MUSEUM NATIONAL D'HISTOIRE NATURELLE

Ecole Doctorale Sciences de la Nature et de l'Homme – ED 227

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THESE

Pour obtenir le grade de

DOCTEUR DU MUSEUM NATIONAL D'HISTOIRE NATURELLE

Spécialité : Physiologie et biologie des Organismes-Populations-Interactions

Clarisse Boulenger

Ajustements dynamiques des sous-populations d'anguilles européennes et traits d'histoire de vie : apport du marquage individuel par PIT-tag pour la conservation.

Sous la direction de **: Monsieur Duhamel, Guy, Professeur et Monsieur Acou, Anthony, Dr.**

JURY :

M. Acou, Anthony	**Chargé de Recherche, Muséum national d'histoire naturelle, Paris (075)**	**Co-directeur de thèse**
M. Bevacqua, Daniele	**Chargé de Recherche, INRA, Avignon (084)**	**Examinateur**
M. Duhamel, Guy	**Professeur, Muséum national d'histoire naturelle, Paris (075)**	**Directeur de Thèse**
M. Feunteun, Eric	**Professeur, Muséum national d'histoire naturelle, Dinard (035)**	**Examinateur**
M. Gimenez, Olivier	**Directeur de recherche HDR, CNRS, Montpellier (034)**	**Examinateur**
M. Lobón-Cerviá, Javier	**Directeur de recherche HDR, CSIC, Espagne**	**Rapporteur**
M. Rivot, Etienne	**Enseignant Chercheur HDR, Agrocampus-Ouest, Rennes (035)**	**Rapporteur**
M. Roussel, Jean-Marc	**Directeur de recherche HDR, INRA, Rennes (035)**	**Examinateur**

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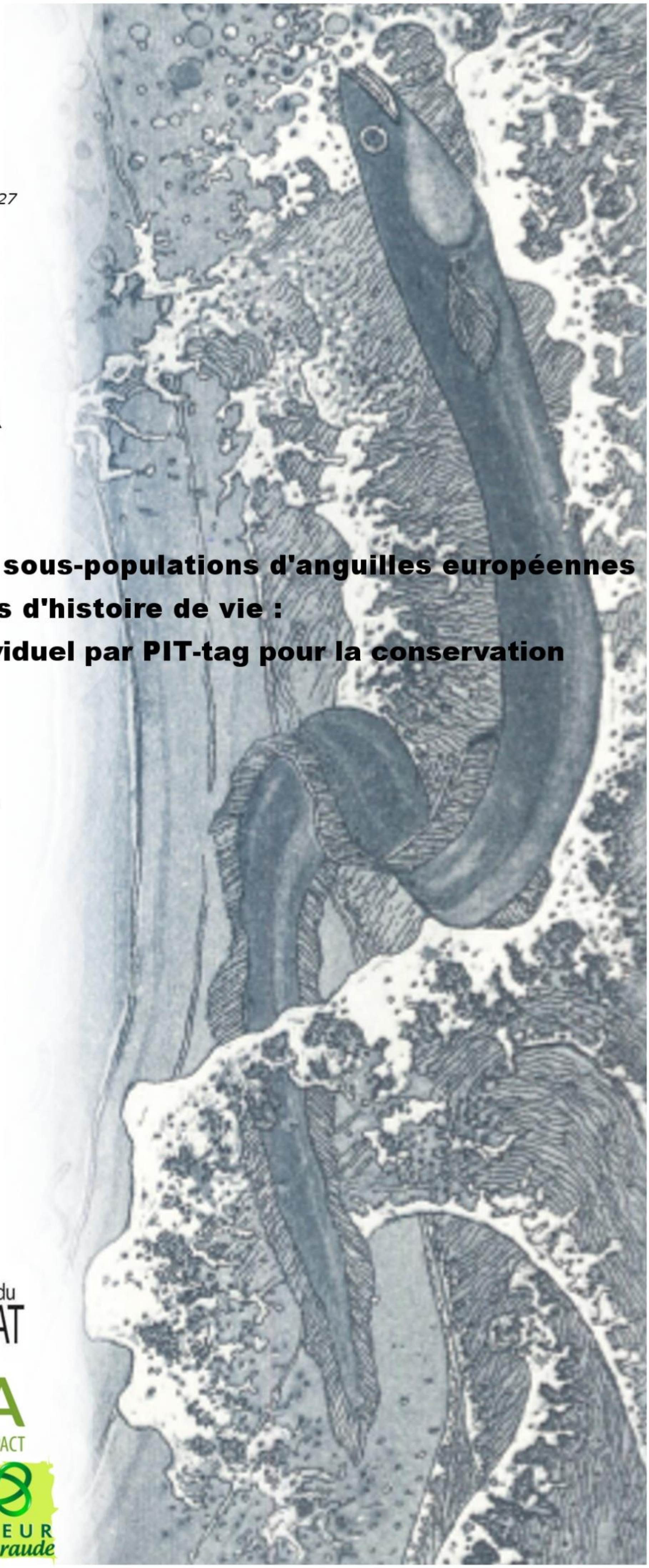

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sous la direction de :
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TOUR DU VALAT

Région BRETAGNE

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Office national de l'eau et des milieux aquatiques

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Et que ceux que j'oublie veuillent bien m'excuser …

A Nonno,

Introduction

La compréhension du fonctionnement des populations animales en interaction avec leur écosystème est l'un des enjeux majeurs en écologie et c'est un pré requis essentiel pour la gestion efficace des populations.

Pour de nombreuses espèces de poissons, la réalisation du cycle de vie se fait via l'utilisation successive de plusieurs habitats, chacun ayant un rôle fonctionnel bien spécifique (reproduction, alimentation ou repos). Pour satisfaire ces différents besoins vitaux, les individus effectuent des déplacements entre ces habitats et ce à différentes échelles spatiales (de quelques centimètres à plusieurs centaines de kilomètres) et temporelles (journaliers, saisonniers,…). Alors que pour la plupart des espèces ces changements d'habitats et les migrations associées se font au sein d'un même milieu (migration potamique : eau douce, migration thalassique : milieu marin), le cycle de vie des espèces diadromes (Myers, 1949) est partagé entre deux phases, une en milieu marin et l'autre en milieu dulçaquicole. Les migrations associées à ces importants changements d'environnement ont lieu à des moments particuliers du cycle de vie et elles sont anticipées et déterminées physiologiquement.

I. La diadromie

1. Définitions

Selon McDowall (1997), trois catégories de diadromie peuvent être distinguées en fonction du sens et de la finalité des migrations. Pour les deux premières catégories (anadromie et catadromie), les migrations s'effectuent pour les mêmes raisons : les zones de reproduction et les milieux de croissance ne se trouvent pas dans les mêmes eaux. Ainsi, les poissons anadromes effectuent la majorité de leur croissance en milieu marin et se reproduisent en eau douce. Parmi les espèces anadromes, on retrouve le saumon atlantique (*Salmo salar*) et les lamproies marine et fluviatile (respectivement *Petromyzon marinus* et *Lampetra fluviatilis*). A l'inverse, les poissons catadromes grandissent en eau douce et se reproduisent en mer comme l'anguille Européenne (*Anguilla anguilla*). La dernière catégorie, les amphidromes, effectuent également des migrations entre le milieu dulçaquicole et le milieu marin mais pour d'autres raisons que la reproduction, par exemple pour l'alimentation.

2. Des espèces pionnières

Ces espèces diadromes, bien qu'elles représentent moins d'1% des espèces de poissons dans le monde, jouent un rôle écologique et socio-économique prépondérant (McDowall, 1988 ; Limburg & Waldman, 2009). En effet, grâce à leur cycle de vie particulier, elles contribuent aux transferts de matière organique sur le *continuum* terre-mer (Helfman 2007). Par exemple, les saumons qui viennent se reproduire puis mourir dans les rivières nord-américaines constituent une source énergétique importante pour la faune (consommation des carcasses) et la flore (nutriments assimilables après décomposition) locales (Willson & Halupka, 1995 ; Gende *et al.*, 2002). Ce transfert d'énergie peut également se faire du milieu continental vers le milieu marin comme c'est le cas lors de la dévalaison des anguilles argentées (Laffaille *et al.*, 2000). Ces espèces sont aussi importantes dans la recolonisation des milieux qui ont subi de fortes perturbations. En Nouvelle Zélande, les seules espèces présentes actuellement dans les cours d'eau autrefois inaccessibles en raison de la glaciation au Pleistocène sont des diadromes (McDowall, 1996). Ainsi, leur grande capacité de dispersion leur confère un rôle d'espèces pionnières. De plus certaines espèces ont un rôle socio-économique très important. En effet, pour beaucoup de communautés d'Indien d'Amérique, l'esturgeon atlantique (Acipenser oxyrinchus), l'anguille américaine (Anguilla rostrata) et d'autres poissons diadromes avaient une importance forte en tant qu'espèces totémiques mais aussi en tant qu'apport de nourriture à la communauté (Bolster 2006). Plus récemment, Moriarty et Dekker (1997) mettaient en évidence que, en plus des pêcheurs, 25 000 personnes dans les zones rurales tirent un revenu de l'exploitation de l'anguille européenne.

3. *Le constat d'un déclin*

Cependant, ces cycles de vie particuliers partagés entre deux milieux exposent ces espèces aux pressions environnementales et anthropiques propre à chaque milieu et depuis plusieurs années cette accumulation de pressions a provoqué un fort déclin des populations diadromes (Fig.1).

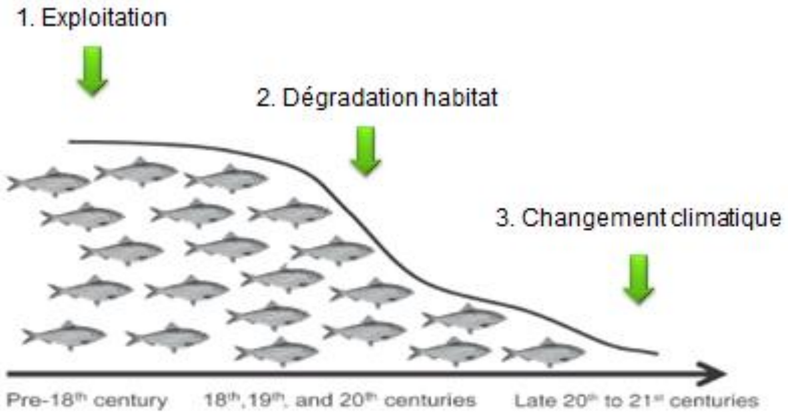

Figure 1 : Les causes du déclin des espèces diadromes au cours des derniers siècles (adaptée de Limburg et Waldman, 2009)

En effet, en étudiant l'évolution temporelle de 24 espèces diadromes (22 anadromes et 2 catadromes) présentes dans la région Atlantique nord, Limburg & Waldman (2009) ont démontré que les abondances de ces espèces avaient chuté de plus de 98% pour 13 d'entre elles et de plus de 90% pour les 11 autres par rapport aux niveaux historiques de référence. De ce fait, la plupart des espèces diadromes ont été classées par l'UICN (Union Internationale pour la Conservation de la Nature) sur la liste rouge des espèces menacées (saumon atlantique) ou en danger critique d'extinction (esturgeon atlantique, *Acipenser sturio* ; anguille européenne *Anguilla anguilla*) (IUCN, 2014). Les raisons de ces déclins sont multiples et peuvent être spécifiques à chaque espèce, cependant ces populations sont toutes affectées par un ensemble commun de facteurs (Limburg & Waldman, 2009), parmi lesquels (par ordre d'apparition, Fig.):

la surpêche : l’exploitation de ces espèces se fait en grande partie dans les couloirs de migrations que sont les estuaires, véritables goulots d’étranglement où les populations se concentrent dans l’espace et dans le temps. Cependant des pêches sont également observées sur les axes principaux des bassins versants et dans les zones côtières. Dans le cas de l’anguille, la surexploitation est considérée comme l’une des causes majeures du déclin (Feunteun 2002). Cela peut s’expliquer par le fait que tous les stades de cette espèce sont pêchés : les post-larves (civelles) à leur entrée dans les zones de croissance, les juvéniles (anguille jaune) dans les zones de croissance que sont les lacs et les fleuves et les sub-adultes lors de leur migration vers la mer des Sargasses pour la reproduction. Cette surpêche peut être expliquée par le fait que la pêche du stade post-larve était très lucrative grâce à la forte demande du marché de l’Asie du sud-est.

La perte ou la dégradation de l’habitat : Différents facteurs peuvent impacter la qualité des habitats nécessaires pour les espèces diadromes. Premièrement les barrages peuvent drastiquement réduire l’accessibilité des habitats nécessaires à l’accomplissement des cycles de vie (Costa *et al.*, 2008 ; Lasne & Laffaille, 2008) mais aussi changer la composition des communautés, modifier les gradients de température ou de débit amont aval ou encore provoquer le colmatage des cours d’eau (Jonsson *et al.*, 1999 ; Limburg & Waldman, 2009). Dynessius & Nilsson (1994) ont montré que 77% des plus grands cours d’eau d’Amérique du Nord, d’Europe et de l’ex-Union Soviétique sont modérément à fortement affectés par des modifications des régimes hydrologiques. Ainsi, environ le tiers des 11200 kms d’habitats normalement disponibles pour la reproduction de l’alose savoureuse (*Alosa sapidissima*) a disparu en raison de l’édification de barrages (Limburg *et al.*, 2003).

La qualité de l’eau peut aussi avoir de gros impacts sur les populations diadromes. Ainsi des études ont montré qu’une contamination même modérée de l’eau, par exemple par les PCBs (Polychlorobiphéniles) ou les métaux lourds (cas du Mercure Hg ou du Cadmium Cd), pouvait affecter les capacités reproductrices des anguilles notamment en limitant la maturation des gonades ou en affectant la condition corporelle (Robinet & Feunteun, 2002, Palstra *et al.*, 2006; Pierron *et al.*, 2008).

le changement climatique: impacte également les populations diadromes. Il modifie les régimes thermiques et hydrologiques affectant ainsi la migration de ces espèces (Baglinière & Porcher, 1994 ; Acolas *et al.*, 2006). Huntington *et al.* (2003) ont montré que les captures du saumon atlantique dans la rivière Penobscot (Maine, Etats Unis) étaient décalées d'1.3 jours chaque année sur la période 1986-2001. Les conséquences de ce décalage sont pour l'instant inconnues mais la rapidité du changement a le potentiel de perturber les relations écologiques qui peuvent exister entre les différents stades de cette espèce. Les changements de températures peuvent également avoir un impact sur d'autres paramètres de la dynamique de population que sont la croissance et la survie (Millers *et al.*, 2009; Daverat *et al.*, 2012 ; Bevacqua *et al.*, 2010; Kettle *et al.*, 2010). Ainsi Daverat *et al.* (2012) ont mis en évidence qu'avec le réchauffement climatique la croissance individuelle des anguilles européennes devrait augmenter spécialement dans la partie nord de l'aire de distribution. Pour de nombreuses espèces diadromes, le changement climatique est aussi annonceur de modifications des aires de distribution. De plus en Europe, les modèles créés par Lassalle et Rochard (2009) prévoient que, en conséquence du scénario de changement climatique le plus probable (une augmentation de la température annuelle entre 1° et 7° et des changements de précipitations), certaines espèces diadromes (22) perdront plus de bassins versants favorables qu'ils n'en gagneront (336 seront perdus contre 113 gagnés).

La gestion de ces espèces diadromes est donc complexe car elle implique de s'attaquer de façon coordonnée aux multiples sources de perturbation des populations qui agissent à différentes étapes du cycle de vie mais aussi de comprendre les stratégies développées individuellement face au caractéristiques propres aux milieux (qualité de l'eau, accessibilité des habitats, compétition, etc.). Ceci implique donc de bien connaître les cycles de vie mais aussi de comprendre la mise en place des différents traits d'histoire de vie et le fonctionnement de la dynamique de population en lien avec leur environnement.

II. Dynamique de population et traits d'histoire de vie

Etudier la dynamique de population revient à identifier les différents mécanismes qui contrôlent l'évolution d'une population dans l'espace et dans le temps mais aussi de comprendre et de mesurer les réactions des individus aux conditions du milieu (Lamotte & Bourlière, 1975 ; Williams, Nichols & Conroy, 2002). Pour cela, il faut identifier et estimer les paramètres faisant évoluer la population entre le temps t et $t+1$, c'est-à-dire les flux entrants et sortants dans ce laps de temps. Une équation simple peut répertorier ces flux (Begon, Harper & Townsend, 1996) :

$$N_{t+1} = N_t + B_t + I_t - E_t - D_t \qquad \text{eq. 1}$$

Avec $N_t$et N_{t+1} représentant la taille de la population au temps *t* et *t+1* respectivement, B_t et D_t représentant la natalité et la mortalité au temps *t*, I_t et $E_t$représentant l'immigration et l'émigration au temps *t*. Ainsi, si des facteurs environnementaux et/ou anthropiques provoquent un changement de la taille de la population, c'est qu'ils auront au moins affecté un des paramètres de la dynamique de population (eq. 1 ; Williams, Nichols & Conroy, 2002).

Cependant, une population n'est pas uniquement constituée d'individus ayant les mêmes caractéristiques. Le sexe, l'âge, le stade (juvénile ou adulte) et d'autres déterminants individuels peuvent être des facteurs influant sur la dynamique de population. Ainsi il a été montré chez l'anguille que la survie augmentait avec l'âge (De Leo & Gatto, 1996 ; Lobón-Cerviá & Iglesias, 2008). Il est donc essentiel, en plus d'étudier la dynamique de population, de caractériser les traits d'histoire de vie que sont la fécondité, la croissance ou encore l'âge (ou la taille) de maturité sexuelle à l'échelle populationnelle mais aussi individuelle.

De plus, une population ne peut être dissociée de son environnement, il est donc nécessaire d'étudier la dynamique de population et les traits d'histoires de vie en lien avec l'écosystème dont elle fait partie (Barbault, 1981). Un écosystème se décomposant en un biotope et une biocénose, les facteurs influençant la dynamique de population et les traits d'histoire de vie seront de deux sortes : (i) les facteurs abiotiques qui incluent tout ce qui est physique et chimique dans le milieu de vie des individus et (ii) les facteurs biotiques qui se présentent sous la forme d'interactions entre organismes vivant dans le même milieu (interaction interspécifique telle que la prédation ou intra-spécifique telle que la compétition pour une ressource au sein d'une même population). A cause de la grande variabilité d'habitats pouvant être colonisés par les espèces diadromes, différentes stratégies peuvent être développées au sein d'une même espèce et même au sein d'une même population afin de s'adapter à leur milieu de vie et d'optimiser la fitness (Gross, 1996). Ainsi, chez la truite commune (*Salmo trutta*), les individus présentant de forts taux de croissance développent des stratégies de plus amples migrations (Cucherousset *et al.*, 2005 ; Acolas *et al.*, 2011).

C'est pourquoi il est essentiel, pour une meilleure gestion de ces espèces, de caractériser la dynamique de population et les traits d'histoires de vie des populations de diadromes dans toute leur aire de répartition et d'identifier les facteurs abiotiques et biotiques, propres à chacun de leur deux milieux de vie, qui régulent ces paramètres.

III. Le cas de l'anguille européenne

Parmi les espèces diadromes, l'anguille Européenne est particulièrement intéressante pour l'étude de la dynamique de population et des traits d'histoire de vie en lien avec leur milieu. En effet c'est une espèce avec une importante variabilité des traits d'histoire de vie à l'échelle de l’aire de distribution mais aussi au sein d’un milieu de croissance. C’est une espèce plastique qui s’adapte à de nombreux environnements et qui au cours de sa longue période de croissance peut subir de nombreuses variations environnementales et anthropiques. De plus le fait que sa phase de croissance se fasse en eau douce facilite son suivi.

1. Le cycle de vie

Comme beaucoup d’espèces diadromes, l’anguille européenne a un cycle de vie complexe (Fig.2a).

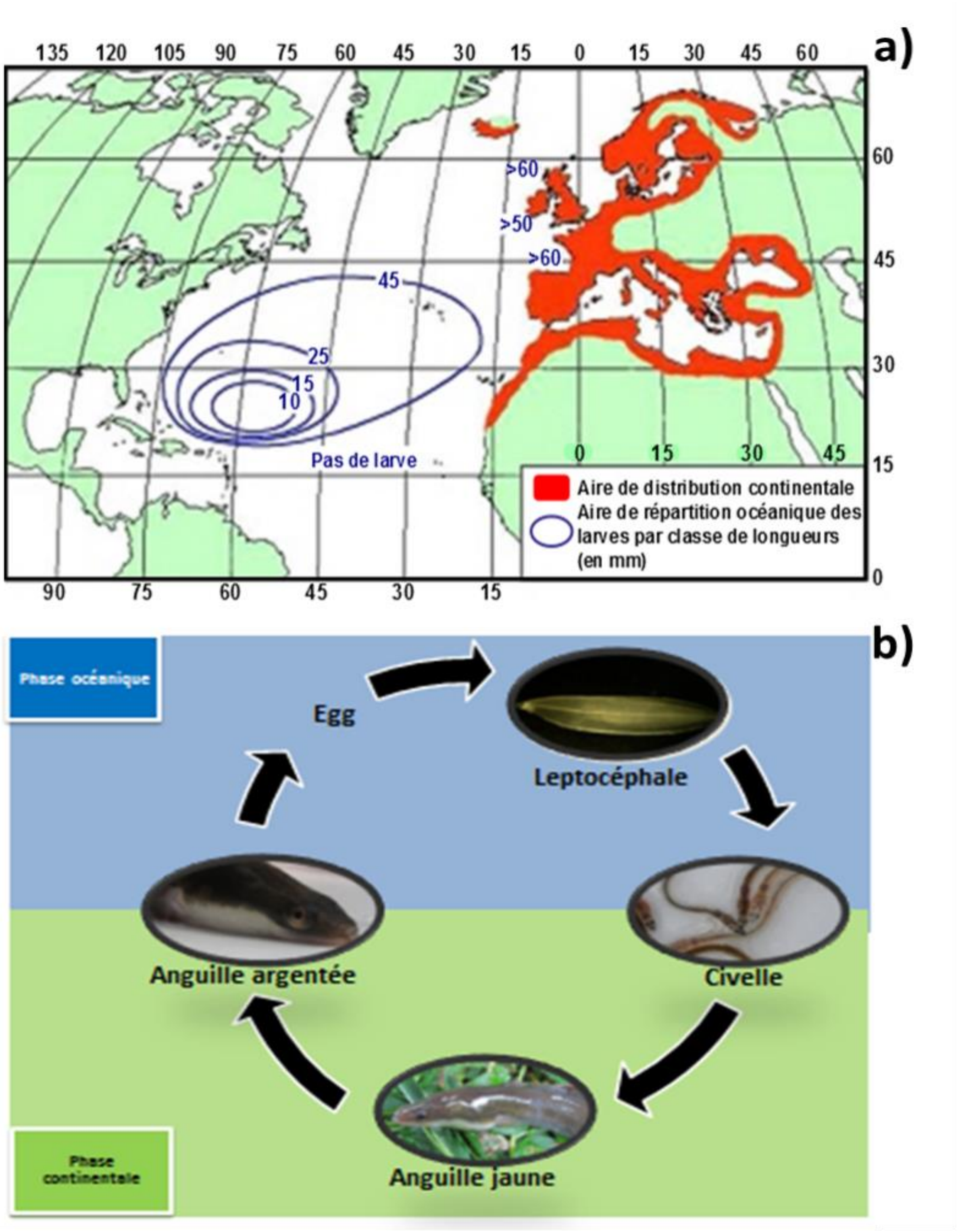

Figure 2: a) Aire de répartition de l'anguille européenne (Anguilla anguilla L. 1758) adaptée de Germain (1927) pour l'aire continentale de Schmidt (1923) pour la répartition océanique des larves, adaptée de Adam (1997). b) cycle de vie simplifié de l'anguille européenne.

Ainsi, l’anguille européenne est une grande voyageuse avec deux migrations transatlantiques, l’une pour atteindre sa zone de croissance (de la Norvège à la Mauritanie, Fig.2a) et la seconde pour rejoindre leur zone de reproduction supposée située dans la mer des Sargasses.

L’aire de ponte supposée se situe dans la mer des Sargasses (Schmidt, 1923) au large des côtes américaines (Fig.2a). Elle s’étend entre 22° et 29° Nord, et entre 50° et 70° Ouest (Tesch, 2003). Après éclosion des œufs, les larves migrent passivement jusqu’aux côtes Européennes et nord africaines en utilisant les courants océaniques et en passant supposément par les Açores (Tesch, 2003; Munk *et al.*, 2010). Le temps de migration de ces leptocéphales, de la zone de reproduction aux zones de croissance, est toujours discuté. Des études effectuées sur des otolithes semblent montrer une migration de 7 à 15 mois (8–9 mois, Lecomte-Finiger, 1992, 1994; 7–9 mois, Arai *et al.*, 2000; ~13–15 mois, Wang & Tzeng, 2000) alors que des estimations faites en prenant en compte les courants océaniques prédisent plutôt une migration de 3 ans (~3 ans, Schmidt, 1923; Tesch, 2003). Une récente synthèse des différentes études faites à ce sujet liste les possibles causes de ce décalage (Miller *et al.*, 2014). Aux abords du talus continental, entre septembre et mars, les leptocéphales se transforment en civelles (aussi appelées pibales). A ce stade, les anguilles sont encore transparentes mais cette transformation s’accompagne de nombreuses modifications physiques, physiologiques et comportementales : (i) une forte diminution du poids et de la longueur est ainsi observée (Elie, 1979), (ii) elles passent d’une forme aplatie à une forme serpentine identique à celle des adultes, (iii) elles arrêtent de se nourrir et perdent les dents caractéristiques de la larve planctonique, (iv) une perte d’eau est également observée et finalement (iv) un changement fonctionnel se déroule avec une activité accrue de la thyroïde et de l’hypophyse.

Après cette transformation, les civelles entreprennent la colonisation des zones de croissance. De récentes études ont montré que la catadromie était facultative chez l’anguille européenne.

En effet des anguilles matures (stade anguille argentée) ont été capturées dans la mer du nord et l'étude isotopique de leur otolithe a permis de montrer qu'elles n'avaient jamais colonisé des milieux d'eau douce pour leur phase de croissance (Tsukamoto *et al.*, 1998 ; Tsukamoto & Arai , 2001). Cependant les proportions d'anguille n'effectuant pas de migration catadrome restent inconnues. Depuis, de nombreuses études ont montré, qu'en effet, une forte variabilité dans le choix d'un habitat de croissance pouvait être observée. Ainsi elles peuvent réaliser leur croissance indifféremment en milieu marin, dans des estuaires, en lagunes, dans des rivières ou encore dans des marais (Feunteun *et al.*, 1998 ; Laffaille *et al.*, 2000 ; Tzeng *et al.*, 2000 ; Acou *et al.*, 2003 ; Limburg *et al.*, 2003 ; Daverat *et al.*, 2006). Selon Edeline *et al.* (2006), le choix de l'habitat préférentiel (eau douce ou eau salée) et le comportement de migration associé sont fortement liés à la température lors de l'entrée dans l'estuaire mais aussi la condition corporelle des civelles. Finalement, au cours de cette phase de colonisation, les transformations amorcées au cours de la métamorphose (leptocéphale→Civelle) se poursuivent : l'alimentation et par conséquent la croissance reprennent (Bardonnet & Riera, 2005) ; la civelle se pigmente et devient alors anguillette (Elie *et al.*, 1982). Dans les milieux continentaux qui ne sont plus sous influence tidale, c'est essentiellement cette écophase qui entreprend la colonisation des hydrosystèmes continentaux (Feunteun *et al.*, 2003).

Après ce stade, les anguilles se « sédentarisent » pour entreprendre une phase de croissance en tant qu'anguille jaune. C'est entre ces deux stades (anguillette et anguille jaune, entre 15 et 30 cm) que l'orientation sexuelle va se faire sous l'induction et le contrôle de facteurs écologiques et environnementaux (Wiberg, 1983). Ainsi des fortes densités semblent induire un sexe ratio à dominance mâle (De Leo & Gatto, 1996) et des faibles densités des femelles. Une répartition géographique différentielle en fonction des sexes semble aussi exister dans les bassins versants: les plus grandes femelles sont dominantes dans les zones situées en de tête de bassin versant alors que les mâles sont majoritaires dans les secteurs en aval des hydrosystèmes (Haraldstad *et al.*, 1985 ; Vollestad 1992, Laffaille *et al.*, 2006).

Les anguilles jaunes se métamorphosent finalement en anguilles argentées. Cette métamorphose s'accompagne de nombreux changements morphologiques et physiologiques qui préparent les individus à la migration transocéanique. Il s'agit d'adaptations préparatoires à l'environnement marin comme l'agrandissement des yeux et des nageoires pectorales, le changement de couleur avec notamment un blanchissement du ventre ou encore la réduction de l'appareil digestif (Pankhurst, 1982 ; Pankhurst & Sorensen, 1984 ; Acou *et al.*, 2005 ; Durif *et al.*, 2005). Des études suggèrent qu'il n'y a pas spécifiquement d'âge ou de taille pour la migration, même s'il y a une différence de taille entre les mâles et les femelles matures, mais que la préparation à la migration est déclenchée lorsque l'anguille a stocké suffisamment d'énergie. Ainsi, en dessous d'une certaine réserve de lipides, l'argenture pourrait ne pas se faire (Larsson *et al.*, 1990). Les réserves lipidiques tiennent un rôle majeur dans la phase migratoire, puisque l'anguille cesse de s'alimenter lors de l'argenture et lors de sa phase reproductrice (appareil digestif se dégrade et l'anus se referme). Cependant des estimations très divergentes des besoins énergétiques minimaux pour l'accomplissement de leur migration et de la reproduction ont été proposées (Böetius & Böetius, 1980: 20%; Palstra *et al.*, 2007: 13,5%; van den Thillart et. al., 2007: 20,7% de matières grasses). Concernant les différences de taille et d'âge à maturité, les anguilles mâles arrivent à maturité à des tailles (29-54 cm) et âges (2-15 ans) plus faibles que les femelles (4-20 ans ; 46-100 cm ; Rossi 1979, Tesch 2003). Dans l'ensemble de l'aire de répartition de cette espèce, ces traits d'histoire de vie sont très variés et fortement liés à la latitude (Vollestad, 1992). Dès les premières variations significatives de température et de débit en début d'automne, les anguilles argentées entament leur migration vers la mer (dévalaison; Vollestad & Jonsson, 1986; Durif *et al.*, 2003). La partie océanique de la migration est beaucoup moins connue mais les travaux de Dufour (1994) présentent des arguments pour une migration à grande profondeur, celle-ci permettant la simulation de la fonction gonadotrope notamment grâce à la pression hydrostatique (Dufour & Fontaine, 1985). Récemment, grâce au suivi d'anguilles argentées en migration par balises satellites, ces importantes migrations verticales ont été confirmées (Aarestrup *et al.*, 2009). Il est supposé que l'acte reproducteur conclut le cycle de vie de cette espèce qui serait donc semelpare (Tesch, 2003; Westeberg; 1979).

2. Une espèce en danger critique d'extinction

Considérée nuisible en France dans les années 1980, l'anguille est désormais classée comme en danger critique d'extinction par l'IUCN. En effet, depuis les années 70, la population d'anguilles européennes, *Anguilla anguilla*, est en nette régression avec une baisse du recrutement de plus de 90 % (Moriarty, 1986; Moriarty, 1990; Dekker, 2000; WGEEL, 2008) et une chute des indices d'abondance de civelles divisés par 10 à 100 lors de cette période (Dekker, 2004). Comme pour la majorité des espèces diadromes, les causes de ce déclin sont en partie dues à la surpêche, la diminution de l'accessibilité aux habitats de croissance lié à la présence d'obstacles (barrages, écluses, turbines, *etc.*), l'augmentation de la pollution ou encore la modification des courants et des températures océaniques (Feunteun 2002; Robinet & Feunteun 2002; Bonhommeau *et al.* 2008 ; Belpaire, 2009; Limburg et Waldman, 2009). A ces pressions subies par l'ensemble des diadromes s'ajoutent des pressions spécifiques à cette espèce. Ainsi l'introduction du parasite de la vessie natatoire, *Anguillicoloides crassus,* au début des années 80 a fortement impacté la santé de l'anguille Européenne d'autant plus que contrairement à l'anguille Japonaise (*Anguilla japonica*) qui a développée des résistances face à ce parasite, on peut observer de très forte densité de ce parasite dans la vessie natatoire de l'anguille Européenne (Kirk, 2003). Pour cette espèce qui effectue d'importantes migrations verticales lors de sa migration reproductrice, le contrôle de la flottabilité est essentielle (Aarestrup *et al.*, 2009). Or la présence de ce parasite dans la vessie natatoire peut fortement affecter leur capacité de nage et donc la capacité des anguilles matures d'atteindre la zone de reproduction. De plus, comme montré par l'étude de Palstra *et al.* (2007), les anguilles affectées par ce parasite ont des demandes en énergie 20% supérieures à celles d'un individu non parasité.

3. *Les mesures de gestion pour soutenir l'espèce*

Pour lutter contre cet effondrement du stock, l'Union Européenne a élaboré un règlement, le règlement Européen n°1100 du 18 septembre 2007, qui oblige les Etats membres à mettre au point un plan de gestion national à l'échelle de leurs bassins versants. L'un des buts de ce règlement est, entre autres, d'inciter les états membres à prendre des mesures pour permettre un échappement de 40 % de la biomasse de géniteurs qui aurait été produite dans un environnement non dégradé et sans impact d'origine anthropique (condition « pristine »; EC 2007). Les mesures appropriées spécifiées sont la réduction de la mortalité par pêche de 60% sur les trois stades pêchés (civelles, anguilles jaunes et argentées) à l'horizon 2015, la restauration des voies de migration tant en montaison qu'en dévalaison, la capture et le transport des anguilles argentées des eaux intérieures fermées vers la mer et le repeuplement de jeunes anguilles dans les eaux intérieures appropriées.

4. *L'importance des milieux de croissance*

La majeure partie de ces mesures sont faites pour favoriser l'entrée de jeunes individus (civelles ou anguillettes) et la sortie d'individus matures (anguilles argentées) mais les processus s'appliquant lors de la phase continentale sont peu ou pas pris en compte. Ainsi le repeuplement vise à augmenter le nombre de reproducteurs partant en mer en augmentant le nombre de recrues entrant dans un système. Cependant les caractéristiques du système où aura lieu le repeuplement, et donc la phase de croissance, vont jouer un rôle majeur dans la définition du nombre de reproducteur mais aussi de leurs qualités. En effet, les individus vont interagir avec leur environnement ce qui va influencer la dynamique de population (mortalité, migration, croissance) et la définition de leur traits d’histoire de vie (sexe, âge à maturité, fécondité,…) (Fig.3).

A l’échelle de l’aire de distribution de nombreux facteurs peuvent influer la dynamique d’une population et la définition des traits d’histoire de vie. Vøllestad (1992) a démontré que l’âge, la taille à maturité ainsi que la croissance étaient corrélés à la latitude du système où elles ont effectué leur croissance. Ainsi, les anguilles les plus au nord sont les plus grandes et les plus âgées. La salinité semble aussi jouer un rôle important puisque les croissances sont plus fortes dans un milieu saumâtre que dans un milieu dulçaquicole (Panfili *et al.* 1994). Bien que ces paramètres expliquent en grande partie les différences de productivité entre les systèmes colonisés par les anguilles, les autres caractéristiques du milieu que sont la densité de congénères, la densité de compétiteurs, la qualité de l’eau, la disponibilité en habitat et en nourriture ou encore la présence d’obstacle à la colonisation peuvent induire des dynamiques de populations et des traits d’histoire de vie différentes entre des systèmes équivalents (taille du bassin versant, type de milieu et salinité)(Fig.3). **Pour pouvoir comparer la dynamique de population et les traits d’histoire de vie observés dans différents systèmes, il faudra donc pouvoir dissocier les effets dus à la latitude et les effets dus réellement aux caractéristiques propres de chacun des systèmes.**

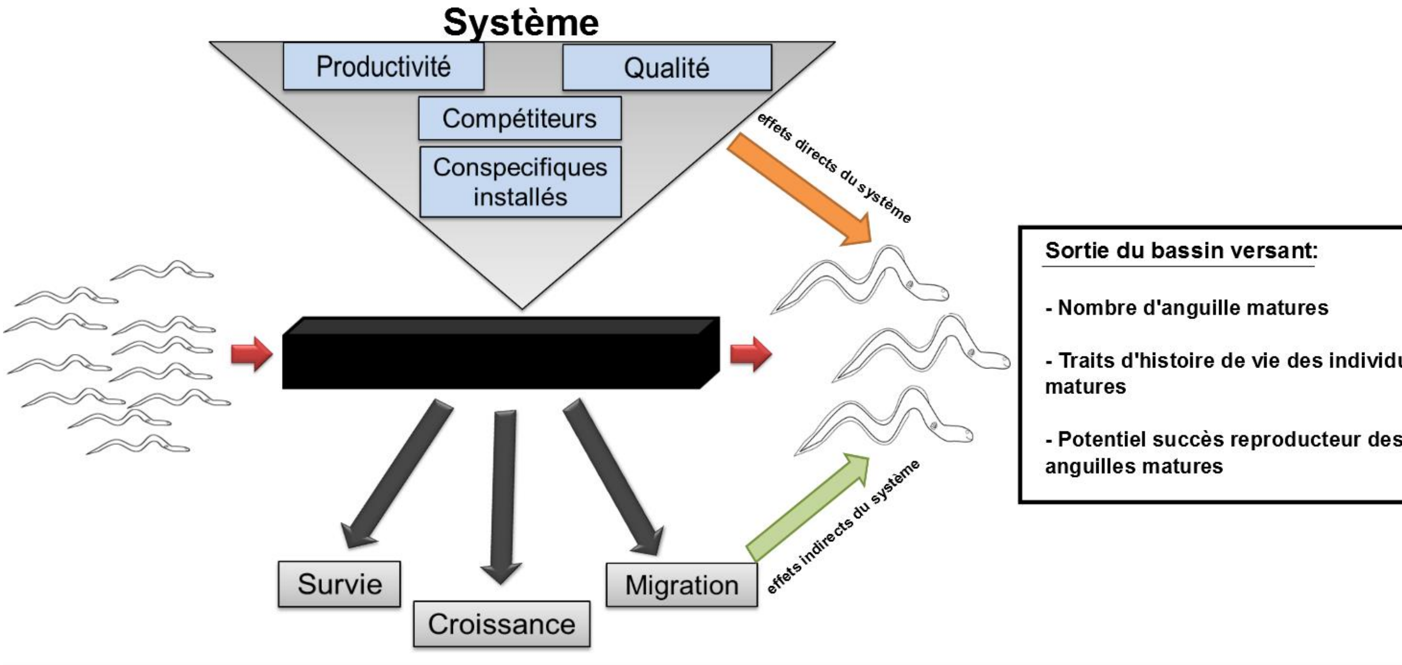

Figure 3: Schéma conceptuel des processus impactant le nombre et les caractéristiques des argentées sortant du système. Le nombre de civelles entrant dans le système sera déterminant mais les caractéristiques du système pourront avoir un effet direct (flèches oranges et grises) en impactant la dynamique de population et la qualité des individus et indirect (flèche verte) en jouant sur les stratégies développées par les individus pour atteindre la maturité.

Ainsi entre des systèmes équivalents (taille du bassin versant, type de milieu et salinité), des différences de capacité d'accueil et de niveau de saturation peuvent impliquer des dynamiques de populations et des traits d'histoire de vie très distincts. En effet, bien que la capacité d'accueil ait été définie de différentes manières (del Monte-Luna *et al.*, 2004), la définition la plus largement acceptée est le nombre maximal d'individus que l'environnement peut supporter, étant donnée la disponibilité en nourriture et en habitats nécessaires pour la population. Ainsi lorsque la population augmente, les ressources disponibles pour chaque individu de la population diminuent et la compétition entre les individus augmente entrainant des modifications de la dynamique de population et des stratégies d'histoire de vie *via* des phénomènes densité-dépendants (Rose *et al.*, 2001). Une augmentation de la compétition peut entraîner une diminution de la croissance individuelle ou à l'inverse une augmentation de la mortalité et de l'émigration (Fig.4). La densité-dépendance sur la mortalité et l'émigration affecte directement le nombre d'individus dans le système. A l'inverse, des changements du taux de croissance individuel vont affecter indirectement la taille de la population en prolongeant par exemple la phase de croissance la plus sensible (augmentant ainsi les risques de mortalité) (Rose *et al.*, 2001). Finalement, lorsque la capacité d'accueil est atteinte, l'ajout de nouveaux individus dans le système entrainera d'importants phénomènes de régulation puisque la taille maximale de population pouvant être soutenue par le système est dépassée (Fig.). **Bien qu'essentiel dans la compréhension de la dynamique de population et des traits d'histoire de vie, l'effet du niveau de saturation atteint par un système sur les populations installées a été peu étudié. Cependant pour cela il faut pouvoir comparer des systèmes équivalents et pouvoir identifier le niveau de saturation atteint par le système.**

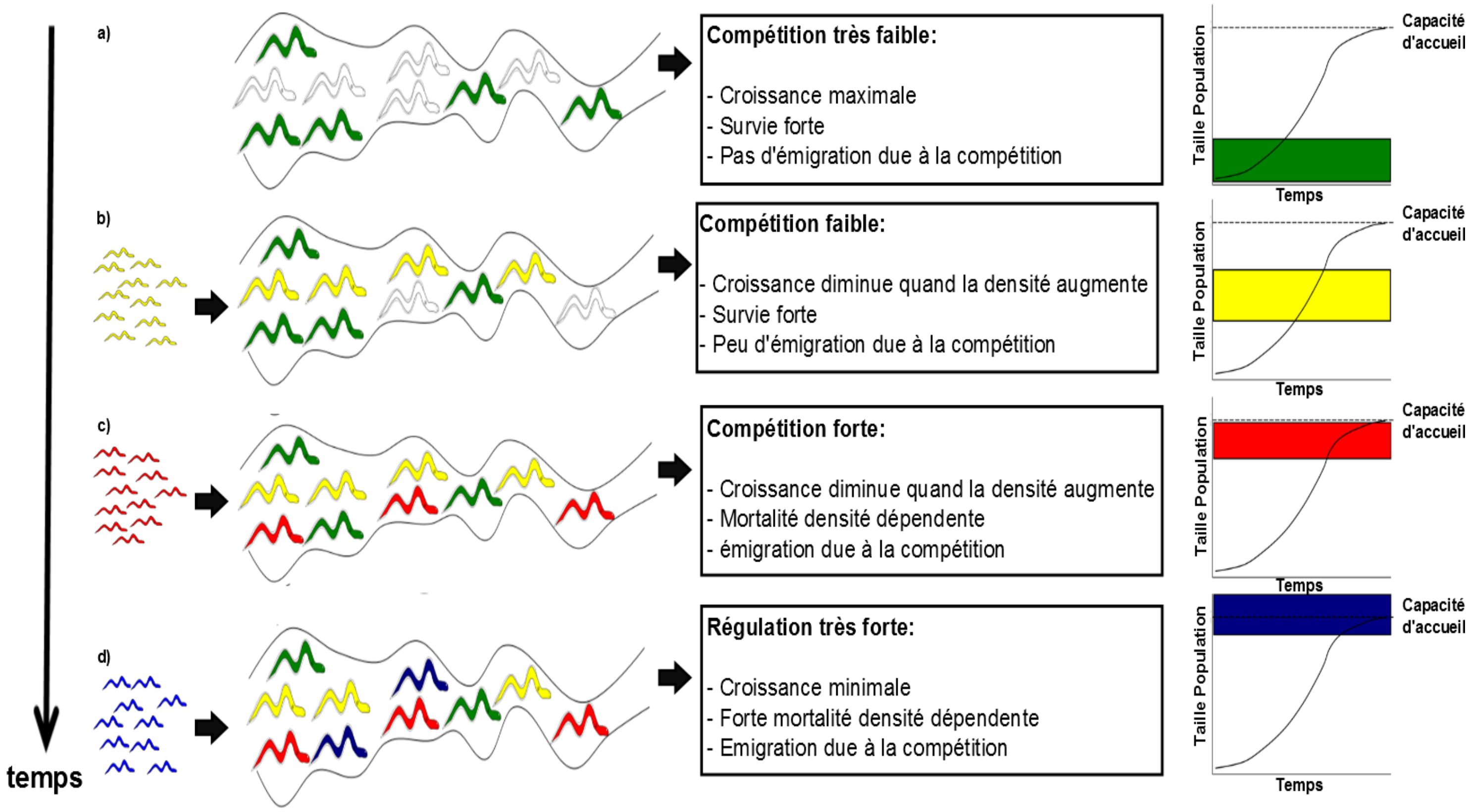

Figure 4: Schéma conceptuel de la saturation d'un système et des impacts que cela pourra avoir sur les paramètres démographiques que sont la croissance individuelle, la survie ou l'émigration. a) Lorsque les densités sont très faibles (relativement à la capacité d'accueil), les processus densité-dépendants sont faibles voire inexistants sur les paramètres démographiques car chaque individu a assez de ressources. b) et c) Lorsque la densité continue à augmenter au sein du système après l'arrivée de recrues, les ressources par individu diminuent et des processus densité-dépendants peuvent être observés d'abord sur la croissance individuelle puis, pour réguler la population plus fortement, sur la survie et l'émigration. Finalement quand la capacité d'accueil est atteinte, toutes les ressources sont limités pour l'ensemble de la population, d) la taille de la population ne peut plus augmenter malgré l'arrivée de nouvelles recrues ce qui implique de fort processus densité-dépendants avec une croissance individuelle minimale et des mortalités (et émigrations) surement dépendantes du nombre d'individus entrant dans le système.

IV. Objectifs scientifiques et plan de thèse

La phase continentale est donc particulièrement importante puisqu'elle déterminera, à partir du nombre de civelles recrutées dans un hydrosystème donné, le nombre et les caractéristiques (sexe, âge à maturité) des anguilles argentées prêtes à migrer pour se reproduire en mer des Sargasses. Les objectifs de cette thèse seront donc de comprendre dans quelle mesure les caractéristiques du site de croissance et les paramètres de la population en place peuvent impacter le nombre et les caractéristiques des anguilles argentées produites et les implications que cela peut avoir sur la gestion des espèces. Afin de répondre à ces questions, nous utiliserons des suivis individuels (grâce à des petits transpondeurs passifs) sur le long terme de 3 populations d'anguille Européenne contrastées dans 3 petits systèmes français (voir sites d'études et données). Pour répondre à ces objectifs, ce travail sera divisé en trois parties :

(1) L'un des principes des mesures prises par la France pour augmenter le nombre d'anguilles argentées prêtes à se reproduire dans un bassin versant consiste à augmenter le nombre de recrues entrant dans ce même bassin versant. La première partie de ce travail consistera à déterminer si ce principe s'applique dans un système naturel où de fortes variabilités de recrutement sont observées. En d'autres termes, **observe-t-on un lien entre le nombre de recrues entrant dans un système l'année *t*, la densité dans le système et le nombre d'anguilles argentées l'année *t+n* ?**

Pour étudier ce lien, nous avons analysé la corrélation entre les séries temporelles de recrutement et de densité dans un petit fleuve côtier breton. Les résultats seront discutés au regard du fait que les habitats étudiés dans ce système semblent avoir atteint la saturation (Acou *et al.*, 2011).

(2) La deuxième partie de ce travail consistera à **déterminer les processus de régulation (densité dépendant et densité indépendant) de la dynamique de population des anguilles jaunes (mortalité et croissance) et d'examiner l'impact de ces processus sur les traits d'histoire de vie.** Si de forts processus densité-dépendants sont observés, les recrues pourront être prélevées pour du repeuplement afin d'éviter des mortalités fortes.

Pour cela nous utiliserons le suivi de deux populations très contrastées à la même latitude et seulement séparées de 65 km : (i) une population majoritairement femelle vivant dans un milieu sans obstacle majeur à la migration et avec une bonne qualité de l'eau où l'on observe de faibles densités d'anguille mais une importante population de salmonidés et (ii) une population, où dans les habitats étudiés, la population d'anguilles est majoritairement mâle vivant dans un milieu cloisonné (plusieurs obstacles à la migration) et avec une qualité de l'eau moyenne. Dans ce système, l'anguille est l'espèce majoritaire en termes de biomasse et on y observe une grande variabilité de recrutement et une très forte densité d'anguilles. De plus, les habitats étudiés dans ce système semblent avoir atteint la saturation (Acou *et al.*, 2011).

Dans un premier temps nous y étudierons la croissance individuelle et déterminerons si les processus de régulation de ce paramètre sont différents entre ces deux milieux. Dans un deuxième temps, nous chercherons aussi à y expliquer les différences de mortalité par stade observées dans chacun des systèmes et nous chercherons à savoir si les différentes pressions appliquées sur chacune de ses populations peuvent déterminer les stratégies développées par les individus pour atteindre la maturité et partir se reproduire. Finalement, nous décrirons un modèle adapté à l'étude de la densité dépendance sur les paramètres démographiques comme la mortalité.

(3) La troisième partie sera consacrée à l’implication que peuvent avoir **ces processus de régulation sur la quantité et la qualité des anguilles argentées prêtes à partir se reproduire.** En effet bien que le nombre d’argentées partant se reproduire est un important déterminant de la production d’œufs, il est aussi nécessaire de prendre en compte la qualité de ces individus. En effet, des individus matures partis avec un mauvais état de santé pourraient ne pas atteindre la zone de reproduction ou ne pas avoir assez d’énergie pour se reproduire. De plus des individus contaminés pourraient transférer les contaminants aux futures générations, entrainant ainsi des problèmes de développement et de mortalité. **Comprendre le rôle du système sur la production d’anguilles argentées en quantité et qualité est en effet nécessaire pour cibler les habitats propices à des mesures de repeuplement.**

Dans un premier temps, nous avons conduit une expérience de repeuplement dans un marais d’eau douce dans le sud de la France (Camargue) et nous avons suivi les individus stockés de la date d’introduction à leur capture au stade argentée grâce au suivi biannuel de marquage-recapture. En estimant la croissance et la mortalité, nous avons pu ainsi estimer le nombre d’individus matures produits par cohorte introduite. La qualité des reproducteurs potentiels a également été évaluée en analysant l’âge et la taille à maturité mais aussi le taux de lipide, les concentrations en divers polluants (PCBs et Cadmium) et l’infection de la vessie natatoire par le parasite *Anguillicoloides crassus*. Ce suivi nous a également permis d’évaluer l’efficacité du repeuplement en comparant le nombre et la qualité des reproducteurs des individus stockés et d’individus ayant naturellement colonisés le système.

Dans un deuxième temps, nous avons étudié les relations taille-poids des anguilles argentées de plusieurs bassins versants à l’échelle européenne pour montrer que les variations observées ne sont pas dues qu’à un effet latitude mais que la qualité du système semble jouer un rôle très important dans la définition des traits d'histoire de vie et donc dans la qualité des anguilles argentées.

Matériels et Méthodes

Pour répondre à ces questions, nous disposons de séries chronologiques d'abondance et de Marquage-Recapture à long-terme (> 7 ans) acquises sur 3 hydrosystèmes différents (Fig.8).

I. Suivi par Capture-Marque-Recapture

1. PIT-tags

Figure 5: Passive Integrated Transponder

Le PIT (Passive Integrated Transponder) (Fig. 5) est un petit transpondeur radio qui contient un code spécifique permettant d'allouer un code unique d'identification à chaque animal marqué. Ils sont « passifs » et donc ne nécessitent pas de batterie, ce qui implique une durée de vie quasi illimitée et une taille minime. Ces marques sont inactives tant qu'elles ne sont pas stimulées par le champ magnétique d'un appareil de lecture (Fig. 6b). Lorsqu'elles sont activées, elles envoient un signal radio codé et normalisé de 8 à 12 caractères. Ce type de marquage a été utilisé sur de nombreuses espèces de poissons comme le saumon atlantique (Roussel, Haro & Cunjak, 2000), la truite commune (*Salmo trutta*; Cucherousset *et al.*, 2005), le brochet (*Esox lucius* ; Cucherousset, Paillisson & Roussel, 2007) ou encore le chabot visqueux (*Cottus cognatus* ; Keeler *et al.*, 2007). Leurs limites principales sont : (i) la distance de lecture qui n'excède pas quelques dizaines de centimètres et (ii) en raison de la taille du PIT-tag seules les anguilles ayant une taille supérieure à 150-200 mm ont pu être marquées. Ces marques sont introduites dans la cavité générale à l'aide d'une seringue (Fig. 6a). Le taux de rejet, considérant notre technique, a été estimé, lors d'essai à 5%, la mortalité induite par le PIT a été estimée nulle.

Dans ce projet, ces tags sont particulièrement importants puisqu'ils vont nous permettre d'avoir une information individuelle précise sur la mortalité, la croissance ou encore l'évolution des stades.

Figure 6 : a) Marquage à l'aide d'une seringue et b) lecture d'un tag

2. *Le suivi*

Dans l'ensemble des systèmes étudiés, les populations d'anguilles ont été suivies par Capture-Marque-Recapture (CMR) à l'aide de l'outil PIT-tag décrit précédemment. Le suivi d'une population par Marquage-Recapture à plusieurs avantages, il permet :

- de suivre non seulement une population mais aussi des individus mettant ainsi en évidence des comportements ou des stratégies au sein d'une même population. Dans le cas de l'anguille cela peut être particulièrement intéressant car au sein d'une même population différents comportements ont déjà été observés. En effet Feunteun *et al.* (2003) ont montré deux types de comportements de colonisation des systèmes au sein d'une même cohorte de recrutement : les pionniers et les fondateurs.
- d'estimer la taille de la population mais aussi des paramètres démographiques tels que la survie, la croissance, la migration ou le succès reproducteur. Pour cela des modèles ainsi que des logiciels d'analyse ont été créés pour analyser ce type de données.

Cependant cette méthode à quelques désavantages. Premièrement le suivi coûte cher en temps en main d'œuvre et en matériel. Par exemple sur l'Oir, le suivi de 14 stations d'échantillonnage (30 m de long) et d'une partie du linéaire nécessite 8 personnes (capture et biométrie/marquage) pendant 12 jours. Deuxièmement, le type de tag utilisé peut ne pas être utilisé pour l'ensemble des individus de la population. Par exemple dans notre étude considérant la taille et le poids des anguilles, seuls les individus ayant une taille supérieure à 150 mm ont pu être marqués.

3. Modèle CMR multi-états

Dans notre étude, nous utiliserons les modèles CMR multi-états et les logiciels E-Surge et U-Care (Lebreton *et al.*, 2009 ; Choquet *et al.*, 2009a ; Choquet *et al.*, 2009b). L'un des avantages de ce type de modèle, est qu'un état peut être défini pour chaque individu capturé (stade, âge, localisation, …). Cet état peut varier dans le temps (vieillissement, maturation, migration, …) et donc la classification d'individus selon leur état permet alors l'évaluation de survie état-dépendante, de probabilités de transition entre deux ou plusieurs états (croissance, migration,…) ainsi que des probabilités de reprise. De plus ces modèles permettent de prendre en compte les détections imparfaites (i.e tous les individus ne sont pas capturés et recapturés) ce qui évitent de sous-estimer la survie (Gimenez *et al.*, 2008). En effet, si l'individu n'est pas capturé, il peut soit être non capturable soit être mort (Fig.7).

Pour estimer ces paramètres, après la définition des différents stades (états), les données individuelles seront traduites sous forme d'histoire de capture[1] (Fig.7). Ces données sont ensuite analysées à l'aide des logiciels E-Surge et U-Care (Fig.7). Ainsi des survies stades-dépendantes ainsi que des probabilités de transitions entre les différents stades pourront être

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[1] Par exemple : 1022030 correspond à une anguille marquée la première année au stade 1, pas recapturée la deuxième année, recapturée vivante la troisième et quatrième année au stade 2, pas recapturée la cinquième année et recapturée vivante la sixième année au stade 3, pas recapturée la dernière année

estimées dans chacun des sytèmes. Des tests permettront de savoir si ces survies et transitions sont variables dans le temps et dans l'espace.

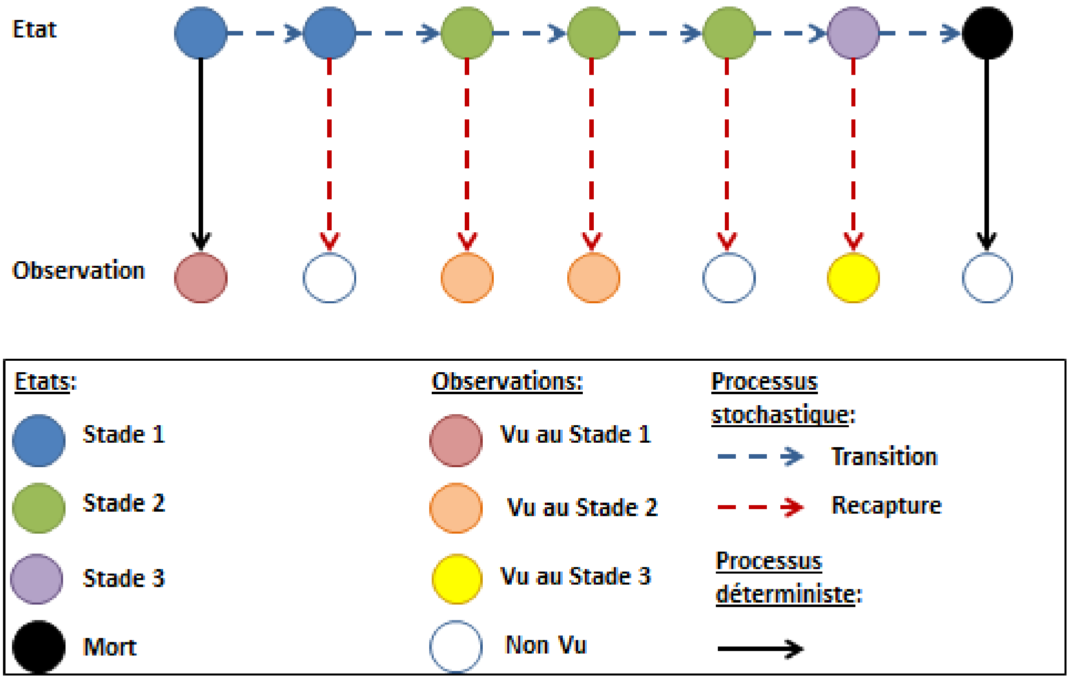

Figure 7: Exemple de processus d'observation et des états d'un individu marqué au cours du temps pour le modèle multi-état. L'ordre de vrais états pour cet individu est 112223M et l'histoire de capture observée est 102203M.

II. Les systèmes d'études

1. *Les sytèmes naturels*

L'Oir, situé dans le sud du département de la Manche, est un **affluent** de la Sélune, petit fleuve côtier normand se jetant dans la baie du Mont Saint-Michel (Fig.8). Le cours de l'Oir, long de 19,5 km, orienté est-ouest, a une pente moyenne de 11‰ et draine un bassin versant de 87 km². L'eau est proche de la neutralité et de **qualité correcte** mais avec des taux de nitrates élevés. Sur ce bassin, les activités humaines, sont essentiellement d'origine agricole (prairies, cultures fourragères, troupeaux laitiers).

Données : (1) Piégeage de Dévalaison au Moulin de Cerisel (2000-2012)

(2) Pêche électrique annuelle (sur station) pour estimation de l'abondance de toutes les espèces (2000-2008), échantillonnage dédié aux salmonidés (anguilles = pas espèce cible), avec Marquage-Recapture par PIT-tags.

Puis changement de protocole en 2009 (sans intercalibration)

(3) Pêche électrique annuelle (sur station) pour suivi de toutes les espèces mais aussi pêche pour le suivi spécifique de l'anguille depuis 2009 avec Marquage-Recapture par PIT-tags.

(4) Pêche spécifique annuelle sur une partie du linéaire avec marquage/recapture (sans estimation abondance)

(5) Données environnementales (température, débit, …)

Le Frémur, est un petit **fleuve** côtier breton (Côtes d'Armor) se jetant dans la Manche aux abords de Saint Malo (Fig.8). Il draine un bassin versant de 60 km2 et a un linéaire de 47 km dont 17 km pour le cours principal. Le cours du Frémur est **cloisonné** par différents obstacles dont 3 classés comme difficilement franchissable : le barrage de Pont Avet, le barrage du Pont es Omnès et le barrage de Bois Joli. Ces trois barrages sont équipés de système d'aide à la montaison. La **qualité de l'eau** est considérée comme **moyenne** avec des taux de phosphores assez élevés en relation avec des blooms de cyanobactéries présents sur la retenue de Bois Joli.

Données : (1) Piégeage de dévalaison au barrage du Pont es Omnès (1996-2012)

(2) Piégeage de montaison au barrage du Bois Joli (1997-2012)

(3) Pêches électrique annuelles sur toutes les espèces (1995-2012) avec changement de protocole en 2006 (avec intercalibration)

(4) Données environnementales (température, débit, …)

Ces deux hydrosystèmes sont à la même latitude et seulement séparés de 65 km, ils sont donc sensés subir des pressions environnementales régionales équivalentes (température, hydrologie, etc). Cependant, ils diffèrent à bien des égards particulièrement en termes de structure de population et en termes de structure du bassin versant. Le Frémur est un petit fleuve côtier où, malgré une qualité de l'eau moyenne, des forts recrutements et des fortes densité d'anguille peuvent être observés (Acou *et al.*, 2011). Dans ce système, l'anguille européenne est l'espèce la plus abondante en terme de biomasse et tandis que les habitats lentiques sont dominés par une population d’anguille féminine, les habitats lotiques sont dominés par des anguilles mâles. L’Oir est un affluent de la Sélune où la population de salmonidés est importante (en moyenne 35% de la population de poisson). On y observe de faible densité d’anguille et la population est majoritairement féminine.

2. Le système expérimental

Pisci sud est un **petit bassin d’eau douce**, qui est un ancien centre de pisciculture, situé dans la Réserve naturelle du « Marais du Vigueirat » en Camargue (Fig.8). Le bassin est composé de deux étangs connectés, de 6 ha et 50 cm de profondeur et de 5.5 ha et de 25 cm de profondeur respectivement, et il est entouré par une roselière de 20.5 ha. En été 2007, le bassin a été vidé entièrement à part une petite rigôle où les anguilles résidentes et d’autres espèces ont trouvé refuge. Le bassin a été de nouveau rempli pour y effectuer des **expériences de repeuplement** en utilisant des anguilles de différents stades (civelle, anguillette et anguille jaune) et venant de milieux différents (saumâtre et eau douce).

Données : (1) Suivi de la population résidente et des individus stockés à l'aide de pêches passives biannuelles et marquage/recapture (PIT-tag)

(2) Captures Par Unité d'Effort (CPUE) grâce des engins passifs (type ganguis) de l'ensemble des espèces présents dans le système

(3) Données environnementales (T°C et abondances de proies potentielles)

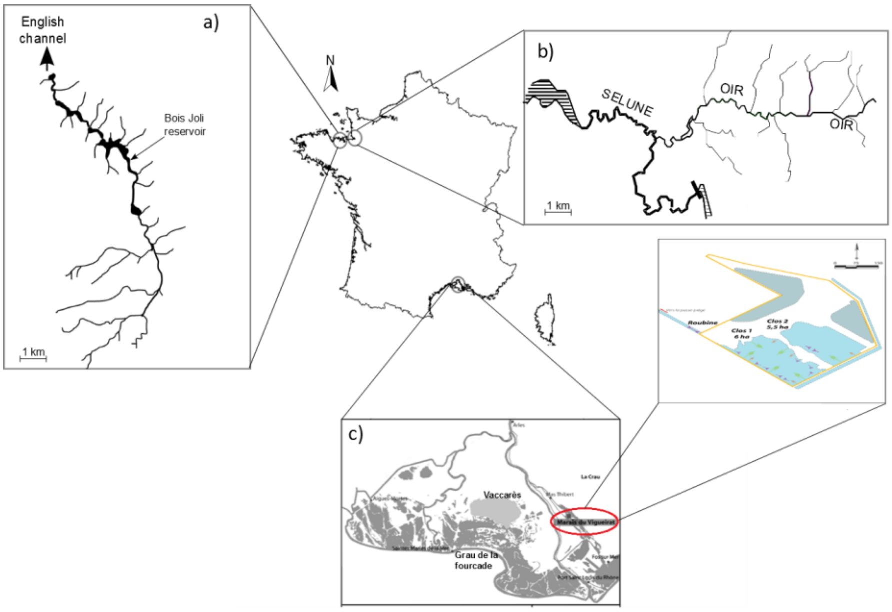

Figure 8 : Carte de France montrant la localisation et la configuration des trois systemes: a) le Frémur, b) l'Oir et c) Pisci-Sud dans le marais du Vigueirat.

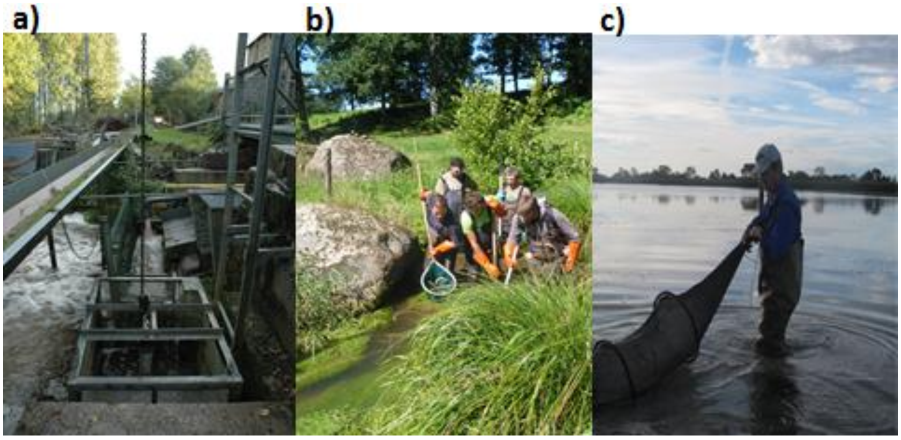

Figure 9 : Méthodes de capture utilisées a) Piège de dévalaison, b) Pêche électrique et c) Pêche passive avec ganguis

Tableau 1 : Données disponibles sur les trois systèmes de 1996 à 2012. P : primptemps, A : automne

		1996	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Frémur	**Recrutement**	-	3454	26765	5995	7965	13578	2457	381	12124	6223	9351	9103	15482	3578	10009	848	4166
	Densité	0,3339	0,5087	0,3061	0,3379	0,4049	0,4524	0,3348	0,4502	0,5153	0,3580	0,4923	0,2481	0,3750	0,2567	0,2225	0,3259	
	Marquée	356	231	82	8	150	87	67	44	x	x	x	x	103	69	80	47	43
	Recapturée dans le stock	0	77	22	22	32	17	33	28	22	6	1	5	0	23	20	24	18
Oir	**Densité**	x	x	x	X	0.041	0.035	0.016	0.017	0.028	0.022	0.027	0.019	0.015	0.12	0.10	0.072	
	Marquée	x	x	x	X	194	203	115	106	150	133	208	58	198	292	269	203	227
	Recapturée dans le stock	x	x	x	X	x	25	30	34	34	36	47	34	37	62	95	118	118
	Recapturée en dévalaison	x	X	x	X	0	0	0	27	6	10	4	2	1	0	7	6	11
	Nb total de dévalantes	X	x	X	x	19	52	4	341	100	142	62	39	90	12	66	65	57
Vigueirat	**CPUE anguille**																	
	Repeuplement	x	x	x	x	x	x	x	x	x	x	X	751 anguillettes et anguilles jaunes	~9000 civelles	~9000 civelles	~9000 civelles	~9000 civelles	~9000 civelles
	Marquée (civelles et résidentes)	x	x	x	x	x	x	x	x	X	X	x	x	P :228 A :95	P :329 A :254	P :486 A :419	P :535 A:267	P :640 A:80
	Recapturée dans le stock	x	x	x	x	x	x	x	x	x	x	x	x	P :53 A :76	P :33 A :63	P :141 A :125	P :117 A :128	P :265 A :81

Partie 1 : Relations entre recrutement, densité de la population

I. Contexte de l'étude

La perte d'habitat liée à la présence d'obstacles à la circulation dans les hydrosystèmes continentaux constituerait le principal facteur historique de la régression de toutes les espèces migratrices (Porcher & Travade, 1992). Feunteun (2002) estime que 33% des habitats potentiellement disponibles et favorables à l'échelle de l'aire de distribution de l'anguille européenne ne sont pas accessibles en raison de la présence de barrages. Pour faire face à cette anthropisation croissante des hydrosystèmes, des programmes de restauration des voies de migration par l'installation de passes migratoires ont vu le jour (Legault, 1994). Ces travaux ont permis de montrer que ces aménagements pouvaient augmenter rapidement l'indice de recrutement (Legault, 1994) et favoriser une colonisation densité-dépendante (Briand *et al.*, 2003) des zones de l'aval vers l'amont. Cependant, l'aménagement des obstacles par des passes anguilles est une mesure efficace si les densités d'anguilles observées en amont sont faibles comme cela a été observé dans la Vilaine (Briand *et al.*, 2003) ou au début du processus de restauration (Laffaille *et al.*, 2005).

En fonction des années, et probablement de la variation des courants océaniques qui influencent l'arrivée des civelles sur le talus continental (Bonhommeau *et al.* 2008), le recrutement observé dans les estuaires peut être massif et dépasser la capacité d'accueil des systèmes continentaux. Cela est particulièrement vrai dans les petits systèmes côtiers (< 100 km²) où les jeunes anguilles recrutées chaque année sont capables de coloniser l'ensemble du système en une saison de migration (Feunteun *et al.*, 2003). L'augmentation du recrutement naturel ne peut entraîner une augmentation des densités à l'amont que si la capacité d'accueil est augmentée via la restauration des habitats.

Le bassin versant du Frémur est un petit bassin côtier breton qui a fait l'objet d'un programme de restauration des voies de migration. Les abondances d'anguilles observées dans ce système sont parmi les plus élevées en Europe (Acou *et al.*, 2011). L'objectif de cette partie est d’évaluer l’effet à long-terme de la restauration des voies de migration sur l’abondance de la population résidente à l’échelle du bassin versant.

II. Article 1 : No relationship between elver recruitment and in-stream densities of European eels in a small obstructed coastal catchment: possible explanations.

Anthony Acou[1], Clarisse Boulenger[1], Fabien Charrier[2], Thomas Trancart[1] and Eric Feunteun[1].

[1]UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC– Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France
[2] Fish Pass, Bureau Expert Gestion Piscicole, Laillé, France

Correspondence : Anthony Acou, Museum National d'Histoire Naturelle, Service des Stations Marines du MNHN, CRESCO, 38 rue du Port Blanc, 35800 Dinard, France.
Email : acou@mnhn.fr

En préparation pour Knowledge and Management of Aquatic Ecosystems

Introduction

The European eel (*Anguilla anguilla*) is a catadromous fish species with a complex life history including two migrations across the Atlantic Ocean to and from the presumed Sargasso Sea spawning grounds (Tesch, 2003; Aarestrup *et al.*, 2009). Larvae (leptocephalli) drift across the Atlantic Ocean in the Gulf Stream to the continental shelf where they metamorphose into glass eels. The tide carries them to the coast, where they transform, first into elvers and then into small yellow eels that colonize growth areas. Some of them settle in coastal water and estuaries, but others colonize freshwater (Daverat *et al.*, 2006). When fat reserves exceed typically 20% of total body weight, after 3-30 years according to local growth conditions, Yellow eels metamorphose into silver eels through the silvering, which is a physiological and morphological adaptation to the last trans-Atlantic journey (Fontaine, 1994). Finally, silver eel migrate downstream towards marine waters and eventually return to the spawning grounds in the Sargasso Sea to reproduce and presumably dye.

Continental phase is particularly important as, with the mortality rates applied on eels during the growing phase, the abundance of the spawning stocks will depend on the abundance of recruits entering the rivers (Lobon-Cervia & Iglesias, 2008). However, study of local population dynamics of river stocks requires the monitoring of inputs (recruits), but also in-stream densities (resident population) and output (silver eels) at relevant spatial and temporal scales (Feunteun, 2002), the minimum time scale being the time needed for an eel to transform into the silver eel stage (3-30 years according to sex and latitude) and the minimum relevant spatial scale being the hydrosystem scale. Considering these requirements, local population dynamics of river stock remain studied in a limited number of European catchments. Vollestad & Jonsson (1988), using a long-term data series from the Imsa River (Norway), developed an input-output model to predict total biomass and age distribution of silver eels from annual recruitment data. The mortality rate was inversely correlated with the number of recruiting elvers, thus giving the first evidence for density-dependence in eel mortality. Such strong density-dependent mortality has more recently been documented for in-stream river-living eel in a pristine river system of NW Spain (Lobon-Cervia & Iglesias, 2008). These results suggest that density-dependence will regulate eel population size, and damp variation at older ages.

The eel population monitoring initiated in the Fremur R. (NW France) in 1995 constitutes one of the longest fishery independent set of data in France and even in Europe. Both upstream and downstream migrations have been studied in details (Acou *et al.*, 2008; Acou *et al.*, 2009; Feunteun *et al.*, 2003) and a positive relationship between silver eels caught in the catchment and effective migrants in the following year has been highlighted (Feunteun *et al.*, 2000). Acou *et al.* (2011) analyzed spatiotemporal in-stream eel densities over an 8-year period (1995-2002). They found that despite a marked variability of recruitment, the density of the oldest size-class remained stable, implying that density-dependent mortality occurred, probably to intraspecific competition for space and food and to predation. These results suggested that despite an increase of the recruitment, a given year, the in-stream densities will not increase. To verify this hypothesis, this paper aims at seeing if a relationship exists between recruitment and eel in-stream densities evaluated by electrofishing surveys led in the watershed over a 17-year period (1997-2013).

Materials and methods

Study site

The Fremur is a small and low gradient coastal river of northern Brittany (France) which discharges into English Channel close to Saint Malo (long. 2°04' W, lat. 48°32' N; Fig. 1). The catchment area is approximately 60 km^2, and the overall distance from source to mouth is

46 km, with 17 km of main stream. Slope ranges from 2% at the source (100 m altitude) to 0.1% near the mouth. Water temperature ranges from 21°C in the summer to 6-8°C in winter. Most of the streams have been degraded through hydraulic re-profiling. Modification of the landscape and loss of riparian plant cover (due to agriculture) have created considerable silt loads. There are many obstructions to eel migration; two major dams (Pont es Omnes and Bois Joli; Fig. 1) were previously impassable until the recent construction of fish lifts (Feunteun *et al.*, 1998). The larger, at Bois Joli, is 14 m high and creates a 3×10^6 m^3 reservoir. A lift for upstream migration of eels was built in 1996. Previous mark-recapture study using fast balneation in calcein for marking suggest a selectivity problem at the Pont es Omnes pass trap with respect to the smallest (≤ 120-140 mm) fish because many were able to climb the wall and cross the dam without passing through the pass trap (Acou *et al.*, 2009). Given this gear selectivity, it is likely that the use of raw total catches at Pont es Omnes may lead to underestimation of both total catches and year-to-year variability. No such selectivity issue has been observed at the Bois Joli trap. For these reasons, only the Bois Joli data set was considered in the present study. Upstream, three minor works, including a culvert under road, a flow gauging device and a sill (step) beneath a bridge, impose temporary obstacles to eel migration which are passable during high flow conditions (Fig. 1; Feunteun *et al.*, 1998). Overall, the Frémur provides a wide range of habitats from turbulent headwater streams with trout to lowland reaches downstream with bream, together with lentic reservoirs. Eel structure and abundance level in the 10-m deep Bois Joli reservoir is not known.

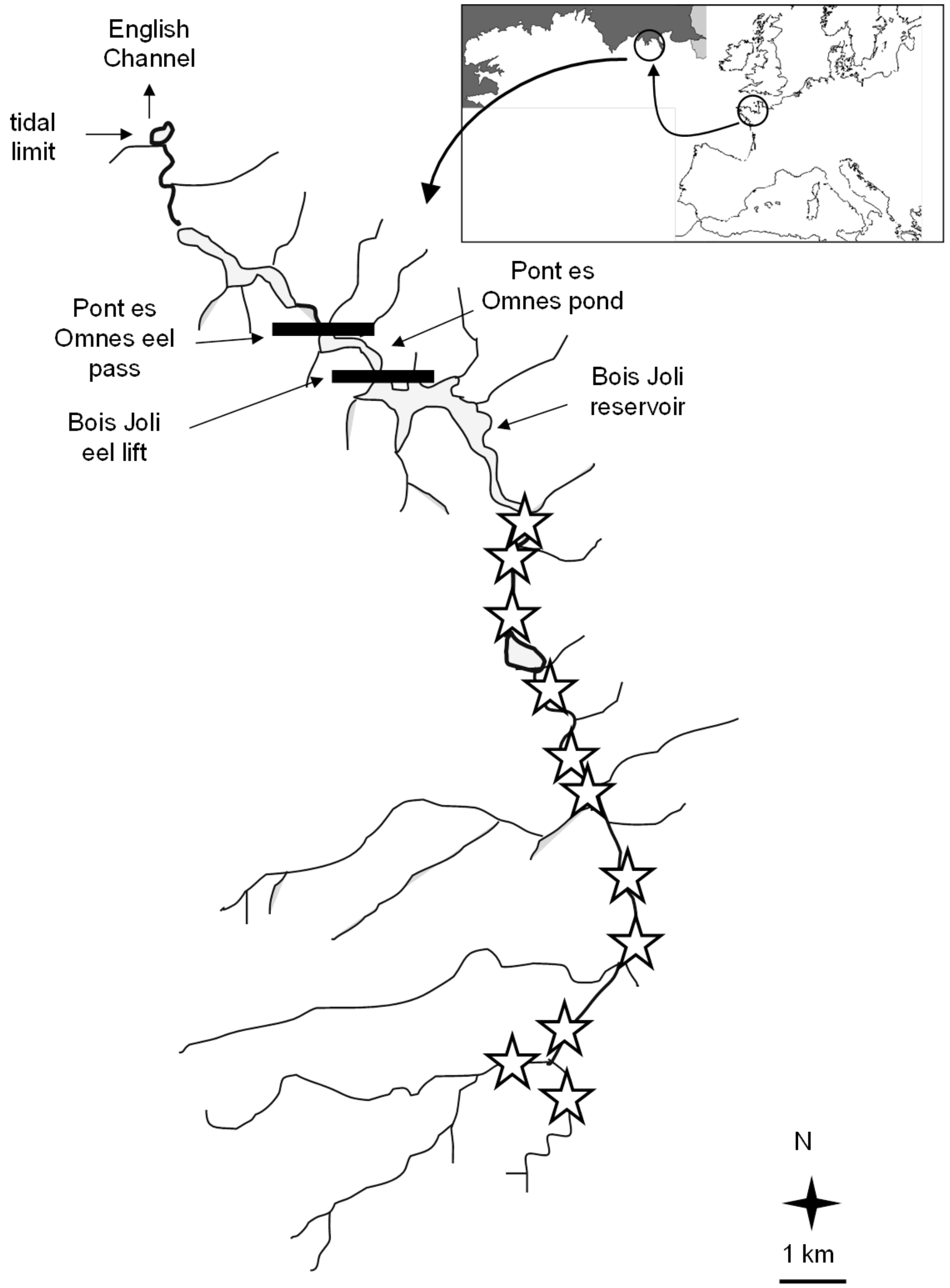

Fig. 1: Location and characteristics of the Fremur catchment (long 2°07'W, lat. 48°35'N). Stars represent batches of from two to four 30-m river sections sampled using electrofishing. Location of major dams equipped with eel passes (i.e. Pont es Omnes and Bois Joli) and tidal limit are indicated.

Fluvial recruitment

Full and comprehensive survey of Bois Joli pass trap was conducted from January 1997 to December 2013 (i.e. over seventeen upstream migration seasons). Over this period, the trap was inspected once every 3 days on average, and every day during migration peaks. All eels captured were anaesthetized with clove oil (Walsh & Pease, 2002) and measured (TL to the nearest mm). Fish were allowed to recover in cool, well-oxygenated water for *c.* 15 min before being released in the water above the dams.

Electrofishing

Abundance was estimated by the removal (depletion) method using electrofishing (Lambert *et al.*, 1994; Feunteun *et al.*, 1998). An average of 26 30-m long river stretches were sampled between 1997 and 2013 (a total of 501), which represented about 2.5% of the overall stream length upstream of the Bois Joli (Fig 1). Sampling sites were located between 8.4 and 17.0 km from the sea, and all had narrow channels (mean ± SD = 2.4 ± 1.0 m) and were shallow (0.5 ± 0.2 m). The habitats consisted of 4.1% of pools, 75.5% riffles and 20.4% of runs (Acou *et al.*, 2011). Sampling was conducted annually in September. This low water level period allows a better capture probability and at this date silver eels have not begun their downstream migration. Each site (30 m) was enclosed with 3 mm mesh stop nets and electrofished with a 'Heron' apparatus (Dream Electronique, Pessac, France) set at DC 300 V and 3 A. Most (> 90%) sites were sampled by a minimum of two successive passes. Some additional passes (three and/or four) were made if necessary until the catch per pass declined by 75% or more between successive passes. Eel numbers at each site were estimated by the weighted maximum-likelihood model of Carle & Strub (1978). As stressed previously (Feunteun *et al.*, 1998), the efficiency of the method is quite good even for large eels because of a high catchability (on average 70% of the eels were caught in the first pass). In total, 9196 eels were captured between 1997 and 2013, ranging in length from 60 to 854 mm (mean 240.1 ± 96.5 mm). Once again, all eels captured were anaesthetized, measured before being returned to the water. Silver eels were identified by three criteria (Acou *et al.*, 2005): colour of the back and belly, presence of a well-defined lateral line and ocular index (OI) ≥ 6.5 according to Pankhurst's silvering threshold value (Pankhurst, 1982). If only one (generally OI value) or none occurred, the eel was recorded as yellow. Eel density (D, number m^{-2}) was estimated at each site as the estimated number of eels per unit area of stream bed. D_{tot} denotes the eel density for all size-classes together. D_{S} represents the density of maturing silver eels (mean length = 382 ± 64 mm, range: 302-722 mm) ready to start their seaward migration.

Statistical analysis

Possible relationships between yearly numbers of immigrating elvers, mean annual $\mathrm{D}_{\mathrm{tot}}$ and D_{s} were examined by correlation analysis between the number of elvers in a given year and $\mathrm{D}_{\mathrm{tot}}$ (or D_{s}) the same year (or few years later). The study period considered here was from 1997 to 2013. Identifying the trend and detrending the data are both of great interest and importance in time series analysis. Therefore, before analysis, linear trends were removed from data series. All statistical analysis were fitted using the R language ⁄ environment (R Development Core Team, 2011).

Results

Fluvial recruitment

In total, 135 860 eels were captured in the Bois Joli trap between 1997 and 2013, ranging in length from 52 and 755 mm (Fig. 2). No glass eels were found, and the smallest fish caught were young pigmented *A. anguilla* ≥ stage VII. Mean length was 128 ± SD 34 mm and population structure was dominated by elvers (fish ≤ 180 mm), which represented roughly

95.0 % of total catches over the study period (Fig. 2). The average annual numbers of ascending *A. Anguilla* recorded at Bois Joli trap was 7985± SD 6515 eels. Numbers of ascending eels decreased according to years (Fig. 3). However, this decrease was not significant ($P > 0.05$). Overall, an important annual recruitment variability was observed in the trap (C.V. = 0.82, range: 381-26765 eels). Highest recruitment was observed in 1998 with 26765 elvers (Fig. 3).

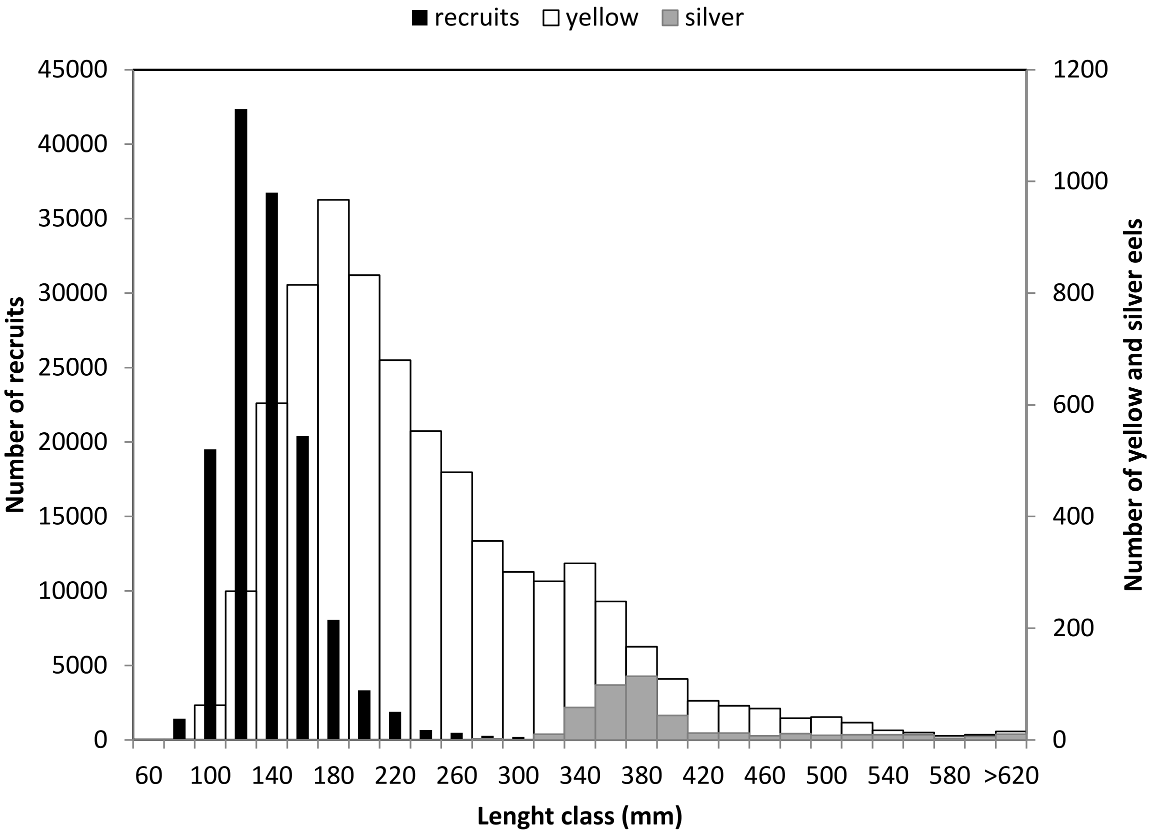

Fig. 2: Length histogram of eels sampled in the Fremur catchment from 1997 to 2013. Solid bars, recruits taken at Bois Joli Dam (N = 135860 ind.); open bars, yellow eels (N = 7399 ind.) sampled during electrofishing surveys; grey bars, silver eels (N = 422 ind.) sampled during electrofishing surveys.

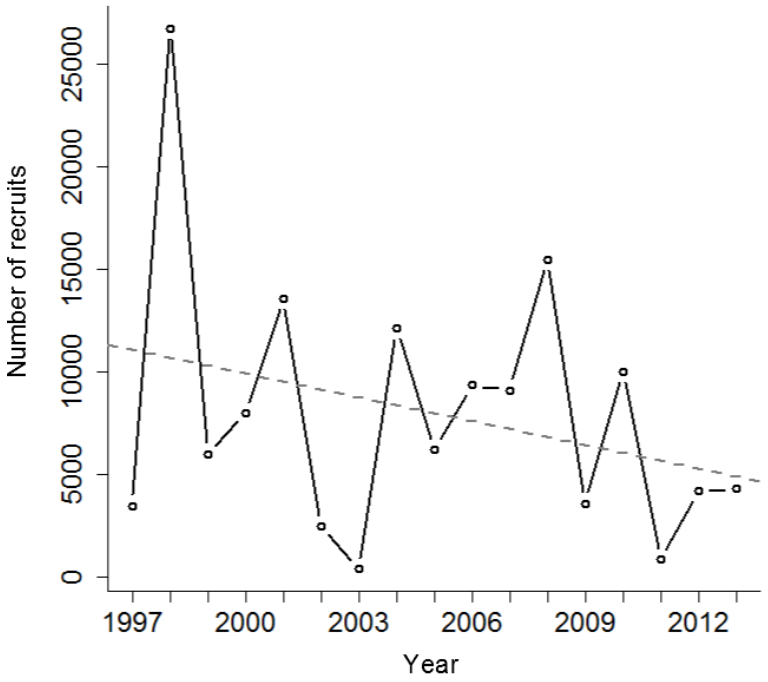

Fig. 3: Annual catches of migrant *Anguilla anguilla* elvers caught at Bois Joli Dam from 1997 to 2013.

<u>In-stream population characteristics</u>

A total of 7821 eels were captured over the study period. The population comprised eels between 56 and 757 mm (Fig. 2). Eels below 200 mm (elvers) made up 45% of total numbers confirming that recruits caught at the Bois Joli Dam reached the upstream areas. Silver eels accounted for only 5.4% of the total. Silver eel population structure is dominated by the 300- to 420-mm size class, which represent 90% of this category. This size-class is dominated by males (Tesch, 2003; Rossi & Colombo, 1979). The estimated total density (D_{tot}) varied between 0.12 eel.m^{-2} in 2012 and 0.52 eel.m^{-2} in 2004, with an overall mean of 0.34 ± SD 0.11 eel.m^{-2}. Before 2007, D_{tot} varied between 0.31 and 0.52 eel.m^{-2} with large annual variation but no particular interannual trend ($P > 0.05$; Figure 4). After 2007, a clear and significant ($P < 0.01$) decrease of D_{tot} was observed. Finally, D_{tot} significantly decreased with years over the study period ($P < 0.05$; Fig. 4).

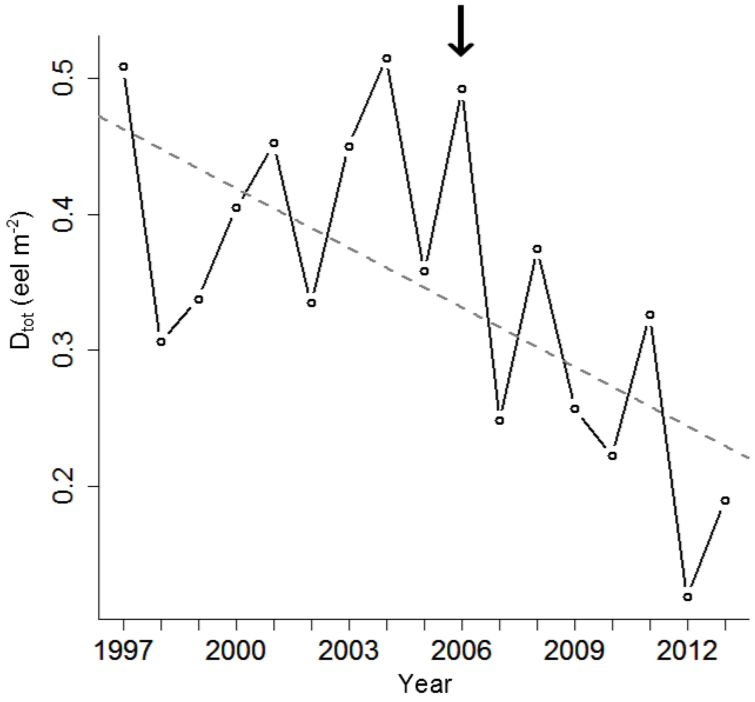

Fig. 4: Mean annual density of in-stream population (D_{tot}) observed during electrofishing survey from 1997 to 2013. The arrow indicates the period when the Bois Joli draining occurred.

Recruits *vs* in-stream densities

Whatever the lag tested (Fig. 1), we found no significant ($P > 0.05$) relationships between yearly numbers of immigrating elvers and D_{tot} in-stream densities (Fig. 5, Fig. 6). A similar result was observed when the in-stream density of silver eels (D_s) was considered (data not represented).

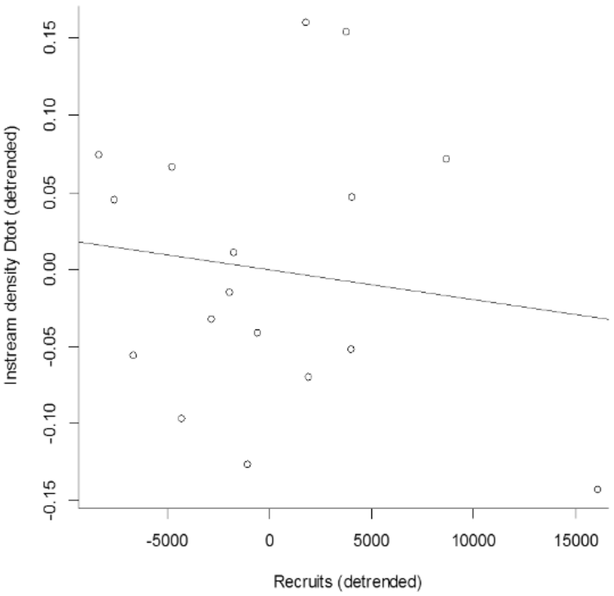

Fig. 5: Relationship between D_{tot} and the number of recruits (detrended data series). The lag represented here is year = 0. The curve was fitted by y = -1.93e-06 x + 6.514e-15 (n = 17, $r^2_{adjusted}$ = 0.01, P = 0.67).

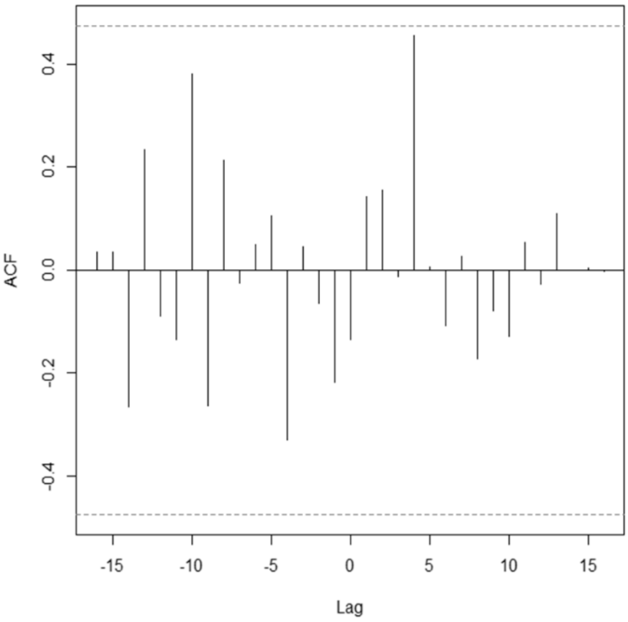

Fig. 6: Cross-correlation plot between the number of elvers in a given year and D_{tot}. Significance levels were represented in blue dashed lines. The most dominant cross-correlations (but not significant) occurs at lag = 4.

Discussion

In a previous study, Acou *et al.* (2011) brought compelling evidence that when Fremur's in-stream density exceeds 0.40 eel.m^{-2}, carrying capacity is reached and that density-dependent mortality occurs. Under the hypothesis of a constant carrying capacity of the system during the study period (1997-2013), it seems that habitat saturation of the Fremur is confirmed for the first part of the time series, between 1997 and 2006 (mean: 0.41 ± SD 0.07 eel.m^{-2}), before a strong reduction starting in 2007 (mean: 0.24 ± SD 0.07 eel.m^{-2}).

Consistent with others similar studies (Naismith & Knights, 1988), recruitment in the Fremur varied greatly according to years (c.v. = 0.82). An exceptional recruitment occurred in 1998 (N = 26765 eels), with catches 3.5 times higher than the overall mean (7985 ± SD 6515 eels). Intraspecific competition and agonistic behaviour that increased with massive recruitment is known to encourage both dispersal and upstream migration (White & Knights, 1997; Briand *et al.*, 2005). Considering that available habitat for eel is 74 000 m² (from Bois Joli to upstream part of the catchment; Acou *et al.*, 2009), this massive arrival of recruits represented roughly an addition of 0.36 eel m^{-2} in the whole system, which means a doubling of the in-stream population. However, upstream migrants this particular year face an overcrowded (or saturated) river habitat and it is likely that density-dependent mortality occurred, caused by limited spatial resources (Moriarty, 1986; Vollestad & Jonsson, 1988; Feunteun *et al.*, 2003). In this context, the absence of relationships between recruits and in-stream density observed here could be explained by density-dependent mortality, at least for the first part of the time series, i.e. between 1997 and 2006 when habitat saturation is confirmed.

However, it is unlikely that this regulation through density-dependent mortality exists for the second part of the time series (from 2007 and afterwards) when in-stream density dropped to lower values (mean 0.24 ± SD 0.07 eel.m^{-2}). An alternative hypothesis must be found. A particular event may explain the observed decline of in-stream density since 2007. Indeed, between June 2006 and February 2007, a complete draining of the Bois Joli was undertaken. The effect of this draining on the eel population is not known as no particular survey was carried out. However, strong diminution of water level was observed in the whole catchment. This might have induced a significant decrease of available habitat or food, increase of predation or migration which could have led in turn to important eel mortalities in the Bois Joli reservoir but also in the upstream part of the river system. Field observations confirmed that eel mortalities occur in summer/autumn 2006, however the magnitude of the mortalities is not known and further studies that aim to estimate annual survival are needed. However, if this hypothesis is accepted, it means that draining may have resulted in vacant habitats in the river systems and reduced both competition and mortality. In this context, successive years of low or moderate recruitment, as observed for the 2007-2013 period, have been needed to fill again the vacant habitats. The observed decrease of in-stream density since 2007 further suggests that recruitment was too low to enhance the density-dependent dispersal up to the upstream part of the river. Finally, recruitment observed since the draining only filled the Bois Joli reservoir, whereas in-stream population upstream decrease through emigration of silver eels.

In conclusion, the absence of relationships between recruits and in-stream density observed in the present study could be explained by two complementary factors: before 2007, a context of over-saturation of all suitable habitats within the river have resulted in strong competitive interactions and probably mortality, that enabled to observe a quantitative link between recruits and in-stream density. In 2007, the Bois Joli draining may have caused such levels of mortality in the population that successive years of low to moderate recruitment did not allow to increase in-stream density. Local eel population dynamic in the Fremur R. seems very complex, as characteristics of the catchment (presence of the Bois Joli reservoir) and the population (high level of abundance) may both play a role. In this context, furthers analysis are needed to better understand local dynamic (growth and survival) of the eel population in this systems.

Partie 2 : Facteurs de régulation de la dynamique de population et conséquences sur les traits d'histoire de vie

I. Contexte de l'étude

Comprendre ce qui fait varier les paramètres de la dynamique de population est un prérequis essentiel pour proposer des outils d'aide à la décision adaptés à la gestion d'une espèce (Caswell, 2000). En effet, ce sont ces paramètres qui vont déterminer l'évolution de la taille de la population mais aussi la définition des traits d'histoire de vie. Par exemple, une faible croissance individuelle prolonge la période durant laquelle les individus sont sensibles à la prédation (Werner & Gilliam 1984; Post & Evans 1989). Les résultats de notre étude précédente, c'est-à-dire l'absence de lien entre recrutement et densité dans le Frémur, semblent indiquer que des processus de régulation agissant sur la population peuvent être très forts. Cependant dans d'autres systèmes, l'augmentation du recrutement a conduit à une augmentation importante de la population (Briand *et al.*, 2003) suggérant que dans ces systèmes la régulation de la population via des processus densité-dépendants est faible, probablement parce qu'une dispersion vers les zones en amont est possible. Ces résultats contrastés pourraient être liés à la capacité d'accueil de chacun des systèmes. En effet contrairement à la Vilaine, l'ensemble des habitats lotiques du Frémur est supposé à saturation. Cependant, pour étudier le réel impact de la capacité d'accueil mais aussi d'autres caractéristiques propres au système, sur les processus de régulation et savoir sur quels paramètre démographiques et à quels stades ces processus s'appliquent, il faut pouvoir comparer des systèmes de taille équivalente et à même latitude.

Afin de déterminer les effets des caractéristiques d'un système (capacité d'accueil, présence d'obstacles aux mouvements, prédateurs, …) sur la régulation d'une population, nous étudierons les patrons de croissance (Chapitre1), et de survie (Chapitre 2), dans deux systèmes proches géographiquement et de taille équivalente. Les pressions appliquées sur chacune de ces populations sont très différentes. En effet, l'un des systèmes est supposé à saturation tandis que le second est supposé insaturé avec notamment des densités d'anguilles 10 fois moins fortes que celles observées dans le premier système. Les patrons observés seront donc analysés en lien avec les paramètres abiotiques et biotiques propres à chaque système. Dans un troisième chapitre, nous décrirons un modèle adapté à l'étude de la densité dépendance sur des paramètres démographiques, tels que la mortalité, et nous testerons si l'utilisation de ce modèle permet d'accroître la précision des estimations de densité dépendance par rapport aux méthodes classiquement utilisées.

II. Article 2 : Difference in factors explaining growth rate variability in European eel sub-populations: The possible role of habitat carrying capacity

Clarisse Boulenger[*], Alain Jean Crivelli[¶], Fabien Charrier[‡], Jean-Marc Roussel[§], Eric Feunteun[*] and Anthony Acou[*]

[*] *UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France*

[¶] *Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France*

[‡] *Fish Pass, Bureau Expert Gestion Piscicole, Laillé, France*

[§] *INRA, UMR 985 INRA-Agrocampus,Ecologie et Santé des Ecosystèmes, 65 rue de Saint Brieuc, CS 84215, F-35042 Rennes cedex, France*

Correspondence: Clarisse Boulenger, UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France.

Email: clarisse.boulenger@edu.mnhn.fr

Running head: Growth in two European eel populations

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Summary

As a key parameter in the management of fish populations, individual Growth Rate (GR) variations were examined in the European eel (*Anguilla anguilla*; > 150 mm) using extensive mark-recapture surveys in the lotic habitats of two small rivers of western France: the Frémur, supposed to be saturated, and at the same latitude the Oir with densities 5-fold lower than those of the Frémur. In both systems, generalised linear models were used to test if spatio-temporal factors such as dominant habitat type or local density affect GR variability. In the presumed unsaturated system, the Oir, GR variability is mainly explained by a set of habitat suitability drivers (density, dominant habitat type). In the Frémur, GRs appear independent of differences in habitat density or productivity. Below saturation, an increase in density will decrease the GR through intraspecific competition. At saturation, intraspecific competition reaches such high levels that regardless of eel density and productivity, the resources available by individual are similar throughout the system. In these circumstances, the effect of density on growth was presumed undetectable. Despite these contrasted results, mean GRs observed in both catchments were closed (~20 mm year^{-1}). This is an unexpected result as GR are expected to be higher in unsaturated systems. This similarity could be explained by the difference between the two systems in term of: (i) sex ratio (the Frémur is dominated by male whereas the female are dominant in the Oir), (ii) habitat type distribution or (iii) possible interspecific competition (important salmonid populations in the Oir).

Introduction

Individual growth is a key parameter in the management of fish populations since it can directly affect reproductive success (Rose *et al.*, 2001). For instance, the slow growth of individual increases their age at maturity, prolongs the period during which individuals are susceptible to size-selective predators (Werner & Gilliam 1984; Post & Evans 1989), and leads to a smaller size at maturity and/or lower fecundity (Werner & Gilliam 1984; Wootton, 1990). Understanding Growth Rate (GR) variability is thus a major component for the management of endangered fish species such as the European eel (*Anguilla anguilla*, L.).

The European eel successfully inhabits a wide range of habitats in Europe and consequently shows considerable variation in GR and size for a given age (Vollestad, 1992). At the scale of the species distribution, eel GR is known to decrease from South to North of Europe (Vøllestad, 1992) as a result of the latitudinal gradients of temperature and environmental correlates (e.g., photoperiod, hydrology, and productivity). Within catchments, eel GR also varies greatly according to environmental drivers such as temperature, salinity, distance to the sea, and productivity of the water body (Berg, 1990; Fontenelle, 1991; Meunier, 1994; Panfili & Ximénès, 1994; Daverat *et al.* 2006; Lasne *et al.*, 2008; Daverat *et al.*, 2012). As a result, eel life-history traits usually covary with distance from the sea because most of the environmental factors (temperature, salinity, productivity) that influence eel growth are structured along the longitudinal gradient (Amoros & Petts, 1993; Lasne *et al.*, 2008; Daverat *et al.*, 2012). Typically, males occupy the most downstream reaches, grow quickly and mature earlier at a smaller size, whereas females develop slowly in upstream reaches and mature later at a larger size (Tesch, 2003).

While density-dependence is known to influence eel migration patterns (Feunteun *et al.*, 2003), demographic parameters such as sex ratio (Krueger & Oliveira, 1999), adult survival

(Vøllestad & Jonsson, 1988; De Leo & Gatto, 1996), or growth has never been confirmed by field data in this species (De Leo & Gatto, 1996; Jellyman, 1997; Aprahamian, 2000). Nonetheless, eels intensively compete for food and space (Tesch, 2003; Cucherousset *et al.*, 2011), and despite compelling evidence that this species is declining throughout its range (ICES, 2009), eel density in catchments can remain at high levels, particularly in small coastal catchments in western France (Acou *et al.*, 2011). In such catchments, major concentrations of glass eels recruited from the ocean are still found, presumably because of different currents, which are the principal vector for eel recruitment in Europe (Dekker, 2003; Bonhommeau *et al.*, 2010). Moreover, in such small rivers young recruits may colonise the whole river in a single wave of upstream migration (Feunteun *et al.*, 2003). It is likely that such massive colonisation of rivers by recruits could limit the potential for eel growth.

The general prediction for density-dependent effects is that growth should be depressed at high densities due to reduced food availability as resources are depleted (Sinclair, 1989). However, identifying Density-Dependent Growth (DDG) in the wild is difficult, both for methodological and ecological reasons. Firstly, the data have to be replicated in time and space in order to disentangle spatio-temporal variations from density effects, and a large range of densities is needed (Strong, 1986; Jenkins *et al.*, 1999). Secondly, the detectability and intensity of DDG may be tightly linked to the habitat Carrying Capacity (CC), defined as the maximum density or biomass that habitat can sustain (Van Gils *et al.*, 2004). Where CC is reached, all the habitats are filled and resources (space and food) are limited in the whole system and equal suitability for all habitats is expected (Fretwell & Lucas, 1969). Consequently, GR should be independent of local habitat density or productivity as suggested by Aprahamian (2000). As far as we know, the only study that analysed European eel DDG was that of Aprahamian (2000). His results showed no relationship between growth and eel density in seven tributaries of the lower Severn (United Kingdom) suggesting that a DDG cannot be detected because the study sites had limited productivity, i.e. their CC have been reached.

Here, we tested the spatio-temporal variability of GRs in relation to environmental and biotic factors. For that, we used an extensive mark-recapture dataset (3 and 6 years) from French sub-populations of European eel in two small (< 100 km²) river systems of Western France: the Frémur (Brittany) and the Oir (Normandy). Both sites are in close proximity (65 km apart) and thus undergo equivalent regional environmental pressures (temperature, hydrology, etc.). However, they differ in many ways. The Frémur is a small river where, despite a medium water quality, high recruitment and density of eel could be observed. In this system, European eel is the most common species in terms of biomass and in lentic habitats major part of eels were female while in the lotic habitats the majority of eels were male. By contrast with the Frémur, the Oir, which is a tributary of the Selune River, is known to be a salmonids river (Baglinière *et al.*, 2005; Rivot *et al.*, 2008). In this system, low densities of eels were observed and the majority of eels were female. These two sites were selected because of the expected differences in their inherent habitat CC. Our hypothesis supported by a previous study (Acou *et al.*, 2011) is that the lotic parts of the Frémur have reached their CC and is thus at habitat saturation (a habitat is saturated when the CC is reached) Indeed, their results highlighted that in the Frémur (i) densities range among the highest values recorded in Europe (a mean of 0.40 ± 0.48 eels m^{-2} between 1995 and 2002), (ii) eels are widely distributed and their densities are similar throughout the lotic habitats of the system (iii) densities of the older eels (individuals with a size superior to higher than 450 mm and silver eels) remains stable over the study despite wide fluctuations of abundance of recruits, suggesting that density-dependent mortality occurred. Whereas in the Oir, a persistent low-density eel population is observed (0.074 ± 0.016 eels m^{-2} between 2009 and 2012) and similar density distribution analyses (unpublished results) suggest that the Oir is below habitat saturation.

We expect that (i) factors explaining GR variability depend on the inherent CC reached by each system, and (ii) that DDG cannot be detected in a system where CC is reached as eel GR is expected to be independent of differences in habitat density or local productivity. For both sites, we focused on the lotic habitats and analysed how eel GR vary with environmental (water temperature and multiscale habitat) and biotic factors (local density and age classes). Results are discussed in the frame of the DDG and CC theories.

Methods

Study systems

The Frémur and the Oir are typical of the numerous small river systems found in Western Europe.

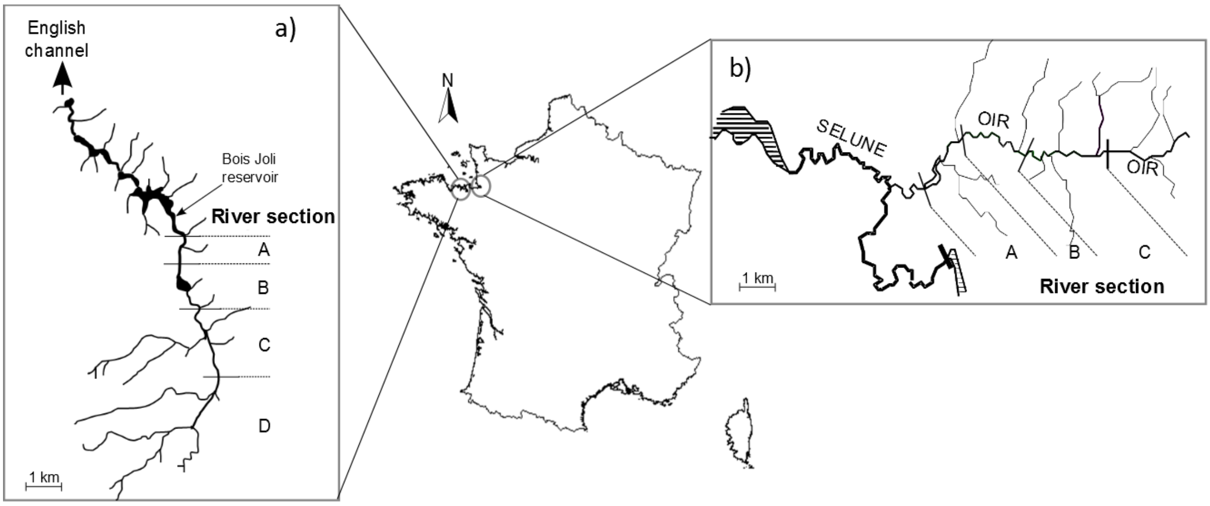

Fig. 1. Map of France, showing the location and configuration of the studied drainage basins: (a) The Frémur River, (b) the Oir River, and the different river sections studied.

The Frémur is a small and low gradient coastal river in Northern Brittany, which discharges into the English Channel close to Saint Malo (2°06′W, 48°34′N; Fig. 1). The catchment area is approximately 60 km^2, and the distance from source to mouth is 46 km, with a 17 km main stem. The gradient ranges from 2% at the source (100 m altitude) to 0.1% near the mouth. The water temperature ranges from 21°C in the summer to 6–8°C in the winter. Two major dams

(Pont es Omnes and Bois Joli) were previously impassable until the construction of fish passes (Feunteun *et al.*, 1998). The highest, at Bois Joli, is 14 m high and holds a 3.10^6 m^3 reservoir. A lift for the upstream migration of eels was built in 1996. Upstream, three minor works, including a culvert under a road, a flow-gauging device, and a sill (step) beneath a bridge, create temporary obstacles to eel migration, but are passable during periods of high flow (Feunteun *et al.*, 1998). These three obstacles lead to an accumulation of eels downstream the hydraulic works and to very low densities immediately upstream the obstacle (Feunteun et al, 1998). Overall, the Frémur provides a wide range of shallow (mean ± SD = 0.5 ± 0.2 m) and narrow (2.2 ± 0.9 m) habitats, from turbulent headwater streams with trout to lowland reaches downstream characteristic of bream habitats, together with lentic reservoirs. In this system, the European eel is the most common species in terms of biomass (41% of the biomass).

At roughly the same latitude (1°16′W, 48°37′N), 65 km eastward, the Oir is a small river tributary of the Sélune, and flows into Mont Saint Michel bay (Fig. 1). The catchment area is 87 km^2, and the main stem is approximately 25 km long. The mean gradient is 1.1%, and the water temperature ranges from 20°C in the summer to 5–7°C in the winter. The Oir is obstructed by only one weir and it dwells significant populations of brown trout *Salmo trutta* and Atlantic salmon *Salmo salar*.

Eel sampling

In each river, sites were sampled by electrofishing (14 sites and between 25 and 31 sites every year for the Oir and the Frémur, respectively). Each site was electrofished with a 'Heron' apparatus (Dream Electronique, Pessac, France) set at DC 300 V and 3 A. Most sites were sampled with a minimum of two successive passes. Additional passes (three or four) were made if necessary, until the catch per pass decreased by 75% or more between successive passes (Acou *et al.*, 2011). As stated previously (Lambert *et al.*, 1994; Feunteun *et al.*, 1998), the efficiency of the method is high, even for large eels, because of the high catching success of these shallow sites; on average, 70% of the eels were caught in the first pass.

In both systems, from 1996 to 2002 for the Frémur, and from 2009 to 2012 for the Oir, sampling was conducted annually in September and October, corresponding to the period when the growth could stop due to low temperatures and before the downstream migration of silver eels (Fontaine, 1994). All eels captured were anaesthetised with clove oil (e.g. Walsh & Pease, 2002) and measured (Total Length [TL], to the nearest mm). In both systems, no glass eels were found, and the smallest eels (60 and 101 mm in the Frémur and the Oir, respectively) were young pigmented eels at stage VII, according to the macroscopic classification of Elie *et al.* (1982). Silver eels were identified by three criteria (Acou *et al.*, 2005; Acou *et al.*, 2006): the colour of the back and belly, the presence of a well-defined lateral line, and an Ocular Index (OI) ≥6.5, according to Pankhurst's silvering threshold value (Pankhurst, 1982). If only two of the criteria (most often the lateral line and the OI value) were met, the eel was considered as a silver eel. If only one (generally the OI value) or none were met, the eel was recorded as a yellow eel.

Eels larger than 150 mm were individually marked with Passive Integrated Transponder (PIT) tags (Prentice *et al.*, 1990). Individuals with a size inferior to 150 mm were not marked because the weight of the tag (0.1g) would have represented more than 2% of the total weight of the individuals (Winter *et al.*, 1996). Recaptured eels were checked for the presence of a PIT tag, and individual information was recorded (TL, stage, site, date of recapture). After handling, the fish were allowed to recover for more than 15 min before being released at the site of capture. Every year, approximately 250 and 150 eels were marked in the Oir and in the Frémur, respectively (Table. 1). From the total number of eels marked in both sites, 22.5% were recaptured in both the Frémur (N=231) and the Oir (N=254) (Table. 1).

Individual growth data

As we want to access the effect of specific parameters in a given year on GRs and avoid to mask possible annual variability using mean growth rates (for example by dividing by 3 the GRs observed between year t and year $t+3$ to have the mean GRs every year), individual Growth Rate (GRt, mm year^{-1}) was calculated only for eels sampled over two consecutive years, in the following manner:

$GRt(i) = TL_{t+1}(i) - TL_{t}(i)$

where $TL_{t}(i)$ is the length (in mm) of the fish i (in the year t).

Table 1 Marking effort and number of eels recaptured in all the lotic habitat sampled since the beginning of the marking campaign in the Oir and in the Frémur. The 69 and 82 individuals used in our growth analysis belong to the 254 and the 231 eels recaptured in the Oir and the Frémur, respectively.

	The Oir R.						**The Frémur R.**								
Year	**2000-2008**	**2009**	**2010**	**2011**	**2012**	Total	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	Total
Number of eels marked	653	139	98	107	131	1128	356	231	82	8	150	87	67	44	1025
Number of eels recaptured	107	30	39	45	34	254	0	77	22	22	32	17	33	28	231

A total of 99 and 76 eels were recaptured two consecutive years during our study period in the Frémur and the Oir, respectively. However some individuals were removed from the data set. Firstly, if GR $_{t-t+1}$ (i) < 0 (due to measurement errors), these data were removed from the dataset (Table. 2). Secondly, as silvering metamorphosis marks the end of the growth period, GR of silver eels were not included in the analysis (Table. 2) and only growing eels (yellow eels) were considered. Thirdly, in order to study the effects of a precise section area and density, only sedentary yellow eels (eels caught in the same sampling site in the years t and t_{+1}) were selected (Table. 2; Laffaille *et al.*, 2003). Finally, our data sets contained 82 and 69 sedentary growing eels in the Frémur and the Oir, respectively (27 and 36% of the total number of recaptured yellow eels, Table. 1). We observed that the distribution in different size classes differed between the two systems with an equivalent number of eels in the three size classes in the Oir and very few individuals in the largest size class (Table. 2). Then our data sets seem to reflect correctly the eel distribution in the different size classes expected: (i) in a predominantly male system with almost only individuals with a size inferior to 450 mm as in the Frémur and (ii) in a female system with an homogeneous distribution between the different size classes as in the Oir.

Table 2 Description of the growth data set before and after remove of certain categories of eels in the Oir and in the Frémur.

	The Oir. R	**The Frémur R.**
Number of eels captured two consecutive years	76	99
Number of eels removed for measurements errors	0	10
Number of silver eels removed	2	2
Number of non-sedentary yellow eels removed	5	5
Number of eels considered in the growth analysis	69 in total 150-300 mm: 21 301-450 mm: 27 >450 mm: 21	82 in total 150-300 mm: 30 301-450 mm: 48 >450 mm: 4

Factors used to explain GR variability

Different factors were selected thanks to previous studies on eel GRs (Jellyman, 1997; Daverat *et al.*, 2012; Aprahamian, 2000; Melia *et al.*, 2006).

Temperature

Water temperature could act on GRs through two mechanisms. Firstly, water temperature could be used as a proxy of the primary productivity of the system (Morin *et al.*, 1999).

Productivity and associated rise of potential prey for eel should increase with increasing water temperatures. Secondly, water temperature is known to influence foraging and feeding activity of eels (Jellyman, 1991) and their subsequent growth. Nyman (1972) has observed that at temperature below 8°C European eels cease feeding (even if offered food items) and burrow in mud but Sadler (1979) demonstrated that eel growth in culture ceased starting at 12°C. As we are not sure about the minimum temperature need to grow, seven temperature variables were calculated: "Tmean" which is the mean water temperature between two sampling sessions, "ND.8", "ND.9", "ND.10", "ND.11", "ND.12", "ND.13" which correspond to the number of days when the water temperature exceeds 8, 9, 10, 11, 12, and 13 °C respectively to assess the possible favourable growth period. In the Oir, water temperatures were recorded using a probe located in the downstream part of the systems. In the Frémur, temperatures in the Bois Joli reservoir were equivalent to the ones measured in lotic habitats downstream the system from July 1999 to October 2009. For the ease of measurements, we thus recorded temperatures at the Bois Joli reservoir durin our study period.

Multiscale habitats

First, in both catchments lotic habitats were divided into river sections, to take into account the distance to the sea and the downstream-upstream productivity of each system (Fig. 1). In the Frémur, four river sections were defined, using temporary obstacles to migrating eels (Feunteun *et al.*, 1998; Acou *et al.*, 2011). In the Frémur, the downstream river section (the river section A) is situated at 8.5 km from the sea and separated from the downstream part of the river by the Bois Joli reservoir. The three river sections of the Oir were chosen according to the location of the principal tributaries of the river (Fig. 1). In the Oir, the downstream river section (the river section A) is situated at 11.5 km from the sea. Secondly, in lotic areas, eels prey on invertebrates and small fish and differences in growth may be attributed to the availability of this kind of prey. As distribution and biomass of macro-invertebrates depend on the variation in physical and morphological conditions (e.g. gradient, substrate, flow, and temperature; Illies & Botosaneanu 1963; Vannote *et al.*, 1980), dominant habitat type could be used as a good proxy of the local productivity. Then to analyse the effect of local productivity on GRs, in the sampling sites where 69 and 82 eels were caught (in the Oir and the Frémur, respectively), habitat types (three categories: run, riffle and pool) were defined from the measurement of depth and flow velocity according to the method defined by Baglinière & Champigneulle (1986). Then a portion of sampling site was defined as run when the depth is inferior to 0.6 m and the mean velocity is superior or equal to 0.2 m s^{-1}, as riffle when the depth is inferior to 0.6 m and the mean velocity is inferior to 0.2 m s^{-1} and as pool when the depth is superior to 0.6 m and the mean velocity is inferior to 0.2 m s^{-1}. The surface areas of the different habitat types found in a site sampled were calculated and the habitat type with the highest surface area was selected as the dominant habitat type of a sampled site. In the Frémur between 1996 and 2002, among the 48 sampling sites colonized by the individuals used for the growth analysis, 2 were defined as pools, 37 as riffles and 9 as runs. In the Oir between 2009 and 2011, the eels used in our study were found in 22 sampling sites, where 2 was defined as pools, 8 as riffles and 12 as runs. The proportion of the different dominant habitat types used in our analysis was representative of the lotic habitats at the scale of the catchment in both rivers (ORE PFC data, Acou *et al.*, 2011).

Age classes

Individual age is an important parameter to take into account for growth analysis as older individuals grow more slowly than younger ones (Vøllestad, 1992). However, a great variation in length within each age class exists for European eel and the only way to evaluate accurate eel individual age is still to apply otolithometry method. However, sacrificing all tagged eels was not a reasonable option particularly for a long-term CMR experiment.

Instead, three Size Classes (SC) of eels taller than 150 mm were created, with different ecological and behavioural characteristics (Baisez, 2001; Laffaille *et al.*, 2004; Acou *et al.*, 2011) as a proxy of age. The SC_1 (150 – 300 mm) consisted of recently recruited elvers that colonise the river (< 200 mm) and of sedentary growing yellow eels. The SC_2 (301 – 450 mm) and SC_3 (> 450 mm) represented the potential reproductive status of future male or female silver eels respectively (Laffaille *et al.*, 2003).

Density

For each sampled site (14 sites and between 25 and 31 sites every year for the Oir and the Frémur, respectively), density (eel.m^{-2}) was calculated by dividing the estimated abundance by the surface area of the sampled site. With the depletion method used in these systems, eel abundance at each sampled site was calculated using a weighted maximum likelihood model (Carle & Strub, 1978). Our sampled sites ranged from 30 to 100 m length and from 30 to 60 m length in the Oir and the Frémur respectively. However, Ovidio *et al.* (2013) showed a longitudinal home range between 33 and 341 m in a small stream in Belgium. Then, to catch the competition effect in their home range, an intermediate scale between the river section and the sampled site, was used to allow a better understanding of the density effect, the river unit, with a scale fine enough to capture the wide range of density of conspecifics experienced by the eel population in the study system and large enough to prevent eel migration for searching food to one unit to another during the studied year. Then a river section was divided into two, three or four river units (9 river units and 10 river units identified for the Frémur and the Oir, respectively). Finally, a river unit density was calculating using the densities observed in each sampled sites situated in the river unit (one to five neighbouring sampled sites were situated in each river unit).The median of the neighbouring sampled sites density placed in a river unit was used as a proxy for river unit density.

Statistical Analyses

All statistical analyses were carried out using R (http:// www.r-project.org/). For each system, generalised linear models were used to assess the statistical associations between GR and independent variables (environmental factors, population, and river system variables), using a Gaussian distribution and an identity link function. Independent variables, and interactions between these variables, were included using a method based on the Akaike Information Criterion (AIC). The R *stepAIC* procedure was used to perform stepwise model selection, to obtain the most parsimonious model (Johnson & Omland, 2004). The significance of the factors remaining in the final models was tested using classical analyses of variance (ANOVA). Tukey post-hoc tests were used to test for differences between subgroups (size class and habitat variables) that remained in the model**.** The modelling assumptions (i.e. residual normality, homoscedasticity) were graphically tested for each model and no major violation was observed for any of them.

Results

On average, European eels captured two consecutive years grew 20.9 mm. year^{-1} in the Frémur and 19.1 mm. year^{-1} in the Oir. The results of the GLMs are presented in the Table. 3. The coefficients and associated probabilities of the parameters selected by the R *stepAIC* procedure are presented in Table 4.

Table 3 Results of the GLM s in the Oir and the Frémur. The factors selected by the procedure stepAIC are noted according to their order of selection (from 1 to 4) into the final models. Factors not selected into the final models are marked with a cross. Results of the F tests and their associated probabilities are figured: ns, not significant; * P < 0.05; **P < 0.01; ***P < 0.001

Parameters		**The Oir**	**The Frémur**
River unit density	Order	1	x
	F	39.7677	
	P(F)	***	
River section	Order	x	1
	F		4.8449
	P(F)		**
Size Class	Order	2	x
	F	7.1442	
	P(F)	**	
Habitat	Order	4	x
	F	4.2293	
	P(F)	*	
Tmean	Order	3	x
	F	5.2008	
	P(F)	*	
ND.8 (9, 10, 11, 12, or 13)	Order	x	x
	F		
	P(F)		

Table 4 Coefficients and associated probabilities from the selected models of GLM of the two systems. ns, not significant; . $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. The factors tested in both systems were: river section (from the downstream part of the study area, river section A, to the upstream part, river section C and D for the Oir and the Frémur, respectively), size class (SC_1: 150-300 mm, SC_2: 301-450 mm, SC_3: > 450 mm), mean water temperature (Tmean) and dominant habitat type (pool, riffle, run).

	Parameters	**Estimate**	**SE**	***t* value**	**Pr (>|t|)**	**Level of significance**
The Oir	Intercept	-103.081	47.022	-2.192	0.032130	*
	River unit density	-54.157	30.001	-1.805	0.075905	.
	SC_2 (301-450 mm)	-6.636	2.731	-2.430	0.018023	*
	SC_3 (> 450 mm)	-11.136	3.082	-3.614	0.000606	***
	Tmean	11.006	3.754	2.932	0.004718	**
	Habitat type riffle	8.955	4.567	1.961	0.054387	.
	Habitat type run	1.540	4.101	0.375	0.708572	ns
The Frémur	Intercept	33.789	4.039	8.365	1.84e-12	***
	River Section B	-15.517	4.833	-3.210	0.00193	**
	River Section C	-15.789	7.785	-2.028	0.04594	*
	River Section D	-21.956	6.492	-3.382	0.00113	**

For the Oir, the selected model explained 53% (adjusted R^2) of the variance of GR. River unit density was the first factor selected by the R *stepAIC* procedure with 31% of the explained variance. GR decreased significantly when the river unit density increased (Fig. 2). Size class was the second factor selected by the R *stepAIC* procedure (11%). As expected, GR decreased when size increased, i.e. young eels had a higher GR than older eels (Fig. 3b). SC_1 was significantly different from SC_2 and SC_3 (Tukey test, $P < 0.05$), but no significant difference was found between SC_2 and SC_3. Tmean was the third factor selected by the R *stepAIC* procedure; this variable only explained 4% of the growth variance with an increase of GR when Tmean increased (Fig. 3c). The other temperature variables did not significantly affect the GR. The last factor selected by R *stepAIC* procedure was the dominant habitat type with 7% of the variance explained. The Tukey post hoc test indicated that the GR was significantly higher in the riffle than in the run (Tukey test, $P < 0.05$; Fig. 3a).

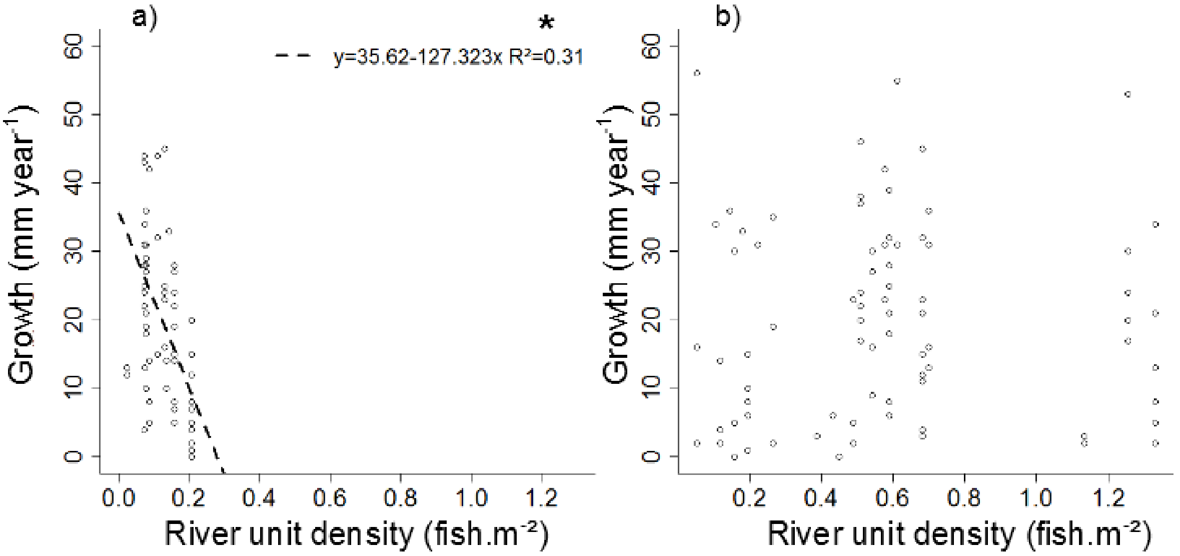

Fig. 2. Growth rate (mm year^{-1}) relative to river unit density of European eels (fish m^{-2}) for (a) the 69 eels studied in the Oir River, and for b) the 82 eels studied in the Frémur River. The best descriptor of the density dependent growth relationship found on the Oir River is represented by a dotted line. The sign * shows that a parameter has a significant effect on growth rate.

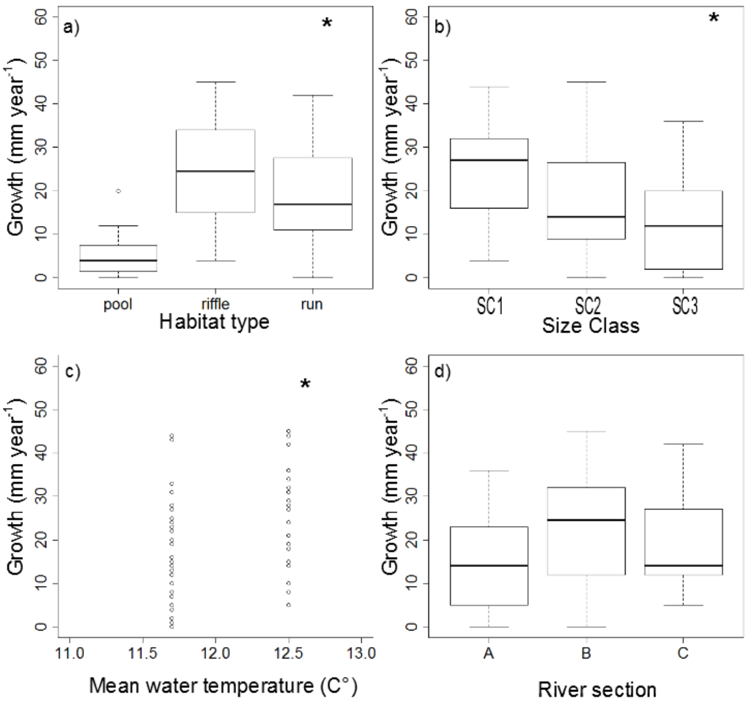

Fig. 3. Box plots showing mean and range of growth rates (mm year^{-1}) in the Oir River according to habitat type (a), size class (SC_1: 150-300 mm, SC_2: 301-450 mm, SC_3: > 450 mm) b) and river section (from the downstream part of the study area, river section A, to the upstream part, river section C) d), and the plot showing the growth rate (mm year^{-1}) relative to mean water temperature c). The sign * shows that a parameter has a significant effect on growth rate.

For the Frémur, only 16% of the GR variance was explained. The only factor selected was river section with significantly higher GR in section A than in B and D (Tukey test, $P < 0.05$). Finally, there was no significant relationship between river unit density and GR (Fig. 4d).

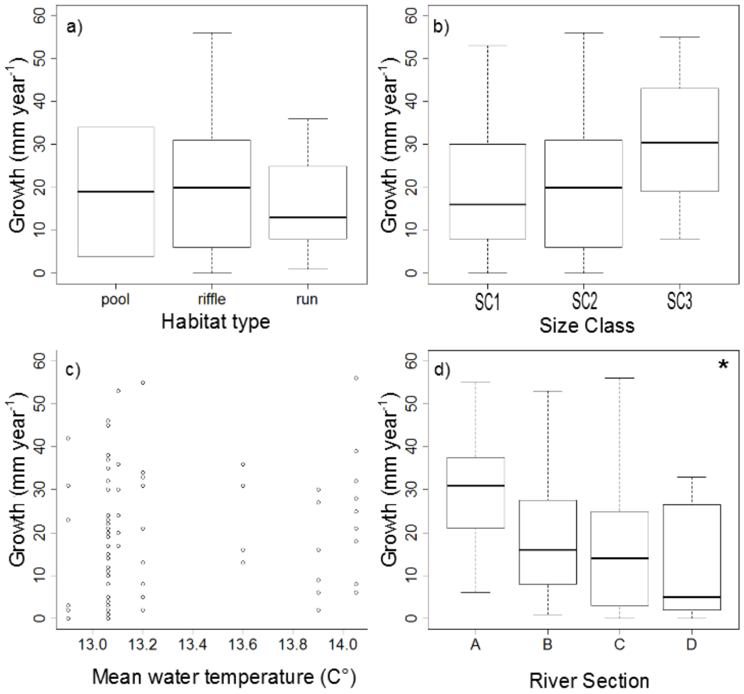

Fig. 4. Box plots showing mean and range of growth rates (mm year^{-1}) in the Frémur River according to habitat type (a), size class (SC$_1$: 150-300 mm, SC$_2$: 301-450 mm, SC$_3$: > 450 mm) (b), and river section (from the downstream part of the study area, river section A, to the upstream part, river section D) d), and the plot showing the growth rate (mm year^{-1}) relative to mean water temperature c). Only the factor 'river section' was selected by the R *stepAIC* procedure. The sign * shows that a parameter has a significant effect on growth rate.

Discussion

Our main results show that despite similar mean eel GR in both rivers, GR variability is not explained by the same factors. In the Oir, GR varies with river unit density, size classes, and Tmean, while the only factor affecting GR in the Frémur is river section. GR variation was better explained in the Oir (53%) than in the Frémur (16%). These contrasted results could be due to the level of CC reached by each system.

In the supposed unsaturated Oir, environmental (Tmean, dominant habitat type) and population variables (size classes and eel density) significantly explained eel GR variability, which is expected in a system below habitat saturation (Fretwell & Lucas, 1969). Indeed, below habitat saturation, differences in habitat suitability will exist depending on the availability and accessibility of resources, together with the density of conspecifics (i.e. the strongest competitors for the available resources). Individuals will then choose the most suitable habitat, i.e. habitat that will favor the higher growth or the lowest mortality (Feunteun *et al.*, 2003; Fretwell & Lucas, 1969).

A part of the difference in habitat suitability for eel population could be attributed to the density of conspecifics. As far as we know, this is the first time that a relationship between GR and density is observed in European eel population. This result is in line with the general prediction for density-dependent effects that growth is depressed at high densities due to decreased food availability as resources are depleted (Sinclair, 1989). Post *et al.*, (1999) pointed out that different forms of DDG occur, depending on the nature of the relationship between predator and prey. Linear DDG is concordant with the prediction of Walters & Post (1993), which is based on a simple prey-predator model. The model assumes that individuals compete for a single limiting resource with a food renewal rate that is independent of predator density, and that metabolic rates are density-dependent. Conversely, if food renewal rates decrease as predator density increases, then GRs should decrease more sharply at low density, resulting in a negative power curve relationship, as found in several taxa, notably in salmonid species (Grant & Imre, 2005; Imre *et al.*, 2005). To understand the processes of DDG in the Oir R., we looked at the best descriptor of the DDG relationship (a linear or a negative power curve relationship) and the model with the lowest Akaike information criterion (AIC; Motulsky & Christopoulos, 2004) was selected. In the present study, a linear relationship was designated as the best descriptor of DDG in the Oir, which is consistent with the hypothesis of Post *et al.* (1999). A point to highlight is that the narrow range of river unit densities observed in the Oir data set, compared to the Frémur data set, seems contradictory to the advice of

Strong (1986) to detect a real density dependent effect. However, this range was representative of the densities observed in the whole system and as suggested by various studies, the study of density dependence is only meaningful if study area is large enough to capture average density of conspecific experienced by a species in this study area (Hassel, 1987; Stewart-Oaten *et al.*, 1995; Ray & Hastings, 1997; Jenkins *et al.*, 1999). The narrower range of river unit densities observed in the Oir could be explained by the low proportion of riffles in the Oir compared to the Frémur (75% of the habitat type observed in the Frémur vs 36% in the Oir). Indeed, riffles seem to be the most productive habitat type, suggesting that the CC, and then the river unit densities, of the Frémur will be higher than the ones of the Oir (Whitledge & Rabeni 2000). Concerning the force (correlation coefficient) and the intensity (slope coefficient) of this linear relationship, it depends on the number of age classes studied. Previous work on salmonid species has reported considerable DDG (up to 90% of growth variance explained by density (Jenkins *et al.*, 1999; Imre *et al.*, 2005) compared to our study (31% of growth variance explained by density). However, these studies were conducted using only young of the year individuals, when the DDG is expected to be at maximum (Cushing 1975). In our study, the DDG was tested on three size classes (SC_1, SC_2, SC_3) representing a wide range of age classes (2 to 15 years old, unpublished data), and especially avoiding young (size below 150 mm). Thus, it was not surprising to find weaker DDG than in salmonids. Although the DDG observed in our study is weak, between size classes comparisons of GR demonstrate that younger individuals grow faster than older ones, which is in accordance with previous works on eel GRs (Vøllestad 1992, Daverat *et al.*, 2012).

Another part of the difference in habitat suitability for eel population could be attributed to habitat productivity. Habitat productivity could be explain, among other factors, by the specific distribution and biomass of macro-invertebrates which depend on the variation in physical and morphological conditions (e.g. gradient, substrate, flow, and temperature; Illies

& Botosaneanu 1963; Vannote *et al.*, 1980). Indeed, in lotic systems such as the Oir, eels prey on invertebrates and small fish and the variation in the species composition of benthic fauna between habitat types. Various studies suggested that primary production is generally higher in riffles than in pools (Keithan & Lowe, 1985; Rosenfeld & Hudson, 1997). Furthermore, the benthic community productivity is generally relatively high in riffles, intermediate in runs and low in pools (Whitledge & Rabeni 2000). This difference in productivity between habitat types could explain the spatial variation in GR of the Oir population with a growth significantly higher in riffles (Fig. 3a). The productivity variability of a system could be also explained by variation in temperature. Our results showed that GR increased with increasing mean temperature (Tmean). However, caution needs to be taken when interpreting this result as only two values of mean temperature were available for the regression (same Tmean in 2009 and 2010). Small variations in mean water temperature, which is the case for the Oir (mean annual water temperature between 11.06°C and 12.6°C), are not expected to alter GR of eels. However, peaks of extreme water temperatures (below 8°C for example) could significantly diminish food availability (Morin *et al.*, 1999), and eel level of activity (Nyman 1972; Sadler 1979), which can traduce periods of growth cease for eels. Our results cannot provide evidence for the effect of mean temperature on eel GR, however, the selection of the Tmean variable, between seven temperatures variables (if not due to hazard) could suggest that food supplies and not low water temperatures altered eel GR in the Oir.

Finally, the results obtained in the Oir are coherent with the expected results of an unsaturated system and strongly link to the variability of habitat suitability.

In the Frémur, there were no differences in eel GR whatever their size classes, location in the catchment, and dominant habitat type. These results are consistent with the Ideal Free Distribution theory (IFD) for a saturated system (Fretwell & Lucas 1969). Indeed the IFD assumes that the gradient of habitat CCs, due to difference in food availability but also to competition, affects the pattern of GR observed, depending on the level of habitat saturation reached by the system. The theory predicts that at a low population density, all individuals will choose the most suitable habitat (H1). When the density increases in H1, the suitability will decrease, until it becomes as suitable as H2. Density should then increase in H1 and H2 to the point at which both will be as suitable as H3. This process will continue until the CC of the system is reached, and at this point, all the available habitats are full. Habitat suitability will be then equivalent throughout the system, and the system is considered as saturated. If GRs are used as a proxy for habitat suitability, when the CC of a system is reached, all the habitats are filled, and an equivalent suitability of the different habitats is expected along the system due to the lack of resources and competition. Therefore, GR should be independent of differences in habitat density or productivity, as observed in the Frémur.

However, the only factor explaining GR variability in the Frémur was the river section, with significant higher GR in the downstream river section A than in others (B and D). At first sight, this result is incoherent with the idea of a saturated system but it could be explained by another factor than the difference in productivity between the river sections. In our study and in the work of Acou *et al.* (2011), the samplings were exclusively made in the lotic parts of the system and the level of habitat saturation of the lentic habitats is unknown. The Bois-Joli reservoir is an important eutrophic and lentic environment close to the river section A (Fig.1). Without obstacle between the river section A and the Bois-Joli reservoir, individuals could have a better growth in the river section A than in other river section by preying in this eutrophic reservoir, disregarding of the habitat saturation of the river section A. This hypothesis seems to be confirmed by the absence of selection of other classical factors and the fact that no difference of GR was found between the river section B, C and D. Furthermore, GRs were homogeneous among the different habitat types independently of their local productivity contrary to the Oir (Fig. 4a) According to the IFD theory, this result was consistent with the hypothesis that all lotic habitats are full and have the same suitability.

None of the seven temperature variables were selected to explain GR variability in the Frémur, highlighting that the variation of global productivity and/or the number of day of activity have no impact on growth (Fig. 4c). European eels will consume any available food and their diets evolve with increasing proportion of fish as their size increases (Schulze *et al.*, 2004; Dörner *et al.*, 2009 Cucherousset *et al.*, 2011). As GR did not vary with eel size classes in the Frémur, this points out that all the type of preys (from small to large eels) are limited (Fig. 4b).

The fact that GR are independent of differences in local density or productivity seems to confirm that all lotic habitats were full and that in those supposed saturated habitats DDG is undetectable. However, in this study, we worked only on the lotic habitats of each system. In this condition, our results could be not representative of the situation of the Frémur where most (91.15%) of the wet area is composed of ponds and reservoirs. However, a previous study on the Frémur highlighted that, using the eel microhabitat selection (Broad *et al.*, 2001), the lotic habitats represented 78% of the available habitat for eel in the Frémur (Acou *et al.*, 2009).

An unexpected result is that our mean GR were not significantly different between the Oir (19.1 mm.year^{-1}) and the Frémur (20.9 mm.year^{-1}). Indeed, GR are expected to be higher in an unsaturated system such as the Oir than in a saturated system such as the Frémur. Three non-mutually exclusive hypotheses can explain this discrepancy.

In the Oir, where we expected the higher mean GR, the sex-ratio is female biased, and females are slow growing eels (SC_3 represents 30.5% of the Oir GRs data set). By contrast, the Frémur sex-ratio is male biased, with females largely under-represented (SC_3 only representing 4% of the Frémur GRs data set). Individual intrinsic GR variation determined by sex might thus explain why mean GR found in these two systems is similar.

The proportion of the different habitat types within a system may also explained the relatively low mean GR observed in the Oir despite it supposed status of unsaturated system, as GRs are significantly higher in riffles than in the other habitat types (Keithan & Lowe, 1985; Rosenfeld & Hudson, 1997, Whitledge & Rabeni, 2000). Indeed, in the Oir, only 36% of the river (36.4% of the Oir GRs data set) is composed of riffles whereas in the Frémur 75% of the lotic habitat (77% of the Frémur GRs data set) is composed of riffles.

Another hypothesis comes from the potential interspecific interaction occurring in the Oir and not in the Frémur. Indeed the dominant species found in the Oir (in average 35% of the fish captured in the Oir are Salmonids, ORE PFC data): the Atlantic salmon, *Salmo salar*, and the brown trout, *Salmo trutta* co-occur with eels (Laffaille *et al.*, 2003; Bardonnet & Baglinière, 2000; Heggenes & Wollebaek, 2013), and feed on the same type of preys (macro-invertebrate and small fishes) (Maitland 1965, Stradmeyer & Thorpe 1987, Bridcut & Giller 1995, Vignes 1995). Whatever the process of interspecific competition (predation, exclusion, segregation, etc.), this is expected to decrease the eel GR potentiality as preys and habitat become less available for the eel population.

Our results give first insight on the possible effect of CC on individual GRs suggesting that the detectability of DDG depends on the status of the system (whether it is below or at habitat saturation). Our results also point out that, despite supposed difference in the status of the status of the system, the mean GR of an eel population could be driven by the structure of the population (sex ratio), the habitat distribution and/or inter-specific competition. However to assess the level of CC reached by each system (below or at habitat saturation) and then confirm that the differences in factors selected to explain GR between the two systems are due to the status of the system (whether it is below or at habitat saturation), mortality have also to been studied. Indeed, in a saturated system, due to a lack of food and space, GRs were low for all the individual eels in the system (independent of the local density or productivity), and the addition of new individuals should trigger an increase in emigration and/or an increase in mortality. So in a saturated system, density dependent mortality should be observed and higher mortality should be linked to reduced growth .This assumption of density dependent mortality seems to be confirmed by previous studies in the Frémur (Acou *et al.*, 2009; Acou *et al.*, 2011). However, future studies should investigate more precisely the mortality, spatially and temporally, to assess quantitatively the effects of density variation in river systems and link this to variation in GR. If the effect of the level of habitat saturation reached (below or at habitat saturation) is not verified, another process than the status of the system (below or at habitat saturation) may explain the difference of DDG detectability. Indeed, Drouineau *et al.* (2014) suggested that the sensibility to density dependent processes (in their case applied on mortality) could be different depending on the sex. Future studies have also to be focused on the DDG of individuals with a size inferior to 150 mm, as young recruits should be the most sensitive to density-dependent processes due to their search of a suitable habitat to live in, which depends on the individuals already present and their competitive advantage, as demonstrated in salmonid species (Johnsson *et al.*, 1999; Johnsson *et al.,* 2000).

Finally the understanding of the density dependent processes are particularly important as a sharp decrease in the best growth habitats for the European eel has occurred in Europe during the last century (Kettle *et al.*, 2011), significantly reducing system CCs. With habitats accommodating fewer individuals, there is a significant risk of an impact on growth, as shown in this study, and consequently on age at maturity, on fecundity, and on survival. Therefore, it is crucial that habitat restoration is carried out for this endangered species.

Acknowledgements

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III. Article 3 : Source of variation in survival of > 150 mm European eels in two contrasted continental populations

Clarisse Boulenger[1], Anthony Acou[1], O. Gimenez[2], F. Charrier[3], Julien Tremblay[4] and Eric Feunteun[1].

[1]UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France

[2] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Campus du CNRS, 1919 route de Mende, 34293 Montpellier cedex 5

[3] Fish Pass, Bureau Expert Gestion Piscicole, Laillé, France

[4] INRA, UMR 985 INRA-Agrocampus,Ecologie et Santé des Ecosystèmes, 65 rue de Saint Brieuc, CS 84215, F-35042 Rennes cedex, France

Correspondence: Clarisse Boulenger, UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France.

Email: clarisse.boulenger@edu.mnhn.fr

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Summary

Estimates of age-specific survival rates and understand the processes (density dependent or independent) that regulate this demographic parameter are key issues to propose adapted decision support tools for the endangered European eel (*Anguilla anguilla*). Here, we propose to analyze the source of variation in natural survival probabilities of two eel sub-populations, using an extensive mark-recapture dataset (13 and 17 years) on eel superior to 150 mm, in relation with density independent factors (temperature, water flow) and density dependent factor. The studied systems in close proximity (65 km apart), the Oir and the Frémur, are two small (< 100 km^2) river systems of Western France that differ in many ways. Whereas in the Frémur, a small river obstructed by dams with a medium water quality, high eel recruitment and density levels (0.37 eel m-^{2}) and male dominant population are observed, in the Oir low densities of eels were observed (0.04 eel m-^{2}) and the sex ratio is skewed towards females. Furthermore, previous study suggested that the lotic parts of the Frémur have reached carrying capacity whereas the Oir is suspected to be below habitat saturation. The results seem to highlight that the differences in the characteristics of the two systems but also of the two sub-populations prompt to different regulatory processes. Indeed whereas in the Frémur, survival probabilities varied significantly along the water course but also in time, in the Oir survival rates observed were stable over time and space in the Oir. The contrasted pressures applied on those two sub-populations impact survival trend which seems to lead to different life history strategies as suggested by the difference in sex ratio.

Introduction

Estimates of accurate population dynamic parameters such as age-specific survival rates are a key issue to propose adapted decision support tools, especially for endangered species (Caswell, 2000). Indeed, estimate population dynamic parameters and identify the processes that influence these parameters may help predicting the future dynamics of population in the face of environmental changes. The factors influencing dynamics parameters are often classified into two groups: density-independent (water flow, temperature, pollutant, dams, etc.) and density dependent factors (competition, parasitism, disease; Williams *et al.*, 2002).

In fish population, density independent factors could act through direct or indirect effects. For example, some studies highlighted that temperature causes both an increase (by direct effect with the critical thermal maximum and minimum which is the temperature at which the fish dies) and a decrease (by hastening body growth and reducing the duration of the continental phase at the optimum temperature; Vøllestad 1992; Angilletta and Dunham 2003) of mortality. Density dependence on demographic parameters could strongly regulated a population by decreasing survival, fecundity rates and growth and then knowledge of density dependence processes could be crucial in practical applications such as conservation or harvest regulations (Hanski *et al.*, 1996; Sinclair and Pech, 1996; Drake, 2005). These processes could be particularly important for populations when the system is near carrying capacity (defined as the maximum density or biomass that habitat can sustain (Van Gils *et al.*, 2004)) as density-dependence through a negative feedback on at least one demographic parameter (survival, fecundity, migration, etc.) is expected. However these processes are often difficult to highlight as long term data sets are required.

Understand these processes are particularly important for the endangered European eel (*Anguilla anguilla*) population. Eels are catadromous, semelparous fish reproducing in the open ocean and spending most of their life in continental waters from recruits (glass eels or elvers) that colonize water courses until sub-adult silver eels that migrate back to the reproductive grounds in the Sargasso Sea (Tesch, 2003). Continental phase is particularly important as the abundance of the spawning stocks will depend on the abundance of glass eels entering the rivers but also on the mortality rates that will apply during the yellow eel stage in the river prior to the silvering downstream migration (Lobón-Cerviá & Iglesias 2008). It is difficult to determine whether natural mortality is a phenomenon rather dependent on the length or age or both (De Leo & Gatto, 1995). Some studies highlighted that mortality decreases with age (De Leo & Gatto, 1995, 1996 ; Lobón-Cerviá & Iglesias, 2008). However, when the age data set were unavailable or unreliable, studies demonstrated that mortality varies also with size (Naismith & Knights, 1990 ; Bisgaard & Pedersen, 1991).

Previous studies on eel population highlighted the sensibility to density dependent processes on natural mortality (Vøllestad and Jonsson 1988; De Leo and Gatto 1996 ; Lobón-Cerviá & Iglesias 2008, Bevacqua *et al.*, 2010; Bevacqua *et al.*, 2011). Bevacqua *et al.* (2010) demonstrated that eel mortality is significantly affected by stock density with a mortality rate at high-density stock about three times larger than that at a low-density one. They also highlighted that European eel mortality increases significantly with temperature, and then eels inhabiting warm waters are potentially subject to a markedly higher mortality. However, few studies if any have distinguished drivers acting on survival among populations in a same region. For conservation, it is particularly important to know whether populations with different life-histories traits are influenced by the same extrinsic and intrinsic factors, and hence whether they vary in their population dynamics and conservation needs. Furthermore, if density dependent processes occur on one or both populations it is particularly important to determine at which stage these processes regulate the population.

Here, we propose to analyze the source of variation in natural survival probabilities of two eel sub-populations in relation with density independent factors (temperature, water flow) and density dependent factor. For that, we used an extensive mark-recapture dataset (13 and 17 years), on eel superior to 150 mm, from French sub-populations of European eel in two small (< 100 km²) river systems of Western France: the Frémur (Brittany) and the Oir (Normandy). In both sites, there is no professional eel fishery, anglers did not target European eels (rather cyprinids, esocids or percids in the Frémur or Salmonids in the Oir), and cormorants and herons are occasional. Therefore, fishing pressure and predation mortality are considered negligible and thereafter mortality rates provided hereafter consisted in natural mortalities. Multistate capture recapture model were built to estimate survival probabilities in each system. Both sites are in close proximity (65 km apart) and thus undergo equivalent regional environmental pressures (temperature, hydrology, etc.). However, they differ in many ways. The Frémur is a small river where, despite a medium water quality, high recruitment and density levels (0.37 eel m-²) of eels could be observed. In this system, European eel is the most common species in terms of biomass and in the shallow (< 1 m) habitats, males are dominant (>80%; study period: 1996-2013). By contrast, the Oir, is a tributary of the Selune River and is known to be a salmonids river (Baglinière *et al.*, 2005; Rivot *et al.*, 2008). In this system, low densities of eels were observed (0.04 eel m-²) and the sex ratio is skewed towards females (>90%; 2000-2013). In addition to these differences in the population structure, differences in the inherent habitat carrying of each system are expected. Indeed, previous study suggested that the lotic parts of the Frémur have reached carrying capacity (Acou *et al.*, 2011) whereas the Oir is suspected to be below habitat saturation (Boulenger *et al.*, in press).

Considering these important differences, we expected that different regulatory processes (density dependent and independent processes) on survival and transition rates exist in these two sub-population maybe driving by the difference in the structure of the population (high/low eel density, level of recruitment, etc.) or by the difference in the structure of each system (dams, level of carrying capacity reached, etc.).

Materials and methods

Study areas

The Frémur and Oir rivers are typical of the numerous small river systems found in Western Europe.

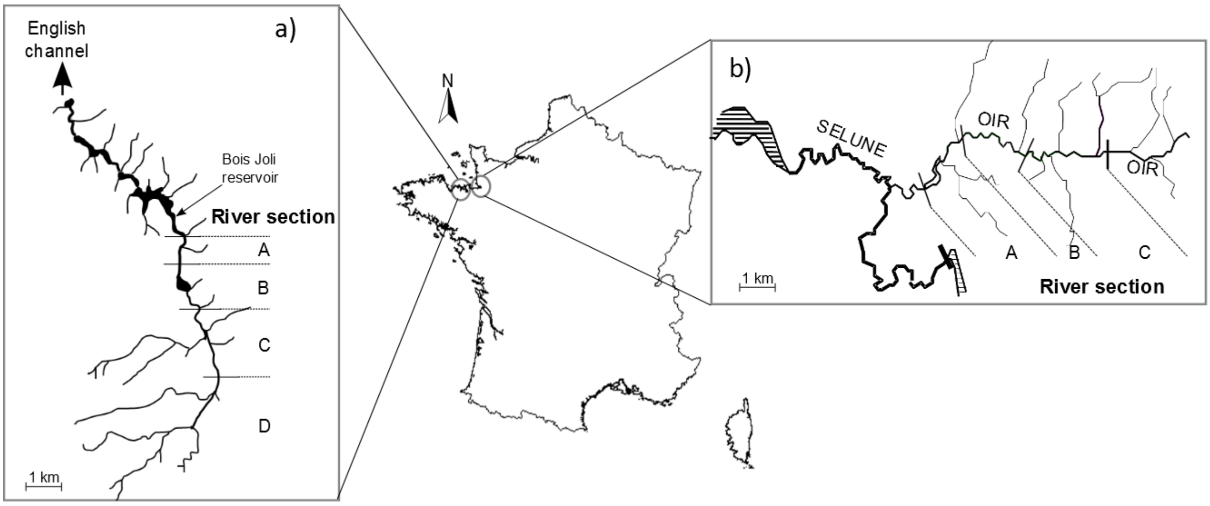

Fig. 1: Map of France, showing the location and configuration of the studied drainage basins: (a) The Frémur River, (b) the Oir River, and the different river sections studied

The Frémur is a small and low gradient coastal river in Northern Brittany, which discharges into the English Channel close to Saint Malo (2°06′W, 48°34′N; Fig. 1). The catchment area is approximately 60 km^2, and the distance from source to mouth is 46 km, with a 17 km main stem. The gradient ranges from 2% at the source (100 m altitude) to 0.1% near the mouth. Overall, the Frémur provides a wide range of shallow (mean ± SD = 0.5 ± 0.2 m) and narrow (2.2 ± 0.9 m) habitats, from turbulent headwater streams with trout to lowland reaches downstream characteristic of bream habitats, together with lentic reservoirs. At roughly the same latitude (1°16′W, 48°37′N), 60 km eastward, the Oir is a small river tributary of the Sélune, and flows into Mont Saint Michel bay (Fig. 1). The catchment area is 87 km^2, and the main stem is approximately 25 km long. The mean gradient is 1.1%.

Whereas the Oir is obstructed by only one weir, the Frémur was obstructed by two major dams (Pont es Omnes and Bois Joli), previously impassable until the construction of fish passes (Feunteun *et al.*, 1998). The highest, at Bois Joli, is 14 m high and holds a 3.10^6 m^3 reservoir. A lift for the upstream migration of eels was built in 1996. Upstream, three minor works, including a culvert under a road, a flow-gauging device, and a sill (step) beneath a bridge, create temporary obstacles to eel migration, but are passable during periods of high flow (Feunteun *et al.*, 1998). These three obstacles lead to an accumulation of eels downstream the hydraulic works and to very low densities immediately upstream the obstacle (Feunteun et al, 1998).

Both sites are in close proximity (65 km apart) and thus undergo equivalent regional environmental pressures (temperature, hydrology, etc.). However, they differ in many ways especially in term of eel population structure. The Frémur is a small river where, despite a medium water quality, high recruitment and density of eel could be observed (Acou *et al.*, 2011). In this system, European eel is the most common species in terms of biomass and in lentic habitats major part of eels were female while in the lotic habitats the majority of eels were male. By contrast with the Frémur, the Oir, which is a tributary of the Selune River, is known to be a salmonids river (in average 35% of the fish population; Baglinière *et al.*, 2005;

Rivot *et al.*, 2008). In this system, low densities of eels were observed (Acou *et al.*, 2009) and the majority of eels were female.

Sampling

Every year (between 1996 and 2012 in the Frémur, and between 2000 and 2012 in the Oir), two methods were used to catch eels in each river. Firstly, between September and October, growing and sub-adult eels were captured thanks to electrofishing sampling, with a 'Heron' apparatus (Dream Electronique, Pessac, France) set at DC 300 V and 3 A, in different sampling sites along the longitudinal gradient of the rivers (between 15 and 32, and between 15 and 39 sampling sites per year for the Frémur and the Oir respectively). Secondly, between September and February (depending on the rise in the level of the rivers), growing and sub-adult eels (essentially mature individuals) that leave the system were caught with a downstream trap placed at the Pont es Omnes dam for the Frémur and at the Cerisel water-mill for the Oir (Fig. 1).

Table 4: transition matrix used for the two eel populations presented the possible transitions (w) from a specific eel life-stage (S1, S2, S3, S4, S5) to another.

		To:				
		S1	S2	S3	S4	S5
From:	S1	$1-\sum_{i=2}^{5} w_{S1\to Si}$	$w_{S1\to S2}$	**0**	$w_{S1\to S4}$	$w_{S1\to S5}$
	S2	0	$1-\sum_{i=3}^{5} w_{S2\to Si}$	$w_{S2\to S3}$	$w_{S2\to S4}$	$w_{S2\to S5}$
	S3	0	0	$1-\sum_{i=4}^{5} w_{S3\to Si}$	$w_{S3\to S4}$	$w_{S3\to S5}$
	S4	0	0	0	$1-w_{S4\to S5}$	$w_{S4\to S5}$
	S5	0	0	0	0	1

All captured eels were anesthetized with clove oil (Walsh & Pease, 2002) and measured (total length, TL, to the nearest mm), weighed (total weight, TW, to the nearest g) and their stage (yellow or silver eel) determined. Silver eels were identified by three criteria (Acou *et al.*, 2005; Acou *et al.*, 2006): the colour of the back and belly, the presence of a well-defined lateral line, and an ocular index (OI) ≥6.5, according to Pankhurst's silvering threshold value (Pankhurst, 1982). If only two of the criteria (most often the lateral line and the OI value) were met, the eel was considered as a silver eel. If only one (generally the OI value) or none were met, the eel was recorded as yellow.

Eels caught during the sampling session, with a length superior to 150 mm, were individually marked with passive integrated transponder (PIT) tags (Prentice *et al.*, 1990). For the newly marked and recaptured eels, individual information was recorded (TL, TW, stage, site, date). After handling, the fish were allowed to recover for more than 15 min before being released at the site of capture.

Survival and transition rates estimates

Multistate capture-recapture models were used to analyze the data (Lebreton *et al.* 2009) and estimate survival (Φ), transition (w) and detection (P) probabilities. Six different stages were created considering different ecological and behavioral characteristics (Baisez, 2001; Laffaille *et al.*, 2004; Acou *et al.*, 2011): the stage "S_1" consisted of recently recruited elvers that colonise the river and sedentary growing yellow eels (yellow eels with a size inferior to 300 mm),the stage "S_2" (yellow eels between 301 and 450 mm) and "S_3" (yellow eels with a size superior to 451 mm) represented the potential reproductive status of future male or female silver eels respectively). The resident and the migratory silver eels (individuals caught as silver eel in the sampling sites and in the downstream trap respectively) made up the stage "S_4" and "S_5" respectively. Finally, the stage "D" represented the dead eels.

The temporal dynamics of stages was governed by transition probabilities (w). Transition probability from a stage to a smaller stage was fixed to 0. Similarly, a silver eel could not return to a yellow eel stage then the transition probabilities from S_4 to S_1, S_2 or S_3 were fixed to 0. Furthermore migratory silver eels could only stay in the stage migratory silver eel (as they leaved the system) then the transition probability from S_5 to S_5 was fixed to 1. The full transition matrix was presented in the Table. 1. These transitions were conditional on survival probability (Φ) and stages were related to observations through detection probabilities (P). We defined a set of candidate models incorporating biologically relevant combinations of year, stages and river section effects on survival, transition and detection probabilities. Regarding temporal effects on survival and transition, we considered continuous effects to test for the influence of environmental conditions. We incorporated a river section effect to assess whether the localization of eels influenced their survival and transition probabilities. Indeed, studies have shown that growth and body conditions near the estuary are often higher than in the upper reaches of a river catchment (Daverat *et al.* 2006; Lasne *et al.* 2008). Regarding recapture probabilities, we considered temporal effect and because silver eels were supposed to be less sedentary than in other stages due to their need to migrate downstream to the sea, we tested for an influence of stage. We incorporated these effects on each parameter (P, Φ and w) sequentially while constraints on remaining parameters were held constant. To build the best model, we firstly selected the most appropriate structure for P testing one by one the different effects. Once the main effect was determined, remaining effects were added in an additive and interactive fashion to assess if one of these combinations was relevant and this operation continue until no better model was selected. Secondly, we repeated the same procedure for Φ using the previously selected structure for P and finally for w using the structures for P and Φ selected in the previous steps. The most parsimonious model was selected using AIC (Akaike information Criterion; Burnham & Anderson, 2002). These analyses were performed with program E-SURGE (Choquet *et al.* 2009a) and the quality of fit of the models (Pradel *et al.* 2003) using program U-CARE (Choquet *et al.* 2009b).

Factors used to explain temporal survival variability in the Frémur

Whereas no temporal or spatial effects on survival were selected in the final multistate model of the Oir, survival probabilities in the Frémur varied greatly in time but also in space. To try to explain this variability, different factors were tested. This analysis was only focused on the eels in the stock which mean the three yellow eel stage (S_1, S_2, and S_3) and the silver eel stage S_4.

Table 5: Time series of the factors used to explain temporal survival variability in the Frémur

		1996	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Number of recruits		-	3454	26765	5995	7965	13578	2457	381	12124	6223	9351	9103	15482	3578	10009	848
Tmean		13,06	12,9	13,6	13,1	13,2	13,9	14,05	13,3	14,43	12,42	13,36	12,92	12,4	13,1	13	14,1
ND.3		5	1	0	0	0	3	0	0	1	3	0	0	1	3	0	2
dt	**Total**	0,3339	0,5087	0,3061	0,3379	0,4049	0,4524	0,3348	0,4502	0,5153	0,3580	0,4923	0,2481	0,3750	0,2567	0,2225	0,3259
	S_1	0,2147	0,3578	0,2434	0,2449	0,2679	0,3762	0,2348	0,3313	0,4308	0,3058	0,4112	0,1855	0,2710	0,1715	0,1635	0,2532
	S_2	0,0651	0,0940	0,0383	0,0632	0,0866	0,0488	0,0700	0,0806	0,0590	0,0391	0,0608	0,0457	0,0666	0,0666	0,0375	0,0546
	S_3	0,0028	0,0036	0,0006	0,0055	0,0160	0,0065	0,0087	0,0157	0,0095	0,0045	0,0122	0,0101	0,0164	0,0076	0,0071	0,0098
	S_4	0.0513	0.0533	0.0237	0.0243	0.0344	0.0208	0.0214	0.0226	0.0161	0.0085	0.0081	0.0067	0.0210	0.0109	0.0143	0.0084
d_A	**Total**	0,5883	0,5790	0,5537	0,3657	0,5789	1,2751	0,6635	1,2895	0,5041	0,6934	1,3895	0,8731	0,7794	0,5995	0,4443	0,6155
	S_1	0,3992	0,3936	0,4653	0,2859	0,3738	1,1091	0,5234	1,0463	0,3598	0,5947	1,1751	0,6527	0,6115	0,4558	0,3687	0,5260
	S_2	0,0510	0,0946	0,0390	0,0440	0,1096	0,0866	0,0872	0,1697	0,0910	0,0674	0,1587	0,1102	0,0990	0,1027	0,0453	0,0634
	S_3	0,0030	0,0076	0	0	0,0365	0,0144	0,0184	0,0509	0,0155	0,0120	0,0257	0,0678	0,0388	0,02053	0,0091	0,0075
	S_4	0.1351	0.0833	0.0494	0.0357	0.0590	0.0650	0.0344	0.0226	0.0378	0.0193	0.0300	0.0424	0.0301	0.0205	0.0212	0.0187
d_B	**Total**	0,3806	0,7004	0,3875	0,6182	0,8443	0,3891	0,5258	0,5310	1,6475	0,7843	0,2690	0,2944	0,3673	0,1738	0,2736	0,2466
	S_1	0,2650	0,5580	0,3391	0,4703	0,6026	0,3113	0,3225	0,3788	1,5078	0,7095	0,2353	0,2227	0,2438	0,0900	0,1584	0,1489
	S_2	0,0795	0,1104	0,0429	0,1027	0,1718	0,0660	0,1382	0,0971	0,1016	0,0554	0,0206	0,0583	0,0768	0,0714	0,0684	0,0791
	S_3	0	0,0029	0	0,01027	0,0204	0,0047	0,0136	0,0130	0,0127	0,0028	0,0103	0,0075	0,0167	0,0031	0,0144	0,0140
	S_4	0.0361	0.0291	0.0056	0.0349	0.0495	0.0071	0.0515	0.0421	0.0254	0.0166	0.0026	0.0060	0.0300	0.0093	0.0324	0.0047
d_C	**Total**	0,1252	0,4991	0,1214	0,1072	0,1775	0,0653	0,1337	0,0676	0,2266	0,0617	0,1528	0,0922	0,1101	0,07	0,0573	0,0517
	S_1	0,0676	0,3068	0,0635	0,0706	0,1017	0,0420	0,0839	0,0434	0,1772	0,0457	0,1194	0,0667	0,0751	0,04	0,0371	0,0287
	S_2	0,0426	0,0916	0,0386	0,0244	0,0536	0,0163	0,0420	0,0217	0,0407	0,0137	0,0334	0,0222	0,0300	0,02	0,0202	0,0230
	S_3	0,0051	0,0046	0	0,0024	0,0055	0,0023	0,0026	0	0,0058	0	0	0	0	0	0	0
	S_4	0.0100	0.0962	0.0193	0.0097	0.0166	0.0047	0.0052	0.0024	0.0029	0.0023	0	0.0032	0.0050	0.01	0	0
d_D	**Total**	0,2547	0,2565	0,1468	0,2779	0,1728	0,1128	0,1294	0,0953	0,1185	0,0907	0,1013	0,1146	0,0549	0,1109	0,0683	0,0519
	S_1	0,1306	0,1411	0,0618	0,1461	0,1057	0,0640	0,0776	0,0426	0,0723	0,0440	0,0624	0,0831	0,0137	0,0525	0,0455	0,0259
	S_2	0,0882	0,0898	0,0425	0,0997	0,0361	0,0335	0,0460	0,0326	0,0347	0,0412	0,0311	0,0258	0,0343	0,0525	0,0152	0,0086
	S_3	0,0033	0	0,0039	0,0109	0,0077	0,0061	0,0029	0,0075	0,0087	0,0055	0,0078	0,0057	0	0,0058	0,0076	0,0173
	S_4	0.0327	0.0256	0.0386	0.0214	0.0232	0.0091	0.0029	0.0125	0.0029	0	0	0	0.0069	0	0	0

Temperature

Sadler *et al.* (1979) determined both upper and lower lethal temperatures for eels (temperature at which the fish becomes incapacitated or dies). They highlighted that the critical thermal maximum varied from 33°C to 39° C and that eels enter a state of torpor at temperatures varying from 1°C to 3°C. In the Frémur, during our study period, temperatures ranged from 0.95 to 25.8°C with an average temperature of 13.05°C so eels never encountered the critical thermal maximum but they could be affected by low temperatures. For this reason, we calculated the number of days when the water temperature is below 3°C (ND.3) between two sampling sessions to study the possible effect of these low temperatures on eel survival (Table. 2). Furthermore, water temperature could be used as a proxy of the primary productivity of the system (Morin *et al.*, 1999) then productivity and associated potential prey for eel should decrease with decreasing water temperatures which could lead to an increase of mortality. Then to understand this possible effect, the mean water temperature between two sampling sessions was calculated (Tmean, Table. 2). Daily river temperature (°C) was recorded with a data logger set at 1 m depth near the Fremur's downstream trap.

Density

As highlighted by previous studies, density could have strong impact on survival (Lobón-Cerviá & Iglesias 2008, Bevacqua *et al.*, 2010). Then, for each sampled site (between 25 and 31 sites every year), thanks to the depletion method used for the samplings, eel abundance was calculated using a weighted maximum likelihood model (Carle & Strub, 1978) and density (eel.m^{-2}) was calculated by dividing the estimated abundance by the surface area of the sampled site. Thus, the total density (regrouping all the stages) but also the specific densities of the three yellow eel stages were estimated for each sampled site every year. Finally the effect of density on survival was studied using different scales. Firstly, the mean of all sampled sites density was used as the proxy of the total density of the system. Then, four variables were created: $dt_{t,tot}$ which is the total density (regrouping all the stages) of the system the year *t* and $dt_{t,s1}$, $dt_{t,s2}$, $dt_{t,s3}$ which are the Frémur total densities of the stage S1, S2 and S3 respectively the year *t* (Table. 2). Secondly, the mean of the neighboring sampled sites density placed in a river section (A, B, C, D; Fig. 1) was used as a proxy for the eel density in a river section. Then, variables were created: $dr_{t,tot}$ which is the total density (regrouping all the stages) in the river section *r* (A, B, C, D) the year *t* and $dr_{t,s1}$, $dr_{t,s2}$, $dr_{t,s3}$ which are the densities of the stage S1, S2 and S3 respectively in the river section *r* the year *t* (Table. 2).

Recruitment

In small catchments such as the Frémur, major concentrations of glass eels recruited from the ocean are still found, presumably because of different currents, which are the principal vector for eel recruitment in Europe (Dekker, 2003; Bonhommeau *et al.*, 2010). Moreover, in such small rivers young recruits may colonise the whole river in a single wave of upstream migration (Feunteun *et al.*, 2003). It is likely that such massive colonisation of rivers by recruits could induce important pressure on individuals already established and lead to increasing inter and intra-cohort mortality. A fish-lift installed at the Bois Joli dam enables the passage and the count of the total number of recruits entering in the system and their characteristics (size and stage). Then we tested if this highly variable number of recruits could explain the temporal survival variability of in-stream eel population of the Fremur.

Statistical Analyses

Generalized linear models were used to assess the statistical associations between survival and independent variables (temperature variables and population variables), using a Gaussian distribution and an identity link function. As survival probabilities were dependent of stages and river sections, we tested the statistical association between the survival of the stage f (f = S_1, S_2, S_3) in the river section r (r = A, B, C and D) and (i) the total eel density in the whole system ($dt_{t,tot}$), (ii) the total density of the stage f in the whole sytem ($dt_{t,f}$), (iii) the total density in the river section r ($dr_{t,tot}$), (iv) the total density of the stage f in the river section r. Independent variables, and interactions between these variables, were included using a method based on the Akaike Information Criterion (AIC). The R *stepAIC* procedure was used to perform stepwise model selection, to obtain the most parsimonious model (Johnson & Omland, 2004). The significance of the factors remaining in the final models was tested using classical GLM deviance tests (ANOVA). The modelling assumptions (i.e. residual normality, homoscedasticity) were graphically tested for each model and no major violation was observed for any of them. All statistical analyses were carried out using R (http:// www.r-project.org/).

Results

For both systems, the best models predicted that detection probabilities varied according to stage and time. However, concerning the survival and transition probabilities, the main effects on these parameters differed. In the Oir, survival probabilities varied according to stage with an increase of survival with size (S_1=0.60, S_2=0.85, S_3=0.80; Fig. 2) but are constant in time and space (absence of river section effect). In the Frémur survival probabilities were slightly different between the yellow eel stages (in average S_1=0.77, S_2=0.72 and S_3=0.81; Fig. 3) but varied with marked fluctuation over the study period (between 0.29 and 0.99; Fig. 3). Drops of survival probabilities were observed in 1998 (0.46), 2000 (0.55) and 2006 (0.46) (Fig. 3). Furthermore survival probabilities varied spatially (on average in the downstream river section A: 0.71, in the river section B: 0.78, in the river section C: 0.68 and in the upstream river section D: 0.73; Fig. 3).

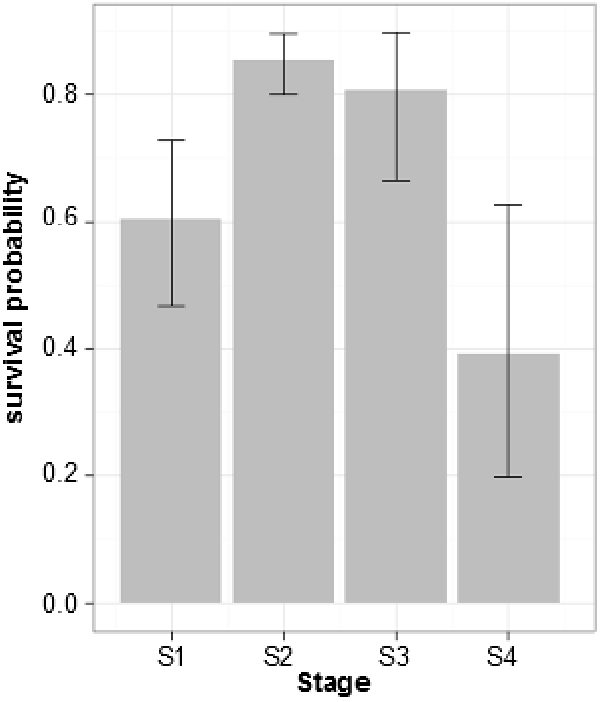

Fig. 2 Survival probabilities of the three yellow eel stages (S_1, S_2, S_3) and of the silver eel stage (S_4) in the Oir. Error bars represented the 95% confidence interval.

In the Oir, transitions probabilities were influenced by time and stage (Fig. 4) whereas in the Frémur transition from a stage to another varied with stage but were constant in time (Fig. 5). The transition probabilities from the stage S_1 to the stage S_2 were higher in the Oir than in the Frémur (in average 0.28 in the Oir, 0.23 in the Frémur). Furthermore, in the Oir, few individuals from the yellow eel stage S_2 change to a silver eel stages (S_4 and S_5, in average transition probabilities from S_2 to S_4 and S_5: 0.02) whereas in the Frémur transition probability from S_2 to S_4 and S_5 was of 0.20).

No significant effects of temperature (Tmean and ND.3) or density (dt, dr, recruitment) were detected to explain temporal variability of survival probabilities of all the stages in all the river sections (P>0.05).

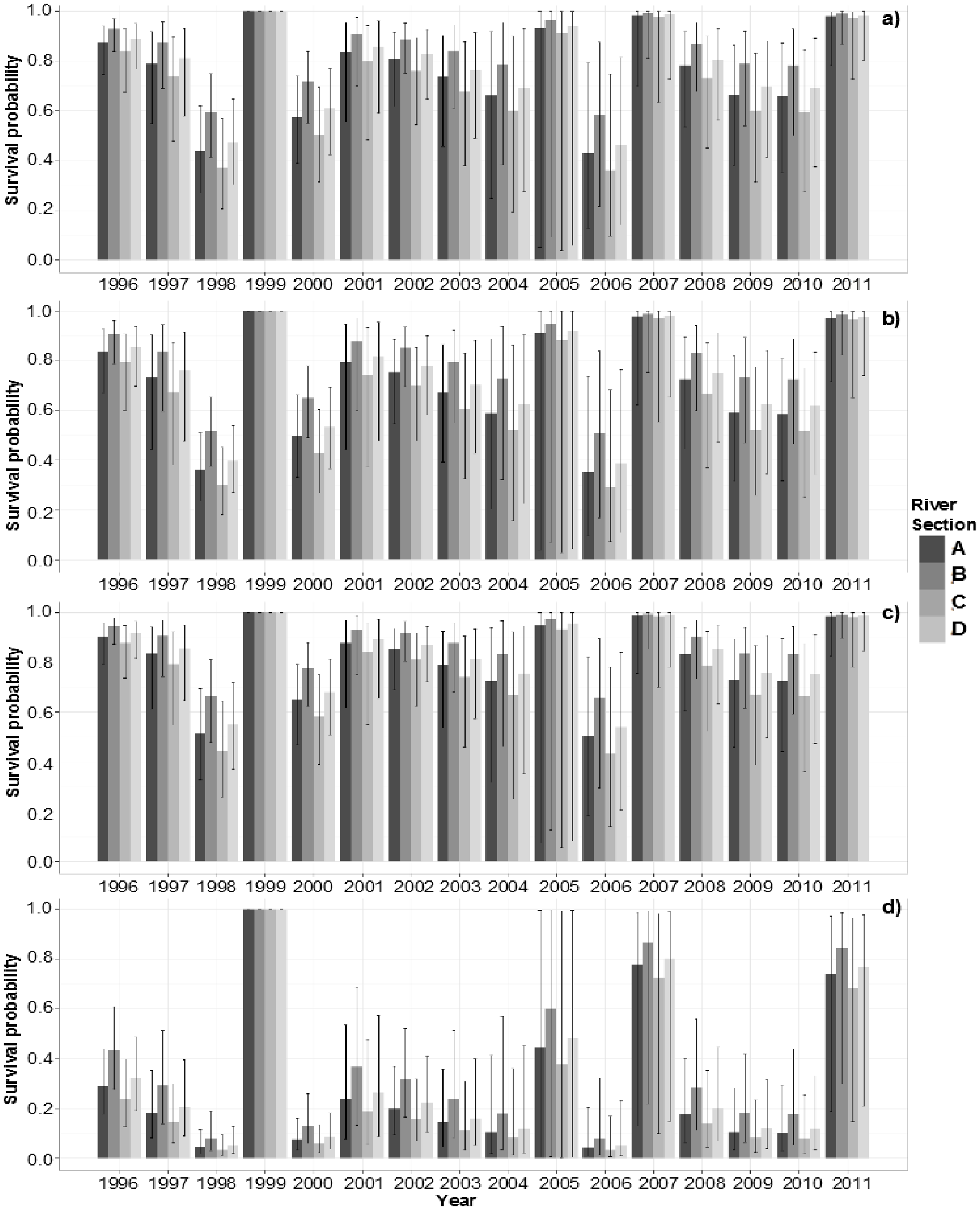

Fig. 3: Survival probabilities on each river section of the Frémur (from the downstream river section A to the upstream river section D) of the three yellow eel stages a) S_1, b) S_2, c) S_3 and of the silver eel stage d) S_4 according to years. Error bars represented the 95% confidence interval.

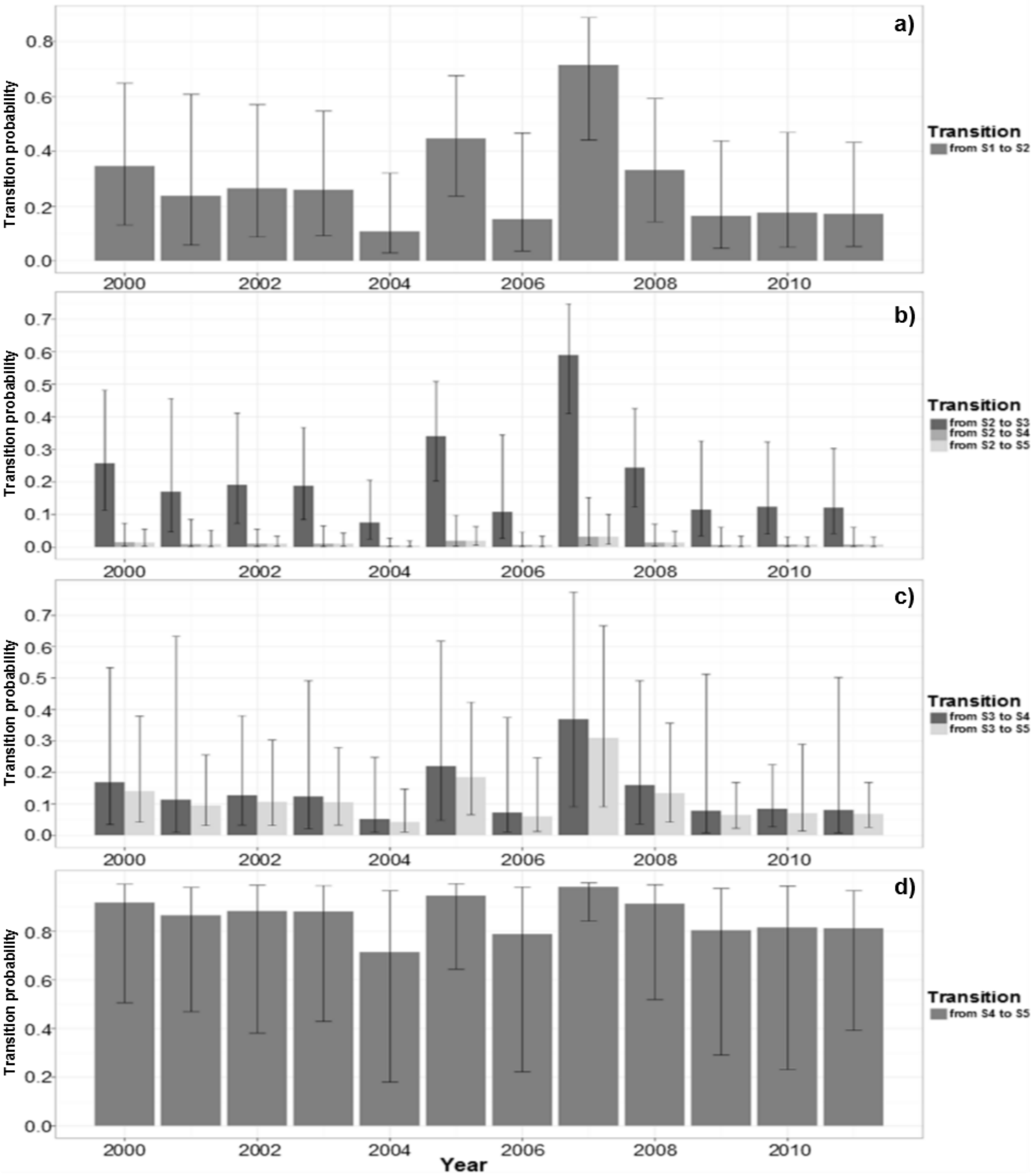

Fig. 4: Transition probabilities (error bars represented the 95% confidence interval) in the Oir a) from the yellow eel stage S_1 to the yellow eel stage S_2, b) from the yellow eel stage S_2 to the yellow eel stage S_3, or to the silver eel stage S_4 or to the migratory silver eel stage S_5, c) from the yellow eel stage S_3 to the silver eel stage S_4 or to the migratory silver eel stage $S_5$and d) from the silver eel stage S_4 to the migratory silver eel stage S_5 according to years.

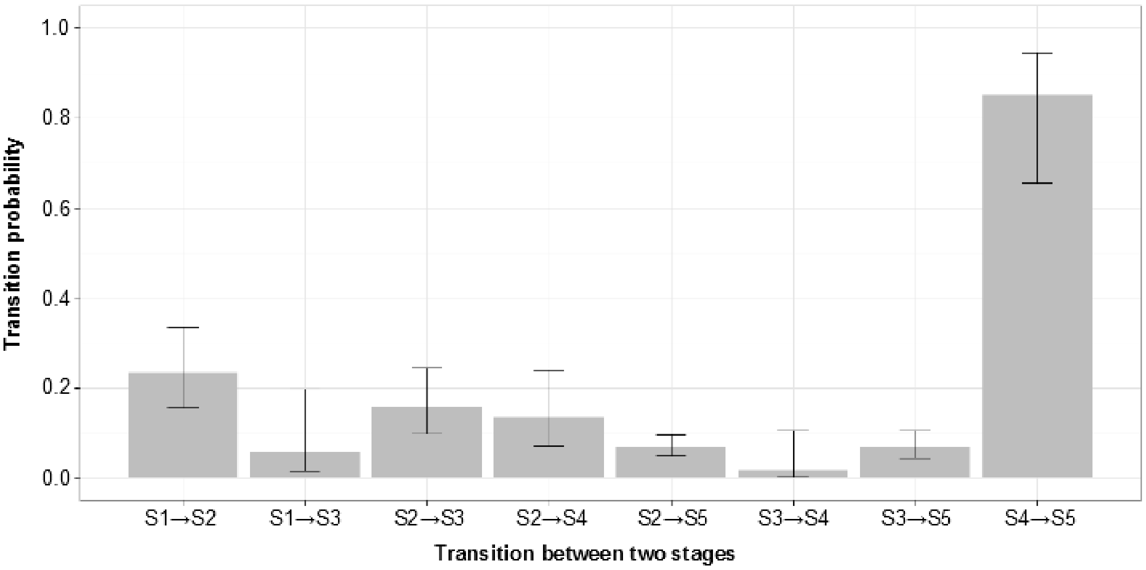

Fig. 5: Transition probabilities (error bars represented the 95% confidence interval) estimated in the Frémur for the different eel life-stages.

Discussion

The mean natural mortality rates observed for yellow eel stages in both systems were 0.24 ± 0.18 (range from 0.01 to 0.71) and 0.25 ± 0.13 (range from 0.15 to 0.40) for the Frémur and the Oir respectively. These estimates are in the range of others values for European catchments such as the Imsa River in Norway (mean mortality: 0.167; Vollestad & Jonsson; 1988) or Esva R. in Spain (0.379; Lobón-Cerviá & Iglesias, 2008). However, our main results show that the population dynamics of the two sub-populations is different. Whereas the survival of the Oir population is stable in time and space, the survival estimated in the Frémur population is highly variable in time and to a lesser extent in space. On the contrary, transition probabilities, which are the probabilities to change from a stage to another, estimated in the Frémur are stable over time whereas those estimated in the Oir are time varying. As our stages represent size classes, transition probabilities reflect growth then our results suggest that growth are stable over time in the Frémur whereas growth in the Oir are time varying. These results suggest that different regulatory processes exist in these two sub-populations.

In the Frémur, survival probabilities varied significantly along the water course (in average in the downstream river section A: 0.71, in the river section B: 0.78, in the river section C: 0.68 and in the upstream river section D: 0.73; Fig. 3). The presence of obstacles between each river section could explain this spatial variability. Indeed, as pointed out by Feunteun *et al.* (1998), the partition of the Frémur creates partially enclosed environment with specific characteristics (available food and space, density of conspecific, contamination). Furthermore, they demonstrated that most of the works are impassable for eels that exceed 180-200 mm, and then even if the local conditions are unfavorable those eels could not migrate to another part of the system which could induce local mortality. In addition to the spatial variability of survival, marked between years variability was observed over the study period (between 0.29 and 0.99; Fig. 3).

One source of temporal variation could be environmental but no effect of temperature was selected to explain the survival temporal variability. However, this species is known to have high plasticity. Then it is coherent that, in this temperate region, the range of water temperatures observed (annual mean between 12.4 and 14.4°C and few days with temperature below 3°C; Table.) did not impact survival.

As highlighted by previous studies, density dependence on survival could strongly regulated eel population and may explain the survival variability (Vollestad & Jonsson, 1988; De Leo & Gatto, 1996; Lobón-Cerviá & Iglesias, 2008; Bevacqua *et al.* 2010). Furthermore, the negative feedback of the population size could be particularly important when populations approach their maximum size (Gaillard *et al.* 1998; Eberhardt, 2002). Previous studies led in the Fremur R. suggested that eel population reach such a level in the lotic habitats (Acou *et* *al.*, 2011; Boulenger *et al.*, in press). However, no significant relationship between eel density (dt,dr, number of recruits) and survival was observed in the present study. This is an unexpected result as the Frémur is supposed to be saturated which mean that an increase of density should lead to a decrease of survival. Four non-mutually exclusive hypotheses could explain this discrepancy. Firstly, as pointed out by previous studies, ignoring measurement error on the density estimates may lead to underestimate the existence of a density-dependent relationship (Barker *et al.*, 2002; Carroll *et al.*, 2006) so to ascertain the fact that survival of the yellow eels (>150 mm) were density independent, another method have to be used. An integrated population model could be used the effect of density on survival while accounting for observation errors as proposed by Abadi *et al.* (2012) for a bird population. Secondly, our measure of density could be inappropriate. Indeed, previous studies highlighted that, in the Frémur, eel density varies with river section but also with instream cover and substratum (Acou *et al.*, 2011). So the use of a simple mean of the sampling sites density could flatten the density variability observed in the system and experienced by eel. Then more appropriate measure has to be used. The build of a model allowing the estimate of river section and habitat effect on density to extrapolate a better estimate of the total density and of the river section density could help to deal with this problem. Previous studies on salmonids species highlighted that a hierarchical Bayesian model could be used to improve our estimates (Wyatt, 2002, Rivot *et al.*, 2008). Thirdly, the scale at which we studied density dependence could be also inappropriate. Indeed, as pointed by various studies, the study of density dependence is only meaningful if study area is fine enough to capture the wide range of density of conspecifics experienced by the eel population in the study system and large enough to prevent eel migration for searching food to one unit to another during the studied year (Hassel, 1987; Stewart-Oaten *et al.*, 1995; Ray & Hastings, 1997; Jenkins *et al.*, 1999). In our study, we estimated density and survival at the scale of the river section. However, Ovidio *et al.* (2013) showed a longitudinal home range between 33 and 341 m in a small stream in Belgium. Then, to catch the competition effect, we should focus our study on density dependent survival at an intermediate scale, between sampling site (30 to 60 m) and river section (2 to 4 km). However, the use of this intermediate scale requires to have enough marked individuals in each of this specific area which is not the case in our study. Finally, our study is focused on the individuals with a size superior to 150 mm (with an overall mean size of tagged eels is 326 mm in our data set) which represent > 2 years old individuals (Acou *et al.*, 2009). However density dependent processes in fish decline with age (Cushing, 1975), then density dependent processes on survival might only applied on the individuals smaller than those studied here. Some studies supported the statement that density dependence is usually restricted to early life stages (Elliot, 1989; Persson & Greenberg, 1990; Dawson, 1991, Jenkins *et al.*, 1991). This could be the case in the Frémur. Comparing time series of the instream density and of the recruitment (Fig. 6), we observed that despite an important inter-annual variability of recruitment (between381 and 26765 recruits, coefficient of variation: 0.82), the eel density in the stock is quite stable (between 0.22 and 0.51 eel m^{-2}, coefficient of variation: 0.24). Considering the important variability of recruitment, the instream density stability and the absence of density dependence on survival of the marked individuals (> 150 mm) suggest that important density dependent processes especially on survival should be applied on the smallest individuals which mean on the recruits (90 to 150 mm). However to confirm this hypothesis, further studies have to be made to check if density dependent processes could be detected on those individuals.

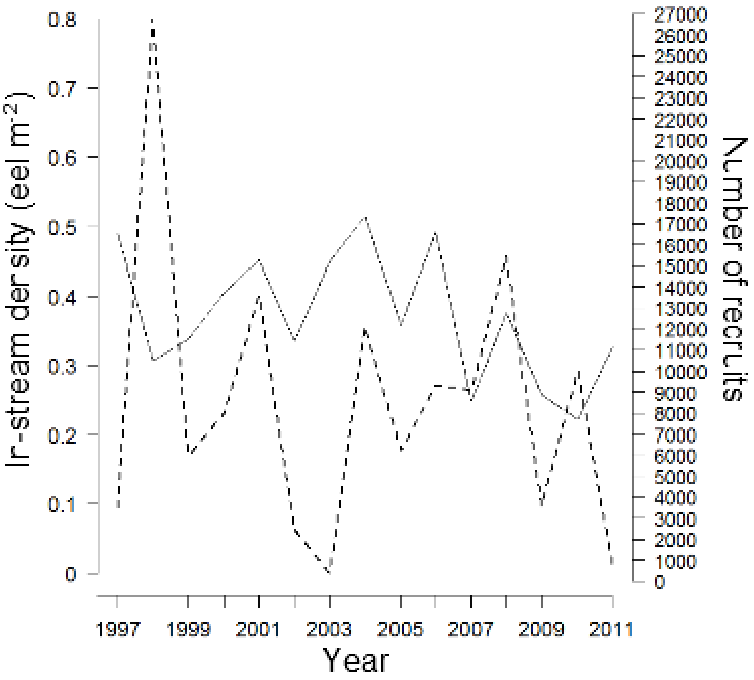

Fig. 6: Time series of instream density (eel m^{-2}; dotted line) and of recruitment (dashed line).

Considering our results, the drop of survival rates observed in the Frémur in 1998 (0.46), 2000 (0.55) and 2006 (0.46) seems to be more due to exceptional events than to systematic effect of temperature or density. Despite the fact that no density dependent effect on survival was detected on our yellow eel stages, an exceptional recruitment may impact the survival of instream population. Indeed, according to a general hypothesis, density-dependent mortality, caused by limited spatial resources, occurs when the colonization of glass eels is sufficiently large and upstream migrants face an overcrowded river habitat (Moriarty, 1986; Vollestad & Jonsson, 1988; Feunteun et al , 2003). Then the high mortality observed in 1998 in the resident population could be explained by the exceptional recruitment observed this particular year. Indeed, in 1998, a recruitment 4 times higher than the overall mean (26765 recruits whereas average annual recruitment is of 7219 individuals) was observed. Considering that 74 000 m² of the Frémur could be considerate as potential eel habitat (Acou *et al.*, 2009), this arrival of 26765 recruits represented an increase of 0.36 eel m^{-2} in the whole system which mean a doubling of the population. Then the large number of recruits observed this particular year might have induced intra- but also inter-cohorts competition for resources and increased mortality of the recruits but also of the resident population (Feunteun *et al.*, 2003). Another particular event may have played a role in explaining the eel survival drop. Between June 2006 and February 2007, a draining of the Bois Joli reservoir, downstream the river section A (Fig.1), was undertaken. The effect of this draining on the eel population upstream is not known however changes in water level may induce decrease of available habitat or food, increase of predation or migration which could lead to the important eel mortality this particular year (0.46). Other factors such as the water quality (anoxia, etc.) can impact the survival of individuals. The Frémur presents a medium water quality and it is a system considered as eutrophic with for example regular blooms of cyanobacteria in the Bois Joli reservoir (Acou *et al.*, 2009). Unfortunately, no quantitative monitoring of the water quality was available for the entire study period. Thus, the water quality parameters were not tested in the present study.

Contrary to the Frémur, survival rates observed are stable over time and space in the Oir. Several hypotheses can be postulated. Firstly, upstream and downstream migrations are not disrupted by any obstacles then when the local conditions are unfavorable for eels, they could migrate to another part of the system. Secondly, recruitment is suspected to be low and densities are 5-fold lower than those of the Frémur suggesting that density dependent processes on survival should be low. Moreover, as in the Frémur, the water temperatures observed (annual mean between 11.06 and 12.5°C and few days with temperature below 3°C) should not impact survival. Finally, interspecific interaction could occur in the Oir. Indeed the dominant species found in the Oir (in average 35% of the fish captured in the Oir are Salmonids, ORE PFC data): the Atlantic salmon, *Salmo salar*, and the brown trout, *Salmo trutta*. Salmonid species co-occur with eels in the same habitat type (Laffaille *et al.*, 2003;

Bardonnet & Baglinière, 2000; Heggenes & Wollebaek, 2013), and feed on the same type of preys (macro-invertebrate and small fishes) (Maitland 1965, Stradmeyer & Thorpe 1987, Bridcut & Giller 1995, Vignes 1995). Different processes of interspecific competition could exist as predation, exclusion or segregation and impact survival as preys and habitat become less available for the eel population. However considering our results, if this interspecific competition occurs, it seems to have low influence on eel survival. Finally, the contrasted survivals observed in the two systems seem to be the results of the differences in the characteristics of the two systems but also of the two sub-populations.

The contrasted pressures applied on those two sub-populations and their impact on survival and transitions rates could lead to different life history strategies as suggested by the difference in sex ratio observed between the lotic habitats of the two rivers (majority of females and males in Oir and Fremur respectively). Indeed, the sexes of eels were hypothesized to develop and mature according to different life history strategies, males using a time-minimizing strategy and females using a size-maximizing strategy which is consistent with our results (Helfman *et al.* 1987; Vøllestad 1992; Oliveira 1999, Oliveira & McCleave, 2002). Indeed, in the Oir, survival rates increase with size classes (S_1=0.60, S_2=0.85, S_3=0.80) but are constant in time and space, then the main advantage for eels in the Oir is to reach quickly the size class S_2 to minimize the mortality and then maximize their size (i.e fecundity). In the Frémur, survival rates were slightly different between the yellow eel stages (in average S_1=0.77, S;$_2$=0.72 and S_3=0.81; Fig. 3) but varied greatly within the study period (between 0.29 and 0.99; Fig. 3). In this situation, the best strategy is to maintain submaximum growth rates to enhance survival and then reach the minimum size necessary to achieve the spawning migration. The transition rates observed in the Oir and the Frémur seems to confirm these strategies. Indeed, the transition rates from the stage S_1 to the stage S_2 were higher in the Oir than in the Frémur (in average 0.28 in the Oir, 0.23 in the Frémur). Furthermore, in the

Oir, few individuals from the yellow eel stage S_2 change to a silver eel stages (S_4 and S_5, in average transition probabilities from S_2 to S_4 and S_5: 0.02) whereas in the Frémur transition probability from S_2 to S_4 and S_5 was of 0.20) highlighting that whereas individuals from the Oir continue to grow in order to reach the highest size at maturity and increase fecundity, eels from the Frémur metamorphose to the migratory silver phase at smaller sizes and certainly younger ages and may begin the shift of resources away from somatic growth in favor of gonadal.

Finally, our results seems to highlight that the pressures (extrinsic and/or intrinsic) applied on eel population will determine the strategy develop by individuals to reach maturity. In the system with the highest pressure (dams, high density, highly variable recruitment, etc.), even if no systematic effect of density or environment were detected, a minimum risk strategy to reach maturity has to be developed as the environment is not stable (time varying survival probabilities). Then, the time-minimizing strategy of male eels, strategy that maintains submaximum growth rates to enhance survival (few variability between stages) to the size necessary to achieve the spawning migration, seems adapted to the system conditions. In contrary, in the system where the pressure are low and stable over time and space, a more risky strategy during the earlier years of an individual (mortality higher in the younger stages) could be developed so they can enter a subsequent niche that allows to have a higher fitness.

Furthermore, our observations pointed out that regulation processes should occur at a size inferior to 150 mm in the Frémur but further studies were need to confirm this hypothesis. If these processes exist in the Frémur and not in the Oir that could confirm that the determination of sex will be strongly correlated to the density pressure on the young individuals (Krueger & Oliveira, 1999; Tesch, 2003).

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IV. Article 4 : An integrated approach to the detection of density-dependence on demographic parameters

Clarisse Boulenger[1], Anthony Acou[1], Eric Feunteun[1], A.J. Crivelli[2] and O. Gimenez[3].

[1]UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France

[2] Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France

[3] CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, 1919 Route de Mende, 34293 Montpellier cedex 5, France

Correspondence: Clarisse Boulenger, UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France.

Email: clarisse.boulenger@edu.mnhn.fr

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Summary

Identifying and understanding the influence of density dependent processes on the regulation of population dynamics and life history traits are important steps in the management and conservation of populations. However, density dependence is generally difficult to detect for several reasons. One of them is that the standard approach of regressing demographic parameters on population counts fails to formally account for the uncertainty in the measurement of population size and ignoring measurement error on the counts may lead to substantial bias in the density-dependent relationship with demographic parameters. Here, we developed an integrated approach to assess density-dependence on demographic parameters using two datasets (survey and mark-recapture datas) while automatically accounting for imperfect detection in both protocols expecting to obtain a more reliable estimation of the relationship between demographic parameters and density than the standard approach. To illustrate our approach, we used data sets on a population of European eel (*Anguilla Anguilla*). The comparison of the results of the standard approach and the integrated approach highlighted that the use of an integrated model increased the precision of the density dependent parameter estimates. This work confirmed the importance to take into account imperfect detections to reliably estimating density dependence in wild animal populations. This approach will hopefully help in improving the knowledge of the mechanisms controlling population dynamics, and in turn help in providing adapted decisions support tools for these populations as long as two sources of information are available on demographic parameters and density.

Introduction

Identifying and understanding the influence of factors that regulate population dynamics and life history traits are important steps in the management and conservation of populations. These factors are often classified into two groups (e.g., Williams *et al.*, 2002), whether these are density-independent processes (seasonal cycles, natural disasters, pollutant, etc) or density-dependent processes (competition, parasitism, disease). Density-dependent processes operate to offset the losses of individuals that can occur from natural fluctuations in environmental conditions or from anthropogenic activities such as agriculture or fishing (Rose *et al.*, 2001). Lowered population density temporarily results in increased survival or reproduction of the remaining individuals that favors an increase in population size. Furthermore, a negative feedback of the population size can also observed in early survival, recruitment, reproductive rate, and adult survival especially when populations approach their maximum size (Gaillard *et al.* 1998, Eberhardt 2002).

Despite its prevalence, density dependence is generally difficult to detect for several reasons. First, long-term datasets are required to reach the sufficient statistical power to detect a potential trend. Second, the standard approach of regressing demographic parameters on population counts fails to formally account for the uncertainty in the measurement of population size. Ignoring measurement error on the counts may lead to substantial bias in the density-dependent relationship with demographic parameters (Barker *et al.*, 2002; Carroll *et al.*, 2006).Several methods have been developed to assess the effect of density dependence on demographic parameters while dealing with observation errors. Using data on marked individuals, Schofield *et al.* (2009) resorted to a Jolly-Seber capture-recapture model to estimate the strength of density dependence on survival while accounting for imperfect detection. Abadi *et al.* (2012) developed an integrated population modeling approach (e.g., Besbeas *et al.*, 2002) to assess the effect of density-dependence on several demographic parameters at once. As predicted in the literature on errors-in-variables models (Carroll *et al.*, 2006), Abadi *et al.* (2012) demonstrated using both simulated data and a real case study that the precision of the slope parameter describing the density-dependent relationship decreased with increasing observation error on the population counts, hence the risk of overcoming density dependence.

Here, we consider the common situation in which a biologist has access to two independent sources of information, one on demographic parameters and the other one on abundance. The method of Schofield is not well suited to this situation as the same dataset is used to estimate survival, abundance and the density-dependence relationship. The integrated population model approach proposed by Abadi *et al.* (2012) would allow combining these two datasets but requires modelling the whole life cycle which adds an unnecessary level of complexity when the interest lies in assessing density-dependence on a single demographic parameter. Using two sources of information combined in a single model via the product of the two likelihoods, we developed an integrated approach to assess density-dependence on demographic parameters using data on marked animals while accounting for imperfect detection in both protocols. Briefly speaking, we parameterized the demographic parameter under scrutiny as a function of density in the same model, hence allowing to automatically handling estimation uncertainty in both abundance and survival; by doing so, we expect improved precision of the intensity of the density-dependence (the slope of the demographic parameter – density relationship). Because estimation error occurs in both the demographic parameters and abundance, it is difficult to predict how the statistical power of the tests to detect density-dependence will be affected (i.e. whether these tests will be too conservative or too liberal). This being said, by explicitly accounting for estimation error, we expect to obtain a more reliable estimation of the relationship between demographic parameters and density.

To illustrate our approach, we used a population of European eel (*Anguilla anguilla*) as a case study. The understanding of density dependent processes possibly controlling population dynamics is particularly important for this species classified as critically endangered. Furthermore, previous studies have highlighted the link between demographic parameters such as migration, sex ratio or even mortality to density dependent processes (Vøllestad and Jonsson 1988; De Leo and Gatto 1996; Feunteun et al, 2003; Lobón-Cerviá and Iglesias 2008), which could be explained by competition for food and space (Tesch, 2003; Cucherousset *et al.*, 2011) exacerbated by the increasing destruction of growth habitats over the past century. However, these studies were performed with classical methods (i.e., regression models that ignored detection error). Here, we used our new approach to test the effect of density-dependence on survival and compared our results with the classical approach.

Materials and methods

Study species

The facultative catadromous European eel is widely distributed on the continent of Europe, spending all or part of its growing phase in fresh, brackish or saline waters, and migrates periodically between habitats of different salinity. The growing stage (yellow eel) ends with metamorphosis to the silver phase and the start of the long-distance migration to the presumed spawning ground in the Sargasso Sea where the adults spawn and die (Tesch, 2003). Leptocephalus larvae are transported from the Sargasso Sea by the Gulf Stream Current and North Atlantic Drift to the Atlantic and Mediterranean coasts of Europe (Tesch, 2003). During this process, leptocephali metamorphose to glass eels long the continental shelf and migrate into coastal and/or inland waters where juvenile development occurs. During three to thirty five years, eels that became yellow eels grow until they have accumulated the critical fat reserve to migrate to the spawning area.

Study system

The Frémur River is a small coastal river in northern Brittany, which discharges into the English Channel close to Saint Malo (2°06′W, 48°34′N; Fig. 1) where a long term monitoring of recruits, yellow eels and silver eels were realized. The catchment area is approximately 60 km^2, and the distance from source to mouth is 46 km, with a 17 km main stem. A wide range of habitats were observed in the Frémur R., from high velocity streams to lentic waters, human made ponds, reservoirs, wetlands, etc. Despite the presence of two major dams (Pont es Omnes and Bois Joli), which were previously impassable until the construction of fish passes (Feunteun *et al.*, 1998), the eel density in the Fremur R.is one of the highest observed in Europe (0.37 eel m^{-2}; Acou *et al.*, 2011). In this system, the European eel is the most common species in terms of biomass (41% of the biomass).

For further analyses, the watershed was divided into four reaches (Fig. 1), from the downstream part (reach A) to the upstream part of the system (reach D). The total surface areas of all the reaches were also measured.

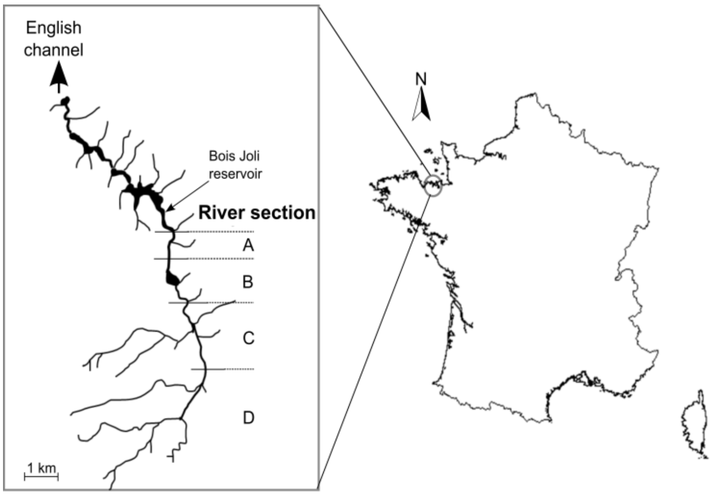

Fig. 1 Map of France, showing the location and configuration of the studied drainage basin: the Frémur and the different reaches studied.

Data

Sampling for density estimation

Over the period 1995-2005, between 25 and 31 sites were sampled every year by electrofishing during autumn (from early September to late October). Each sampled site is a small section of the stream with a wetted surface between 15 and 202.5 m². Before electrofishing, the sampled site was blocked with barrier nets to prevent fish movement inside or outside the site. Then the sampled site was electrofished with a ‘Heron’ apparatus (Dream Electronique, Pessac, France) set at DC 300 V and 3 A. Most sites were sampled with a minimum of two successive passes. Additional passes (three or four) were made if necessary, until the catch per pass decreased by 75% or more between successive passes (Acou *et al.*, 2011). The efficiency of the method was high because of the high catching success of these shallow sites (Lambert *et al.*, 1994; Feunteun *et al.*, 1998); on average, 70% of the eels were caught in the first pass. After all the catches, fishes were released back into the sampled site from which they were captured. During these samplings, eels from 70 mm to 1124 mm were captured.

Sampling for demographic parameter estimation

Between 1996 and 2005, 1457 eels with a size >150 mm were marked using passive integrated transponder tags (PIT-tags). Two methods were used to follow the marked individuals. First, every year between September and October, growing and sub-adult eels in the system were captured thanks to electrofishing sampling in different sites along the longitudinal gradient of the river (~25). Second, between September and February (depending on the rise in the level of the river), growing and sub-adult eels (essentially mature individuals) that leave the system were captured with a downstream trap placed at the Bois Joli dam. With this method, 365 eels were recaptured between 2 and 6 times.

Model

A hierarchical capture model was built to estimate the density of fish (eel m^{-2}) at different scales (sites, reaches and the whole river stretch) using the number of fish caught during the successive removal pass in each sampling site. This model was combined with a multistate capture-recapture model (described further below) that allows estimating survival and transition probabilities. These two components were linked by regressing survival in the multistate capture-recapture model to the density in the capture model.

A hierarchical capture model with density as a parameter

The whole data set for successive removal data consists in the number of fish caught during the 2 to 4 successive removals for a total of 306 sampling units. Each sampling unit is identified by the indices *(y,r,n)* where:

- y = 1,…,11 stands for years 1995, …, 2005;
- r = 1,…,4 stands for the 4 reaches A, B, C, D;
- n(y,r)= 1,…,10 stands for the measure made in year y in reach r.

For each sampling unit *(y,r,n)*, the number of fish caught during the jth pass (j = 1, ..., 4) was denoted $C_j(y,r,n)$. Based on the successive removal experiment in each site, a capture model was built using binomial distributions (Wyatt 2002; Rivot *et al.* 2008; Brun *et al.* 2011). As the majority of our removal experiments consisted in only two removal passes, there would not be much information under our data collection setting to estimate separate probability of capture between each removal in a site. Therefore, we used a more parsimonious model by considering the probability of capture constant between successive removal pass. Under this assumption, $C_j\ (y,r,n)$ is a binomial distribution with parameters the number of fish present before the jth pass, say $N_j\ (y,r,n)$ and the probability of capture $p\ (y,r,n)$:

$$C_j(y,r,n) \sim Binomial(N_j\ (y,r,n), p\ (y,r,n)) \qquad \text{eq. 1}$$

Before the first pass, the initial number of fish in each sampling unit is denoted $N_1(y,r,n)$. The number of fish present in each site before the pass j (for j = 2 to 4) is defined as:

$$N_j\,(y,r,n) \;=\; N_{j-1}\,(y,r,n) - \;C_{j-1}(y,r,n) \qquad \text{eq. 2}$$

The initial number of fish $N_1\,(y,r,n)$ depends on the fish density (fish.m^{-2}) $d(y,r,n)$ and on the surface area of the sampling sites $S(y,r,n)$. We suppose that the fish are randomly distributed in the whole river, then, $N_1\,(\,y,r,n)$ is distributed as a Poisson distribution with parameter $\lambda(y,r,n) = \; d(y,r,n) \times \; S(y,r,n)$:

$$N_1\,(y,r,n) \sim Poisson\,(\lambda(\,y,r,n)) \qquad \text{eq. 3}$$

A fully exchangeable hierarchical structure between all sampling units was used on the probability of capture (no systematic effect of year or reach). We assumed that $p(y,r,n)$ was distributed on the logit scale as a normal distribution with mean μ_z and standard deviation sd_z^2:

$$logit\; p(y,r,n) \sim \; Normal(\mu_z, \sigma_z) \qquad \text{eq. 4}$$

The densities $d(\,y,r,n)$ were considered to be partially exchangeable and follow a Gamma distribution conditionally on the shape $r_d(y,r,n)$ and the inverse scale $\mu_d(y,r,n)$. These two parameters were functions of the expected mean $E_d(y,r)$ and the coefficient of variation $CV_d(y,r)$ of the density (Table. 1):

$$\begin{cases} d(\,y,r,n) \sim \; Gamma(r_d(y,r,n), \mu_d(y,r,n)) \\ \qquad r_d(y,r,n) = \frac{1}{CV_d(\,y,r)^2} \\ \quad \mu_d(y,r,n) = \frac{1}{E_d(y,r) \times CV_d(y,r)^2} \end{cases} \qquad \text{eq. 5}$$

The spatial distribution of European eel could be highly heterogeneous between different reaches and the abundance is known to decline from downstream to upstream (Feunteun *et al.*, 2003). Moreover, an important inter-annual variability of density could exist in such river. Indeed, a great variability of the number of recruits entering in a system could be observed and, in such small river, young recruits may colonize the whole river in a single wave of upstream migration (Feunteun *et al.*, 2003). As a consequence of this spatio-temporal variability, the expected mean of the density was modeled on the log-scale as a linear combination of a random year effect $\beta_d(y)$ normally distributed with mean equal to 0 and standard deviation sd_β and a fixed reach effect and $\alpha_d(r)$.

$$\log\big(E_d(y,r)\big) = \beta_d(y) + \alpha_d(r) \qquad \text{eq. 6}$$

We extrapolated fish densities and abundance at the scale of the reaches and for the whole watershed while accounting for uncertainties. We resorted to the method proposed by Brun *et al.* (2011) which consists, for each combination of factor *Year* × *Reach*, in drawing the number of fish on the whole reach in the posterior predictive Poisson distribution:

$$N'_t(y,r) \sim Poisson\ (S_t(r) \times\ E_d(y,r)) \qquad \text{eq. 7}$$

where $S_t(h,r)$ is the total surface area for the reach r and $E_d(y,r)$ is the expected mean of the Gamma distribution given in eq. 6 drawn in its posterior predictive distribution. The number of fish estimated from the sites sampled was not considered in this approach but the small surface area sampled compared to the total surface area (sampling rate is about 3%) minimizes the effect of such an approximation.

The total number of fish in the whole watershed, $Ntot(y)$, was obtained by summing the $N'_t(y,r)$ over all reaches and the density of fish in the whole watershed, $d_{tot}(y)$, and divided this total number of fish by the total surface area of the watershed.

Multistate capture-recapture models for demographic parameters

We developed multistate capture-recapture models (Lebreton *et al.*, 2009) to estimate survival and transition probabilities. We considered seven stages (3 yellow eel stages and 4 silver eel stage) depending on differences in ecological and behavioral characteristics (Baisez, 2001; Laffaille *et al.*, 2004; Acou *et al.*, 2011). Stage S_1 (<301 mm) consisted of recently recruited elvers that colonise the river (< 200 mm) and of sedentary growing yellow eels. Stages S_2

(301 – 450 mm) and SC_3 (> 450 mm) represented the potential reproductive status of future male or female silver eels respectively (Laffaille *et al.*, 2003). Stages S_4 and S_5 represent respectively male and female silver eels captured in the system. Stages S_6 and S_7 consisted of male and female migratory silver eels captured at the downstream trap.

Following recent works (Gimenez *et al.*, 2007; Royle, 2008; Servanty *et al.*, 2010; Gimenez *et al.*, 2012), we used a state-space formulation of capture-recapture models to explicitly separate the demographic process of interest (survival status at a given stage) from the observations (data). Firstly, we considered eight states: alive S_1 (AS_1); alive S_2 (AS_2) ; alive S_3 (AS_3); alive S_4 (AS_4); alive S_5 (AS_5); alive S_6 (AS_6); alive S_7 (AS_7) and dead (D). We denoted $X_{i,t}$, the random state vector taking values (1,0,0,0,0,0,0,0), (0,1,0,0,0,0,0,0), (0,0,1,0,0,0,0,0), (0,0,0,1,0,0,0,0), (0,0,0,0,1,0,0,0), (0,0,0,0,0,1,0,0), (0,0,0,0,0,0,1,0), (0,0,0,0,0,0,0,1) if at time *t* individual *i* was in the state AS_1, AS_2, AS_3, AS_4, AS_5, AS_6, AS_7 or D, respectively. Secondly, in accordance with the differences in ecological and behavioral characteristics depending on eel size, we considered different possible observations that were created from those underlying states: eel is not seen (coded 0), eel seen in stage S_1 (coded1), eel seen in stage S_2 (coded 2), eel seen in stage S_3 (coded 3), eel seen in stage S_4 (coded 4), eel seen in stage S_5 (coded 5), eel seen in stage S_6 (coded 6) and eel seen in stage S_7 (coded 7). Then we denoted $Y_{i,t}$ the random observation vector taking values (1,0,0,0,0,0,0,0), (0,1,0,0,0,0,0,0), (0,0,1,0,0,0,0,0), (0,0,0,1,0,0,0,0), (0,0,0,0,1,0,0,0), (0,0,0,0,0,1,0,0), (0,0,0,0,0,0,1,0), (0,0,0,0,0,0,0,1), if at time *t*, eel *i* is not seen or seen in stage S_1, S_2, S_3, S_4, S_5, S_6 or S_7 respectively. Different parameters were involved in the models. We modeled the probability $\Phi^{f}_{i,t}$ that an individual *i* is alive in stage *f* (*f* = S_1, S_2, S_3, S_4, S_5, S_6 or S_7) at time *t* may survive at time *t+1* and the probability $\varphi^{f,to}_{i,t}$ that an individual *i* in stage *f* change to stage *to* between *t* and *t+1*(*f*, *to* = S_1, S_2, S_3, S_4, S_5, S_6 or S_7). The transitions from a stage to another were governed by biological processes. An individual in a size class could not return to a smaller size class and male (female) silver eel could only change to male (female) migratory silver eel. Furthermore as male silver eels did not have a size >450 mm, yellow eels in stage S_3 (> 450mm) could not become male silver eels or male migratory silver eels. Finally, we modeled the probability $po_{i,t}^{f}$ that an individual i was recaptured at time t in state *f*. We did not consider individual effect on those parameters, so the individual index *i* was removed.

The state space formulation of the capture-recapture model (Gimenez *et al.*, 2007) relies on a combination of two equations, the state and the observation equations (eq. 8 and eq. 9, respectively).

$$X_{i,t+1}|X_{i,t} \sim multinomial\ (1, X_{i,t}w_t) \qquad \text{eq. 8}$$

where

$$w_t = \begin{pmatrix}
\Phi_t^{S1}\varphi_t^{S1\to S1} & \Phi_t^{S1}\varphi_t^{S1\to S2} & 0 & 0 & 0 & 0 & 0 & 1-\Phi_t^{S1} \\
0 & \Phi_t^{S2}\varphi_t^{S2\to S2} & \Phi_t^{S2}\varphi_t^{S2\to S3} & \Phi_t^{S2}\varphi_t^{S2\to S4} & \Phi_t^{S2}\varphi_t^{S2\to S5} & \Phi_t^{S2}\varphi_t^{S2\to S6} & \Phi_t^{S2}\varphi_t^{S2\to S7} & 1-\Phi_t^{S2} \\
0 & 0 & \Phi_t^{S3}\varphi_t^{S3\to S3} & 0 & \Phi_t^{S3}\varphi_t^{S3\to S5} & 0 & \Phi_t^{S3}\varphi_t^{S3\to S7} & 1-\Phi_t^{S3} \\
0 & 0 & 0 & \Phi_t^{S4}\varphi_t^{S4\to S4} & 0 & \Phi_t^{S4}\varphi_t^{S4\to S6} & 0 & 1-\Phi_t^{S4} \\
0 & 0 & 0 & 0 & \Phi_t^{S5}\varphi_t^{S5\to S5} & 0 & \Phi_t^{S5}\varphi_t^{S5\to S7} & 1-\Phi_t^{S5} \\
0 & 0 & 0 & 0 & 0 & \Phi_t^{S6} & 0 & 1-\Phi_t^{S6} \\
0 & 0 & 0 & 0 & 0 & 0 & \Phi_t^{S7} & 1-\Phi_t^{S7} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$

and

$$Y_{i,t}|X_{i,t} \sim multinomial\ (1, X_{i,t}H_t) \qquad \text{eq. 9}$$

where

$$H_t = \begin{pmatrix}
1-po_t^{S1} & po_t^{S1} & 0 & 0 & 0 & 0 & 0 & 0 \\
1-po_t^{S2} & 0 & po_t^{S2} & 0 & 0 & 0 & 0 & 0 \\
1-po_t^{S3} & 0 & 0 & po_t^{S3} & 0 & 0 & 0 & 0 \\
1-po_t^{S4} & 0 & 0 & 0 & po_t^{S4} & 0 & 0 & 0 \\
1-po_t^{S5} & 0 & 0 & 0 & 0 & po_t^{S5} & 0 & 0 \\
1-po_t^{S6} & 0 & 0 & 0 & 0 & 0 & po_t^{S6} & 0 \\
1-po_t^{S7} & 0 & 0 & 0 & 0 & 0 & 0 & po_t^{S7}
\end{pmatrix}$$

In Eq. 9 (the state equation), the matrix contains the condition probabilities of being in a state at particular time occasion (columns) given the state at the previous occasion (rows). Given that an eel is alive at given state, it can survive and remain in the same state, survive and move to another state or die. To ensure that these probabilities are within the interval [0,1] and sum to 1, a generalized (or multinomial) logit link function were used for the transition probabilities (Choquet, 2008). In Eq. 9 (the observation equation), the matrix gathers the conditional probabilities of being observed or not at a particular time occasion (columns) given the state at this current occasion (rows). Given that an individual is alive at a given state, it can be recaptured or not in this given state.

For the detection and transition probabilities of each state, we assumed a random year effect.

Assessing density dependent survival using an integrated model

Using the two models previously described, we firstly built a joint model as the product of both likelihoods and made an explicit link between the two components by relating survival in the multistate capture-recapture model to the density in the capture model. This integrated approach allows assessing density dependence on survival while accounting for estimation errors in density in the survival regression. We used the relation:

$$logit(\Phi_t^f) = \alpha_f + \beta_f \times d_{tot}(t) + \varepsilon_t^f \quad \text{eq. 10}$$

where Φ_t^f is survival probability of the state *f* the year *t*, $d_{tot}(t)$, is the density of eel in the whole watershed the year *t* (obtained thanks to the eq. 7). Parameters α_f and β_f , which depend on the state, are the signal components representing the predictable part of the response and ε_t^f following a normal distribution with a mean equal to 0 and standard deviation sd_f , which depend on the year and the state, is the noise component representing the unpredictable part of the response (Table. 1).

The density dependent survival was only estimated for the first three stages (S_1, S_2, S_3) which correspond to the different yellow eel stages. Indeed, silver eels should be less sensible to density dependent survival as when transformed into silver eel, eels ceased to feed (Pankhurst *et al.*, 1984) and waited to meet the environmental conditions to migrate to the spawning area. For the survival of these silver eels stage (f=S_4, S_5, S_6 or S_7), we assumed a random year effect, thus logit(Φ_t^f)=N($\mu_\Phi^f, sd_\Phi^{f\,2}$) with the mean $\mu_\Phi^f$and the standard deviation sd_Φ^f(Table. 1).

Bayesian implementation

The joint posterior distribution of all unknown quantities (parameters, latent variables and missing data) was estimated through Markov Chain Monte Carlo (MCMC) simulations (Robert, 1996; Gelman *et al.*, 2004) using WinBUGS (Lunn *et al.*, 2000). Three independent chains were used and the first 150000 iterations were discarded. Then 150 000 iterations were used to get posterior results and the convergence of the MCMC chains was tested via the Gelman-Rubin diagnostics (Gelman & Rubin, 1992).

A rather diffuse (weakly informative) prior distribution was assigned to all free parameters in order to let the Bayesian posterior inferences reflect the information brought by the data (Table. 1). Furthermore the sum of the $\alpha_d(r)$ was set to 0 to avoid confusion between the reach effects on the density.

Comparison of the integrated model with a classical regression

We compared the results of the integrated population model with those of a more classical method to see the importance of the choice of an integrated method. The classic method consists in two-step approach i.e. by firstly estimate densities using the hierarchical model and secondly use the estimate median of the density, $d_{med}(t)$, to regress survival in the state space model (we replaced $d_{tot}(t)$ by $d_{med}(t)$ in the eq. 10). With this two-step method, we ignored the estimates error around density. This could lead to uncertainty and bias in estimated survival as the same statistical weight is given at all the density points when regressing survival.

Table 6: Prior distribution of parameters

Parameters	Distribution
μ_z	$Normal(0{,}100)$
sd_z	$Uniform(0{,}10)$
$CV_d(y,r)$	$Uniform(0{,}10)$
sd_β	$Uniform(0{,}10)$
$\alpha_d(r)$	$Normal(0{,}100)$ (sum up to 0)
α_f	$Normal(0{,}100)$
β_f	$Normal(0{,}100)$
sd_f	$Uniform(0{,}10)$
μ_Φ^f	$Normal(0{,}100)$
sd_Φ^f	$Uniform(0{,}10)$

Results

Posterior estimates of the overall mean of the capture probability showed that on average, 46 % of the fish was captured at the first pass during electrofishing sampling. As expected, the density decreased from the downstream to the upstream reach of the catchment (posterior mean of the reach effect $\alpha_d(r)$= 0.73, 0.53, -0.73 and -0.57 for the reach A, B, C and D, respectively). The results of the total density estimates (d_{tot}) showed a low inter-annual variability with a stable period between 1998 and 2003 with a density of 0.4 and only one peak in 1997 with density of 0.55 (Fig. 2). A larger posterior uncertainty was observed around this peak than in the stable period (between 0.39 and 0.75, and between 0.27 and 0.55, for the peak and the stable period respectively; Fig.2).

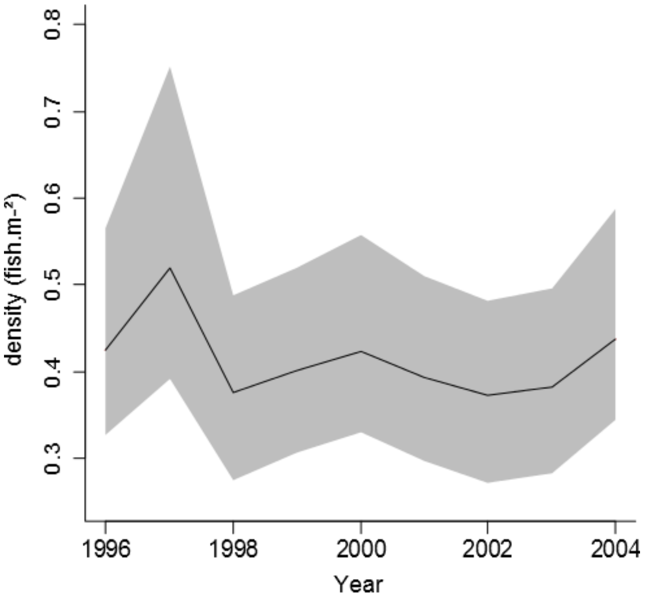

Fig. 2 Time series of estimated densities of European eels in the Frémur, 1996-2004. The thick line represents the posterior median and the shaded area is the posterior uncertainty (95% credibility interval).

Posterior estimates of the detection probability (po) showed that for each stage the trends and posterior means were equivalent between the two approaches (two-step approach and integrated model). Average posterior estimates of the detection probability for each stage were, for integrated model and classical regression respectively, of 0.064 and 0.066 for stage S_1, 0.22 and 0.21 for S_2, 0.10 and 0.11 for S_3, 0.050 and 0.051 for S_4, 0.07 and 0.09 for S_5, 0.93 and 0.95 for S_6, 0.76 and 0.80 for S_7.

Posterior estimates of the detection probability (po) showed that for each stage the trends and posterior means were equivalent between the two approaches (two-step approach and integrated model; Table. 2). On average, an important part of the yellow eels with a size between 300 and 450 mm (~40% of the S_2) stopped growing and became mature silver eels (S_4), which is expected for an eel population with a majority of male as in the Frémur.

No density dependent effect was detected on stages S_2 and S_3 with either method. For these two stages the parameters representative of the density dependent relationship α_f and β_f, were equivalent in term of value. The precision (width of the posterior densities, Fig. 3& 4) of these two parameters was equivalent for stage S_2 but for stage S_3, the precision was higher with the integrated model than with the two-step approach. With the two methods, survival estimated for these two stages were high and slightly variable (Fig. 5).

In the case of the two-step approach, our study showed a negative effect of density on survival for stage S_1 (posterior mean β_1= -3.8) with a decrease of the predicted survival of 0.34 when the density increases from 0.1 to 0.9 eel m^{-2}. In the case of the integrated model, a weak negative effect of density on survival was observed for stage S_1 (posterior mean β_1= -1.1) with a decrease of the predicted survival of 0.008 when the density increases from 0.1 to 0.9 eel m^{-2}. For this stage, the strength of density dependence (β_1, slope of the density dependent relationship) obtained from the integrated model was more precise compared to that of the regression analysis, indicated by a narrow width of the posterior densities (Fig. 4).

The parameters of the density dependent relationship obtained via both methods were identifiable (for all stages) as the posterior densities were different of the specified prior distribution (Gimenez *et al.*, 2009). However, important posterior uncertainties were observed on the parameters of the density dependent relationship (Fig. 3 & 4).

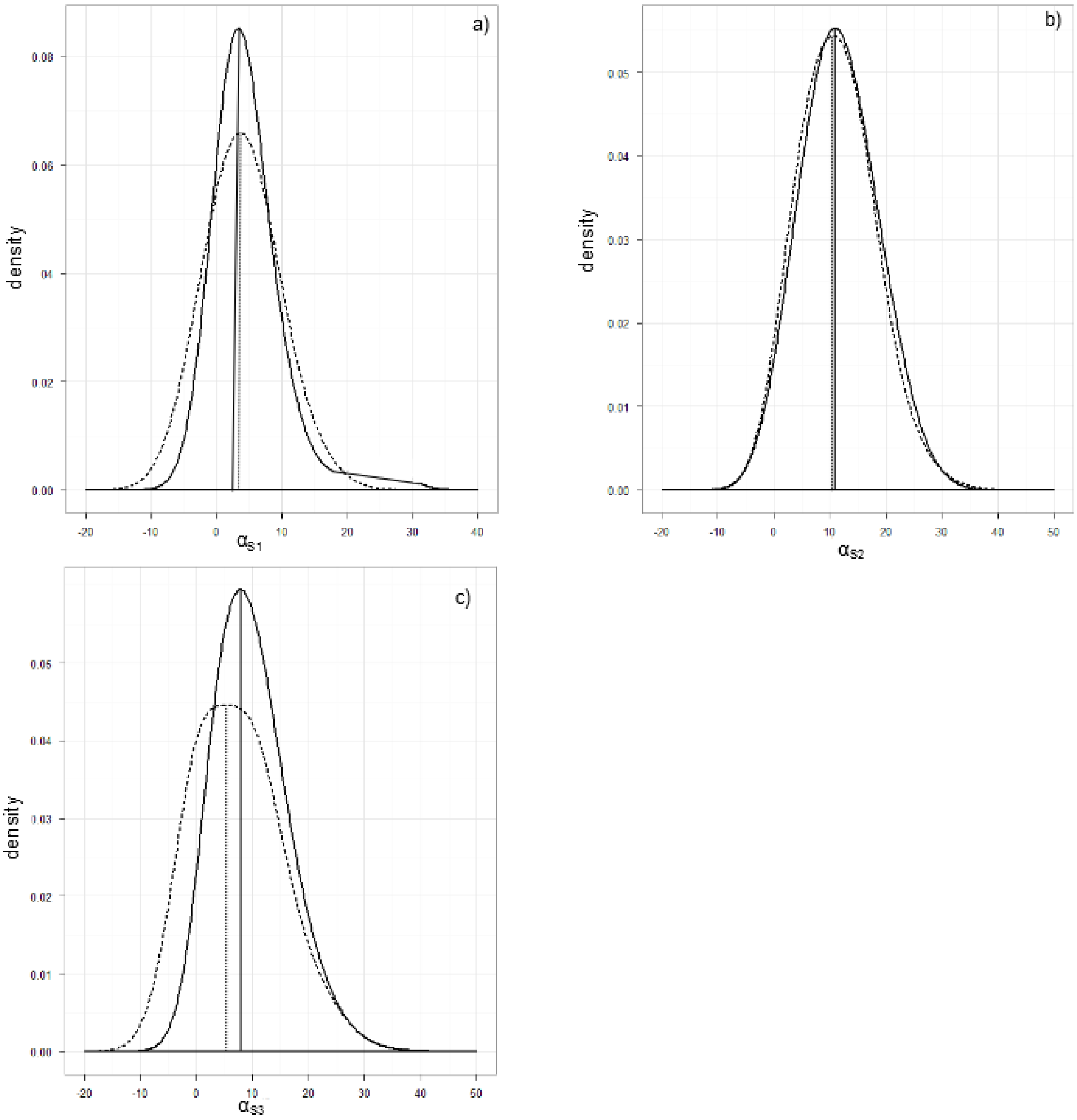

Fig. 3 Density plots of estimated posterior means of the intercept of the density dependent relationship (α_f) on survival of the three yellow eel stages, a) S$_1$, b) S$_2$ and c) S$_3$, obtained from integrated population models (solid line), and from single data analysis ignoring observation error (dashed line). Vertical lines are the means of the estimated posterior means of the intercept of the density dependent relationship (α_f).

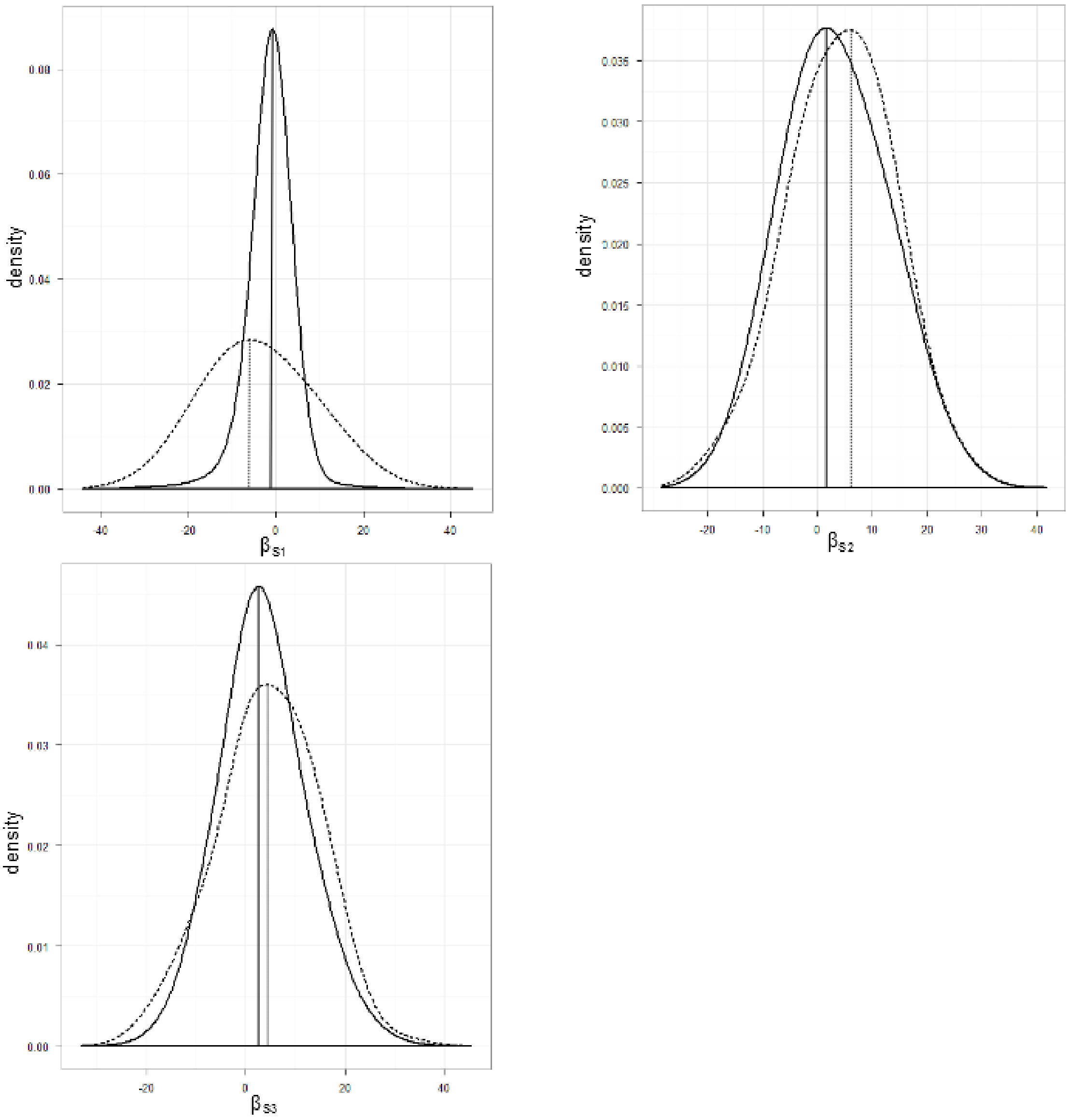

Fig. 4 Density plots of estimated posterior means of strength of density dependence (slope of the density dependent relationship, β_f) on survival of the three yellow eel stages, a) S_1, b) S_2 and c) S_3, obtained from integrated population models (solid line), and from single data analysis ignoring observation error (dashed line). Vertical lines are the means of the estimated posterior means of the strength of density dependence (β_f).

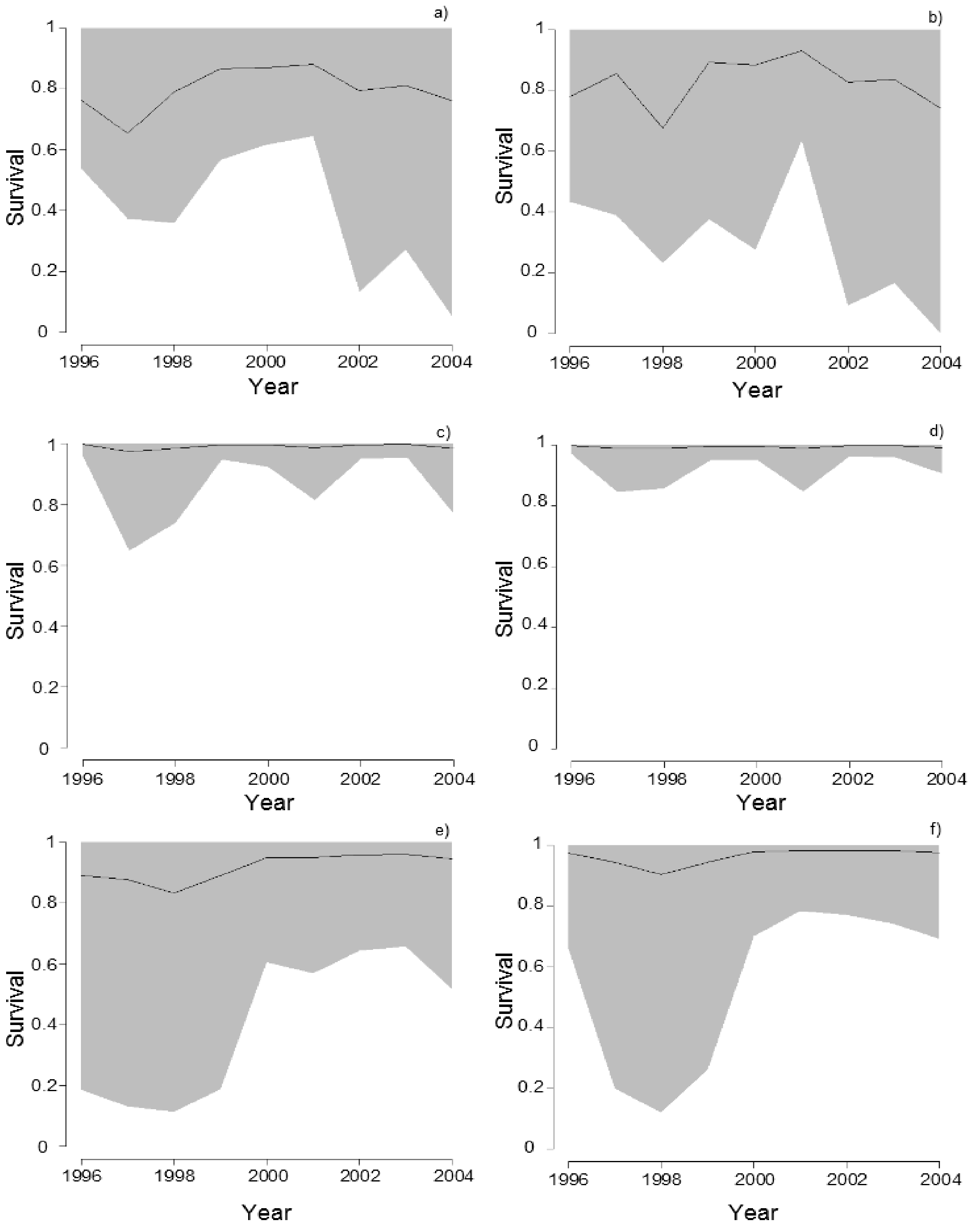

Fig. 5 Time series of estimated survival probabilities of the three yellow eel stages, a) & b) S_1, c) & d) S_2, e) & f) S_3 in the Frémur for the two methods used: a), c) & e) classical regression model and b), d) & f) integrated model. The thick line represents the posterior mean and the shaded area is the posterior uncertainty (95% credibility interval).

Table 7: Average posterior mean of the transition probability for the integrated method and the two-step approach

Transition	Average posterior estimates of the transition probability for the integrated model ± SD	Average posterior estimates of the transition probability for the two-step approach ± SD
$\varphi_t^{S1\rightarrow S1}$	0.71 ± 0.1	0.70 ± 0.1
$\varphi_t^{S2\rightarrow S2}$	0.45 ± 0.04	0.45 ± 0.03
$\varphi_t^{S2\rightarrow S3}$	0.059 ± 0.03	0.060 ± 0.03
$\varphi_t^{S2\rightarrow S4}$	0.41 ± 0.06	0.39 ± 0.05
$\varphi_t^{S2\rightarrow S5}$	0.006 ± 0.04	0.010 ± 0.01
$\varphi_t^{S2\rightarrow S6}$	0.083 ± 0.04	0.080 ± 0.04
$\varphi_t^{S2\rightarrow S7}$	0.0006 ± 0.0005	0.0003 ± 0.0001
$\varphi_t^{S3\rightarrow S3}$	0.72 ± 0.17	0.76 ± 0.17
$\varphi_t^{S3\rightarrow S5}$	0.19 ± 0.18	0.17 ± 0.18
$\varphi_t^{S3\rightarrow S7}$	0.082 ± 0.016	0.065 ± 0.01
$\varphi_t^{S4\rightarrow S4}$	0.72 ± 0.024	0.74 ± 0.03
$\varphi_t^{S5\rightarrow S5}$	0.83 ± 0.02	0.81 ± 0.02

Our analyses revealed that the mean annual survival probabilities using the integrated model were 0.82 (sd = 0.07), 0.99 (sd = 0.003) and 0.96 (sd=0.03), for stage S_1, S_2 and S_3 respectively. For comparison, the mean annual survival probabilities using the two-step approach were 0.79 (sd = 0.06), 0.99 (sd = 0.01) and 0.92 (sd=0.04), for stages S_1, S_2 and S_3 respectively. For stages S_2 and S_3, the survival patterns were equivalent and stable in time for both methods but posterior uncertainties were larger for the two-step approach (Fig. 5). For stage S1, survival probabilities estimates were slightly lower using the two-step approach models than with the integrated model. The patterns observed were equivalent between 1999 and 2004 with survival probabilities quite stable in time (Fig. 5). However a peak of mortality was observed in 1997 with the two-step approach models in accordance with the peak of density observed this same year whereas a peak of mortality is only observed in 1998 with the integrated model (Fig. 5). We observed also for this stage that the posterior distributions of survival were wider for the integrated model compared to the two-step approach method (Fig. 5).

Discussion

Density dependence can have a strong impact on population dynamics by affecting different demographic parameters (survival, growth, fecundity, etc.). Understanding and quantifying the intensity of this process is crucial for accurate demographic projections, with important consequences in conservation and population harvesting (Sinclair and Pech, 1996; Lande *et al.*, 2003).

The model we propose has several advantages. First, because the population survey dataset consists of successive removals in portions of a river using electrofishing, it allows building a hierarchical structure that makes density explicit and accommodates uncertainty at different scales (sampled site, reach, whole watershed; Wyatt, 2002; Rivot *et al.*, 2008). Besides, it is possible to assess density dependence based on estimates of population abundance corrected for detection errors. Second, because demographic parameters (e.g. survival and transition probabilities) are estimated with a multistate capture-recapture structure, it allows testing density-dependence at a given stage, and therefore to determine when in the life cycle the demographic mechanisms of density-dependent population regulation occur. Third, the use of two independent datasets for estimating both survival and density and build an integrated model resulted in improved precision of the density dependence intensity estimate.

While we found that the parameters of the density-dependent relationship were similar for stages S_2 and S_3 whatever the method we used, hence highlighting no significant effect of density on survival, we found differences for stage S_1. The two-step approach model tended to estimate a strong density dependence on survival while the integrated model showed no density dependent. This discrepancy between the two approaches could be explained by the fact that the classical method assigns the same statistical weight to all the density estimates when regressing survival, which could lead to an overestimation of the density effect; in contrast, the integrated method incorporates estimation errors. The results of the integrated model seems more reliable as, in agreement with the results of Abadi *et al.* (2012), the precision of the density dependent parameter estimates was better with the integrated model than with the two-step approach (Fig. 4).

The non-detection of density-dependent survival for any of the three yellow eel stages using the integrated population model was an unexpected result as the study area, the lotic habitats of the Frémur, was supposed to have reached carrying capacity (Acou *et al.*, 2011). Three non-mutually exclusive hypotheses can explain this discrepancy.

First, we estimated demographic parameters and density over a short period of time (i.e., 9 years). This situation met conditions where the estimation of density dependence was difficult as the ability to detect density dependence usually increases with long time series data (Brook and Bradshaw, 2006). Furthermore during this period, variation in densities of the lotic habitats of the Frémur was relatively low (min: 0.3652 eel m^{-2}; max= 0.5329 eel m^{-2}).

Second, in our study, the errors in density estimates were quite large (Fig. 2) and as demonstrated by Abadi *et al.* (2012) the estimates of density dependent parameters were less precise when the error was large than small. Furthermore, the influence of density on biological processes can be overlooked due to an inappropriate measure of density (Barker *et al.*, 2002; Williams *et al.*, 2002). To estimate density, we modelled the spatio-temporal variability of the density using a linear combination of a year and a reach effects. However, in the Frémur, density also varies with instream cover and substratum (Acou *et al.*, 2011). The addition of these two covariates may improve the precision of our density estimates and then modify the density dependent relationship on survival.

Finally, we only studied survival probabilities of eel with a size >150 mm as smaller eels were not marked because the weight of the tag (0.1g) would have represented more than 2% of the total weight of the individuals (Winter *et al.*, 1996). However, these individuals, representing young recruits, should be the most sensitive to density-dependent processes due to their research of a suitable habitat to live in, which depends on the individuals already present and their competitive advantage, as demonstrated in salmonid species (Johnsson *et al.*, 1999; Johnsson *et al.*, 2000). Indeed, in such small rivers, young recruits may colonize the whole river in a single wave of upstream migration (Feunteun *et al.*, 2003). It is likely that such massive colonization of rivers by recruits would induce density dependent processes. The field observations and our results seemed to highlight that if density dependent mortality existed in the eel population of the Frémur, this process was mostly applied on this juvenile stage. Indeed, between 1997 and 2007, the number of recruits that entered in the system was highly variable (between 381 and 26765 young recruits) whereas the eel density in the river remained quite stable (between 0.373 and 0.5329 eel m^{-2}; Fig. 2&6) suggesting density dependent mortality. However as no density dependent mortality was detected on eels with a size >150 mm, the increased numbers of recruits should lead to increase of mortality of this young stage due to lack of available habitat to settle in or to predation pressure (predators or larger conspecifics; Tesch, 2003).

Finally, our results confirmed that the use of an integrated model increased the precision of the density dependent parameter estimates. This model was tested using European eel subpopulation but it could be used for the study of other riverine fish species where density dependent processes are expected to be strong regulator of the population dynamics such as salmonids species (Elliott, 1994). Furthermore, this model could be improved as the integrated population model is a very flexible tool that allows to simultaneously estimating the effect of density dependence on different demographic parameters such as survival, growth, migration or fecundity (Abadi *et al.*, 2012). The integrated model could also be extended to assess nonlinear density dependence, for instance by using penalized splines (Gimenez *et al.*, 2006) or thresholds (Besbeas and Morgan, 2012) but also to study delayed density dependence.

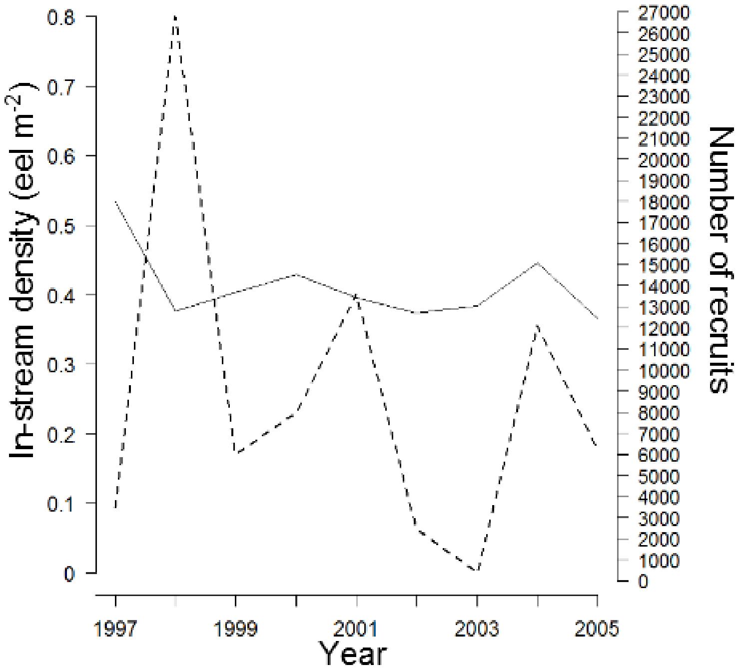

Fig. 6 Time series of in-stream density (eel m^{-2}; dotted line) and of recruitment (dashed line).

Overall, our model provides an efficient statistical tool for reliably estimating density dependence in wild animal populations as long as two sources of information are available on demographic parameters and density. This approach will hopefully help in improving the knowledge of the mechanisms controlling population dynamics, and in turn help in providing adapted decisions support tools for these populations.

Acknowledgements

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Partie 3 : Impacts des systems sur la dynamique de population et les traits d'histoire de vie : Apport pour la conservation

I. Contexte de l'étude

Pour une espèce en danger critique d'extinction comme l'anguille européenne, il est essentiel de mettre au point des plans de gestions adaptés pour permettre le soutien voire la restauration du stock. Cependant à cause de leur cycle de vie particulier, la mise en place de mesures de protection est souvent compliquée. En effet, la phase marine est rarement accessible, comme pour la plupart des espèces diadromes. Il faut donc se résoudre à gérer cette espèce là où elle est la plus accessible, c'est-à-dire dans les habitats continentaux. Pourtant, les processus ayant lieu dans les systèmes continentaux sont rarement pris en compte. En effet, l'une des mesures phares de gestion préconisées par l'Europe consiste à réserver 60% des captures d'anguilles de moins de 12 cm (civelle et anguillette) à des fins de repeuplement (EC, 2014). En France, sur les 42.5 t accordées par quota aux pêcheurs entre 2013 et 2014, 20.2 t devront donc être réservées à des fins de repeuplement. Cette mesure vise à augmenter le nombre de reproducteurs partant en mer en augmentant le nombre de recrues entrant dans un système. Cependant, les résultats de nos précédentes analyses semblent indiquer que les processus de régulation au sein du système peuvent avoir lieu, en induisant par exemple de fortes mortalités. Ainsi, selon le rapport français sur les opérations de repeuplement, le repeuplement ne peut être considéré comme efficace que si le nombre et la qualité des anguilles argentées produites issues des individus repeuplés sont au moins équivalents à ceux des individus ayant naturellement colonisé le système (Frotté *et al.*, 2012). Comprendre le rôle des caractéristiques du système (disponibilité en nourriture et en habitat, compétiteurs, qualité du milieu, …) sur la production d'anguilles argentées, en termes de quantité et de qualité, est donc nécessaire pour déterminer l'efficacité du repeuplement et pour finalement cibler les habitats propices.

Pour étudier l'efficacité du repeuplement en lien avec les caractéristiques du milieu et son évolution et proposer des aides à la décision, nous avons, dans un premier temps, suivi le destin de groupes d'anguilles stockées à différents stades et provenant de milieux différents dans un marais d'eau douce du le sud de la France (Camargue) qui évolue rapidement d'un statut de système quasiment vierge vers un statut de système à saturation. L'impact des stades de stockage, des milieux d'origine et de l'évolution du système sur le nombre et les caractéristiques des anguilles argentées produites par chaque groupe sera discuté afin de mettre en évidence les précautions à prendre pour augmenter les chances de succès de repeuplement. Dans un deuxième temps, nous allons étudié les relations taille-poids des anguilles argentées, qui sont des bonnes indicatrices de la condition corporelle, dans plusieurs bassins versants à l'échelle européenne afin de montrer l'importance de la qualité du système dans les stratégies de traits d'histoire de vie développées par toutes les anguilles.

II. Article 5 : Is Stocking an Efficient Measure to Sustain the Freshwater Eel Populations?

Clarisse Boulenger[1, 2], Anthony Acou[1], R.K. Gallon[1], M. Desprez[3], J. Panfili[4], I. Lebel[5], M. Pascal[6], Eric Feunteun[1] and Alain Jean Crivelli[2],

[1]UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France

[2]Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France

[3] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Campus du CNRS, 1919 route de Mende, 34293 Montpellier cedex 5

[4] UMR 5119 ECOSYM, CNRS-UM2-IFREMER-IRD-UM1, Université Montpellier 2, cc093, place E. Bataillon, 34095 Montpellier Cedex 5, France

[5] Association Migrateur-Rhône-Méditerranée, ZI Nord, rue A. Chamson, 13200 Arles, France

[6] Association les Amis du Vigueirat, 13104 Mas Thibert, France

Correspondence: Clarisse Boulenger,UMR BOREA 7208 Muséum National d'Histoire Naturelle, CNRS, IRD, UPMC – Service des stations marines du MNHN, CRESCO, 38 rue du Port Blanc 35800 Dinard, France.

Email: clarisse.boulenger@edu.mnhn.fr

Running head: Efficiency of European eel stocking

Keywords: stocking, European eel, glass eel, silver eel, survival, mark-recapture experiment

En Préparation pour Biological Conservation

Summary

Stocking is one of the the key measures to fight against the European eel (*Anguilla anguilla*, L.) stock collapse. However, few studies have been conducted to demonstrate the effectiveness and suitability of such conservation measure. Here, we evaluated the stocking effectiveness by assessing the number and quality of silver eels yielded by both stocked eels from different origins and life-stages versus naturally recruited ones. Five groups of different eel life-stages (glass eels, bootlace eels and yellow eels) and origins (brackish and freshwater) were successively stocked and sampled during 6 years in a controlled freshwater marsh of southern France (Rhône River delta). The fate of these stocked eels, from the date of introduction until the silver eel stage, was studied using a biannual eel sampling associated with an extensive mark-recapture study. Multistate models were used to estimate survival and transition probabilities which were then used to calculate the final number of silver eels yielded per 100 eels for the 5 stocked groups and the naturally recruited group. Quality of potential spawners was assessed using lipid content (%), pollutant contents (PCBs and Cd) and *Anguillicoloides crassus* infection in swimbladder observed in silver eels originated from the different groups. Our results highlighted that the number of silver eels yielded is dependent of the origin, the stage and the size at introduction whereas the quality of silver eels is equivalent among eel groups. Finally, we demonstrated that the characteristics of the system (food and space availability, water quality) where the eels will be stocked are particularly critical for the stocking success as it will govern both the quality and quantity of silver eel produced. Considering our results, recommendations for future stockings were addressed.

Introduction

Considered as a pest species in France until 1984, the European eel, *Anguilla anguilla*, is now listed as critically endangered by the IUCN. Since the 70's, the population of European eel is in sharp decline with a decrease in recruitment superior than 90% (Moriarty, 1986 Moriarty, 1990 Dekker, 2000 WGEEL, 2008, ICES 2012) and an abundance in glass eels divided by 10 to 100 (Dekker, 2004). Several causes of this decline have been proposed such as climatic variation, overfishing, habitat loss and degradation, pollution with PCB's and heavy metals and infections with the swimbladder parasite *Anguillicoloides crassus* (Feunteun *et al.*, 1998; Dekker, 2003a; Pierron *et al.*, 2008a; Pierron *et al.*, 2008b; Limburg and Waldman,2009; Lefebvre *et al.* 2012a). To fight against this stock collapse, the European Union, through the European Regulation No.1100 of September 18, 2007, requested all member states to implement an Eel Management Plan aiming to increase the number of potential spawners capable of reproduction. As the fishing of juvenile eels (glass eels and elvers) is still authorized in some member states (including France), one of the key measures is to reserve 60% of the catches of eels < 12 cm for stocking in European waters by 2013. Stocking is the practice of adding fishes (eels) to a water body from another source to supplement existing populations or to create a population where none exists (ICES, 2013). However, few studies have been conducted to demonstrate the effectiveness and suitability of such measure (ICES 2013). In particular, there is a lack of quantitative studies that would help in formulating advice on if, when, where and how much to stock (Desprez *et al.*, 2013).

As explained in the French report on stocking operations (Frotté *et al.*, 2012), stocking would be considered as an efficient measure if (i) stocked eels produced more silver eels than if they had naturally colonized the system (*i.e.* mortality rates between the glass eel and silver stages are lower for the stocked eels than for eels from natural colonization) (ii) stocked silver eels had an equivalent or superior quality (*i.e.* mean reproductive success) than naturally recruited eels and (iii) stocked silver eels had the ability to find their way back to the spawning area in the Sargasso Sea and to produce viable eggs and larvae.

Westerberg *et al.* (2014) have recently shown that, during their marine migration from Baltic to the spawning areas, stocked adult eels have similar behaviors and routes than eels from natural recruitment suggesting that stocking does not hinder the marine migration. On the contrary, Wickström *et al.* (2014 québec AFS conference) have suggested that the silver eels breeding migration inside the Baltic sea is altered. A debate is thus still ongoing to understand if translocated and stocked eels correctly perform their breeding migration. While this question is currently studied, thanks to the recent improvement of telemetry, the two first points (quantity and quality of stocked eels) still need to be analyzed to demonstrate the efficiency of stocking.

The number of potential spawners produced depends mainly on the number of recruits (juveniles as glass eels or elvers) and the survival of eels during the whole continental life, *i.e.* from recruits (juveniles as glass eels or elvers) to the silver eel stage (last continental life stage). Estimating these parameters is difficult because of imperfect detection that needs to be accounted for in order to avoid underestimating survival probabilities (Gimenez *et al.*, 2008). One method to deal with this issue is to use a multistate capture-recapture modeling approach (Lebreton *et al.*, 2009).

It is also necessary to take into account the quality of silver eels produced. Indeed, quality might be a key factor in explaining the stock decline as silver eels with a poor health status might not be able to reach the spawning area or might not have enough energy to reproduce successfully. Among numerous factors, three have been particularly studied for their impacts on the reproductive success. Indeed, because silver eels fast during their breeding migration, lipid content is crucial (i) to fuel this migration across the Atlantic ocean and (ii) for the sexual maturation of ovaries and testis that happens mostly during the trip to the reproductive areas (Böetius 1980; van den Thillart *et al.*, 2004; Palstra *et al.*, 2007; van den Thillart *et al.*, 2007). Pollutants, especially lipophilic persistent contaminants such as PCBs, are known also strongly affect the reproductive success of eels as this long-lived species presents high body lipid content making it more sensible to the bioaccumulation of this kind of pollutants (Roche *et al.*, 2000). Numerous studies have shown that eels migration and reproduction could be seriously affected by PCB-levels (Larsson *et al.*, 1990; Robinet & Feunteun 2002; Palstra *et al.*, 2006a; Van Ginneken *et al.*, 2009) as lipids are metabolized during the spawning migration, the lipophilic contaminants, as PCBs, are remobilized and transferred to the blood and finally to the gonads. This could interfere with the energy metabolism reducing the chances to reach the spawning area. Furthermore, trans-generation transfer of this kind of pollutants from a mother to her eggs is thought to impair larval survival and development (Gutleb *et al.*, 1999; Gutleb *et al.*, 2007 and Palstra *et al.*, 2006). Heavy metals could also strongly impact reproductive success (e.g. cadmium (Cd) can induce oocyte atresia and eel mortality (Pierron *et al.*, 2008, 2009)). Finally, an infection by the swimbladder parasite *Anguillicoloides crassus* may affect the silver eels capacity to migrate by decreasing their oxygen transport capacity and thus reducing their swimming performance (Molnar, 1993; Palstra *et al.*, 2007).Therefore, Silver eel quality assessment must considerate once lipid content, pollutants (PCBs and Cd levels) and swim bladder infection.

Here, we evaluated the stocking effectiveness by assessing the number and quality of silver eels yielded by both stocked and naturally recruited eels. To do so, we conducted a 6-years stocking experiment in a controlled freshwater marsh ofsouthern France (Rhône River delta). Between October 2007 and April 2013, five groups of different eel life-stages (glass eels, bootlace eels and yellow eels) and origins (brackish and freshwater) were successively stocked. The fate of these stocked eels, from the date of introduction until the silver eel stage, was studied using a biannual (spring and autumn) eel sampling associated with an extensive mark-recapture study. Multistate models (Lebreton *et al.*, 2009) were used to estimate survival and transition probabilities between continental eel life-stages for each stocked eel group. These parameters were then used to calculate the final number of silver eels yielded per 100 eels for the 5 stocked groups. Quality of potential spawner was assessed using lipid content (%), pollutant contents (PCBs and Cd) and *A. crassus* infection in swimbladder observed in silver eels originated from the different groups. The stocking efficiency was assessed by comparing the number of silver eel yielded and the quality of potential spawners of each group to those of a native eels group that naturally colonized the pond. Finally, we discussed about the factors (stage of introduction, origin, characteristics of the system where eels are stocked) that could influence the efficiency of stocking.

Materials and methods

Study system

The study site is a closed freshwater pond called "Pisci-Sud", which is a former fish farm, located in the Natural Nature Reserve of the "Vigueirat Marshes", in the River Rhône Delta, France (Fig.1). The basin is composed oftwo interconnected ponds, respectively 6 ha and 50 cm deep and 5.5 ha and 25 cm deep, surrounded by a 20.5 ha reedbed and a meadow. In summer 2007, the pond was entirely emptied except for a deep ditch where native eel (Vig) found refuge with other fish species and refilled for the stocking experiment.

Water temperature ranged from 0°C to 33°C with a mean water temperature of 7°C in winter and 23°C in summer (overall mean = 19.05°C). The period during when eels were active in the basin (temperature above 8°C) is long and varied between 177 and 249 days a year. Under this latitude (43°31'36), the eel growth is in the upper range of other values in for European catchment (117 mm year^{-1} in average in the Vigueirat; Vollestad, 1992; Aprahamian, 2000; Daverat *et al.*, 2012).

Stocked eel collection, origins and characteristics

Between October 2007 and February 2009, five groups of eels with different origins (brackish water, BW, or freshwater, FW) and life-stages (glass eels, bootlace eels or yellow eels) were introduced in Pisci-Sud.

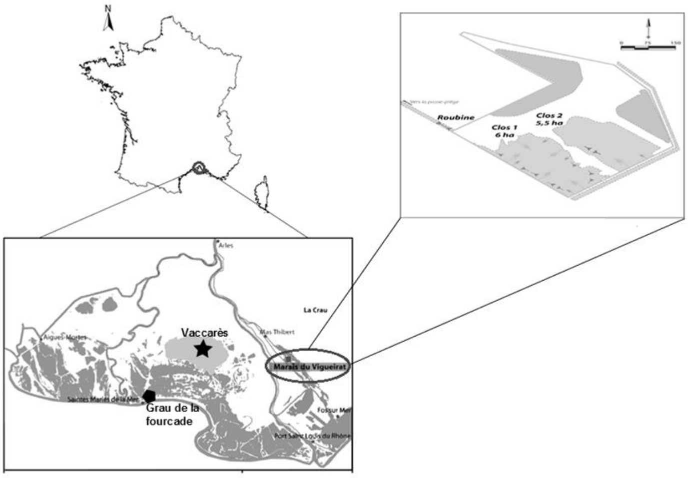

Fig.1 Map of France, showing the location and configuration of Piscisud. The star and the polygon show the localization of where the eels from Vacc1 and Vacc2 were caught and where the eels from Grau1, C08 and C09 were caught, respectively, for the stocking experiment.

The first three groups (Vacc1, Vacc2 and Grau1) were stocked in October 2007 (Table 1). Eels from Vacc1 and Vacc2 were both collected in the brackish lagoon of Vaccares using fyke-nets (Fig. 1, Table 1). Eels from Grau1 were collected in a freshwater canal at the entry of the lagoon (Grau de la Fourcade fish-pass, Crivelli *et al.*, 2008). Eels from Grau 1 and Vacc1 groups were introduced at a size between 200-299mm, whereas eels from the group Vacc2 were added at a size superior to 300 mm long.The total length (TL, to the nearest mm) of each stocked eel and the associated total body weight (TW, to the nearest g) were recorded, together with the averaged eye diameter (ED, to the nearest mm) to determine their EELREP stage according to Durif *et al.* (2005). Finally, we grouped EELREP stages into three classes as proposed by Desprez *et al.* (2013): undifferentiated, yellow and silver eel. When the EELREP stage was NA or I, eels were considered as sexually undifferentiatedeel (E). Eels were considered as yellow eel (Y) when EELREP index was FII or FIII and as silver eel (S) for EELREP stages FIV, FV (female silver eel) and MII (male silver eel).On this basis, all individuals from Vacc1 and Grau1 groups were classified as sexually undifferentiated eels (E) while individuals from group Vacc2 were classified as yellow eels (E) and sexually undifferentiated eels(Y; Table 1). Before introduction in Pisci-Sud, all eels from the Vacc1, Vacc2 and Grau1 were individually marked with PIT-tag (Passive Integrated Transponder tags).

The two last stocked groups were composed of glass eels (mean length = 80 +/- SD mm) collected at the Grau de la Fourcade (freshwater canal) using a glass eel trap (Crivelli *et al.*, 2008) in January 2008 (C08) and February 2009 (C09). Around 2.5 kg of glass eels were collected, corresponding to 9358 and 9257 glass eels for C08 and C09 respectively (Table 1). Prior to introduction in 'Piscisud', all glass eels were batch marked with Tetracycline.

Table 8: Origin and characteristics of individuals stocked in PisciSud for the five groups (Vacc1, Vacc2, Grau1, C08 and C09).

Group	Origin	Life-stage introduced	Range of size	Number of eel stocked	Period of introduction	Marking method
Vacc1	Brackish water (Vaccares lagoon)	Sexually undifferentiated eel	200-299	390	October 2007	PIT-tag before stocking
Vacc2	Brackish water (Vaccares lagoon)	Sexually undifferentiated eel and Yellow eel	300-399	404	October 2007	PIT-tag before stocking
Grau1	Freshwater (Grau de la Fourcade)	Sexually undifferentiated eel	200-299	297	October 2007	PIT-tag before stocking
C08	Freshwater (Grau de la Fourcade)	Glass eel	<80	~2.5kg = 9358	January 2008	Tetracycline and PIT tag
C09	Freshwater (Grau de la Fourcade)	Glass eel	<80	~2.5kg = 9257	February 2009	Tetracycline and PIT tag

Sampling

In Pisci-Sud, two removal samplings of nine consecutive days, in May and in October, were conducted every year from 2008 to 2013. Eels were captured by passive trapping using different nets: 13 fyke nets with a 6 mm mesh size and 11 "capetchades" nets, 6 with a 6 mm mesh size in the funnel and a leading net of 40 m, and 5 with a 0.5 mm mesh size in the funnel and a leading net of 20 m. The use of different mesh sizes allowed the capture of eels of all lengths (Bevacqua *et al.*, 2007; 2009). During the removal sampling, the nets were visited every morning and releasedback to the capture sitemaking fishing effort constant over years.

All captured eels were anesthetized with phenoxyethanol, measured, weighed and the life stage was determined using the methodology described before. All eels captured during the sampling session were checked for a PIT-tag. If the individual was not marked (individuals from 'Vig, 'C08 or 'C09') and the the length was superior to 160 mm, a PIT tag was inserted. Regarding the glass eel group assignment (C08 and C09), we considered that a small unmarked eel (<250mm) caught during the sampling following the stocking of a given group belonged to this group. To validate the group assignment, silver eels were sacrificed and the tetracycline mark was checked for each otolith in order to confirm affiliation to groups C08 and C09. If no tetracycline mark was observed, individuals were assigned to Vig groups.

Capture-Mark-Recapture analysis

Data were analyzed using multistate capture-recapture models (Lebreton *et al.*, 2009) to estimate survival rates and transition probabilities between stages. Following Desprez *et al.* (2013), three different stages were considered: sexually undifferentiated eels (E), yellow eel (Y) and silver eel (S). Individuals were allowed to make transition from E to Y or S, and from Y to S. Yellow eel could not return to the undifferentiated stage then transition probability from Y to E was fixed to 0. Silver eels could not return to previous stage so transition probabilities from S to E or Y were fixed to 0 and transition probability from S to S was fixed to 1. We investigated various effects on transitions (w), survival (Φ) and detections (P) probabilities such as temporal effects (continuous and seasonal effects), stage effects or group effect (except on detection probabilities as sampling efforts did not vary). We tested a group effect (Vig, Vacc1, Vacc2, Grau1, C08, and C09) to determine whether the stage in which eels were stocked influenced their survival or their probability to pass from a stage to another. We also examined a stage effect on survival and transition probability as it was suspected to differ. To build the best model, we firstly selected the most appropriate structure for P testing one by one the different effects. Once the main effect was determined, remaining effects were added in an additive and interactive fashion to assess if one of these combinations was relevant. This operation continues until no better model was selected. We repeated the same process for Φ using the previously selected structure for P and finally for w using the structures for P and Φ selected in the previous steps. The most parsimonious model was selected using AIC (Akaike information Criterion; Burnham & Anderson, 2002). These analyses were performed with program E-SURGE (Choquet *et al.*, 2009a) and the models quality of fit (Pradel *et al.*, 2003) using program U-CARE (Choquet *et al.* 2009b).

Number of silver eels yielded for each group

Survival and transition rates (see results, Fig. 2 and 3), obtained from the selected model, were used to determine the fate of 100 eels from undifferentiated eel to silver eel over the study period for each group. The simulations were realized in R software (http:// www.r-project.org/) using repeated Bernoulli trials for survival and multinomial trials for transition (function "rbinom" and "rmultinom" in package "stats"). Firstly we estimated the number of individual that survive from the stage f (*f*= E, Y or S) between the sampling session *t-1* and *t*,$Ns_{t,f}$, using the survival probability $s_{t,f}$ and the total number of individuals from the stage f at the sampling session *t-1*,$NT_{t-1,f}$ (eq. 1). Secondly, we estimated the number of individuals that pass from the stage *f* (*f*= E, Y or S) to the stage *to* (*to* = E, Y or S) between the sampling session *t-1* and t,$Nt_{t,f,to}$, using the transition probability $g_{t,f,to}$ and $Ns_{t,f}$ (eq. 2). Finally, the total number of individuals from the stage *f* at the sampling session t, $NT_{t,f}$, is calculated (eq. 3).

$$Ns_{t,f} = Bernouilli(s_{t,f}, NT_{t-1,f}) \qquad \text{eq. 1}$$

$$Nt_{t,f,to} = Multinomial(g_{t,f,t,1}, g_{t,f,2}, g_{t,f,t,3}, Ns_{t,f}) \qquad \text{eq. 2}$$

$$NT_{t,f} = \sum_{to} Nt_{t,f,to} \qquad \text{eq. 3}$$

This process was made for each group and repeated 1000 times to account for demographic stochasticity.

Quality of silver eels in relation with life history traits (age and size at silvering)

During each sampling period, all silver eels identified according to the methodology of Durif *et al.* (2005) were collected, measured, weighed and frozen the day of capture before subsequent dissection. As female were dominant in the silver eel catches (91% of silver eel catches), only female were considered for quality analysis.

Lipids

Muscle samples from 180 female eels from the different groups were collected and analyzed by LABEXIA laboratory (Quimper, France) to quantify the lipid weight. Total lipid content (expressed in %) was determined according the French norm NF V 04-403(AFNOR, 2001).

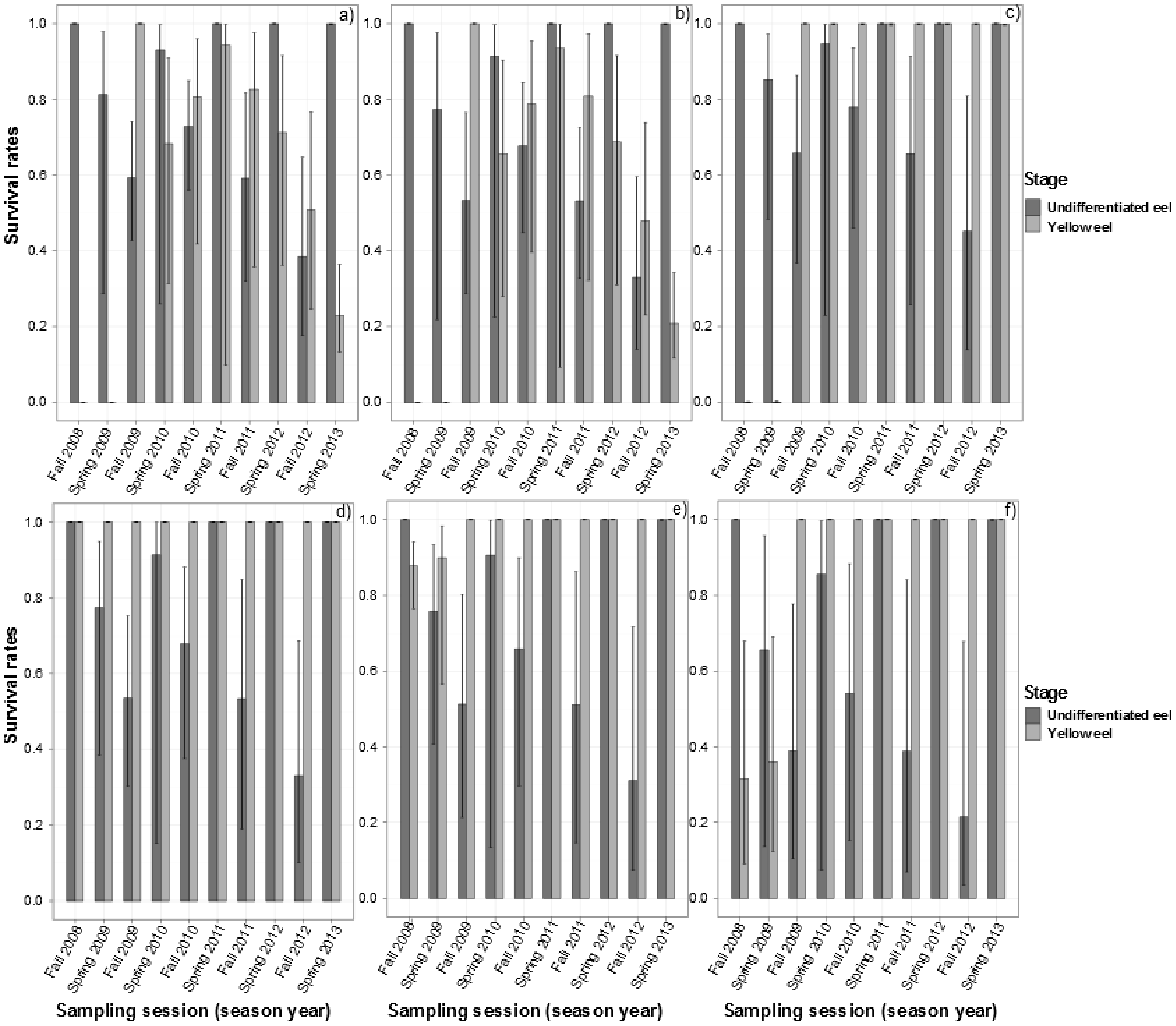

Fig.2 Survival probabilities of undifferentiated and yellow eel (error bars represented the 95% confidence interval) according to time for the stocked eels from a) C08, b) C09, c) Grau1, d)Vacc1, e) Vacc2 and and for the native eel from f) Vig.

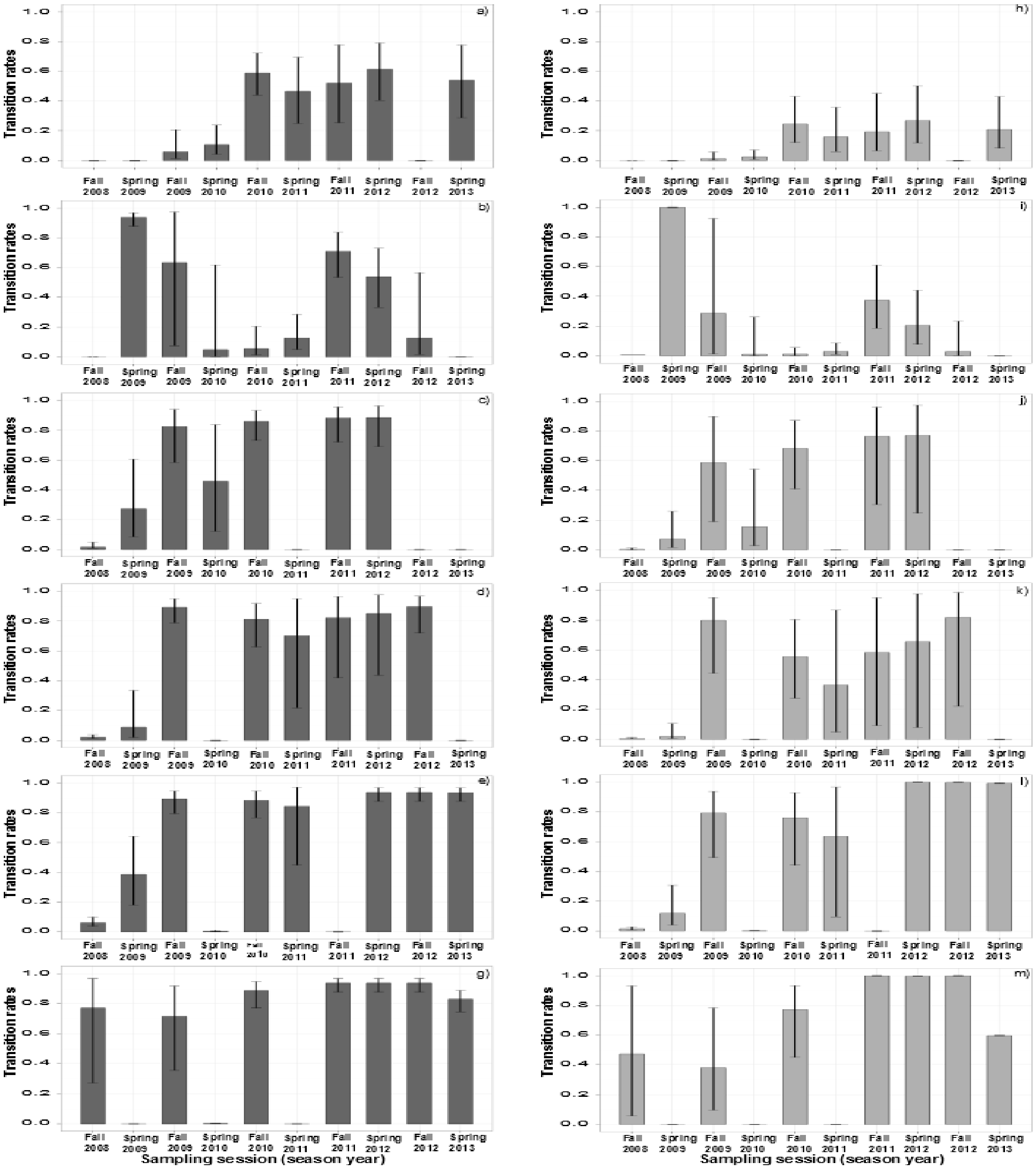

Fig. 3 Transition probabilities (error bars represented the 95% confidence interval) from sexually undifferentiated eel to yellow eel (a to g) and from yellow eel to silver eel (e to m) according to time for stocked groups C08 (a and h), C09 (c and i), Grau1 (c and j), Vacc1 (d and k), Vacc2 (e and l), and the native group Vig (f and m).

Swimbladder infection

Three parameters were collected after dissection of the swimbladder (Table 2): prevalence (absence/presence data) of worms, number of *A. crassus* in the swimbladder and swimbladder degenerative index (SDI). SDI is based on three criterions (transparency-opacity of the swimbladder wall, presence of pigmentation and exudate in the swimbladder lumen, and thickness of the swimbladder wall), each one coded by 0, 1 or 2 (increasing degradation). As proposed by Lefebvre *et al.* (2002), eels that present SDI ≤ 3 correspond to individuals with low/medium degradation (LMD group), whereas eels with SDI ≥ 4 have serious degradation (SD group) and this low probability to reach the spawning area.

Table 9: Silver eels yielded and quality characteristics (Life history traits, Lipid content, and *A. crassus* infection) of the stocked groups (Vacc1, Vacc2, Grau1, C08, C09) and the native group (Vig).

Group	**umulative r of silver rom 100 erentiated eels**	**Mean Age at silvering (month)**	**Mean Size at silvering (mm)**	**Mean Weight at silvering (g)**	**Lipid content (%)**	**Prevalence (% infected eel)**	**Mean Number of *A. crassus* when infected**	**% SDI≥4**
Vacc1	45	50 [24-72]	706 [601-795]	656 [406-834]	19 [14-26]	70.6	10 [1-96]	20.6
Vacc2	56	50 [35-84]	717 [583-801]	653 [256-871]	19 [10-33]	67.6	16 [1-63]	26.5
Grau1	62	46 [29-72]	681 [576-802]	597 [357-923]	19 [8-28]	80	15 [4-50]	12
C08	10	46 [36-53]	636 [480-818]	515 [279-930]	17 [5-25]	55	11 [1-69]	15.9
C09	13	38 [24-41]	644 [453-755]	496 [196-777]	20 [9-29]	76	19 [1-169]	22.4
Vig	37	93 [36-168]	732 [603-869]	779 [395-1431]	22 [4-37]	61	11 [1-68]	26.5

Pollutants

Due to budget limitations, pollutant analyses were only conducted on 29 female silver eels from the group 'Vig'. This group was selected because silver eels showed greatest variability in terms of lipid concentration, but also in age, size and weight at silvering (Table 2).

PCBs analysis- Eel muscle samples were analyzed by CARSO-LSEHL laboratory (Lyon, France) according to the method US EPA 1668 (US EPA method 1668, 1999). Each muscle sample was mixed and freeze dried and 10g was spiked with isotopically labeled standards (12 PCB Dioxin like standard and 6 indicators PCBs standard marked with ^{13}C). Then extractions were performed with a mixture of toluene/cyclohexane (30/70). The extracts were purified using multilayer silica columns. The identification and quantification of the PCBs were performed using a gas chromatography (Agilent 6890) coupled with a high-resolution mass spectrometry (MicromassUltima Waters). Chromatographic separation was achieved with an HT8 column. Uncertainty of measured concentrations was about 20%. Concentration of 12 PCB "dioxin like" congeners was then estimated to determine the Toxic equivalent-value (TEQ-value; 77, 81, 126, 169, 105, 114, 118, 123, 156, 157, 167, 187) and secondly the concentration of 7 indicators PCBs (28, 52, 101, 118, 153,180) which the sum was used to have a PCB indicator. Results are expressed as pg g^{-1} wet weight for the further analyses.

Cadmium analysis: Liver samples from the same 29 individuals were analyzed by CARSO-LSEHL laboratory (Lyon, France) to quantify Cd concentration (mg kg^{-1}) in accordance with the norms NF EN 13805 and NF EN 15763. Quantitative analyses were performed by inductively coupled plasma (ICP-MS) after pressure digestion.

Life history traits

Previous study suggested that both lipid content and contaminants increase with increasing length or age at silvering (Degani *et al.*, 1986; Ferrante *et al.*, 2010). When objective is to compare quality of silver eels between groups, first step is to test for age and size at silvering differences between groups. Age at silvering (in months) was estimated by otolithometry according to the method of Panfili & Ximenes (1994) for a sub-sample of silver eels in each group (282 eels in total).

Statistical analysis

All the statistical analyses were made with the R-Cran project free software (R Development Core Team, 2013). Generalized linear models were used to assess statistical associations of age and size at silvering with groups (Vac1, Vac2, Grau1, C08, C09 and Vig). A Gaussian distribution and identity link were used, and significance of the group factor was tested using classical GLM deviance tests (ANOVA). Multiple pairwise comparisons were made using the Post-hoc test. To assess differences in quality between groups,for each parameters (lipid content, pollutants content, SDI, prevalence and intensity of parasitism), generalized linear models were used to assess their statistical associations with groups, size and age at silvering, using a Gaussian distribution and identity link (except for the prevalence and SDI where a binomial distribution and probit link were used). As PCBs are known to be fat-soluble pollutants, the statistical association between PCBS and lipid content was also analyzed. ANCOVA were realized to determine if the relationship between parameters and life history traits depends on group.Graphical analysis showed that there was no violation of the modelling assumptions (i.e. residual normality, homoscedasticity).

Results

Capture-Mark-Recapture results

The best model predicted that detection probabilities varied according tostage and time, butnotrend wasobserved. Survival probabilities varied according to stage, group and time with marked fluctuation over the study and increase with age (from E to S; Fig. 2). For a given stage (E, Y or S), the same survival patterns was observed for all groups except for the stage Y where individuals introduced as glass eel (C08 and C09) had a survival lower than the individuals introduced later (Fig. 2). Transitions between stages were influenced by time, group and stage with transition probabilities higher during spring /summer (from May to October) than during autumn/winter (from October to May; Fig.3). Transition probabilities of individuals stocked as glass eels (C08 and C09) were close to 0 during afew months following stocking (Fig.3).

Number of silver eels yielded for each group

Mean cumulative number of silver eels reached a plateau starting between 3.5 and 4 years after introduction for all the groups (Fig. 4). The number of silver eels predicted from 100 undifferentiated eels, at the end of our study period, differed between groups (Fig. 4). As the cumulative number of silvers eels reached a quite low threshold for individuals from C08 and C09 (10 and 13 silver eels, ± 6, respectively), thresholds for other groups were rather high (37, 45, 56 and 62 silver eels, ± 10, for Vig, Vacc1, Vacc2 and Grau1, respectively). For all groups, transition into silver eels seemed close to zero during autumn/winter (from October to April).

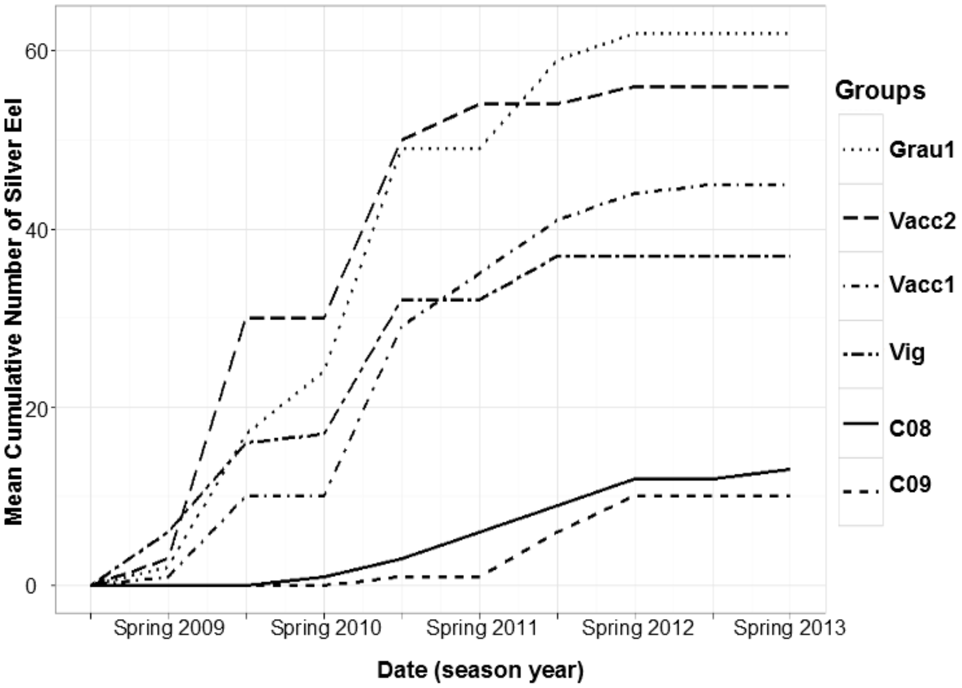

Fig.4 Mean cumulative number of silver eel yielded by stocked groups (Vacc1, Vacc2, Grau1, C08 and C09) and the native group (Vig) according time.

Silver eel quality in relation to age and size at silvering

Age and size at silvering were significantly different between the groups (p<0.05, 58 and 36% of explained variance respectively).Silver eels produced from the native group (Vig) showed significant higher age (Fig. 5a) and size (Fig. 5b) at silvering than all the stocking groups (Table. 2; Tukey test p<0.05). Silver eels belonging to stocked glass eel groups (C08 and C09) have the lowest age and size at silvering with respectively (Table. 2; Tukey test p<0.05) but for size at silvering no significant differences were observed between C08 and C09. However, eels from C09 matured more quickly than those from C08 and Vacc2 (Table. 2; Tukey test: p<0.05). C08 had a smaller age at silveringthan Grau1 (Table. 2; Tukey test p<0.05).

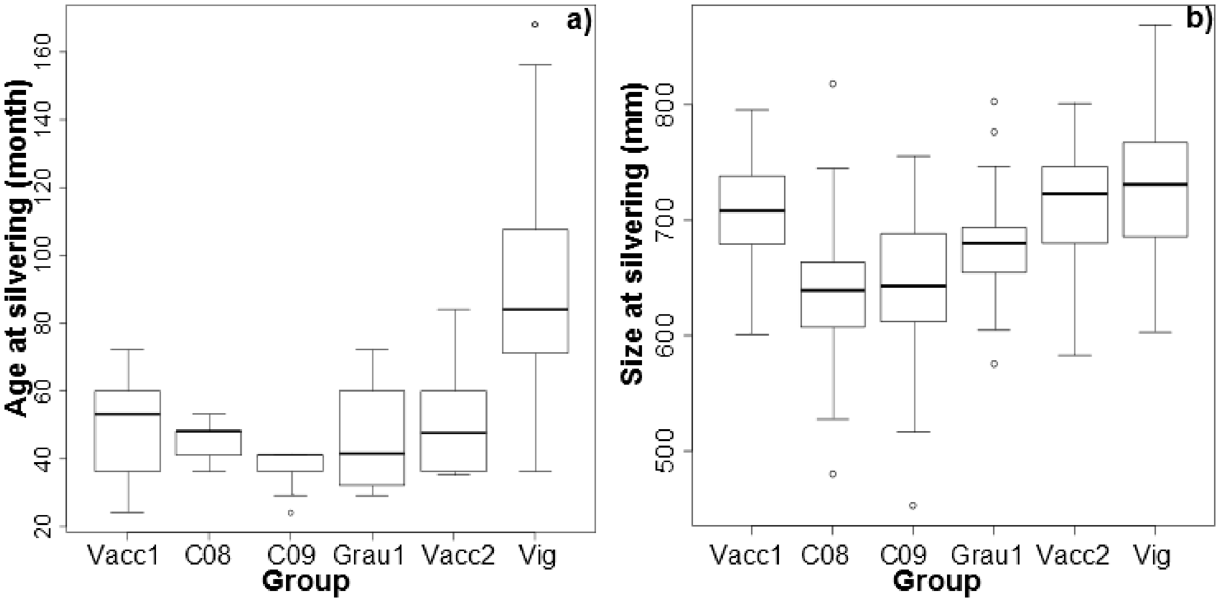

Fig.5. Box plots showing mean and range of a) age at silvering and b) size at silvering (month and mm, respectively) in PisciSud according to groups affiliation (Vacc1, C08, C09, Grau1, Vacc2 and Vig)

Lipid content significantly increased with size but not with age (Fig.6a) but the significant relationship did not differ between the groups (ANCOVA, $p>0.05$). Prevalence and number of worms in swimbladder, as SDI did not vary significantly between groups, size and age at silvering ($p>0.05$).

For the native eels from Vig group, PCBs concentration increased significantly with lipid content (Fig.6b, $p<0.05$) but no significant relationship were found with age and size at silvering. Concerning Cd concentration, no significant effect of size or age at silveringwas detected ($p>0.05$).

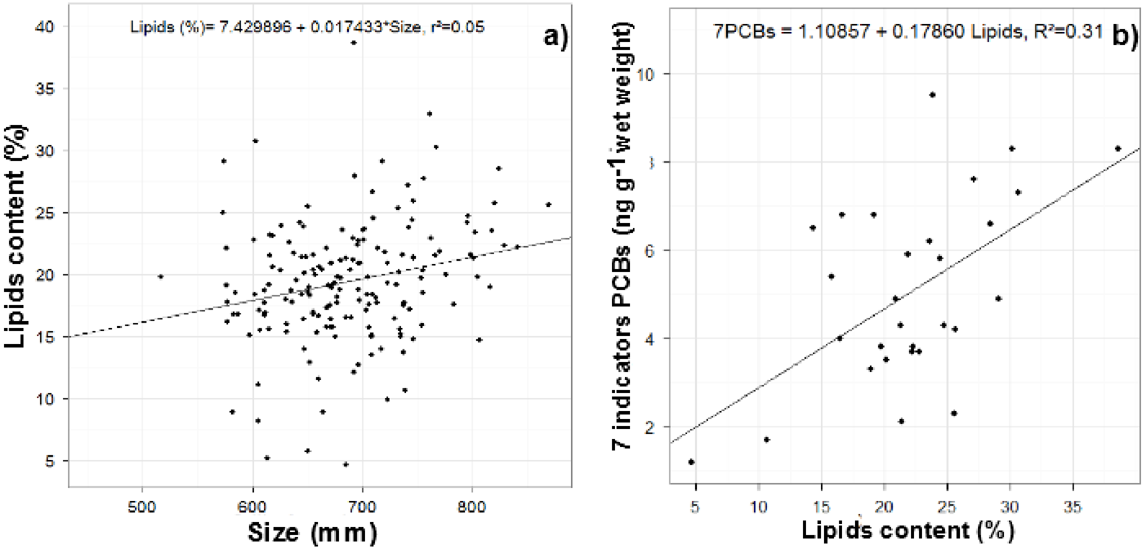

Fig.6. Plots showing a) lipids content (%) relative to size at silvering (mm) and b) 7 indicators PCBS level (ng g^{-1} wet weight) relative to lipids content (%).

Discussion

Silver eel yields vary greatly according to stocking groups

In the present study, a great variation of silver eel yields from 100 recruits was observed according to the eel stocking groups. Three patterns were observed. The highest silver eel yields per 100 recruits were observed for individuals from sexually undifferentiated or yellow eels > 200 mm originated from either freshwater (Grau1: 62 silver eels per 100 recruits) or brackish water (Vacc2: 56). Intermediate silver eel yields were observed for eels from undifferentiated sexually eels from brackish water (Vacc1: 45) and the native eel population (Vig: 37). Lowest silver eel yields were observed for individuals originated from the freshwater canal of the Grau de la Fourcade and introduced as glass eel (C09: 13; C08: 10).

Such a contrasted pattern must be linked to the differential survival experienced by the individuals during their growth phase and to their capacity to grow from a stage to another. Indeed, survival probability is lower for the *E* stage (sexually undifferentiated eels: 0.74 ±0.24) than for the *Y* stage (yellow eels: 0.83 ±0.34). Consequently the less eels stay in the *E* stage, the more the silver eel production will be important. For instance, Vacc2 and Grau1 groups produced the highest number of silver eel as transition probabilities from *E* to *Y* were high (between spring and fall 2009, 83% and 89% of individuals shifted from E to Y stages for Grau1 and Vacc2 respectively). Thus, eels from these two groups spent a small amount of time in the more sensible *E* stage, increasing the probability to survive and reach *S* (silver eel stage). By contrast, the probability to stay in *E* stage could be twice higher for individuals from C08 and C09 than for the other groups (mean transition probability to stay at stage undifferentiated eels: 0.70 and 0.76 for C08 and C09 respectively and between 0.37 and 0.55 for the other stocked groups). So individuals from C08 and C09 experienced a far longer period of high mortality rates at the E stage compared to others eel stocking groups.

Stocking bigger eels is better ?

The differences of survival and transition probabilities observed between the groups led to disparate silver eel yields. The understanding of these differences, which could be explained by several phenomena, could help to improve future stocking.

At first sight, our results suggested that stocking is more efficient, in terms of number of silver eels yielded, when eels are stocked at a size superior to 200 mm (Grau1, Vacc2, Vacc1). Indeed, as shown previously, the smaller eel is the smaller survival will be, implying that for individuals from the same source (FW or BW) the number of silver eels produced increased with the size of introduction (Vacc2>Vacc1 and Grau1>C08 or C09; Fig. 4). However, the results highlighted that other important factors need to be taken into account to increase the efficiency of stocking.

Both the size at introduction and the change of environment between the site where eels were caught and the site where eels were stocked may also impact the stocking efficiency. For example, individuals from Grau1 and Vacc1 were both stocked at a size between 200 and 299 mm but the number of silver eels yielded from 100 undifferentiated eels from Grau1 was higher than the onefromVacc1 (62 and 45 silver eels respectively). This difference could be explained by their origin (FW and BW, respectively) as individuals from Grau1 did not undergo an important change of environment during stocking (from a freshwater canal to a freshwater basin) unlike individuals from Vacc1 caught in brackish water and replaced in freshwater pond. This could induce a physiological cost to adjust to the change of salinity and of diet that undifferentiated eels caught in freshwater in Grau1 do not undergo. The change of environment, for stage older than glass eel, could then lead to slower growth and higher mortality implying a low number of silver eels produced compared to the group Grau1. The lowest transition probabilities from a stage to another and the highest mortality at the undifferentiated stage observed for Vacc1 compared to Grau1 seem to confirm this hypothesis (Fig. 2 & 3).

Density dependent processes on growth and survival probabilities could also explain the differences of silver eels yield between groups and especially the relatively low number of silver eels produced by the glass eel groups (13 and 10 silver eels for C08 and C09 respectively). Indeed, previous studies have shown that stocked glass eel undergo high mortality throughout few months following stocking especially when stocked in large number (Bisgaard & Pedersen, 1991; Pedersen, 2009). Musseau *et al.* (in press) demonstrated that the carrying capacity of Piscisud, reached in October 2009, is around 4152 eels which mean 346 eels ha^{-1}, and yet every year we added around 9000 glass eels, more than twice the carrying capacity of the pond. The important number of glass eels stocked every year (considering the carrying capacity of the pond) could then lead to density dependent processes (intra-group competition) on growth and mortality on this specific stage due to limited food, limited space and/or cannibalism. Inter-groups competition at older stages could also explain this low production of silver eels. In this system, an important part of individuals are identified as yellow eels at sizes between 300 and 400 mm. However a shift in behavior and habitat preferences occurs around a size of 300 mm for European eels (Baisez *et al.*, 2001; Laffaille *et al.*, 2004), eels became more sedentary, territorial and live in deeper habitat where they feed and rest (Glova, 1988; Chisnall and Hicks, 1993; Baisez *et al.*, 2001; Laffaille *et al.*, 2004). Most individuals from groups Grau1, Vacc2 and Vacc1 rapidly became yellow eels between, 6 months and 1 year after stocking, whereas individuals from C08 and C09 became yellow eels mostly one year and two years, respectively, after the other groups. Yellow eels from Grau1, Vacc1 and Vacc2 were then the first to colonize suitable habitats and settle, reducing the number of available habitat for the latest individuals from C08 and C09. This situation could lead to an intra and inter-group competition for resources more and more limited increasing mortality and decreasing growth for the groups C08 and C09 due to a lack of feeding and resting sites which is consistent with Feunteun et *al*'s (2003) hypothesis. This hypothesis seems to be confirmed by the significant decline of the main food item, the crayfish, that occurred in the pond since October 2011 implying a lack of food especially for the latest stocked individuals (that grow slowly) but also by high mortality and slow growth observed at the stage yellow eel for individuals from C08 and C09 (Fig. 2 and 3). Simon & Dorner (2014) observed this phenomenon in the lake Godnasse (Germany) with an advantage in growth and survival of the farmed eels compared to the glass eel due to the fact that farmed eels were stocked one year prior to the glass eel.

Another hypothesis may explain the relatively low production of silver eels by the glass eel groups (C08 and C09). Indeed, the majority of eels from the glass eel groups may not have yet reached the maturity suggesting that only individuals with early maturation were detected during the study period. This hypothesis will be verified during the next samplings.

An equivalent quality of silver eels despite a variability of life history traits

We found that age and size at silvering were significantly different between groups ($p < 0.05$). Native eels (Vig group) were the largest and the oldest but we also observed an important variability of their life history traits. Among the stocking eel groups, silver eels from C08 and C09 were generally younger (on average 46 and 38 month) and smaller (636 and 646 mm, respectively) than those from Grau1 (on average 46 months and 681 mm), Vacc1 (on average 50 months and 706 mm) and Vacc2 (on average 50 months and 717 mm). Size and age at silvering are known to vary greatly between catchments from south to north of Europe (Vollestad, 1992) as the result of the latitudinal gradients of temperature and environmental correlates (e.g., photoperiod, hydrology, productivity). This study brought evidences that both size and age at silvering may vary greatly within the same growing sites for different eel groups.

The high variability of the life history traits observed in the group Vig could be explained by the fact that eels from Vig are from the individuals trapped in the pond (more precisely in the deep ditch) when it was emptied in summer 2007 which mean they were in the pond before any other stocked eels and that they could belong to different age cohorts. The small size and the young age at silvering of individuals from C08 and C09 could be explained by two hypotheses. Firstly, as explained before the majority of eels from the glass eel groups may have not yet reached the maturity suggesting that only individuals with early maturation were detected during the study period. Secondly, as showed before the intra-specific competition seems unfavorable for individuals stocked as glass eel. This competition could lead to an earlier maturation. Indeed, for a plastic species as European eel, the choice of an early maturation needs to be seen in relation to the balance of the advantages obtained from early maturation and the costs incurred by individuals. As individuals with early maturation (as eels from C08 and C09) spend less time as juvenile, they have higher probability of surviving to maturity (Bell, 1980; Stearns, 1992). The cost for this early maturation is, in our case, a size at silveringsmaller which mean a lower fecundity (Wenner & Musick, 1974; Vøllestad & Jonsson, 1986) but also a lower chance of a successful migration because body size is related to swimming performance (Brett, 1965; Brett & Glass, 1973; Videler & Nolet, 1990; Palstra, 2006).

However, despite this life history traits variability between groups, we found that silvers eel produced have equivalent reproductive success if we referred to the quality parameters tested.

Firstly, lipids content increased with the size at silveringsuggesting that individuals from Vig will have a higher spawning success than eels from other groups, especially from C08 and C09. Indeed, using this relationship, an increase of less than 2% was predicted in averagebetween the smallest and the biggest group. However, size at silvering explain only 5 % of the lipids content variability and few individuals with a size inferior to 600 mm were analyzed suggesting that more precise analyses have to be done to ascertain this relationship. In any event, as showed by Van den Thillart *et al.* (2004), a minimum of 13% of lipid reserve is required for migration and in our study between 0 and 8 % (depending of the group) have a lipids content lower than this level but proportion of such 'lean' silver eels were not statistically different ($P > 0.05$) between stocking groups. So, except if the lipids content/Size at silvering relationship is ascertain, lipids content was not a factor of discrimination concerning reproductive success between groups.

Secondly, prevalence and number of A. crassus in the swimbladder, as health state of the swimbladder (SDI) were not significantly different between groups. This result suggests that Anguillicolosis affect eels, whatever their origin and life history traits, in the same way.

Pollutant analysis realized on native eel group (Vig) first showed that Cd concentrations in the liver were independent of the size (range: 603-869 mm) and age at silvering (range: 48-161 months). Furthermore, Cd concentrations were lower than those reported in wild populations from the Camargue Reserve (Ribeiro *et al.*, 2005) and below to 0.3 µg g^{-1}ww which is the maximum allowable concentration under E.C. Directives (Mason and Barak, 1990). PCB levels significantly increased with lipid content (Figure 6) which is in line with study that previously showed that PCBs are fat soluble pollutants. As no difference in lipid content is observed between stocking groups, it can be assumed that PCB levels are equivalent between eel groups. Furthermore, the PCBs' contents observed in the Vigueirat (mean 5.06 ng g^{-1}, min 1.2 ng g^{-1} and max 9.5 ng g^{-1}) are among the lowest compared to those found in eels in other Mediterranean regions, where concentrations were 10–100 times higher (Bordajandi *et al.*, 2003; Oliveira Ribeiro *et al.*, 2008; Ferrante *et al.*, 2010; Bettinetti *et al.*, 2011) but also compared with other European countries (7 PCBs indicator; Belpaire *et al.*, 2011b). This suggests that silver eels of Vigueirat, even the Vig group, are less impacted by PCBs content compared to other systems. Finally, in our study, the reproductive success related to pollutant contents was equivalent between groups.

These results suggest that the quality of silver eels is independent of the origin, stage or length at the introduction, and that finally only the characteristics of the site where eels where introduced play a role.

Conclusion and recommendations

To conclude, we found that Grau1, Vacc2 and Vacc1 eel groups produce more silver eels than native Vig groups with equivalent quality. This suggests as proposed by Frotté *et al.* (2012) that stocking eels > 200 mm is an efficient measure to sustain European eel population. The apparent failure of the stocking for the glass eels group (C08 and C09) provides clues for future stockings. Further studies are needed to elucidate the reason of this failure, but the firsts elements provided here suggests some habitat limitations which were critical for this risky life-stage. A precaution principle will be to limit successive batch of stocked eels in the same site in order to limit intraspecific competition and increase high levels of survivals. Finally, we demonstrate that the characteristics of the system where the eels will be stocked are particularly critical for the stocking success as it will govern both the quality and quantity of silver eel produced. We thus recommend to conduct stocking operation in highly suitable habitats to promote efficient stocking operation.

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III. Article 6 : Length-Weight relationships of the silver European eel (*Anguilla anguilla*, Linnaeus 1758) across its geographic range

C. Boulenger [1,*], A. Acou[1], T. Trancart[1], A.J Crivelli[2] and E. Feunteun[1]

[1] Muséum National d'Histoire Naturelle, UMR BOREA, Station Marine de Dinard, CRESCO, 38 rue du port blanc, 35800 Dinard, France ; [2] Station Biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France.

Summary

Length-Weight relationships for European silver eels sub-populations (*Anguilla anguilla*) in 6 countries (13 catchments) along the latitudinal gradient of the distribution area are provided in this study using three important programs of sampling in Europe. The results observed were coherent with previous studies on European eel with an equation: W=0.0010 $L^{3.148}$ for the whole data set (sex combined). Significant differences were observed between the 13 catchments that could imply differences in body conditions. Male and female LWRs vary significantly between catchments suggesting that the capacity of silver eels to migrate and reproduce successfully vary according to European growing sites.

* Correspondence : clarisse.boulenger@edu.mnhn.fr

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Introduction

The European eel (*Anguilla anguilla*, L.) is a catadromous fish species with a complex life history that includes two migrations across the Atlantic Ocean to and from the presumed Sargasso Sea spawning grounds (Tesch, 2003; Aarestrup *et al.*, 2009). During their continental phase eels, at the yellow eel stage, will grow and store lipids to provide sufficient energy to support the journey across the Atlantic Ocean and to produce fully develop gonads and gametes. When the critical fat reserve to migrate to the spawning area is reached, yellow eels metamorphose into silver eel which is a physiological and morphological adaptation to the last trans-Atlantic journey (Fontaine, 1994). Silver eel then migrate downstream towards marine waters and eventually return to the spawning grounds to reproduce and presumably die. In the last 30 years, recruitment has decreased by about 95%, and current population levels are outside safe biological limits in many parts of the distribution range that includes all accessible European hydrosystems (Dekker, 2003; ICES, 2010). The reasons for this decline are poorly understood as the species range is so vast, the life cycle complex and is subjected to such a range of pressures in both marine and continental habitats.

In this context, ICES recommended that all means should be taken to restore the depleted stocks (ICES, 2012). Length-Weight relationships (LWRs) have many applications in fisheries assessment as the latter could be used to estimate the body condition, biomass from length observations or growth (Le Cren, 1951, Froese, 2006). However, LWR remains poorly documented at the scale of the distribution range of the European eel. Up to now, only 14 LWR studies were listed in FishBase (www.fishbase.org accessed on 21/03/2014). They refer to different life stages and correspond to different study period and half were made in France for this species with a large distribution area. Few are dedicated to silver eels which represent a serious lack for management decisions. Indeed, silver eel LWRs could provide important insights on reproductive success which mean on their capacity to migrate to the spawning area, to maturate their gonad and mate (Boëtius & Boëtius 1980). Smaller size at maturity lead to a lower fecundity (Wenner & Musick, 1974; Vøllestad & Jonsson,1986) but also to a lower chance of a successful migration because body size is related to swimming performance (Brett, 1965; Brett & Glass, 1973; Videler & Nolet, 1990; Palstra, 2006). Results about silver eels LWRs would be thus of great interest for member states that have to implement Eel Management Plan (Regulation No. 1100/2007, European Commission) with the objective to increase both quantity and quality of silver eels in their river systems.Furthermore, Robinet and Feunteun (2002) hypothesized that the probability that silver eels reach the spawning grounds and reproduce successfully varies among continental growing sites. So, for this species with a large distribution area, the comparison of silver eel LWRs between catchments could help to verify this hypothesis and provide adapted decisions support tools.

The aims of this study is to provide LWRs for silver eels and to compare the results obtain by sex and catchment using an important data set, 766 individuals in 13 catchments distributed from the south (Spain) to the north (Denmark) of the distribution area.

Materials and methods

To estimate LWR parameters, data from 13 European eel stocks were used. Eleven datasets were collected as part of the EELIAD program that aims to assess quality of silver eels that escape from European freshwater systems (Table 1). This program enables to intercept a total of 522 silver eels at the beginning of their seaward migration in early winter 2008, 2009 and 2010 in European catchments belonging to 6 countries across Europe (Spain, France, United Kingdom, Belgium, Ireland, and Denmark). To ensure a wider coverage of the distribution range of the species, we completed the data with older datasets of the Loire and the Fremur River. Moreover, two others datasets in France were added: the first (49 individuals including

38 females and 11 males) was collected in the Oir River (NW France) between 2001 and 2013; the second (26 females) was collected between 2002 and 2004 in a small drainage basin of the Camargue (southern France). All individuals were captured during the migration period and their status of migrant was determined thanks to the EELREP stages (EELREP, 2005). Only individuals with the migrant EELREP stages FIV, FV and MII were keep in the data set. Then, a total of 766 migrating silver eels were available for the present study (Table 1).

Each fish collected was anaesthetised with clove oil (Walsh & Pease, 2002), measured (TL to the nearest millimeter) and weighted (TW to the nearest gram). The silver eel stage was determined according to three criteria: colour of the back and belly, presence of a well-defined lateral line and eye diameter (Acou *et al.*, 2005, 2006). Individuals were then dissected in order to assign sex by macroscopic observation of gonads, using the criteria described by Colombo *et al.* (1984). Silver eels identified as male by this method ranged from 288 and 512 mm (N = 210, mean TL = 370 ± 38 mm), and silver eels identified as female ranged from 406 mm to 1005 mm (N = 557, mean TL = 665 ± 120 mm). Around 98% of silver eels greater than 440 mm were females, as has been shown in other studies (Rossi and Colombo, 1979; Tesch, 2003).

The Length-Weight relationships was calculated using the equation $TW = a \times TL^b$ and logarithmically transformed into: $\log_{10}(TW) = \log_{10}(a) + b \times \log_{10}(TL)$, where TW and TL are respectively the total weight in gram and the total length in centimeters, a is a coefficient relative to body form and b is an exponent indicating isometric growth when equal to 3.0 (Froese, 2006). Fit of the model to the data were measured by the coefficient of Pearson r-squared, r^2. Length-Weight relationships were calculated for the whole data set independently of the origin and the sex of individuals, for the whole data set by sex independently of the origin and for each catchment by sex or not. The relationship was only calculated if the number of individuals was superior to 10. Effect of origin on the log-transformed relationships, for female and male data sets (separately), was analysed using a covariance analysis (ANCOVA) as proposed by Cornillon *et al.* (2008). Statistical analyses were performed using R software (http://www.r-project.org/). The modelling assumptions (i.e. residual normality, homoscedasticity) were graphically tested for each model and any major violation was observed for any of them.

Results and discussions

LWRs are given in Table 2 for female, male and sex combined (respectively F, M, and C). The results are similar to those found in Fishbase (mean a = 0.0008, mean b = 3.22 for the 14 selected studies) with a b equal to 3.148 and an a equal to 0.0010 for the whole data set. Among the catchments, for the sex combined data set, b ranged between 2.446 and 3.326 and a between 0.005 and 0.0242. For the male data set, b ranged between 2.348 and 3.405 and a between 0.0004 and 0.0175. For the female data set, b ranged between 2.507 and 3.670 and a between 0.0001 and 0.0123. When LWRS using separately male and female data sets for each catchment were compared, slopes and intercepts were significantly different between the catchment demonstrating that difference in body condition could be observed for the both sex. Numerous local factors could impact the LWRs and explain these differences such as, waterbody type, water quality (Organic pollutants, heavy metals, eutrophication; Robinet & Feunteun, 2002; Acou *et al.*, 2008) or density of conspecifics which could imply strong competition for resources. These results highlighted that further studies have to be conducted to understand more precisely inter-catchment variability of silver eel LWRs, which mean silver eel quality, and to develop adapted management rules for each catchment.

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Table 1. Characteristics of the fourteen European catchments sampled and associated numbers of male and female silver eels per sites.

Sampling site	Latitude (N)	Waterbody type	Distance to the sea (km)	Sampling date	Number of males	Number of females	Total number of silver eels
Gudenna (Denmark)	55°58'01.31"	River	100	Nov-2009	**1**	**39**	**40**
Burrishoole (Ireland)	53°55'13.51"	Coastal river & lakes system	5	Nov-2008	**2**	**48**	**50**
Corrib (Ireland)	53°16'32.05"	Coastal river & lakes system	1	Nov-2009	**12**	**38**	**50**
Warwickshire Avon (United Kingdom)	52°10'00.46"	River	75	Nov-2009	**0**	**41**	**41**
Scheldt (Belgium)	51°03'58.53"	Canal & ponds	75	Oct-2009	**3**	**42**	**45**
Stour (United Kingdom)	50°44'41.56"	River	2	Nov-2009	**4**	**34**	**38**
Oir (France)	48°37’39.10’’	River	10	2001-2013	11	38	49
Fremur (France)	48°34'39.80"	Coastal river	4	Jan-2010 1999-2000	**12** 33	**37** 17	**49** 50
Loire (France)	47°22'59.80"	River	150	Dec-2009 Dec-2003 & Dec-2014	**13** 11	**39** 116	**52** 127
Esva (France)	43°34'09.00"	River	2	Oct-2009	**49**	**1**	**50**
Bages-Sigean (France)	43°03'39.61"	Lagoon	5	Nov-2009	**39**	**11**	**50**
Fumemorte canal (France)	43°31'36"	Canal	20	2002-2004	0	26	26
La Albufera de Valencia (Spain)	39°20'59.58"	Lake	0	Nov-2010	**20**	**31**	**51**

[1] numbers in bold refer to silver eels caught for the EELIAD program.

Table. 2. Descriptive statistics and LWRs estimated parameters for the fourteen catchments: male (M), female (F) and combined sexes (C); Sample size (n); Confidence limits (95% CL), Coefficient of determination (r^2).

Catchment	Sex	n	Length range (mm)	Weight range (g)	b	95 %CL of b	a	95% CL of a	r^2
All	C	767	288-1005	39.5-2420	3.148	3.130-3.190	0.0010	0.0009-0.0010	0.98
	M	210	288-512	39.5-232.7	3.015	2.871-3.159	0.0016	0.0009-0.0026	0.89
	F	557	406-1005	112.8-2420	3.108	3.076-3.140	0.0012	0.0010-0.0013	0.94
La Albufera de Valencia (Spain)	C	51	351-852	112.8-1661	3.316	3.201-3.431	0.0005	0.0003-0.0008	0.98
	M	20	351-437	75.7-142	2.980	2.530-3.430	0.0018	0.0003-0.0094	0.90
	F	31	577-852	288.3-1661	3.670	3.126-4.214	0.0001	0.00009-0.0001	0.86
Bages-Sigean (France)	C	50	354-875	77.5-1573	3.164	3.056-3.272	0.0009	0.0006-0.0014	0.99
	M	39	354-442	77.5-148.4	2.942	2.371-3.513	0.0020	0.0003-0.0165	0.73
	F	11	470-875	164.8-1573	3.424	2.976-3.872	0.0003	0.00004-0.0027	0.96
Fumemorte (France)	F	26	492-810	198-1250	3.289	2.912-3.666	0.0006	0.0001-0.0027	0.93
Esva (Spain)	C	50	288-610	39.5-344.4	3.002	2.928-3.176	0.0016	0.0009-0.0030	0.96
	M	49	288-512	39.5-232.7	3.071	2.854-3.288	0.0013	0.0006-0.0027	0.94
Loire (France)	C	179	334-1005	48.6-2420	3.326	3.255-3.397	0.0005	0.0003-0.0006	0.98
	M	24	334-458	48.6-149	3.405	2.704-4.106	0.0004	0.00003-0.0046	0.80
	F	155	495-1005	195-2420	3.325	3.190-3.461	0.0005	0.0002-0.0008	0.94
Frémur (France)	C	99	300-796	47-929.2	3.053	2.977-3.129	0.0014	0.0010-0.0019	0.98
	M	45	300-434	47-149	3.075	2.690-3.460	0.0013	0.0003-0.0051	0.85
	F	54	414-796	117-929.2	2.939	2.800-3.078	0.0022	0.0013-0.0039	0.97
Oir (France)	C	49	334-769	44-905	2.981	2.781-3.181	0.0020	0.0009-0.0045	0.95
	M	11	334-437	44-154	2.565	1.901-3.228	0.0090	0.0008-0.0998	0.86
	F	38	429-769	112.8-905	2.824	2.434-3.214	0.0039	0.0008-0.0183	0.85
Stour (United Kingdom)	C	38	333-710	59-770.2	3.203	3.023-3.383	0.0008	0.0004-0.0016	0.97
	F	34	481-710	146-770.2	3.179	2.875-3.483	0.0008	0.0002-0.0029	0.93
Scheldt (Belgium)	C	45	354-837	62-1008.3	2.258	1.983-2.533	0.0065	0.0020-0.0205	0.89
	F	42	496-837	198.7-1008	2.507	2.073-2.941	0.0123	0.0020-0.0775	0.76
Warwickshire Avon (United Kingdom)	F	41	538-833	276.6-1204	2.948	2.613-3.283	0.0023	0.0006-0.0094	0.88
Corrib (Ireland)	C	50	336-970	60-1627	3.087	2.993-3.181	0.0012	0.0008-0.0018	0.99
	M	12	336-410	60-99	2.348	1.593-3.102	0.0175	0.0012-0.2671	0.79
	F	38	406-970	132-1627	3.114	2.914-3.314	0.0011	0.0004-0.0025	0.96
Burrishoole (Ireland)	C	50	318-635	60-405	2.863	2.633-3.093	0.0031	0.0012-0.0076	0.93
	F	48	443-635	160-405	2.532	2.187-2.877	0.0101	0.0026-0.0396	0.82
Gudenna (Denmark)	C	40	387-787	110-973	2.922	2.724-3.120	0.0025	0.0.001-0.0058	0.96
	F	39	486-787	207-973	2.917	2.674-3.160	0.0026	0.0009-0072	0.94

Discussion générale-Limites-Perspectives

I. Discussion et conclusions

A l'échelle de son aire de répartition, le stock d'anguilles européennes est dispersé en une multitude de sous-populations indépendantes qui réalisent leur croissance au sein d'hydrosystèmes aux caractéristiques très différentes (fleuves côtiers, rivières, lacs, lagunes, marais, etc). Cette variété d'habitats de croissance semble induire une large variabilité des traits d'histoire de vie au sein de l'espèce liée à la grande plasticité phénotypique de l'anguille (Stearns, 1992 ; Matthews, 1998). Vollestad (1992), en analysant 38 sous-populations d'anguilles européennes échantillonnées à travers l'Europe et l'Afrique du Nord, a montré que les âges moyens de la métamorphose en anguilles argentées étaient fortement influencés par les variations du taux de croissance qui varient eux-mêmes en fonction de gradients thermiques et de photopériodes qui s'expriment aux échelles latitudinale et longitudinale. Cette variation géographique de l'âge à maturité a également été démontrée chez d'autres espèces diadromes que sont l'anguille américaine *A. rostrata* (Helfman *et al.*, 1987) et les Salmonidés (*Salmo trutta* ;Baglinière *et al.*, 2001).

Cependant, à l'échelle locale, l'influence des caractéristiques des hydrosystèmes (structure, niveaux trophiques ou caractéristiques physico-chimiques) sur l'ensemble des paramètres de la dynamique de population et variabilité des traits d'histoire de vie est rarement abordée. **L'étude de la croissance et de la survie des populations d'anguilles réalisée dans cette thèse a permi de mieux comprendre le rôle de l'hydrosystème sur (i) la dynamique des sous-populations d'anguilles et (ii) la variabilité des traits d'histoire de vie. Ces résultats fondamentaux trouvent également des prolongements intéressants en matière de conservation comme pour les mesures de repeuplement.**

1. *L'absence de relation recrutement-stock dans un système à saturation*

Les analyses menées sur le Frémur semblent montrer qu'il n'existe pas de lien quantitatif entre le nombre de recrues colonisant le système l'année *t* et les densités observées dans les habitats lotiques du système à *t+n* (n variant de 0 à 15). Deux hypothèses complémentaires liées aux caractéristiques du système peuvent expliquer cette absence de lien.

Premièrement la configuration du système et notamment la présence de la retenue d'eau du Bois Joli peut impacter la colonisation des recrues. En effet pour atteindre les zones lotiques du Frémur les recrues doivent traverser une importante retenue d'eau (3.10^6 m^3). Si **des habitats sont disponibles dans cette importante zone lentique, une grande partie des individus peut alors s'y sédentariser et y grandir.** En effet, Feunteun *et al.* (2003) considèrent qu'une partie des recrues adopte un comportement de « founders » c'est à dire qu'elles arrêtent leur migration dès qu'elles rencontrent un habitat favorable. Si la majorité du recrutement à un comportement migratoire de « founders » alors la majorité des recrues peut s'installer dans la réserve du Bois Joli et ainsi peu influencer les densités dans les habitats lotiques en amont.

La deuxième hypothèse est que de **forts processus de régulation peuvent s'appliquer sur les recrues et/ou sur les individus déjà installés**. En effet malgré l'arrivée massive de recrues certaines années (particulièrement en 1998) et la disparition des anguilles argentées par émigration, les densités dans les zones lotiques restent stables entre 1996 et 2007 suggérant une régulation de la population notamment par des processus de mortalité densité-dépendance. Cette hypothèse semble cohérente avec le fait que les habitats lotiques du Frémur sont supposés à saturation (Acou *et al.*, 2011) ce qui peut induire de forts processus de régulation lorsque la population augmente notamment en réduisant la survie des juvéniles et des adultes (Gaillard *et al.* 1998, Eberhardt 2002).

Conclusion : Ces résultats montrent qu'une augmentation du recrutement (naturelle ou par repeuplement) n'implique pas systématiquement une augmentation de la densité au sein du système et donc du nombre de reproducteurs potentiels. Dans une précédente étude menée sur la Vilaine, il a été montré qu'après la construction de passes à poissons permettant l'arrivée d'un plus grand nombre de recrues dans le système (jusqu'à 2.4 millions de civelles par an), une augmentation d'un facteur 6 des densités et un bouleversement de la structure de population avec les densités d'anguilles d'âge 0 et 1 multipliées par 29 étaient observés (Briand *et al.*, 2005). Dans notre petit système côtier, où les relations recrutement/stock devraient être plus faciles à mettre en évidence que dans des systèmes comme la Vilaine (forte dilution du recrutement), l'absence d'influence du recrutement sur la densité au sein du système semble mettre en évidence de fort processus de régulation de la population. Cette différence entre les deux systèmes pourrait être liée à la capacité d'accueil de chacun des systèmes. En effet contrairement à la Vilaine, l'ensemble des habitats lotiques du Frémur est supposé à saturation entrainant des processus de régulations densité-dépendants (comme la mortalité) lorsque la population augmente. Dans la Vilaine, au contraire, ces processus devraient être faibles voire inexistants. Cependant, pour étudier le réel impact de la capacité d'accueil sur les processus de régulation et savoir sur quel paramètre démographique et quand ils s'appliquent, il faut pouvoir comparer des systèmes de taille équivalente et à même latitude. Les analyses réalisées dans la deuxième partie de la thèse devraient pouvoir permettre cette comparaison.

2. *Les impacts des caractéristiques d'un système de croissance sur la dynamique de population et les traits d'histoire de vie.*

Des patrons survie/croissance très contrastés

Les patrons de croissance et de survie de deux sous-populations d'anguilles ont été étudiés dans deux systèmes proches géographiquement et de taille équivalente. Pour autant, les pressions appliquées sur chacune de ces populations sont très différentes. Les habitats étudiés dans le Frémur sont supposés saturés au moins jusqu'en 2007 (Acou *et al.*, 2011), les densités sont élevées et stables malgré un recrutement très variable et parfois très important, de plus le cours d'eau est fragmenté à cause de nombreux ouvrages. Au contraire l'Oir est un système supposé insaturé avec des faibles densités d'anguilles (environ 10 fois moins fortes que celles observées dans le Frémur) et sans obstacle majeur. Ces pressions différentielles qui s'exercent sur les populations semblent être responsables de la grande variabilité observée des dynamiques des deux sous-populations. En effet les croissances observées dans le Frémur sont équivalentes entre les plus petites et les plus grandes anguilles étudiées et elles sont indépendantes de la productivité du milieu (température et habitat). Au contraire les survies varient dans le temps et dans l'espace suggérant que des variations au sein du système ont provoquées des mortalités. Dans l'Oir, les individus de petites tailles grandissent plus vites que les individus de grandes tailles. De plus, la croissance varie en fonction de la productivité du milieu (type d'habitat, température). La survie, elle, est stable dans le temps et l'espace mais les anguilles les plus petites ont une survie plus faible (0.60) que les anguilles plus grandes (~0.80).

Des stratégies d'histoire de vie liées aux pressions du milieu ?

Ces patrons contrastés semblent être contraints par les différences de niveau de pressions appliqués sur ces deux populations, fort sur le Frémur (barrage, fort recrutement, saturation) et faible sur l'Oir (faible recrutement, faible compétition) et suggèrent le développement de différentes stratégies de vie. En effet, bien qu'une détermination génétique de l'orientation sexuelle des anguilles n'ait jamais été réellement écartée, il y a aujourd'hui de nombreuses preuves pour une détermination environnementale de l'orientation sexuelle. Cette différenciation sexuelle s'effectue au-delà de 20 cm (Colombo et Grandi, 1996 ; Melià *et al.*, 2006), mais la détermination, elle, semble s'effectuer au stade civelle. Depuis plusieurs années, la majorité des observations réalisées suggèrent que la densité est le facteur principal responsable de la différentiation sexuelle, avec lorsque le système est saturé une orientation vers le sexe mâle (Tesch, 2003). Ainsi dans le Fleuve Esva (Espagne) où les densités sont très fortes (3-5 anguilles par m^{-2} dans l'estuaire et 1.2 anguille par m^{-2} à l'amont), 99% des anguilles sexuellement différenciées sont des mâles (Lobón-Cerviá *et al.*, 1995). Les mâles prédominent aussi en aquaculture où les densités sont très fortes (Egusa 1979). Différentes stratégies semblent donc se développer en fonction des pressions de densité appliquées sur les individus. Helfman *et al.* (1987) suggèrent ainsi que les mâles suivent une stratégie « time-minimizing » qui leur permet de réduire le temps de croissance en migrant à la taille minimum pour survivre à la migration de reproduction. Les femelles, elles, au contraire suivent une stratégie « size-maximizing » qui leur permet d'avoir une fécondité élevée (corrélée à la taille ; Barbin & McCleave, 1997) mais la durée plus importante de la phase de croissance augmente aussi les risques de mortalité au stade jaune. Cependant, les processus derrière ces stratégies sont peu connus. Le travail d'Oliveira et McCleave (2002) sur la différenciation sexuelle de l'anguille américaine a mis en évidence que les anguilles femelles grandissaient plus vite que les mâles et qu'un « trade off » (mortalité) devait y être associé. Nos résultats suggèrent que **la différentiation sexuelle se fera à travers le « trade off » mortalité/croissance**. En effet, au cours de sa vie un individu doit nécessairement faire des choix, prendre des décisions, par exemple décider de se reproduire jeune ou plus âgés. Ces choix ont des effets positifs sur certains traits et négatifs sur d'autres. Le but étant de toujours transmettre le maximum ses gènes au cours de sa vie (optimiser sa fitness) (Stearns 1992). Quand les conditions de vie sont difficiles (forte compétition par exemple dans le cas du Frémur), les individus optimisent leur survie (en moyenne la probabilité de survie des individus de moins de 300 mm est de 0.77) au détriment d'une forte croissance (croissance annuelle de 20 mm en moyenne entre 1996 et 2003 pour les individus de moins de 300 mm). L'investissement (couteux) dans la reproduction est minimal, et c'est le sexe mâle qui est privilégié (les mâles représentent 90% des anguilles argentées produites dans les zones lotiques du Frémur). Dans un milieu moins dense en congénères, les jeunes individus grandissent plus vite (croissance annuelle de 26 mm en moyenne entre 2009 et 2012 pour les individus < 300 mm) et l'orientation femelle devient alors possible. Mais cela a un coût : une plus forte mortalité des individus (mortalité estimée : 0.40). Les raisons de cette mortalité ne sont pas connues mais il est probable qu'il soit risqué d'accéder à plus de nourriture pour une jeune anguille. Cette stratégie plus risquée pour les jeunes stades permet d'accroitre la fitness en promouvant une période de croissance plus longue ce qui aboutit à une plus grande taille à maturité c'est-à-dire une plus grande fécondité et une meilleure efficacité de nage. A notre connaissance c'est la première fois que ce « trade off » mortalité /croissance est observé chez l'anguille européenne.

L'absence de mortalités densité-dépendantes dans des habitats supposés saturés ?

Un des résultats surprenant de ces analyses est l'absence d'effet clair et significatif de la densité (ou du recrutement) sur la survie des individus installés dans le Frémur, excepté en 1998 où le très fort recrutement semble avoir provoqué de fortes mortalités au sein de la population résidente. Le postulat de départ était que dans ce système supposé à saturation (du moins les habitats lotiques), la mortalité devait être fortement liée aux changements de la taille de la population (Gaillard *et al.* 1998, Eberhardt 2002). Tout d'abord cette absence de détection de la densité-dépendance aurait pu être liée à un problème méthodologique. En effet, nos analyses ne prennent pas en compte les erreurs autour de nos estimations de survie et de nos densités et des études ont démontré que ne pas prendre en compte ces erreurs pouvait induire des biais dans l'estimation de la relation entre ces deux paramètres (Barker *et al.,* 2002 ; Carroll *et al.*, 2006). Le modèle décrit dans la partie 2 permet d'estimer la relation entre la survie et la densité en prenant en compte ces erreurs d'observations. Cependant, les résultats du modèle semblent confirmer qu'il n'existe pas de mortalité densité-dépendante, tout du moins sur les anguilles avec une taille supérieure à 150 mm. D'autres hypothèses peuvent expliquer l'absence de mortalité densité-dépendante sur les stades étudiées :

- Premièrement, la période où la densité est mesurée n'est peut-être pas adéquat. En effet, s'il y a une augmentation de la population dans le bassin versant ce sera après le pic de recrutement qui a lieu entre Mai et Juin à Bois Joli. Idéalement il faudrait donc pouvoir faire les estimations de densités à cette période car elles représenteraient les pressions de compétition les plus fortes sur la population. Deuxièmement dans notre étude, les survies sont estimées pour les individus ayant une taille supérieure à 150 mm. Or les individus d'une taille inférieure (recrue et jeune anguillette) sont sûrement les plus sensibles aux processus densité-dépendants en raison de leur recherche d'un habitat favorable pour vivre, ce qui va majoritairement dépendre des individus déjà présents et de leur avantage compétitif, comme démontré chez les salmonidés (Johnsson *et al.*, 1999; Johnsson *et al.*, 2000). Lors d'une arrivée importante de recrues dans le système, les effets de la compétition interspécifique devraient donc être plus forts sur ces individus nouvellement recrutés que sur les individus déjà sédentarisés.

Conclusion : Les dynamiques de population contrastées entre les deux systèmes semblent être fortement liées à la structure des bassins versants (cloisonnés ou non) et au niveau de saturation atteint par le système. Ces différences de pressions impliquent des comportements divergeants entre une population subissant de faibles pressions et une population en subissant des fortes. Ainsi, **le niveau de saturation du système va jouer un rôle essentiel dans l'orientation sexuelle puisque quand les densités seront trop fortes (et que l'espace manquera) les jeunes individus développeront une stratégie qui permet une maturation**

à petite taille et jeune, c'est-à-dire que le sexe mâle sera favorisé (Colombo et Rossi, 1978). Cependant, une phase d'expérimentation aiderait à déterminer plus clairement quelles sont les phases (civelle, anguillette, anguille jaune) les plus sensibles à ces processus de régulation de la dynamique de population et des traits d'histoire de vie

3. *L'importance de la compréhension de ces processus de régulation pour la conservation*

L'une des mesures phares pour lutter contre le déclin de cette espèce est le repeuplement. Le principe consiste à prélever des jeunes anguilles (civelle et anguillette principalement) dans un milieu et les replacer dans un milieu plus favorable pour augmenter leur chance de devenir mature. Cependant l'absence de relation recrutement/stock dans le Frémur et la possibilité de forts processus de régulation lorsque les densités sont trop fortes (recrutement et densité au sein du système) laissent envisager que cette mesure pourrait ne pas être efficace pour augmenter le nombre de reproducteurs potentiels si le protocole (nombre d'individus introduits) et le choix du milieu où aura lieu le repeuplement ne sont pas adaptés. De plus même si le nombre de reproducteurs est augmenté via cette mesure il faut également vérifier que ces individus sont capables d'atteindre la zone de fraie et de se reproduire avec succès. Pour cela la qualité des anguilles argentées c'est-à-dire le potentiel reproducteur doit être aussi étudié. La troisième partie de la thèse s'est intéressée à la production d'argentée en terme de quantité et de qualité.

Efficacité du repeuplement

L'efficacité du repeuplement comme mesure de gestion de l'anguille européenne reste à ce jour peu connue (EC, 2014). Le rapport français sur les opérations de repeuplement (Frotté *et al.*, 2012) propose d'évaluer cette mesure de la façon suivante : le repeuplement est efficace quand le nombre et la qualité des anguilles argentées introduites sont au moins équivalents à

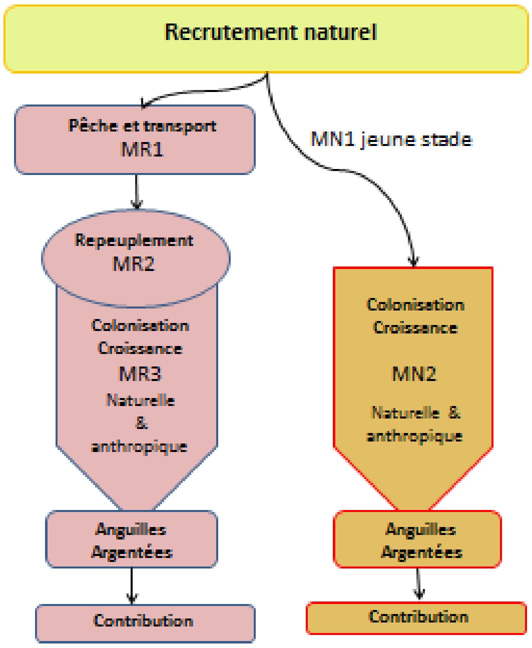

Figure 10 : Schéma conceptuel montrant les différents processus subis par les anguilles repeuplées et les anguilles colonisant naturellement le système. (d'après Frotté *et al.*, 2012)

ceux d'individus ayant colonisé naturellement le système repeuplé. Pour cela il faut notamment que les mortalités accumulées tout au long du processus de repeuplement (MR) soient inférieures à celles subies par des individus qui auraient colonisé le système naturellement (MN) (Fig.). Pour étudier l'efficacité du repeuplement, différents groupes d'individus de stades (civelle, anguillette, anguille jaune) et de provenances (eau douce et eau saumâtre) différents ont été ajoutés dans un petit marais de Camargue, préalablement vidé, tout au long de la période d'étude (2008-2013). Les résultats ont montré que les individus repeuplés aux stades anguillette et jaune (i) produisaient plus d'anguilles argentées que les anguilles « indigènes » (ii) et avaient une qualité, en terme de capacité reproductrice, équivalente. A l'inverse, les résultats ont montré que les individus repeuplés au stade civelle présentaient des survies beaucoup plus faibles que les stades plus âgés (anguillettes ou anguilles jaunes). Ces résultats suggèrent que le repeuplement est une mesure efficace quand les individus les plus vieux sont introduits, car ces stades sont les plus compétitifs en matière de croissance et survie. Cependant, l'ordre d'introduction des cohortes dans le système peut également avoir une importance primordiale. En effet, les cohortes jaunes et anguillettes ont été introduites en premier, quand le milieu était quasiment vierge, alors que les civelles ont été stockées quand le milieu avait vu son abondance fortement augmentée par des introductions successives. Une nouvelle fois, le niveau d'abondance (et plus globalement le niveau de saturation du système) est fondamental pour bien appréhender les performances des cohortes introduites et améliorer les opérations de repeuplement.

Effets de la saturation du système sur la dynamique de population et les traits d'histoire de vie

Le protocole prévoyait l'ajout d'environ 9000 civelles chaque année (entre janvier et février). L'objectif était de saturer progressivement le système afin (i) d'étudier la dynamique de population et l'évolution des traits de vie des différentes cohortes introduites en fonction du niveau de saturation du système (passage d'un système vierge à saturé) et (ii) d'estimer la capacité d'accueil du système.

Avant la saturation, de forts niveaux de compétition intra-groupes peuvent déjà avoir affectés la mortalité des civelles. En effet, il a été montré que les civelles subissaient de fortes mortalités les quelques mois suivants le stockage surtout lorsque qu'elles ont été stockées en grand nombre (Bisgaard & Pedersen, 1991; Pedersen, 2009) comme dans notre expérimentation. Après la saturation du système, les processus de régulation sur ces individus semblent s'accroitre avec des survies et des croissances faibles comparées à celles observées avant la saturation mais aussi comparées à celles observées chez les autres anguilles stockées. Cet effet plus fort de la saturation sur les individus issus de civelles peut s'expliquer par le fait qu'étant plus petits, ils sont plus sensibles aux compétitions intragroupes et intergroupes. Des civelles ont été introduites dans le système après la saturation (~ 9000 en janvier 2010, 2011 et 2012) mais elles sont très peu recapturées dans le système ce qui suggèrent que les processus densité-dépendants ont été encore plus forts sur ces individus. Une vidange du système qui aura lieu au printemps 2015 pourra nous indiquer si les individus qui n'ont pas eté recapturés sont effectivement morts ou s'ils étaient trop petits pour pouvoir être recapturés traduisant dans ce cas une croissance très faible.

De plus, les traits d'histoire de vie ainsi que le succès reproducteur des individus peuvent être impactés par la qualité du milieu où aura lieu le repeuplement (capacité d'accueil, pollution, compétiteur). Ainsi dans l'étude sur l'efficacité du repeuplement, les anguilles argentées issues des groupes de civelles (C08 et C09) sont plus petites et plus jeunes que les anguilles argentées issues d'autres groupes cela étant sûrement le résultat de la forte pression de compétition appliquée sur ces individus durant la majorité de leur croissance. L'augmentation de la compétition au fur et à mesure des ajouts de civelles semble avoir un impact modéré sur l'orientation sexuelle des deux groupes de civelles. En effet, alors que 5% des anguilles argentées issues des civelles introduites en 2008 sont des mâles, 11% des anguilles argentées issues des civelles introduites en 2009 sont des mâles. Cette légère augmentation de la proportion de mâle entre les deux cohortes peut s'expliquer par l'augmentation des pressions dues à la densité entre les deux introductions. Il serait intéressant de voir si la proportion de mâle est plus importante encore chez les anguilles issues des civelles introduites en 2010, c'est à dire lorsque le système est à saturation.

Le succès reproducteur

Le succès reproducteur a été évalué en analysant trois paramètres (taux de lipides, infection par *Anguillicoloides crassus* et contamination par des polluants) pouvant affecter la migration et/ou la reproduction des anguilles argentées. Malgré les différences d'origines (milieu saumâtre et milieu dulçaquicole), de stades d'introduction (civelle, anguillette, anguille jaune) et de dynamique de population, le succès reproducteur est équivalent entre les différents groupes. Ces résultats suggèrent que la qualité des anguilles argentées est indépendante de l'origine, du stade ou de la taille à l'introduction, et que finalement c'est la qualité du milieu où les anguilles vont être introduites qui va définir le succès reproducteur des anguilles argentées. Le choix du système où seront stockées les anguilles est donc primordial puisque ces caractéristiques détermineront également le succès reproducteur des futurs géniteurs.

Cette importance de la qualité des milieux sur le succès reproducteur des anguilles semble confirmée par notre dernière étude. En effet, à l'échelle européenne, une grande variabilité des relations taille-poids existe indépendamment la latitude, ce qui suggère des effets propres à la qualité du milieu sur la condition corporelle des anguilles. Ainsi pour une même taille (60 cm), les femelles provenant d'un bassin très contaminé par les PCB et métaux lourds (Scheldt, Belgique) ont un poids plus faible que celles provenant d'un système moins pollué (rivière Avon, United Kingdom).

Conclusion : Les résultats montrent que **le repeuplement est une mesure efficace** pour augmenter localement le nombre de reproducteurs potentiels. Cependant **des précautions restent à prendre** pour augmenter les chances de succès : (i) l'introduction sur un même site doit être limité en nombre d'individus et en frequence (ii) le choix du site est également déterminant puisqu'il déterminera à la fois la quantité d'anguilles argentées produites mais aussi leur succès reproducteur. D'autres études sont cependant nécessaires pour déterminer si les individus issus du repeuplement arrivent à atteindre la zone de fraie de la mer des Sargasses et se reproduirent puisque ce sujet fait encore débat (Westerberg *et al.*, 2014 ; Wickström *et al.*, 2014 (Québec, AFS conference)).

II. Perspectives

L'objectif principal de ce travail était de comprendre comment les caractéristiques (productivité, densité de congénères et de compétiteurs, qualité de l'eau, …) du système dans lequel vont s'établir les anguilles pendant plusieurs années vont pouvoir impacter le nombre et les caractéristiques (traits d'histoire de vie et condition) des anguilles sortant du système pour la reproduction. Les résultats ont montré que, en lien avec la capacité d'accueil, le système pouvait réguler la population via des processus densité-indépendants et densité-dépendants. Pour s'adapter au système de croissance et aux pressions appliquées sur la population, les anguilles vont donc développer différentes stratégies d'histoire de vie en lien avec la dynamique de population. Ces informations sont nécessaires pour l'application de méthodes de gestion adaptées en prédisant par exemple dans quel système les individus pourront être prélevés afin d'être stockés dans des milieux plus favorables et ainsi éviter de forts processus densité dépendants. Cependant certains points restent encore à étudier.

1. Les processus de régulation sur les anguilles de moins de 150 mm

Nos analyses se sont concentrées sur l'étude des processus de régulation des anguilles de plus de 150 mm. Or, sur le Frémur, compte tenu de l'importante variabilité du recrutement (entre 3 et 26 765 recrues, coefficient de variation: 0.94) et de la relative stabilité de la densité au sein du bassin versant (entre 0.22 et 0.51 anguille par m^{-2}, coefficient de variation: 0.24), l'absence de densité-dépendance sur la survie des individus marqués (> 150 mm) suggère que les processus de régulation doivent être appliqués sur les individus de moins de 150 mm. De plus si ces processus existent dans le Frémur et pas dans l'Oir cela pourrait confirmer que la détermination de sexe serait fortement corrélée à la pression de densité sur les jeunes individus (Krueger et Oliveira, 1999; Tesch, 2003). Cependant pour confirmer ces hypothèses, d'autres études doivent être réalisées et de nouvelles méthodes de suivi doivent être mises en place. En effet, la méthode de marquage que nous utilisons n'est pas adaptée au suivi de ce type d'individu à cause de la taille du PIT-tag (11 mm). D'autres méthodes existent pour suivre ces populations cependant elles ne sont pas toutes adaptées à un suivi sur le long terme, à notre espèce, ou à l'estimation des paramètres démographiques. Par exemple, le marquage de masse avec des produits de type tétracycline, alizarine ou alcéine permettrait de marquer des individus de petites tailles en fixant une marque sur les pièces calcifiées. A l'aide de ce type de marque la croissance d'un individu peut être estimée par retro calcul sur l'otolithe, cependant il est nécessaire de le sacrifier pour extraire les pièces calcifiées ce qui n'est pas souhaitable pour une espèce en danger critique d'extinction. Des tags sous-cutanés type VIE-tag (Visible Implant Elastromer tag) peuvent aussi être utilisés sur les petits individus, cependant avec la pigmentation de l'anguille la lecture du tag pourrait devenir difficile.

L'utilisation d'une marque externe de type tags spaghetti attachée à la nageoire dorsale ainsi que l'utilisation de plus petits PIT-tag pourraient être une solution pour suivre ces petits individus mais des analyses restent à faire pour estimer la rétention de ses marques.

2. Les mouvements au sein des bassins versants

Le travail réalisé dans cette thèse a permis d'étudier les processus densité-dépendants et densité-indépendants appliqués sur deux paramètres affectant la dynamique de population : la croissance et la mortalité. Cependant un paramètre important n'a pas été pris en compte, les mouvements des anguilles jaunes au sein du bassin versant. En effet, lorsque les pressions dans leur habitat sont trop fortes, les individus peuvent se déplacer pour chercher un habitat plus adapté. Nos échantillonnages nous permettent de confirmer que d'importants déplacements au sein du système ont lieu. Ainsi sur 580 individus recapturés au moins une fois sur l'Oir, 47 changent de compartiment avec principalement des mouvements de l'aval vers l'amont. Dans le Frémur, sur les 461 anguilles recapturées au moins une fois, 19 changent de compartiment. Cependant, il est difficile d'établir avec un suivi annuel : (i) quand ces mouvements ont lieu ? (ii) pour quelles raisons ? (iii) quel en est l'avantage ?

La mise en place de nouvelles antennes dans le système de l'Oir devrait nous permettre d'étudier ces mouvements plus précisément afin d'affiner notre compréhension de la dynamique de population dans ce système. Une mise en place équivalente dans le Frémur serait intéressante puisqu'elle permettrait de mettre en évidence la présence ou non de mouvements entre les zones lotiques et les zones lentiques telles que le réservoir d'eau du Bois Joli qui reste à ce jour encore une boite noire.

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Annexes

ANNEXE I

Script Winbugs du modèle bayésien pour l’étude de la survie densité dépendence

```
model
{
#####################
# Density estimates #
#####################
     #  parameters  for  probability  of  capture  and  density
estimates
               mu.z~dnorm(0,0.001)
               tau.z<-1/(sd.z*sd.z)
               sd.z~dunif(0,100)

               mu.d~dnorm(0,0.001)
               CV.d~dunif(0,10)
               r.d<-1/(CV.d*CV.d)

     # Random effect year
               tau.a<-1/(sd.a*sd.a)
               sd.a~dunif(0,10)

          for (a in 1:11)
          {
               a.d[a]~dnorm(0,tau.a)
          }

     # Fixed effect Reach
          for (b in 1:4)
          {
               bl.d[b]~dnorm(0,0.001)
               b.d[b]<-bl.d[b]-mean(bl.d[])
          }
     # Extrapolation
          for (a in 1:11)
          {
          for (b in 1:4)
          {
               logE.dextra[a,b]<-mu.d+a.d[a]+b.d[b]
               E.dextra[a,b]<-exp(logE.dextra[a,b])
               Nr[a,b]<-E.dextra[a,b]*Sr[b]
          }
               Nt[a]<-sum(Nr[a,])
               dt[a]<-Nt[a]/St
          }
     # Probability of capture
          for (i in 1:K)
          {
               p[i]<-exp(z[i])/(1+exp(z[i]))
               z[i]~dnorm(E.z[i],tau.z)
               E.z[i]<-mu.z
     # density and abundance
               logE.d[i]<-mu.d+a.d[y[i]]+b.d[R[i]]
               E.d[i]<-exp(logE.d[i])
```

```
               d[i]~dgamma(r.d,m.d[i])
               m.d[i]<-1/(E.d[i]*CV.d*CV.d)
               lambda[i]<-d[i]*S[i]

               N1[i]~dpois(lambda[i])I(,1500)
               N2[i]<-N1[i]-c1[i]
               N3[i]<-N2[i]-c2[i]
               N4[i]<-N3[i]-c3[i]
     # Likelihood
               c1[i]~dbin(p[i],N1[i])
               c2[i]~dbin(p[i],N2[i])
               c3[i]~dbin(p[i],N3[i])
               c4[i]~dbin(p[i],N4[i])
          }
#########################################
#Multistate Capture-recapture structure #
#########################################
# Priors
      #initial state
          for (a in 1:6)
          {
          bb[a]~dnorm(0,0.01)
          }
     pis[1]<-
1/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(bb[5])+ex
p(bb[6]))
     pis[2]<-
exp(bb[1])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))
     pis[3]<-
exp(bb[2])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))
     pis[4]<-
exp(bb[3])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))
     pis[5]<-
exp(bb[4])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))
     pis[6]<-
exp(bb[5])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))
     pis[7]<-
exp(bb[6])/(1+exp(bb[1])+exp(bb[2])+exp(bb[3])+exp(bb[4])+exp(
bb[5])+exp(bb[6]))  pis[8]<-0
     # Parameters for survival, transition and observation
          for (a in 1:7)
          {
               mu.po[a]~dnorm(0,0.01)
               tau.po[a]<-1/(sd.po[a]*sd.po[a])
               sd.po[a]~dunif(0,10)
          }
```

```
            mu.phi1~dnorm(0,0.01)
            tau.phi1<-1/(sd.phi1*sd.phi1)
            sd.phi1~dunif(0,10)

            mu.phi4~dnorm(0,0.01)
            tau.phi4<-1/(sd.phi4*sd.phi4)
            sd.phi4~dunif(0,10)

            mu.phi5~dnorm(0,0.01)
            tau.phi5<-1/(sd.phi5*sd.phi5)
            sd.phi5~dunif(0,10)
        for (a in 1:5)
        {
            mu.cc[a]~dnorm(0,0.01)
            tau.cc[a]<-1/(sd.cc[a]*sd.cc[a])
            sd.cc[a]~dunif(0,10)
        }
        for (a in 1:2)
        {
            mu.ee[a]~dnorm(0,0.01)
            tau.ee[a]<-1/(sd.ee[a]*sd.ee[a])
            sd.ee[a]~dunif(0,10)
        }
    # Survival
        for (t in 1:(k-1))
        {
            dx[t]<-cut(dt[t+1])
        for (a in 1:5)
        {
            eps[a,t]~dnorm(0,tau.s[a])
            mu.s[a,t]<-alpha[a]+beta[a]*dx[t] + eps[a,t]
            logit(s[a,t])<-mu.s[a,t]
        }
        }
        for (a in 1:5)
        {
            alpha[a]~dnorm(0, 0.01)
            beta[a]~dnorm(0,0.01)
            tau.s[a]<-1/(sd.s[a]*sd.s[a])
            sd.s[a]~dunif(0,10)
        }
    # Transition
        for (t in 1:(k-1))
        {
            z.phi1[t]~dnorm(mu.phi1,tau.phi1)
            phi1[t]<-exp(z.phi1[t])/(1+exp(z.phi1[t]))
            z.phi4[t]~dnorm(mu.phi4,tau.phi4)
            phi4[t]<-exp(z.phi4[t])/(1+exp(z.phi4[t]))
            z.phi5[t]~dnorm(mu.phi5,tau.phi5)
            phi5[t]<-exp(z.phi5[t])/(1+exp(z.phi5[t]))
        for (a in 1:5)
```

```
        {
            cc[a,t]~dnorm(mu.cc[a],tau.cc[a])
        }
    phi2[1,t]<-
1/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[4,t])+exp(c
c[5,t]))
    phi2[2,t]<-
exp(cc[1,t])/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[
4,t])+exp(cc[5,t]))
    phi2[3,t]<-
exp(cc[2,t])/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[
4,t])+exp(cc[5,t]))
    phi2[4,t]<-
exp(cc[3,t])/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[
4,t])+exp(cc[5,t]))
    phi2[5,t]<-
exp(cc[4,t])/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[
4,t])+exp(cc[5,t]))
    phi2[6,t]<-
exp(cc[5,t])/(1+exp(cc[1,t])+exp(cc[2,t])+exp(cc[3,t])+exp(cc[
4,t])+exp(cc[5,t]))
        for (a in 1:2)
        {
            ee[a,t]~dnorm(mu.ee[a],tau.ee[a])
        }
            phi3[1,t]<-1/(1+exp(ee[1,t])+exp(ee[2,t]))
            phi3[2,t]<-
exp(ee[1,t])/(1+exp(ee[1,t])+exp(ee[2,t]))
            phi3[3,t]<-
exp(ee[2,t])/(1+exp(ee[1,t])+exp(ee[2,t]))
        }
    # Observations
        for (a in 1:7)
        {
        for (t in 1:(k-1))
        {
        z.po[a,t]~dnorm(mu.po[a],tau.po[a])
        po[a,t]<-exp(z.po[a,t])/(1+exp(z.po[a,t]))
        }
        }
    # Matrices state transition
        for (i in 1:nind)
        {
        for (t in 1: (k-1))
        {
            px[8,i,t,1]<-0
            px[8,i,t,2]<-0
            px[8,i,t,3]<-0
            px[8,i,t,4]<-0
            px[8,i,t,5]<-0
            px[8,i,t,6]<-0
```

```
px[8,i,t,7]<-0
px[8,i,t,8]<-1

px[1,i,t,1]<-s[1,t]*phi1[t]
px[1,i,t,2]<-s[1,t]*(1-phi1[t])
px[1,i,t,3]<-0
px[1,i,t,4]<-0
px[1,i,t,5]<-0
px[1,i,t,6]<-0
px[1,i,t,7]<-0
px[1,i,t,8]<-1-s[1,t]

px[5,i,t,1]<-0
px[5,i,t,2]<-0
px[5,i,t,3]<-0
px[5,i,t,4]<-0
px[5,i,t,5]<-s[4,t]*phi5[t]
px[5,i,t,6]<-0
px[5,i,t,7]<-s[4,t]*(1-phi5[t])
px[5,i,t,8]<-1-s[4,t]

px[6,i,t,1]<-0
px[6,i,t,2]<-0
px[6,i,t,3]<-0
px[6,i,t,4]<-0
px[6,i,t,5]<-0
px[6,i,t,6]<-s[5,t]
px[6,i,t,7]<-0
px[6,i,t,8]<-1-s[5,t]

px[7,i,t,1]<-0
px[7,i,t,2]<-0
px[7,i,t,3]<-0
px[7,i,t,4]<-0
px[7,i,t,5]<-0
px[7,i,t,6]<-0
px[7,i,t,7]<-s[5,t]
px[7,i,t,8]<-1-s[5,t]

px[2,i,t,1]<-0
px[2,i,t,2]<-s[2,t]*phi2[1,t]
px[2,i,t,3]<-s[2,t]*phi2[2,t]
px[2,i,t,4]<-s[2,t]*phi2[3,t]
px[2,i,t,5]<-s[2,t]*phi2[4,t]
px[2,i,t,6]<-s[2,t]*phi2[5,t]
px[2,i,t,7]<-s[2,t]*phi2[6,t]
px[2,i,t,8]<-1-s[2,t]

px[3,i,t,1]<-0
px[3,i,t,2]<-0
px[3,i,t,3]<-s[3,t]*phi3[1,t]
```

```
          px[3,i,t,4]<-0
          px[3,i,t,5]<-s[3,t]*phi3[2,t]
          px[3,i,t,6]<-0
          px[3,i,t,7]<-s[3,t]*phi3[3,t]
          px[3,i,t,8]<-1-s[3,t]

          px[4,i,t,1]<-0
          px[4,i,t,2]<-0
          px[4,i,t,3]<-0
          px[4,i,t,4]<-s[4,t]*phi4[t]
          px[4,i,t,5]<-0
          px[4,i,t,6]<-s[4,t]*(1-phi4[t])
          px[4,i,t,7]<-0
          px[4,i,t,8]<-1-s[4,t]
          }

# Matrice observation
     for (t in 1:(k-1))
     {
          pob[1,i,t,1]<-1-po[1,t]
          pob[1,i,t,2] <- po[1,t]
          pob[1,i,t,3] <- 0
          pob[1,i,t,4] <- 0
          pob[1,i,t,5] <- 0
          pob[1,i,t,6] <- 0
          pob[1,i,t,7] <- 0
          pob[1,i,t,8] <- 0

          pob[2,i,t,1]<-1-po[2,t]
          pob[2,i,t,2] <- 0
          pob[2,i,t,3] <- po[2,t]
          pob[2,i,t,4] <- 0
          pob[2,i,t,5] <- 0
          pob[2,i,t,6] <- 0
          pob[2,i,t,7] <- 0
          pob[2,i,t,8] <- 0

          pob[3,i,t,1]<-1-po[3,t]
          pob[3,i,t,2] <- 0
          pob[3,i,t,3] <- 0
          pob[3,i,t,4] <- po[3,t]
          pob[3,i,t,5] <- 0
          pob[3,i,t,6] <- 0
          pob[3,i,t,7] <- 0
          pob[3,i,t,8] <- 0

          pob[4,i,t,1]<-1-po[4,t]
          pob[4,i,t,2] <- 0
          pob[4,i,t,3] <- 0
          pob[4,i,t,4] <- 0
          pob[4,i,t,5] <- po[4,t]
```

```
          pob[4,i,t,6] <- 0
          pob[4,i,t,7] <- 0
          pob[4,i,t,8] <- 0

          pob[5,i,t,1]<-1-po[5,t]
          pob[5,i,t,2] <- 0
          pob[5,i,t,3] <- 0
          pob[5,i,t,4] <- 0
          pob[5,i,t,5] <- 0
          pob[5,i,t,6] <- po[5,t]
          pob[5,i,t,7] <- 0
          pob[5,i,t,8] <- 0

          pob[6,i,t,1]<-1-po[6,t]
          pob[6,i,t,2] <- 0
          pob[6,i,t,3] <- 0
          pob[6,i,t,4] <- 0
          pob[6,i,t,5] <- 0
          pob[6,i,t,6] <- 0
          pob[6,i,t,7] <- po[6,t]
          pob[6,i,t,8] <- 0

          pob[7,i,t,1]<-1-po[7,t]
          pob[7,i,t,2] <- 0
          pob[7,i,t,3] <- 0
          pob[7,i,t,4] <- 0
          pob[7,i,t,5] <- 0
          pob[7,i,t,6] <- 0
          pob[7,i,t,7] <- 0
          pob[7,i,t,8] <- po[7,t]

          pob[8,i,t,1]<-1
          pob[8,i,t,2] <- 0
          pob[8,i,t,3] <- 0
          pob[8,i,t,4] <- 0
          pob[8,i,t,5] <- 0
          pob[8,i,t,6] <- 0
          pob[8,i,t,7] <- 0
          pob[8,i,t,8] <- 0
     }
     }
# Likelihood
     for (i in 1:nind)
     {
          Z[i,f[i]]~ dcat(pis[1:8])
     for (t in (f[i]+1):k)
     {
          Z[i,t]~dcat(px[Z[i,t-1],i,t-1,])
          ye[i,t]~dcat(pob[Z[i,t],i,t-1,])
     }
     }         }
```

ANNEXE II

Script R pour l’estimation du nombre d’argentées par groupes dans le Vigueirat

```
model.abond <-
function(filename,work_rep=work_rep,N0=100,repetition=10)
{
   #################################################

  croise=function(abond,esp,ue,FUN="sum"){

    if (FUN=="sum")
    {
      mat=xtabs(abond~esp+ue)
      mat=cbind(apply(mat,1,sum),mat)
      mat=subset(mat,mat[,1]!=0,select=2:dim(mat)[2])
    }

    if (FUN=="mean")
    {
      mat=xtabs(abond~esp+ue,aggregate(abond~esp+ue,FUN=mean))
      mat=cbind(apply(mat,1,sum),mat)
      mat=subset(mat,mat[,1]!=0,select=2:dim(mat)[2])
    }
    return(mat)
  }

  #################################################
  nstade=3

  require(xlsx)
  model.init.princ <-
read.xlsx(paste0(work_rep,filename),sheetName="Reduced Set of
Parameters")

  cat(paste(length(unique(model.init.princ$Time))-1,"ans de
suivi \n"))
  cat(paste(length(unique(model.init.princ$Group)),"groupes
\n"))
  cat(paste(length(unique(model.init.princ$From)),"stades
\n"))
  cat(paste("Fichiers sauvegardés dans :",work_rep,"\n \n
\n"))

  wb <- createWorkbook()
  wb2 <- createWorkbook()

#   i=0
  for (group in unique(model.init.princ[,"Group"]))
  {
print(group)
    #     i <- i+1
#
cat(paste(round((i/length(unique(model.init.princ$Group)))*100
,2),"% de progression","\n \n"))
```

```
    for (boot in 1:repetition)
    {
      print(boot)
      model.init <-
model.init.princ[which(model.init.princ[,"Group"]==group),]
      model.survie <-
model.init[which(model.init[,"Parameters"]==" Survie"),]
      if (boot==1)
      Ntot <-
array(dim=c((length(unique(model.survie$Time))),nstade,repetit
ion))
      model.croissance <-
model.init[which(model.init[,"Parameters"]==" Croissance"),]
      model.croissance <-
model.croissance[,c("Time","From","To","Estimates")]
      model.croissance2 <- data.frame(matrix(nc=4,nr=0))
      for (i in unique(model.croissance$Time))
      {
        selection1 <- c(i,1,1,1-
(model.croissance[which(model.croissance[,"Time"]==i &
model.croissance[,"From"]==1 &
model.croissance[,"To"]==2),]$Estimates

+model.croissance[which(model.croissance[,"Time"]==i &
model.croissance[,"From"]==1 &
model.croissance[,"To"]==3),]$Estimates))
        selection2 <- c(i,2,2,1-
model.croissance[which(model.croissance[,"Time"]==i &
model.croissance[,"From"]==2 &
model.croissance[,"To"]==3),]$Estimates)
        selection3 <- c(i,3,3,1)
        model.croissance2 <-
rbind(model.croissance2,selection1,selection2,selection3)
      }

      names(model.croissance2) <- names(model.croissance);
model.croissance <- rbind(model.croissance,model.croissance2)

      PT <- NT <- NS <-
array(dim=c(length(unique(model.survie$Time)),nstade,nstade))
      PS <-
as.data.frame(matrix(nc=nstade,nr=length(unique(model.survie$T
ime))))
      NS[1,2,2] <- 0;NS[1,3,3] <- 0

      #PS[an,from]
      PS <-
croise(model.survie$Estimates,model.survie$Time,model.survie$F
rom,FUN="mean")
      rownames(PS) <- 1:dim(PS)[1]
      PS[,nstade] <- rep(1,dim(PS)[1])
```

```

      #PT NS NT [an,to,from]
      PT[,,1]                                                   <-
croise(model.croissance[which(model.croissance[,"From"]==1),]$
Estimates,

model.croissance[which(model.croissance[,"From"]==1),]$Time,

model.croissance[which(model.croissance[,"From"]==1),]$To,FUN=
"mean")

      PT[,2:3,2]                                                <-
croise(model.croissance[which(model.croissance[,"From"]==2),]$
Estimates,

model.croissance[which(model.croissance[,"From"]==2),]$Time,

model.croissance[which(model.croissance[,"From"]==2),]$To,FUN=
"mean")
      PT[,1,2] <- rep(0,length(unique(model.survie$Time)))

      PT[,,3]                                                   <-
croise(model.croissance[which(model.croissance[,"From"]==3),]$
Estimates,

model.croissance[which(model.croissance[,"From"]==3),]$Time,

model.croissance[which(model.croissance[,"From"]==3),]$To,FUN=
"mean")
      PT[,1:2,3]                                                <-
cbind(rep(0,length(unique(model.survie$Time))),rep(0,length(un
ique(model.survie$Time))))

      NTtot                                                     <-
data.frame(matrix(nc=3,nr=length(unique(model.survie$Time))))

      an <- length(unique(model.survie$Time))
      #  Function ---------------------------------------------
-------------------

      for (a in 1:(an))
      {
        if (a==1)
        {
          NS[1,1,1]   <-   rbinom(1,N0,PS[1,1])#Probabilité   de
survie
          NT[1,,1] <- rmultinom(1,NS[1,1,1],PT[1,,1])
        }

        if (a==2)
        {
```

```
          NS[2,1,1] <- rbinom(1,NT[1,1,1],PS[2,1])
          NT[2,,1] <- rmultinom(1,NS[2,1,1],PT[2,,1])

          NS[2,2,2] <- rbinom(1,NT[1,2,1],PS[2,2])
          NT[2,,2] <- rmultinom(1,NS[2,2,2],PT[2,,2])

          NS[2,3,3] <- rbinom(1,NT[1,3,1],PS[2,3])
          NT[2,,3] <- rmultinom(1,NS[2,3,3],PT[2,,3])

          for (st in 1:nstade)
            NTtot[2,st] <- sum(NT[2,st,])

        }
        if (a!=1 & a!=2)
        {
          NS[a,1,1] <- rbinom(1,NTtot[(a-1),1],PS[a,1])
          NT[a,,1] <- rmultinom(1,NS[a,1,1],PT[a,,1])

          NS[a,2,2] <- rbinom(1,NTtot[(a-1),2],PS[a,2])
          NT[a,,2] <- rmultinom(1,NS[a,2,2],PT[a,,2])

          NS[a,3,3] <- rbinom(1,NTtot[(a-1),3],PS[a,3])
          NT[a,,3] <- rmultinom(1,NS[a,3,3],PT[a,,3])

          for (st in 1:nstade)
            NTtot[a,st] <- sum(NT[a,st,])
        }
      }
      NTtot[is.na(NTtot)] <- 0
      Ntot[,,boot] <- as.matrix(NTtot)
    }
    Ntotmean <- round(apply(Ntot,c(1,2),mean),2)
    Ntotsd <- round(apply(Ntot,c(1,2),sd),2)
    sheet  <- createSheet(wb, sheetName=paste("group",group))
    addDataFrame(Ntotmean, sheet)
    sheet  <- createSheet(wb2, sheetName=paste("group",group))
    addDataFrame(Ntotsd, sheet)
  }
  saveWorkbook(wb, paste0(work_rep,"result_model_mean2.xlsx"))
  saveWorkbook(wb2, paste0(work_rep,"result_model_sd2.xlsx"))
return(list(Ntotmean=Ntotmean, Ntotsd=Ntotsd))
}
work_rep="C:/Users/cbouleng.IFR/Documents/these/Données
Camargue/Analyse Qualité Géniteurs/modele_abondance/"
filename="Model60ttest.xlsx"


result                                                          <-
model.abond("Model60ttest.xlsx",work_rep,N0=100,repetition=100
0)
```

ANNEXE II

Native European eels as a potential biological control for invasive crayfish

Freshwater Biology

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Native European eels as a potential biological control for invasive crayfish

CAMILLE MUSSEAU*,†, CLARISSE BOULENGER‡, ALAIN J CRIVELLI§, ISABELLE LEBEL¶, MARINE PASCAL**, STÉPHANIE BOULÊTREAU*,† AND FRÉDÉRIC SANTOUL*,†

*Ecolab (Laboratoire d'Ecologie Fonctionnelle et Environnement), Université de Toulouse, UPS, INP, Toulouse, France
†Ecolab, CNRS, Toulouse, France
‡Muséum National d'Histoire Naturelle, UMR BOREA, CRESCO, Dinard, France
§Station Biologique de la Tour du Valat, Arles, France
¶Association Migrateurs-Rhône-Méditerranée, Arles, France
**Association les Amis du Vigueirat, Arles, France

SUMMARY

1. Invasive species may have strong negative impacts on ecosystems. Invasive crayfish are well known to cause ecological imbalances in freshwater systems and have become targets in eradication programmes.
2. The red swamp crayfish (*Procambarus clarkii*) is vulnerable to predation by several fish species. The European eel (*Anguilla anguilla*) appears to be a very good candidate given its benthic feeding activity and ability to recognise prey by odour.
3. Our study took place from 2009 to 2013 in a closed system in south-eastern France in which ponds were sampled twice a year by passive capture methods to evaluate trends in populations of potential prey. Eel population dynamics were assessed by means of a multistate capture–recapture model, and diet assessment was performed using stable isotope analysis in October 2010 and October 2012.
4. Our results show that the invasive crayfish was the most important prey in the eel diet, and every size-class of crayfish was preyed upon by the predator.
5. A high predator density, approaching carrying capacity for the European eel in this system, strongly affects *P. clarkii* populations, leading them to their collapse, but not eradication.

Keywords: diet, ontogeny, predation, red swamp crayfish, stable isotope

Introduction

Biological invasions are among the main causes of biodiversity decline (Mack *et al*., 2000; Clavero & García-Berthou, 2005). Non-native species can have strong impacts on biological communities and are responsible for altering ecosystem functioning and ecosystem services and for homogenising biota (McKinney & Lockwood, 1999). Non-native species can strongly affect freshwater systems (Moyle & Light, 1996; Dudgeon *et al*., 2006; Strayer, 2010). While fish are the most commonly introduced organisms outside their native ranges (Gozlan *et al*., 2010; Cucherousset & Olden, 2011), non-native invertebrate species are also known to produce adverse effects (Hakenkamp & Palmer, 1999; Dick, Platvoet & Kelly, 2002; Miehls *et al*., 2009). In European fresh waters, arthropods are the second most commonly reported group in terms of introductions that have established self-sustaining populations (Strayer, 2010).

Crayfish are the largest invertebrates living in freshwater systems, often in high density (Usio & Townsend, 2004). European ecosystems have been threatened by a number of non-native crayfish species, the red swamp crayfish (*Procambarus clarkii*) being one of the most significant (Gherardi *et al*., 2011). *P. clarkii* represents an important source of prey for several species of birds (Barbraud *et al*., 2001; Poulin, Lefebvre & Crivelli, 2007), mammals (Beja, 1996), reptiles (Ottonello, Salvidio &

Correspondence: Camille Musseau, Ecolab (Laboratoire d'Ecologie Fonctionnelle et Environnement), Université de Toulouse, UPS, INP, 118 Route de Narbonne, Bât. 4R1, Door 342, Toulouse 31062, France. E-mail: camille.musseau@univ-tlse3.fr

Rosecchi, 2005) and fish (Martino *et al.*, 2011). However, the introduction of *P. clarkii* may have severe impacts, affecting many ecosystem properties ranging from physical habitat structure to food webs. The species is known for its omnivorous diet, with the potential to generate trophic cascades by preying on native species (Gherardi & Acquistapace, 2007). Its grazing activity can lead to dramatic reductions in aquatic vegetation, with loss of biodiversity and cascading changes to food webs (Rodríguez *et al.*, 2005). Furthermore, *P. clarkii* is responsible for damage to agricultural irrigation systems and production and also impacts on the fishing industry (Lodge *et al.*, 2012).

For all these reasons, *P. clarkii* populations are targeted in management and control programmes, like other invasive crayfish (Hein, Vander Zanden & Magnuson, 2007). Different methods have been adopted to reduce the impacts of this species: mechanical removal using various traps or electrofishing; physical management using drainage, barriers or river diversions; natural or chemical biocides; autocidal methods; and biological control (Nystrom, 2002; Gherardi *et al.*, 2011). Biological control (biocontrol) is based on the use of natural enemies to limit the invader (Freeman *et al.*, 2010). Predators appear to be one of the best biocontrol agents for red swamp crayfish (Gherardi *et al.*, 2011). While burbot (*Lota lota*), perch (*Perca fluviatilis*), pike (*Esox lucius*) and wels catfish (*Silurus glanis*) are well-known predators of *P. clarkii* (Westman, 1991; Martino *et al.*, 2011), the European eel (*Anguilla anguilla*) is also known to prey on benthic invertebrates and fish, especially when the prey are large (Dörner *et al.*, 2009). Eels might prove effective predators of the crayfish because of two morphological advantages: they can detect crayfish by odour (Blake & Hart, 1995), and their body shape allows them to enter crayfish burrows and consume hidden crayfish (Aquiloni *et al.*, 2010). While *P. clarkii* is known to be vulnerable to different eel species (Hicks, 1997; Wysujack & Mehner, 2005; Gualtieri *et al.*, 2006; Kaifu *et al.*, 2012), the efficacy of *A. anguilla* in mitigating *P. clarkii* damage has only been shown experimentally, in laboratories and enclosures, when preying on soft and small-sized crayfish (Aquiloni *et al.*, 2010). These experiments need to be validated at a larger scale and under natural conditions.

Here, we assess the efficiency of the European eel as a biocontrol agent for the red swamp crayfish in a natural eel-stocked pond by (i) quantifying the contribution of crayfish to eel diet using stable isotope analysis and (ii) measuring the effect of eel predation on crayfish population trends. We expected a decline of the invasive crayfish population via fish predation on small crayfish.

Methods

Study area

The Pisci-Sud freshwater pond is located in the natural reserve of the Vigueirat Marshes in the Camargue close to the River Rhône Delta (south-eastern France). It is a closed 32-ha basin divided into a dense reed bed and two interconnected open water ponds of 6 ha and 5.5 ha. This area has been used for eel stocking and annual restocking experiments since 2007 (European Council Regulations, N° 1100/2007). More details on this experiment can be found in Desprez *et al.* (2013). The designated area is totally closed, and the sources of water include rain and a pumping station. The water depth is maintained at 50 cm to avoid fish predation by birds.

Eel, other fish and crayfish sampling

Eels were stocked as yellow eels in October 2007 and as glass eels every February from 2008 to 2012. Nine consecutive days of eel sampling was conducted in May and October from 2008 to 2013. Eels were captured by passive trapping using capétchade nets (which consist of a barrier leading into an enclosure surrounded by three trap nets and which keep alive the fish that enter them) with a 6 mm mesh size in the funnel and a leading net of 40 m. As eels were marked using PIT tags, their abundance was estimated for each sampling session from 2008 to 2013 using multistate capture–recapture models (Lebreton *et al.*, 2009). More details about this method and the model selection can be found in Desprez *et al.* (2013).

Freshwater fish species and red swamp crayfish were trapped by passive methods in May and October from 2009 to 2013 using the same trapping devices as for eels, but only for five consecutive days. Each fish and crayfish trapped was identified to species, counted and weighed; fish were measured (TL, nearest millimetre) and crayfish were individually weighed (nearest gram) instead of taking their carapace length. For potential prey, mean catch per unit effort (CPUE) was expressed in grams of fish or number of crayfish caught per 24 hours per capétchade net (for biomass and number, respectively) and then standardised by a logarithmic transformation [ln(CPUE + 1)]. For fish prey, we focused on the top-mouth gudgeon (*Pseudorasbora parva*), a small, elongated fish representing substantial biomass in the studied system. Crayfish were categorised into three weight classes: small (<10 g), medium (10.1–25 g) and large (>25 g).

To ensure that any observed trend was not simply a broader regional trend, crayfish abundances were compared with those obtained using the same trapping devices and with the same mesh size from October 2008 to October 2012 in a canal adjoining the Pisci-Sud.

Stable isotope analysis

Tissue samples of European eels and their potential prey were collected to quantify eel diet using stable isotope analysis in October 2010 and October 2012. A total of 86 eels (TL ranging from 170 to 808 mm) and 88 eels (TL ranging from 210 to 885 mm) were analysed in 2010 and 2012, respectively. Each eel was measured and weighed. Tissue samples of the potential prey were also collected in 2010 and 2012. For isotopic analysis using a Bayesian mixing model (n = 3–6 for each five groups, Fig. 1), prey were categorised into five groups: 'fish', including topmouth gudgeons; 'invertebrates', including chironomids and freshwater shrimps (*Palaemon* spp. and *Atyaephyra desmarestii*); and three weight classes of *P. clarkii*. Then, the three weight classes were pooled into a group called 'crayfish'. Stable isotope analysis (δ^{13}C and δ^{15}N) was performed on fin samples for eel, on muscle samples for *P. parva* and *P. clarkii* and on the whole organism for other invertebrates. To assess the validity of fin sampling as a non-lethal proxy for muscle, we sampled additional fin and muscle tissues from 12 individuals.

Samples were oven-dried (60°C for 48 h) and ground into a fine homogenous powder using a mixer mill (Retsch MM 200, Hann, Germany). Approximately 1.0 mg of sample was accurately weighed into a small tin cup, and stable isotope ratios of carbon and nitrogen were analysed in a Carlo Erba NC2500 elemental analyser coupled to a Thermo Finnigan Mat Delta XP isotope ratio mass spectrometer. Stable isotope ratios are expressed in per mill (‰) delta values (δ^{13}C or δ^{15}N) referring to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen): δ^{15}N or δ^{13}C (‰) = $[(R_{\mathrm{sam}} - R_{\mathrm{std}})/R_{\mathrm{std}}] \times 1000$. Data were corrected using working standards (fish tissue, mink tissue and methionine SD < 0.2‰ for both δ^{13}C and δ^{15}N) that were previously calibrated according to International Atomic Energy Agency (IAEA) standards. All stable isotope analyses were performed at the Cornell Isotope Laboratory, Cornell University, U.S.A.

Statistical analyses

The three classes of *P. clarkii* showed diet variation due to ontogenetic shifts among different types of food. Differences among prey isotopic signatures (Fig. 1) reflected diet variations between prey groups and were essential for the use of the diet model.

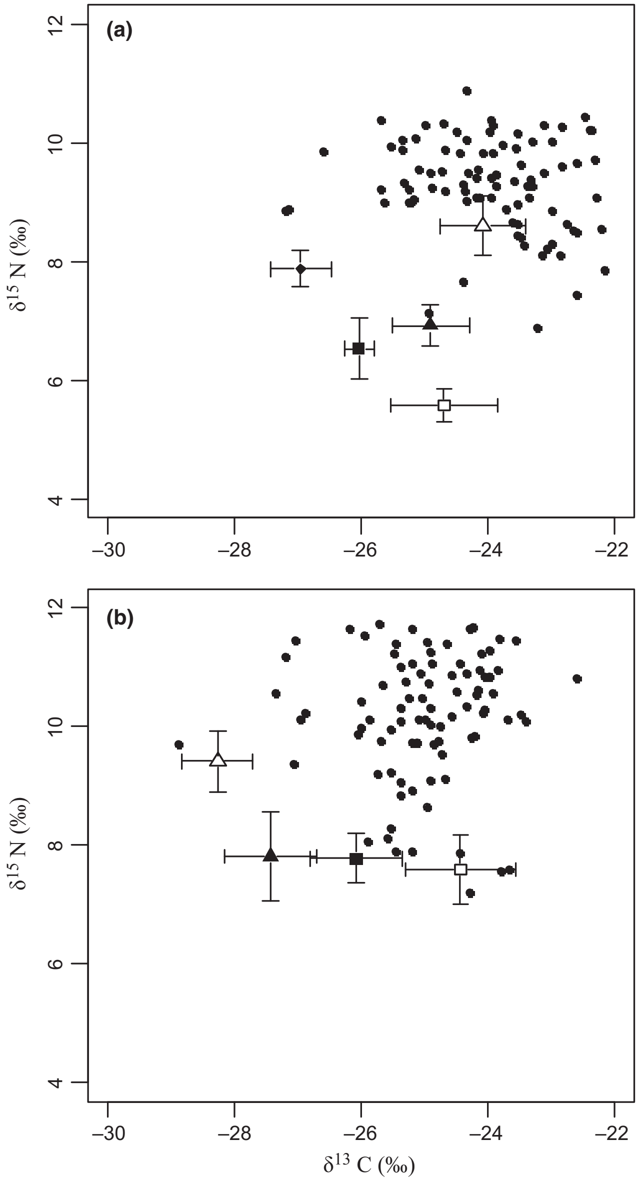

Fig. 1 δ^{13}C and δ^{15}N biplot of the experimental pond in (a) 2010 and (b) 2012. Mean values (±SE) are shown for *Pseudorasbora parva* (Δ), invertebrates (□), small (▲) medium (■) and large (♦) *P. clarkii*. Closed circles are individual values for *Anguilla anguilla*.

Linear regressions were run to compare isotopic signatures between fin and muscles samples. Significant relationships were found between eel muscle and fin tissues, for both δ^{13}C and δ^{15}N (F = 11.3, P < 0.05, R^2 = 0.53 and F = 10.7, P < 0.05, R^2 = 0.52, respectively). Subsequent analyses focus on fin isotopic signature for eels.

A Bayesian mixing model Stable Isotope Analysis in R (SIAR, Parnell *et al.*, 2010) was used to estimate the contribution of each group of prey; the three weight classes of crayfish were run separately to estimate the diet contribution of each class. For each prey group, the mean and standard deviation were used in the mixing model. After sensitivity tests on different fractioning factors, 3.3 ± 1.0‰ for δ^{15}N and 1.0 ± 1.0‰ for δ^{13}C were used in this study (Post, 2002 and Inger *et al*., 2010). The following analyses were performed on the median of 500 000 simulations for each individual.

Quadratic regressions were developed to characterise ontogenetic changes in δ^{15}N, δ^{13}C and the contribution of each prey to the eel diet. Linear models including the quadratic term $(TL)^2$ and its interaction term with the year of the study were used to assess potential ontogenetic diet changes. Non-significant interactions were removed from models. Spearman regressions were used to test the relationship between eel total length and the size of *P. clarkii* consumed: small (0–10 g), medium (10.1–25 g) and large (>25 g).

ANOVA tests were conducted to assess differences between sampling seasons for both fish and crayfish temporal trends, and Tukey *post hoc* tests were run to perform pairwise comparisons. When conditions for the application of a parametric test were not met, Kruskal–Wallis tests were used and Kruskalmc tests (package: pgirmess) for pairwise comparisons. Statistical analyses were performed using R software version 3.1.0 (R Development Core Team, Vienna, Austria).

Results

Eel abundance

The total number of eels increased strongly between October 2008 and May 2009 but declined quickly to the carrying capacity of the pond, approximately 4000 eels (348 eels ha^{-1}, Fig. 2).

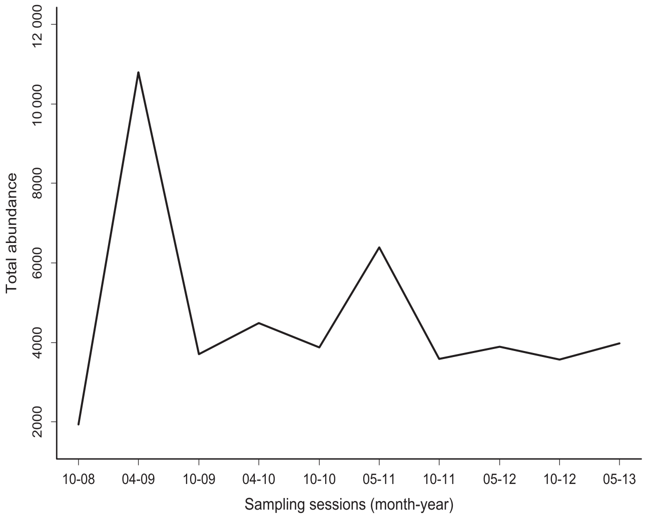

Fig. 2 Time series of the total abundance (per ha) of European eels estimated in the experimental pond between October 2008 and October 2013.

Eel diet

Eel δ^{13}C and δ^{15}N exhibited high trophic niche variability in the 2 years. The δ^{13}C values had a range of 5.0‰ (from −27.2 to −22.1‰) in 2010 and 6.3‰ (from −28.9 to −22.6‰) in 2012. The δ^{15}N values had a range of 4.0‰ (from 6.9 to 10.9‰) in 2010 and 4.5‰ (from 7.2 to 11.7‰) in 2012.

Mixing model results revealed that the red swamp crayfish made the greatest contribution to eel diet in both years with a mean (±SD; from min. to max.) proportion of 0.53 (±0.09; from 0.23 to 0.64) in 2010 and 0.50 (±0.05; from 0.22 to 0.55) in 2012. The mean rate of consumption of crayfish was significantly lower in 2012 than in 2010 ($t = 2.8$, $df = 141$, $P < 0.05$). Chironomids and shrimps represented the second most important food group for eels, with a mean proportion of 0.27 (±0.07; from 0.16 to 0.60) in 2010 and 0.30 (±0.07; from 0.11 to 0.62) in 2012. The contribution of invertebrates to eel diet was significantly higher in 2012 than 2010 ($t = -3.1$, $df = 171$, $P < 0.001$). The proportion of fish prey in eel diets averaged 0.17 (±0.04) in 2010, ranging from 0.05 to 0.27, and 0.17 (±0.05) in 2012, ranging from 0.05 to 0.28. This mean proportion did not differ between years ($t = -0.37$, $df = 167$, $P = 0.71$).

Ontogenetic changes in eel diet

Eel δ^{15}N was significantly and positively correlated to TL in 2010 ($R^2 = 0.51$, $n = 86$, $P < 0.001$) and in 2012 ($R^2 = 0.36$, $n = 86$, $p < 0.001$). The relationship between carbon (δ^{13}C) and TL was also significant in both 2010 and 2012 ($R^2 = 0.41$, $n = 88$, $P < 0.05$ and $R^2 = 0.30$, $n = 88$, $P < 0.001$, respectively).

Rates of consumption of crayfish increased with TL ($R^2 = 0.36$, $P < 0.001$; Fig. 3a and b; Table 1) to a proportional contribution of more than 0.60. A significant effect of the interaction between TL and year ($P < 0.01$; Table 1) indicated that the relationship between eel TL and crayfish consumption rate differed among years. The consumption rates on medium crayfish increased with TL in both 2010 (Spearman rho = 0.23, $n = 86$, $p < 0.05$) and 2012 (Spearman rho = 0.22, $n = 88$, $P < 0.05$). The consumption rate on large crayfish showed a significant positive correlation with eel TL in

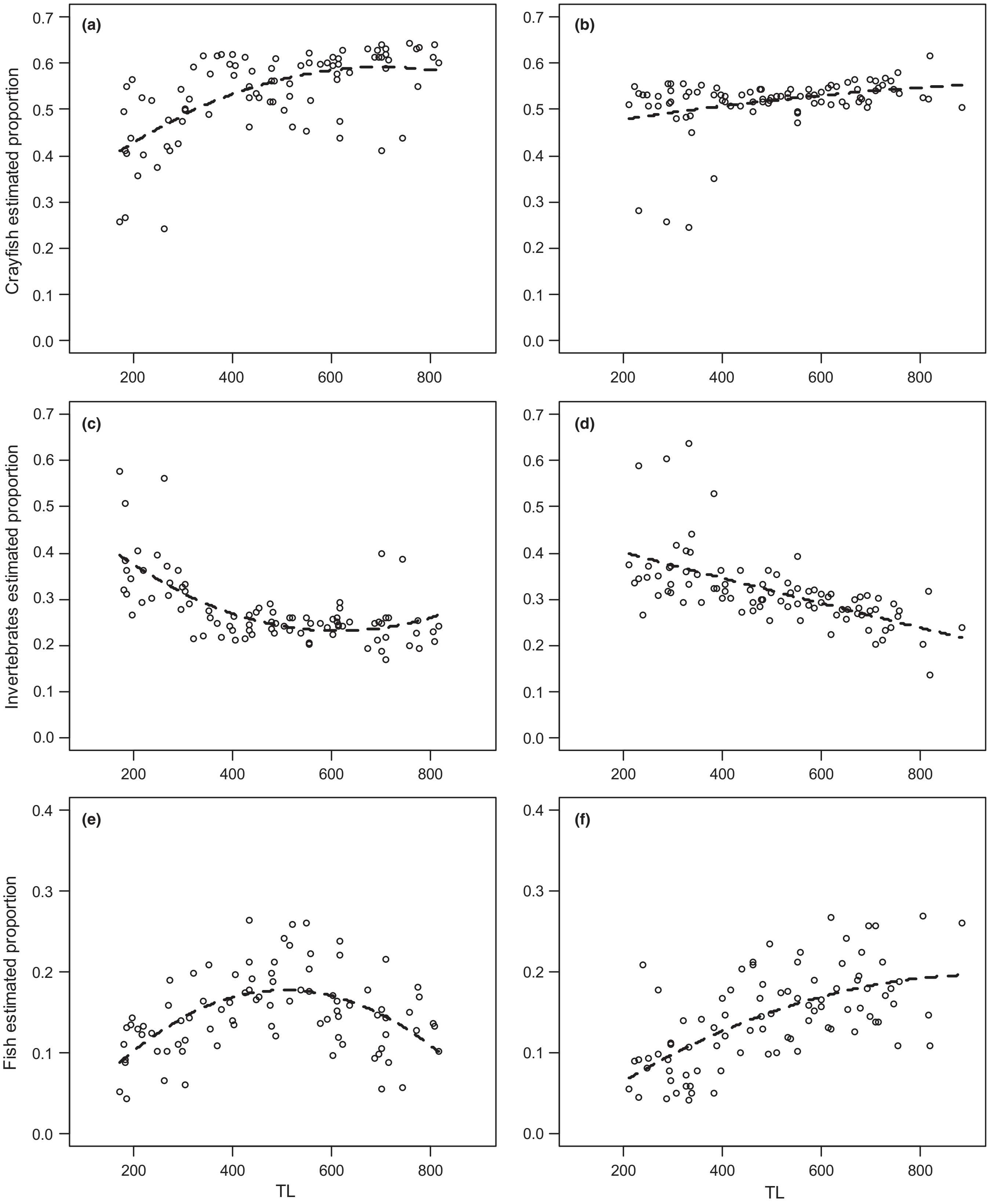

Fig. 3 Relationship between European eel total length (TL) and the estimated proportion of crayfish (a and b), invertebrates (c and d) and fish (e and f) in eel diets in 2010 (a, c and e) and 2012 (b, d and f). Dashed lines correspond to predictions from each linear model.

Table 1 Effects of eel total length (TL) and sampling year (Year) on the estimated proportion of fish, invertebrates and crayfish in eel diets using linear models

Variable	Parameters	Estimate	*F*-value	*P*
Crayfish	TL	7.1×10^{-4}	60.0	<0.001
	TL^2	-4.6×10^{-7}	11.9	<0.001
	Year	-9.8×10^{-3}	17.9	<0.001
	(TL:Year)^2	-1.1×10^{-7}	4.2	<0.05
Invertebrates	TL	-7.2×10^{-4}	98.6	<0.001
	TL^2	4.7×10^{-7}	8.0	<0.01
	Year	4.5×10^{-2}	25.1	<0.001
	(TL:Year)^2	–	–	NS
Fish	TL	5.4×10^{-4}	61.2	<0.001
	TL^2	-5.1×10^{-7}	11.1	<0.01
	Year	-5.4×10^{-2}	0.1	0.73
	(TL:Year)^2	1.8×10^{-7}	29.7	<0.001

Significant *P*-values correspond to $\alpha = 0.05$, NS, non-significant.

2010 (Spearman rho = 0.72, $n = 86$, $P < 0.001$). However, no correlation was found between small crayfish consumption rate and eel TL in 2010 or 2012 (Spearman rho = 0.15, $n = 86$, $P = 0.15$ and Spearman rho = 0.01, $n = 88$, $P = 0.89$), indicating that they are consumed by all eels regardless of eel size. These results show that all *P. clarkii* size classes are vulnerable to eel predation.

The estimated proportion of invertebrates in the eel diet changed during ontogeny with a positive correlation with TL ($R^2 = 0.43$, $P < 0.001$; Fig. 3c and 3d; Table 1).

The fish proportion in the eel diet was positively and significantly correlated with TL ($R^2 = 0.38$, $P < 0.001$; Fig. 3e and f; Table 1). Similarly, for crayfish proportion, the interaction between TL and years was significant, indicating a difference in the relationship between the two factors in 2010 and 2012.

Prey abundance

Pseudorasbora parva biomass showed seasonal variations between the spring and autumn (ANOVA test, $F = 15.1$, $df = 9$, $P < 0.001$; Fig. 4a). Fish biomass in October 2012 was significantly different from other autumn sampling values (Tukey test, $P < 0.001$ for all pairwise comparisons).

Similar to fish biomass, the trend for crayfish biomass showed seasonal variations between the spring and autumn sampling periods and also showed a substantial decline throughout the study period (ANOVA test, $F = 24.6$, $df = 9$, $P < 0.001$; Fig. 4b.). Putting aside the seasonal effects, biomass decline occurred during summer 2011 and biomass stayed low (CPUE above 2), but stable, from autumn 2011 to the end of the experiment in autumn 2013. Focusing on crayfish weight classes, small crayfish (0–10 g) did not exhibit significant temporal changes in abundance between 2009 and 2013 (Kruskal–Wallis test, $\chi^2 = 8.51$, $df = 4$, $P = 0.07$; Fig. 5), but medium (10–25 g) and large crayfish (>25 g) abundances did change significantly over time (Kruskal–Wallis test, $\chi^2 = 30.17$, $df = 4$, $P < 0.001$ and $\chi^2 = 39.53$, $df = 4$, $P < 0.001$, respectively). The biggest organisms disappeared totally from catches in 2012 and 2013 (Fig. 5).

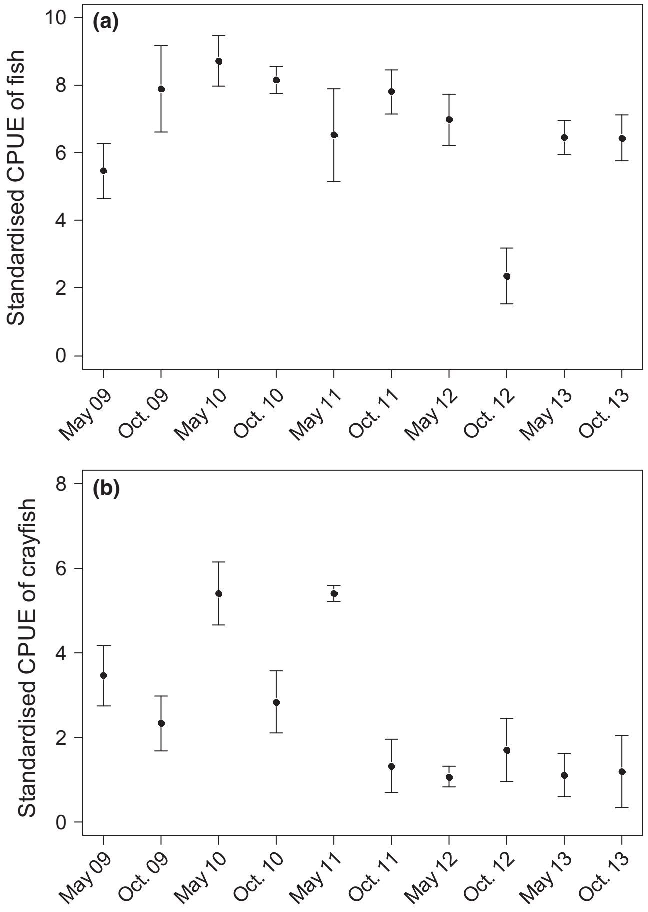

Fig. 4 Trends for (a) fish and (b) crayfish catch per unit effort (standard deviations shown) in the experimental pond from 2009 to 2013.

In the site used as a control for eel density, the crayfish population was stable, showing no trend (Kruskal–Wallis test, $\chi^2 = 9.52$, $df = 4$, $P = 0.05$, Fig. 6).

Discussion

Our results show that the European eel preys effectively on the invasive crayfish, which represented more than half of eel diet in both 2010 and 2012, and reaching 63% for the largest eels. This is consistent with the literature;

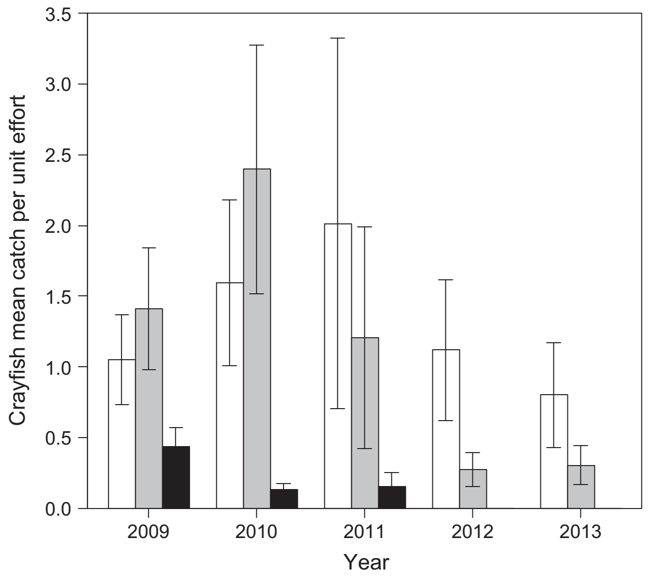

Fig. 5 Mean catch per unit of effort [ln(CPUE + 1)] for *Procambarus clarkii* weight classes (white: 0–10 g, grey: 10–25 g and black: >25 g) (standard deviations shown). Large crayfish disappeared from the system from 2012.

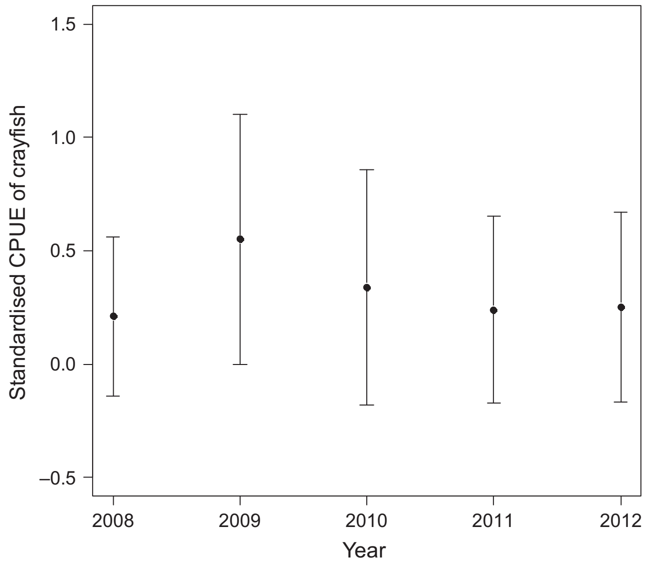

Fig. 6 Crayfish population trend in the canal adjoining the experimental pond from 2008 to 2012.

A. anguilla (Frutiger & Müller, 2002; Aquiloni *et al.*, 2010) and other *Anguilla* species consume *P. clarkii*. Stomach content analyses have revealed that crayfish comprised between 25 and 32% of the total diet of the long-finned eel (*A. dieffenbachii*) and from 43 to 57% for the short-finned eel (*A. australis*) (Hicks, 1997). *P. clarkii* was also the main food item in the stomach contents of the Japanese eel (*A. japonica*), comprising 37–90% (Kaifu *et al.*, 2012).

Isotopic analysis results highlighted that all weight classes of *P. clarkii* were subject to predation by eels. As reported in previous studies, smaller crayfish were most strongly preyed upon regardless of predator size (Englund & Krupa, 2000; Aquiloni *et al.*, 2010). In our study, larger crayfish (>25 g) became more important in the diet of the largest fish, mainly because eels are gape-limited. As observed in a laboratory experiment, adult crayfish are vulnerable to eels when crayfish are soft-shelled during the moulting period in open water (Aquiloni *et al.*, 2010).

Two years after the start of our experiment, the system seemed to have reached a carrying capacity for *A. anguilla* of 346 ind$\cdot$ha^{-1} (0.030 ind$\cdot$m^{-2}). This implies that resources (food and/or space) have been limiting for the eel population since October 2009. While fish prey have been quite stable since 2009 (except in October 2012, when there was poor reproduction by *P. parva*, but subsequent recovery in 2013), the crayfish population exhibited a significant decline, with CPUE decreasing from 5.6–7.7 to 2.6–3.4 on average between 2010 and 2013. The invasive species became scarcer in the system, and the observed trend in 2011 was confirmed in both 2012 and 2013. This trend was not observed in the nearby control population, highlighting that the main cause of the *P. clarkii* decline was local eel predation and not a regional effect. Although we observed a decline in the *P. clarkii* population, eradication of the population was not observed. However, organisms over 25 g disappeared from the system in 2012, and the number of adult animals and their size both declined.

Eel consumption of invertebrates was stable across years, while fish consumption increased. The bell-shaped curve for 2010 illustrates a clear ontogenetic effect with a rise in the proportion of fish in the eel diet until 500 mm and then a reduction in the largest eels (>500 mm), indicating a switch to crayfish prey. However, in 2012, the proportion of fish in the diet increased, especially for the largest eels. Concurrently, the fraction of crayfish prey in the eel diet was lower in 2012 than in 2010, and this was particularly obvious for the largest eels, which switched to fish prey. However, the estimated predation rate on *P. clarkii* in 2012 means that even if crayfish were scarce, eels were still looking for them in the system, highlighting the selective feeding behaviour of this predator. *A. anguilla* is known to be an opportunistic species whose diet can change according to prey availability (Lammens & Visser, 1989), but stomach contents analyses have shown that *A. anguilla* often forage on a single species

(Lammens & Visser, 1989; Dörner *et al.*, 2009). Other eels species (*A. australis*, *A. dieffenbachii*) are also known to be selective for a single prey species (Jellyman, 1989), and the Japanese eel is known to have selective behaviour towards the red swamp crayfish (Kaifu *et al.*, 2012). This predatory selectivity is likely to be the cause of the *P. clarkii* decline in our study. Further, this selective feeding appears to have consequences for the eel population, with a decrease in individual eel body weight indicating food limitation (C. Boulenger & A. J. Crivelli, pers. comm).

The decline of *P. clarkii* could also be partly due to indirect effects of eel predation. Previous study of the rusty crayfish (*Orconectes rusticus*) suggested that selective trapping of females may have strong consequences for reproductive success of the species (Hein *et al.*, 2007). Selective feeding on female crayfish deserves further research to understand whether the predator can alter the sex ratio of crayfish. Our results showed that predation affects juvenile crayfish (young of the year) and the stock of reproductive adults, resulting in a rapid decline. Furthermore, under fish predation pressure, threatened crayfish are known to change their behaviour and reduce activity. Time spent in the burrow increases, leading to a decrease in feeding rate, which could lead to mortality from starvation (Aquiloni *et al.*, 2010). Moreover, swimming, digging, touching and copulating behaviours may dramatically decline to minimise predation risk (Stein & Magnuson, 1976; Blake & Hart, 1995). By stimulating costly defensive behaviours, the presence of a predator may have significant demographic costs involving low fecundity and survival rates, decreased density and a negative impact on population growth rate (Preisser, Bolnick & Benard, 2005).

Reducing the number of *P. clarkii*, even without eradication, seems to have already had a beneficial impact in our study area. Indeed, in May and October 2013, the aquatic vegetation had totally recovered (A. J. Crivelli, personal observations) compared to previous years when crayfish occurred at high density. This improvement could be due, among other factors, to the indirect effects of eel predation on *P. clarkii*. Since *P. clarkii* mainly feeds on plants (Gutiérrez-Yurrita *et al.*, 1998), a predator-induced reduction in feeding rate would lead to reduced impact on aquatic vegetation. Thus, although the invasive species was still present in the study system at the end of our experiment, our study shows the potential of the European eel as an efficient management tool in its native range, to reduce red swamp crayfish abundance and control their negative effects.

Acknowledgments

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Ajustements dynamiques des sous-populations d'anguilles européennes et traits d'histoire de vie : apport du marquage individuel par PIT-tag pour la conservation.

Résumé :

L'anguille européenne *Anguilla anguilla* est un poisson catadrome, c'est-à-dire qu'il croît dans les eaux continentales (rivières, lacs, lagunes, etc.) avant de rejoindre son lieu de reproduction supposé dans la mer des Sargasses. Longtemps considérée comme nuisible, elle est désormais classée en danger critique d'extinction. La connaissance des facteurs qui influencent la dynamique des sous populations d'anguilles en milieu continental reste lacunaire et rend sa conservation difficile. Cette thèse a pour objectif d'étudier les facteurs qui influencent le nombre et les caractéristiques d'adultes (anguilles argentées) partant se reproduire en mer. Dans une première expérience, des suivis à long-terme (6 à 17 ans) de capture-marquage-recapture réalisés en conditions naturelle et expérimentale ont été utilisés pour étudier les patrons de croissance et de survie de trois sous-populations françaises. Les résultats montrent que la capacité d'accueil des systèmes influence l'orientation sexuelle, non déterminée génétiquement chez cette espèce. Par exemple, quand la compétition est forte, les individus optimisent leur survie au détriment de la croissance, et le sexe mâle est privilégié probablement pour limiter l'investissement couteux dans la maturation des gonades femelles. Une seconde expérience, menée dans un marais Camarguais, consistait à augmenter progressivement la densité d'anguilles par ajouts successifs d'individus jusqu'à la saturation du milieu. Les cohortes introduites lorsque le milieu arrive à saturation ont subi des mortalités plus élevées que celles déjà installées, suggérant une forte compétition entre les cohortes introduites. Finalement, les résultats de cette thèse montrent que les caractéristiques des hydrosystèmes (niveau de saturation et qualité de l'eau) influencent directement le nombre et les caractéristiques des futurs reproducteurs. Les implications de cette étude pour la conservation de cette espèce sont discutées.

Mots Clés : Anguille Européenne, dynamique de population, traits d'histoire de vie, croissance, survie, repeuplement, conservation, marquage-recapture, PIT-tag

Dynamical adjustments and life history traits of European eel sub-populations: Insights from the use of individual and PIT tags for conservation.

Abstract:

The European eels (*Anguilla anguilla*), which are catadromous fishes, grow in continental waters such as rivers, lakes, and lagoons before reaching the presumed Sargasso Sea spawning ground. This species, considered as a pest for a long time, is now classified as critically endangered. While attempts to preserve this species are now developed, they are limited by lacks of data on factors influencing eel population dynamics in continental environments. The aims of this PhD thesis were to study the factors influencing the abundance and features of adults (silver eels) when they leave continental waters to go to reproduce in the sea. Methods used were long-term mark-recapture monitoring (between 6 and 17 years) in natural and experimental conditions in ordered to study patterns of growth and survival in three French sub-populations. Results of the first experiment showed that the level of carrying capacity reached by the systems influences sexual orientation, which is not genetically determined in this species. For instance, individuals developed as males when the level of competition is strong, trading off to maximize survival at the cost of growth, probably to limit the costly investment in reproduction experienced by the female sex. Another experiment conducted in a freshwater march located in Camargue (South of France) consisted in successively increasing eel density up to system saturation. At saturation of the system, cohorts introduced suffered higher mortality than those previously installed, suggesting a strong competition between the different introduced cohorts. Finally, this PhD thesis provides strong support that the hydrosystem characteristics (saturation level and water quality) are determinant for eel populations as they directly influence the abundance and characteristics of futur spawners. Implications of these results for eel preservation are discussed.

Key words: European eel, population dynamic, life-history traits, growth, survival, stocking, preservation, mark-recapture, PIT-tag

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CRESCO, MNHN, Station Marine de Dinard, 38 du port blanc, 35800 Dinard, FRANCE