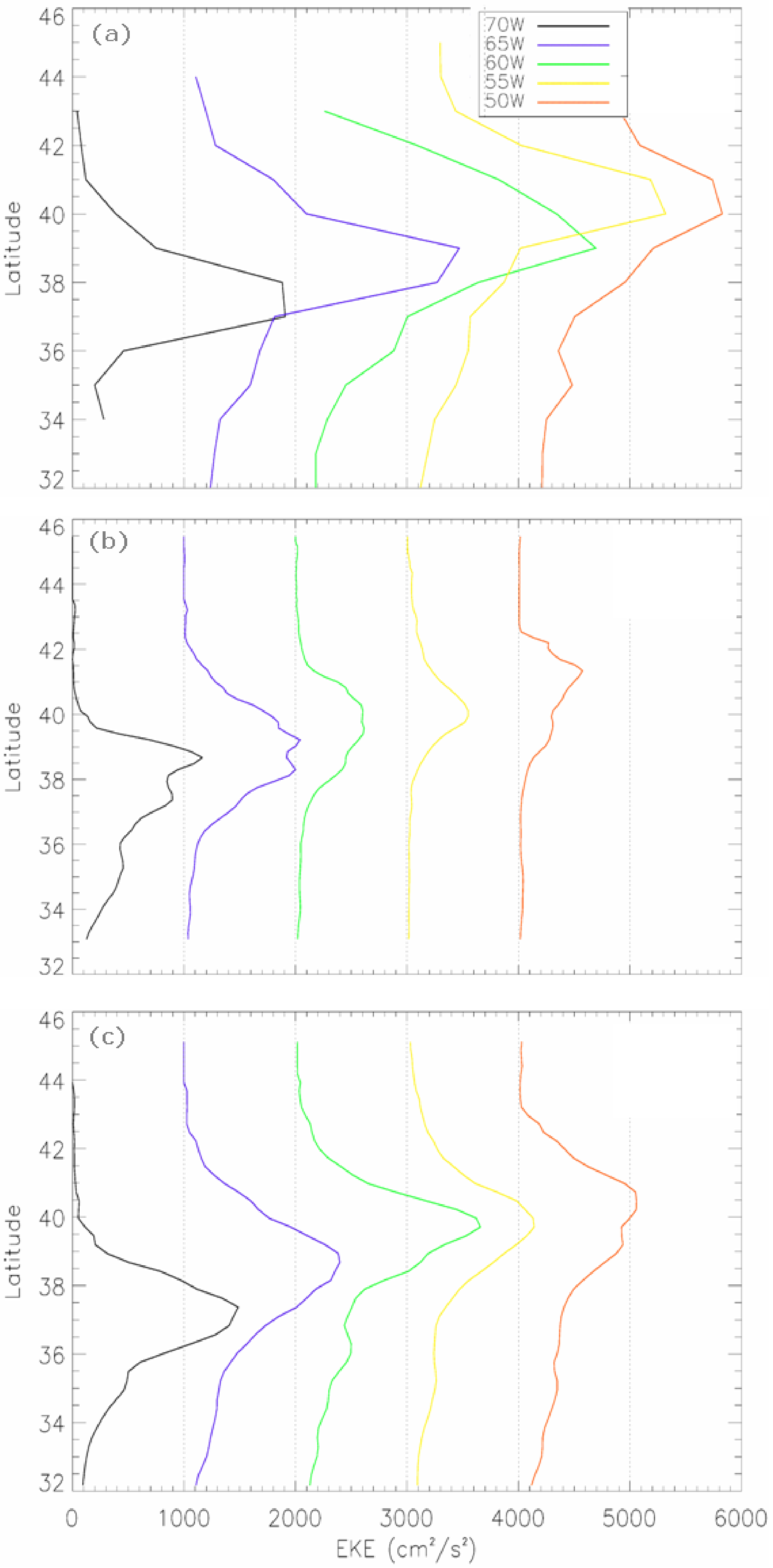

FIG. A.9: Comparaison des profils méridionaux d'énergie cinétique turbulente, *EKE*, à 70, 65, 60, 55 et 50°W entre les données observées (a) de Fratantoni (2001) et le modèle Drakkar (b) et Mercator (c).

Ces différents résultats montrent que les modèles ont une bonne estimation des vitesses moyennes des différents courants et en particulier dans les zones qui vont nous intéresser par la suite. Une bonne cohérence avec les indices de circulation océanique est trouvée. Les modèles sous-estiment l'énergie cinétique turbulente et la vitesse maximale des courants.

A.4 Discussion

L'objectif de ce chapitre n'est pas de valider les modèles physiques car cela est déjà fait mais de comprendre leur fonctionnement et leurs caractéristiques en relation avec notre problématique. Ces informations pourront nous être utiles pour l'interprétation des différences observées entre les modèles lors des simulations lagrangiennes.

Un réalisme satisfaisant et des différences à prendre en compte pour l'interprétation lagrangienne

La température Les données de température sont cohérentes avec les résultats des modèles excepté pour les couches d'eau plus profondes de Drakkar qui ne nous intéressent finalement que très peu dans notre cas d'application étant donné que les larves ne sont pas observées à ces profondeurs. Nous n'avons pas comparé les données de température des modèles avec des données plus globales comme les données du satellite SeaWif car ces validations ne relèvent pas de notre objet d'étude et sont analysées par les différents laboratoires qui développent les modèles. L'objectif est de conforter les données de température des modèles dans une zone qui va être utilisée par la suite (cf chap 5 et 6) car elle est située proche de l'aire de ponte estimée des Anguilles.

Le Gulf Stream index est bien reproduit par les modèles Certaines différences entre les observations et le modèle Drakkar apparaissent pour des évènements particuliers comme la diminution du Gulf Stream index observée au le milieu des années 90. Ces diminutions comme celle de la NAO à cette période ne sont toujours pas expliquées par les scientifiques. Les modèles physiques ont quant à eux une certaine inertie de fonctionnement qui ne leur permet pas de retranscrire ces variations d'amplitudes rapides

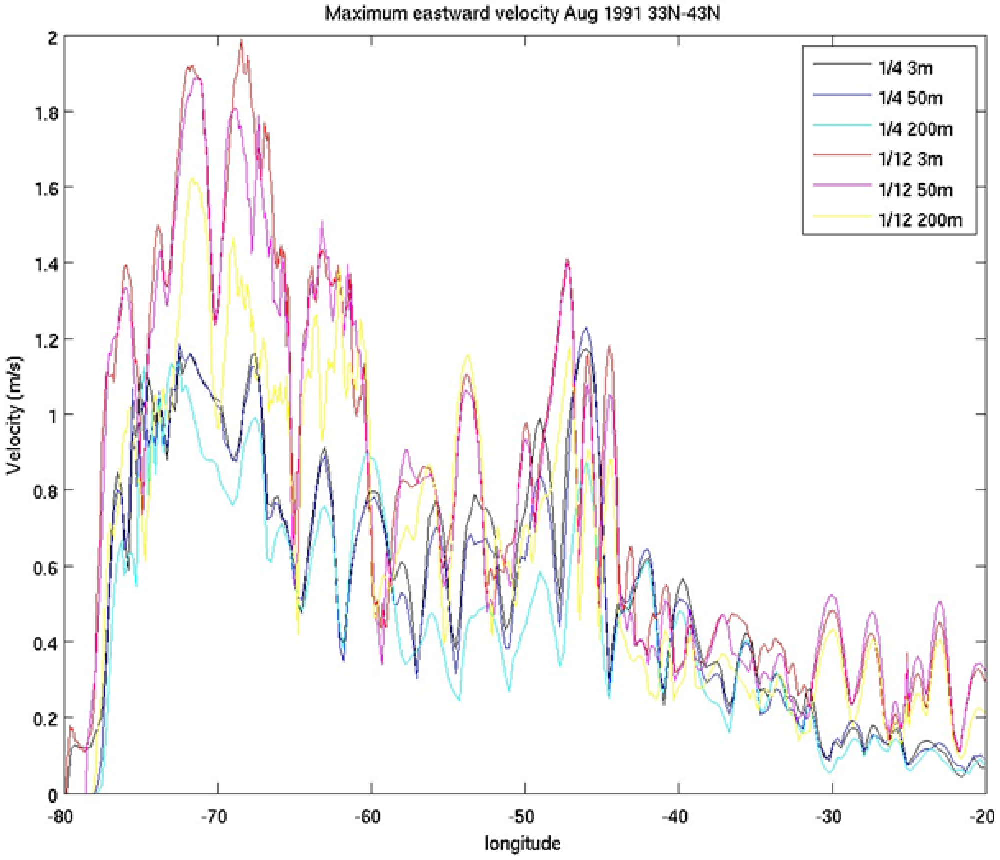

FIG. A.10: Comparaison des profils méridionaux de vitesses maximales entre le modèle Drakkar à 1/12 de degré et Drakkar à 1/4 de degré à trois profondeurs différentes entre les latitudes 33°N et 43°N dans l'Atlantique Nord en Août 1991. Figure fournie par Anne-Marie Tréguier (LPO, Brest).

difficilement compatibles avec une conservation exacte d'invariants physiques. Pour l'Atlantique Nord, cette variabilité océanique devrait être partiellement conditionnée par l'atmosphère qui est prise en compte par les modèles utilisés. Une des sources des écarts entre les modèles et les données pourrait être à rechercher dans la nature "forcée" des simulations océaniques, sans prise en compte possible d'une rétroaction active de l'océan sur l'atmosphère. Dans la réalité, l'état de surface de la mer (température, rugosité,...) module la couche limite atmosphérique et a ainsi un impact à petite et à grande échelle sur la dynamique de l'atmosphère. Une autre source possible d'erreurs tient à la nature "lente" de l'océan. Certaines rétroactions océan-atmosphère mettent en jeu des propriétés océaniques induites par la remontée d'anomalies de température (ou de salinité), issues du déplacement sur de grandes distances de masses d'eau (Bruno Blanke, comm. pers.). Par exemple, les eaux qui remontent à la surface de l'océan dans le Gulf Stream ont en partie été "formées" (c'est-à-dire qui ont quitté la couche de mélange océanique) dans des régions aussi distantes que les tropiques, avec des trajets de plusieurs années (voire plusieurs dizaines d'années). Aussi bon que soient le modèle d'océan et les forçages appliqués à sa surface, la complexité du processus est telle qu'il peut être mal représenté, et donc impacter certains indices “grande échelle” (Bruno Blanke, comm. pers.).

Vitesses des courants Les modèles physiques sous-estiment les vitesses maximales mais estiment bien les vitesses moyennes. Ce phénomène s'explique par le besoin de conserver la masse entre les différentes couches modélisées. Une couche beaucoup plus rapide à certains endroits va nécessiter un transfert de masse important dans une autre couche par la suite et ces phénomènes locaux sont très difficiles à retransmettre dans les équations de la dynamique des fluides. Ainsi, lorsque l'on considère une particule d'eau, il est probable que le transport moyen d'un bout à l'autre de l'Atlantique ne change pas beaucoup entre les modèles et la réalité physique (Anne-Marie Tréguier, comm. pers.). Anne-Marie Tréguier nous a fourni un autre élément de comparaison qui permet de bien comprendre les phénomènes en jeu. La comparaison de la vitesse maximale vers l'Est entre les latitudes 33N et 43N à trois profondeurs différentes en aout 1991 pour chacun des modèles ORCA025 1/4 degré (le modèle DRAKKAR utilisé) et NATL12 (nouveau modèle à plus haute résolution, $1/12^o$) montre qu'il y a pratiquement un facteur 2 entre les vitesses maximales des deux modèles (Fig. A.10). Ainsi, les particules d'eau vont plus vite avec un modèle ayant une meilleure résolution mais seront aussi plus sujettes à des méandres, des tourbillons, des recirculations qui les dispersent, et en fin de compte les ralentissent comme le montre la Figure A.11.

Dans notre cas d'implication, les particules des simulations lagrangiennes auront une vitesse moyenne qui correspond à la réalité physique de l'océan. Dans l'hypothèse où les larves peuvent choisir les courant les plus rapides, les simulations vont néanmoins sous-estimer la vitesse maximale qu'elles peuvent avoir par rapport à la réalité. Cependant, ces forts courants sont associés à de fortes turbulences qui ralentissent la dérive des particules.

L'énergie cinétique turbulente La Fig. A.8 confirme que l'EKE est plus faible dans les modèles que dans les données observées. La turbulence est plus faible dans ces modèles qui sont considérés comme “eddy permitting” et non “eddy resolving”. Cela signifie qu'ils sont capables de reproduire l'existence des tourbillons d'une taille d'environ 40 km mais pas de résoudre les turbulences plus fines qui sont très souvent observées dans cette région de l'Atlantique Nord. Les particules relâchées ont ainsi des trajectoires plus linéaires que

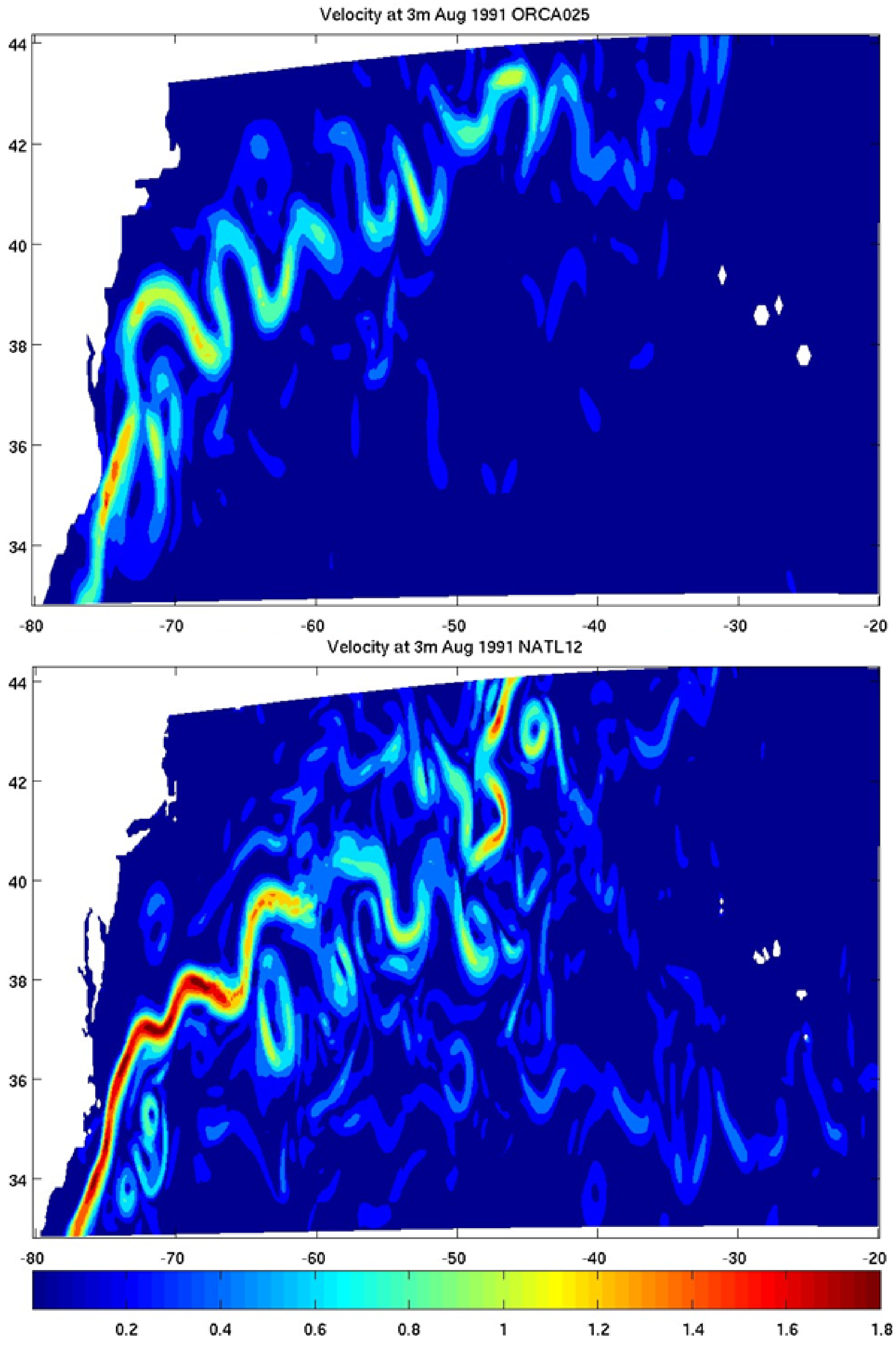

FIG. A.11: Représentation des modules de vitesse $(|\vec{u}+\vec{v}|)$ dans la zone du Gulf Stream pour le modèle Drakkar à 1/4 de degré (haut) et à 1/12 de degré (bas). Figure fournie par Anne-Marie Tréguier (LPO, Brest).

la réalité mais aussi moins de chances de se faire piéger dans des zones tourbillonnaires. Les deux modèles semblent aussi avoir des comportements différents de par la localisation des courants. Le courant des Açores est bien représenté dans la cas de Mercator et semble faible pour Drakkar.

Cette comparaison entre les données et les modèles mais aussi entre les modèles nous permet de mieux comprendre le fonctionnement global des modèles et de leurs limites. Ces modèles sont validés, font partie des plus précis à l'heure actuelle dans la communauté scientifique européenne et retranscrivent une bonne réalité physique de l'océan. Trois principaux résultats sont à retenir :

- les vitesses moyennes sont une bonne représentation de la réalité physique,
- les vitesses maximales sont sous-estimées par les modèles physiques,
- les tourbillons sont moins bien représentés que dans la réalité,
- des différences de comportements des modèles sont observées, notamment au niveau du courant des Açores

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$\mathcal{B}$

Tendance des stocks et des recrutements en Europe

Status and trends in European eel (*Anguilla anguilla* L.) stocks and recruitment in north west Europe

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In prep.

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Summary/Abstract For 54 eel stock datasets from North West Europe (indexed to their 1979-94 means), inter-annual variability was high during 1970-2006 but 61% showed no significant changes, 35% showed significant declines and 4% showed significant increases. Comparable trends in 31 of these datasets comprising continuous time series were 55%, 39% and 6% respectively.

Geomeans of combined time series for glass eel recruitment in North Atlantic/North Sea sites have declined by ≈200% from a peak in 1979 with a significant downward regime shift in 1983. Baltic yellow eel recruits have shown a decline of ≈650% from a peak in 1958, with a negative regime shift in 1961. Stocks have however only declined by about 90% and 200% respectively over the same time period. Direct and indirect evidence shows that similar or larger (but not such prolonged) fluctuations in recruitment and stocks have occurred historically. Buffering of fluctuations in stock levels may be due to compensatory changes in density-dependent mortality and sex determination and/or reductions in competition and hence enhancement of survival, growth rates and biomass. It is also possible that upstream and inter-habitat migrations of yellow eels during summer (especially from brackish/coastal waters) may be very important in determining stock status, in comparison with glass eel recruitment *per se*.

Glass eel recruitment and stock geomeans have tended to show fluctuations over about 4 to 8 years (comparable to those in the North Atlantic Oscillation (NAO)) and to be positively correlated at lags of -3 to +1 year. However, peaks and troughs in glass eel

recruitment would be expected to lag those in stocks by a larger number of years, as needed to complete maturation, emigration, spawning and leptocephalus/glass eel migrations. It is possible that recruits to northern Europe are actually mainly derived from production of spawners in more southerly European countries, seeing that commercial landings of eels in South Europe tend to be negatively correlated over time with those from North Europe (Kettle *et al.*, in press). Longer lags would also be expected between maxima in recruitment and stock geomeans, to account for the time taken to grow to catchable size. It is possible that higher temperatures and precipitation during periods of high NAO enhance growth rates and/or overall activity levels and migrations and hence earlier and more efficient capture. Correlations are unclear for Baltic yellow eel v. stock geomeans, this may be partly due to the sparse and variable data available.

Prior to 1980, recruitment of glass eels was significantly negatively correlated at lags of 1-2 and 7 years with the NAO and positively correlated with the Sargasso Sea sea surface temperature anomaly (SS-SST). Relationships were less clear in subsequent years when the NAO, SS-SST and North Hemisphere Temperature (NHT) increased to sustained high levels and autocorrelation interferences high. The evidence supports hypotheses that oceanic changes associated with warming have had negative impacts on leptocephalus nutrition and transport. Key transitions after 1980 include a rise in SS-SST to 21.6°C and a decline in primary productivity in the Sargasso Sea (Bonhommeau *et al.*, 2008) and to northward shifts in isotherms defining the spawning area and declines in mixed layer depths (Friedland *et al.*, 2007)

Major declines in recruitment of yellow eels in Baltic sites occurred from the 1960s but geomeans shows unclear inter-annual relationships to the winter NAO, NHT and SS-SST. Transport of recruits from the North Sea into the Baltic via the Danish Straits has probably been particularly dependent on high NAO/strong westerly winds and also on Major Baltic inflows of saline water (MBI). The latter only occur after a period of high easterlies/low NAO in the autumn followed by high winter-spring westerlies / high NAO. Such conditions have been uncommon since the 1960s and only three MBIs have occurred in the last 35 years.

Although (sometimes unclear) inter-annual variations in recruitment and stocks have occurred in response to the environmental indices, major decadal trends have been clearly related to the NAO. Glass eel recruitment to the North Atlantic / North Sea tended to fall or be relatively low during the high NAO/warming periods around 1900-1920 and in the 1940-50s, 1960-70s and, most notably, since about 1980, probably because of changes in oceanic conditions unfavourable for leptocephali. Conversely, yellow eel recruitment in the Baltic has shown positive relationships to the NAO over the long term, supporting the hypothesis that high NAO / high westerly wind conditions have encouraged transport of recruits from the North Sea into the Baltic. Lack of recovery in recent decades may be due to the lack of MBIs and/or the species-wide decline in numbers of recruits. Despite some stabilisation of the NHT and falls in the NAO in recent years, recruitment and stocks are still relatively low, but some evidence is revealed of recent and possible future recoveries.

Results support the hypothesis that ocean-climate factors exert the major controls on recruitment and thence stocks. However, in the light of uncertainties, especially about future warming trends predicted by different climate-change models, application of the precautionary principle may be needed to protect the European eel during its continental life stages. Pragmatic management implications are therefore discussed, including the challenges in determining recruitment and stock reference status and targets, formulation and execution of Eel Management Plans, modelling and monitoring.

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C

Evolution du marché de l’Anguille et implications dans la gestion

An appraisal of historical glass eel fisheries and markets: landings, trade routes and future prospect for management

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Abstract Using commercial and fishery data, we recount the main features and key points of the historical trade of the European eel. Glass eel fisheries have been already active at the end of the XIXth century with landings estimated around 200t, and fisheries and trade mainly developed in the south of France. From this southern point, the market has progressively expanded along the Atlantic coast during the first 30 years of the XXth century. Export of eel towards Spain is accurately reported by the railway statistics and was 531t at its peak in 1925. The Spanish war closed trade, and during Franco regime, the trade route towards Spain, although representing 80 % of the total volume has remained totally opaque. In 1969, the first onset of the Japanese demand in Europe has increased the profitability of a fishery having already introduced push nets all along the coast. The landings in Europe have culminated around 1976 at 2700t. From 1982 to 1995, the drop in recruitment and collapse of Japanese imports have made the fishery less attractive. In 1995, the surge in demand from the Chinese market on a then dwindling stock has brought a large increase in prices, only levelled by the Asian financial crisis in 1997 and the malachite green residues in 2006. The cross analysis from various source of data shows that landings are now below 100t. The increasing profitability despite the severe decline in recruitment brings up the possibility of an 'economic' Alee effect. This effect and the

changes brought by CITES and European regulation are discussed along with the element needed for achieving a sustainable status in the glass eel fisheries.

C.1 Introduction

After a transatlantic migration from the Sargasso Sea to the European and North African shelves, European eel (*Anguilla anguilla*) larvae begin their metamorphose into glass eels. They are juvenile eels that accomplish the final migration from the continental shelf (Tesch, 1977) to the estuaries using a behaviour of tidal stream transport (Gascuel, 1986; Wippelhauser and McCleave, 1987). From transparent, they become pigmented (Elie *et al.*, 1982), resume feeding, and become small yellow eels that will colonize the Inland and coastal waters (Moriarty, 1986a).

The seasonal inshore migration of glass eels occurs in winter (Bertin, 1956; Tesch, 1977; Elie and Rochard, 1994). The distribution area spreads from North Africa (Morocco) to Northern Europe (Norway) including the Mediterranean basin (Schmidt, 1909). Within this distribution, the main fisheries are concentrated in the western Mediterranean, Portugal, the Bay of Biscay, Ireland and the western coast of England (Dekker, 2003). In these areas, the concentration of glass eels in estuaries is large enough to enable glass eel fisheries to be a profitable activity.

In France the glass eel fishery employed 1050 marine professional fishermen and 240 fluvial professional fishermen in 2001 (Castelnaud *et al.*, 2006). The access to an estuary is restricted by the purchase of a stamp. The turnover per boat is around 100 k€ with the glass eel fishery representing from 62 to 100 % of the annual turnover (ICES, 2007).

Glass eel migrations of a lesser importance are known to occur in the Channel (Strubberg, 1923; Tesch, 1977), Skagerak-Kattegatt (Hagström and Wickström, 1990), central and eastern Mediterranean (Schmidt, 1922; Dekker, 2002). In these areas, the glass eel migration has historically supported various trap fisheries and transport operations for restocking purpose. The eel aquaculture has been based on live seeds since European eel reproduction is not currently controlled. For the Japanese eel (*A. japonica*, Japanese researchers have succeeded in reproduction and breeding of larvae to the glass eel stage but no commercial hatchery exists hitherto because of the financial costs of artificial reproduction (Tanaka *et al.*, 2001). The decline in glass eel recruitment for the three main species, the European, American and Japanese eel, has brought large changes in the international glass eel trade (Guérault *et al.*, 1986; Moriarty, 1986b; Moriarty and Dekker, 1997; Anonymous, 2003). Japanese people have a long culinary culture of eel, especially *kabayaki*, roasted eel using a secret soy sauce. At the end of the 1960's, they were confronted to the decline in glass eel catch of Japanese eels. The supplies were no longer sufficient for Japanese market. As an answer to this problem, they imported live European glass eels to provide their aquaculture farms with seeds. The strong Japanese demand has switched to European eel fry rather than American glass eels because of rearing potential and importance of European landings (Bonhommeau Patrick, pers. com.). It has in turn modified the profitability of European glass eel fisheries, in a European context where most eel fisheries are now dwindling to a shadow of their past extent.

The decline in glass eel resources has led to the inclusion of eel in the Annex II B of the Convention on International Trade on Endangered Species of wild fauna and flora in 2007, which will mean that the exporting country will have to prove the sustainable exploitation of each lot traded outside Europe. It has also brought the European commission to adopt a new regulation (1100/2007), which will bring large changes in glass eel trade. The glass eel fisheries will have to reserve a part of their catch, from 35 % in 2009 to 60 % in 2013, for restocking within Europe. In addition, national management plans will have to account for the sustainability of human impacts. In this context, we provide an appraisal of the European glass eel market which has not been studied recently (but see for instance Elie and Fontenelle (1982); Castelnaud *et al.* (1994)). Starting from 1900, we provide an overview of the changes brought in the glass eel fishery, try to rebuild a series of landings and trade from the best available information, and finally try to provide the best description of the current state of glass eel fisheries and trade. From this overview we analyse the risk of economic extinction of the species and give a hint of the possible consequence of the new regulation on trade; we analyse also the basis of a sustainable management.

C.2 Materials and Methods

C.2.1 Analysis of trade data

A database on glass eel trade is built from various sources of trade data:

- the French Custom data (OFIMER) with 580 annual data from 1962 to 2006 reporting trade towards 32 countries,

- the European database EUROSTAT; 12 567 monthly trade data from 1995 to 2007 towards 23 countries,
- Daily shipping records from an independent French glass eel trader which were converted into 256 annual mean export prices and total quantity towards 16 countries from 1961 to 2005 (Bonhommeau Gilbert and Patrick, Somme & Loire, Saint Nazaire, France, personal communication),
- 24 annual glass eel prices from the Asturian market from 1983 to 2006 (Estibalitz Diaz, AZTI, personal communication). Prices are corrected from French and Spanish local inflation to obtain constant current money (basis 2006 for French and Spanish currencies). All prices hereafter are expressed in constant money and correspond therefore to the equivalent price in 2006.

Except for the French trader, trade data do not discriminate eel stages, i.e. , glass eels, yellow eels or silver eels. They only indicate the process applied while preparing the eels: frozen, smoked, alive, or fresh. Based on prices, destination, total weight and process, some monthly or annual records are identified as being constituted of either glass eels or (yellow/silver) eels. For instance, regular trade of small weight and high value between France and Germany, Mexico or Asia can in most of cases be identified as glass eel shipping. By contrast, trades of low value and large weight can be ascribed to eels. All trade towards Italy was identified as being eels. Glass eels have been known to be exported there in the Naples area before the 1980s for food consumption. However, this market has not gone on because of the ban of glass eel fishery in Italy. However, since the largest part of trade has always concerned small eels caught in the French Mediterranean lagoons, and sent to Italy for aquaculture purpose, and since eels have always had a larger value than those eels sold for food consumption in the European market, a unique category was chosen for Italy. The trend in glass eel price is extracted from the previously selected values and compared to the various sources of data. A general linear model is fitted on both import and export data using a weighting according to the trade volume. It is then used to compute the annual mean price per destination. For data where an annual price per destination could not be calculated, the mean or weighted mean price of the four series has been used.

A general trend for the mean price of yellow/silver eel is also calculated. Missing years are interpolated and the whole series is smoothed. As in the case of glass eels, import and export prices are mixed in the analysis. The share between glass eel and eel among values previously identified as a blend of glass eel and eel data is calculated according to the mean annual price of both stages. Commercial data are then used to reconstruct a time series of glass eel export towards various countries.

C.2.2 Analysis of catch data

The annual landings per marine area have been computed both in quantity and value from 1895 to 1983 from the French statistics of the marine administration (Boude, 1987). The records starts in 1902 in the Atlantic region. They are compared to historical trade series available (Gandolfi Hornyold, 1933, 1936) and punctual expert estimates of the volumes landed by the fishery (Arne, 1908; Popelin, 1971; Castelnaud *et al.*, 1994; Castelnaud, 2000, 2002; Léauté and Caill-Milly, 2002). More recent statistics collected by the administration for small boats from 2000 to 2006 have been analysed. They have been discarded as incomplete or irrelevant. When compared with local records from other source, the estimation of the real landings is underestimated by a factor 2 to 10.

C.2.3 Time series of landings

An attempt has been made to rebuild the possible series of landings of glass eel from trade and catch data, by using expert estimates of the volume of export in 1975 and by correcting the volume of trade towards Spain to account for the underreporting of the trade of frozen glass eels. For the current European market, the mean value of 1996-2006 Eurostat trade statistics have been used to analyse volumes exchanged across Europe and towards Asia.

C.3 Results

In the OFIMER database, 129 annual exports or imports have been identified as eels, 155 as glass eels, and 296 as a blend of glass eel and eel data. In the EUROSTAT database, 2 263 monthly exports or imports have been identified as glass eels, 6474 as eel and 3830 as a blend of glass eel and eel. The glass eel prices show an exponential rise from around 5€ in the 1960's to a maximum of 500€ per kg in 2005 (Fig. C.1). The peak in

1969 corresponds to the first onset of Japan on the French market. The prices are quite synchronous among series, and those could be combined to obtain a consistent price series (Table C.1).

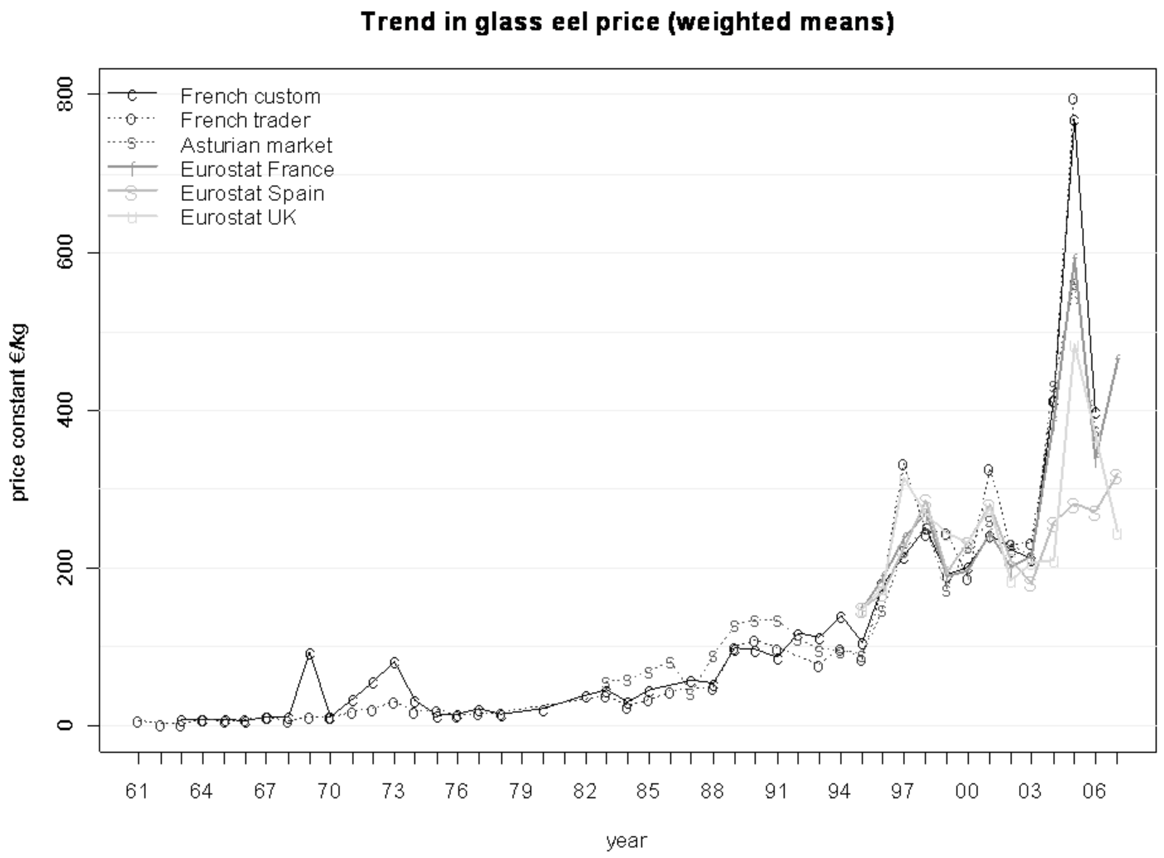

Figure C.1: Trend in glass eel prices, weighted means computed from the OFIMER annual import and export data, eurostat monthly data, a French trader annual data, and from the Asturian Market annual price series

The mean eel price drops abruptly from 5 to 1€/kg in the 1970's due to the import of large volumes of eels from New Zealand. From this low level, the price rises back progressively to 7€ at the beginning of the 1990's (Fig. C.2, Table C.2). A more detailed analysis of Eurostat database shows that the prices are highly variable within a single year ranging from 1 to 13€kg in 1995 for instance. The data identified as a blend of glass eels and eels represent 56 % of the total glass eel export weight. For some years, the Spanish trade, which represents the largest volume, has been identified as a blend. Indeed for these years, large volumes of export are recorded at a low price. This might have been the consequence of the trade of frozen glass eel sold at a lower price for the food market, but

Table C.1: Trend in glass eel prices (€/kg). Mean value from the four sources of data (€ 2006)

	1960	1970	1980	1990	2000
0		12	22	104	196
1	6	27	22	93	271
2	4	40	39	118	218
3	6	57	43	95	220
4	9	26	28	120	404
5	8	17	40	114	719
6	8	14	45	183	369
7	11	19	57	263	464
8	10	16	52	255	
9	53	16	100	209	

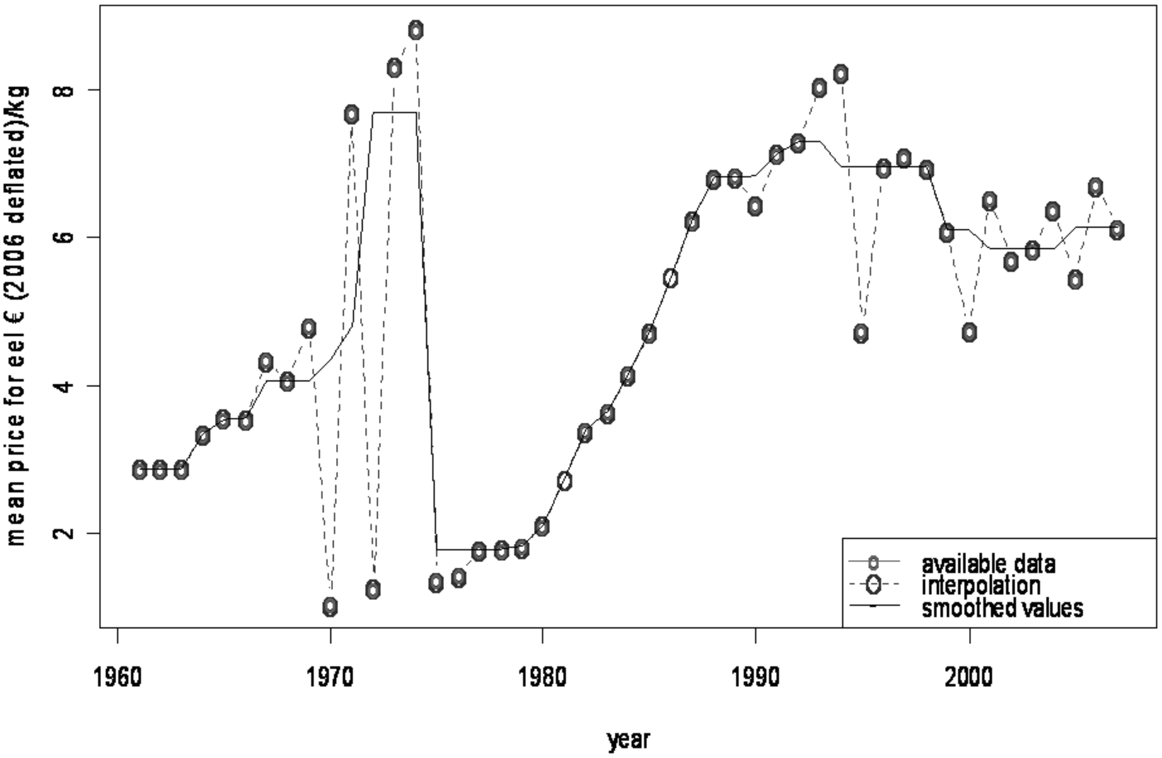

Figure C.2: Trend in yellow eel prices computed from EUROSTAT and OFIMER trade data. Single circles indicate interpolation for a missing value. Solid line indicate the smoothed trend (€ 2006) also could have been the consequence of a blend of glass eel and yellow eel in the export. However, the analysis of the glass eel trade towards Spain shows the consistency of the time series and of the calculations of glass eel volumes.

Table C.2: Trend in eel (Bootlace - Yellow or silver undifferentiated) prices per kg (€ 2006) from OFIMER (1961-2006) and Eurostat (1995-2007)

	1960	1970	1980	1990	2000
0		4.3	2.1	6.8	6.1
1		4.8	2.8	7.1	5.9
2		7.7	3.4	7.3	5.9
3	2.9	7.7	3.7	7.3	5.9
4	3.4	7.7	4.2	7.0	5.9
5	3.5	1.8	4.7	7.0	6.1
6	3.6	1.8	5.5	7.0	6.1
7	4.1	1.8	6.2	7.0	6.1
8	4.1	1.8	6.8	7.0	
9	4.1	1.8	6.8	6.1	

The OFIMER and EUROSTAT statistics series show consistent results during their common period. The trade statistics from OFIMER show that official export have decreased from a maximum of 1200t in 1978 to less than 100t in 2006 (Fig. C.3). Two phases of export towards Asia are reported in the series. First exports to Japan from 1969 to 1980 also correspond to the first increase in prices and the second towards China via-Hong-Kong which started in 1994 and was responsible for the second rise in prices (Fig. C.1). The landings collected from the marine administration are, as in the case of commercial data, a blend of glass and yellow eels (Fig. C.4). The landings are detailed precisely by maritime region. Over the period 1902 to 1938, they display a steady trend, which values range from 86 to 280t. After Word War II in 1947, a first peak in catch (444t) is reported. It is followed by low landings in the 1950's and a resumption after 1958.

These landings are far lower than the commercial data collected by the railway administration on the glass eel trade before 1936. For instance, in 1924 the total landings of both glass eel and eel are estimated at 168 t while the export of glass eel by train is estimated as 420t. They are also largely underestimated in the 1970's. After 1975 the "official" open-

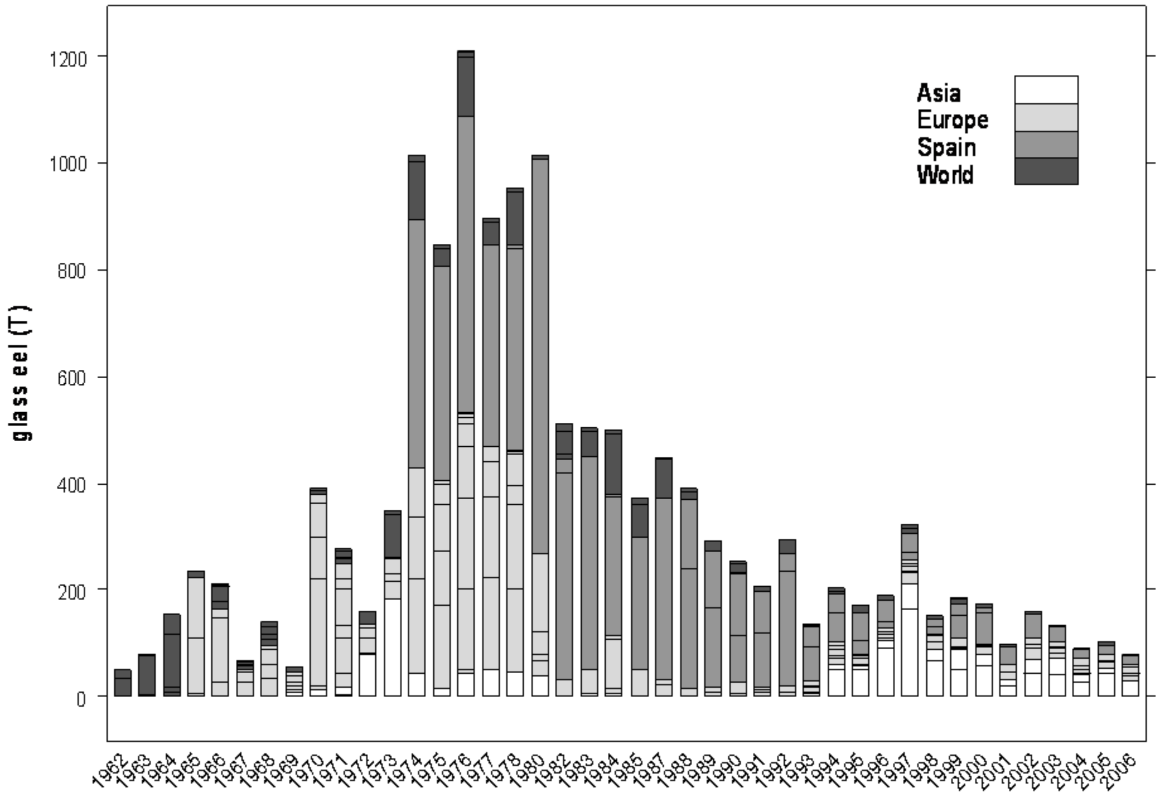

Figure C.3: Historical trend in weights of glass eel exported from France, data computed from OFIMER statistics

ing of the Spanish trade market, they are more consistent with the reports from trade but remain about half the true size of the landings. A series consistent with punctual expert estimates (Table C.3) has been built to generate a more realistic time series than using underestimated data. Different coefficients have been applied to correct the export towards Spain, considered as biased, by experts. The final export towards Spain covers both Spanish and French consumption. These coefficients have been assessed as following: before 1936, the export statistics are considered as accurate, from 1965 to 1973 we assume a constant trade of 1000t towards Spain to be able to reach 1970 level (Table C.3). From 1974 to 1983 the export towards Spain is multiplied by 3, from 1980 to 1997 the export towards Spain is multiplied by 1.3, after 1998 the export towards Spain is multiplied by 1.2 (Fig. C.4).

The Eurostat statistics provide an overview of European trade. Most of European trade goes to Asia with a mean value of 123t per year during the period 1996-2006, 38t are sent by truck in northern Europe mostly for aquaculture. Out of 38t, the weight of glass eel used for restocking is estimated as 3t (ICES, 2007). These statistics also describes

Table C.3: Expert estimates of landings and trade volume

Year	Quantity (t) marine Fishermen	Quantity (t) fluvial Fishermen	Total landings (t)/ export	Description	Reference
1895			200	France	Vaillant (1889)
1906			73	Landes (South of France)	Arne (1908)
1927			350.6	San Sebastian Market	Gandolfi Hornyold (1936)
1927			362.5	Export by train from the Loire to the Bidassoa	Gandolfi Hornyold (1933)
1933			202.6	San Sebastian Market	Gandolfi Hornyold (1936)
1933			271.3	Export by train from the Loire to the Bidassoa	Gandolfi Hornyold (1933)
1970	450	895	1345	Bay of Biscay (Brittany not included)	Popelin (1971)
1976	1455	700	2150	French glass eel fisheries	Elie (1979)
1979	1175	675	1850	French glass eel fisheries	CIPE,Castelnaud *et al.* (1994)
1983	591		1000	French glass eel fisheries	Castelnaud *et al.* (1994)
1986	260		500	French glass eel fisheries	CIPE, Castelnaud *et al.* (1994) Désaunay and Aubrun (1988)
1989			300	French glass eel fisheries	Castelnaud *et al.* (1994)
1997			410.5	French glass eel fisheries	Castelnaud (2000)
1999	222	17.4+5.6	245	French glass eel fisheries	Castelnaud (2002)
2000	180	16.6	196.6	French glass eel fisheries	Castelnaud (2002)
2004			92.5	Trade overview	(Anonymous)

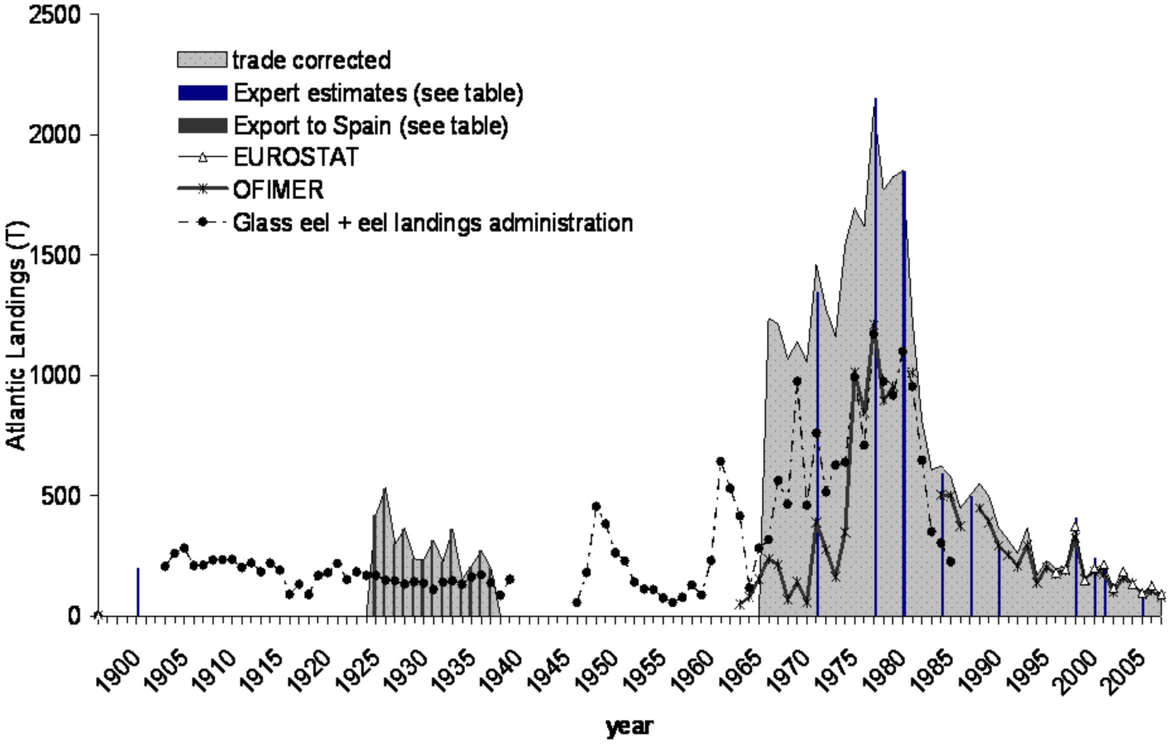

Figure C.4: Landings and export of glass eel from France. Series of landings from the administration and official export from eurostat and OFIMER. The corrected trade series represents an attempt to rebuild the historical landings from corrected trade data

well the internal trade between glass eel traders, with large exchange to and from Spain, and to a lesser extend, cross trade between the continent and the UK, glass eel being exchanged to constitute lots before plane shipment (Fig. C.5). Our treatment of Eurostat data lacked consistence for the UK. The sum of France and Spain export towards the UK minus the export from the UK (net export) ranged from -21t in 2000 to 20t in 2004.

C.4 Discussion

C.4.1 An historical overview of glass eel fishing and trade

The development of the glass eel fisheries has been operated in five phases:

1850-1936 : development of commercial fisheries Glass eel fisheries have already been active at the end of the 19th century with landings estimated around 200t (Vaillant,

Figure C.5: Mean trade volumes of glass eels (t) 1996-2006 in Europe analysed from Eurostat database

1889). Fishermen used hand nets from the banks of river or from an anchored boat (Elie and Fontenelle, 1982; Castelnaud *et al.*, 1994) and the destination of glass eels was mostly local. In 1908, the glass eel fishery was already well developed in the south of France due to the proximity of the Spanish consumption and market (Arne, 1908). The volumes exported by train from the two southernmost regions, Landes and Basses Pyrénées were 73t in 1906. Some years later, in 1923 they were still at the same level, i. e. 76t (Gandolfi Hornyold, 1933), suggesting that the southernmost fishery was already fully developed by the beginning of the XIX$^{\text{th}}$ century. In fact, from this southern point, the market has progressively expanded along the Atlantic coast, and led to the development of glass eel fisheries that were already at this time shifting from traditional and local to commercial 'international' activities (Gandolfi Hornyold, 1933; Gascuel, 1987).

From 1920 to 1936, a precise description of the weight of glass eels transported by train and of the volumes sold at the San Sebastian market enables us to rebuild a time series of glass eel landings (Fig. C.4, Gandolfi Hornyold, 1933, 1936). From both series, it is possible to evaluate that total glass eel production has varied from 531t (1925) to 199t (1936). The level of production from the marine administration which sums glass eel and yellow and silver eel reported for the Atlantic coast is steady around 140t, so this source of data is clearly underreported and completely irrelevant (Fig. C.4). The price values from the marine administration have been steady around 15 € for half a century. Their analysis against other data series collected in the 1960's prove again that they are too high to be reliable.

1936-1969 : the Spanish ghost trade and transition to push net fisheries After 1936, the Spanish war and Franco's regime closed the Spanish borders and hence restricted the trade of eel to Spanish buyers. This market "officially" disappeared until 1975 although smugglers still supplied Spanish Basque market and buyers crossed the frontier. However, international troubles at that time suggest that the glass eel fisheries have probably been restricted to a local market until 1945.

From 1945 to 1969 the main export routes were for glass eel consumption, in France, Spain and Mexico. The fishery progressively shifted from practicing hand net to push nets which were allowed by a decree in 1952 (Elie and Fontenelle, 1982) and extended in many areas on the Atlantic coast in 1958 (Castelnaud *et al.*, 1994). But the attractiveness of the glass eel prices remained low. Our earliest reliable records of glass eel prices indicate that the market price was between 6 and 12 € (2006) per kg before the onset of the Japan market (Table C.1). Fishing power of glass eel fishing boats also increased during the 1960's and the 1970's (Elie and Fontenelle, 1982).

1969-1979: golden years and first onset of Asian market The change in the fishing techniques initiated during the 1960's has turned out into a large increase in glass eel landings. Commercial statistics (Fig. C.4) and expertise (Table C.3) agree with the fact that landings have culminated around 1976. The landings of glass eel in Europe at their bulk are estimated at 2700 t, with France at more than 2000 t, Spain (200 to 300 t), Portugal (220 to 250 t), the United Kingdom (40 to 50 t) and Morocco (10 to 30 t) (Elie and Fontenelle, 1982). An analysis of the catches in the Gironde River (Fig. C.6) shows that local landings could already have been diminishing in the 1960's, and that the apparent increase of landings in the 1960's and 1970's might be both the consequence of a large increase in effort on a fishery turned profitable by the international demand and the onset of the Japanese market in 1969, and also a more accurate reporting of catches (see below).

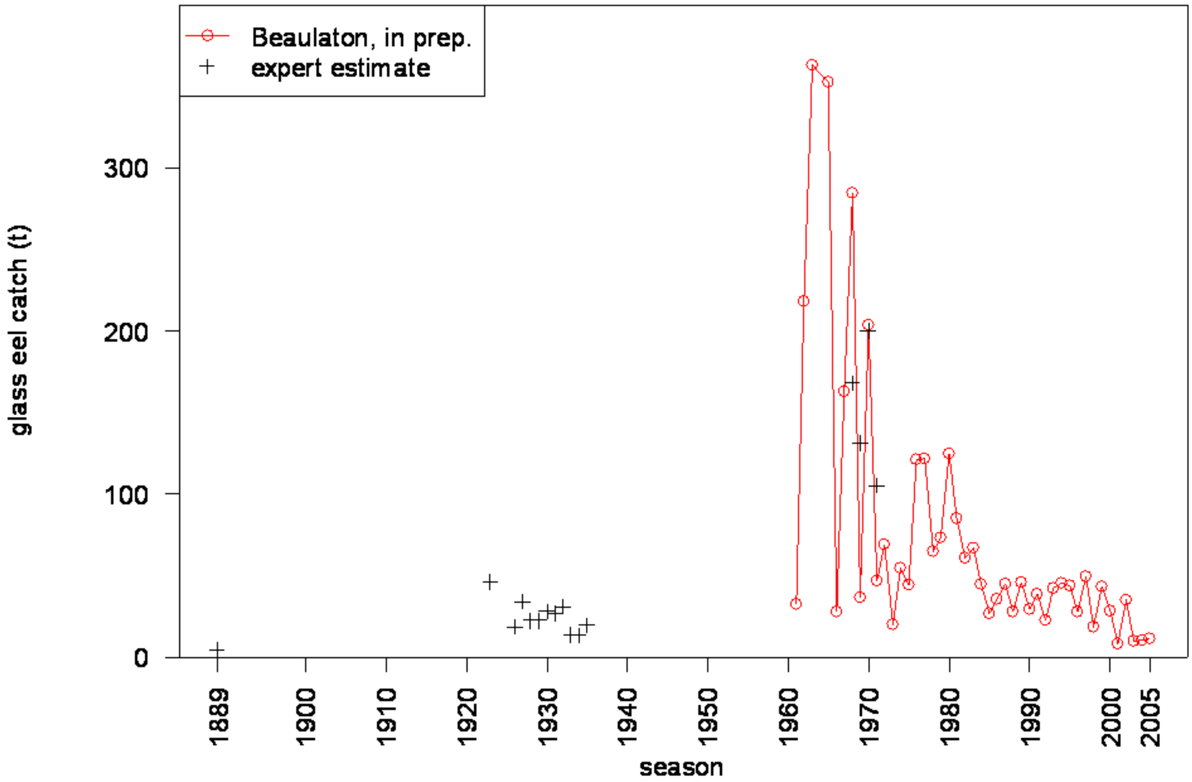

Figure C.6: Trend in glass eel catch in the Gironde, Beaulaton in prep., (analysis of cooperative fisherman data) , expert estimates (Vaillant, 1889; Gandolfi Hornyold, 1933, 1936; Popelin, 1971)

Because of Franco's Regime, glass eel trade towards Spain was forbidden and inexistent in the official trade statistics until 1975. However, it was probably the largest trade route and represented around 80 % of the total (Popelin, 1971). After Franco's death, this trade route appears in the official statistics (Fig. C.4), but the level of exports, reported from 378 to 555 t between 1975 and 1979, is surely still underestimated by factor 3. Indeed, Popelin (1971) indicates that this level was already 1070 t in 1970. Export for food market was also done towards Mexico and Venezuela. France exported glass eels in many countries, either for restocking (Germany, the Netherlands, Russia, Poland), or for intensive or extensive aquaculture (Denmark, Germany, United Kingdom, Benelux). It is noteworthy that Germany was also a transit country for live glass eels to restock East European countries (East block) such as Hungary. The market for live glass eel represented probably 10 to 20 % of the total trade.

1980-1994: landings falling down In the 1980's, the European glass eel recruitment suddenly declined and Japan ceased to import glass eel from France in 1982 because of the high mortality rate of exported glass eels. These mortality rates were mainly due to new French traders that wanted to export live glass eels but had no skills at maintaining glass eels alive during more than 30 h in airplanes. In addition, Japanese aquaculture has progressively shifted to Taiwan with lower handling prices, and the Asian market only resumed in 1994. The opening of the Chinese market at that time enabled Japanese industrialists to invest massively in China whether in huge extensive farms and transformation industries. These investments were mainly motivated by the huge space available that Japanese farms could not afford, by low costs of working force, and by financial allocation to invest in China. The number of fishing licences has dropped slightly at that time indicating that during this period of still high abundance, the fishery was probably less profitable (ICES, 2007). Export towards Spain is more accurately covered than in the preceding period, the sum of local consumption and underreporting in trade statistics is about a third of the total trade.

1994-2006: back to Asian market From 1994, glass eel landings have kept on dropping, but glass eel prices have shown an unprecedented rise. Two major events have disrupted the trend in glass eel price: in 1997, the Asian financial crisis, and in 2006, the export closure of Chinese eels to many markets due to the presence of residues of malachite green in the flesh of eels. The largest prices have been met in 2005 because of the coincident high demand of Spanish, North European, and Asian markets. Two other factors may have played a key role in this price explosion. First, the licence regime of glass eel imports has been opened to Chinese farmers. They were thus allowed to import directly glass eels and not constrained to buy only from authorized Chinese importers. Second, the year 2004 was a very low recruitment year in Europe (the landings fell below 100t in France for the first time), Chinese farms could therefore not produce enough eel to supply the Japanese market. It has induced the next year (2005) a strong competition between Chinese farms to fill their ponds and led to the peak in price.

The current trade across Europe Three countries are the main producers and traders of glass eels: France, Spain, and the United Kingdom (sorted by importance). Portugal is a producer as well even if the fishery is legally banned. Portuguese glass eels have a high attractiveness since they are of a smaller size than in other countries and are caught mostly with hand nets. In 2006, the export routes are Asia (50 %-36t) (living glass eels) Northern Europe (44 %-living glass eels-32t), Spain (4 %-t) and restocking (2 %-1t).

When compared with mean 1996-2006 Eurostat trade statistics (Fig. C.5), the volume of trade has clearly decreased due to the shortage in resource, and the part of glass eel with a final use to aquaculture has progressively increased to reach 94 % in 2006.

From 2000 to 2006, the statistics available from the database for small vessels sum up between 57 and 76.8 t. These values represent only half of true landings. The catch is largely underreported, both by understatement of reports and lack of computation, so we considered those data as not relevant to analysis. The latest accurate estimation of the size of landings in the season 2003-2004 indicates that total landings were 92.5 t. This level is consistent with the total export from France from Eurostat 97t or OFIMER 92t. One must be reminded that a statistical year from eurostat or OFIMER mixes two glass eel season which last from October to March, precluding a full comparison of the two series.

The network for glass eel trade is complex since there are several products and markets: dead glass eel for food consumption, living glass eels for Chinese and Northern Europe aquaculture and for restocking. Few companies share these markets and underground money and financial tricks are commonly used in this connection.

The frozen glass eel market is the most opaque part of the market as it is used to replace dead glass eels with glass eels caught from poachers. Prices for that market are lower than the price for living glass eels as illustrated by Spanish trade series (Fig. C.1). The frozen glass eel allow to sell the glass eel dead from fishing injury during their preparation for the Asian market.

This illegal fishery has a double asset. First, buying prices are lower than official prices since the unscrupulous traders have risk to buy and can bring pressure on illegal fishermen. Second, because the quality of “hand-caught” glass eels is far better than those caught by professional fishermen using towed nets and thus, mortality rates are far much lower using this product.

In 2004 the part of glass eel purchased from “non licensed fishermen” was estimated as 16 % but this value did not include glass eel caught by poachers and sold by fishermen. The volume of illegal trade is estimated between 20 to 40 % by our contact trader (Bonhommeau Patrick, com. pers.).

It is thus possible that the frozen glass eel shipment to Spain and local consumption are underestimated in the official statistics. This market initiated during the Franco’s years, still remains opaque and forms the highest source of uncertainty on the real size of the glass eel trade. However, given the large prices for living glass eel, a quantity larger than the number of glass eel dead after fishery, 40 % in the case of the most impacting fishery in the Vilaine and the Loire, seems improbable in the recent period.

A volume of underreported trade around 20 % is also consistent with the correction of export statistics estimated as about 20 % of the total trade from 1998 (Fig. C.4, corrected trade series). Prouzet and Nielsen (in press) have provided data from T. Nielsen own inquiry among the traders. The volumes estimated for shipment towards Asia or Northern Europe agree well with our series. The main difference is the volume of glass eel used as local consumption, for instance 100 t estimated in 2002 where our trade statistics to Spain only sum up to 12t.

C.4.2 Glass eel prices keeping profitability of fisheries

Standard economic theory predicts that exploitation alone is unlikely to result in species extinction because of the escalating costs of finding the last individuals of a declining species (Clark, 1990; Courchamp *et al.*, 2006). The eel species is worrying for three reasons. First, the costs of finding do not increase since the fishing methods has remained unchanged after the 1960's. Increasing oil prices have impacted the fishermen income but glass eel fisheries require little power and fishing grounds are close. Second, the international demand described above has led to the explosion in prices (Fig. C.7). The similarity between the prices extracted from various sources of data shows that the glass eel price is set by the worldwide demand (Fig. C.1). Hence, the sharp decrease in volumes has been more than counterbalanced by the increase in price. The prices for a fisherman at the beginning of 2008 was 750 € per kilo. For instance, a fisherman fishing 0.5 kg per day will have a turnover of 11 250 € per month, and most catches are larger than this. Third a possible ecological Allee effect has been pointed out in eel as the recruit to spawner ratio has been decreasing since the 1970's (Dekker, 2004; ICES, 2005).

We postulate that unless a proper mechanism of regulation takes place, as rarity makes the European glass eel more attractive, efficient enough glass eel fisheries might drive the species to extinction, as a large part of the European resource is concentrated in the estuaries where glass eel fisheries occur. Such a phenomenon is called Anthropogenic Allee effect (Courchamp *et al.*, 2006).

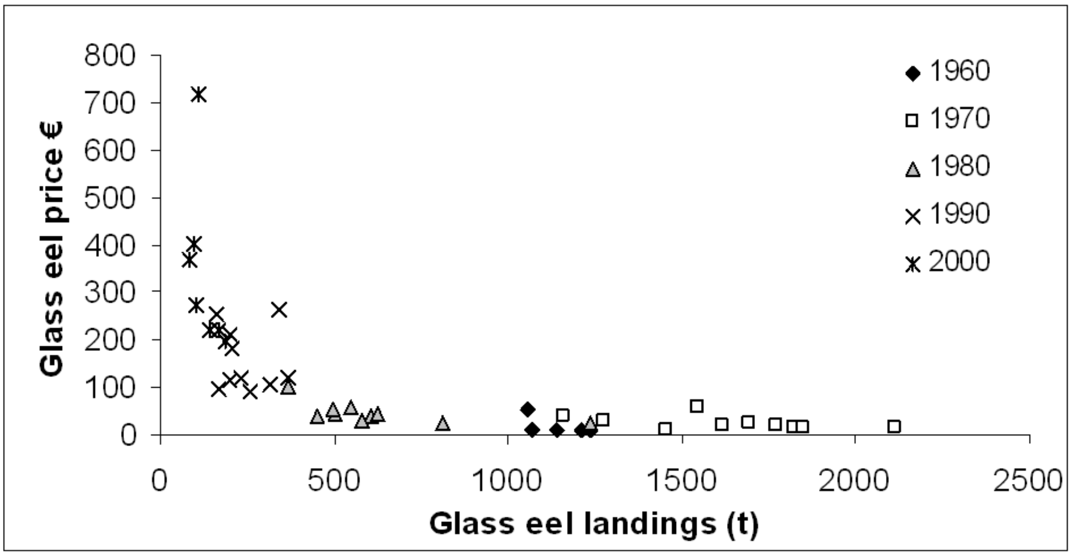

Figure C.7: Relationship between landings, computed from the corrected export data series (see text) and glass eel prices. Prices are corrected from inflation and expressed as 2006 values

C.4.3 Insight on the changes to come

From the present level of 2 % the percentage of glass eel used for restocking will have to increase to 35 % in 2008 and then to 60 % in 2012. The maximum level affordable for the European aquaculture is 700 € (Prouzet and Nielsen, in press). However, prices could get a higher level in Asia as illustrated by prices already reached in 2005. The price consented for restocking is probably less than 100 €, especially if a large weight of glass eels is to be sent for aquaculture purpose.

The difference in price will clearly affect the profit of glass eel fisheries, prices for restocking will surely be too low to maintain an acceptable profitability of fishing activities for fishermen who use to have such prices levels. On the contrary, the further reduction in glass eel available for aquaculture will provoke a further rise in price, and an incentive for black market.

ICES (2005) argued that there was a risk of Allee effect or depensatory mechanism on the spawner recruitment curve, and that because of this risk, transporting glass eel throughout Europe would be an option to enhance the stock in a short while, and overcome the depensatory trap. However, this analysis did not account for the fact that the current level of landings was already too low to permit a pan European restocking as proposed by Moriarty and Dekker (1997). The next year ICES drew up a decision tree, whose first choice was the demonstration of a local surplus. An outcome of the risks associated with restocking, is indeed that sending glass eel for restocking is justified if we think that the global survival at the stock level will be increased.

Though the recruitment level in the French estuaries is still high when compared to rest of Europe, yellow eel densities have been now diminishing for more than two decades (Briand, unpublished), and it is from our point of view improbable that current recruitment could achieve the carrying capacity of estuaries.

The European commission has set up the objective of restoring the eel stock at a safe biomass level of 40 % of its pristine state in the long term, i. e. several eel generations. To reach this objective, each basin will have to enhance the spawner output, and the European countries will have to achieve a spawner escapement larger than the replacement level, to reverse the declining trend in recruitment. The CITES listing of eel will have further consequence for glass eels. Each lot of glass eel traded outside Europe will have to be accompanied by a certificate showing that the commercial use of those glass eels does not endanger the stock.

So basically each basin will have to restrict anthropogenic mortalities at level permitting a level of escapement larger than the replacement level, and permitting the achievement of the long term goal. This means that achieving a proper management of a glass eel fishery means to analyse other sources of mortalities as well as the glass eel fishery mortality (Beaulaton and Briand, 2007), to get a picture of the total mortality in a basin. A pan European analytical assessment of the stock will also be necessary to compute the mortality level permitting the achievement of the long term objective.

Conclusion

Checking and cross checking different sources of data is a long and tedious task. So in the end, getting only a part of the real size of trade could be considered as a poor result. However, the attempt was never made to check catch and glass eel trade statistics against each other, in a long series that covers the XX$^{\text{th}}$ century. The analysis brings knowledge on the increasing quality of trade data, and permits to get a picture of the eel trade and landings and their evolution.

The European eel listing in the Annex IIB of the Convention on Trade of Endangered Species (CITES) and the European eel Management Plans that will impose European

Members to allocate 60 % of their production to restocking in 2013 are a necessity for glass eel fisheries more than eel fisheries: the reduction of landings has been compensated by higher market prices to such an extent that the licensed fishermen have kept on harvesting, thus increasing the pressure on stocks.

In the short future, a further increase in prices is highly probable on the international glass eel market as the quantity of glass eel available will decrease. On the European side, the combination of the reduced recruitment and the price affordable for restocking (far much lower than East Asian market) will probably not permit to maintain the profitability of the glass eel fishery. As a consequence, a strong incentive for black market will probably build up. To our mind, the carrying capacity of French basins is no longer achieved, achieving and controlling a sustainable anthropogenic impact is probably more important than building up a massive export of glass eel throughout Europe, because of the risks associated with the latter. Either way, a large change in the glass eel fisheries is probably to come.

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ABSTRACT

The PhD thesis aims to contribute to the study of environmental impacts on European glass eel recruitment. We chose a modelling approach for two reasons. First, the observation of the larval stage over the trans-atlantic migration is difficult to carry out. Then, the modelling approach enables us to explore the complexity of eel ecology. Different physical an biological hypotheses are tested to understand processes whereby environment may impact on recruitment that is declining for 25 years. Two modelling approaches are developed:

In a **first part**, a deterministic modelling using hydrodynamic models enables us to study the passive drift of larvae released in the spawning area, the Sargasso Sea. One of the originalities of this work is to implement realistic hypotheses of behaviour and mortality in simulations. On one hand, our simulations show that a 6-month migration duration, as suggested by the analysis of otolith microstructure, would imply a fast active swimming. This energy expenditure would be too high in an oligotrophic environment such as open ocean. The mean migration duration is estimated to 22 months in accordance with previous approaches of cohort analyses. On the other hand, our results suggest a weak impact of oceanic transport intensity on recruitment success. Simulations also provide evidence of the influence of starting locations and dates on arrival areas and larva life histories in accordance with previous results of genetic and otolith microchemistry.

In a **second part**, a statistical modelling focuses on the links between environmental conditions experienced by larvae (oceanic transport and food availability) and the recruitment assessed by glass eel quantities entering European estuaries. Recruitment is not impacted by transport conditions described by large-scale oceanic indices. We show that glass eel recruitment variations are related to primary production in the Sargasso Sea. The recent increase in sea temperature in the spawning area led to a decrease in food availability and thus, in glass eel recruiment. These trophic relationships are also found for two other eel species of the Northern Hemisphere: American and Japanese eels. At the scale of two oceans, similar ecological processes related to global warming seem to have concurred to the strong synchronous decrease in recruitment of three eel species.

The use of ocean general circulation models proves to be a very promising tool to look holistically at ecological processes such as migration and larval stage of marine species. This work enables us to consider future developments such as the coupling of physics to biology to understand and reproduce life histories of the earliest life stages that are difficult to observe in the wild. This work is finally put into perspective with eel ecology and life cycle: its resiliency over the last ten millions years seems to be weakened by recent anthropogenic disturbances such as climate change and overexploitation and pose the problem of the management measures envisaged.

Keywords : lagrangian modelling, larva migration, climate change, bottom-up, *Anguilla*, larval survival, Sargasso Sea.

RÉSUMÉ

L'objectif de ce travail de thèse est de contribuer à l'étude des effets de l'environnement sur le recrutement de civelles d'Anguille européenne. Nous avons adopté une approche de modélisation, et cela pour deux raisons. Tout d'abord, l'observation de la phase larvaire durant la migration trans-atlantique est très difficile à mettre en œuvre. Ensuite, la démarche de modélisation permet d'explorer la complexité de l'écologie de l'Anguille. Des hypothèses physiques et biologiques sont formulées pour comprendre les processus par lesquels l'environnement agit sur le recrutement, en fort déclin depuis 25 ans. Deux approches de modélisation sont menées :

Dans une **première partie**, une modélisation déterministe basée sur des modèles hydrodynamiques permet d'étudier la dérive passive de larves relâchées dans la zone de reproduction, la mer des Sargasses. Une des originalités de ce travail est de rendre ces simulations réalistes en implémentant des hypothèses de comportement et de mortalité. D'une part, nos simulations montrent qu'une traversée trans-océanique en 6 mois, suggérée par l'analyse de la microstructure des otolithes, impliquerait une nage active rapide et donc trop coûteuse en énergie dans un milieu oligotrophe comme l'océan ouvert. La durée moyenne de migration est estimée à 22 mois, en conformité avec des approches préalables d'analyse de cohortes. D'autre part, nos résultats suggèrent un faible impact de l'intensité du transport océanique sur le succès du recrutement. Ils démontrent aussi l'influence des dates et lieux de départ des larves sur leur histoire de vie au cours de la migration ainsi que sur leur aire d'arrivée, en conformité avec les résultats préalables de génétique et de microchimie des otolithes.

Dans une **seconde partie**, une modélisation statistique étudie les liens entre les conditions environnementales rencontrées par les larves (transport océanique et disponibilité en nourriture) et le recrutement évalué par les quantités de civelles européennes en estuaire, en tenant compte de la durée de migration estimée au préalable. Le recrutement n'est pas influencé par les conditions de transport décrites par les indices océaniques à grande échelle. Nous montrons que les variations du recrutement de civelles sont reliées à celles de la production primaire dans la mer des Sargasses. L'augmentation de la température dans la zone de reproduction a entraîné une diminution de la disponibilité en nourriture et ainsi du recrutement. Ces relations trophiques sont mises en évidence pour deux autres espèces d'Anguille de l'hémisphère nord: l'Anguille américaine et japonaise. A l'échelle de deux océans, des processus écologiques communs reliés au changement climatique semblent avoir participé à la forte diminution synchrone du recrutement de trois espèces d'Anguille.

L'utilisation des modèles physiques se révèle très prometteuse pour appréhender certains processus écologiques comme la migration et la phase larvaire des espèces marines. Ce travail permet d'envisager le couplage physique-biologie afin de comprendre et de reproduire les histoires de vie des plus jeunes stades difficilement observables en milieu naturel. Les acquis de ce travail sont finalement mis en perspective avec l'écologie et le cycle de vie de l'Anguille: sa résilience au cours des dix derniers millions d'années semble affaiblie par les perturbations anthropiques récentes comme le changement climatique et la surexploitation et pose le problème des mesures de gestion envisagées.

Mots clés : modèle lagrangien, migration des larves, changement climatique, bottom-up, *Anguilla*, survie larvaire, mer des Sargasses.