Histoires de vie larvaire et dispersion des Anguillidés : vers une approche bio-évolutive

Elodie Réveillac

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Université de La Rochelle
École Doctorale de La Rochelle
Littoral Environnement et Sociétés

Histoires de vie larvaire et dispersion des Anguillidae : vers une approche bio-évolutive

THÈSE DE DOCTORAT

Soutenue le 2 Décembre 2008

pour l'obtention du grade de Docteur de l'Université de La Rochelle

Spécialité : Océanologie Biologique et Environnement Marin

par

Élodie RÉVEILLAC

Composition du Jury :

M. Patrick PROUZET, Cadre de Recherche, LRHA IFREMER Anglet	Rapporteur
M. Philippe KEITH, Professeur, MNHN Paris	Rapporteur
Mme. Raymonde LECOMTE-FINIGER, C.R. au CNRS, Perpignan	Examinateur
M. René GALZIN, Professeur, CNRS-EPHE-UPVD, Perpignan	Examinateur
M. Olivier LE PAPE, Maître de Conférence, Université de Rennes	Examinateur
M. Paco BUSTAMANTE, Professeur, Université de La Rochelle	Examinateur
M. Éric FEUNTEUN, Professeur, MNHN Dinard	Directeur de thèse

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PUBLICATIONS ACCEPTÉES (en annexe)

1 - Réveillac E., Feunteun E., Gagnaire P.A., Berrebi P., Bosc P., Lecomte-Finiger R. & Robinet T. (**2008**). A*nguilla marmorata* larval migration plasticity as revealed by otolith microstructural analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(10): 2127-2137.

2 - Robinet T., **Réveillac E.**, Kuroki M., Rabenevana M.W., Valade P., Aoyama J., Gagnaire P.A., Berrebi P., Tsukamoto K. & Feunteun E. (**2008**). New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands. *Marine Biology*, 154: 453-463.

3 - Robinet T., Feunteun E., Keith P., Marquet G., Olivier JM., **Réveillac E.** & Valade P. (**2007**). Eel community structure, fluvial recruitment of Anguilla marmorata and indication for a weak local production of spawners from rivers of Réunion and Mauritius islands. *Environmental Biology of Fishes*, 78 : 93-105.

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2 - Réveillac E., Gagnaire PA., Berrebi P., Valade P., Lecomte-Finiger R., Robinet T. & Feunteun E. *Soumis à Journal of Fish Biology, Special Issue on Eels.* Reassessment of south-western Indian Ocean Anguillid glass eels identification protocols on morphological and genetic characteristics.

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5 - Réveillac E., Gagnaire PA., Berrebi P., Lecomte-Finiger R., Robinet T. & Feunteun E. Mise au point d'un protocole de détermination des civelles d'anguilles du sud-ouest de l'Océan Indien sur des critères morphologiques et génétiques. *Anguilles du Sud-ouest de l'Océan Indien: bilan des connaissances en vue de la mise en place d'une gestion durable de la ressource* (St Leu, Ile de La Réunion, Novembre 2006).

6 - Robinet T., **Réveillac E.**, Kuroki M., Feunteun E., & Lecomte-Finiger R. Identification des périodes de reproduction et localisation des aires de ponte potentielles. *Anguilles du Sud-ouest de l'Océan Indien: bilan des connaissances en vue de la mise en place d'une gestion durable de la ressource* (St Leu, Ile de La Réunion, Novembre 2006).

7 - Réveillac E., Lecomte-Finiger R., Robinet T., Valade P., Sasal P. & Feunteun E. Caractéristiques des peuplements et des recrues des Anguillidés du sud-ouest de l'Océan Indien : perspectives biogéographiques. *3èmes Rencontres de l'Ichtyologie en France* (Paris, France, Mars 2006). 3ème prix de la communication orale.

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1 - Martin S., Lacoue-Labarthe T., Oberhänsli F., **Réveillac E.**, Teyssié J-.L., Houlbreque F., Comeau S., Boisson F., Gattuso J-.P., Orr J. & Jeffree R. Effects of ocean acidification on early life stages of sea bream. *The Ocean in a high CO_2 World* (Monaco, Principauté de Monaco, Octobre 2008).

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SOMMAIRE

INTRODUCTION GENERALE **1**

CHAPITRE I

METHODOLOGIES **17**

PARTIE 1
L'OTOLITHE: ENREGISTREUR DE VIE 19

PARTIE 2
IDENTIFICATION DES CIVELLES DU SUD-OUEST DE L'OCEAN INDIEN SUR CRITERES MORPHOLOGIQUES ET GENETIQUE 33

CHAPITRE II

MECANISMES ET CARACTERISTIQUES SPECIFIQUES DE LA DISPERSION LARVAIRE **47**

PARTIE 1
DIVERSITE DES HISTOIRES DE VIE LARVAIRE D'*ANGUILLA MOSSAMBICA*: INDICES SUR LES MECANISMES DE LA DISPERSION LARVAIRE VERS MADAGASCAR 49

PARTIE 2
PLASTICITE DE LA DISPERSION LARVAIRE D'*ANGUILLA MARMORATA* REVELEE PAR L'ANALYSE DE LA MICROSTRUCTURE DES OTOLITHES 67

PARTIE 3
DISPERSION LARVAIRE DE L'ANGUILLE EUROPEENNE *ANGUILLA ANGUILLA* EXAMINEE AU TRAVERS DES VARIATIONS SPATIO-TEMPORELLES DES HISTOIRES DE VIE LARVAIRE ET DES CARACTERISTIQUES BIOMETRIQUES AU RECRUTEMENT 89

CHAPITRE III

BIOGEOGRAPHIE DE LA DISPERSION LARVAIRE DES ANGUILLES DU SUD-OUEST DE L'OCEAN INDIEN RECONSTITUEE PAR EXAMEN DES TRAITS DE VIE LARVAIRE **113**

CHAPITRE IV SYNTHESE

IMPLICATIONS EVOLUTIVES DES VARIATIONS DES TRAITS DE DISPERSION LARVAIRE CHEZ LES ANGUILLES **135**

CONCLUSIONS ET PERSPECTIVES **159**

GLOSSAIRE **167**

BIBLIOGRAPHIE **171**

ANNEXES **193**

INTRODUCTION GÉNÉRALE

INTRODUCTION GÉNÉRALE

L'Évolution[1], telle qu'énoncée par Darwin (1859), a apporté une vision dynamique des processus fondamentaux régissant l'existence des êtres vivants. "Rien n'a de sens en biologie, si ce n'est à la lumière de l'Évolution" (Dobzhansky 1973). Objets de nombreux débats et fascinations, les causes et les mécanismes impliqués dans ce processus complexe sont, aujourd'hui encore, abondamment étudiés en vue de reconstituer les changements passés, de comprendre les mutations en cours, et d'augurer de leur nature face aux futures modifications de l'environnement. Dans cette entreprise, la diversité des histoires de vie[2] a été maintes fois reconnue comme une caractéristique clef de l'évolution des espèces en raison de la résilience[3] qu'elle leur confère (Hilborn et al. 2003, Beechie et al. 2006). Cette caractéristique est en effet source "d'adaptabilité" dont les limites gouvernent la fixation, l'extinction, le morcellement et la divergence des populations et des espèces.

Parmi les processus qui caractérisent les histoires de vie et sont susceptibles d'alimenter leur diversité, la dispersion[4] est probablement celui le plus impliqué dans la persistance et l'évolution des espèces (Clobert et al. 2003). D'une part, la dispersion régule la charge en individus d'un habitat alors plus propice au maintien des populations. D'autre part, l'émigration et donc l'exploration du milieu environnant augmente les probabilités de rencontrer des habitats favorables et de fonder de nouvelles colonies entretenant ou non des liens avec la population d'origine.

A ce titre, les anguilles sont parmi les animaux les plus illustres en terme de capacité de dispersion de leurs larves, qui réalisent la première phase, clef, du cycle de vie complexe de ce poisson vieux de plusieurs dizaines de millions d'années (Aoyama et al. 2001, Lin et al. 2001).

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[1] Évolution: modification au fil des descendances (Darwin 1859), changements opérés entre les générations d'une même lignée (Ridley 2004)

[2] Histoire de vie : déroulement du cycle de vie (Stearns 1992)

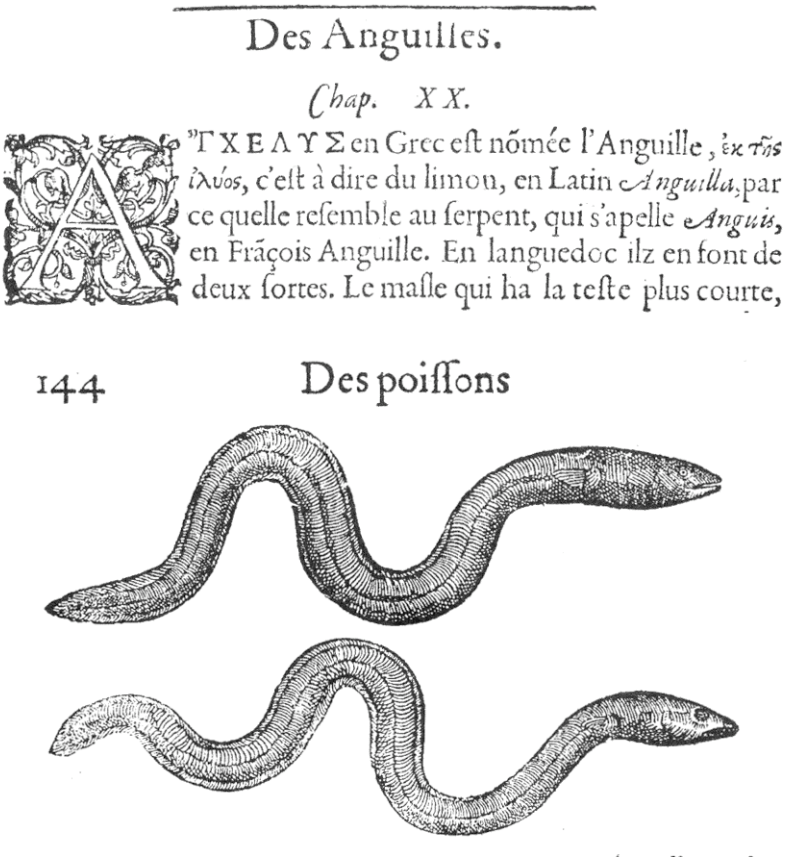
[3] Résilience: mesure de la persistance des systèmes ou des populations et de leur capacité à absorber les changements et les perturbations tout en maintenant la même relation entre les populations ou les variables d'état (Holling 1973)

[4] Dispersion: mouvement définitif d'un organisme d'un lieu à un autre (Roff et Fairbairn 2003)

L'anguille et son cycle de vie

"ΑΓΧΕΛΥΣ en Grec est nommée l'Anguille, εχ τηςιλυος, c'est à dire du limon, en Latin Anguilla, parce qu'elle ressemble au serpent, qui s'appelle Anguis, en Français Anguille". C'est ainsi que Guillaume Rondelet, premier auteur d'une grande compilation illustrée sur la vie maritime, entame la description de l'anguille dans le *Libri de piscibus marinis in quibus verae piscium effigies expressae sunt* paru en 1554 et traduit en Français par son élève Laurent Joubert dans L'Histoire entière des poissons en 1558. S'en suivent anecdotes et hypothèses sur son cycle de vie, alors emprunt d'un grand mystère, qui contribuèrent à alimenter le mythe du poisson serpent à génération spontanée (cf. Extrait ci-après).

Extrait de "L'Histoire entière des poissons" par Guillaume Rondelet (1558), réédition CTHS (2002), sur la description de l'anguille.



Des Anguilles.

Chap. XX.

"ΓΧΕΛΥΣ en Grec eſt nõmée l'Anguille, ἐκ τῆς ἰλύος, c'eſt à dire du limon, en Latin *Anguilla*, par ce quelle reſemble au ſerpent, qui s'apelle *Anguis*, en Frãçois Anguille. En languedoc ilz en font de deux ſortes. Le maſle qui ha la teſte plus courte,

144 Des poiſſons

plus groſſe,é plus large.é l'appellẽt *Margaignon* La femelle qui ha la teſte plus petite, é plus pointüe, qu'ilz nomment *Anguille fine.* De ceſte differẽce nous en parlerons ci apres. Toute Anguille naiſt aux eaux douces, é ſeule de tous poiſſons ſemblables entre aux eſtangs de mer, é en la mer meſme, autrement elle vit aux riuieres, lacs, é eſtangs. C'eſt poiſſon long, gliſſant, ſans ecailles, couuert de cuir, duquel on le depouille aiſemẽt. Ell'ha la bouche aſſes grande, garnie de petites dens, les ouies petites, couuertes de peau, d'ouuerture petite, qui eſt la cauſe pourquoi toſt ſont eſtouffées aux eaux troubles, é pourquoi elles viuent aſſes long tems hors de l'eau. Tout prés les ouies ont deux fort petites æles. Par les flechiſſemens du reſte du corps elles ſe meuuent, é ſe pouſſent dans l'eau. Au lieu d'æles, depuis le millieu du dos, é depuis le trou des excremẽs elles ont comme vn bord, plus toſt peau que æle qui enuironne tout le reſte du corps. Elles ont vn long conduit par où deualle leur viande, l'eſtomac long, le foïe grand é rouge, d'où pend la bourſe du fiel cler cõme eau. La chair eſt graſſe é gluante. Les Anguilles naiſſent dans la pourriture, comme les vers en terre, ce que lon trouue par experience. Car autresfois vn cheual mort eſtant ietté dans leſtang de Maguelone, vn peu apres on i vit innumerables Anguilles, ce qui ne faut entendre, qu'elles naiſſent ſeulement en la pourriture d'vn cheual mort, mais auſsi des autres beſtes, é es autres pourritures. Aucuns dient que les Anguilles s'engẽdrent de celles qui meurent de force de vielleſſe, é pourries. Ariſtote eſcrit que les

Anguilles ne s'engendrent point par fraier, qu'elles n'ont point d'œufs, é qu'on n'en trouua iamais vne qui eut ou œufs ou ſemence, ne aucuns conduits ou pour ſemence, ou pour matrice. Parquoi ceſte ſorte de poiſſon aiant ſang, eſtre engendrée ſans œufs, é ſans fraier, ce que lon a conneu de ce qu'en aucuns eſtangs limonneux tout le limon ietté hors, de rechef ſi engendrent des Angnilles, s'il i tumbe de la pluie, car en tems ſec elles ne peuuent eſtre engendrées, par ce qu'elles viuent de pluies. é s'en nourriſſent. Il ni a point donc entre les Anguilles de difference de maſle é de femelle. Pour cela difference ſuſdite priſe de la teſte d'icelles, ſera difference d'eſpece, non pas de ſexe. Pline a eſté d'autre opinion touchant la generation des Anguilles. Les Anguilles, dit il, ſe frottent contre les rochiers, ceſte craſſe qui ſe raele prend vie, é n'i a autre generation d'icelles. Athenée en eſcrit ainſi. Les anguilles fraient en s'entrebraſſant, d'où ſort quelque craſſe, ou humeur gluante, de la quelle tumbée au limon l'Anguille s'engendre. Oppian en eſcrit ne plus ne moins. Certainement i'ai veu des Anguilles s'entrembraſſer, é fraier, é croi que toutes parties neceſſaires à leur generation ne leur manquent, car au bas du ventre les femelles ont conduit pour matrice, les maſles de la ſemence. Mais ces parties ne paroiſſent

eſtans toutes couuertes de greſſe,comme ne les œufs auſsi pour ceſte meſme raiſon.Parquoi ie penſe qu'il i a des Anguilles qui naiſſent par le fraier du maſle auec la femelle,d'autres qui naiſſent dãs la pourriture.Les Anguilles viuent d'eau douce é clere, pour ceſte raiſon ceux qui font des Viuiers d'Anguilles,comme eſcrit Ariſto te prennent bien garde,que par les lieux où ilz, les baſtiſſent, n'i coure qu'eau nette,car ſi l'eau eſt trouble, elles eſtouffent. Voila pourquoi en aucunes riuieres de France l'hyuer, quand pour les grandes pluies,ou neges fondües, les eaux accroiſſent, é ſe troublent fort,dans des naſſes é autres rets propres à prendre poiſſon, on prend fort grande quantité d'Anguilles,leſquelles on ſale pour le prochain careſme.Pour ceſte raiſon Ariſtophane compare ceux qui font leur prouſit des guerres é perturbations des Republiques, aux peſcheurs d'Anguilles, leſquels ne prennent rien ſi ne troublent l'eau.De là meſme,ſelon mon aduis,vient le prouuerbe commun,peſcher en eau trouble.qui ſe dit de ceux qui ne font leur proſit,ſi non que de guerres,de mutineries,de noiſes, é de procés. Les Anguilles ne flottent point ſur l'eau eſtans viues,é ne s'eſleuent pas gueres au haut de l'eau comme les autres poiſſons, car elles ont le ventre petit,par conſequent peu d'air dedans peut eſtre ſouſtenües en haut. On ſale les Anguilles pour eſtre meilleures, car leur viſcoſité eſt corrigée par le ſel.Celles qu'on prend en la mer ſont meilleures.On en prend en noſtre eſtang de Lates,de fort grãdes,comme de trois coudées.Au Gange i en a de longues de trente pieds.Les Anguilles ſont viſqueuſes,aſsés nourriſſantes, mauuaiſes à toutes perſones ſubiettes à maladies prouenantes de phlegme,comme la grauelle,les goutes,certaines douleurs de teſte. Elles ne ſont pas ſaines en paſte,é les faut manger à l'entrée de table.Celles qui ſont roſties en la Broche ſont meilleures.

Il faut attendre la fin du XIXème siècle pour que le mystère de la naissance et du développement larvaire de l'anguille soit élucidé par Grassi et Calandruccio (Grassi 1896). Ils furent en effet les premiers à établir que l'espèce marine alors connue sous le nom de *Leptocephalus brevirostris* était en fait la forme larvaire de l'anguille (Fig. 1). Cette **larve leptocéphale** (du grec: tête mince) transparente, classiquement décrite comme ayant la forme d'une feuille de saule, éclot en milieu océanique quelques heures après la fécondation (Tanaka 2003). Elle possède des tissus et des organes internes peu développés, peu de myomères, ne présente pas de mélanophores, et est composée majoritairement de matière gélatineuse acellulaire comprenant en forte proportion des glycosaminoglycanes (GAGs, Otake 2003). Cette matrice imbibée d'eau confère à la larve une turgescence qui remplace la colonne vertébrale inexistante, ainsi qu'une réserve d'énergie utilisée par la larve

uniquement pour son métabolisme basal (Bishop et Torres 1999, 2001). Les mécanismes d'alimentation ainsi que la nature de la ressource énergétique de la larve leptocéphale sont encore mal connus. Les contenus du tube digestif ont souvent révélé la présence de matières détritiques, mais les capacités de digestion des leptocéphales ont été remises en cause en raison de la faible activité enzymatique du système digestif. D'autres hypothèses ont proposé une nutrition par voie de diffusion transcutanée (Hulet et Robins 1989 in Mochioka 2003). Il demeure, néanmoins, dans tous les cas, que la faible demande en nutriments liée à un métabolisme très faible par rapport aux autres larves de poisson est reconnue comme une particularité conférant à la leptocéphale des possibilités de maintien dans le milieu océanique hors du commun (Pfeiler et Govoni 1993, Bishop et Torres 2001). Ainsi, grâce à cette capacité, la larve leptocéphale peut parcourir jusqu'à de très grandes distances (8000 km pour l'anguille Européenne) transportée par les courants océaniques et, potentiellement, aidée par un comportement de nage active et/ou orientée (Williamson 1987, Lecomte-Finiger 1992, Bishop et Torres 1999, 2001). Au bout d'un laps de temps variable selon les individus et les espèces (de quelques mois à plus d'une année) la larve subit, sous l'action de facteurs mal identifiés, une profonde métamorphose[5] en **civelle** (aussi appelée "pibale" ou encore "civette"). Elle acquiert alors une forme cylindrique par remaniement de toute sa structure interne, se dote d'un squelette et de myomères développés. Parallèlement, son acuité visuelle augmente avec l'apparition de cônes rétiniens en plus des bâtonnets présents chez la larve. Son tube digestif est également totalement remanié et ne devient fonctionnel qu'une fois la métamorphose terminée, si bien que la larve, qui ne se nourrit donc pas pendant cette phase, utilise l'ensemble des réserves préalablement accumulées sous forme de GAGs (Otake 2003). La civelle, armée pour quitter le milieu pélagique, gagne par nage active et orientée les habitats côtiers, estuariens ou dulcicoles (remontée en eau douce facultative, Tsukamoto 1998, Tsukamoto et Arai 2001) où elle s'établit pour entamer une phase de croissance sous forme d'**anguille jaune**. Durant cette étape, différents comportements allant de la complète sédentarité au nomadisme peuvent être observés et se succéder chez un même individu selon son âge, son statut physiologique, les paramètres de densité-dépendance de la

[5] Métamorphose: processus du développement précédé par une phase larvaire fonctionnelle, libre et qui produit une phase juvénile fonctionnelle.

population, la température, la disponibilité de la ressource ou encore le régime hydrologique de son habitat (Feunteun et al. 2003). Après une durée variable (de l'ordre moyen d'une dizaine d'années), l'anguille jaune entame une phase dite de dévalaison et de retour vers la zone de reproduction océanique, accompagnée d'une métamorphose en adulte mature dit **argenté**. La durée de cette migration et les mécanismes d'orientation mis en place sont mal identifiés. Néanmoins, il est certain que les adultes ne reviennent pas de ce voyage, et que donc la reproduction leur est fatale (espèce semelpare).

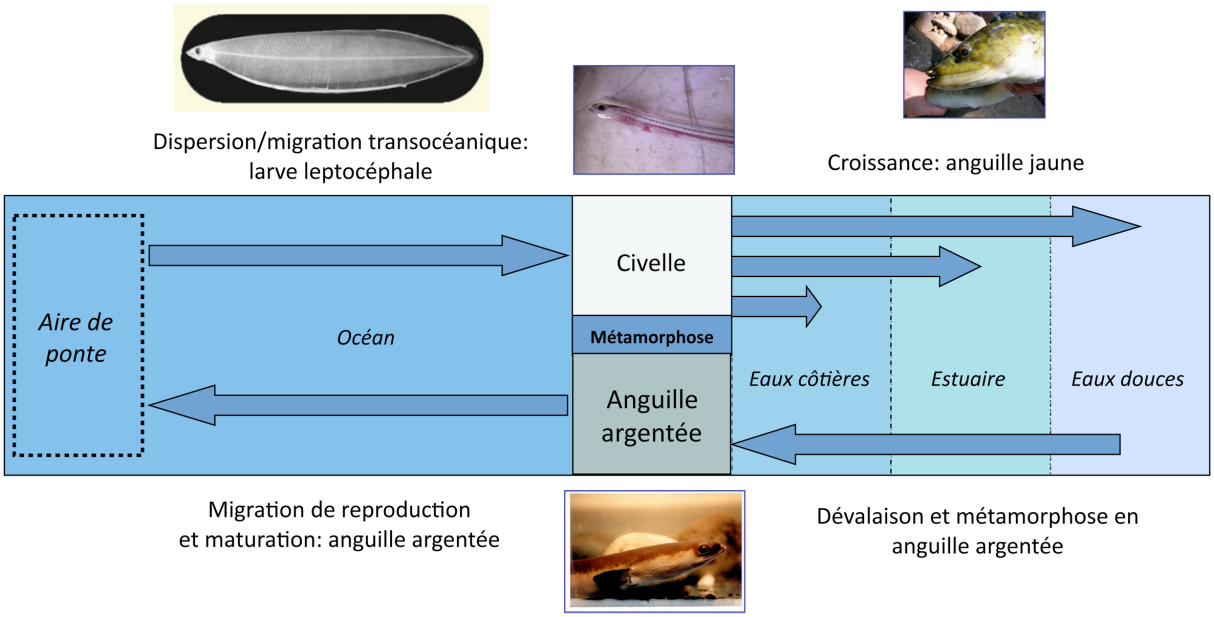


Figure 1. Cycle de vie de l'anguille et habitats colonisés par les différentes phases de développement.

L'origine exacte de ce cycle est inconnue. Le genre *Anguilla*, composé aux deux tiers d'espèces tropicales, appartient au superordre des Elopomorphes caractérisé par le développement indirect via la larve marine de type 2, qu'est la larve leptocéphale (Bishop et Torres 2001). A l'exception des espèces du genre *Anguilla*, tous les Anguilliformes et les très proches Saccopharyngiformes (anguilles abyssales) (Inoue et al. 2004), réalisent leur cycle de vie entièrement en milieu marin. Cet ensemble d'informations a conduit certains auteurs à proposer que les anguilles descendraient de poissons marins tropicaux déjà possesseurs de la larve leptocéphale et donc d'une phase de dispersion larvaire (Tsukamoto et al. 2002, Minegishi et al. 2005). L'anguille, ainsi à tort qualifiée d'eau douce (freshwater eel), semblerait avoir évolué

secondairement vers la catadromie, supposément pour diminuer la compétition pour la ressource et l'espace (Tsukamoto et al. 2002). Le caractère facultatif de la remontée en eau douce et donc de la diadromie (Tsukamoto 1998, Tsukamoto et Arai 2001) observé sur certaines espèces tempérées trouverait donc son explication dans l'origine marine du genre. De plus, le retour de ces espèces à un cycle de vie totalement marin semblerait dénoter qu'elles ne trouvent plus d'avantage à gagner les eaux continentales. Tsukamoto et al. (2002) suggèrent que la colonisation des eaux douces en milieu tropical se serait faite pour des raisons de compétition mais aussi d'abondance de la ressource, avantage que perdraient les espèces qui "s'exportent" en milieu tempéré où les eaux marines sont plus riches que les eaux douces.

Distribution géographique actuelle

De nos jours 15 espèces, dont 2 ou 3 sont subdivisées en sous-espèces (litige sur *A. australis*, Dijkstra et Jellyman 1999), peuplent la quasi-totalité des côtes mondiales à l'exception de l'Atlantique Sud, du Pacifique Est et des régions polaires (Ege 1939) (Fig. 2). Cinq seulement sont tempérées et toutes les autres réalisent leur cycle de vie totalement en milieu tropical.

L'océanographe Danois Johannes Schmidt (1922) fut le premier à localiser, dans la Mer des Sargasses, les aires de ponte partiellement communes des deux espèces de l'Atlantique Nord, *i.e.* l'anguille Américaine *A. rostrata* et l'anguille Européenne *A. anguilla*. Ce n'est que soixante-dix ans plus tard que Tsukamoto (1992) localisa celle de l'anguille Japonaise *A. japonica* au niveau des monts sous-marins situés à l'Est des Mariannes dans le Pacifique Nord. Il faudra attendre encore dix ans pour que Miller et al. (2002) obtiennent de solides preuves sur l'emplacement de l'aire de ponte de la population nord Pacifique de l'anguille marbrée *A. marmorata*, tout près de celle de l'anguille Japonaise. En ce qui concerne les autres espèces, aucune aire de ponte n'a jamais été délimitée avec certitude. Néanmoins, des hypothèses ont été émises pour la majorité d'entre elles grâce aux travaux de Jespersen (1942) basés sur la collecte de larves leptocéphales au cours d'une expédition océanographique autour du monde. Malheureusement, les larves échantillonnées à cette occasion n'ont pu

être toutes identifiées au niveau de l'espèce, rendant impossible une interprétation très précise des collectes.

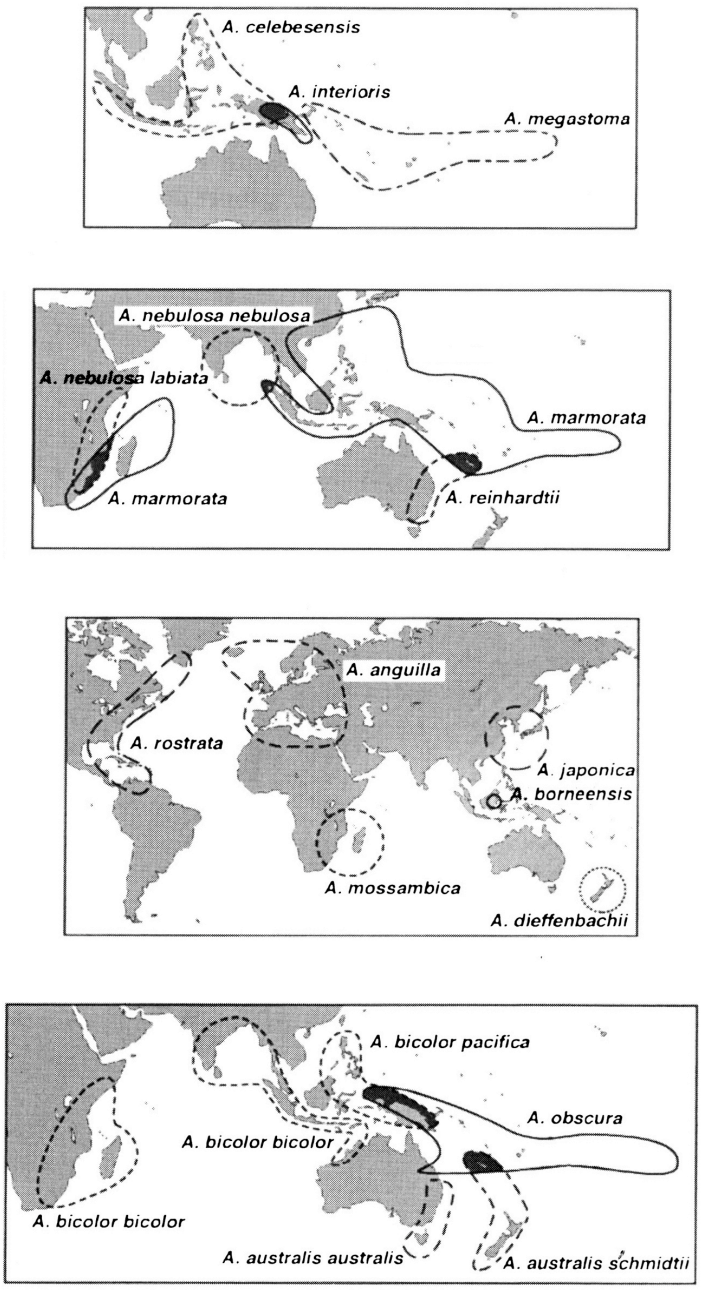


Figure 2. Distribution mondiale des 15 espèces et 6 sous-espèces d'anguilles (*Anguilla* spp.) d'après Aoyama (2003).

Anguilla spp.: origine et phylogéographie

C'est d'Indonésie, considérée comme le centre de la biodiversité marine (Briggs 1999), que le départ de la radiation du genre *Anguilla* est supposé avoir eu lieu (Tsukamoto et al. 2002). Ege (1939) fut le premier à ériger *Anguilla celebesensis* au

rang d'espèce la plus ancienne sur des critères anatomiques. Une soixantaine d'années plus tard, grâce à l'analyse moléculaire, Aoyama et Tsukamoto (1997) et Aoyama et al. (2001) proposèrent que ce titre devait revenir à l'anguille de Bornéo *A. borneensis*. A partir de l'arbre phylogénétique généré par l'examen de l'ARN 16S mitochondrial, ils suggérèrent également un scénario d'évolution et d'expansion biogéographique intitulé "l'hypothèse du Corridor de Téthys" (Fig. 3), basé sur un retro-calcul de période d'apparition du genre estimée à 50-60 millions d'années avant notre ère. Selon cette hypothèse, les anguilles se seraient dispersées à partir de l'Indonésie pour atteindre, via la mer de Téthys, l'actuel Océan Atlantique, fondant alors les deux espèces les plus apparentées et les plus récentes, *i.e.* l'anguille Américaine *A. rostrata* et l'anguille Européenne *A. anguilla*.

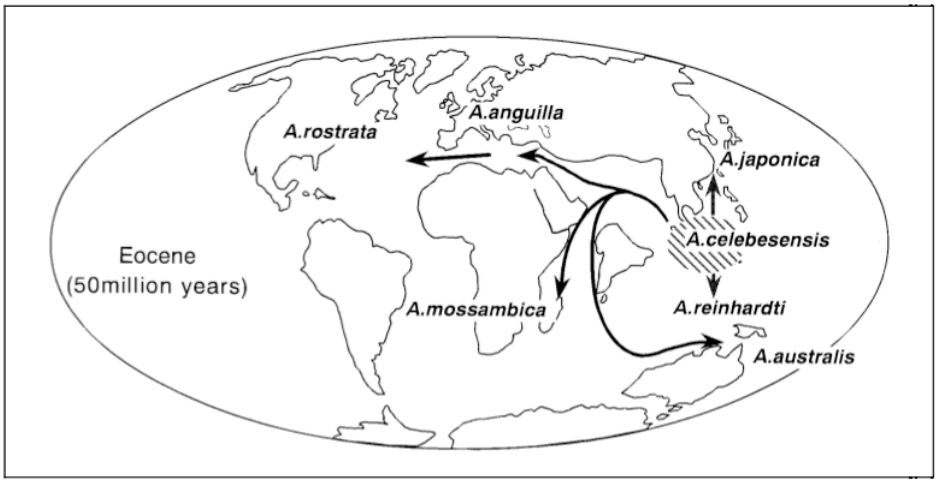


Figure 3. Représentation schématique de l'hypothèse du "Corridor de Téthys" proposée par Aoyama et Tsukamoto (1997) pour expliquer l'expansion du genre *Anguilla* qu'il font remonter à -50 Ma.

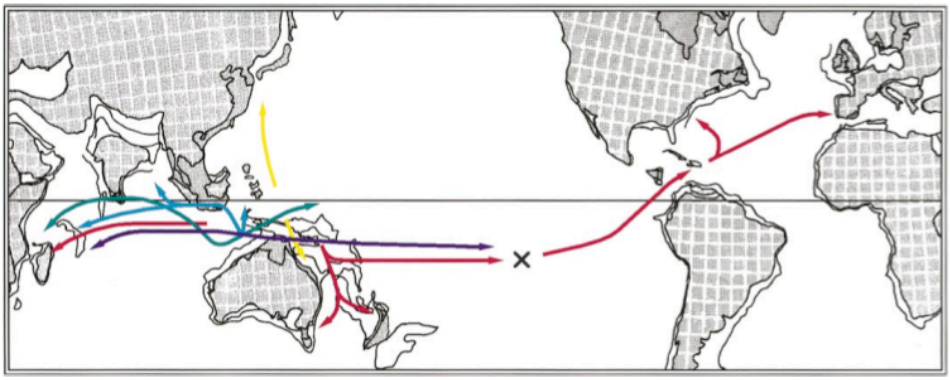


Figure 4. Scénario d'expansion du genre *Anguilla* (-20 Ma) proposé par Lin et al. (2001) intitulé "Hypothèse de la Route Panaméenne". La croix représente l'aire de ponte présumée d'*Anguilla obscura* qu'ils supposaient être l'ancêtre des espèces Atlantiques.

Lin et al. (2001) proposèrent, dans le même temps, un scénario d'expansion et de diversification du genre totalement opposé à celui d'Aoyama et Tsukamoto (1997) qu'ils nommèrent "la route Panaméenne" (Fig. 4). Leur proposition s'est appuyée sur une estimation de l'origine du genre à seulement 20 millions d'années, alors que la mer de Téthys était déjà fermée, et sur le fait que l'espèce qu'ils identifiaient comme l'ancêtre commun aux anguilles Atlantiques était *A. obscura* distribuée dans le Pacifique ouest. La dernière étude en date ne supporte aucun de ces scenarii (Minegishi et al. 2005). Basée sur la cartographie de l'ensemble des séquences du génome mitochondrial des 15 espèces du genre, le nouvel arbre phylogénétique propose qu'*A. mossambica* serait l'espèce la plus ancienne. De plus les résultats montrent que de probables épisodes de dispersion multidirectionnelle et/ou d'extinction empêchent la reconstruction complète de l'arbre phylogénétique (Minegishi et al. 2005). Ainsi, il semble encore difficile et prématuré de reconstituer l'expansion géographique et la radiation du genre *Anguilla*, néanmoins réaffirmé comme étant originaire du milieu tropical.

Modes de spéciation

Sans pouvoir donc reconstituer géographiquement l'expansion du genre, il est tout de même certain qu'elle a engendré les espèces répertoriées aujourd'hui. Ishikawa et al. (2004) ont proposé que deux principaux mécanismes régissent la spéciation des anguilles au vu du fonctionnement de leur cycle de vie en boucle migratoire (Tsukamoto et Aoyama 1998).

Le premier scénario (Fig. 5, I) décrit une dissociation géographique et/ou temporelle des boucles de migration, induisant un asynchronisme de ponte ou une dissociation de l'aire de reproduction entre les sous-unités générées. Cette situation peut également survenir suite à l'émergence, plus ou moins soudaine, de barrières géographiques et/ou temporelles à la dispersion larvaire ou à la migration génésique des adultes. Le second scénario (Fig. 5, II) implique le rôle d'individus fondateurs qui colonisent de nouveaux habitats à la faveur d'un changement courantologique ponctuel. L'existence de ce comportement fondateur a d'ailleurs déjà été décrit comme étant un trait caractéristique des anguilles (Feunteun et al. 2003).

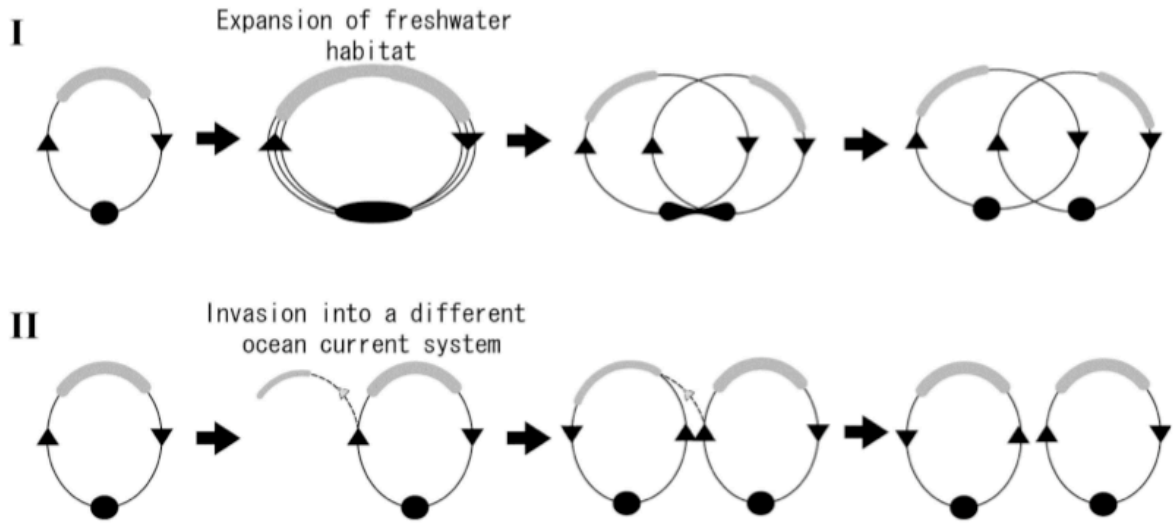


Figure 5. Scenarii alternatifs de spéciation chez les Anguillidae (*Anguilla* spp.) (I) par dissociation des boucles migratoires et (II) par invasion d'un nouveau système océanique par un ou plusieurs individus. Cercles: boucles de migration (Tsukamoto et al. 2002); ellipses noires: aires de ponte; arcs grisés: habitats de croissance; flèches ascendantes: dispersion larvaire; flèches descendantes: migration des adultes (de Ishikawa et al. 2004).

Contexte de la thèse

Les anguilles semblent donc avoir évolué par élargissement et fractionnement des boucles de migration depuis les espèces tropicales aux boucles courtes, jusqu'aux espèces tempérées qui continuent de se reproduire en milieu tropical mais émigrent vers de plus hautes latitudes pour effectuer leur phase de croissance (Fig. 6). Cette évolution apparait étroitement liée (cause ou conséquence) à celle des capacités de dispersion de la phase larvaire, étape cruciale pour le renouvellement des populations, la colonisation des habitats de croissance, la dynamique de la distribution géographique et la connectivité des localités continentales et insulaires.

Quelles sont les capacités de dispersion larvaire des anguilles? Quels sont les processus biologiques et les mécanismes physiques mis en jeu? Les capacités de dispersion varient-elles entre individus d'une même espèce, et si oui, pourquoi? Comment ces variations nous renseignent-elles sur la biogéographie des boucles migratoires des espèces? Varient-elles d'une espèce à une autre? Quelle est leur contribution à l'évolution passée des anguilles? Quel peut être leur rôle dans le futur

pour faire face aux changements environnementaux annoncés? Voici autant de questions importantes qui manquent aujourd'hui de réponses, notamment dans un contexte de déclin des stocks d'anguilles tempérées qui nécessite la mise en place de plans de gestion draconiens basés sur la connaissance du cycle de vie.

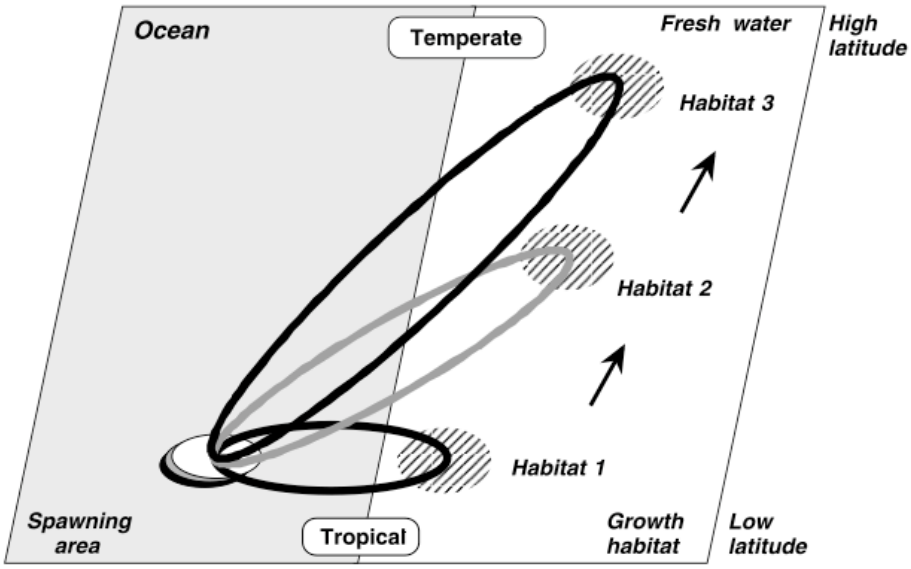


Figure 6. Schéma représentant la boucle de migration d'une espèce tropicale, qui en se modifiant, devient une espèce tempérée: les larves leptocéphales sont dispersées et recrutent à des latitudes de plus en plus élevées induisant un changement des habitats de croissance alors même que les adultes continuent de retourner se reproduire en milieu tropical (de Tsukamoto et al. 2002).

Les objectifs de cette thèse s'inscrivent dans cette problématique.

Un premier chapitre méthodologique consistera, d'une part, à présenter l'outil permettant d'examiner les caractéristiques de la phase de dispersion larvaire: l'analyse de la microstructure des **otolithes**. D'autre part, puisque l'intégralité des analyses des traits de vie larvaire se fait a posteriori sur des civelles capturées au recrutement, un **outil diagnostique d'identification** spécifique des civelles d'espèces recrutant en sympatrie dans le sud-ouest de l'Océan Indien sera fournit.

Le deuxième chapitre examinera les mécanismes de dispersion mis en place actuellement par trois espèces du genre. Ces trois espèces ont été sélectionnées parmi les 15 existantes en raison de leur représentativité en terme de diversité des tailles d'aires de distribution, de structure génétique et de statut phylogénétique. ***A. mossambica*** est la plus ancienne du genre (Minegishi et al. 2005). Elle est aussi

endémique du milieu tropical du sud-ouest de l'Océan Indien où elle est supposée être panmictique et posséder une seule aire de reproduction (Jespersen 1942). ***A. marmorata*** est apparue en milieu de radiation du genre. Tropicale, elle est la plus largement répartie de toutes les espèces, mais est aussi subdivisée en six populations génétiques (Ishikawa et al. 2004). Cette thèse se focalisera sur sa population du sud-ouest de l'Océan Indien, en partielle sympatrie avec *A. mossambica*. Enfin, l'anguille Européenne ***A. anguilla*** est l'espèce la plus récente. Qualifiée de tempérée, elle est aussi celle qui présente la plus grande boucle de migration et donc les plus grandes capacités de dispersion, tout en conservant une apparente panmixie néanmoins débattue (Wirth et Bernatchez 2001, Maes et al. 2006, Pujolar et al. 2006).

Un troisième chapitre illustrera les variations inter-spécifiques des caractéristiques de la phase larvaire de trois espèces qui cohabitent dans le sud-ouest de l'Océan Indien *A. mossambica*, *A. marmorata* et *A. bicolor bicolor*, et examinera leur incidence sur la géographie des boucles de migration.

Un quatrième chapitre fera la synthèse des connaissances acquises sur les mécanismes de dispersion larvaire des trois espèces mises en exergue dans cette thèse et intègrera les données disponibles de la littérature sur les autres espèces du genre. Le but de ce chapitre sera d'explorer le passé évolutif des anguilles selon un nouveau point de vue, celui de l'évolution des capacités de dispersion larvaire. Cette approche permettra d'émettre des hypothèses sur le devenir possible des anguilles face aux changements environnementaux majeurs prévus dans les prochaines décennies.

Cette thèse se terminera par un ensemble de **conclusions** ouvrant sur des **perspectives** de recherche en modélisation de la dispersion larvaire, en génétique, en analyse de la microchimie de l'otolithe.

CHAPITRE I

Méthodologies

Partie 1. L'otolithe: enregistreur de vie

Partie 2. Identification des civelles

Partie 1

L'otolithe: enregistreur de vie

L'OTOLITHE: ENREGISTREUR DE VIE

La sclérochronologie[6] est une discipline phare en ichtyologie car elle permet de reconstituer l'histoire vie d'un individu à une échelle temporelle précise. Trois méthodes existent selon les pièces anatomiques examinées. Les écailles (scalimétrie), les rayons des nageoires, les opercules et les vertèbres (squelettochronologie) sont les premières structures à avoir été étudiées pour estimer l'âge des poissons (Anonymous 1913, Meunier 1988). Ce n'est qu'en 1971, lorsque Pannella décrivit le caractère journalier de la formation des otolithes chez les poisons ostéichtyens (du grec *oto*: l'oreille et *lithos*: la pierre), que l'otolithométrie prit son essor, surpassant les autres méthodes en terme d'utilisation et de précision.

GÉNÉRALITÉS

1. Position anatomique

Tous les poissons ostéichtyens possèdent trois paires d'otolithes (Campana et Neilson 1985). Chaque pierre d'oreille est enfermée dans une des trois capsules paires, semi-perméables et remplies d'endolymphe de l'oreille interne (Fig. 1 et 2). Les plus gros otolithes, appelés **sagittae**, sont contenus par les **saccules**. Les otolithes de taille intermédiaire, les **lapilli**, sont retrouvés dans les **utricules**. Et enfin, les plus petits, nommés les **asteriscii**, sont logés dans un diverticule du saccule, la **lagena**.

2. Fonction

Le rôle des otolithes est crucial puisqu'ils participent à l'ensemble des fonctions de l'oreille interne: réception des signaux acoustiques et réponse à des forces d'inertie et de gravité (Lecomte-Finiger 1999). Pour ce faire, chaque otolithe est relié à la macula acustica, surface riche en cellules ciliées sensorielles (mécanorécepteurs), elle-même reliée au nerf auditif (Grassé 1958 dans Pothin 2005). Lors de tout mouvement du poisson (*e.g.* accélération, nage oblique), le déplacement consécutif de l'otolithe renseigne l'individu sur son positionnement et son déplacement dans l'espace.

[6] Sclérochronologie: science qui étudie les pièces calcifiées des êtres vivants pour reconstituer leur histoire de vie (Panfili et al. 2002)

Chaque otolithe joue un rôle différent et complémentaire de celui des autres (Popper et Platt 1993 dans Pothin 2005).

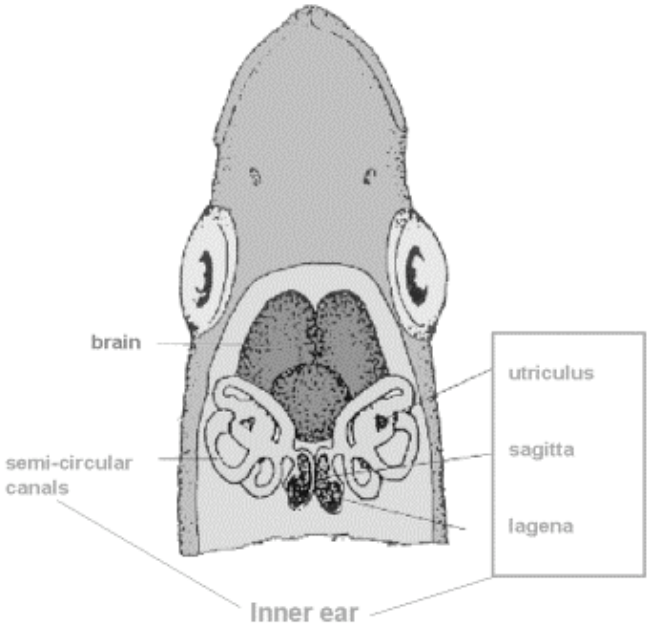


Figure 1. Position anatomique de l'oreille interne chez le poisson (crédits AFORO, adapté de Secor et Dean 1992)

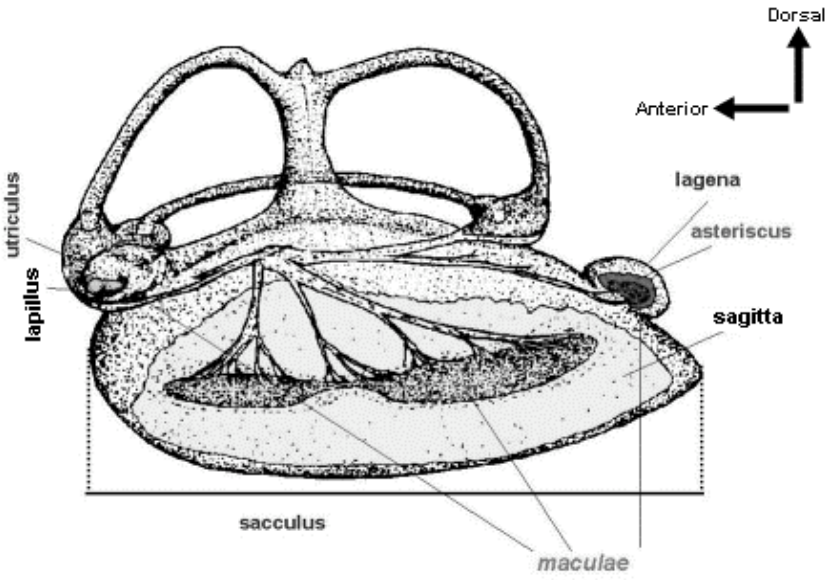


Figure 2. Structure de l'oreille interne d'un poisson et position des otolithes (crédits AFORO, adapté de Lombarte 1990)

3. Structure et composition

Les otolithes sont des pièces minéralisées acellulaires formées par dépôts de couches alternativement calcique et protéique (Campana et Neilson 1985). Les couches minérales sont constituées de cristaux de carbonate de calcium ($CaCO_3$) agencés en aragonite et parfois en vatérite (Carlström 1963 dans Arai et al. 2003a, Mugiya et al. 1981 dans Campana et Neilson 1985). La matrice protéique de nature fibrillaire (otoline), quant à elle, est principalement constituée d'amino-acides (Degens et al. 1969 dans Campana et Neilson 1985).

Le dépôt des couches est supposé être sous contrôle endocrinien (Simkiss 1974 dans Campana et al. 1995). Le rythme circadien, bien inscrit sur les otolithes des larves et des juvéniles, s'estompe avec l'âge jusqu'à ne plus marquer que les saisons ou les années (Campana et Neilson 1985). Le taux de croissance de l'otolithe est directement influencé par le métabolisme individuel (Wright 1991) et l'est donc aussi indirectement par les facteurs qui peuvent moduler le métabolisme tels la température (Brothers 1981 dans Pothin 2005, Mosegaard et al. 1988 dans Armstrong et al. 2004).

31 éléments ont étés répertoriés dans la composition chimique des otolithes. Puisés dans le milieu environnant, ils passent successivement dans le plasma sanguin puis dans l'endolymphe, principalement par voie dissoute (via les branchies ou l'absorption d'eau; Campana 1999) mais aussi par voie trophique dont la contribution est cependant jugée minimale (Limburg 1995, Hoff et Fuiman 1995). Les éléments constitutifs du carbonate de calcium sont largement dominants, tandis que les autres éléments sont en concentrations mineures (>100 ppm; Na, Sr, K, S, N, Cl et P) et traces (<100 ppm; Li, Ba, Ni, Al). Plusieurs études ont révélé une bonne corrélation entre les concentrations de certains éléments dans l'eau et dans l'otolithe des poissons (Sr, Zn, Pb, Mn, Ba, Fe), permettant de reconstituer fidèlement le milieu de vie des individus et leurs déplacements d'un milieu à l'autre (Campana et al. 2000, Elsdon et Gillanders 2006).

4. Avantages de l'otolithe en sclérochronologie

L'otolithe, à la différence des autres pièces calcifiées, croît tout au long de la vie de l'animal même en conditions de jeûne ou d'arrêt de la croissance somatique et n'est pas sujet à résorption (Campana et Neilson 1985, Maillet et Checkley 1990 dans

Campana et Thorrold 2001). De plus, contrairement aux écailles, aux opercules et aux rayons des nageoires, l'otolithe est protégé par la boîte crânienne et n'est donc pas directement exposé à l'environnement et à ses agressions. Il n'est enfin pas renouvelé au cours de la vie du poisson.

L'OTOLITHE DES CIVELLES D'ANGUILLES

1. Structures et correspondances

Le centre d'accrétion de l'otolithe (primordium) est supposé être formé dès le début de l'embryogénèse par fusion de granules protéo-calciques (Radtke et Dean 1982 dans Tzeng 1990, Brophy et al. 2004). Sur cette base présente à l'éclosion, le carbonate de calcium va ensuite s'accumuler pour former une couronne cristalline épaisse jusqu'à la première prise de nourriture ou la résorption des réserves vitellines. L'ensemble primordium + couronne constitue le nucleus (Fig. 3 et 4). Les couches accumulées ensuite correspondent à la vie larvaire leptocéphale. Un changement soudain de la largeur des incréments marque la fin de la vie larvaire et le début de la métamorphose en civelle (Lecomte-Finiger 1992, Arai et al. 1997; Fig. 5). La largeur des incréments s'accroît puis décroît vers la marge de l'otolithe (Fig. 5). Arai et al. (1997) ont montré que la métamorphose s'achevait avant que le pic de largeur des stries ne soit atteint. Enfin, en bordure d'otolithe, une double-marque peut être observée. Elle signale le passage de la civelle en eau douce (Kawakami et al. 1999, Kuroki et al. 2005).

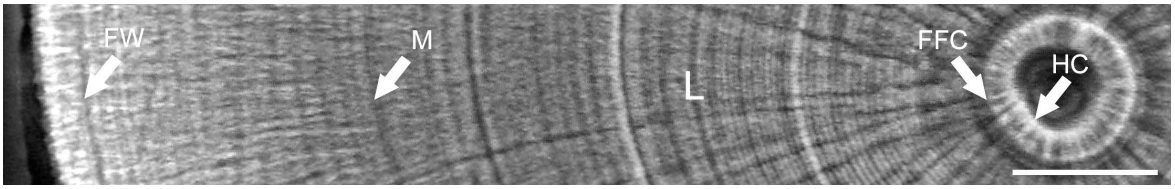


Figure 3. Photographie au MEB du transect d'un otolithe de civelle d'anguille. Au centre se trouve le primordium délimité par la marque d'éclosion (HC); le nucleus délimité par la marque de première prise de nourriture ou de résorption des réserves vitellines (FFC); puis la phase larvaire leptocéphale (L); la marque de début de métamorphose en civelle (M); et enfin, à la marge, la marque d'entrée en eau douce (FW). Barre d'échelle = 20 μm.

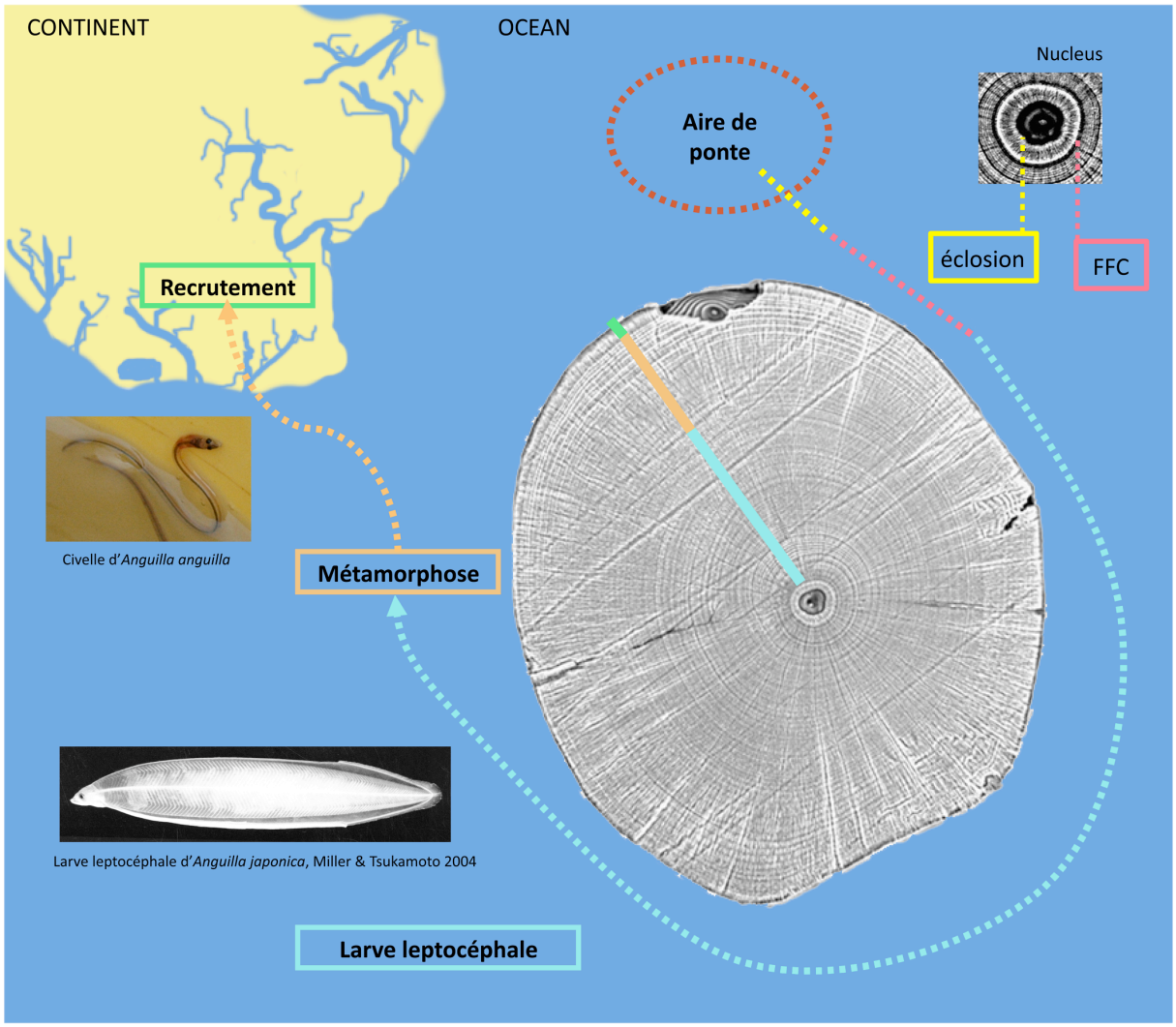


Figure 4. Reconstitution du passé larvaire d'une anguille par analyse de la microstructure de l'otolithe d'une civelle capturée au recrutement. FFC: first feeding check (marque de première prise de nourriture/résorption des réserves vitellines).

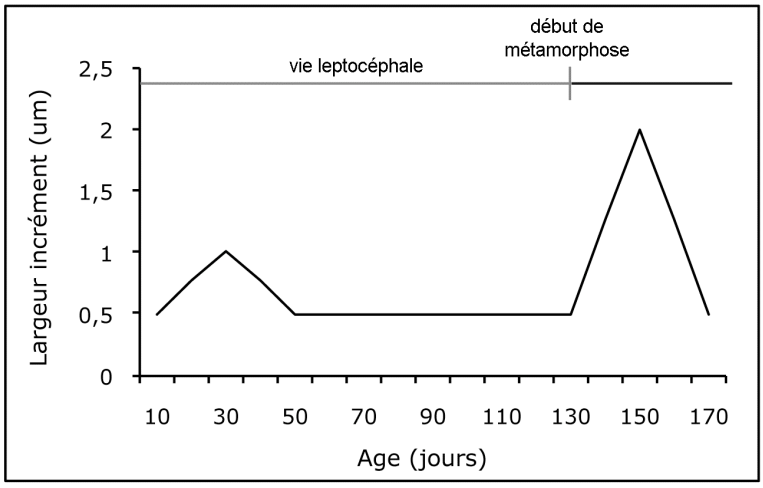


Figure 5. Représentation schématique de la croissance de l'otolithe de l'éclosion au début de la phase anguille jaune (d'après Arai et al. 1997).

2. Rythme de formation

L'examen des otolithes n'a de sens, en sclérochronologie, que si les couches sont déposées de façon chronique avec un rythme bien identifié. Dès lors, il convient de valider cette propriété préalablement à toute étude visant à reconstituer les histoires de vie individuelles. C'est ce qu'on entrepris de faire différentes équipes de recherche sur les larves et les civelles d'anguilles. Pour ce faire, plusieurs techniques peuvent être mises en oeuvre.

La première méthode consiste à élever des larves depuis leur éclosion, à les sacrifier et à comparer le nombre d'incréments observé sur l'otolithe à l'âge connu du poisson. C'est cette technique qu'ont appliquée Shinoda et al. (2004) sur 20 larves leptocéphales d'anguille japonaise *A. japonica*. Pour 30 jours d'élevage à partir de l'éclosion, ils ont dénombré 26.8 ± 0.8 incréments. Très proche de l'âge réel, ce résultat a supporté l'hypothèse du rythme journalier du dépôt de couches sur l'otolithe. La marge d'erreur a été imputée, par les auteurs, à la difficulté de distinguer les incréments déposés avant la marque de première prise de nourriture (FFC).

La seconde technique est un système de marquage au fluomarqueur (hydrochloride de tétracycline ou alizarine complexone (ALC ou AC)) par balnéation. Cette méthode a permis de valider la croissance journalière de l'otolithe sous forme d'incréments chez deux espèces tempérées, l'anguille Américaine *A. rostrata* (Martin 1995, Cieri et McCleave 2001) au stade civelle et l'anguille japonaise *A. japonica* (Tsukamoto 1989, Umezawa et al. 1989) aux stades larve et civelle; ainsi que chez les civelles de deux espèces tropicales *A. marmorata* (Sugeha et al. 2001) et *A. celebesensis* (Arai et al. 2000a). Sugeha et al. (2001), ont notamment obtenu un compte de 20.1 ± 0.7 incréments pour 20 jours d'élevage.

3. Traitement de l'otolithe pour la lecture de l'âge

Afin d'observer la structure en couches de l'otolithe et ainsi pouvoir estimer l'âge, un traitement mécanique et chimique doit être préalablement appliqué.

L'extraction. La sagitta est préférentiellement utilisée en raison de sa relative grande taille (env. 200 μm de diamètre chez une civelle peu pigmentée d'anguille européenne). L'otolithe est extrait de la tête de la civelle par la cavité palléale

faiblement calcifiée à ce stade du développement (Fig. 6). Il est ensuite nettoyé aux ultrasons pour éliminer les résidus de tissus qui pourraient nuire aux étapes suivantes.

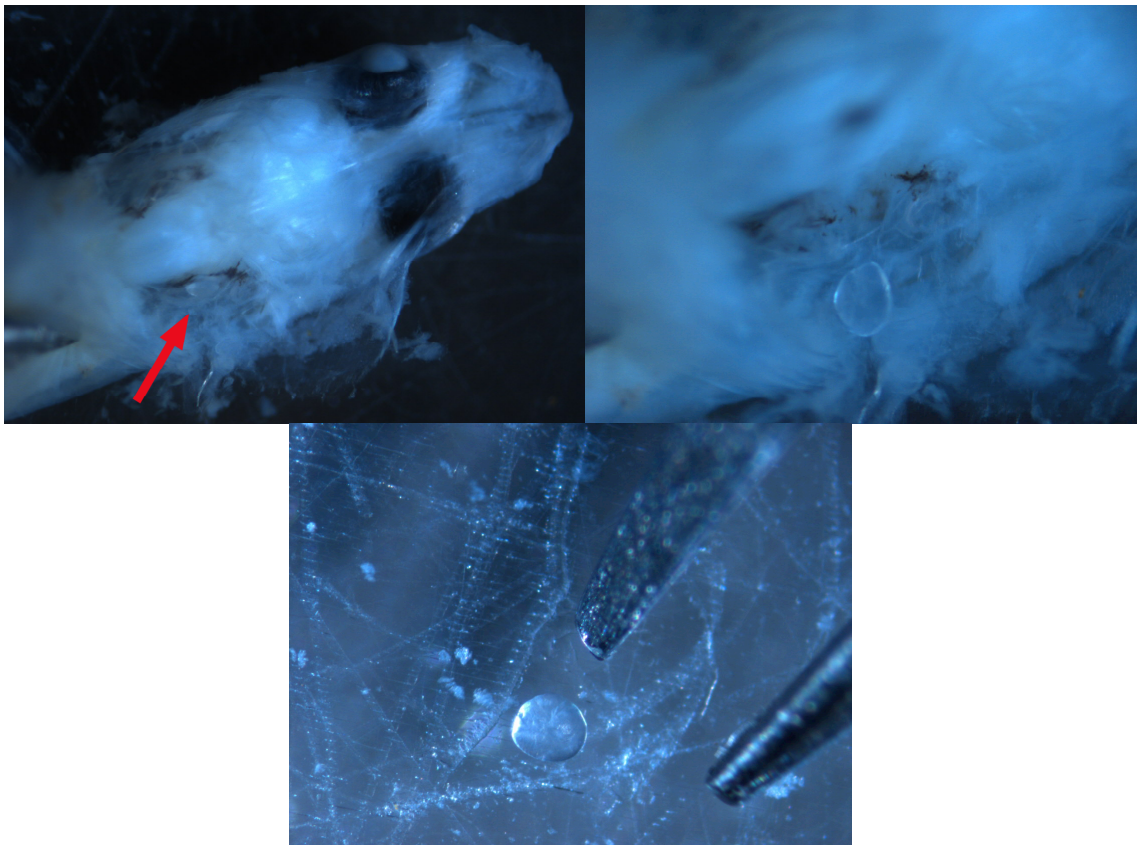


Figure 6. Extraction de la sagitta gauche d'une civelle d'anguille par la cavité palléale.

L'inclusion et le ponçage. Afin de révéler sa structure depuis les premières couches déposées après l'éclosion, l'otolithe doit être sectionné sur le plan sagittal au niveau du nucleus (Fig. 7). Il est pour cela inclus dans de la résine Epoxy ou dentaire, polymérisante à froid ou à chaud qui assure une bonne cohésion avec toute la surface de l'otolithe. L'inclusion est ensuite poncée sur du papier abrasif de grain décroissant à mesure que le manipulateur se rapproche du centre de l'otolithe.

A ce niveau, deux options sont possibles. Une lame mince peut être réalisée en ponçant l'autre face de l'otolithe. Cette technique est utilisée pour visualiser les couches sous microscope optique. Ou, tel qu'il l'a été réalisé pour cette thèse, l'otolithe subit un traitement chimique qui va mettre en relief sa structure pour être ensuite observée au microscope électronique à balayage (MEB).

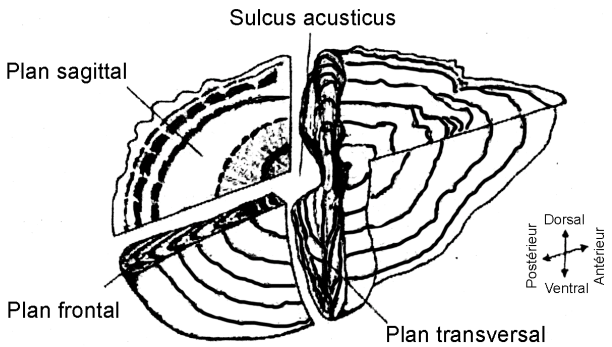


Figure 7. Plans de coupe d'une sagitta (d'après Pannella 1980)

Décalcification. Afin de mettre en relief la structure en couches de l'otolithe sur la face poncée, un acide est appliqué de quelques secondes à quelques minutes en fonction de sa concentration et du relief souhaité. Parmi différents acides possibles, l'acide éthylène-diamine-tétra-acétique (EDTA), chélateur du calcium, a été choisi pour cette thèse car, par rapport aux acides acétique, chlorhydrique ou nitrique, il dégrade la matrice protéique plus progressivement et précisément (Campana et Neilson 1985, Panfili et al. 2002, observation personnelle). Un simple rinçage à l'eau distillée stoppe son activité.

Métallisation. Afin de rendre l'échantillon opaque aux électrons pour l'observation au MEB, l'otolithe est métallisé à l'or qui se dépose en une fine couche sans combler le relief créé par la décalcification.

Observation. L'otolithe est ensuite observé au MEB dont le principe est basé sur le processus d'interaction électrons-matière. La résolution du modèle JEOL JSM 5410 LV utilisé ici est de 35 nm avec un grossissement x350 pour visualiser l'intégralité de la surface de l'otolithe, et une magnification x2000 ou x3500 pour réaliser les clichés détaillés qui servent ensuite au comptage des incréments. Un système d'acquisition d'image est relié au microscope et permet de récupérer des photographies au format numérique, qui sont ensuite interprétées pour estimer les durées des différentes phases du développement du poisson telles qu'illustrer en figures 3 et 4.

Expérience de l'observateur. Le dernier point essentiel à la réussite de la lecture de l'otolithe concerne l'expérience de l'observateur. Pour illustrer l'importance de cet aspect, une expérience simple a été réalisée. 22 étudiants, totalement novices en

matière de lecture de la microstructure des otolithes se sont prêtés au jeu de l'estimation de l'âge à partir de clichés pris au MEB. Quatre otolithes d'individus différents ont été étudiés par chacun des étudiants. La figure 8 indique qu'il faut moyenner les résultats de plus de cinq observateurs inexpérimentés pour stabiliser l'estimation d'âge. Pour cette raison, des doubles comptages avec un observateur expérimenté ont été réalisés pour former l'observateur novice à l'interprétation de la microstructure des otolithes.

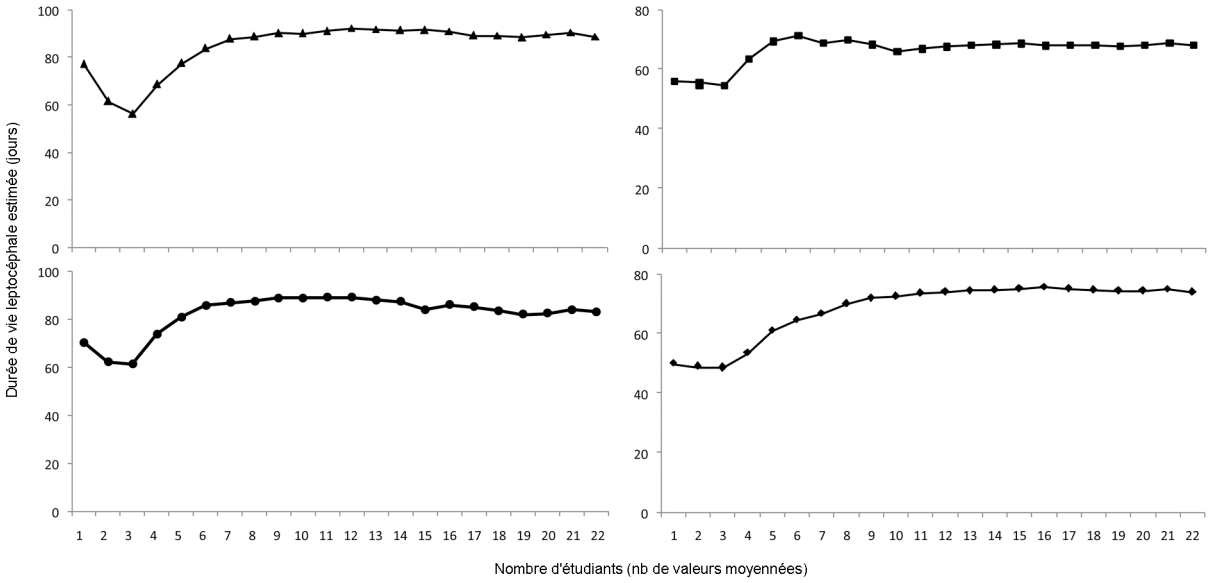


Figure 8. Courbe des moyennes cumulées des estimations de durée de vie leptocéphale obtenues par interprétation de la microstructure des otolithes de civelles d'anguilles réalisée par des observateurs novices en la matière.

3. Analyse critique de la méthode

En écologie, l'utilisation d'un outil quel qu'il soit s'accompagne d'incertitudes qu'il faut savoir évaluer et prendre en compte. L'otolithe, grâce aux propriétés précédemment citées et bien d'autres encore, est un outil à fort potentiel. Néanmoins, préalablement à toute étude, il est essentiel de s'assurer de la stabilité des propriétés utilisées. Ainsi, en ce qui concerne l'utilisation de l'otolithe pour estimer l'âge des poissons, la validation du rythme de dépôt des couches est nécessaire. Comme décrit précédemment, cette étape a été réalisée chez deux espèces tempérées et deux espèces tropicales d'anguilles à différentes phases du développement validant le caractère journalier du dépôt.

Cependant, l'utilisation de l'otolithe pour estimer les durées de vie larvaire des anguilles fait l'objet d'une controverse qui persiste depuis une quinzaine d'années. Le litige vient du fait que les estimations réalisées sur l'anguille européenne *A. anguilla* par otolithométrie (Lecomte-Finiger et Yahyaoui 1989, Lecomte-Finiger 1992, 1994) sont en désaccord avec celles réalisées par le biais (1) de l'analyse des courbes de croissance des larves leptocéphales capturées entre la zone de ponte en Mer des Sargasses et les côtes Européennes (Schmidt 1923), et (2) de la simulation numérique de la dispersion larvaire basée sur des modèles courantologiques (Kettle et Haines 2006, Bonhommeau 2008). La première méthode estime la durée de dispersion à environ 1 an, tandis que les autres approches proposent 2 à 3 ans de dérive.

Dans ce contexte, les incertitudes liées à l'utilisation de l'otolithe doivent être passées en revue:

- La validation du caractère journalier n'a pas été réalisée chez l'anguille Européenne. Néanmoins, la confirmation de cette propriété sur 4 autres espèces évoluant en milieux tempéré et tropical laisse fortement présager de la validité de ce caractère chez *A. anguilla.*

- L'otolithe est la seule pièce calcifiée dont la croissance soit continue et dont la résorption n'a été démontrée chez aucun ostéichtyen. Il semble donc raisonnable de supposer que l'anguille ne fait pas exception à ces règles.

- En 1991, Umezawa et Tsukamoto ont montré, sur des civelles d'anguille Japonaise élevées en aquaculture, que la faible température et la privation de nourriture pouvaient ralentir la croissance de l'otolithe et empêcher de distinguer les couches déposées. Dès lors, il a été suggéré que la limite de résolution des instruments d'observation de la microstructure des otolithes pourrait conduire à sous estimer le nombre de couches accumulées. Si cette hypothèse est techniquement difficile à tester, il faut cependant mettre en exergue que l'expérience conduite par Umezawa et Tsukamoto (1991) a été réalisée sur des civelles, et non des leptocéphales dont les performances métaboliques sont reconnues pour être importantes, y compris en milieu tempéré, comparativement à la demande énergétique (Bishop et Torres 1999, 2001). Néanmoins, dans l'incapacité de contester cette théorie, elle fera l'objet d'une discussion plus poussée, basée sur de nouveaux résultats acquis au moyen de l'otolithométrie, dans le chapitre traitant de l'anguille Européenne (Chapitre II, partie 3).

4. Postulat

Après cette revue des caractéristiques des otolithes et des incertitudes liées à leur utilisation, un postulat, qui sera celui admit dans cette thèse, doit être énoncé. "**Il sera considéré que l'otolithe des larves et des civelles d'anguilles, quelle que soit l'espèce, est formé par accrétion journalière et continue de couches discernables au MEB et non sujettes à la résorption".**

Partie 2

Identification des civelles du sud-ouest de l'Océan Indien sur critères morphologiques et génétique

Résumé: Quinze espèces d'anguilles sont répertoriées dans le monde entier. Elles sont reconnues pour leur importance écologique et font également l'objet d'enjeux économiques importants. Néanmoins, leur cycle de vie catadrome rend difficile la mise en place de plans de gestion viables. Les civelles, qui constituent le stade de transition entre la phase larvaire océanique et la phase de croissance en eau douce, déterminent la colonisation continentale et insulaire des populations et des espèces. Ainsi, la compréhension de la dynamique de leur recrutement aux échelles spatiale et temporelle est de première importance. Cependant, la première étape pour ce type d'étude est compliquée par la difficulté d'identifier l'espèce à ce stade particulier du développement. Ceci est d'autant plus vrai lorsque plusieurs espèces cohabitent dans les mêmes rivières. Dans le Sud-Ouest de l'Océan Indien, où 4 espèces sympatriques sont enregistrées, il a été développé un protocole d'identification des civelles à partir de leurs caractéristiques morphologiques, ainsi facilement applicable lors des campagnes de recensement sur le terrain. La clé d'identification proposée par Ege en 1939 a été réexaminée et deux caractères pertinents ont été retenus : la pigmentation au niveau de la nageoire caudale ainsi que le ratio entre les longueurs des nageoires dorsales et anales. Le protocole proposé a enfin été validé par analyses génétiques des civelles.

Mots-clef: *Anguilla* spp., civelles, identification spécifiques, morphologie, analyses génétiques

Reassessment of southwestern Indian Ocean anguillid glass eels identification protocols on morphological and genetic characteristics

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In preparation

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Abstract: Fifteen species of Anguillid eels are recorded worldwide. They are recognized as ecologically important species and are also the purpose of huge economical stakes. Their catadromous life cycle makes difficult to establish suitable management plans for their conservation. Glass eels, that represent the transition phase between the oceanic larval stage and the freshwater growth stage, determine the continental and insular colonization of populations and species. Understanding of their recruitment dynamics in space and time is thus of first importance. However, the first step of that kind of studies is problematic, as difficulties in species identification at this developmental stage have been reported. This is especially problematic when several species can be encountered in the same river. In the South-Western Indian Ocean, where four sympatric species are recorded, we aimed at developing a protocol of for glass eels identification based on morphological characteristics. We focused on the objective that this protocol would be applicable on the field during monitoring surveys. We reexamined the identification key proposed by Ege in 1939, and retained two characteristics that are the caudal pigmentation and the proportion between the length of the dorsal and the anal fins. The relevance of the proposed protocol has been verified with genetic methods.

Keywords: *Anguilla* spp., glass eels, species determination, morphology, molecular analysis

INTRODUCTION

The genus *Anguilla* Schrank, 1798, is widely distributed and recorded in most of the world oceans coasts through its 15 tropical and temperate species (Aoyama et al. 2001). Their particular catadromous life cycle proceeds between oceanic spawning areas and inland, estuarine or coastal growth waters (Tsukamoto 1998, Tesch et al. 2003), depending on the developmental stage. This leads to high difficulties in their management as ecologically important species (Feunteun 2002) that are also the purpose of huge economical stakes (Tesch et al., 2003). The decline of temperate species since approximately thirty years, led to establish management plans that have now to be held for tropical species which increasingly focus commercial attention. In this context, intensive studies on the life-cycle have to be conducted and must be based on approved identification protocols at every developmental stage. On this depend successful monitoring surveys of the resource as well as commercial surveys of species import/export, relative to the legislation concerning each of them (FAO EIFAC/ICES 2006).

In some regions, several species are partially or totally sympatric, inhabiting the same continents, islands, watersheds, and sometimes the same rivers (Aoyama & Tsukamoto 1997, Watanabe 2003, Robinet et al. 2003a). This kind of situation induces a need of plurispecific management plans as it is the case in the western part of the Indian Ocean, where the distribution areas of *Anguilla marmorata*, *A. mossambica*, *A. bicolor bicolor* and *A. nebulosa labiata* have been reported to overlap (Jespersen 1942, Jubb 1961, Robinet et al. 2007, 2008). And, because glass eels colonise growth areas and determine the geographic distribution of populations and species, they represent a key stage to study within a management framework.

In such context, individual identification at the species level is the first step to conduct any study. Ege proposed, in 1939, a protocol of specific identification using 14 morphological characteristics. This protocol has been discussed and reassessed for yellow eels (body size from 115 to 1248 mm) through genetic analysis (ARN 16s, RFLP) by Watanabe et al. (2004). They concluded that the 3 characters of skin coloration patterns, width of maxillary bands of teeth and length of fins were the most important as valid characters for the taxonomy of the genus *Anguilla*. However, species recognition at the larval and early juvenile (glass eel) life is

difficult as these morphological characteristics are not established, e.g. the incomplete pigmentation (Watanabe et al. 2004). Recent molecular progress has enabled to propose specific mtDNA amplification caled semi-multiplex identification method (Gagnaire et al. 2007), but this method requires high technical skills and expensive equipment, which are not often available for routine surveys, especially in developing countries. This represents a major problem when field monitoring for species management is conducted.

The present paper aims at proposing a simplified protocol of glass eels identification based on the comparative morphology of the four species recorded in the South-Western Indian Ocean. Effort has been made to propose characteristics that can be easily used on the field without sacrifice of the specimens. The protocol relevance has been verified through genetic analysis.

MATERIALS AND METHODS

1. Sampling sites and methods

Individuals were sampled during several electric fishing sessions made between April 2005 and February 2006 in Mauritius (5th to 7th April 2005), Réunion (11th to 12th April 2005), Mayotte (15th to 19th April 2005) and Madagascar (September 2005 to February 2006) islands (Fig. 1) in the South-Western Indian Ocean. All specimens were preserved in 95% ethanol.

2. Morphological identification

We considered and tested the relevance of the two characteristics described by Ege (1939) as the most discriminant between juveniles of *Anguilla marmorata*, *A. mossambica*, *A. nebulosa labiata* and *A. bicolor bicolor*, which are: the caudal pigmentation (tail and fin), and the distance between dorsal and anal fins as related to the fish total length (Equation 1, Fig. 2)

$$A\text{-}D\% = (LD\text{-}LA)/LT*100$$

Equation 1. Distance between the origins of the dorsal (LD) and anal (LA) fins as a percentage of the fish total length (LT).

Glass eels are the metamorphosing stage from translucent and non-pigmented leptocephalus larvae to fully pigmented yellow eels (Elie et al. 1982). The body area where the melanophores appear first within the pigmentation process, has been described as a valid characteristic of species identification.

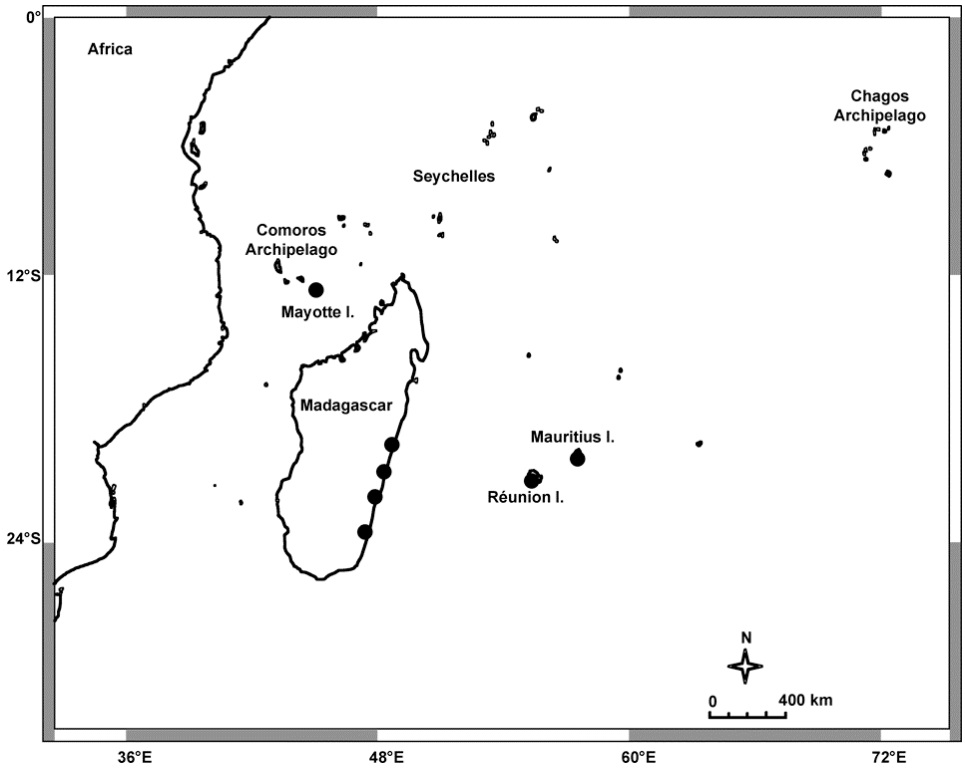

Figure 1. Map of the sampling locations in the South-western Indian Ocean.

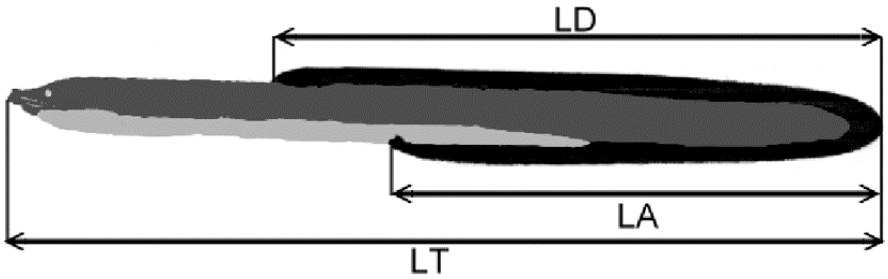

Figure 2. Measures for the ano-dorsal fin relation calculation (A-D%). LT = total length (mm); LA = anal fin length (mm); LD = dorsal fin length (mm).

According to Ege (1939): *A. marmorata* early glass eels (V_B) show pigmentation only on the tail, not on the fin. "Along the mediolateral line there is a streak of pigment, which extends, in the early glass eels stages, through the posterior two-thirds of the area. At the tip of the tail, this streak forms a fairly broad belt with many

melanophores close together, changing further forward to a single, irregular row of relatively large stellate melanophores, the spaces between being filled up with faint, structureless pigment" (Fig. 3a). *A. mossambica* shows "at the outermost end of the tail, a belt of somewhat diffuse pigment with cleft basal region and extending a little further forward on the tail than the length of the pigment area on the caudal fin. The latter occupies about three-fourth of the length of the fin. The basal part of a few adjacent rays in the dorsal and anal fins is faintly pigmented" (Fig. 3b). *A. bicolor bicolor*'s pigmentation is somewhat similar to that of *A. mossambica*. The end of the tail "bears mediolaterally a double row of five large, stellate melanophores, continued forward by a single row of three melanophores. The pigment on the caudal fin is a network of melanophores, which extends over more of the length of the fin. (…) From there it decreases faintly on both sides, with a somewhat greater decrease towards the final surrounding" (Fig. 3c). *A. nebulosa labiata* shows "a row of large, stellate, quadrilateral, diffuse melanophores in the mediolateral line at the tip of the tail. The latter mediolateral pigment in the posterior part forms a belt of more complex composition" (Fig. d).

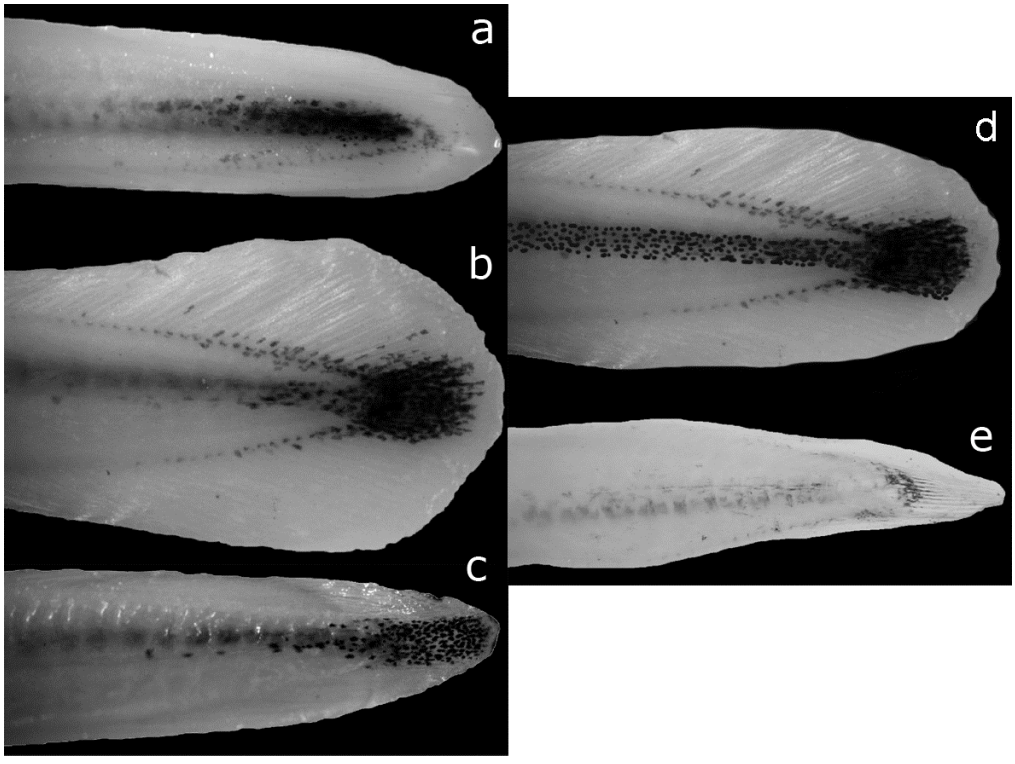

Figure 3. Caudal fin photographs of (a) *Anguilla marmorata*, (b) *A. mossambica*, (c) *A. bicolor bicolor*, (d) modified photograph to display the pigmentation characteristics of *A. nebulosa labiata* based on Ege (1939) and (e) photograph of an example of morphologically unidentified specimen (Photographs Réveillac 2007).

A. marmorata, *A. mossambica* and *A. nebulosa labiata* are long-finned species, i.e. their dorsal fin origin is closer to the jaw than to the anus. Conversely, *A. b. bicolor* is a short-finned species having its dorsal fin beginning closer to the anus than to the jaw. According to Ege (1939), A-D% of the three first species is approximately 16.3% for *A. marmorata*, 14.8% for *A. mossambica* and 11.9% for *A. n. labiata*, as that of *A. b. bicolor* is only approximately 0.8%, which might allow the discrimination of these species. In a more recent work, Jubb (1961) reported overlapping ranges between species, with values comprised between 7% and 13%, between 9% and 15% and between 14% and 17% respectively for *A. n. labiata*, *A. mossambica* and *A. marmorata* individuals of 50 mm long.

3. Genetic identification by semi-multiplex PCR analysis

The semi-multiplex PCR analysis is based on the differential amplification of various length mitochondrial 16SrRNA fragments in the four Indian Ocean eel species (Gagnaire et al. 2007). A common eel-specific forward primer (L1854') is jointly used with four different species-specific reverse primers in the same PCR mixture. The reverse primer R0253 only hybridizes in *A. bicolor bicolor*, R0341 is specific for *A. mossambica*, R0439 for *A. marmorata*, and R0537 for *A. nebulosa labiata*. This method leads to a species-specific amplification of a 253 bp fragment in *A. bicolor bicolor*, 341 bp in *A. mossambica*, 439 bp in *A. marmorata*, and 537 bp in *A. nebulosa labiata*. The method enables producing short, easily distinguishable amplification products, after separation on a 1% agarose gel.

RESULTS

4099 glass eels from stage V_A to stage VI_{A1} (Elie et al. 1982), sampled in Mauritius, Réunion, Mayotte and Madagascar rivers between April 2005 and February 2006, have been submitted to morphological identification based on the pigmentation characteristic. Caudal fin pigmentation analysis allowed to identify 205 individuals of *A. marmorata* and to exclude 3834 individuals from this species, i.e. belonging to *A. mossambica* and/or *A. n. labiata* and/or *A. b. bicolor*. However, 60 individuals could not be classified into those groups thanks to the sole caudal pigmentation characteristic (Table 1). The principal reason was an anarchistic and little spread

pigmentation that didn't exhibit characteristics described in the identification key (Fig. 3e). The pigmentation, used alone for identification, enabled to identify only *A. marmorata* individuals thus 5% of the sampled glass eels.

The long-finned/short-finned characteristic was examined the 4099 glass eels, but measures of the A-D% was performed only on 427 individuals. Thanks to this characteristic 63 short-finned (mean A-D% at 1.7 +/- 0.7%) glass eels have been identified and were assigned directly to *A. bicolor bicolor*, which is the only short-finned eel recorded in the region. The rest of the individuals were long-finned. However, their A-D% did not enable to discriminate *A. marmorata, A. mossambica* and *A. n. labiata*, as the distribution of A-D% frequencies strongly overlapped between values reported by Ege (1939) for these three species (Fig. 4). The short or long-finned characteristic used alone thus enabled to identify only *A. b. bicolor*.

The combination of morphological and pigmentation analysis methods gave a far better result as 98.5%, i.e. 4039 individuals were identified to the species level (205 *Anguilla marmorata*, 3771 *A. mossambica* and 63 *A. bicolor bicolor*).

A sub-sample of 50 *A. marmorata*, 33 *A. mossambica* and 58 *A. b. bicolor* was submitted to molecular analysis to test the validity of the morphological identification, which was validated, except for three *A. mossambica* identified first as *A. marmorata*.

In final, 1.5% of the glass eels (60 individuals) still unidentified after morphological examination. This was mainly because of unusual pigmentation patterns, and insufficient discrimination of the short/long-finned species on the A-D% characteristic. Genetic identification revealed they were 73% of *A. marmorata* (44 ind.) and 27% of *A. mossambica* (16 ind.,).

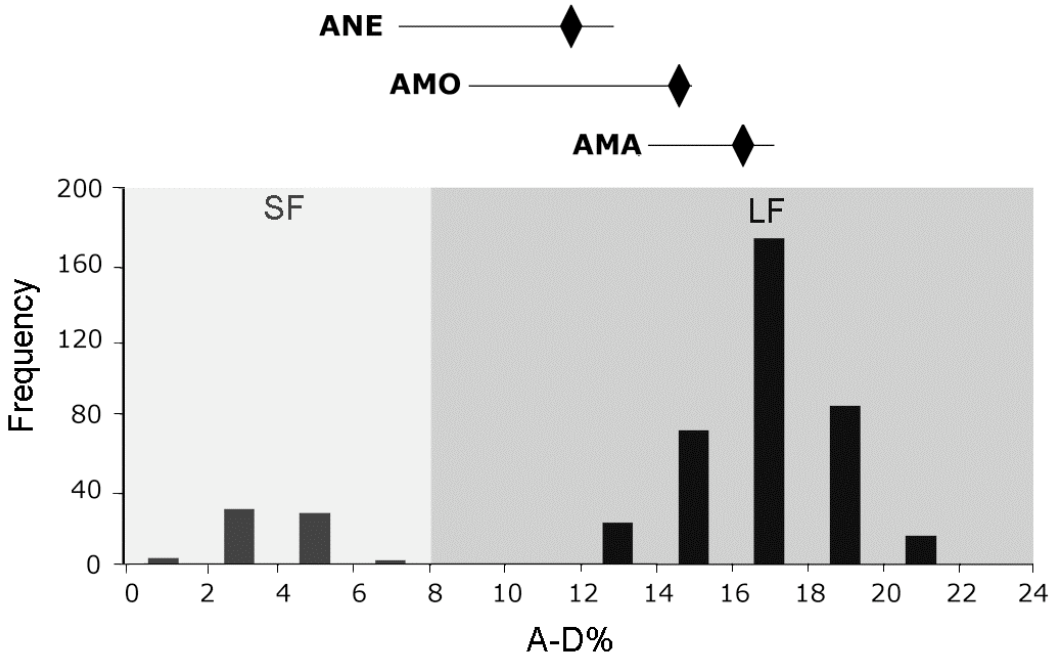

Figure 4. Ano-dorsal values distribution for glass eels sampled in the South-Western Indian Ocean, and specific values described by Ege (1939) (♦) and Jubb (1961) (–). N = 427. SF = short-finned, LF = long-finned, ANE = *A. n. labiata*, AMA = *A. marmorata*, AMO = *A. mossambica*.

In summary, among the 4099 glass eels sampled between April 2005 and February 2006 in Reunion, Mauritius, Mayotte and Madagascar rivers, there were 246 *A. marmorata*, 3790 *A. mossambica*, 63 *A. b. bicolor*, and 98.5% have been successfully identified thanks to the combination of only two morphological characteristics. No *A. nebulosa labiata* glass eels have been identified nor morphologically nor genetically.

DISCUSSION

Accurate species identification is the first step in any organism study with ecological and/or conservation aim (Avise 1989). Anguillid glass eels identification at the species level is the starting point for studying their watershed and riverine recruitment variations in space and time (Feunteun 2002), as so as their individual migration traits such as spawning areas location and migration routes and periods (Robinet et al. 2003a, 2008, Réveillac et al. 2008). It is obvious that field identification for monitoring surveys within a resource management framework

must require as less material as possible and must be as fast, as cheap and as much reliable as possible. The relevance of the identification by semi-multiplex PCR has been confirmed by parallel RFLP analysis. Genetic identifications were not therefore ambiguous. The molecular analysis method is the absolute specific identification tool. In counterparts, its use necessitates a complex and expensive material, and does not provide immediate results. It is also a destructive method, because, at least, tissues have to be taken on the fins of pretty small individuals during their upstream migration and at most, a number of individuals have to be sacrificed. Moreover, the technique requires high technological skills. Therefore molecular methods are only necessary for studies that require strict reliable species identification (*i.e.* life-history traits).

Ege (1939) gave the basis for Anguillid eels morphological identification at every developmental stages. However, like Jubb (1961) for elvers and more recently Watanabe (2003) and Watanabe et al. (2004) for yellow eels, this study demonstrated that external morphological characteristics used for glass eels must be carefully examined, as diagnostic characters may overlap between species. Combination of at least two characteristics, which are the pigmentation and the A-D%, enable a fairly correct identification. Considered separately, these characteristics didn't allow the assignment to more than one species.

Therefore, we propose the following simple identification key for Indian Ocean glass eels: *A. mossambica*, *A. marmorata*, *A. n. labiata* and *A. b. bicolor*

1- Caudal pigmentation distribution

_ Mainly on the tail: *A. marmorata*

_ Mainly on the fin: see 2

2- A-D%

_ Short-finned: *A. b. bicolor*

_ Long-finned: see 3

3- Pigmentation

_ Large pigment drag on the tail and triangle of pigment on the fin: *A. n. labiata*

_ Triangle of pigment on the fin: *A. mossambica*

Neither the morphological nor the genetic analysis revealed clearly the presence of the species *A. nebulosa labiata*. Although this species has been reported as inhabiting the regional rivers (Frost 1957, Jubb 1964, Keith et al. 1999), some recent studies and field sampling qualified this species as rare or failed to observe it in regional islands (Robinet et al. 2007). Therefore its occurrence in these localities must be recalled in question, and its presence in the eastern coast of Africa where, historically, few sampling studies have been conducted, has to be verified (Frost 1957).

Incapacities of identification of some glass eels on morphological characteristics left gaps in describing recruitment composition in some islands. Nevertheless, the A-D% characteristic enabled to determine if unidentified individuals belonged to a short or to a long-finned species. In parallel, genetic analysis demonstrated that unidentified individuals on morphological characteristics belonged most often to the species reported to dominate the local communities described by Marquet et al. (1997), Keith (2002) and Robinet et al. (2003b, 2007). The comparison between recruitment composition before and after the genetic analysis, showed no significant differences (Khi-Square Test, $p > 0.05$) for *A. mossambica*. However differences were significant ($p < 0.05$) for *A. marmorata* because the unidentified individuals almost belonged exclusively to this species. Thus, if precise identifications are required, as for studies at the individual scale, genetic analysis should be performed. Otherwise, assigning unidentified glass eels to the local dominant species seems to be a reasonable assumption.

Acknowledgements

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CHAPITRE II

Mécanismes et caractéristiques spécifiques de la dispersion larvaire

Partie 1. *Anguilla mossambica*

Partie 2. *Anguilla marmorata*

Partie 3. *Anguilla anguilla*

Partie 1

Diversité des histoires de vie larvaire d'*Anguilla mossambica*: indices sur les mécanismes de la dispersion larvaire vers Madagascar

Résumé: Les traits d'histoires de vie larvaire d'*Anguilla mossambica* ont été étudiés à travers l'analyse de la microstructure des otolithes de civelles collectées le long de la côte Est de Madagascar. Les variations de ces traits ont été examinées entre 5 localités d'échantillonnage (variation spatiale) ainsi qu'au sein de chacune d'elle. Les variations temporelles ont été, quant à elles, étudiées au rythme d'une collecte par mois pendant 4 mois dans la seule localité de Mananjary. Des relations significatives ont été mises en évidence entre les différents traits de vie larvaire (durée de la phase leptocéphale (LD), durée de la métamorphose (MD), âge au recrutement (AR), taux de croissance de l'otolithe (OGR)) et la longueur totale au recrutement (TL). Ces traits ont montré des variations plus importantes entre les sites d'échantillonnage qu'au sein d'une même localité. Aucune variation temporelle ne s'est, par contre, montrée significative. Les possibles contributions des facteurs innés et environnementaux à l'existence de ces variations ont été discutées et de nouvelles informations quant à la migration des larves d'anguilles et les mécanismes de métamorphose et de recrutement ont été apportées. Ces résultats supportent, de plus, l'hypothèse d'une seule aire de ponte régionale au Nord-Est de Madagascar.

Mots-clef: *Anguilla mossambica*, histoires de vie larvaire, variabilité, analyse de la microstructure des otolithes.

Early-life histories diversity of *Anguilla mossambica*: clues for larval dispersal mechanisms toward Madagascar.

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In preparation

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Abstract: *Anguilla mossambica* early-life traits (ELT) were studied through the otolith microstructural analysis of glass eels collected along the eastern coast of Madagascar. Spatial variations of simultaneously recruited individuals were examined within and between 5 localities and temporal variations were studied throughout 4 consecutive months in a single locality. Significant relationships were detected between early-life traits (leptocephalus duration (LD), metamorphosis duration (MD), age at recruitment (AR), otolith growth rate (OGR)) and body length at recruitment (TL). Those traits showed variations at different scales with latitudinal variations being more important than local ones, whereas temporal variations were not significant. Possible contributions of innate and environmental factors to these variations are discussed and new insights on anguillid eel's larval migration, metamorphosis and recruitment mechanisms are provided. Results furthermore supported the hypothesis of a single regional spawning area at the northeast of Madagascar.

Keywords: *Anguilla mossambica*, early-life histories, variability, otolith microstructure.

INTRODUCTION

Anguillid eels are semelparous and catadromous fish, which larval dispersal toward coastal, estuarine or continental waters govern their renewal, distribution range and ability to spread over new areas (Arai et al. 2001a, Réveillac et al. 2008). By determining the extension capabilities of their growth areas and the connectivity between localities and between populations, the larval phase drives also the evolution and the phylogeography of the genus *Anguilla* (Tsukamoto 1998). This explains why the early-life history (ELH) of eels has been intensively studied during the last decades.

In that context, the analysis of the otolith microstructure is commonly investigated, as otoliths are considered to be a reliable recorder of the ELH (Lecomte-Finiger 1994, Campana 2001, Robinet et al. 2008, Réveillac et al. 2008). Several studies have demonstrated the daily deposition of increments in the otolith of tropical eel larvae (Umezawa et al. 1989, Arai et al. 1997, Sugeha et al. 2001). Several remarkable checks, which are thought to correspond to particular changes in the larval development (first feeding, onset of metamorphosis into yellow eel, entry to freshwater), are visible on the otolith, and age at which they occur can be determined (Campana and Thorrold 2001, Jessop et al. 2006, Lecomte-Finiger 1994, Wang and Tzeng 2000). Furthermore, the otolith daily growth rate is supposed to reflect the individual metabolic rate (Wright 1991).

The long-finned eel *Anguilla mossambica* is found only in the southwestern Indian Ocean (Ege 1939, Jubb 1961, Robinet et al. 2003a), and despite it has recently been described as the oldest *Anguilla* species (Minegishi et al. 2005), few investigations were conducted on its life cycle. Only three studies reported on its larval dispersal features at temporary sampling time and locations (Jespersen 1942, Robinet et al. 2003a, 2008). After a campaign of larvae sampling during the Carlsberg Foundation's Oceanographic Expedition Around the World in the years 1928-1930, Jespersen (1942) suggested that the spawning area of this species was located somewhere East off Madagascar coasts (Fig. 1). This theory has been documented by Robinet et al. (2008), who suggested that the area between Madagascar Island and the Mascarene Archipelago could shelter the reproductive area. However, Robinet et al. (2008) based their analysis on larval dispersal duration recorded punctually in

2001 and 2005 in Réunion Island and in 2005 in two localities of Madagascar Island. Thus this study did not examine either extended simultaneous spatial or intra-annual variations of early-life traits[7] (ELT) to test confidently the possible fluctuations of larval dispersal associated to these components. Variations of the dispersal duration have already been reported in other *Anguillidae* (Arai et al. 1999a, 2000b, Shiao et al. 2002, Robinet et al. 2008, Réveillac et al. 2008) at small spatial and temporal scales.

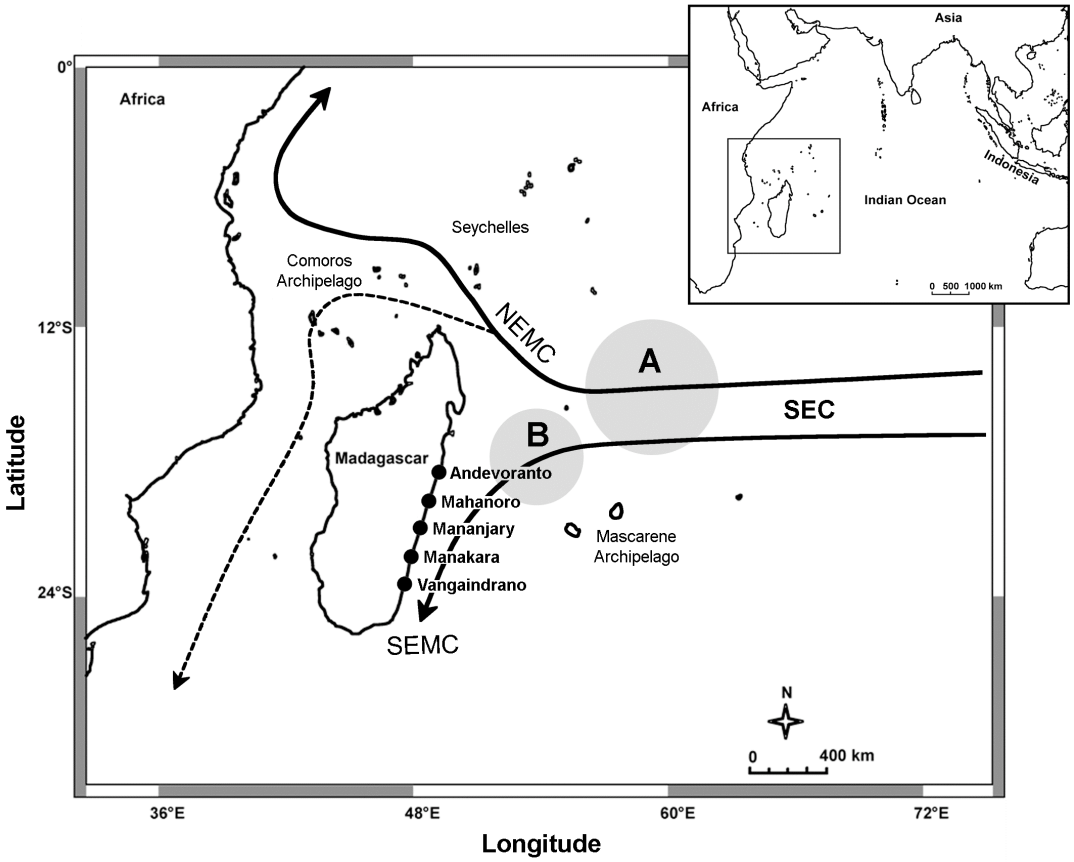

Figure 1. Localities sampled in Madagascar in the South-Western Indian Ocean. Arrows represent the main regional currents (SEC: South-Equatorial Current, SEMC: South-Equatorial Madagascar Current, NEMC: North-Equatorial Madagascar Current) and the grey areas represents the spawning area proposed (A) by Jespersen (1942) and (B) by Robinet et al. (2008).

The objectives of the present study were in part to fulfil these lacks and to deepen the knowledge on larval dispersal, metamorphosis and recruitment mechanisms in eels. 1) As Madagascar seems to be located in a strategic geographic place in regard to *A. mossambica* migration loop, we investigated the species ELTs spatio-temporal

[7] Trait: Any morphological, physiological or phenological feature measurable at the individual level, without reference to the environment (Violle et al. 2007).

variations along the eastern coast of the island. 2) From on, we discussed the hypotheses about the spawning area's location proposed by Jespersen (1942) and Robinet et al. (2008) based on new and more complete dataset. Finally 3) we examined the possible mechanisms that could drive larval dispersal and recruitment in this species.

MATERIALS AND METHODS

1. Study area and sampling protocol

122 glass eels of *A. mossambica* were collected by traditional fisheries along the eastern coast of Madagascar in the South-Western Indian Ocean (Fig. 1). The spatial sampling occurred in December 2005 in five localities, from North to South: Andevoranto (18°58' S; 49°06' E), Mahanoro (19°54' S; 48°48' E), Mananjary (21°14' S; 48°20' E), Manakara (22°08' S; 48°01' E) and Vangaindrano (23°20' S; 47°42' E). The temporal sampling was conducted in Mananjary from November 2005 to February 2006.

2. Species identification

After fixation in 90% ethanol, eels were measured and identified using Ege's (1939) glass eel determination key. Characteristics used were the caudal pigmentation and the distance between the origins of the dorsal and anal fins as percent of the fish total length: A-D% = [(DL-AL)/TL]*100 where DL is dorsal length, AL is anal length and TL is total length. Identifications were confirmed through molecular analysis using semi-multiplex PCR (Gagnaire et al. 2007). The pigmentation stage was determined according to Elie et al. (1982).

3. Otolith microstructural analysis

Left sagittae of *A. mossambica* were extracted under binocular microscope, cleaned, embedded in epoxy resin and ground with grit paper until the nucleus was visible. Once polished, etched with 9% EDTA solution and coated with gold, they were examined with a scanning electron microscope SEM (JEOL JSM 5410 LV) and developmental stages checks were located (Fig. 2).

The duration of the leptocephalus (LD) and the metamorphosis (MD) stages, the larval otolith growth rates during the leptocephalus stage (OGR), the age at recruitment (AR) and, by back-calculation, the hatching date (HD), were determined for each individual. Otolith daily growth rates (μm d^{-1}) were calculated along the longest radius, from the first feeding check to the edge of each otolith.

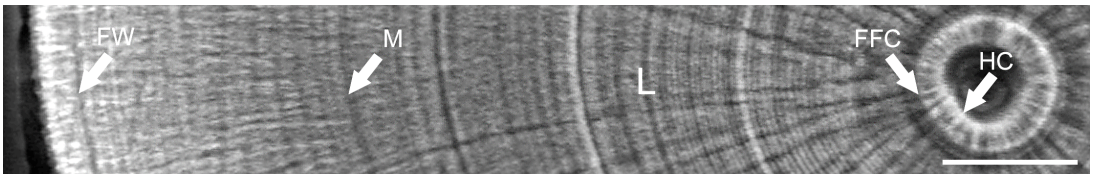

Figure 2. *Anguilla mossambica*. SEM photograph of the transect of an etched otolith. HC: Hatch Check, FFC: First Feeding Check, L: Leptocephalus stage, M: Metamorphosis onset, FW: FreshWater entry. Scale bar = 20 μm.

4. Statistical analysis

Boxplots were used to illustrate the ELT variations within and between sampling localities. Statistical analyses were performed with R software (R Development Core Team 2007). One-way ANOVA and Tukey HSD post-hoc tests were performed after verifying the normality (Anderson-Darling test) and the homoscedasticity of data (Bartlett test). Correlation tests were performed using Pearson test for parametric data. Means (± SD) and minimum and maximum values of each ELT were calculated for localities and months of sampling.

RESULTS

Values of TL and ELT identified through otolith microstructure are listed in Table 1 for each locality and sampling date. All trait frequencies were normally distributed in each sampling location and date (Anderson-Darling Normality test, $p > 0.5$).

1. Spatial variations of early-life traits

Glass eels collected in early December 2005, between north to south of the eastern coast of Madagascar hatched from the 30th of June 2005 to the 22nd of September 2005 (Fig. 3, Table 1). LD was negatively correlated to the HD ($R^2 = 0.902$, $p < 0.0001$), to the OGR ($R^2 = 0.348$, $p < 0.0001$) and to the TL ($R^2 = 0.194$, $p < 0.001$).

Conversely, it was positively correlated to the AR ($R^2 = 0.239$, $p < 0.001$). Freshwater recruitment checks only occurred in glass eels from Manakara. In this site, they also exhibited the longest MD (Tukey HSD, $p < 0.05$, Fig. 3). Other ELT varied along a latitudinal gradient (Tukey HSD, $p < 0.05$). Northern localities exhibited earlier HD, shorter LD, higher OGR, younger AR and smaller TL than southern localities (Table 1, Fig. 3). Between localities, LD and TL differences increased with the distance ($R^2 = 0.350$, $p < 0.01$ and $R^2 = 0.729$, $p < 0.001$ respectively for LD and TL, Fig. 4).

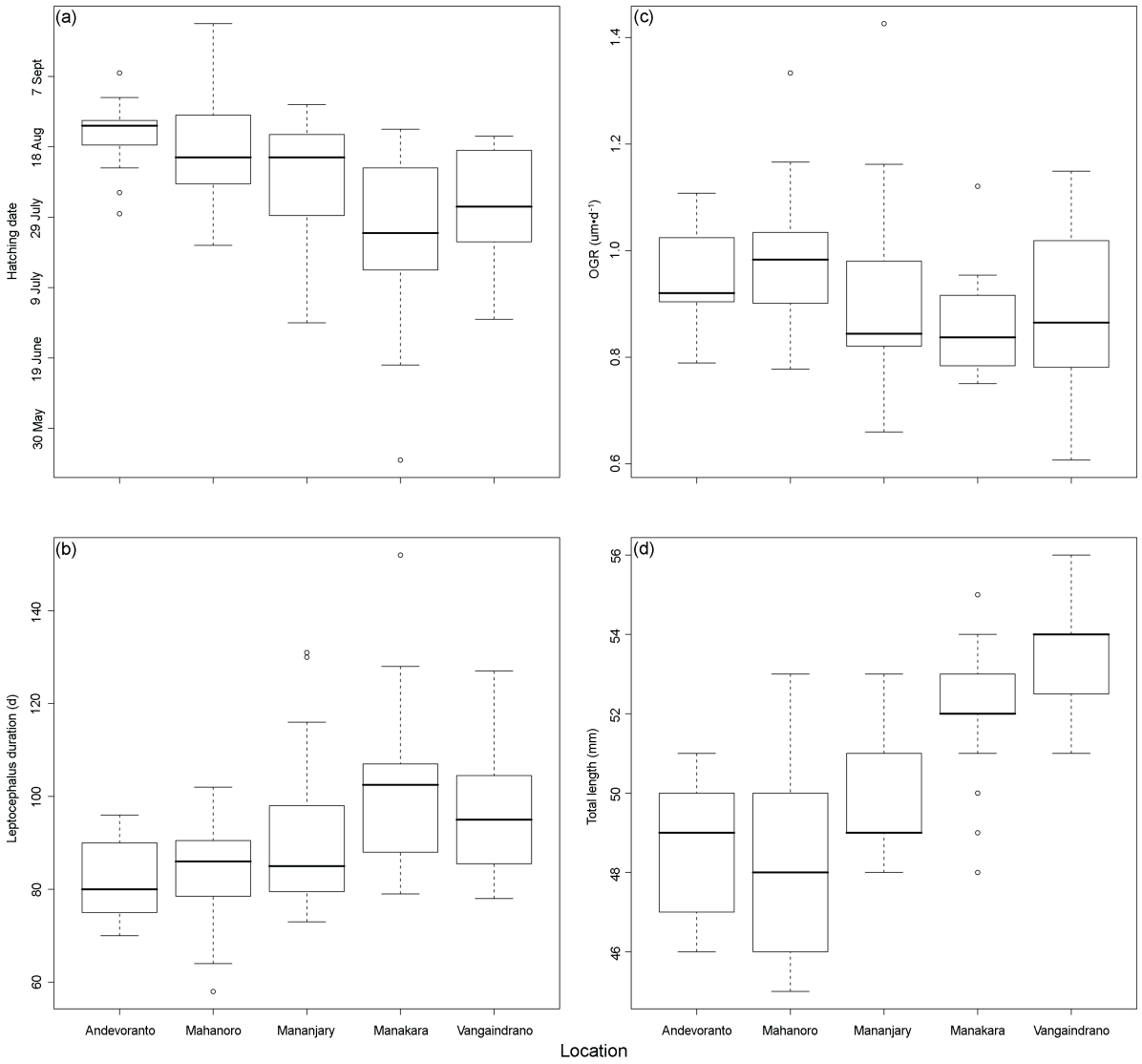

Figure 3. *Anguilla mossambica*. Boxplots representing spatial variations of (a) hatching date, (b) leptocephalus stage duration, (c) otolith growth rate (OGR) and (d) body total length of glass eels caught in December 2005 in Madagascar. Localities are ordered from North on the left to South on the right.

Table 1. *Anguilla mossambica*. Mean ± SD and range for the hatching date (HD), leptocephalus duration (LD), otolith growth rate (OGR), metamorphosis duration (MD), age at recruitment (AR) and total length at recruitment (TL), for glass eels sampled in different localities in December 2005 and in Mananjary at different months.

	N	HD (± days)	LD (days)	OGR (µm • d-1)	MD (days)	AR (days)	TL (mm)
Spatial variations from North to South							
Andevoranto	15	23-aug-05 ± 8.1 Aug 7 to Sep 8 2005	82.5 ± 8.2 70 to 96	0.95 ± 0.10 0.79 to 1.11	22.4 ± 3.7 17 to 28	105.0 ± 8.1 89 to 121	48.6 ± 1.7 46 to 51
Mahanoro	15	21-aug-05 ± 13.0 Aug 1 to Sep 17 2005	84.8 ± 10.8 64 to 102	1.00 ± 0.14 0.78 to 1.33	21.9 ± 4.6 15 to 30	106.7 ± 13.0 80 to 127	48.3 ± 2.1 45 to 53
Mananjary	15	08-aug-05 ± 19.0 Jun 29 to Aug 30 2005	92.5 ± 18.8 73 to 131	0.90 ± 0.19 0.66 to 1.42	22.5 ± 3.4 18 to 29	115.0 ± 17.5 99 to 152	50.0 ± 1.7 48 to 53
Manakara	15	26-jul-05 ± 22.8 Jun 3 to Aug 23 2005	103.0 ± 20.3 79 to 152	0.86 ± 0.10 0.75 to 1.12	27.2 ± 4.3 19 to 32	130.2 ± 21.7 105 to 181	52.3 ± 1.4 50 to 54
Vangaindrano	15	31-jul-05 ± 16.9 Jun 30 to Aug 21 2005	96.6 ± 14.5 78 to 127	0.90 ± 0.17 0.60 to 1.15	22.4 ± 2.9 18 to 29	119.0 ± 14.8 100 to 149	53.5 ± 1.5 51 to 56
Temporal variations in Mananjary							
November 2005	16	16-jul-05 ± 7.4 Jul 6 to Aug 8 2005	85.5 ± 10.2 71 to 104	0.90 ± 0.10 0.74 to 1.07	25.2 ± 4.6 16 to 33	110.7 ± 8.4 96 to 123	47.9 ± 1.5 43 to 49
January 2006	15	29-aug-05 ± 13.3 Aug 10 to Oct 1 2005	104.1 ± 11.4 78 to 120	0.82 ± 0.06 0.68 to 0.91	24.2 ± 5.8 13 to 33	128.3 ± 13.3 96 to 148	51.2 ± 1.5 49 to 54
February 2006	16	24-oct-05 ± 13.8 Sep 27 to Nov 12 2005	96.4 ± 15.5 77 to 126	1.00 ± 0.20 0.69 to 1.31	22.9 ± 4.5 17 to 32	119.4 ± 14.2 102 to 148	51.0 ± 1.4 48 to 53

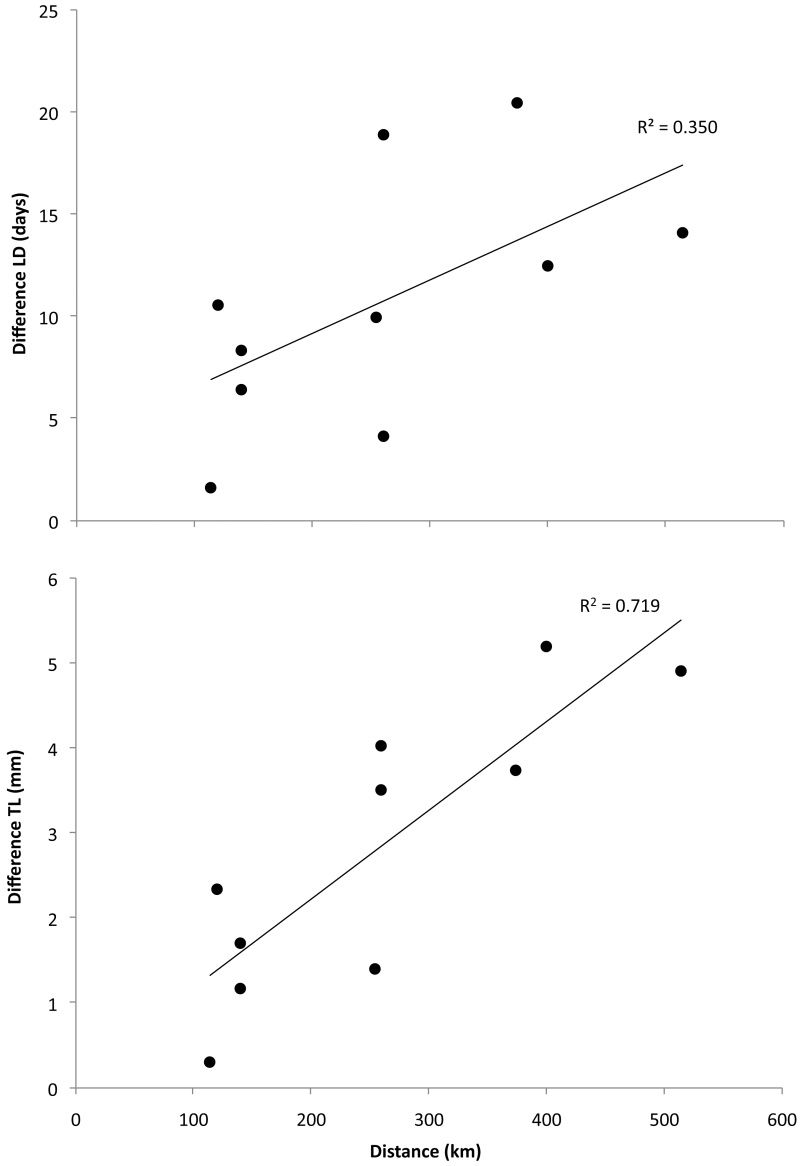

Figure 4. *Anguilla mossambica*. Mean differences of (a) leptocephalus duration (LD) and (b) body total length (TL) according to the coastal distance separating the localities of recruitment sampled in December 2005 in Madagascar.

2. Temporal variations of early-life traits

The temporal sampling revealed continuous spawning from the 3rd June to the 12th November 2005 (Fig. 5). Large variations of LD were observed between simultaneously hatched larvae. The variation range seemed constant throughout the hatching period, with all the values of LD being comprised between a minimum of 71 days and a maximum of 131 days.

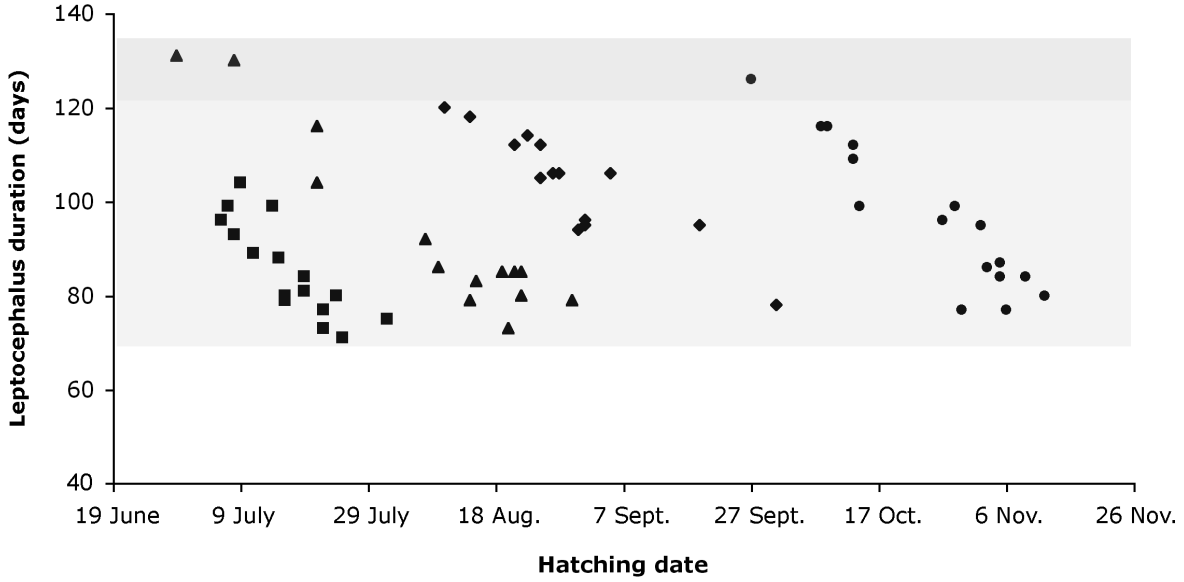

Figure 5. *Anguilla mossambica*. Correspondence between hatching dates and leptocephalus durations (LD) of glass eels collected in Mananjary (Madagascar) the 6th November 2005 (■), the 8th December 2005 (▲), the 5th January 2006 (◆) and the 22nd February 2006 (●).

DISCUSSION

1. Anatomical clue of dispersal duration

Estimates of the LD seemed to be possible through the examination of the TL of recruited glass eels, as both traits were positively correlated. The same observation has been made at the inter-specific level. Temperate eels exhibit, indeed, longer larval dispersal and longer TL at recruitment than tropical eels (Marui et al. 2001, Kuroki et al. 2006). Our results thus support the observation of Kuroki et al. (2006) who found the TL of 4 tropical species leptocephali to be correlated to their LD. They showed a non-linear body growth during the larval life, which best fitted to a Gompertz growth curve. This growth model supposes that leptocephalus larvae reach a fully-grown size before or at the onset of the metamorphosis. The positive correlation between TL and LD suggest that larvae with a short LD had a smaller size at the metamorphosis onset than larvae with a long LD. Thus, conversely to Bishop and Torres's (1999) hypothesis, the maximum size reached by leptocephali before their metamorphosis onset could rather be typical of their dispersal duration rather than of their species.

2. Variability of the larval dispersal duration

At the individual level, the duration of the larval dispersal results from the combination of two parameters. (**1**) On the one hand, it depends on the duration of the larval stage and the extent to which it can vary. (*i*) This parameter, controlled by the metabolic rate (O'Connor et al. 2007), can be innate/genetically determined and immutable for each larva (Russell 1987). (*ii*) Alternatively, larvae can exhibit individual plasticity[8], and can generate different responses to variations of environmental conditions such as water temperature (Anderson 1988 in Jenkins and King 2006, Meekan et al. 2003). (**2**) On the other hand, the larval dispersal duration depends on the time necessary to reach the final recruitment place. This duration might be modulated (*i*) by the distance that separates the spawning area from the recruitment place, (*ii*) by currents velocity and complexity, and (*iii*) by the swimming capacity of larvae (Bradbury et al. 2003). Although active migration has not been demonstrated in eel leptocephali, it has never been excluded (McCleave et al. 1998, Shiao et al. 2002). Its contribution to migration and dispersion thus remains to be studied. In the present study, LD variations, repeatedly observed at a small scale in each of the five estuaries studied, could have been produced by a mix of the two aforementioned individual and environmental parameters. Nevertheless, considering the uniform pattern of variation recorded in each locality (Gaussian variation), we suggest that a single pathway fed each locality in larvae. This supports the existence of a single spawning area, accordingly to Jespersen (1942) and Robinet et al. (2008).
Whether individual plasticity or phenotypic polymorphism explain that the larval phase duration varies in *A. mossambica* is unknown. Nevertheless this is an important issue that has to be addressed. Indeed, even if both would increase the number of larvae reaching a changing recruitment place thanks to the resilience capacities these processes provide to face environmental changes (Holling 1973, Hilborn et al. 2003, Beechie et al. 2006), they would not have the same evolutionary implications.

[8] Plasticity: Genetically controlled response to the environment (Murren et al. 2003).

3. Latitudinal variation of larval dispersal

Inter-localities variations of larval life duration overwhelmed intra-locality ones. Moreover, LD variations went with those of other traits such as the OGR, and followed a latitudinal cline. Larvae had shorter LD and higher OGR in northern localities than in southern ones. As larval traits seemed stable through time within the recruitment period studied in Mananjary, it is likely that spatial heterogeneity have generated the latitudinal gradient. The same kind of latitudinal variation of LD has been reported for *A. australis* along the eastern coast of Australia (Shiao et al. 2001), for *A. rostrata* along the eastern coast of North America (Wang and Tzeng 1998) and for *A. japonica* along Japanase coasts (Tsukamoto 1990). In each of these studies, the gradient was supposed to be related to the presumed or known location of the spawning area. In the SWIO, Jespersen (1942) and Robinet et al. (2008) have proposed that *A. mossambica* spawning area could be located in Madagascar northeastern waters, between Madagascar and the Mascarene Ridge. From this presumed spawning area, currents carrying larvae would flow southward along the eastern coast of Madagascar. Our results strongly support this hypothesis, as larvae exhibited shorter dispersal durations in the North. Furthermore, according to mean regional current speeds (varying from 10 to 20 $cm.s^{-1}$, Penduff et al. 2007), larval dispersal in *ca.* 100 days would enable them to cross about 1500 to 2000 km which limits the dispersal origin to the Mascarene Ridge as fairly suggested by Jespersen (1942) and clearly proposed by Robinet et al. (2008).

From this area, Padfield and Coward (1998) and Schott and McCreary (2001) models reported the flow reaching Madagascar to be about 2°C warmer in the North than in the South. This seemed well translated into the individual metabolic rate directly influenced by the environmental temperature in fish larvae (Pepin et al. 1997, O'Connor et al. 2007). As temperature decreases, the metabolism slows down. This induces larvae to develop slowly thus delays the time at which they reach the metamorphic competence[9] (Hadfield et al. 2001) and prolongs their dispersal phase in the pelagic environment. The fact that the spawning area of *A. mossambica*, and other eels, still lie in tropical areas after millions of years of evolution may results in the advantage it provides the species to colonize both close areas in warm waters

[9] Metamorphic competence: developmental capacity to undergo metamorphosis when triggered by internal or external factors (Hadfield et al. 2001).

thanks to a rapid development, and distant habitats in colder waters thanks to high dispersal capacities.

4. Clue for recruitment determinism

Previously, we discussed the causes for dispersal duration variability among a population of larvae. We might also wonder what may stop the larval dispersal. No previous studies succeeded in determining the mechanisms that trigger metamorphosis in leptocephalus larvae and further, recruitment (Otake 2003, Miller et al. 2006). On the one hand, it has been proposed that metamorphosis could be initiated by a "biological clock" governed by intrinsically determined factors such as the developmental rate and hormonal factors, influenced or not by environmental parameters like temperature (Gillooly et al. 2002, Otake 2003). This theory suggests that, in a pool of simultaneously hatched larvae, some individuals could become competent (defined as the developmental capacity to undergo complete metamorphosis; Victor 1986, Hadfield et al. 2001, Hickford and Schiel 2003), for metamorphosis and recruitment earlier than others. On the other hand, it has been suggested that the detection of cues associated to coastal waters (Sola 1995, Miller et al. 2006) could initiate the metamorphosis and the recruitment. This would mean that larvae transported by different routes could recruit at different times of the dispersal, depending on their distance to the coastal area influence.

In the light of the results recorded in this study, we propose that metamorphosis and recruitment are initiated by a subtle combination of both biological clock and detection of coastal cues. Indeed, the previous discussion on the mechanisms that might generate variations in the larval dispersal duration supports the role of a biological clock. This process might determine the time at which larvae attain the metamorphic competence. After what, the detection of coastal cues could induce metamorphosis and/or recruitment. We propose that if, at least, one condition was not respected, larvae would continue to disperse or would die in the open ocean.

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Conclusions:

- La variabilité des traits et donc des histoires de vie larvaire a été observée aux échelles locale, ponctuelle et régionale dans des limites stables.

- Cette variabilitié pourrait être imputée à la combinaison des propriétés individuelles et des caractéristiques de l'environnement.

- L'examen de la variabilité a donné des informations sur les caractéristiques de la dispersion et sur son origine géographique.

Perspectives:

- Savoir si ces caractéristiques sont maintenues chez d'autres espèces.

- Observer la structuration de la variabilité des traits de vie par la configuration géographique du recrutement.

Partie 2

Plasticité de la dispersion larvaire d'*Anguilla marmorata* révélée par l'analyse de la microstructure des otolithes

Résumé: L'histoire de vie larvaire d'*Anguilla marmorata* a été examinée dans le sud-ouest de l'Océan Indien à Mayotte, Maurice et La Réunion, par analyse de la microstructure des otolithes des civelles. Les traits de vie tels les dates d'éclosion, la marque de première prise de nourriture (FFD), les durées de vie leptocéphale (LD) et de métamorphose (MD), l'âge au recrutement (AR) et les taux de croissance de l'otolithe (OGR), se sont montrés variables et diversement corrélés. Trois types d'histoires de vie larvaire discriminés par analyse de groupement agglomératif hiérarchique, ont été observés à l'échelle géographique: (*i*) migrateurs rapides à LD et MD courtes, AR jeunes, et FFD et OGR forts, dominants à La Réunion et à Mayotte; (*ii*) migrateurs intermédiaires à LD, MD, AR, FFD et OGR intermédiaires, dominants à Maurice; (*iii*) migrateurs lents à LD et MD longues, AR avancés, et FFD et OGR faibles, observés seulement à Maurice. Toutes les stratégies possibles n'ont pas été observées et donc n'ont pas toutes été efficaces pour la période échantillonnée L'expression simultanée de plusieurs stratégies laisse supposer, à l'échelle de la population, une plasticité de la migration larvaire chez *A. marmorata*. L'information est cruciale au regard des capacités de dispersion et du scénario d'évolution du genre *Anguilla* qui suppose une émergence des espèces tempérées aux migrations larvaires longues à partir des espèces tropicales aux migrations larvaires courtes.

Mots-clef: *Anguilla marmorata*, traits et histoires de vie larvaire, plasticité, microstructure des otolithes.

Anguilla marmorata larval migration plasticity as revealed by otolith microstructural analysis

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Abstract: The oceanic early-life history of *Anguilla marmorata* was examined in the southwestern Indian Ocean in Mayotte, Mauritius, and Réunion islands through otolith microstructural analysis. The study of the hatching dates, the first feeding check diameter (FFD), the leptocephalus (LD) and metamorphosis (MD) durations, the age at recruitment (AR) and the leptocephalus otolith growth rate (OGR) of glass eels, revealed great variations in early-life traits (ELT) and relationships between them. An agglomerative nesting analysis discriminated three early-life histories, differently represented according to the locality: (*i*) fast migrants with short LD, short MD, young AR, large FFD and high OGR dominated in Réunion and Mayotte; (*ii*) mid-speed migrants with intermediate LD, MD, AR, FFD and OGR dominated in Mauritius; (*iii*) slow migrants with long LD, long MD, old AR, small FFD and low OGR were recorded only in Mauritius. All possible strategies were not observed and therefore not successful at the sampling time. However, several were simultaneously expressed, which suggests larval migration plasticity at the population level. This evidence is crucial information regarding both the species dispersal capabilities and the evolution from short-migratory tropical species towards long-migratory temperate ones in the genus *Anguilla*.

Keywords: *Anguilla marmorata*, early-life traits and histories, plasticity, otolith microstructure.

INTRODUCTION

The duration of a fish larval stage, and therefore, its metamorphosis timing, might be key factors determining distances of dispersal and species distribution range (Arai et al. 2001a, Hoareau et al. 2007). Variation in oceanic migration duration of successfully recruited larvae probably reflects the species capabilities to delay metamorphosis and therefore the ability to maximize chances of finding suitable growth areas (Victor 1986). This delay has been observed to be very flexible in some fish groups and mostly for those composing the monophyletic group of the Elopomorpha (*i.e.* Elopiformes, Albuliformes, Saccopharyngiformes and Anguilliformes; Inoue et al. 2004).

In the complex catadromous Anguillid eel life cycle, the duration of the leptocephalus stage, which undergoes an oceanic migration from spawning areas to growth coastal or inland waters, can vary widely among species. In eels, this larval phase is known to be shorter in tropical ancestral species than in the most recent temperate ones (Kuroki et al. 2006). Migration loops made by tropical species from inter-tropical spawning areas seem to have enlarged during evolution, offering the emergence of new species with large migration loops, with spawning areas still located in tropical waters while growth areas shifted toward temperate waters (Tsukamoto et al. 2002). This evolution could be consecutive to an intraspecific variability in the oceanic larval life duration, found in a number of recent studies, as for *Anguilla marmorata* (Marui et al. 2001, Arai et al. 2002a, Robinet et al. 2003a; Table 1), which is the most widespread species of the genus (Jubb 1961, Ishikawa et al. 2004, Robinet et al. 2007). This plasticity in the duration of the larval migration at the population scale might be the expression of selected strategies, which are defined here as genetically determined life histories or behaviours. Each individual will not show the whole strategy, but rather one of several tactics that the strategy may be composed of. The selection of strategies might occur according to environmental conditions (currents, water physico-chemical characteristics, trophic resource…) and distance of the recruitment areas from the spawning location, maximizing the number of larvae that reach growth zones.

In the southwestern Indian Ocean (SWIO), *A. marmorata* spawning area was proposed to be unique and roughly localized northeast off the Mascarene Ridge by Jespersen (1942), Jubb (1961) and Robinet et al. (2008) (Fig. 1). In the present paper,

we compare, through otolith microstructural analysis, the early-life traits (ELT: hatching dates, timing and duration of metamorphosis, age at recruitment and otolith growth rate) of *A. marmorata* glass eels, sampled within the same month in three localities of the SWIO. On the one hand, Jespersen's hypothesis about a single regional spawning area is discussed in the light of the regional current circulation. On the other hand, variability of ELT is discussed in terms of response to variations of the pelagic environment and in terms of intra- and inter-specific dispersal capabilities.

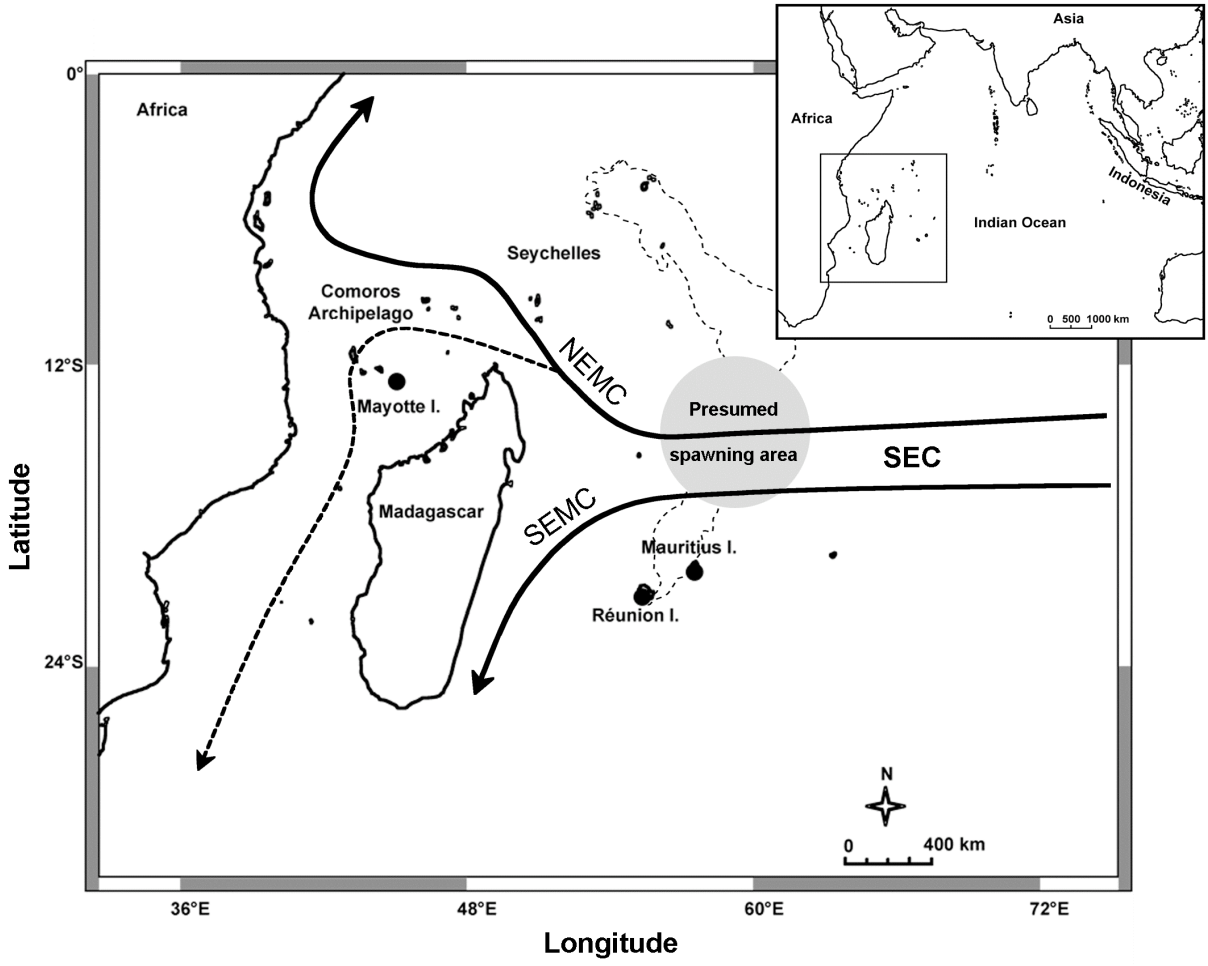

Figure 1. Location of Mayotte, Mauritius and Réunion islands in the southwestern Indian Ocean. The presumed spawning area of *Anguilla marmorata* by Jespersen (1942) is shown in grey; the Mascarene Ridge (thin dotted line) and main regional currents (solid and dotted lines with arrows) are also indicated: SEC, South-Equatorial Current (dividing into the NEMC (Northeast Madagascar Current) and the SEMC (Southeast Madagascar Current)).

Table 1. Duration (mean ± standard deviation, SD) of the leptocephalus stage of *Anguilla marmorata* reported in literature for glass eels sampled throughout the species distribution range from 1994 to 2005.

Locality	Year	N	LD (d)	SD (d)	Min. (d)	Max. (d)	Range (d)	Source
Indonesia	1996	18	120	15.6	96	147	51	Arai et al. 1999b
	1996	1	162	14.0	-	-	-	Marui et al. 2001
	1997	68	128	15.2	114	158	44	Arai et al. 2001b
	1999	23	79	11.2	-	-	-	Budimawan & Lecomte-Finiger 2005
Philippines	1994	10	120	13.0	105	140	35	Arai et al. 1999b
	1998	16	146	19.5	112	183	71	Marui et al. 2001
Taiwan	1999	15	114	13.8	92	141	49	Arai et al. 2002a
Japan	1999	15	123	13.9	100	155	55	Arai et al. 2002a
Réunion	2001	9	97	26.4	60	135	75	Robinet et al. 2003a
	2005	15	111	15.8	94	142	48	Present study
Mauritius	2005	30	139	24.0	91	180	89	Present study
Mayotte	2005	29	120	13.1	104	151	47	Present study

MATERIALS AND METHODS

1. Study area and sampling

Réunion (21°S, 56°E; 2507 km²) and Mauritius (20°S, 57°E; 1865 km²) islands belong to the Mascarene Archipelago and are the most southern islands of the Mascarene Ridge (Fig. 1). Mayotte (12°S, 45°E; 374 km²) is a part of the Comoros Archipelago located 1300 km northwest of the Mascarene Islands at the northern entry of the Mozambique Channel. These two archipelagos are bathed, respectively, by the southern and the northern bifurcation of the main regional current, the South-Equatorial Current (SEC), flowing westward and splitting on the Mascarene Ridge and on the east coast of Madagascar (Schott and McCreary 2001).

74 glass eels and young elvers of *A. marmorata* were sampled in April 2005 in Mauritius (30 individuals), Réunion (15 individuals) and Mayotte (29 individuals)

islands in the SWIO, with a portable electroshocker delivering electric impulses (DEKA 3000, EFKO manufacturer, DC 30 impulses·s-1, 350 V, 4 A). Sampling occurred in the estuary of 26 permanent rivers as follow: 8 rivers in Mauritius (April 5-7th), 4 in Réunion (April 11-12th), and 14 in Mayotte (April 15-19th).

2. Species identification

After fixation in 90% ethanol, eels were measured and identified using Ege's glass eel determination key (Ege 1939). Criteria used were caudal pigmentation and the distance between the origins of the dorsal and anal fins as a percentage of the fish total length: A-D% = [(LD-LA)/LT]*100 where LD is dorsal length, LA is anal length and LT is total length (Ege 1939, E. Réveillac et al., unpublished data). Identifications were confirmed through molecular analysis using semi-multiplex PCR (Gagnaire et al. 2007). The pigmentation stage was determined according to Elie et al. (1982).

3. Otolith microstructural analysis

Otoliths can be regarded as a reliable record of early-life history (ELH) (Lecomte-Finiger 1992, Campana 2001). Previous works on eels otolith microstructure revealed by scanning electron microscope (SEM) concluded that growth increment deposition occurs daily with a low error margin (Martin 1995, Sugeha et al. 2001, Shinoda et al. 2004). Moreover, remarkable checks are thought to correspond to shifts between the different ontogenetic stages and, if increment deposition is clear, enable the determination of the age of the individual at every shift (Wang and Tzeng 2000, Campana and Thorrold 2001, Jessop et al. 2006; Fig. 2). The otolith core can be observed as a deep hole in the centre of the etched otolith, with a surrounding ring described as the hatch check. The first feeding check, which is thought to correspond to the end of the preleptocephalus stage and to the complete absorption of the yolk reserve, is in the vicinity of the crystalline crown surrounding the core (Marui et al. 2001, Kuroki et al. 2005). The metamorphosis check, which marks the transition from the leptocephalus stage to the metamorphosis stage, is usually observed when increment widths start to increase suddenly (Lecomte-Finiger 1992). The end of metamorphosis, and therefore the onset of the glass eel stage, is represented by one

or two successive annuli from which increment widths start to decrease towards the otolith edge (Lecomte-Finiger 1992).

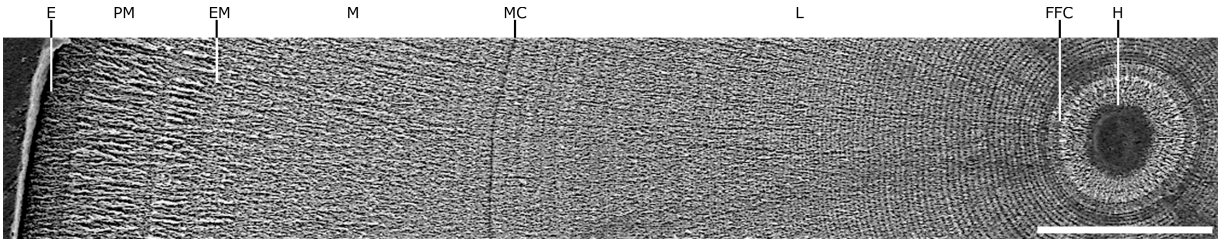

Figure 2. Scanning electron microscope (SEM) photograph of the microstructure of an etched otolith of *Anguilla marmorata* with marks of developmental events. H: Hatch check; FFC: First Feeding Check; L: Leptocephalus stage; MC: Metamorphosis Check; M: Metamorphosis; EM: End of Metamorphosis; PM: Post-Metamorphic stage; E: otolith Edge. Scale bar = 20 μm.

A total of 74 left sagittae of *A. marmorata* (30 from Mauritius, 15 from Réunion and 29 from Mayotte) were extracted under binocular microscope, cleaned, embedded in metacrylate resin and ground with 150, 9 and 3 μm grit paper until the nucleus was visible. Once polished, etched with 9% EDTA solution and coated with gold, they were examined with a SEM (JEOL JSM 5410 LV). The age at first feeding could not be precisely determined because layers deposited within the crystalline crown surrounding the otolith core are not always well visible. Therefore, to characterize the preleptocephalus stage, we measured the diameter of the first feeding check (FFD in μm). This parameter and the duration of the leptocephalus (LD) and the metamorphosis (MD) stages, the larval otolith growth rates during the leptocephalus stage (OGR), the age at recruitment (AR) and, by back-calculation, the hatching date (HD), were determined for each individual. Otolith average growth rates ($\mu m \cdot d^{-1}$) were calculated by the average thickness of every 10 increments from the FFD to the margin of each otolith, along the measurement axis.

4. Statistical analysis

Agglomerative nesting ("agnes"; hierarchical clustering), developed for R (R Development Core Team 2007, Kaufman and Rousseeuw 1990) was performed on the regional sample for FFD, LD, OGR, MD and AR variables. The Euclidean metric system and the average method of linkage were used after the variables were standardized. A bootstrap analysis was performed to test the strength of the structure. An analysis of vairance (ANOVA) was performed to test the differences for

each variable between groups computed by the cluster analysis. The shape of the LD frequencies distribution was tested with MCLUST density test analysis of data aggregation (MCLUST: model-based clustering normal mixture modeling) (Fraley and Raftery 2003, 2007), developed for R (R Development Core Team 2007). Means (± SD) of each variable were calculated for groups of individuals computed by the cluster analysis. Comparisons were made after performing Anderson-Darling normality tests and verifying variance equality, with Student's *t*-test or Kruskal-Wallis (KW) test. Correlation tests between variables were performed with the Spearman test for nonparametric data.

RESULTS

1. Pigmentation and size at recruitment

The pigmentation of the 30 individuals caught in Mauritius was only developed on the caudal and rostral regions of the body (stages V_A to VI_{A0}), classifying them all as glass eels (Elie et al. 1982). Among the 15 individuals sampled in Réunion, 4 eels were at a more advanced pigmentation stage (VI_{A1} to VI_B) and 1 was classified as a stage VII (elver). In Mayotte, 14 eels were classified as stages VI_{A1} to VI_B.

Mean body length of all eels (*i.e.* all stages included) and only glass eels (V_A to VI_{A0}) were respectively 67.53 +/- 32.97 mm (range: 50 to 178 mm) and 52.40 +/- 1.07 mm (range: 50 to 54 mm) in Réunion Island, and 59.76 +/- 8.86 mm (range: 47 to 79 mm) and 52.53 +/- 3.74 mm (range: 47 to 55 mm) in Mayotte Island. Mean body length of glass eels caught in Mauritius was 52.13 +/- 2.60 mm (range: 46 to 56 mm). No significant variability in the size of glass eels occurred between the sites (KW test, $p > 0.05$).

2. Oceanic life

A. marmorata glass eels sampled simultaneously in April 2005 showed a wide distribution range of HD from late August to late December 2004 (Fig. 3). The glass eels from Mauritius hatched significantly earlier (hatching date: 8 Oct 04 +/- 26.70 d) than those of Réunion and Mayotte, which showed quite similar distributions and

mean HD (5 Nov 04 +/-36.21 d and 6 Nov 04 +/- 23.11 d, respectively; KW test, $p > 0.05$).

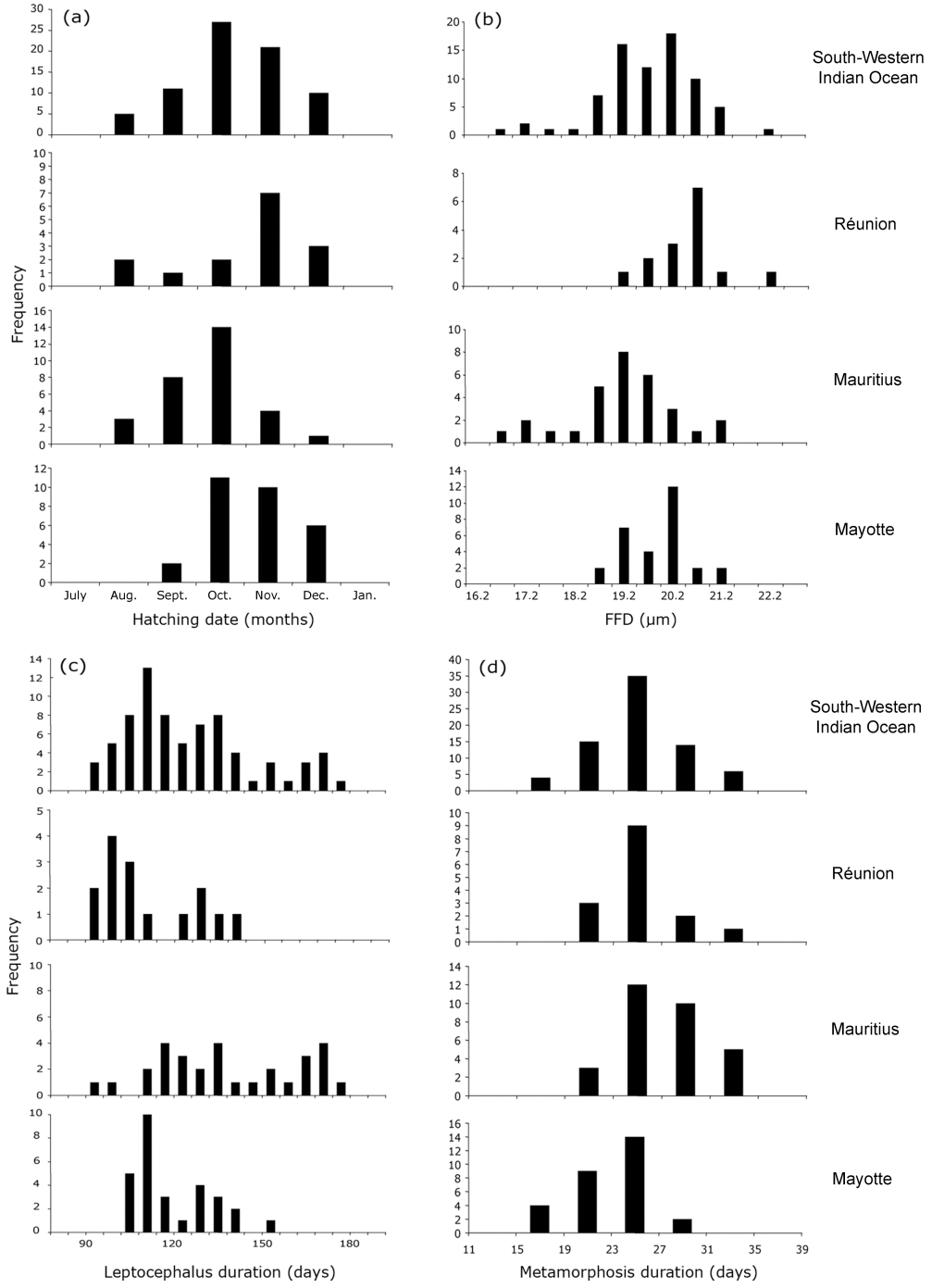

Figure 3. Hatching date (a), first feeding check diameter FFD (µm) (b), leptocephalus duration (days) (c) and metamorphosis duration (days) (d) frequencies distribution, determined by otolith microstructural analysis of 74 glass eels (*Anguilla marmorata*) sampled in the southwestern Indian Ocean in Réunion (N = 15), Mauritius (N = 30) and Mayotte (N = 29) islands in April 2005.

The other ELT showed wide ranges of values at insular and regional scales (Fig. 3). They also exhibited interrelationships (Fig. 4) with LD being negatively correlated to FFD (Spearman, $R^2 = 0.746$, $p < 0.0001$) and to OGR (Spearman, $R^2 = 0.142$, $p < 0.01$), and positively correlated to MD (Spearman, $R^2 = 0.284$, $p < 0.0001$), and to AR (Spearman, $R^2 = 0.982$, $p < 0.0001$).

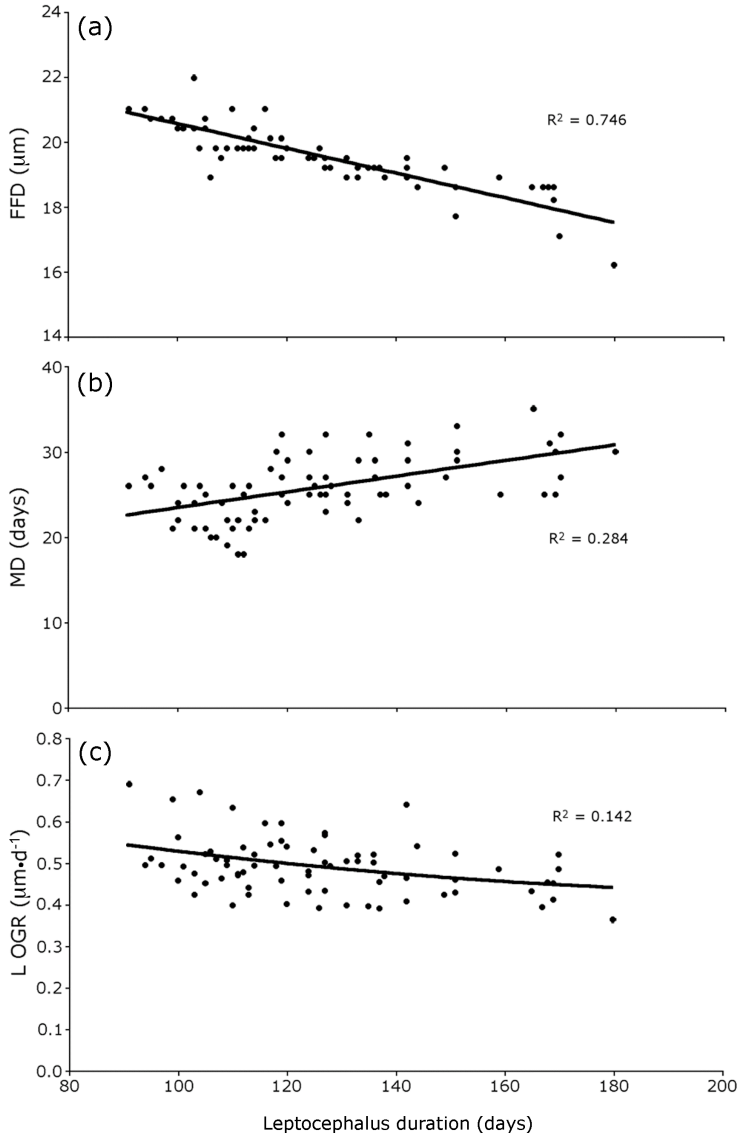

Figure 4. *Anguilla marmorata*. Relationship between the first feed check diameter FFD (µm) (a), the metamorphosis duration (days) (b), the leptocephalus daily otolith growth rate (L OGR) ($\mu m \cdot d^{-1}$) (c) and the leptocephalus duration (days), in glass eels caught in the South-Western Indian Ocean (N = 74) in April 2005.

Three main clusters of individuals were computed by the agnes hierarchical cluster analysis (agglomerative coefficient = 0.88, bootstrap values > 98%; Fig. 5). They showed statistically different ELT values (ANOVA, $p < 0.05$) and corresponded to 3

modes of LD distribution frequencies observed at the regional scale (MCLUST density test, E = 3). The first group was composed of 30 individuals sampled in all 3 islands (N = 10 in Réunion, N = 4 in Mauritius and N = 16 in Mayotte). Their life history was characterized by large FFD (mean 20.4 ± 0.5 µm), short LD (mean 104.6 ± 6.2 d, range 91 to 116 d), high OGR (mean 0.64 ± 0.08 $\mu m \cdot d^{-1}$), short MD (mean 22.9 ± 2.5 d) and young AR (mean 127.5 ± 5.7 d). They were qualified as fast migrants.

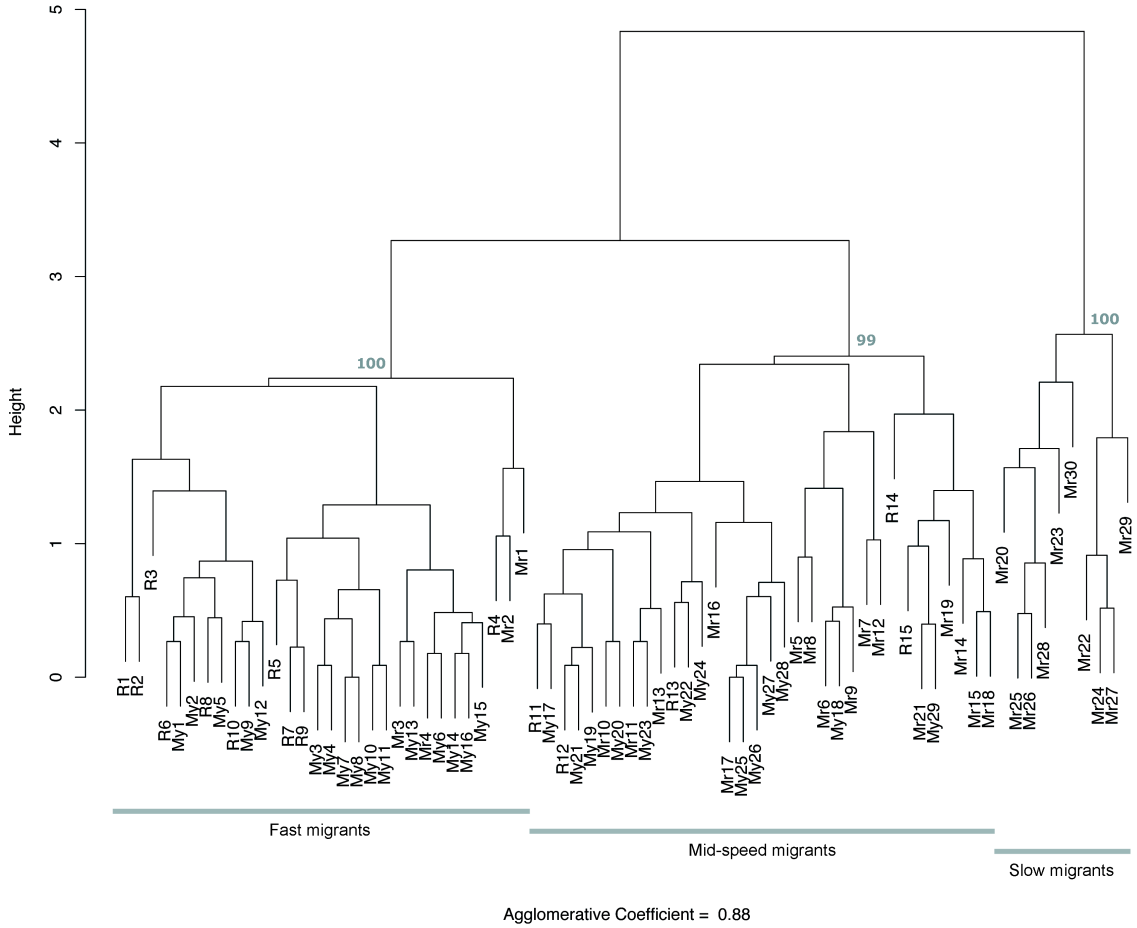

Figure 5. Dendrogram computed by agglomerative nesting analysis (agnes; hierarchical clustering) of 74 individuals glass eels (*Anguilla marmorata*) characterized by 5 early-life traits: first feed check diameter, leptocephalus duration, metamorphosis duration, otolith growth rate and age at recruitment. Variables were standardized before the analysis of Euclidean distances. Bootstrap values are reported for the 3 identified strategies of larval migration: fast, mid-speed and slow migrants. R plus sample number, Mr plus sample number, My plus sample number represent glass eels collected in Réunion, Mauritius and Mayotte islands respectively.

The second group (mid-speed migrants) included 34 individuals also sampled in the 3 islands (N = 5 in Réunion, N = 16 in Mauritius and N = 13 in Mayotte). They had

intermediate values of FFD (mean 19.3 ± 0.4 µm), LD (mean 129.4 ± 10.3 d, range 117 to 151 d), OGR (mean 0.59 ± 0.06 µm•d^{-1}), MD (mean 26.7 ± 2.8 d) and AR (mean 156.1 ± 11.8 d). The third group (slow migrants) was composed of 10 individuals only sampled in Mauritius. They had small FFD (mean 18.1 ± 0.8 µm), long LD (mean 166.8 ± 47.6 d, range 159 to 180 d), low OGR (mean 0.55 ± 0.05 µm•d^{-1}), long MD (mean 29.3 ± 3.5 d) and old AR (mean 196.1 ± 8.0 d).

Geographical differences were observed, as each type of ELT combinations, *i.e.* ELH was not similarly represented among islands. Indeed, fast migrants were dominant in Réunion and Mayotte, while mid-speed migrants were the most represented in Mauritius recruitment. Slow migrants only occurred in Mauritius, where they were more abundant than fast migrants. The 3 types of ELH were therefore different in terms of ELT values and in terms of geographical occurrence.

3. Otolith growth rate pattern

The OGR pattern from the centre to the edge of the otolith is shown in figure 6. It comprised 4 phases as described for *A. japonica* (Arai et al. 1997); *A. rostrata* (Arai et al. 2000b); *A. australis*, *A. dieffenbachii and A. b. pacifica* (Marui et al. 2001); *A. celebesensis*, *A. marmorata* and *A. b. bicolor* (Arai et al. 1999b); and *A. anguilla* (Lecomte-Finiger 1992). High individual variations were recorded within each phase, independently from the general pattern (Fig. 6).

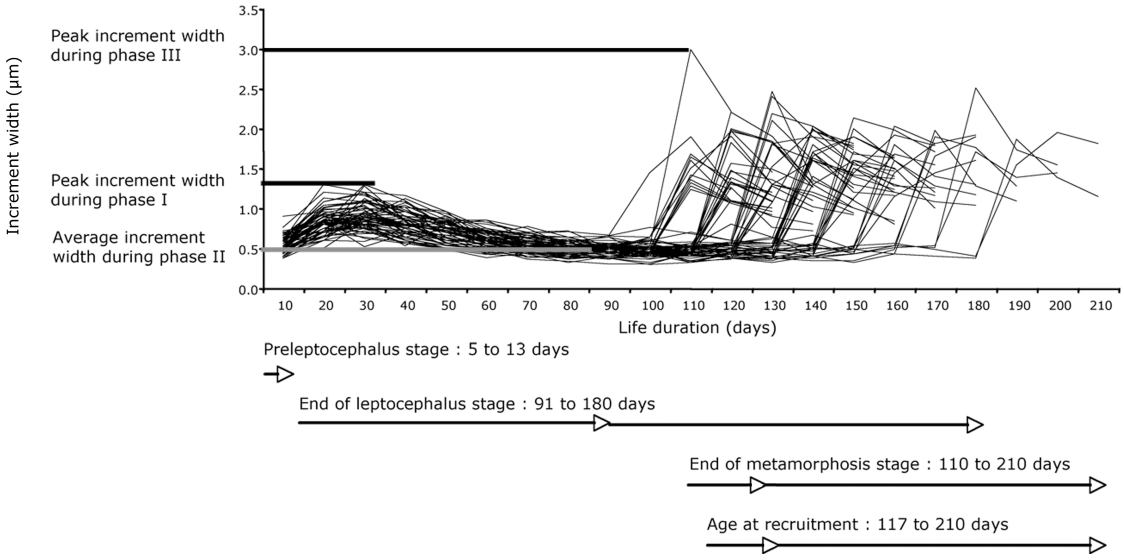

Figure 6. Otolith increment widths along the preleptocephalus, leptocephalus, and metamorphosis stages of 74 glass eels (*Anguilla marmorata*) sampled in the southwestern Indian Ocean in April 2005.

During the first phase, otolith increment widths increased between the hatch check and age 20 to 40 d (maximum peak average 0.94 ± 0.15 µm•d^{-1}, range: 0.68 to 1.30 µm•d^{-1}) and then gradually decreased until almost constant during the second growth phase (mean values 0.49 ± 0.08 µm•d^{-1}, range: 0.29 to 0.80 µm•d^{-1}). At the end of the steady growth phase, a sudden increase of the OGR occurred, corresponding to the third phase (maximum peak average 1.73 ± 0.35 µm•d^{-1}, range: 1.08 to 2.99 µm•d^{-1}). Increment widths then decreased afterward (fourth growth phase).

DISCUSSION

1. Size at recruitment

In the present study, the body size at recruitment of *A. marmorata* (*i.e.* for juveniles at stages V_A to VI_{A0}) was poorly correlated to the migration duration, indicating no clear correspondence between these parameters at the intraspecific level. Nevertheless, mean sizes observed in each island (52.13 ± 2.60 mm in Mauritius, 52.40 ± 1.07 mm in Réunion and 52.53 ± 3.74 mm in Mayotte), were close to those previously recorded for the same species recruiting into Indonesia (Arai et al. 1999b, 2001b) into Taiwanese and Japanese coastal waters (Arai et al. 2002a) and into Réunion estuaries (Robinet et al. 2003a). Also, as observed in previous studies, these mean values were smaller than for temperate species at the same pigmentation stages, such as *A. anguilla* (68 mm) (Lecomte-Finiger 1992), *A. japonica* (57 mm) (Arai et al. 1997), *A. rostrata* (58 mm) (Arai et al. 2000b), *A. dieffenbachii* (64 mm) (Marui et al. 2001) and *A. australis* (59 mm) (Shiao et al. 2001). Therefore, there is an obvious difference in length at recruitment between temperate and tropical species. As temperate eels undergo much longer migrations than tropical ones (Lecomte-Finiger 1992, 1994, Kuroki et al. 2006), the size at recruitment seems, at the interspecific level, to be influenced by the LD, as suggested by Marui et al. (2001).

2. Clues for a single regional spawning area

In the years 1928-1930, leptocephalus larvae were sampled in the Indian Ocean during the Carlsberg Foundation's Oceanographic Expedition Around the World. The results conducted Jespersen (1942) to locate a regional spawning area for Anguillid eels at the northeast of Madagascar on the Mascarene Ridge (discussed by Robinet et al. 2008). However further studies should be conducted to test Jespersen's hypothesis. Indeed, a model combining life history traits and oceanic circulation would help to simulate larval transport under various conditions. The global model NEMO (simulation DRAKKAR ORCA025-G70 over years 1959 to 2004, resolution 1/4°; Penduff et al. 2007) computed 45 years of currents speeds and directions in the SWIO (Fig. 7).

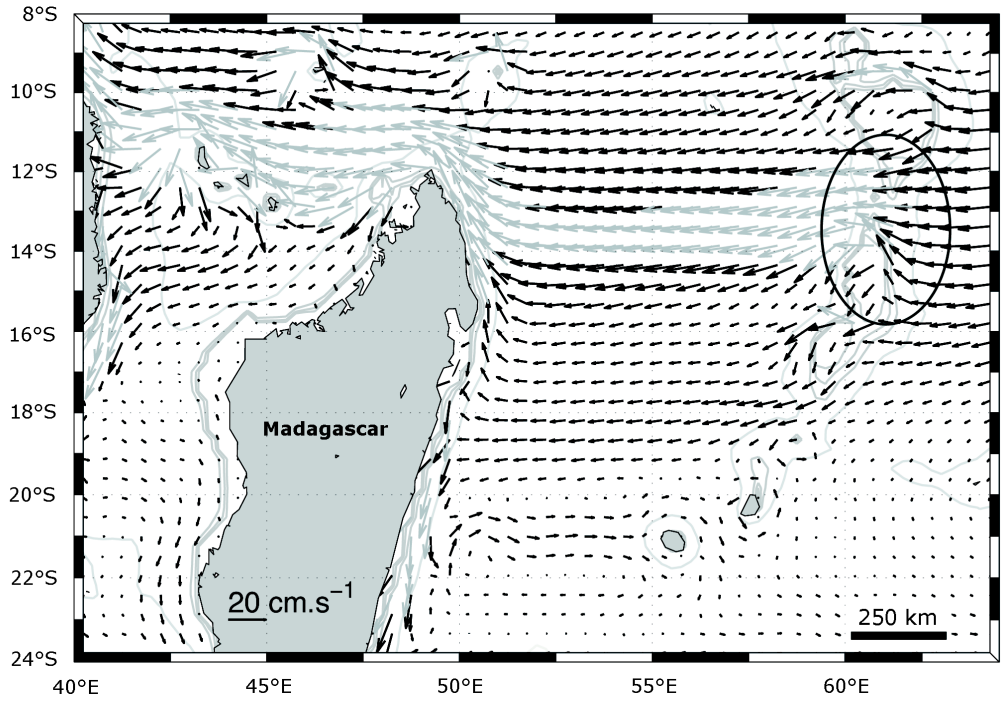

Figure 7. Southwestern Indian Ocean mean currents speeds and directions (0 to 100 m depth) computed over years 1959 to 2004 by the global oceanographic model NEMO (simulation DRAKKAR ORCA025-G70, resolution 1/4°; Penduff et al. 2007). The spawning area of *Anguilla marmorata* proposed by Jespersen (1942) is delimited by a black ellipse on the Mascarene Ridge. Grey-shaded current vectors correspond to current velocities higher than 20 cm • s^{-1}.

This model, roughly combined with migration durations we recorded in this study, seems to support the spawning area proposed by Jespersen (1942) and supported by Robinet et al. (2008). From this area, indeed, the SEC, and the North Equatorial Madagascar Current could have transported larvae to Mayotte at the speed of about

20 cm•s^{-1} (Fig. 1, 7). In that case, larvae would have crossed 1500 km in about 90 days, which roughly corresponds to the LD recorded for larvae recruited in this island. As well, from the Mascarene Ridge, the SEC and the South-Equatorial Madagascar Current could have carried larvae first to Mauritius and then to Réunion at the speed of about 10 cm•s^{-1}. Thus those larvae would have crossed 1000 km in about 110 days, which is also consistent with the mean LD registered in those two islands.

3. Variability of early-life history traits

Developmental variability was clearly expressed through obvious variations of early-life stages durations (Fig. 8). The sum of these durations resulted in variations of ages at recruitment. This variability seemed to be also related to fluctuations of the OGR, which reflects individual somatic metabolic rates (Wright 1991).

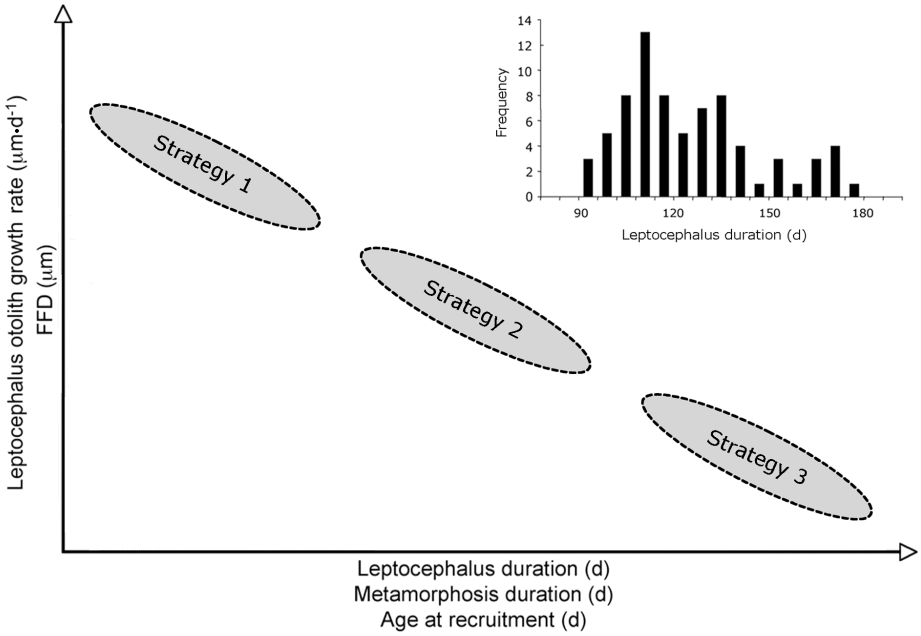

Figure 8. Schematic representation of the three strategies (1, fast; 2, mid-speed; and 3, slow migrants) discriminated by cluster analysis based on early-life traits combinations of glass eels (*Anguilla marmorata*) caught in April 2005 in the South-Western Indian Ocean. Frequencies of each strategy occurrence are shown in the top right corner. Other possible strategies were not observed. FFD: first feeding check diameter.

Relationship between developmental stages duration and OGR has already been described in other anguilliform larvae such as *Anguillidae* (Tzeng 1990, Robinet et al. 2008) and the American conger eel *Conger oceanicus* (Correia et al. 2004), but also

in Pleuronectiforms with *Limanda ferruginea* (Benoit and Pepin 1999) or in some reef fishes (Wellington and Victor 1992). This study goes further, demonstrating correlations between more than two ELTs. These complex relationships discriminated individuals into 3 groups and revealed the existence of, at least, three ELHs (Fig. 8).

Observed ELT variations may be explained by two alternative or complementary hypotheses: (*i*) the intrinsic metabolism hypothesis and (*ii*) the environmental conditions hypothesis. Indeed, both may govern modalities of energy expense and may have repercussions on ELT and then on ELH. Environmental conditions such as water temperature (Høie et al. 1999, Otterlei et al. 2002, Bang et al. 2006) and food availability (Takasuka and Aoki 2006) are thought to be the primary determinant of larval growth rate and subsequent larval duration (Anderson 1988, Jenkins and King 2006). Then, their variations are thought to have mainly produced the different ELHs recorded. As the HD was not related to the other ELTs, observations of several different ELHs might not be related to temporal heterogeneity, but rather to spatial heterogeneity of environmental conditions. As the hypothesis of a single spawning area seemed plausible, it is likely that heterogeneous conditions in this spawning area and/or several migration routes have produced the different ELHs observed. The global NEMO model showed that migrations were possible within the mean durations recorded through otolith microstructural analysis. However, complexity of currents was undervalued because this model calculated the mean circulation over several decades. Over shorter periods of time, like a season, those currents are indeed reported to have more complex trajectories (Schott & McCreary 2001, Pous et al. unpublished data). As they encounter islands or shallow waters like the Mascarene Ridge, gyres are created (Padfield & Coward 2001). The turbulence of this system could partly explain how different migration routes could have transported larvae to different localities in different environmental conditions, inducing disparities in ages at recruitment and delays of arrival between localities.

In light of these results, more precise modeling is required to test hypotheses on *A. marmorata* migration routes in the SWIO. Active swimming, diffusion mechanisms, larval mortality and water temperature are some of the parameters that would have to be introduced in the model. In parallel, growth dynamic, which seemed to influence and/or be influenced by the developmental rhythm at every stage of the

oceanic life, has to be further examined in order to analyze the contribution of environmental and intrinsic factors to the Anguillid eel larval life course.

4. A plasticity of larval migration in the anguillid eel?

As previously mentioned, variability of migration traits led to the observation of three ELH patterns, which respond to the following trend: the migration duration is inversely proportional to OGR and the associated metabolic rate. This variability demonstrates that *A. marmorata* larval migration can be achieved at various times. This might be a key in the migratory anguillid eel life-cycle success. Indeed, several ELH patterns, qualified here as strategies, were expressed in variable proportions according to the recruitment place, while other strategies were not expressed. There is a possible trade-off between these various strategies. On the one hand, fast migration (linked to high metabolic rate) probably reduces mortality (Takasuka & Aoki, 2006) while it also reduces the probability to find growth habitats. On the other hand, slow migration (low metabolic rate) might reduce larval survival while it might increase the probability to find suitable growth habitats. The existence of such a range of larval migratory strategies might globally increase the fitness of the population. It might also represent a strong selective advantage for *A. marmorata* because it sustains an extraordinary dispersion capacity among fish species. Indeed, a short duration of the leptocephalus stage might favour geographical retention, while a long migration duration might favour both emigration (Correia et al. 2004) and connectivity among populations separated during their growth phase in continental systems.

The fact that no other strategies were observed could reflect unsuccessful or inexistent combinations of ELT. As McCormick (1999) proposed, larval duration of a fish may result from the interactions between its genotype, its larval environment and the capacity of the species to delay metamorphosis. The lower age limit for settlement is governed by the rate of larval development, while the upper age limit is determined by the extent to which a delay of metamorphosis is possible, both also linked to the timing of finding suitable places to settle. On the one hand, short migration with low growth rate might be lethal because larvae that reach rapidly coastal shelves are not ready to undergo metamorphosis (*i.e.* are not competent for recruitment; Victor 1986, Hickford and Schiel 2003). On the other hand, long

migration with high growth rate might induce rapid consumption of energy reserves, leading to body depletion and therefore death before coastal waters are reached.
Regarding the evolution of the genus *Anguilla*, short migration with high metabolic rate could be seen as the ancestrally successful strategy in tropical waters wherein the genus seems to have originated (Aoyama et al. 2001, Lin et al. 2001). Long migration with low growth rate could then be regarded as the strategy that has generated large migration loops leading to the emergence and establishment of temperate species. This strategy could have started to be profitable and widely represented when oceans opened, allowing larger dispersal toward temperate waters. This possibility of extending the dispersal range could have been supported by a lower temperature of migration, which, by decreasing the larval metabolic rate, led to viable migration strategies establishment (Gillooly et al. 2002, O'Connor et al. 2007). This scenario hypothesis must be examined in Anguillid eels to deepen the knowledge on their evolution.

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Conclusions:

- Contrairement à ce qui a été observé chez *Anguilla mossambica*, la longueur totale au recrutement ne s'est pas montrée corrélée à la durée de la dispersion chez *A. marmorata*. Ceci pourrait être du au temps de résidence en estuaire/rivière plus important chez la seconde espèce.

- La variabilité à différentes échelles spatiales a été réaffirmée et semble être une caractéristique importante pour la réussite de la phase de dispersion.

- La structuration de la variabilité s'est montrée étroitement liée à la géographie du recrutement qui a donné des informations, comme pour *A. mossambica*, sur la position de la zone de ponte.

Perspectives:

- Compléter l'analyse par l'examen des paramètres biométriques taille, poids et coefficient de condition.

- Continuer d'investiger la typologie des variations des traits de vie sur une espèce à longue dispersion qui recrute en milieu tempéré.

Partie 3

Dispersion larvaire de l'anguille Européenne *Anguilla anguilla* examinée au travers des variations spatio-temporelles des histoires de vie larvaire et des caractéristiques biométriques au recrutement

Résumé: Les histoires de vie de 385 civelles d'anguilles européennes ont été étudiées par analyse de la microstructure de leur otolithes, dans le but d'estimer les variations spatio-temporelles de la dispersion larvaire. Les variations de durée de la phase leptocéphale, non graduelles sur la façade Altantique, ont révélé un gradient d'augmentation de l'ouest à l'est de la Méditerranée. Ces résultats pourraient illustrer une arrivée frontale des larves sur les côtes européennes, suggérant ainsi l'existence de plusieurs routes (latitudinales) de dispersion. La métamorphose a semblé coïncider avec l'arrivée sur le plateau continental mais la relation mise en évidence entre le déclenchement de la métamorphose et le taux métabolique larvaire suggère la contribution d'une horloge biologique déterminant la compétence des larves à se métamorphoser. Les caractères biométriques (longueur totale, poids et condition) de 1789 civelles, collectées lors du recrutement en estuaire, sur différents sites, à différents moments, ont montré des variations spatiales supportant l'existence de différentes routes latitudinales de dispersion larvaire. Les variations temporelles de la longueur et du poids ont, quant a elles, révélé la même tendance de décroissance saisonnière observée par d'autres auteurs. Cette observation pourrait être imputée aux changements des conditions environnementales au long de cette période, ou plus largement, à une variation des combinaisons des traits de vie conférant à la larve la capacité de coloniser les zone de croissance dans un état physiologique stable. Les résultats confortent les estimations des durées de dispersion larvaire faites lors de précédents travaux basés sur l'otolithométrie, mais alimentent, en retour, la controverse existante quant à la durée de traversée de l'Atlantique par les larves d'anguilles. Dans ce contexte, la contribution d'un comportement de nage des larves leptocéphales est discutée.

Keywords: Anguille Européenne *Anguilla anguilla*, traits de vie larvaire, caractéristiques biométriques, dispersion, otolithométrie.

Larval dispersal of the European eel *Anguilla anguilla* as revealed by spatio-temporal variability of early-life histories and biometric characteristics at recruitment

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In preparation

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Abstract: The early-life histories of 385 European glass eels were studied through otolith microstructural analysis to examine the spatio-temporal variations of larval dispersal. Leptocephalus duration variations were poorly gradual along the Atlantic coast but showed a clear gradient from western to eastern Mediterranean Sea. This highlighted a frontal arrival on the European coasts and suggested the existence of different latitudinal routes of dispersal. Metamorphosis seemed to be correlated with the arrival above the continental shelf but the relationship between the early metamorphosis onset and a high metabolic rate suggested also a contribution of the biological clock determining the metamorphic competence. The diversity of early-life histories displayed by *A. anguilla* reflected different trades-off between larval traits and also the ability for the species to recruit at different times and thus over a large distribution range. The biometric characteristics (total length, weight and condition) were examined on 1789 glass eels collected at recruitment. Spatial variations seemed to support the existence of different latitudinal dispersal routes with one flowing directly to the Mediterranean Sea. Temporal variations were similar to those observed in previous studies showing a decrease of both total length and weight through the season. This could be imputed either to temporal variability of environmental conditions, or to different trades-off made between larval traits that enable larvae to colonize growth habitats with a constant physiological state. Results finally comforted larval dispersal durations estimated by previous authors through otolith analysis. This still feeds the controversy about the duration of the transatlantic journey of *A. anguilla* larvae. In this context mention the importance that could have a potential swimming behaviour on the migration efficiency.

Keywords: European eel *Anguilla anguilla*, early-life traits, biometric characteristics, dispersal, otolith microstructural analysis.

INTRODUCTION

350 years BC, Aristotle stated that eels don't mate, that they do not have eggs and that we will never find an eel either with eggs, seed, or seed conducts or matrix (Rondelet 1558). Since that time, many theories followed one another about the origin of eels, until Grassi and Calandruccio (Grassi 1896) determined that the marine species known as *Leptocephalus brevisrostris* was in fact the larval form of the European eel. Chasing the smallest larvae like a treasure hunt, Schmidt (1922) then discovered that all begins in the Sargasso Sea. Few days' incubation of fertilized eggs gives birth to leaf-like transparent larvae called leptocephali (Yamamoto and Yamauchi 1974). These larvae spend their whole phase crossing the ocean toward the coasts of Europe. At their arrival near the continental area, they start to metamorphose into glass eels and reach a recruitment place in coastal, estuarine or freshwater habitats from North Africa to North Europe along the Atlantic and the Mediterranean coasts (Lecomte-Finiger 1992, Arai et al. 2006).

About 2300 years after Aristotle, Lecomte-Finiger (1994) cited Kleckner and McCleave (1988) while beginning her letter to Nature by "the early life history of the European eel *Anguilla anguilla* is still something of a mystery". Twenty years later again, this assessment is always of topicality. How long is dispersal? How do larvae come back to continental growth areas? What conditions do they experience during their journey? These are some of the remaining questions that find hypotheses but no certainties. Moreover, controversy exists about dispersal duration estimates since otolith microstructural analysis revised the generally accepted 2-3 years estimate made by Schmidt (1922), by providing shorter estimates (less than one year, Lecomte-Finiger 1992). Those discrepancies challenge subsequent studies on the early-life of the European eel that are of first importance to understand and manage this species. Indeed, the transatlantic dispersal of eels' larvae is a key phase as it determines the species distribution area, plays a role in geographic units connectivity, and governs partly the renewal of the species (Tsukamoto and Aoyama 1998). In a context of fairly unresolved panmictic status of the European eel (Wirth and Bernatchez 2001, Maes et al. 2006, Pujolar et al. 2006) listed in the Appendix II of the International Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES 2007) in regard to its dramatic decline since the end of the XXth

Century (Feunteun 2002), the examination of larval life histories and biometric characteristics at recruitment seems a major concern. Such studies have been conducted since several years (Lecomte-Finiger and Yahyaoui 1989, Lecomte-Finiger 1994, Désaunay et al. 1996, Désaunay and Guérault 1997, deCasamajor et al. 2001a, 2001b, 2006, Pujolar et al 2007). However they examined trends of both larval life histories and biometric characteristics in one locality, or trends of only one characteristic but in different localities sampled more or less simultaneously.

The purposes of the present study were (1) to examine early-life histories and biometric characteristics of glass eels collected, on the one hand, simultaneously in different localities and, on the other hand, during 9 months over two consecutive seasons in one locality, (2) to learn about the migratory strategy success of *A. anguilla* according to its life-histories variability, and finally (3) to review and re-examine the estimates of larval dispersal durations made by otolith microstructural analysis.

MATERIALS AND METHODS

1. Sampling sites

1749 glass eels and elvers were collected from 10 localities on both the Atlantic (Carlingford Lough in Ireland, Den Oever estuary in the Netherlands, Vilaine estuary and Aiguillon Bay in France, Oria and Butron estuaries in Spain, Oued Loukkos in Morocco) and the Mediterranean coasts (Saintes Maries de la Mer in Camargue in the South of France, Oued Mejerdah in Tunisia, Sagiada Marsh in Greece) coasts (Fig. 1). Spatial sampling occurred in February 2006 in all localities except in the Netherlands and in Tunisia, sampled respectively in April 2006 and in February 2007. A temporal monitoring was conducted in the Vilaine estuary in France and in the Oria and Butron estuaries in northern Spain. Samples occurred every month from February to April 2006, in June 2006 and from December 2006 to April 2007 in the Vilaine estuary and every month from January to April 2007 in 2 localities in northern Spain.

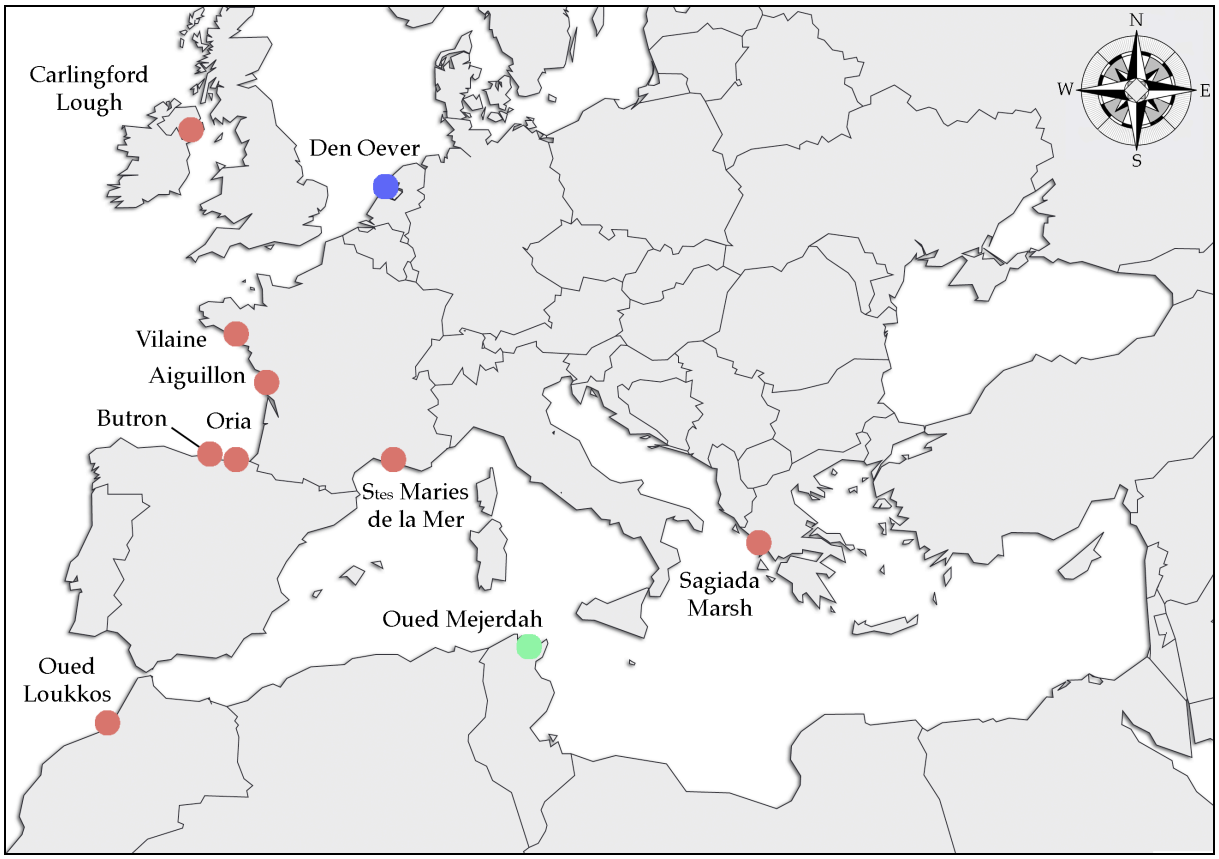

Figure 1. Locations of sampling sites. (Red dots = collected in February 2006; blue dot = collected in April 2006; green dot = collected in February 2007)

2. Biological examination

After preservation in absolute ethanol, the pigmentation stage of eels was determined according to Elie et al. (1982). Only eels at the V_B stage were considered as they characterize the immigrating glass eels (Désaunay et al. 1996). They were measured to the nearest millimetre and weighted to the nearest 10^{-1} milligram. Their coefficient of condition was calculated according to Fulton K-index, $K = (\text{weight} \cdot 10^5)/\text{total length}^3$.

3. Otolith microstructural analysis

Only glass eels at the stage V_B were selected for otolith analysis to allow the comparison of simultaneously recruited individuals. A total of 385 otolith left sagitta were extracted under binocular microscope, cleaned, embedded in epoxy resin and ground with grit paper until the nucleus was visible. Once polished, etched with 9% EDTA solution and coated with gold, they were examined under scanning electron

microscope SEM (JEOL JSM 5410 LV). From the center to the edge (Fig. 2), marks of hatching, first feeding, metamorphosis onset and entry to freshwater were used to delimit the preleptocephalus, leptocephalus (LD), metamorphosis (MD) and beginning of the yellow eel phases (Lecomte-Finiger 1994, Arai et al. 2000b). The otolith daily growth rate (OGR) was calculated in order to consider variations of the individual metabolic rate (Bang et al. 2006).

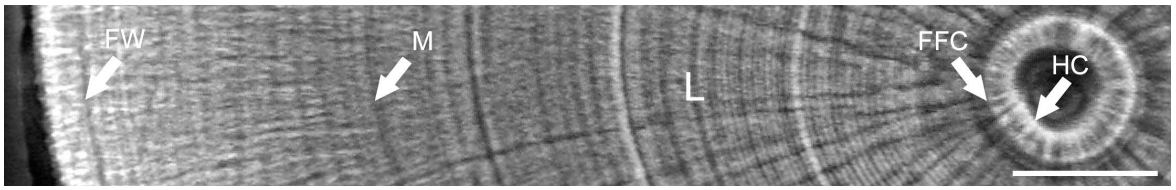

Figure 2. SEM photograph of the transect of an etched glass eel otolith. HC = Hatch Check; FFC = First Feeding Check; L = Leptocephalus stage; M = metamorphosis onset; FW = FreshWater check. Scale bar = 20 μm.

4. Statistical analyses

Statistical analyses were performed with R software (R Development Core Team 2007). One-way ANOVA, Tukey HSD and pairwise Student *t*-tests were performed after evaluation of the normality (Anderson-Darling test) and the homoscedasticity of data (Bartlett test). Boxplots were used to illustrate variations within and between sampling localities and months. Correlation tests were performed with Pearson test for parametric data. Means (± SD), minimum and maximum values were calculated for localities and months of sampling.

RESULTS

1. Biometric characteristics at recruitment

Temporal variations. Results illustrated in Fig. 3 show that biometric parameters tended to decrease through time both in 2006 and 2007 (ANOVA $p < 0.01$) in the Vilaine estuary. Values differed between the two consecutive years studied. Total body length was quite the same, except in March 2006, whereas body weight and condition were significantly lower in early 2006 than in early 2007 (ANOVA $p < 0.01$).

Spatial variations. Results illustrated in Fig. 4 show, from left to right, biometric variations from North to South on the Atlantic coast and from West to East in the Mediterranean Sea. In all localities, biometric parameters were highly variable between individuals. On the Atlantic coast, Aiguillon Bay received the longest and almost the lightest glass eels with the lowest body condition of all the localities studied. A gradient in body length was observed with decreasing lengths towards both North and South from Aiguillon Bay. From the entry of the Mediterranean Sea, in Oued Loukkos, body length increased toward Camargue and decreased toward Greece. Variations of body weight were not significant (ANOVA, $p > 0.05$), whereas body condition was higher in Greece than in the other two localities (Tukey HSD, $p < 0.0001$). Body length and weight were significantly lower for Mediterranean localities grouped with Oued Loukkos than for the group of other Atlantic localities (Student *t*-test, $p < 0.001$).

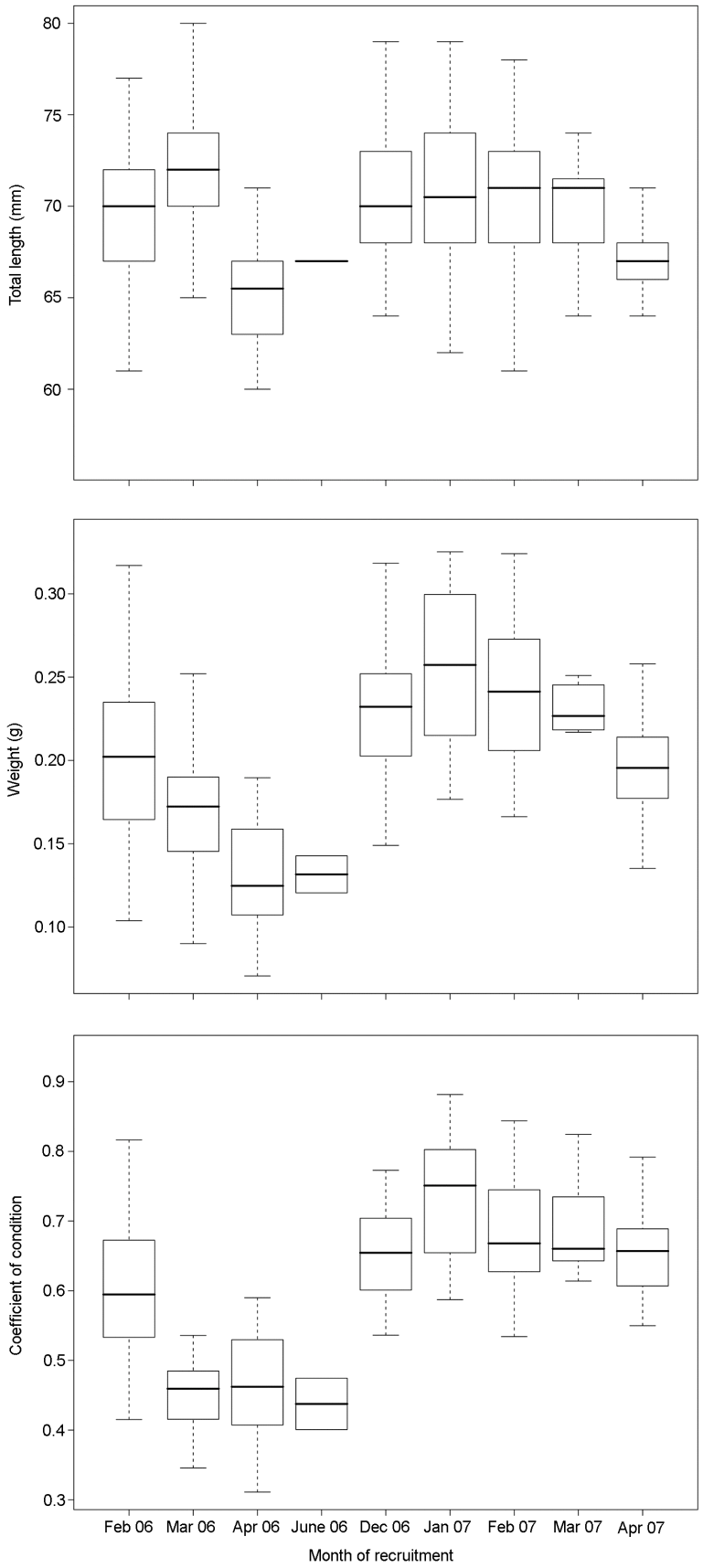

Figure 3. Temporal variations of biometric characteristics (body length, weight and Fulton coefficient of condition) of *Anguilla anguilla* glass eels recruited in the Vilaine estuary in 2006 and 2007.

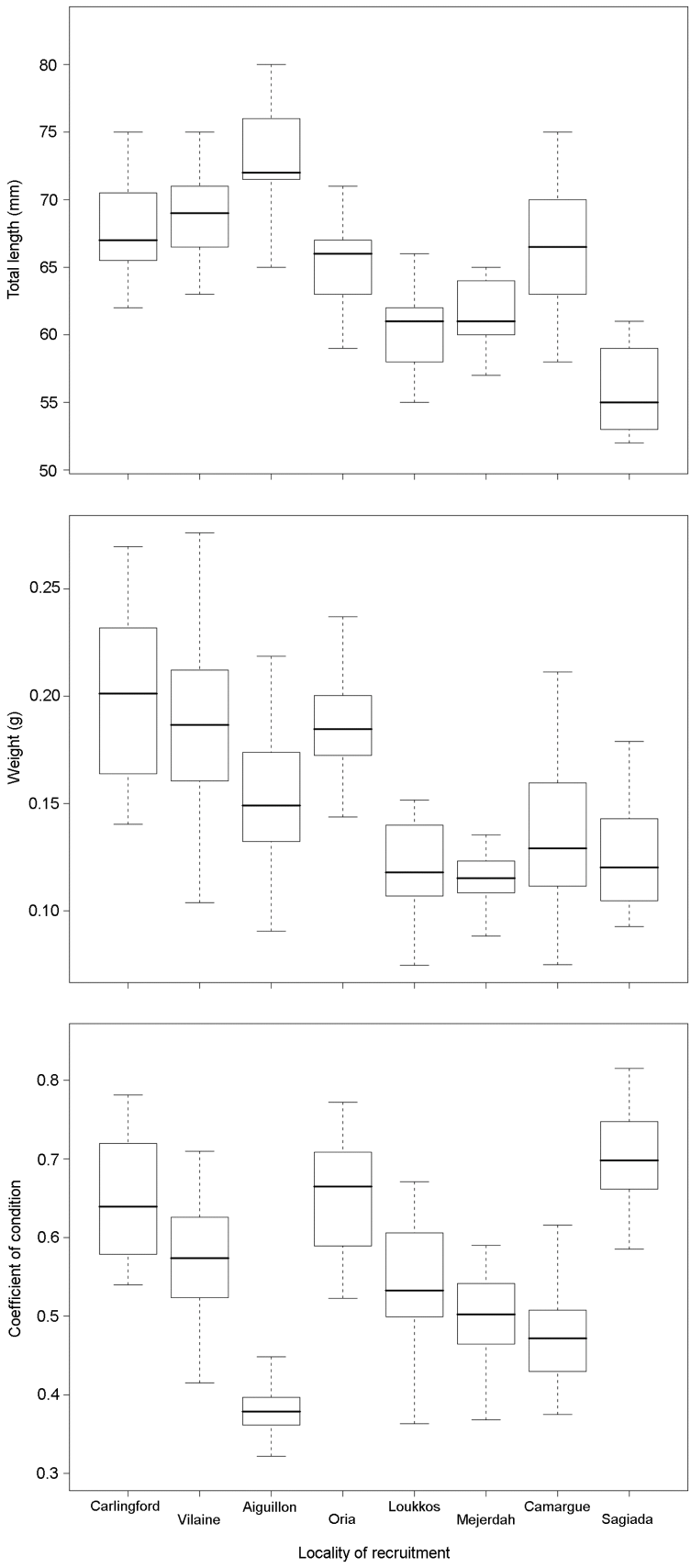

Figure 4. Spatial variations of biometric characteristics (body length, weight and Fulton coefficient of condition) of *Anguilla anguilla* glass eels recruited in February 2006.

2. Early-life traits

A. anguilla displayed negative relationships between leptocephalus duration (LD) and leptocephalus otolith growth rate (LOGR) (Pearson, $r^2 = 0.530$, $p < 0.0001$) and between MD and metamorphosis otolith growth rate (MOGR) ($r^2 = 0.339$, $p < 0.001$) (Fig. 5 and 6).

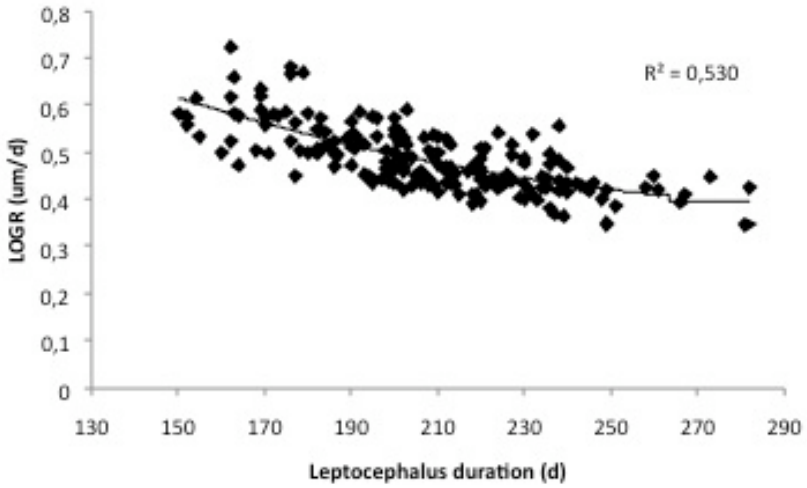

Figure 5. Relationship between leptocephalus duration (LD) and otolith growth rate during the leptocephalus phase (LOGR) in *Anguilla anguilla.*

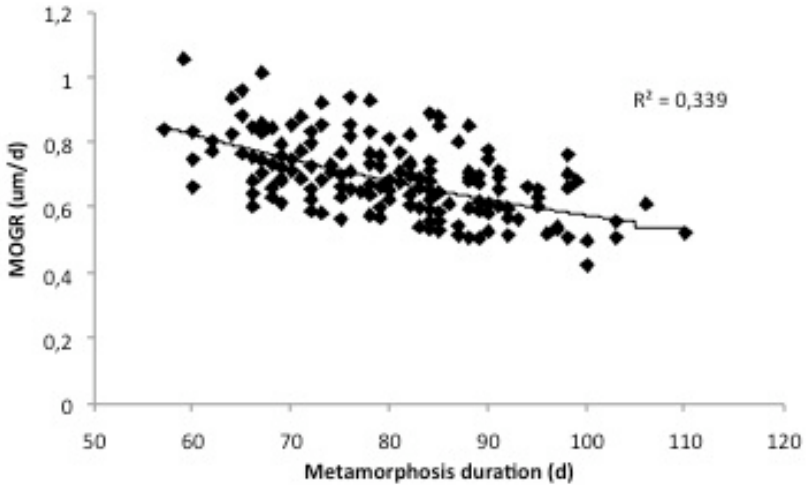

Figure 6. Relationship between leptocephalus duration (LD) and otolith growth rate during the leptocephalus phase (LOGR) in *Anguilla anguilla.*

Temporal variations. 90 and 95 early-life histories of glass eels recruited respectively to the Vilaine estuary in France and to the Oria and Butron estuaries in northern Spain in 2007, have been studied by otolith analysis. Individuals sampled each month in the Vilaine hatched at significantly different periods from the 5th February

2006 for eels sampled in January 2007, to the 9th June 2006 for eels sampled in April 2007. The LD shortened significantly throughout the 4 months from 241.7 ± 37.7 d to 211.7 ± 21.4 d (ANOVA $p < 0.02$, Fig. 7a), independently from the MD that did not vary during this period with a mean of 102.21 ± 9.73 d (ANOVA $p > 0.05$). As a sum of these durations, the age at recruitment (AR) shortened slightly but without significance from 342.1 ± 47.1 d to 311.2 ± 27.8 d (ANOVA $p > 0.05$). In Spain, a 4 months sampling led to sample 3 hatching periods as individuals collected in February 2007 in the Oria estuary hatched at the same period as those collected 60 km away in March 2007 in the Butron estuary (*t*-test, $p > 0.05$). Simultaneously hatched eels arrived later in the westernmost estuary with an age of 318.3 ± 28.4 days at recruitment instead of 286.3 ± 26.7 d in the Oria. Both LD and MD were longer in Butron (*t*-test, $p < 0.005$, Fig. 7b). In both estuaries, a decrease trend of all phases' durations through time has been observed.

Spatial variations. 200 early-life histories of glass eels have been studied over 9 localities on the distribution area of *A. anguilla* (Fig. 8). All localities were sampled in February 2006, except Den Oever and Oued Mejerdah where sampling occurred in April 2006 and in February 2007 respectively. On the Atlantic coast, the 3 northernmost localities (Carlingford Lough, Den Oever and the Vilaine) showed similar LD that were significantly shorter than those recorded in the 2 localities enclosed in the Bay of Biscay, Aiguillon Bay and Oria estuary (Tukey HSD, $p < 0.05$). The southernmost Atlantic locality, Oued Loukkos, showed the shortest LD of the Atlantic coast (Tukey HSD, $p < 0.005$). From this locality, LD increased inside the Mediterranean Sea toward Greece (Tukey HSD, $p < 0.05$). The longest MD was recorded in the Netherlands. The shortest was observed in Morocco. Between those two Atlantic localities, MD increased progressively from in Ireland to northern Spain (Tukey HSD, $p < 0.05$). In the Mediterranean Sea, Oued Mejerdah showed similar MD as Oued Loukkos (*t*-test, $p > 0.05$), while Camargue and Sagiada Marsh exhibited longer MD (*t*-test, $p < 0.05$).

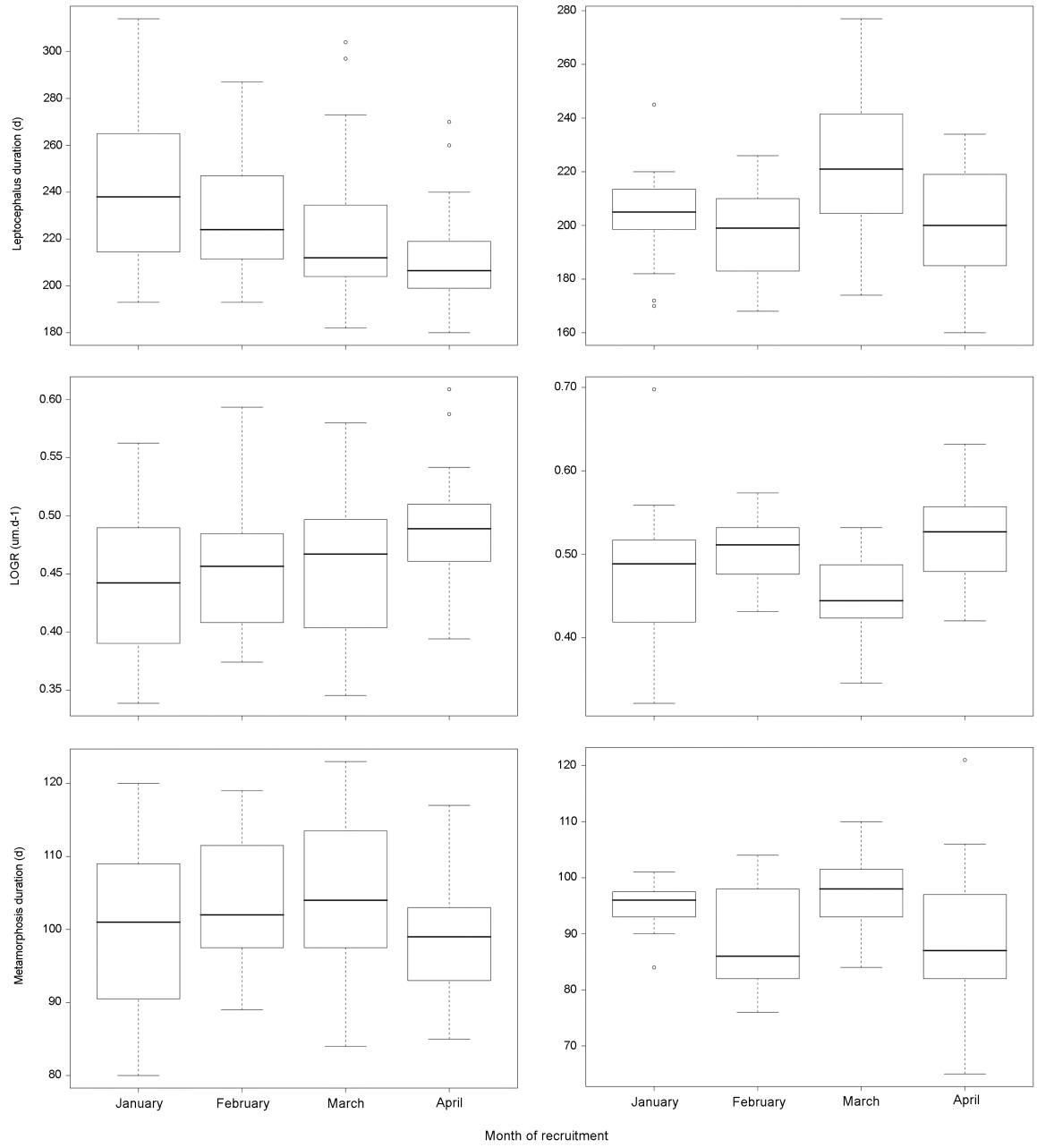

Figure 7. Temporal variations of early-life traits of *Anguilla anguilla* (leptocephalus duration; LOGR, otolith growth rate during the leptocephalus phase; metamorphosis duration) in the Vilaine estuary (left) and in northern Spain (right) in 2007.

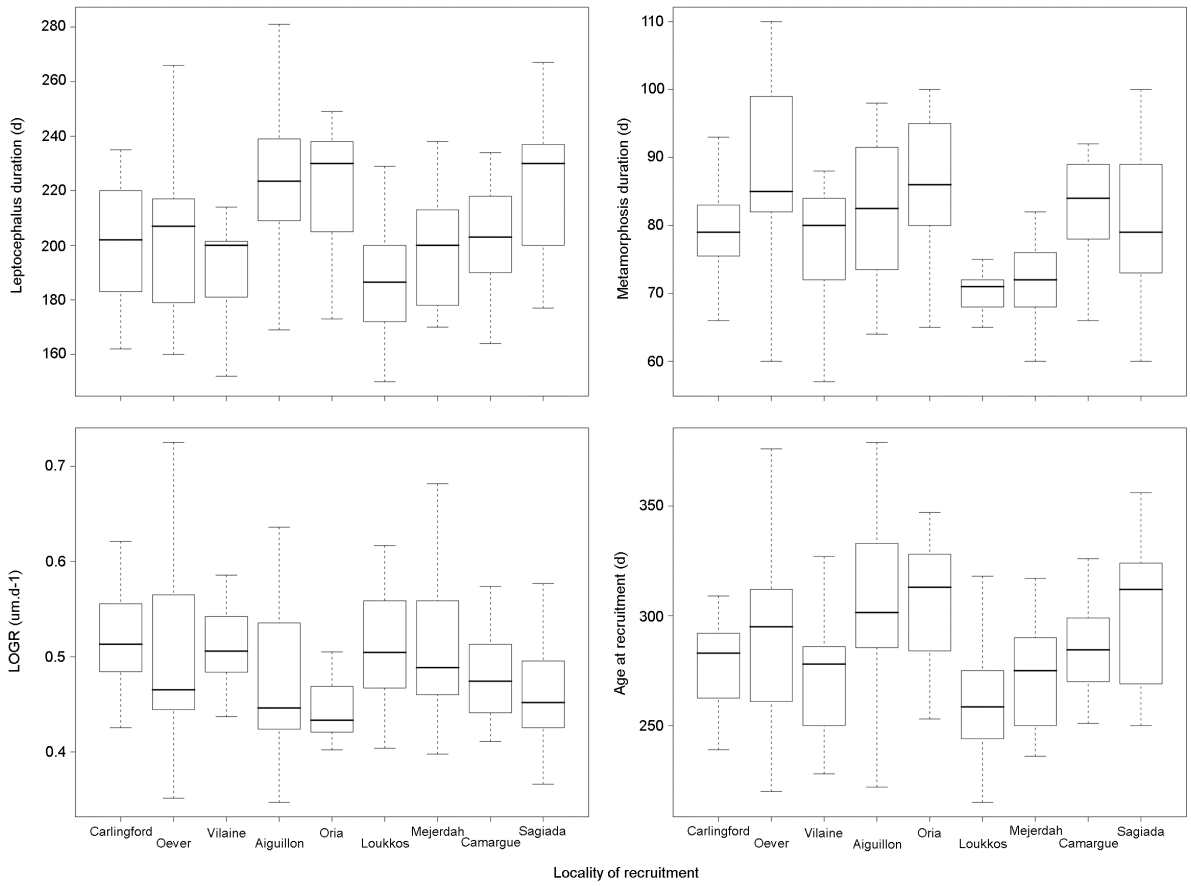

Figure 8. Spatial variations of early-life traits of *Anguilla anguilla* (leptocephalus duration; LOGR, otolith growth rate during the leptocephalus phase; metamorphosis duration, age at recruitment) in February for all localities except Den Oever estuary sampled in April 2006 and Oued Mejerdah sampled in February 2007.

3. Early-life history vs biometric characteristics at recruitment

In the Vilaine estuary, the temporal decrease of LD went along with those of biometric characteristics. Individuals recruited earlier showed longer leptocephalus durations and were longer heavier and in better condition than those recruited at the end of the season. Conversely, no clear correspondence has been observed at the spatial scale between early-life histories and biometric characteristics at recruitment.

DISCUSSION

1. Spatio-temporal variations of early-life histories

Different early-life histories were recorded according to the locality of recruitment. Two main groups were distinguished. On the one hand, on the European Atlantic coast from Ireland to northern Spain, spatial LD variations were poorly gradual and seemed rather to depend on the geographical configuration. Indeed Aiguillon Bay and localities in northern Spain wedged in the Bay of Biscay showed longer LD than others localities more directly exposed to oceanic currents. Thus arrivals seemed to have occurred frontally rather than along a longitudinal flow. On the other hand, in the Mediterranean Sea, an eastward flow of larvae seemed to have occurred as LD increased from Oued Loukkos in Morocco towards Sagiada Marsh in Greece.

Those patterns raise questions about mechanisms that trigger the leptocephalus metamorphosis into glass eel. The hypothesis generally proposed is that metamorphosis would be triggered when larvae reach the continental shelf and encounter the bottom during their vertical (McCleave 1993, Lecomte-Finiger 1992, Désaunay et al. 1996, deCasamajor et al. 2001a). Castonguay and McCleave (1987) found, indeed, that leptocephali ≥ 20mm migrate as deep as 275m at daytime, which would enable larvae to reach the bottom of the continental shelf laying at about 200m deep. Our results on the European Atlantic coast seem congruent with this hypothesis. Indeed, LD were significantly longer in the two localities wedged in the Bay of Biscay, where the continental edge begins more eastward than in other localities. Recorded MD also support this hypothesis. The Netherlands, located the farthest from the shelf edge, exhibited the longest MD. In contrast, Morocco, located very close to the shelf edge, showed the shortest MD.

To enter the Mediterranean Sea, larvae must cross the Strait of Gibraltar (300m deep at the Camarinal Sill, Vargas et al. 2006). However, the crossing of this strait does not trigger metamorphosis. Proof is the work of Grassi (1896) who described the larval metamorphosis of *A. anguilla* on leptocephali collected in the Mediterranean Sea. This explains that the present study recorded different LD and MD in the different Mediterranean localities. According to the "Shelf Hypothesis", these observations would mean that larvae do not encounter the bottom of the Strait. This is supported by the fact that the entering current carrying larvae from the Atlantic

Ocean flows from surface to about 150 m deep while the Mediterranean outflow runs deeper, 'isolating' the bottom of the Strait.

McCleave (1993) reported another important point that seems essential in some other anguillid eels' species metamorphosis process (Réveillac et al. Chapitre II, partie 1). This is about competence/capability to metamorphose, defined as the developmental capacity to undergo complete metamorphosis when triggered by internal of external factors (Hadfield et al. 2001). In tropical species recruiting in volcanic islands (without continental shelf), the metamorphic competence is thought to be governed by the "biological clock hypothesis", which supposes that intrinsically determined factors, influenced or not by environmental parameters, may lead individuals to become competent to metamorphose at different timings (Victor 1986, Hickford and Schiel 2003, Otake 2003). In the European eel, this parameter could combine to the "shelf hypothesis" that could act as an environmental cue triggering metamorphosis in competent larvae. The oldest recruits (longer LD) were recorded in Greece, the farthest locality from the spawning area and from the Strait of Gibraltar. They displayed, among other Mediterranean recruits, the lowest LOGR. It thus seemed that to migrate a long time, individuals must have had a lower metabolic rate than those recruiting more rapidly. Larvae recruited in Greece could have, due to their low metabolic and developmental rates, attained later the metamorphic competence, prolonging their migration eastward. Thus, the appearing variability in early-life histories and trade-offs between traits seem to ensure the species recruitment in the closest localities to the spawning area and also seem to favour dispersal and range extension.

The temporal decrease trend of LD, independently from other traits observed in the Vilaine and in two localities of northern Spain over a two months period could be explained by the arrival of successive cohorts of larvae that could have experienced different environmental conditions during their journey (faster transport, faster swimming). Alternatively, spawning areas could shift eastward or northward according to seasonal variations of oceanographic conditions, thus shortening the distance to cover.

2. Biometry at recruitment

When metamorphosis occurs, eels stop feeding. The end of their oceanic journey is thus a starvation period during which glass eels must survive on their energetic reserves (Boëtius and Boëtius 1989 in Désaunay and Guérault 1997). Biometric characteristics of glass eels at recruitment are thus supposed to reflect the conditions they experienced during their larval life. But interpretation of these characteristics is delicate as biometry reflects both growth performances and energy stored during the leptocephalus life, and energy spent during metamorphosis. The spatial variations were fairly gradual along the Atlantic coast. Glass eels collected in northern localities were heavier and longer than those sampled in Morocco. Mediterranean recruits displayed different characteristics than Atlantic ones. These observations seem to support the aforementioned hypothesis on various latitudinal routes of dispersal, which would transport larvae in environmental conditions varying along a latitudinal gradient. Temporal variations observed in this study agreed with those reported in other works, which described a global decrease of body total length and weight during the recruitment season (Désaunay et al. 1996, Désaunay and Guérault 1997, deCasamajor 2001a, 2001b, 2006). To explain this recurring trend over different estuaries and years, two main hypotheses have been raised. On the one hand, Désaunay et al. (1996) proposed that the average quality of recruits could depend on the trophic capacity of the ocean, which is translated into mean length and weight of the larval cohort. Thus, according to their hypothesis, the observed decrease of biometric characteristics could be imputed to more favourable conditions of migration at the beginning of the season than at the end. On the other hand, deCasamajor et al. (2001b) proposed another hypothesis based on the examination of variations of both biometric characteristics and physiological state of glass eels studied through DNA/dry weight ratio and %H2O. They suggested that, according to the temporal stability of the physiological condition of recruits, geographic origin/date of hatching could have produced eels with different biometric characteristics that arrived on the European coast, spread out in time, but with the same physiological state. In the light of our results, showing a slight decrease of LD along with those of biometric characteristics, we propose that a particular physiological state could be required to cross a particular distance and thus to reach a particular recruitment locality. There could be a trade-off between other larval

traits than physiological condition, which would be influenced by changing environmental conditions through the season. In the most favourable conditions described by Désaunay and Guérault (1997) at the beginning of the season, larvae could have had a better growth, stored more energy and thus stayed longer at the leptocephalus stage before metamorphosis. Conversely, at the end of the season, in less favourable conditions, only larvae that rapidly attained the good physiological state (metamorphic competence) could have recruited. This would support the hypothesis of the benefit for the species of having a great diversity of life histories.

3. Estimate of the duration of the larval transatlantic journey

Since Pannella (1971) demonstrated the presence of daily growth increments in otoliths of marine fish, a huge number of studies using ear-stones have been carried out (Campana and Thorrold 2001). Since that time too, several studies focused on validating otolith use for ageing and life history reconstruction (Campana 2001). Work on otoliths of eels leptocephali and glass eels concluded that growth increment deposition occurs daily with a low error margin, both during the leptocephalus and the metamorphosis phases (Martin 1995, Cieri and McCleave 2001, Sugeha et al. 2001, Shinoda et al. 2004, Powles et al. 2006). Remarkable microstructural checks have been observed to be deposited between different ontogenetic stages from the centre to the edge of sectioned otoliths (Umezawa et al. 1989, Kuroki et al. 2005). When clear increment deposition between those checks occurs, it is possible to determine the age of the individual at different ontogenetic shifts (Wang and Tzeng 2000, Campana and Thorrold 2001, Jessop et al. 2006). For these reasons, otolith is assumed to be a reliable record of eel's early-life history as well as other fish species (Lecomte-Finiger 1992, Campana 2001).

However, controversy exists. Different estimates of the European eel larval migration duration have been obtained using different techniques. Cohort and body growth curve analysis (Schmidt, 1923), numerical models (Power and McCleave 1983, Kettle and Haines 2006, Bonhommeau et al. in prep) and otolith microstructural analysis (Van Utrecht and Holleboom 1985, Boëtius and Boëtius 1985, Lecomte-Finiger and Yahyaoui 1989, Arai et al. 2000b, Wang and Tzeng 2000, this study) gave estimates of respectively 2-3 years, 10 months to 2 years and 6 to 16 months. As a result, otolith microstructural analysis has been finger-pointed as to

underestimate larval durations. Otolith resorption has never been demonstrated in fish otoliths (Campana and Thorrold 2001); neither has been the growth stop in eels' leptocephali. Thus, the main hypothesis raised to propose that otolith could underestimate larval duration is that daily increment could be forming below the resolution limit of either light or scanning electron microscopy (Campana et al. 1987). This assumption is consecutive to Geffen's (1982) hypothesis on growth rate limitation according to which slow-growing larvae evolving in temperate waters may deposit such thin increments that they would be undetectable (Campana et al. 1987, Geffen 1992). As *Anguilla anguilla* larvae evolve in temperate waters, this hypothesis has been proposed to explain the discrepancies between techniques used to evaluate the time needed for larvae to cross the Atlantic Ocean. However, such hypothesis has never been proposed for other temperate eels such as the Japanese eel *A. japonica*, because no discrepancies have been observed between larval durations estimated by otolith microstructural analysis and by numerical models (Kimura et al. 1994, Kimura 2003). The present study estimated the transatlantic journey of *A. anguilla* larvae to last between 7 to 14 months. This comforts estimations made by other authors using otolith microstructural analysis (Lecomte-Finiger and Yahyaoui 1989, Lecomte-Finiger 1992, Désaunay et al. 1996, Arai et al. 2000b). These durations seem coherent with distances crossed (about 6000 km) compared to *A. japonica* (2600 km in 5 months to Taiwan, 3800 km in 7 months to Japan). Furthermore, the hatching period and the glass eels detrainment period along shelves corresponding to these durations extended from December to July and from October to January respectively, which is coherent with periods reported in the literature (Désaunay et al. 1996, Bonhommeau et al. in prep, McCleave 2008). Thus, as well as there are many arguments to question otolith use accuracy, arguments do not miss to say that estimations made by otolithometry could describe reality.

To explain that larvae can separate from the hydrological reality, which would transport them over a 2 to 3-year period (Kettle and Haines 2006, Bonhommeau 2008), the swimming behaviour must be taken into account. At a first sight, one can be sceptical about the swimming capability of a leaf-like larvae composed mainly of water and glycosaminoglycans (GAGs), without a functional bony-skeleton. However, Bishop and Torres (1999) reported their GAGs act as a firm gelatinous skeleton, conferring an exceptional swimming ability, without appreciable metabolic costs other than that needed for acquiring and depositing GAGs. Furthermore, Wegner

(1982 in Lecomte-Finiger 1992) reported leptocephali could cross 300 km in 7 days and Williamson (1987) described them as vigorous swimmers. Bishop and Torres (1999) also reported that leptocephali exhibit well-developed backward and forward anguilliform locomotion. They concluded that leptocephali are highly competent swimmers for a larval form, for which category Leis and Carson-Ewart (1997) reported that coral reef fish larvae can swim faster than 13.7 times their body length per second, and Miller et al. (1988) and Meng (1993) reported that temperate larvae can swim at a mean speed of 1 to 3 times their body length per second. As *A. anguilla* leptocephali first experience tropical waters before entering temperate waters, their swimming behaviour could shift from those of reef fish larvae to those of temperate fish larvae. According to all these elements, we could assume that *A. anguilla* leptocephali are not just driven passively by oceanic currents. This hypothesis, proposed by other authors (Lecomte-Finiger 1992, Umezawa 1991 in Arai et al. 1999b) could explain the discrepancies observed in estimating the duration of the transatlantic journey of *A. anguilla* leptocephali.

CONCLUSION

Latitudinal variations of biometric characteristics observed along the European Atlantic coast, as well as those of early-life traits seem to support the hypothesis according to which different migrations routes could feed different localities, or a least different latitudinal zones (deCasamajor et al 2001, Bonhommeau 2008). This brings new clues to explain the temporal and geographic genetic structures observed by different scientists (Wirth and Bernatchez 2001, Dannewitz et al. 2005, Maes et al. 2006).

In parallel, the great diversity of early-life histories recorded along with the relationships identified between early-life traits seemed to confer to *A. anguilla* its great ability to disperse over 6000 km and colonize a large distribution area. Whether limits of this variability are or could be reached is an important factor that has to be examined in the context of the climate change and eel stock decline.

Furthermore, such diversity and relationship patterns have already been described in other anguillid species (Réveillac et al. 2008, Chapitre II, partie 1). They were supposed to reflect selection of environmental conditions on traits trade-offs, by

acting on individual plasticity or by selecting pre-determined (innate) early-life histories in a specific diversity. Compared to tropical species (*A. marmorata* and *A. mossambica*, Réveillac et al. 2008, in prep), *A. anguilla* displayed relatively low OGR variations in regard to those of stages durations. It thus seems that the amplitude of the metabolic rate variation in the temperate European eel is more constrained than that of the cited tropical species. This could reveal that *A. anguilla* is submitted to smaller variations of environmental conditions or that its range of response to environmental conditions is more restricted than for tropical species. These characteristics of variability and relationships between traits among and between species have to be further examined within the hypothesis of phylogenetic and phylogeographic evolution of the genus *Anguilla* (Aoyama et al 2003, Kuroki et al 2006, Réveillac et al. 2008).

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Conclusions:

- La variabilité des traits et donc des histoires de vie larvaire a été, encore une fois, observée à différentes échelles spatiales. Elle l'a également été à l'échelle temporelle.

- La variabilité des traits de vie larvaire et des paramètres biométriques au recrutement a, là encore, montré un lien avec la géographie du recrutement et a donné des indications sur la géographie et les mécanismes de la dispersion.

Perspective:

- Réaliser une analyse comparative des mêmes traits de vie larvaire sur trois espèces distribuées dans la même région pour examiner la géographie de leur dispersion de façon relative.

CHAPITRE III

Biogéographie de la dispersion larvaire des anguilles du sud-ouest de l'Océan Indien reconstituée par examen des traits de vie larvaire

Résumé : Un total de 4172 anguilles ont été collectées par pêche électrique dans la partie amont des estuaires de Madagascar (côte Est), des Mascareignes (îles de la Réunion et Maurice), des Comores (île de Mayotte) et de l'archipel des Seychelles (îles de Mahé et Praslin) entre Octobre 2003 et Février 2006. La composition spécifique des anguilles dans les stations échantillonnées apparaît contrastée entre l'est de Madagascar (*Anguilla mossambica* 96.0%, *A. marmorata* 3.9% et *A. bicolor bicolor* 0.2%), les Comores (*A. marmorata* 56.1% et *A. bicolor bicolor* 43.9%), les Mascareignes (*A. marmorata* 91.4%, *A. bicolor bicolor* 5.4% et *A. mossambica* 3.2%) et l'archipel des Seychelles (*A. bicolor bicolor* 100.0%). Bien qu'ayant été observé sur une courte période d'échantillonnage, ce gradient de la composition spécifique sous-tend l'existence de routes de migration propres à chaque espèce. L'âge de 168 civelles a été déterminé par lecture de la microstructure des otolithes. De plus, la croissance des otolithes a été calculée du stade pré-leptocéphale (post-éclosion) à la métamorphose, *i.e.* jusqu'à la marque d'entrée en eau douce. Pour toutes les espèces, le taux de croissance moyen de l'otolithe (OGR) a pu être mis en relation avec les routes de migration spécifiques : *A. bicolor bicolor*, distribuée au niveau des latitudes les plus faibles montrent les plus forts OGR pendant la phase leptocéphale, alors qu'*A. marmorata*, endémique de la zone Malgache, possède l'aire de distribution la plus sud et présente les OGR les plus faibles. L'OGR durant la phase leptocéphale est négativement corrélé à la durée de cette phase, signe d'une diminution du métabolisme global en fonction du temps, typique chez les leptocéphales. Cette relation s'est montrée significative pour *A. marmorata* et *A. mossambica*, impliquant que leurs larves aient été exposées aux mêmes conditions environnementales, mais pas pour *A. bicolor bicolor*, dont les larves ont probablement traversé d'autres zones pélagiques. Ces informations alimentent donc l'hypothèse de larves provenant de différentes origines.

New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands

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Abstract: A total of 4,172 freshwater eels have been collected by electrofishing in upper estuaries from Madagascar (East coast), Mascarene (Réunion and Mauritius Is.), Comoros (Mayotte Is.) and Seychelles (Mahé and Praslin Is.) Archipelagos, between October 2003 and February 2006. Eel species composition in the sampling stations was contrasted between eastern Madagascar (*Anguilla mossambica* 96.0%, *A. marmorata* 3.9% and *A. bicolor bicolor* 0.2%), the Comoros (*A. marmorata* 56.1% and *A. bicolor bicolor* 43.9%), the Mascarene (*A. marmorata* 91.4%, *A. bicolor bicolor* 5.4% and *A. mossambica* 3.2%) and the Seychelles Archipelagos (*A. bicolor bicolor* 100.0%). This gradient in species composition, even concerning the short time-range of our sampling, argued for separate migration routes between species. A total of 168 eels were aged by reading their otolith microstructure, and otolith growth rates were calculated from pre-leptocephalus stage (post-hatching) to metamorphosis, until freshwater check. For all species, mean otolith growth rate (OGR) was related to specific migration routes: *A. bicolor bicolor* is distributed in the lowest latitudes and showed the highest OGR during leptocephalus stage, whereas *A. mossambica*, endemic of the Malagasy area, has the most southern distribution and showed lowest OGR. OGR during leptocephalus stage was negatively correlated to the leptocephalus stage duration, showing a decrease of global metabolism with time, classical in leptocephali. This relationship was found significant for *A. marmorata* and *A. mossambica*, probably because all these larvae crossed successively the same environments, but not for *A. bicolor bicolor*, probably because their larvae crossed different pelagic environments, opening the hypothesis of larvae from different origins.

INTRODUCTION

Freshwater eels are represented by a single genus, *Anguilla* Schrank 1798, and 15 species distributed in the Atlantic, Indian and Pacific oceans (Castle 1984, 1986, Watanabe 2003; Lecomte-Finiger 2003). *Anguilla* sp. spawn in the ocean and grow in coastal, estuarine or continental areas (Tsukamoto et al. 2002). To link these two zones that compose lifecycle, eels disperse first from their oceanic hatching area to coastal areas as pelagic, flattened and transparent leptocephalus larvae (Mochioka 2003). Leptocephali, when they approach the continental shelf, metamorphose into glass eels that will settle in the continental system to grow for years as yellow eels. The marine dispersal of leptocephali drives the continental distribution of freshwater eel species, but also their evolution and the phylogeography of the genus (Tsukamoto and Aoyama 1998).

In the south-western Indian Ocean (SWIO), four eel species occur: *Anguilla mossambica* and *A. nebulosa labiata* are endemic of the Madagascar area, *A. bicolor bicolor* is present along the coasts from Western to Eastern Indian Ocean, and the marbled eel *A. marmorata* spreads widely from the East African coast, through the Indo-Pacific area, far to the Mid-Pacific Islands (Ege 1939; Jubb 1961; Nishi and Imai 1969; Marquet and Lamarque 1986; Jellyman 1987; Marquet and Galzin 1991; Williamson and Boëtius 1993; Budimawan 1997; Marquet et al. 1997; Robinet et al. 2007). Eels in the SWIO are facing a growing interest from the fisheries international markets in Madagascar and South Africa. Knowing their patterns of larval dispersal would be of prime importance for managing this resource. However, freshwater eels spawning location and migration routes in the Indian Ocean are still unknown, as whether there is a single or several spawning places per species. In parallel with population genetic studies, description of species local assemblages and analysis of larval life-histories would provide useful information on species dispersal patterns on one hand, and on the ontogenic metabolism of these tropical species on the other.

Among the few studies available on larval life history of tropical eels, most of them concern the Indo-Pacific (Indonesia, Philippines and Sulawesi; Arai et al. 1999b, 2001a) and western Pacific regions (Taiwan and Japan; Arai et al. 2001b, 2002a, 2002b; Miller et al. 2002). In the Indian Ocean, early life-histories of freshwater eels were studied on the eastern part (Java Is., Arai et al. 1999a; Aoyama et al. 2007;

Budimawan and Lecomte-Finiger 2008) and on the western part (Réunion Is., Robinet et al. 2003a), but both were limited in time and space. Since Jespersen (1942) and Jubb (1961) suggested a single large spawning area in SWIO, common to all the freshwater eel species somewhere in the NE waters of Madagascar, there has been no real progress concerning the western spawning area(s) location. Based on local species composition and larval life-histories, the present study proposes new information for migration routes of freshwater eels that recruit in estuaries of eastern Madagascar and surrounding islands.

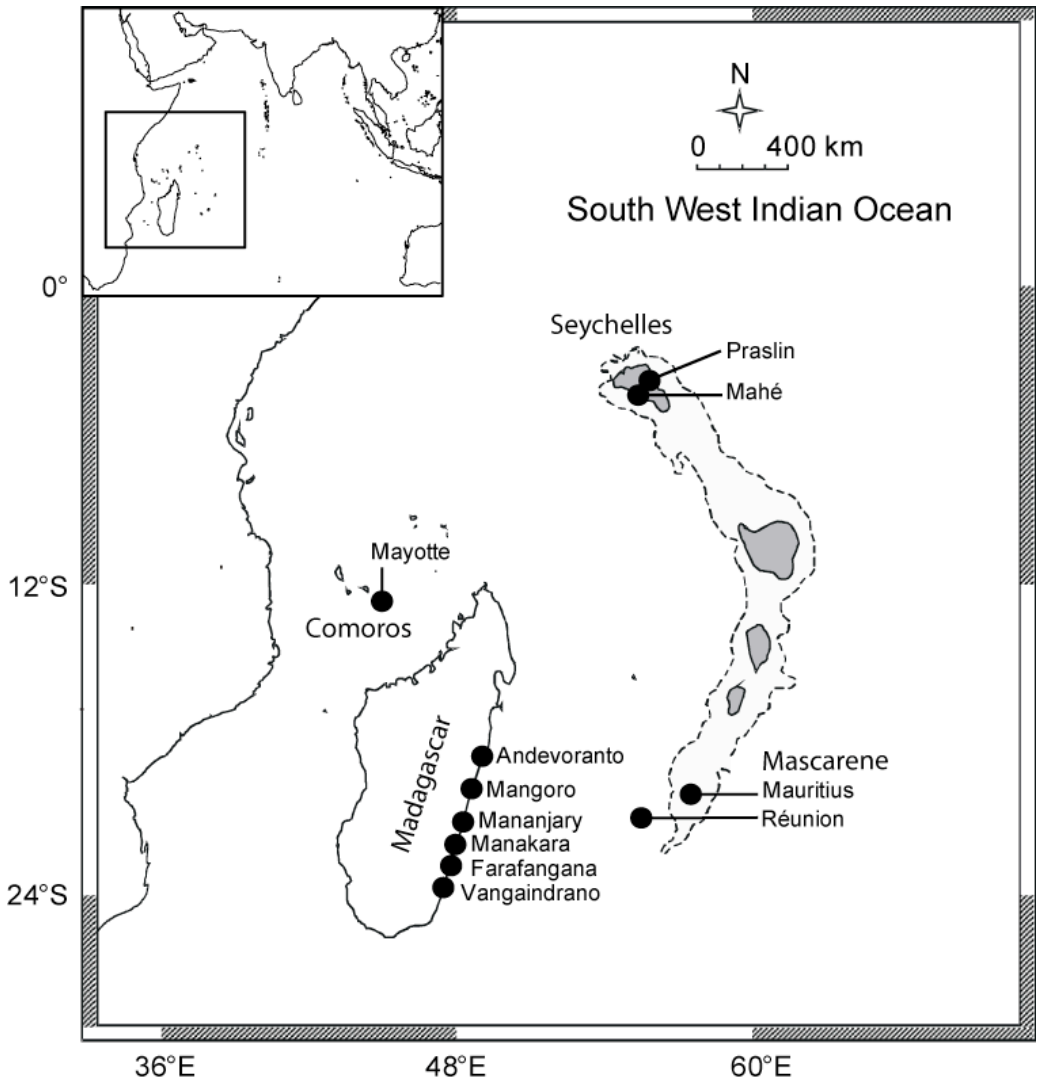

Figure 1. Location of sampling sites (black circles) in SWIO. Hashed line represents the 1200m depth isobaths, sand beds of the Mascarene ridge are in plain grey (isobaths 200m, after Padfield and Coward 1998).

MATERIALS AND METHODS

1. Sites and sampling protocol

Eels were sampled in estuaries of Réunion Is. (21°S 56°E), Mauritius Is. (20°S 57°E), Mayotte Is. (Comoros, 12°S 45°E), Mahé and Praslin Is. (Seychelles, 4°S 55°E), Mananjary and Vangaindrano (Madagascar, 22°S 48°E and 24°S 48°E, respectively, Fig. 1). For all the sites except those of Madagascar, sampling was conducted with a portable electroshocker delivering electric impulses (DEKA 3000, EFKO manufacturer, DC 30 i.s-1, 350 V, 4 A). Glass eels were sampled at the tidal limit of the permanent rivers in Mauritius (5–7 April 2005), Réunion (11–12 April 2005), and Mayotte (15–19 April 2005). In Madagascar, glass eels were collected in traditional fyke-nets with the collaboration of local fishermen, from September 2005 to February 2006. Because no glass eels were present during the sampling campaign in Mahé and Praslin Is. (Seychelles, October 2003), only riverine yellow eels were sampled.

2. Species determination

After fixation in 90% ethanol, eels were measured and identified using Ege's determination key (Ege 1939), based on the caudal pigmentation (for glass eels), the skin colour (for yellow eels), and the distance between the origins of the dorsal and anal fins as percent of the fish total length (Robinet et al. 2003a). Undetermined specimens were identified using semi-multiplex PCR (Gagnaire et al. 2007).

3. Otoliths preparation and reading

To sub-sample according to species and sites, in a maximum of 15–30 specimens by species and by site, 168 eels were selected for aging, regarding to their otolith microstructure (160 glass eels or elvers of less than 120 mm total length (TL): Réunion, Mauritius, Mayotte and Madagascar; and 8 yellow eels: Seychelles). In Réunion Is., elvers reach a TL = 120 mm 2–4 months after their freshwater entrance (Robinet et al. 2003b), so eels of TL < 120 mm entered estuaries at the same season than sampling. For microstructure analysis, otoliths were extracted and embedded in epoxy resin (Epofix Struers), ground with 1,000 and 5 _m grit paper, or using a Struers Discoplan with a grit stone, until the nucleus was visible, and polished with 1 _m grit paper (Rotopol 35, Struers) and colloidal silica suspension (OP-S, Struers).

Then the otoliths were etched with 5% EDTA solution, and coated with gold (10 nm) before examination with a scanning electron microscope (SEM, Hitachi S-520) at various magnifications.

Using SEM microphotographs of otolith sections, different patterns were identified in accordance with conventional characteristics established for other eel species (primordium and core, first feeding-check, leptocephalus zone, metamorphosis zone, and transition mark to freshwater: Castonguay 1987; Tabeta et al. 1987; Tsukamoto 1989; Umezawa et al. 1989; Tsukamoto and Umezawa 1990; Lecomte-Finiger 1992; Tzeng and Tsai 1992). Wider growth increments that have been interpreted by previous authors to occur in association with metamorphosis were used to separate the leptocephalus zone from the metamorphosis zone. Since Umezawa et al. (1989), Arai et al. (2000b) and Sugeha et al. (2001) established that otolith increment-deposition occurs daily in *Anguilla japonica*, *A. celebesensis* and *A. marmorata*. the number of these increments for the oceanic larval stages were counted from the hatching check (HC) to the freshwater recruitment-check (FWC). The beginning of metamorphosis was identified by the sudden increase of the increments width (Arai et al. 2001a). The number of increments from the HC to the beginning of metamorphosis represented the leptocephalus stage duration (LD), and those from the beginning of metamorphosis to the FWC represented the marine life duration after metamorphosis (MD). The number of increments counted between HC and FWC was interpreted as the age at recruitment (AR, Lecomte-Finiger 1992). General patterns of otolith microstructure are presented in Fig. 2. Hatching dates were back-calculated based on AR and sampling dates. LD and MD were counted for each otolith, AR and hatching date calculated, and means (±SD) were calculated for each species. After testing that the basic assumptions of normality of each sample were verified (Kolmogorov-Smirnov and Liliefors tests), a pairwise comparison (Student's *t* test) was used to compare LD of each species and each site.

4. Otolith growth

The mean increment width was calculated by measuring the width of every 10 increments, from HC to FWC. This measure was considered as the instantaneous growth rate of the otolith (OGR), pooled by groups of 10 days. A linear regression was used to test the correlation between LD (days) and the mean OGR (μm days-1)

during the leptocephalus stage of each species.

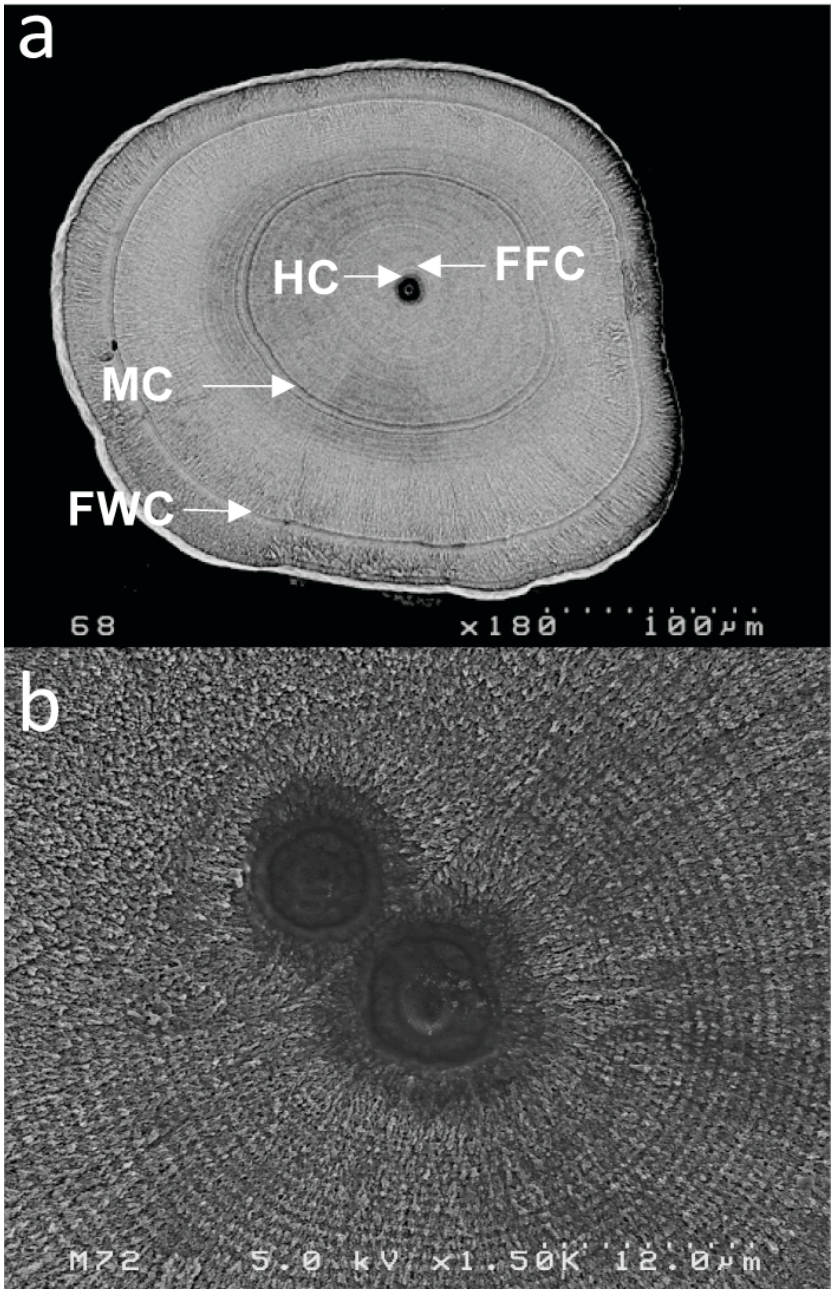

Figure 2. (a) Otolith section from a glass-eel of *A. bicolor bicolor* (Mayotte), viewed with Scanning Electron Microscope. *FFC* First feed check; *FWC* freshwater check; *HC* hatching check; *MC* metamorphosis check. **(b)** Detail of an otolith section from a glass-eel of *A. bicolor bicolor* (Mayotte), showing an atypical double-core.

RESULTS

1. Specimens collected

A total of 4,172 eels were collected in the sites sampled. The species composition was very heterogeneous between sites (Table 1). *A. bicolor bicolor* was the only species in the Seychelles, and was fairly present in Mayotte (43.9% of the eels sampled). Elsewhere, 1–3 species occurred, with *A. marmorata* as dominant species in Mauritius (93.3%), Réunion (89.5%) and Mayotte (56.1%), and *A. mossambica* in Madagascar (96.0 %). The eels collected sized from 43 up to 1140 mm, but 60% were glass eels (total length < 60 mm, newly recruited), and 10% elvers (total length up to 150 mm, recruited at the same season than sampling).

Table 1. Species composition of eel [post-larvae (glass-eels) and juveniles eels (yellow eels) samples collected in prospected estuaries. N. Number of eels collected.

Site	River	Date	N	*A. mossambica* %	*A. marmorata* %	*A. bicolor bicolor* %
Seychelles	All rivers	Oct. 2003	8	-	-	100.0
Mauritius	All rivers	Apr. 2005	80	1.1	93.3	5.6
Réunion	All rivers	Apr. 2005	19	5.3	89.5	5.3
Mayotte	All rivers	Apr. 2005	98	-	56.1	43.9
Madagascar	Andevoranto	Sept. 2005	72	98.6	-	1.4
		Nov. 2005	27	100.0	-	-
	Mananjary	Nov. 2005	693	99.4	0.3	0.3
		Nov. 2005	621	99.5	-	0.5
	Manakara	Dec. 2005	50	100.0	-	-
	Mangoro	Dec. 2005	50	100.0	-	-
	Andevoranto	Dec. 2005	50	100.0	-	-
	Vangaindrano	Dec. 2005	56	100.0	-	-
	Mananjary	Dec. 2005	989	99.2	0.7	0.1
	Farafangana	Jan. 2006	211	77.3	22.7	-
	Manakara	Jan. 2006	175	99.4	0.6	-
	Mananjary	Jan. 2006	227	98.7	1.3	-
		Feb. 2006	337	98.8	0.9	0.3
		Feb. 2006	409	72.4	27.6	-

2. Early-life histories

The duration of larval stages, otolith growth rates, ages at recruitment and hatching dates are listed in Table 2 and compared in Table 3. For each species and locality, LD was normally distributed (Kolmogorov-Smirnov and Liliefors tests, $p > 0.05$ for both). Among the three species, *A. mossambica* had the shortest LD (all sites 95.1 ± 16.7 days), especially those recruited in Madagascar (94.5 ± 16.6 days), which were significantly shorter than those of *A. marmorata* in the same island (115.6 ± 13.9 days). *A. marmorata* was the species with the longest leptocephalus mean duration (all sites 123.0 ± 20.3 days), and showed significant differences with *A. bicolor bicolor* in sites where both species coexisted (Mauritius and Mayotte). Between site comparisons showed different patterns according to the species. In *A. bicolor bicolor*, mean leptocephalus stage was shorter in Mayotte (100.9 ± 8.5 days, 87–117 for all specimens) than any sampling sites, but not significantly (paired *t* test $p > 0.05$, excluding Réunion—151 days, the single LD could not be tested). In *A. marmorata*, leptocephalus stage was shorter in Réunion (111.1 ± 15.9 days and Farafangana (108.8 ± 8.4 days) than in Mayotte (119.9 ± 13.2 days), Mananjary (122.5 ± 15.2 days) and Mauritius (139.2 ± 24.0 days). *A. marmorata* from Mauritius showed the highest mean LD with a twice higher standard deviation than the other localities. *A. mossambica* had a similar duration of leptocephalus stage whether they recruited in the Malagasy sites (Mananjary and Vangaindrano, 92.5 ± 18.8 and 96.6 ± 14.5 days, respectively, paired *t* test $p = 0.506$), or in Réunion (75 days, the single LD could not be tested).

3. Otolith growth

Otolith growth patterns are represented for all the specimens analysed in Fig. 3. All showed general patterns described in Arai et al. (2001a) and Kuroki et al. (2007): a slight increase during the first 15 days, then a continuous decrease until the end of the leptocephalus stage, followed by a drastic increase corresponding to the metamorphosis of the leptocephalus into glass eel. Glass eels of *A. mossambica* seemed to enter in estuaries less than 10 days after metamorphosis, whereas *A. bicolor bicolor* and A. *marmorata* glass eels recruited in estuaries 10–30 days after metamorphosis was completed. LD was negatively correlated to OGR in *A. marmorata* ($r2 = 0.113$, $p = 0.003$) and *A. mossambica* ($r2 = 0.208$, $p = 0.014$), but not

in *A. bicolor bicolor* ($r2 = 0.025$, $p = 0.376$, Fig. 4).

Table 2. Early-life history of *A. bicolor bicolor*, *A. marmorata* and *A. mossambica* based on the otolith microstructure of eels collected in estuaries of different locations of the SWIO. N. Number of eels analysed; TL. Total length; LD. Leptocephalus duration; OGR. Otolith growth rate during the leptocephalus stage; MD. Marine life duration after metamorphosis. AR. Age at recruitment in estuary; HP. Hatching period. * without specimens from Seychelles. ** Nc. Not calculated (hatching dates were not calculated for eels from the Seychelles because they were 4-8 years old at sampling).

	N	TL (mm)	LD (d)	OGR ($\mu m.d^{-1}$)	MD (d)	AR (d)	HP
A. bicolor bicolor							
All sites	33	158.4 ± 174.7 50 to 644	106.1 ± 13.1 87 to 139	0.67 ± 0.08 0.50 to 0.83	32.8 ± 8.1 15 to 49	138.9 ± 14.1 108 to 179	Mar 1 to Dec 12 2004*
Mauritius	9	52.6 ± 2.0 50 to 56	110.6 ± 16.7 87 to 139	0.59 ± 0.06 0.50 to 0.66	32.0 ± 9.9 15 to 44	142.6 ± 19.2 108 to 179	Oct 7 to Dec 12 2004
Mayotte (1)	12	54.8 ± 3.0 51 to 62	101.8 ± 9.2 87 to 117	0.69 ± 0.07 0.59 to 0.81	36.3 ± 6.8 24 to 49	138.3 ± 11.3 120 to 157	Oct 8 to Dec 12 2004
Mayotte (2)	3	169.7 ± 32.5 163 to 205	97.0 ± 4.4 92 to 100	0.76 ± 0.07 0.71 to 0.83	33.3 ± 5.0 28 to 38	130.3 ± 3.5 127 to 134	Mar 1 to Aug 14 2004
Réunion	1	53	151	0.60	32	183	Sep 10 2004
Seychelles	8	452.4 ± 98.9 364 to 644	110.9 ± 13.8 87 to 128	0.68 ± 0.06 0.61 to 0.79	28.0 ± 7.3 20 to 38	138.9 ± 14.4 117 to 158	Nc**
A. marmorata							
All sites	104	55.6 ± 14.6 46 to 178	123.0 ± 20.3 91 to 180	0.61 ± 0.08 0.47 to 0.76	26.7 ± 4.2 18 to 39	149.6 ± 22.2 114 to 211	Aug 25 to Nov 8 2005
Mauritius	30	52.1 ± 2.6 46 to 58	139.2 ± 24.0 91 to 180	0.61 ± 0.07 0.47 to 0.76	28.1 ± 3.5 21 to 35	167.3 ± 25.6 117 to 211	Aug 28 to Dec 5 2004
Mayotte	29	59.8 ± 8.9 47 to 79	119.9 ±13.2 104 to 151	0.63 ± 0.08 0.49 to 0.82	23.7 ± 3.2 18 to 29	143.7 ± 15.0 126 to 180	Sep 21 to Dec 21 2004
Réunion	15	67.5 ± 33.0 50 to 178	111.1 ± 15.9 94 to 142	0.56 ± 0.07 0.48 to 0.71	25.5 ± 3.2 21 to 32	136.6 ± 17.7 121 to 173	Aug 25 to Dec 4 2004
Madagascar (Farafangana)	15	49.4 ± 1.3 48 to 52	108.8 ± 8.4 94 to 120	0.62 ± 0.04 0.56 to 0.59	28.5 ± 3.7 20 to 34	129.6 ± 10.8 113 to 145	Aug 15 to Sep 16 2005
Madagascar (Mananjary)	15	48.9 ± 1.0 47 to 50	122.5 ± 15.2 92 to 145	0.60 ± 0.05 0.52 to 0.69	28.8 ± 5.4 22 to 39	143.8 ± 17.1 108 to 167	Sep 14 to Nov 8 2005
A. mossambica							
All sites	31	52.5 ± 4.8 48 to 75	95.1 ± 16.7 73 to 131	0.47 ± 0.09 0.34 to 0.76	22.6 ± 3.2 18 to 29	117.7 ± 16.3 99 to 152	Jun 28 to Aug 29 2005
Madagascar (Mananjary)	15	50.0 ± 1.7 48 to 53	92.5 ± 18.8 73 to 131	0.47 ± 0.08 0.38 to 0.65	22.5 ± 3.4 18 to 29	115.0 ± 17.5 99 to 152	Jun 28 to Aug 29 2005
Madagascar (Vangaindrano)	15	53.5 ± 1.6 51 to 56	96.6 ± 14.5 78 to 127	0.48 ± 0.10 0.34 to 0.76	22.4 ± 2.9 18 to 29	119.0 ± 14.8 100 to 149	Jun 29 to Aug 20 2005
Réunion	1	75	113	0.51	27	140	Oct 2 2004

Table 3. T-test pairwise comparisons of LD (mean ± sd, in brackets) between sites. Far. Farafangana; Man. Mananjary; Mau. Mauritius; May. Mayotte; Réu. Réunion; Sey. Seychelles; Van. Vangaindrano. ns. not significant (t-test p>0.05). nt. not tested because only 1 specimen in each. Significant differences: • p<0.05, •• p<0.01, ••• p<0.001.

	A. bicolor bicolor				*A. marmorata*					*A. mossambica*		
	Mau (110.6 ± 16.7)	May (100.9 ± 8.5)	Réu (151)	Sey (110.9 ± 13.8)	Mau (139.2 ± 24.0)	May (119.9 ± 13.2)	Réu (111.1 ± 15.9)	Fara (108.8 ± 8.4)	Man (122.5 ± 15.2)	Man (92.5 ± 18.8)	Van (96.6 ± 14.5)	Réu (113)
A. bicolor bicolor												
Mau (110.6 ± 16.7)		ns	ns	ns	•••	••	ns	ns	•	ns	ns	ns
May (100.9 ± 8.5)	ns		•••	ns	•••	•••	••	••	•••	ns	ns	ns
Réu (151)	ns	•••		•	ns	ns	ns	•••	ns	•	••	nt
Sey (110.9 ± 13.8)	ns	ns	•		•••	•	ns	ns	•	ns	ns	ns
A. marmorata												
Mau (139.2 ± 24.0)	•••	•••	ns	•••		•••	•••	•••	•	•••	•••	ns
May (119.9 ± 13.2)	••	•••	ns	•	•••		ns	••	ns	•••	•••	ns
Réu (111.1 ± 15.9)	ns	••	ns	ns	•••	ns		ns	ns	••	•	ns
Fara (108.8 ± 8.4)	ns	••	•••	ns	•••	••	ns		••	••	••	ns
Man (122.5 ± 15.2)	•	•••	ns	•	•	ns	ns	••		•••	•••	ns
A. mossambica												
Man (92.5 ± 18.8)	ns	ns	•	ns	•••	•••	••	••	•••		ns	ns
Van (96.6 ± 14.5)	ns	ns	••	ns	•••	•••	•	••	•••	ns		ns
Réu (113)	ns	ns	nt	ns	ns	ns	ns	ns	ns	ns	ns	

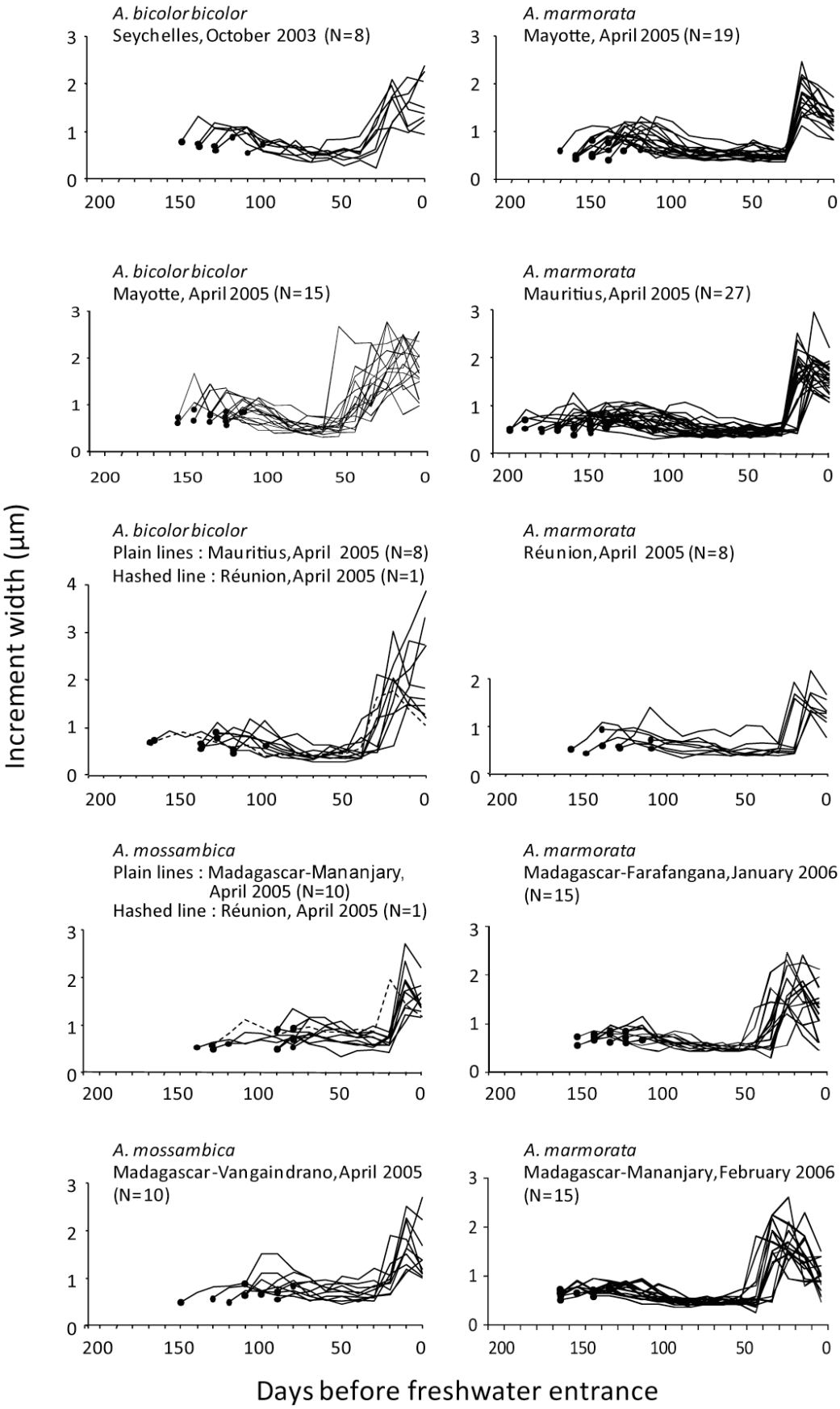

Figure 3. Otolith growth history, from HC (*black dot* on the left end of the curves) to FWC (right end of the curves), for the 168 specimens analysed.

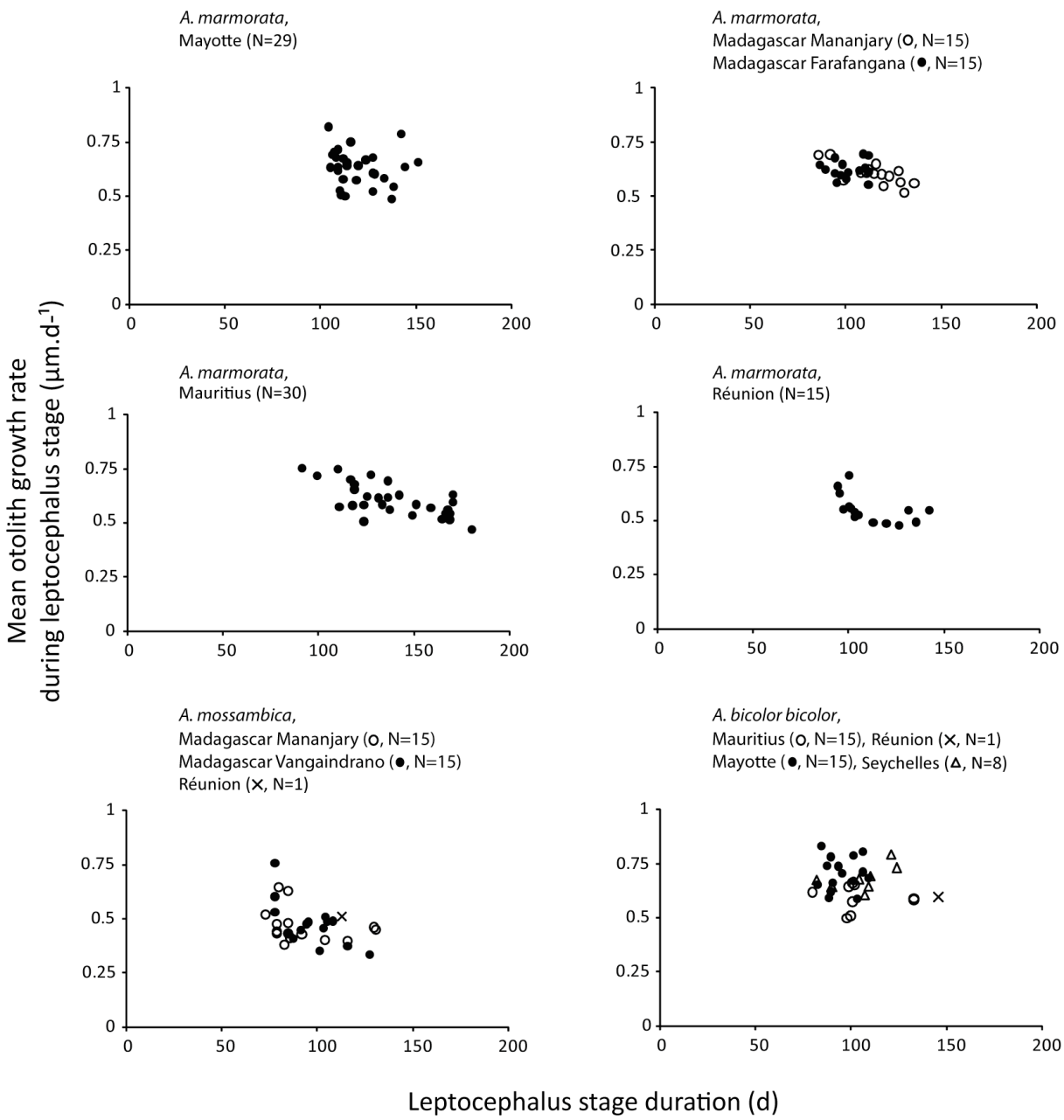

Figure 4. Representation of OGR (µm days-1, *y*-axis) in function of LD (days, *x*-axis) for the 168 eels analysed.

DISCUSSION

1. Otolith growth

Otolith microstructures showed growth patterns usually observed in anguillid eels (Arai et al. 2001b; Kuroki et al. 2007): just after FFC, the increment width increased until a first peak at *c.* 10–15 days after HC (up to *c.* 1.0– 1.5 µm days-1), after what the increment width decreased to a minimum value (*c.* 0.4–0.5 µm days-1) until

metamorphosis. The metamorphosis began with a drastic growth increase, usually up to 2 μm days-1 and with a maximum of 3.88 μm days-1 for a specimen of *A. bicolor bicolor* in Mauritius.

OGRs during leptocephalus stage of *A. bicolor bicolor* (mean 0.67 ± 0.08) were comparable to those described for the same sub-species in North eastern Indian Ocean during the year 2003 (mean 0.78 ± 0.12 from core to the first peak, 1.13 ± 0.16 at the peak, 0.52 ± 0.05 after the peak and before metamorphosis, Kuroki et al. 2007). Mean OGRs of *A. bicolor bicolor* in the present study (Seychelles 2003, other sites 2005–2006) were lower than that observed in 2001 in Réunion Is. (mean 0.90 ± 0.20 μm days-1, Robinet et al. 2003a). This could reflect changes in pelagic environments, that is known to have an influence on natural larval growth (Sponaugle and Pinkard 2004). OGR of *A. bicolor bicolor* in the present study was a bit lower than those of the other sub-species in western Pacific (*A. bicolor pacifica*, mean 0.79 ± 0.11, Arai et al. 2001b). *A. marmorata* OGRs (mean 0.61 ± 0.08) were similar to those of *A. bicolor bicolor*, but lower than those of the same species in western Pacific (mean 0.96 ± 0.07, Arai et al. 2001b). For SWIO species, it is likely that the mean OGR is related to specific migration routes: *A. bicolor bicolor* is distributed in the lowest latitudes and showed the highest OGR during leptocephalus stage, whereas *A. marmorata*, has a most southern distribution and showed lowest OGR.

2. Leptocephali metabolism as revealed by otolith growth

Through the analysis of the otolith growth patterns, the present study retraces the very singular ontogenic metabolism of eel leptocephali in the SWIO. The pre-metamorphic OGR of analysed eels decreased with age, until metamorphosis. This pattern clearly appeared for *A. marmorata* and *A. mossambica*. In the present study, the growth patterns observed are similar to those described in other families of Anguilliforms (Congridae, Muraenidae, Ophichthidae, Bishop and Torres 1999): the more the leptocephalus body weight increases, the more its metabolism per unit of wet weight slows down (O2 consumption, enzymatic activity, osmoregulation and excretion, Pfeiler and Govoni 1993; Bishop and Torres 1999; Bishop et al. 2000). This trend, that seems to be common to all elopomorph fishes, is not a true metabolic dormancy: metabolically inert glycosaminoglycans (GAGs) replace progressively the

actively metabolizing tissues in the larvae (Bishop and Torres 1999), allowing leptocephali to reach a large size with a minimal metabolic penalty. This growth strategy, singular among fishes, probably reduces the spectrum of potential predators and maximizes the lift ability (Bishop and Torres 1999; Pfeiler 1999).

A slackening growth rate of leptocephali, waiting for favourable conditions to metamorphose, allows anguillid larvae to survive to long dispersals and to reach growing areas far away from the hatching zone. Same patterns were observed in temperate species: a longer duration of the leptocephalus stage in *A. Anguilla*, compared to *A. rostrata* (European and American eel, respectively), has been attributed to a slower growth rate during the leptocephalus stage (Arai et al. 2000b; Wang and Tzeng 2000; Kuroki et al. 2007). These considerations has lead some authors to develop the hypothesis that the timing of metamorphosis, triggered by the larval growth rate, was accounting for larval segregation between two species that spawns in close areas (e.g. the Atlantic eels species). This "Timing of Metamorphosis" hypothesis, as proposed by Kuroki et al. (2008), is probably also accounting in the Indian Ocean eels that would spawn in adjoining areas, and for whose different growth rates would control different dispersal ranges.

3. Larval migration routes in the Indian Ocean

During sampling period in the prospected estuaries, eel species composition was contrasted between sites. This gradient in species composition argued for separate migration routes between species, as suggested by Jubb (1961). However, we combined data from the few historical oceanographic cruises in the Indian Ocean with the LD of the different species analysed in the present study to synthesize the present information concerning these migration routes of eels that reach the SWIO.

A. marmorata is present in the Indian Ocean, but the number and location of its spawning places in this ocean remain unclear. The Dana expedition collected 1,225 leptocephali off Sumatra (September–December 1929, Jespersen 1942), but without genetic identification, it was impossible to distinguish species for the smallest ones (<20 mm, N = 408). Among the large leptocephali collected (>20 mm), 696 were *A. bicolor bicolor* (short-finned), and the 121 others, all long-finned, could be *A. marmorata* as well as *A. nebulosa nebulosa*. Thus, even if they were mostly *A. marmorata*, these larvae were too large to come with certainty from south-western

Sumatra area, and could have come from elsewhere. Moreover, a recent oceanographic cruise off Sumatra only collected a single specimen (June 2003, Aoyama et al. 2007). In the northern waters of Madagascar, also prospected during the Dana expedition (December 1929–September 1930), only a few large *A. marmorata* leptocephali were collected (Jespersen 1942). On the other hand, *A. marmorata* glass eels collected in eastern Madagascar and surrounding islands in 2001 (Robinet et al. 2003a) and 2005–2006 (this study) showed ages at metamorphosis that make possible any hypothesis for reproduction places (60–135 days in Réunion in 2001, 94–142 days in Réunion in 2005, 104–151 days in Mayotte in 2005, 91–180 days in Mauritius in 2005, and 92–145 days in eastern Madagascar in 2005). It is worth noting that the high standard deviation in *A. marmorata* LD from Mauritius, twice higher than those from the other localities, could be a consequence of heterogeneous origins of larvae recruiting there. The probable explanation is separated spawning areas (completely distinct or slightly overlapping) for the *A. marmorata* matured eels coming from SWIO and western Indonesian areas. This has to be explored by molecular analysis.

Anguilla bicolor bicolor extends all along the Indian Ocean coasts, from South-Africa (Bruton et al. 1987), Arabian peninsula (Attaala and Rubaia 2005), Sri Lanka (Wicktröm and Enderlein 1988), to western Indonesia and north-western Australia (Ege 1939). This species probably spawns in the eastern Indian Ocean, *c.* south-western Sumatra, because small leptocephali (20–40 mm) were collected there during the Dana expedition (1929–1930, lead by Johannes Schmidt; Jespersen 1942; Miller 2003). However, recent analysis argued for a spawning area not directly located above the Mentawei trench as Jespersen (1942) proposed: leptocephali trawled in June 2003 during the Baruna Jaya VII expedition off Sumatra were large (TL > 40 mm, Indonesian Institute of Science RV, Aoyama et al. 2007; Kuroki et al. 2007). A western spawning place was also suspected by several authors in the eastern Malagasy region (Jespersen 1942; Jubb 1961; Robinet et al. 2003a), but remains to be validated because only a few large leptocephali were collected there (Jespersen 1942). Otolith microstructures showed that ages at metamorphosis of *A. bicolor bicolor* recruited in various places around Madagascar were quite variable: 39–57 days (in Réunion in 2001), 87–139 days (in Mauritius in 2005), 87–125 days (in Mayotte in 2005), and 87–128 days (in Seychelles in 2005, Robinet et al. 2003a, this study). However, a spawning place in north-eastern Madagascar is highly

probable because (1) these ages at metamorphosis were similar to those of the endemic species (*A. mossambica*), except in Réunion in 2001 where they were much shorter, and (2) *A. bicolor bicolor* silver eel sexual maturity is quite advanced at the onset of their spawning migration in Réunion Is., supplying the hypothesis of a rather close spawning place (Robinet and Feunteun 2002; Robinet et al. 2003b). Recent population genetics works in *A. bicolor bicolor* did not show evidence of genetic structure between East and West Indian Ocean samples (Minegishi 2006). Glass eels of *A. bicolor bicolor* arriving in SWIO could therefore originate from the same spawning area as those recruiting in Sumatra.

Anguilla mossambica is endemic of the SWIO, so its spawning area must be in this region. However, the Dana expedition only collected a few large specimens in the northern Malagasy waters (Jespersen 1942). Age at metamorphosis recorded for this species ranged 72–130 days in Réunion Is. (2001, Robinet et al. 2003a), and 73–131 days in Madagascar (2005, this study). *A. mossambica* was dominant in eastern Madagascar estuaries but less dominant in Mayotte (Comoros), and rare in Mascarene Archipelago. Among the three eel species studied here, *A. mossambica* had the shortest leptocephalus duration (95.1 ± 16.7 days). Because the South Equatorial Current sweeps the SWIO westwards (Schott and McCreary 2001), the origin of *A. mossambica* larvae should lay in the Madagascar eastern waters, between Madagascar and the Mascarene Archipelago.

Acknowledgments

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Conclusion:

- L'approche comparative a permis de changer de point d'observation et a donné un autre type, complémentaire, d'information sur la géographie de la dispersion et son incidence sur les aires de distribution spécifiques.

Perspective:

- La dispersion doit maintenant être examinée d'un point de vue évolutif au regard de l'expansion géographique du genre durant laquelle ont émergé les différentes espèces actuelles.

CHAPITRE IV

SYNTHÈSE

Implications évolutives des variations des traits de dispersion larvaire chez les anguilles

Résumé: La dispersion est un des processus les plus importants dans la persistance et l'évolution des espèces puisqu'il assure le maintien local des populations, favorise l'émigration d'individus vers de nouvelles aires de distribution et contribue aux échanges entre différentes populations. Les anguilles sont des poissons reconnus pour la grande capacité de dispersion de leurs larves leptocéphales. La boucle migratoire du cycle de vie des anguilles s'est initialement mise en place dans les eaux tropicales, puis s'est progressivement élargie vers les zones tempérées au fur et à mesure de la spéciation du genre, probablement initiée par une augmentation des capacités de dispersion. Dans cette revue, nous avons examiné les possibles implications des traits de dispersion larvaire dans l'évolution biogéographique et phylogénétique du genre *Anguilla*. D'une part, les traits larvaires ont montré une grande variabilité à l'échelle intra-spécifique, ce qui a été proposé comme étant le reflet de leur plasticité. La diversité des histoires de vie générée par l'interaction de l'individu avec son environnement a été proposé comme ayant favorisé la persistance de la stratégie de dispersion grâce aux compromis que cette diversité permet de faire entre les risques et les avantages à moduler la durée de la dispersion. D'autre part, la variabilité des traits a montré des limites propres à chaque espèce. Ceci tend à montrer que l'évolution des traits de vie larvaire a accompagné la spéciation du genre pour laquelle les deux scénarios, proposés par de précédentes études, sont discutés du point de vue de l'évolution des capacités de dispersion larvaire. Cette approche met, de plus, en lumière la contribution de l'environnement et du déterminisme génétique aux processus moteurs de l'évolution. Enfin, il a été proposé que la résilience, conférée par la diversité des histoires de vie larvaire, ait favorisé la persistance des Anguilles, lors des changements climatiques et océaniques passés. Néanmoins, cette faculté d'adaptation est aujourd'hui remise en question au vu de la rapidité des changements globaux à venir.

Keywords: Capacités de dispersion, traits de vie larvaire, évolution des Anguillidae, plasticité, résilience, changements environnementaux.

Evolutionary implications of variability of larval dispersal traits in fish: the case of Anguillid eels

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Abstract: Dispersal is one of the most important processes involved in both species persistence and evolution as it grants local retention, emigration toward new areas and connectivity between centre and peripheral population units. Anguillid eels are famous fish species for the huge dispersal capacities of their leptocephalus larvae. Eel's life-cycle loop that first occurred in tropical waters progressively enlarged toward temperate areas along with speciation, probably promoted by an increase in larval dispersal capacities. In this review, we examined the implications of larval dispersal traits in the biogeographical and phylogenetic evolution of the genus *Anguilla*. Intraspecific variability of larval traits was proposed to reflect their plasticity. The diversity of early-life histories generated by the interaction between individual inner characteristics and environmental conditions was then proposed to have favoured the persistence of the dispersal strategy thanks to successful trades-off between risks and advantages of delaying the metamorphic competence. Traits variability displayed limits for each species, which ones exhibited fairly unshared traits' attributes. This evidenced that evolution of dispersal traits occurred along with speciation for which two scenarii drawn by previous authors are developed from the evolution of dispersal capacities point of view. This approach highlighted the support of the environment and its limits as well as the genetic determinism implication in this evolution. Finally, resilience conferred by early-life histories diversity was proposed to have supported the persistence of Anguillid species such as the temperate ones during past climate and oceanic changes, but its efficiency was ultimately thoroughly questioned in regard to the forthcoming rapid global change.

Keywords: Dispersal capacities, early-life traits, evolution of Anguillid eels, plasticity, resilience, environmental changes.

INTRODUCTION

Evolution of the living being has always fascinated scientists that still debate about its causes and mechanisms almost 150 years after Darwin's "Origin of species" (Darwin 1859). Studies of that process mainly aim at reconstructing the evolutionary past of species within the scope to predict their future becoming in regard to forthcoming environmental shifts. Life histories diversity is a key contributor to the evolutionary success of species as it confers resilience to face of environmental perturbations (Hilborn et al. 2003, Beechie et al. 2006). This characteristic is common to a vast range of organisms at both inter- and intra-specific levels (Roff 1992). But though the diversity of life histories is readily apparent, attempts to understand its origin and maintenance are still in their infancy (Roff 1992). Among life-history processes that contribute to this diversity, dispersal, defined as the movement of an organism from one location to another in a permanent way (Roff and Fairbairn, 2003), is probably the most important one involved in both species persistence and evolution (Clobert et al. 2003). It grants escapement from competition and unfavourable conditions, permits to keep connections between isolated populations, and enlarges or displace distribution areas by exploration of the environment. Anguillid eels are famous fish species for the huge dispersal capacities of their leaf-like transparent larvae. These leptocephali can indeed cross thousands to hundreds of kilometres to reach coastal, estuarine or freshwater growth habitats from which adults escape to return to natal waters to spawn and die (Tesch 1977, Tsukamoto and Arai 2001). This migration loop (Tsukamoto and Aoyama 1998) is thought to have first occurred entirely in tropical marine waters. The so-called "freshwater eels" are indeed supposed to have originated several million years ago from a marine deep-sea fish that lived in marine tropical areas and already had a leptocephalus pelagic phase but that did not undergo diadromous migrations (Tsukamoto et al. 2002, Aoyama 2003, Inoue et al. 2004 in Kuroki et al. 2006). The phylogeny and phylogeography of the genus that now comprises 15 species distributed almost worldwide and among which ten grow in tropical continental waters whereas five grow in temperate habitats is still under debate (Aoyama et Tsukamoto 1997, Aoyama et al. 2001, Lin et al. 2001, Minegishi et al. 2005). Nevertheless, it has been proposed that diadromous movements first occurred in order to avoid intra-specific competition and that geographical expansion followed for

the same reason (Tsukamoto et al. 2002). Then evolution apparently promoted range expansion from tropical species making short and thus local migration to temperate species that still reproduce in tropical waters but that make large migrations toward temperate habitats to grow. This evolution is thus likely to have been consecutive to diversity and adaptability of larval dispersal capacities. This has been reported in many studies among which only few attempted to explain its origin and probable implications for the evolution of the genus *Anguilla* (Aoyama et Tsukamoto 1997, Tsukamoto et Aoyama 1998, Tsukamoto et al. 2002).

In this paper, we examined the intra- and inter-specific variations of larval life histories among species of the genus *Anguilla* with an emphasis on three representative species of the genus' evolution. The aims were (1) to review and provide some new insights on the possible mechanisms that favoured past evolution of Anguillid eels and (2) to set the scene of species capabilities to face forthcoming environmental changes.

METHODS

1. Literature review

To compare intra- and interspecific variations of early-life traits of anguillid eels, a literature review was carried out. Early-life traits of the five temperate species *A. anguilla*, *A. rostrata*, *A. japonica*, *A. australis* and *A. dieffenbachii* and of the six tropical species *A. celebesensis, A. bicolor pacifica, A. bicolor bicolor, A. reinhardtii, A. mossambica* and *A. marmorata* were extracted from 24 publications and assembled in the present study (Table 1). Early-life histories of glass eels collected at recruitment and of leptocephali collected at sea were usually reconstructed by otolith microstructural analysis (see Lecomte-Finiger 1992, Kuroki et al. 2005, Réveillac et al. 2008). Examined traits were the body total length at recruitment (TL), the leptocephalus phase duration (LD), the metamorphosis duration (MD), the age at recruitment (AR) and the otolith growth rate during the leptocephalus life (LOGR). Unfortunately, all studies did not report exactly the same traits, and sometimes, information was only scarce. Furthermore, examination protocols of these traits sometime differed between studies. Thus, as only comparable data were taken into account, between 7 and 11 species were compared according to the biological trait.

2. Statistical analysis

Statistical analyses were performed with R statistic software (R Development Core Team 2007). Plots displaying means ± SD of each trait as a variable, were used to illustrate early-life traits variations within and between species. The Student's *t*-test, analysis of variance (ANOVA) and the Tukey's HSD post-hoc test for parametric data or the Kruskal-Wallis' for nonparametric data were performed to investigate traits differences between species. Relationships between early-life traits were examined using the correlation tests of Pearson for parametric data or Spearman for nonparametric data.

RESULTS

Specific early-life traits characteristics and length at recruitment are reported in table 1 with reference to their original publication and are illustrated in figures 1 to 3.

1. Intra-specific variability of early-life histories

All species displayed early-life traits variations. Temperate species exhibited high variances of TL, LD, MD and AR and small variances of LOGR compared to tropical species (Fisher's test, $p < 0.02$). A negative relationship was also observed at the specific level between LD and LOGR (Fig. 3). The correlation coefficients (R^2) calculated on raw data of the 3 species *A. mossambica*, *A. marmorata* and *A. anguilla* were $R^2 = 0.33$, 0.38 and 0.53 respectively. This specific trend was confirmed in the other species by calculating correlations between means of LD and means of LOGR reported in different publications on *A. rostrata*, *A. anguilla*, *A. marmorata*, *A. bicolor bicolor* and *A. mossambica* ($R^2 = 0.61$, 0.91, 0.28, 0.91 and 0. 63 respectively).

2. Inter-specific variability of early-life histories

Interspecific variations of early-life traits exceeded intra-specific ones and displayed a continuous pattern among the genus *Anguilla*, as illustrated in Fig. 1 and 2 (ANOVA, $p < 0.05$ for each trait). Tropical species had different early-life histories

than temperate ones, exhibiting shorter LD, MD, AR and higher LOGR and somatic growth rates (Student *t*-test, $p < 0.001$). Within tropical species, *A. mossambica* had the shortest LD and AR (mean 93.6 ± 8.6 d and 116.6 ± 9.7 d respectively) and the highest LOGR (mean 0.88 ± 0.1 µm/d). LD and AR reached a maximum in *A. bicolor pacifica* (mean 151.0 ± 14.1 d and 186.0 ± 18.4 d respectively). LOGR was lower in *A. bicolor bicolor* and reached a minimum in *A. marmorata* (mean 0.71 ± 0.12 µm/d). Within temperate species *A. japonica* showed the shortest LD and AR (mean 148.3 ± 10.6 d and 189.8 ± 17.5 d respectively) and the highest LOGR (0.54 ± 0.064 µm/d), conversely to *A. anguilla* (230.6 ± 66.0 d, 302.2 ± 79.4 d and 0.42 ± 0.10 µm/d respectively). Between these two extremes, variations between *A. dieffenbachii*, *A. australis* and *A. rostrata* were not always significant and their classification differed according to the trait considered. Variations of the metabolic rate were likely to be greater in tropical species and the opposite trend was observed for larval duration that tended to be more variable in temperate eels (Fisher's test *F*, $p < 0.05$).

The total length at recruitment was closely related to the MD ($R^2 = 0.62$) but its variations were also explained by the LD ($R^2 = 0.45$; Fig. 3). The same relationship between LD and LOGR as observed at the specific level was observed at the genus scale with a significant negative correlation between these traits ($R^2 = 0.58$). The regression slope decreased toward the highest values of LD to reach a LOGR threshold of approximately 0.4 µm/d around 180 d.

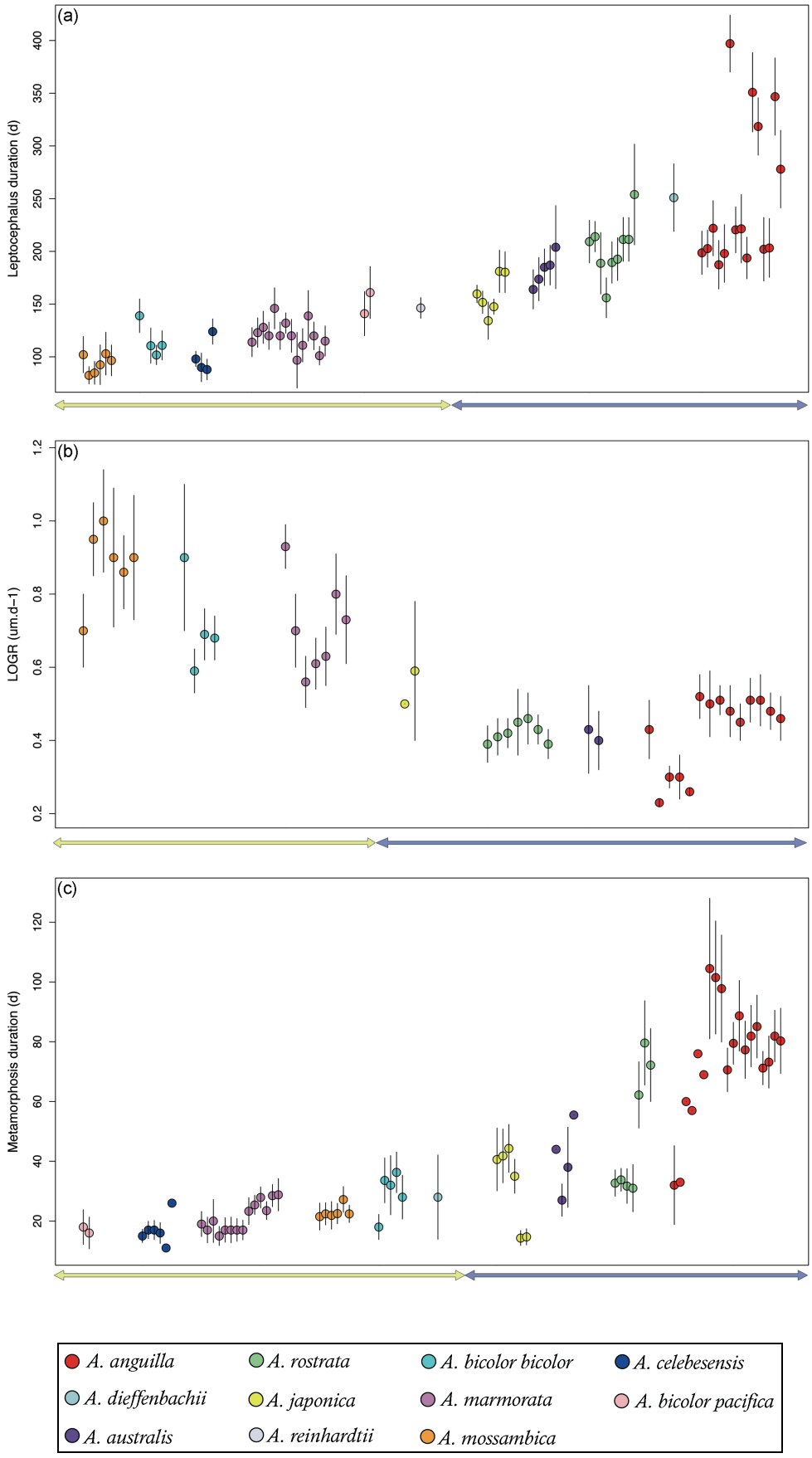
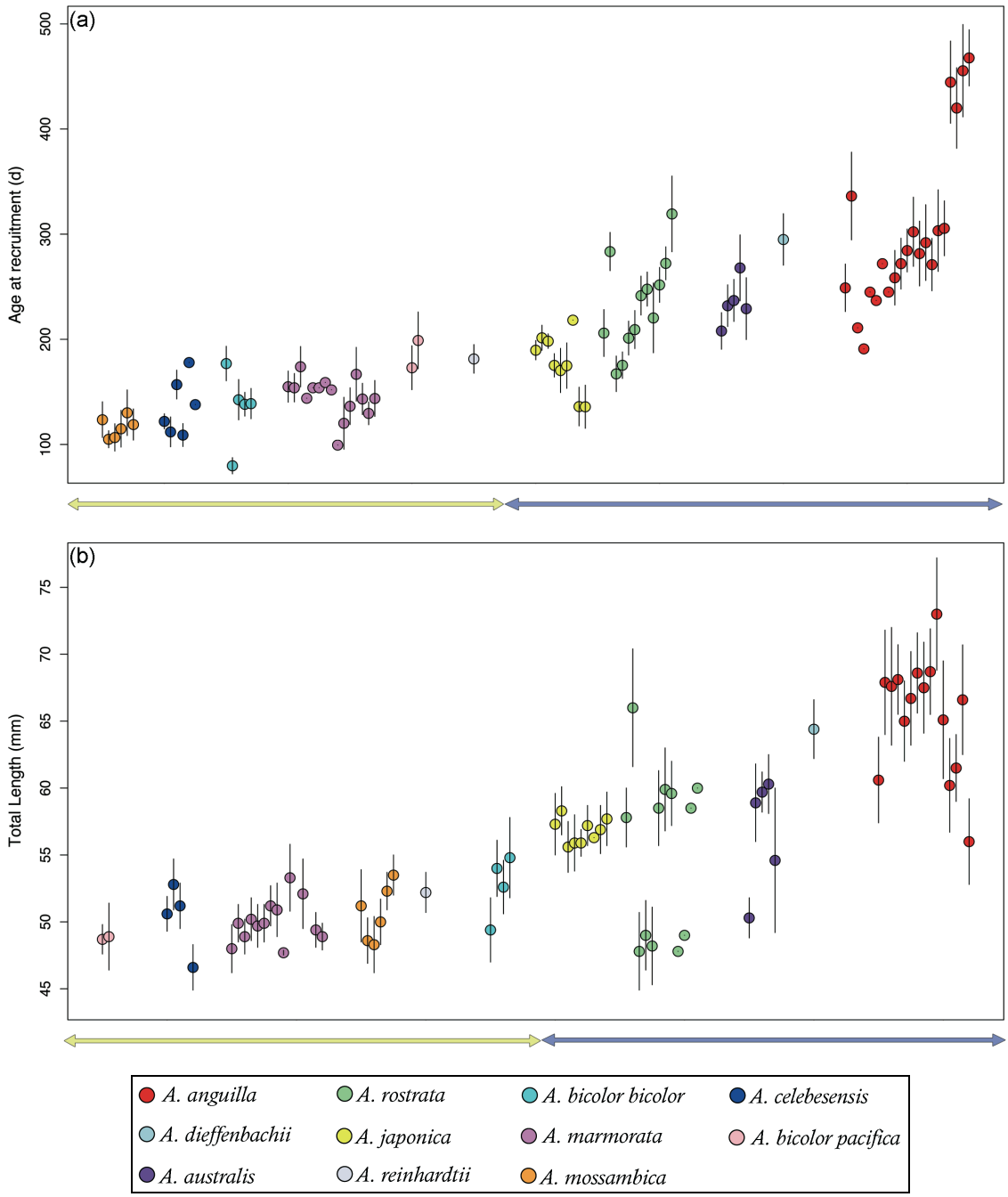

(a)
Leptocephalus duration (d)
100
150
200
250
300
350
400
(b)
LOGR (um.d−1)
0.2
0.4
0.6
0.8
1.0
1.2
(c)
Metamorphosis duration (d)
20
40
60
80
100
120
A. anguilla
A. rostrata
A. bicolor bicolor
A. celebesensis
A. dieffenbachii
A. japonica
A. marmorata
A. bicolor pacifica
A. australis
A. reinhardtii
A. mossambica

Figure 1



Figures 1 and 2. Plots showing intra- and inter-specific variations of (Fig. 1a) leptocephalus duration (LD in days), (Fig. 1b) otolith growth rate during the leptocephalus phase (LOGR in $\mu m \cdot d^{-1}$), (Fig. 1c) metamorphosis duration (MD in days) among 11 species of anguillid eels, (Fig. 2a) age at recruitment (AR in days) and (Fig.2 b) total length at recruitment (TL in mm) among 11 species of anguillid eels (legend of specific colours given apart). Each dot represents the mean (± SD) of a biological trait reported by one study on one locality (*e.g.* mean LD of *A. marmorata* glass eels sampled in Réunion Island reported by Réveillac et al. 2008). The yellow and the blue arrows at the bottom of each graphic represent tropical and temperate species respectively. They were classified by increasing or decreasing trait attribute in order to display easier the variation pattern of each biological trait. Each dot represents the mean (± SD) of a biological trait reported by one study on one locality (*e.g.* mean LD of *A. marmorata* glass eels sampled in Réunion Island reported by Réveillac et al. 2008).

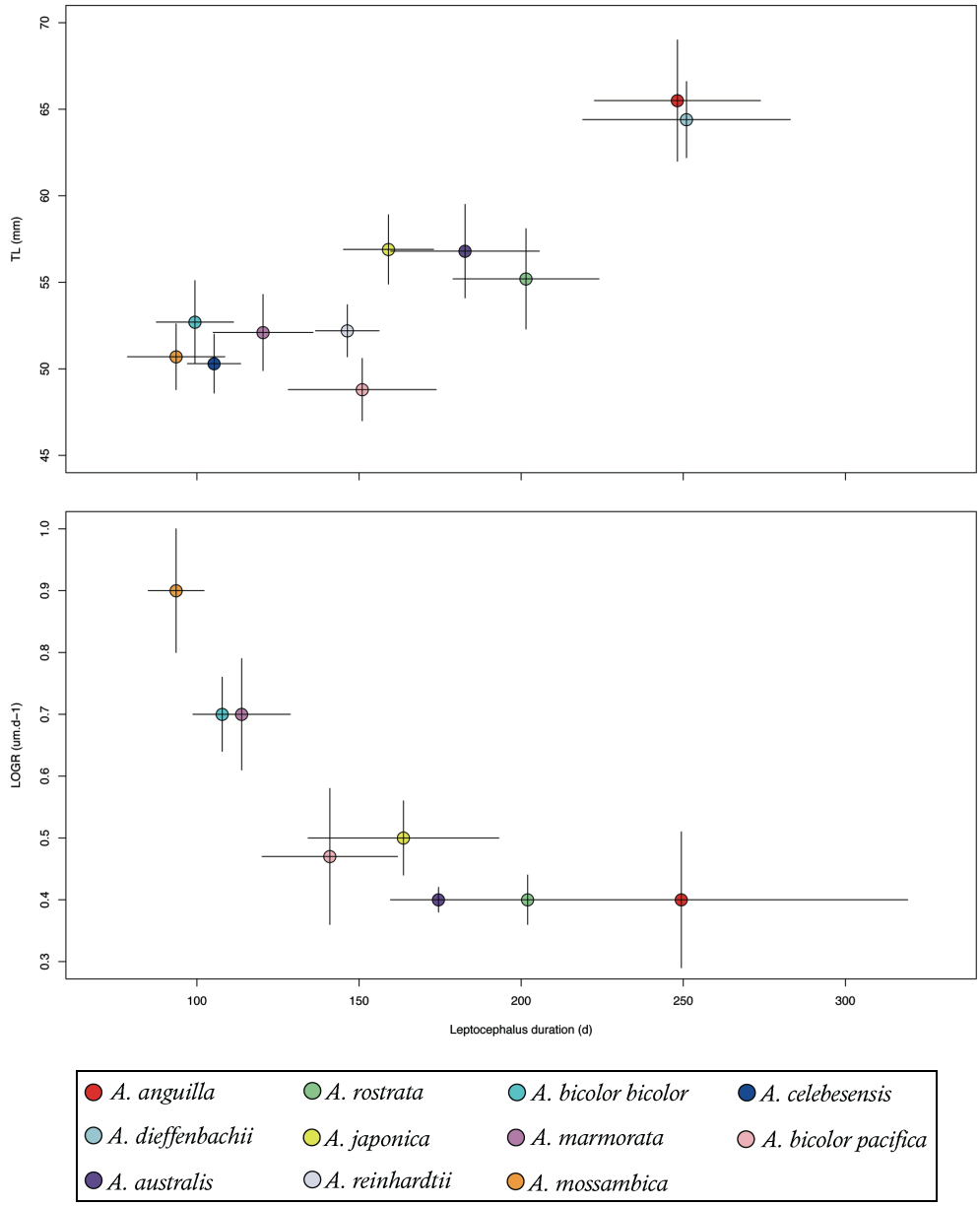


Figure 3. Plots showing the evolution of the correspondence between the leptocephalus duration (days) and (a) the total length at recruitment (mm) and (b) the leptocephalus otolith growth rate (LOGR in $\mu m \cdot d^{-1}$) among species of anguillid eels.

DISCUSSION

1. Intra-specific diversity of early-life histories

The variability of life histories observed in this study is not particular to eel's larvae. It is the attribute of many species that find great advantages in this strategy. This property enables vegetal species like the canopy lianas to live in patchy and chronically perturbed environments like are tropical forests submitted to fires (Gerwing 2004). Also, it confers the ability to the migratory sand cricket *Gryllus firmus* to escape from unfavourable environments (Roff and Fairbairn 2003) and enables the sedentary garter snake *Thamnophis elegans* to optimize its fitness in different conditions of weather, diet composition and prey availability (Bronikowski and Arnold 1999). Genetic determinism and environmental pressures are classically assumed to generate this variability and to influence covariation of traits composing the life histories (Armbruster and Schwaegerle 1996). On the one hand, environmental conditions can select individuals according to their genetically determined life histories within a specific reservoir of diversity, defined as the genetic polymorphism[10] (Russell 1987, Murren et al. 2003, Roff and Fairbairn 2003). On the other hand, individual phenotypic plasticity[11] can occur, increasing the phenotypic alternatives available to an individual that experiences fluctuations of its environment conditions (Murren et al. 2003). In eel's larvae genetic support to this variability has not been investigated yet. Therefore, it is difficult to assess whether phenotypic plasticity occur at the individual level as a response to environmental drives or if alternative strategies are innate. Nevertheless, the genetic variance of migratory species has shown to be high and dispersal traits, such as dispersal duration, to be heritable (Roff and Fairbairn 2003). In parallel, some experiments conducted on leptocephali reported water temperature to influence the larval metabolic rate, which is likely to have repercussions on larval durations and subsequent dispersal capacities (Umezawa et Tsukamoto 1991, O'Connor et al. 2007, Okamura et al. 2007). From these indications, we propose that eel larval traits are

[10] Genetic polymorphism: Genetically determined life histories forming a reservoir of diversity in which environment can select some histories (from Murren et al. 2003).

[11] Individual phenotypic plasticity: genetically controlled response to the environment experienced by the individual (Murren et al. 2003).

genetically determined, as in other species, with a propensity to be influenced by the environment, which thus plaids for plasticity. Such plasticity of migratory traits accounts for the dispersal capacities of eels, and certainly represents a key evolutionary factor and an advantage for anguillid eels that appeared several ten million years ago. So far, such a bioevolutionary approach has been largely neglected in anguillid eels as well as for many other species (Ronce et al. 2003).

The fact that various early-life histories with various larval life durations were recorded at recruitment suggests that eel species are able to generate different successful trades-off between risks and advantages of shortening or lengthening their larval life. On the one hand, short dispersal and subsequent migration loop might reduce the probability to find suitable growth habitats but might allow species to maintain local distribution at low risk by reducing larval mortality by predation or loss in currents (Takasuka and Aoki 2006, Réveillac et al. 2008). On the other hand, long dispersal and subsequent large migration loop might enable the species, in counterparts to a probable higher larval mortality, to explore new areas (Correia et al. 2004). This increases its probabilities to find new suitable places for growth and might enable individuals to escape from competition. Recently, the Australasian spotted eel *A. reinhardtii* seems to have given an ostensible proof of the advantages conferred by this ubiquitous strategy. This species, originally distributed in eastern Australian rivers, has newly colonized New Zealand freshwaters (Jellyman et al. 1996, McDowall et al. 1998). While oceanic current changes are supposed to have opened the possibility to reach a new area (McDowall 2008), the present study points out the possible crucial role that the intra-specific larval plasticity might have played in this neo-colonization process.

2. Specific limits of dispersal, structure and speciation

However, each species exhibited limits of its larval traits variations. Furthermore, each species displayed its own and fairly unshared traits attributes[12]. These observations are evidences that evolution of the genus *Anguilla* occurred through speciation, and that, according to the continuous inter-specific variation pattern, it left few to no ecological gap. Haldane (1990) argued that species ranges could be set

[12] Attribute: value or modality taken by a trait at a point of a gradient (Violle et al. 2007).

intraspecifically when gene flow from a species populous centre overwhelms local adaptation at the periphery. In this context, speciation might occur when gene flow is not strong enough to prevent isolation of peripheral units barely connected to the species centre (Haldane 1990 in Case and Taper 2000). In eels, barriers between local dispersal ensuring maintenance of the species populous centre and long dispersal ensuring gene flow to the periphery of the species distribution range would lead to the emergence of new populations or to the extinction of peripheral units. Ishikawa et al. (2004) proposed two main scenarii of speciation based on the functioning of migration loops (Tsukamoto et al. 2002). The first scenario describes a progressive temporal or geographical dissociation of migration loops inducing spawning asynchronism and/or spawning area dissociation. This scenario can be associated to the vicariant speciation hypothesis that can be triggered by the emergence of physical or temporal barriers to either larval dispersal or adult migration. The second scenario is the founder hypothesis, which implies that individuals colonize another circulation system and found a new migration loop in the favour of temporary hydrological changes.

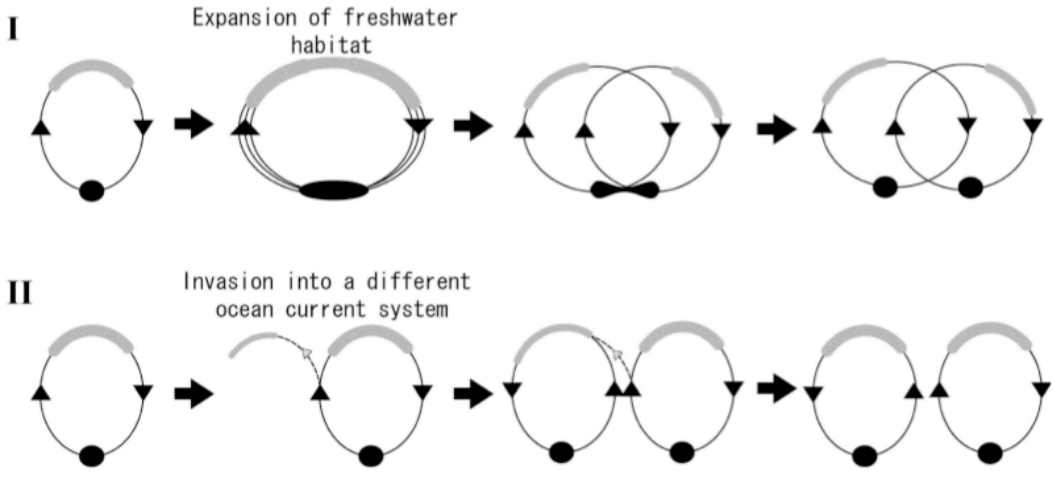


Figure 4. Two alternative models of the speciation process in anguillid eels. Model I shows speciation within an ocean current system; model II shows speciation beyond the margin of an ocean current system. Circles represent migration loops (Tsukamoto et al. 2002); small solid circles, spawning grounds; shaded arcs, freshwater habitats; lines connecting these with upward arrowheads, transportation of eggs and larvae to the freshwater habitats; lines with downward arrowheads, spawning migration by adults (in Ishikawa et al. 2004).

According to these scenarii, speciation is inclined to occur when intra-specific limits of variability of the dispersal capacities, *i.e.* elasticity, are reached. When it is the case, species stop their range expansion or start to divide up into populations that will extinct, become new species or that will reconnect later. Among all anguillid eels, three species seem to be representative of this process. *A. mossambica* has been recently described as the most ancient and basal species of the genus *Anguilla* (Minegishi et al. 2005). It exhibits the shortest LD and the smallest variances of dispersal duration, which is congruent with the fact that this tropical species is (*i*) endemic to the southwestern Indian Ocean, and (*ii*) probably not genetically structured as only one spawning area is presumed to feed its whole distribution range (Robinet et al. 2008, Réveillac et al. in prep). (2) *A. marmorata* presumably appeared intermediately among actual species (Minegishi et al. 2005). This tropical eel displayed mean LD and variances, which fit with the relatively large distribution ranges of its six genetic populations, which, together, constitute the largest specific distribution range of the genus (from the western Indian Ocean to the western Pacific in both hemispheres). Each of these populations have successfully separated by founding independent migration loops, but some joined again by introgression in a secondary contact like the two populations of the Indian Ocean (Gagnaire et al. in prep). (3) *A. anguilla* is the most recent species of the genus (Minegishi et al. 2005). It showed the longest LD and the highest variances. This seems to match with the large migration loop and distribution of this temperate species (in the northwestern Atlantic Ocean from Iceland to North Africa, including the Mediterranean Sea), and with the seemingly existing, but poor, genetic structure that is still debated (Wirth and Bernatchez 2001, Dannewitz et al. 2005, Maes et al. 2006, Pujolar et al. 2006). Thus, *A. mossambica* might have not enough dispersal capacities and variance to colonize distant areas, *A. marmorata* might have not enough dispersal capacities to maintain one population in its patchy tropical environment but might have enough variance to found new populations, and *A. anguilla* might have enough of both to emigrate far from its spawning area and maintain as one genetic population.

In the light of these observations, specific distribution range and genetic structure seem to be dependent on the species elasticity conferred by the dispersal capacities and amplitude of variance. These two characteristics seem to have genuinely increased from ancient tropical species to young temperate eels.

3. Environment supports and limits the strategy evolution

The evolution of dispersal capacities from tropical to temperate waters reflects adaptation to new environmental conditions. Among all, temperature has been reported to have a major influence on dispersal capabilities (O'Connor et al. 2007). Indeed, colder water temperatures slow down the metabolism of fish larvae, that thus develop slower. This cascade of processes has the consequence to delay the timing of metamorphic competence, and to subsequently increase the larval dispersal capacities. In addition, the lower metabolic rate lengthens the competence period of larvae, preventing them from spontaneous metamorphosis that would automatically result in death, as described in marine invertebrates (Hadfield et al. 2001). This is probably what happens in eel's larvae as the recorded otolith growth rate, proxy of the metabolic rate (Wright 1991), is lower in temperate species than in tropical ones. Thus, more than a "simple" adaptation, evolution of eel's dispersal capacities might have been supported by the environment. Furthermore, both average and the variance of the metabolic rate decreased from tropical to temperate waters. This could be the sign that the amplitude of metabolic response to environmental fluctuations is more constrained in species that develop slowly and have a lower metabolic rate.

As a result, the genus seems to be limited "on the tropical side" by the high rate of energy expense which constrains species to recruit rapidly and thus locally. And, "on the temperate side", limitation might occur because the low temperatures delay the metamorphic competence of species that are obliged to undergo long dispersal. Furthermore, the potential variability in metabolic rate increases toward lower latitudes and warmer waters; whereas the opposite trend is observed for larval durations, which tend to be both long and potentially variable in high latitudes (Fig. 5). This is almost word for word the general trend described by Houde (1989) for marine fish larvae. And, it is obvious that these characteristics drive the dispersal capacities of larvae, which in turn, govern the structure, the adaptability and thus the evolution of species.

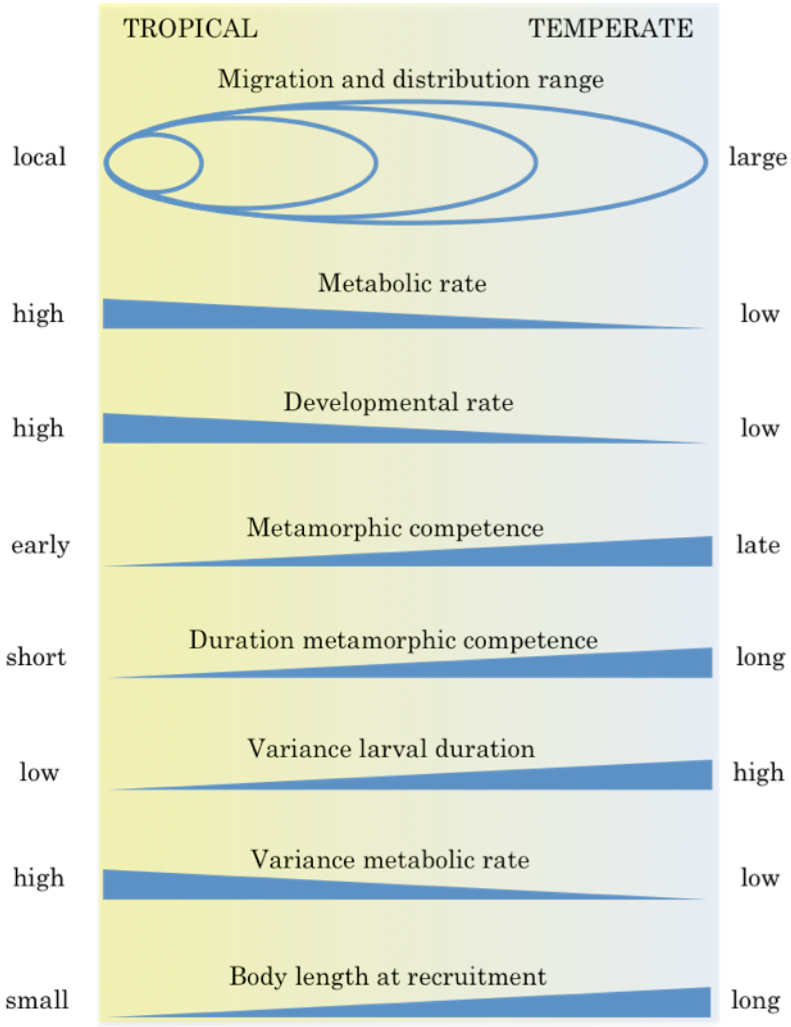


Figure 5. Schematic representation of early-life traits variations and evolution from tropical to temperate species of the genus *Anguilla*.

4. Genetic determinism of dispersal and sympatric speciation

The metabolic and subsequent metamorphic competence constraints, limiting whether local or distant recruitment, design the heart of the "timing of metamorphosis" hypothesis raised to explain the segregation between the two Atlantic eel's species (Kuroki et al. 2008). Although they recruit in two different continents, *i.e.* in northwestern Atlantic for *A. rostrata* and in northeastern Atlantic for *A. anguilla* with an overlap in Iceland, they spawn in relatively close areas from western to eastern side of the so-called Sargasso Sea (Schmidt 1922). Thus a difference in the timing of metamorphic competence seems to occur with *A. rostrata* recruiting at a younger age and closer to the spawning area than *A. anguilla* larvae. As phylogeographic hypotheses suppose that *A. anguilla* and *A. rostrata* diverged from a common species (Avise 2003), it seems likely that isolation barriers,

supposedly related to the continental drift, emerged and that the ancestral species migration loop was not elastic enough to maintain as one population. Thus, type I mechanism of speciation (Ishikawa et al. 2004) could have occurred, with an enlargement of the migration loop that progressively divided in two loops that still meet in the reproduction area. The increasing asynchrony of reproductive migrations made by adults coming from differently distant areas has been proposed to induce a temporal reproductive isolation and initiate the sympatric speciation (van Ginneken and Maes 2005). But to maintain this isolation throughout the life-cycle, differential dispersal is likely to have reinforced the loops segregation. Only heritability of dispersal traits (Roff and Fairbairn 2003) acting jointly with differential environmental pressures selecting different phenotypes, could have induced such an ecological speciation[13] by disruptive selection[14] resulting in the segregation of the two Atlantic species (Schluter 2001). As both species occur in Iceland, this locality might represent the break point, *i.e.* the limit of the ancestral species elasticity, which hybrids witness that we may be in presence of two incipient species[15] that are still diverging or that join again in a secondary contact (Albert et al. 2006).

4. Resilience: answers to the past and interrogations for the future

Life history diversity, through the subjacent trades-off between life history advantages and risks, is a key contributor to population and species persistence as it confers resilience in the face of environmental fluctuations (Hilborn et al. 2003, Beechie et al. 2006). This might have been the key for the survival of the two Atlantic species *A. rostrata* and *A. anguilla* which have been highly impacted by the reduced speed of the Gulf Stream during the Wisconsinan glaciation and the Younger Dryas cold event (Duplessy 1999, Wirth and Bernatchez 2003; Fig. 6). These

[13] Ecological speciation: the evolution of reproductive isolation caused ultimately by divergent natural selection on traits between populations (or disruptive selection between phenotypes of a single population) in different environments. (Trends in Ecology & Evolution, Speciation Glossary, 2001).

[14] Disruptive selection: natural selection within a single population towards different phenotypes. (Trends in Ecology & Evolution, Speciation Glossary, 2001).

[15] Incipient species: two or more diverged populations hat are substantially, but not completely, reproductively isolated (Trends in Ecology & Evolution, Speciation Glossary, 2001).

events of major oceanic current changes have probably reduced and/or moved the distribution areas of the species (Keffer et al. 1988).

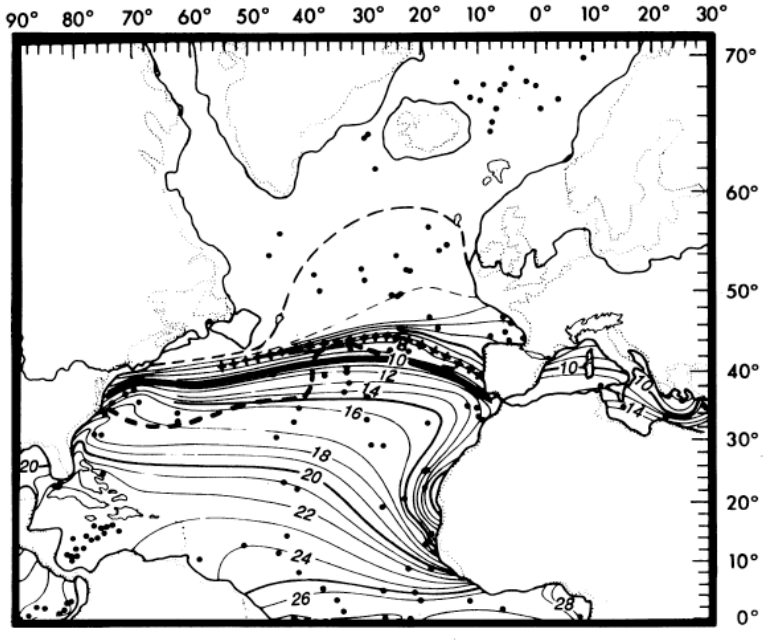


Figure 6. January sea-surface temperature in the Atlantic Ocean 18,000 years ago (original figure from Keffer et al. 1988). The heavy solid line represents the 10°C isotherm; the crossed line represents the position of the polar front as determined by Ruddiman and McIntyre (1977).

Thanks to their plasticity they might have been able (1) to maintain their life-cycle migration loops in changing environmental conditions and (2) to redeploy during subsequent warming events. Thus, the characteristics of the marine larval phase already rescued the eel. However, whether limits of plasticity identified in this work could evolve rapidly enough to face the forthcoming major climate changes (Knights 2003) is a crucial question. Indeed, if climate and oceans warm too quickly, temperate species with long distances to cross will suddenly lose their environmental support to delay their metamorphic competency. A question, universal to Anguillid species, and other species displaying strong dispersal strategies, remains: what is the reactivity of eel's plasticity? Is extinction their fate? Or will the marine larval dispersal again rescue this remarkable fish in displacing its distribution area?

Acknowledgements

This work was supported by the European INTERREG IIIB Indo-Eel and the INTERREG II INDICANG research programs. E. Réveillac was supported by a Ph.D. grant of the French Conseil Général de Charente Maritime.

Table 1. *Anguilla* spp. Mean ± SD for the total length at recruitment (TL), leptocephalus duration (LD), metamorphosis duration (MD), age at recruitment (AR), leptocephalus otolith growth rate (LOGR) reported in different studies on leptocephalus and glass eel phases.

Species	Locality	Date	TL (mm)	LD (days)	MD (days)	AR (days)	LOGR ($\mu m\ d^{-1}$)	Authors
Temperate species								
A. australis	Australia	1996	50.3 ± 1.5	164.0 ± 18.6	44.0	208.0 ± 17.4	0.43 ± 0.12	Arai et al., 1999c
A. australis	New Zealand	1996	58.9 ± 2.9	185.0 ± 17.3	27.0 ± 5.4	232.0 ± 19.8	0.40 ± 0.08	Arai et al., 1999c
A. australis	New Zealand	1996	59.7 ± 1.5	187.0 ± 18.9	-	237.0 ± 20.0	-	Arai et al., 1999c
A. australis	New Zealand	1996	60.3 ± 2.2	204.0 ± 39.4	38.0 ± 13.4	268.0 ± 31.3	-	Marui et al., 2001
A. australis	Australia	1998	54.6 ± 5.4	173.7 ± 20.5	55.5	229.2 ± 29.4	-	Shiao et al., 2002
A. dieffenbachii	New Zealand	1996	64.4 ± 2.2	251.0 ± 32.0	28.0 ± 14.1	295.0 ± 24.5	-	Marui et al., 2001
A. japonica	Japan	1994	57.3 ± 2.3	147.6 ± 7.2	40.6 ± 10.5	189.7 ± 9.2	-	Cheng and Tzeng, 1996
A. japonica	Korea	1993	58.3 ± 1.8	159.7 ± 8.3	41.8 ± 9.0	201.5 ± 11.9	-	Cheng and Tzeng, 1996
A. japonica	China	1993	55.6 ± 1.9	151.7 ± 10.6	44.3 ± 8.0	198.3 ± 6.9	-	Cheng and Tzeng, 1996
A. japonica	Taiwan	1993	55.9 ± 2.1	134.3 ± 17.7	35.0 ± 5.7	175.3 ± 11.1	-	Cheng and Tzeng, 1996
A. japonica	Taiwan	1990	55.9 ± 1.0	-	-	170.4 ± 21.0	0.50	Tzeng and Tsai, 1992
A. japonica	Japan	1997	57.2 ± 1.5	-	-	175 ± 21.6	0.59 ± 0.19	Arai et al., 1997
A. japonica	Japan	1990	56.3	-	-	218.3	-	Tsukamoto et al., 1990
A. japonica	Japan	1995	56.9 ± 1.8	181.1 ± 20.0	14.3 ± 2.5	136.1 ± 18.4	-	Kawakami et al., 1999
A. rostrata	Maine	1997	57.8 ± 2.2	156.0 ± 18.9	31.0 ± 7.9	206.0 ± 22.3	0.45 ± 0.09	Arai et al., 2000b
A. rostrata	Iceland	1999	66.0 ± 4.4	254.0 ± 47.7	-	319.3 ± 36.0	-	Kuroki et al. 2008
A. rostrata	Haiti	1995	47.8 ± 2.9	209.3 ± 20.2	32.7 ± 4.4	241.6 ± 18.5	0.39 ± 0.05	Wang and Tzeng, 2000
A. rostrata	Florida	1995	49.0 ± 2.6	214.0 ± 14.4	33.8 ± 3.8	247.8 ± 16.2	0.41 ± 0.05	Wang and Tzeng, 2000

Species	Locality	Date	TL (mm)	LD (days)	MD (days)	AR (days)	LOGR ($\mu m\ d^{-1}$)	Authors
Temperate species (continuation)								
A. rostrata	Carolina	1995	48.2 ± 2.9	188.8 ± 29.1	31.7 ± 5.8	220.4 ± 33.2	0.42 ± 0.04	Wang and Tzeng, 2000
A. rostrata	Rhode Island	1995	58.5 ± 2.8	189.5 ± 19.6	62.2 ± 11.1	251.8 ± 16.6	0.46 ± 0.07	Wang and Tzeng, 2000
A. rostrata	New Brunswick	1995	59.9 ± 3.1	192.7 ± 20.3	79.6 ± 14.1	272.3 ± 15.7	0.43 ± 0.04	Wang and Tzeng, 2000
A. rostrata	Nova Scotia	1995	59.6 ± 2.4	211.4 ± 20.8	72.2 ± 12.2	283.5 ± 18.2	0.39 ± 0.04	Wang and Tzeng, 2000
A. rostrata	Carolina	1994	-	-	-	167.2 ± 16.9	-	Powles and Warlen, 2002
A. rostrata	Carolina	1994	-	-	-	175.4 ± 12.6	-	Powles & Warlen, 2002
A. rostrata	New Jersey	1994	-	-	-	201.2 ± 16.1	-	Powles & Warlen, 2002
A. rostrata	New Brunswick	1994	-	-	-	209.3 ± 18.1	-	Powles & Warlen, 2002
A. anguilla	Portugal	1996	60.6 ± 3.2	198 ± 27.4	32 ± 13.2	249.0 ± 22.6	0.43 ± 0.08	Arai et al., 2000b
A. anguilla	Iceland	1999	67.9 ± 3.9	278 ± 36.8	-	336.3 ± 41.7	-	Kuroki et al., 2008
A. anguilla	Morocco	1989	-	178	33	211	-	Lecomte-Finiger, 1992
A. anguilla	Spain	1987	-	186	-	191	-	Lecomte-Finiger, 1992
A. anguilla	Loire	1989	67.6 ± 4.4	185	60	245	-	Lecomte-Finiger, 1992
A. anguilla	Vilaine	1989	-	180	57	237	-	Lecomte-Finiger, 1992
A. anguilla	Severn	1988	-	196	76	272	-	Lecomte-Finiger, 1992
A. anguilla	Netherlands	1990	-	176	69	245	-	Lecomte-Finiger, 1992
A. anguilla	Sweden	1995	68.1 ± 2.6	346.8 ± 36.6	104.5 ± 23.5	444.6 ± 39.1	0.23 ± 0.01	Wang and Tzeng, 2000
A. anguilla	Severn	1995	65.0 ± 3.0	318.5 ± 27.2	101.5 ± 18.9	420.0 ± 38.3	0.30 ± 0.03	Wang and Tzeng, 2000
A. anguilla	Vilaine	1995	66.7 ± 3.5	350.9 ± 37.6	97.8 ± 17.9	455.5 ± 43.9	0.30 ± 0.06	Wang and Tzeng, 2000
A. anguilla	Portugal	1995	68.6 ± 3.0	397.1 ± 27	70.6 ± 7.3	467.7 ± 26.7	0.26 ± 0.01	Wang and Tzeng, 2000
A. anguilla	Ireland	2006	67.5 ± 3.4	202.1 ± 30.1	79.5 ± 7.0	281.6 ± 30.8	0.52 ± 0.06	Réveillac et al., *in prep*
A. anguilla	Netherlands	2006	-	203.3 ± 27.9	88.7 ± 11.8	292.0 ± 36.0	0.50 ± 0.09	Réveillac et al., *in prep*
A. anguilla	Vilaine	2006	68.7 ± 3.2	193.8 ± 19.7	77.3 ± 9.6	271.1 ± 24.9	0.51 ± 0.04	Réveillac et al., *in prep*
A. anguilla	Aiguillon	2006	73.0 ± 4.2	221.5 ± 32.4	81.9 ± 10.3	303.4 ± 38.8	0.48 ± 0.07	Réveillac et al., *in prep*

Species	Locality	Date	TL (mm)	LD (days)	MD (days)	AR (days)	LOGR ($\mu m\ d^{-1}$)	Authors
Temperate species (continuation)								
A. anguilla	Spain	2006	65.1 ± 4.4	220.5 ± 21.8	85.1 ± 10.5	305.6 ± 26.1	0.45 ± 0.05	Réveillac et al., *in prep*
A. anguilla	Morocco	2006	60.2 ± 3.5	187.4 ± 23.0	71.2 ± 5.6	258.6 ± 26	0.51 ± 0.06	Réveillac et al., *in prep*
A. anguilla	Tunisia	2007	61.5 ± 2.5	198.7 ± 20.5	73.2 ± 8.7	272.0 ± 24.2	0.51 ± 0.07	Réveillac et al., *in prep*
A. anguilla	Camargue	2006	66.6 ± 4.1	202.7 ± 17.6	81.9 ± 8.6	284.5 ± 20.4	0.48 ± 0.05	Réveillac et al., *in prep*
A. anguilla	Greece	2006	56.0 ± 3.2	222.0 ± 26.1	80.3 ± 10.9	302.3 ± 32.9	0.46 ± 0.06	Réveillac et al., *in prep*
Tropical species								
A. celebesensis	Indonesia	1999	50.6 ± 1.3	98.0 ± 7.2	15.0 ± 2.2	122.0 ± 7.2	-	Arai et al., 2003b
A. celebesensis	Indonesia	1997	52.8 ± 1.9	90.0 ± 13.6	17.0 ± 2.9	112.0 ± 14.2	-	Arai et al., 2003b
A. celebesensis	Philippines	1994	51.2 ± 1.7	124.0 ± 12.0	17.0 ± 3.2	157.0 ± 13.7	-	Arai et al., 2003b
A. celebesensis	Indonesia	1997	-	88.0 ± 9.8	16.0 ± 3.5	109.0 ± 10.9	-	Arai et al., 2001b
A. celebesensis	Indonesia	1998	41.5	154	11	178	-	Marui et al., 2001
A. celebesensis	Philippines	1996	46.6 ± 1.7	109	26	138	-	Marui et al., 2001
A. pacifica	Indonesia	1997	48.7 ± 1.1	141.0 ± 20.9	18.0 ± 5.8	173.0 ± 20.9	0.47 ± 0.11	Arai et al., 2001b
A. pacifica	Philippines	1998	48.9 ± 2.5	161.0 ± 24.6	16.0 ± 5.3	199.0 ± 27.0	-	Marui et al., 2001
A. marmorata	Indonesia	1997	48.0 ± 1.8	128.0 ± 15.2	19.0 ± 4.2	155 ± 14.8	-	Arai et al., 2001b
A. marmorata	Philippines	1994	49.9 ± 1.4	120.0 ± 13.0	17.0 ± 4.3	154 ± 13.5	-	Arai et al., 1999a
A. marmorata	Philippines	1998	48.9 ± 1.3	146.0 ± 19.5	20.0 ± 7.2	174 ± 19.2	-	Marui et al., 2001
A. marmorata	Taiwan	1999	50.2 ± 1.6	114.0 ± 13.8	15.0 ± 3.2	144	-	Arai et al., 2002a
A. marmorata	Japan	1999	49.7 ± 1.6	123.0 ± 13.9	17.0 ± 4.1	154	-	Arai et al., 2002a
A. marmorata	Philippines	1999	49.9 ± 1.4	120.0 ± 13.0	17.0 ± 4.3	154	-	Arai et al., 2002b
A. marmorata	Indonesia	1999	51.2 ± 1.5	132.0 ± 9.7	17.0 ± 3.8	159	-	Arai et al., 2002b
A. marmorata	Indonesia	1999	50.9 ± 2.0	120.0 ± 15.6	17.0 ± 3.3	152	-	Arai et al., 2002b
A. marmorata	Indonesia	1999	47.7 ± 0.2	-	-	99.5	0.93 ± 0.06	Budimawan and Lecomte-Finiger, 2005
A. marmorata	Reunion	2001	53.3 ± 2.5	96.9 ± 26.4	23.3 ± 4.5	120.2 ± 24.7	0.70 ± 0.10	Robinet et al., 2003a

Species	Locality	Date	TL (mm)	LD (days)	MD (days)	AR (days)	LOGR ($\mu m\ d^{-1}$)	Authors
Tropical species (continuation and end)								
A. marmorata	Reunion	2005	-	111.0 ± 15.8	25.4 ± 3.2	136.4 ± 17.5	0.56 ± 0.07	Réveillac et al., 2008
A. marmorata	Mauritius	2005	52.1 ± 2.6	138.9 ± 24.0	27.9 ± 3.5	166.8 ± 25.6	0.61 ± 0.07	Réveillac et al., 2008
A. marmorata	Mayotte	2005	59.8 ± 8.9	119.9 ± 13.1	23.5 ± 3.0	143.3 ± 14.9	0.63 ± 0.08	Réveillac et al., 2008
A. marmorata	Madagascar	2005	49.4 ± 1.3	101.1 ± 8.8	28.5 ± 3.7	129.6 ± 10.8	0.80 ± 0.11	Réveillac et al., 2008
A. marmorata	Madagascar	2005	48.9 ± 1.0	115.0 ± 14.3	28.8 ± 5.4	143.8 ± 17.1	0.73 ± 0.12	Robinet et al., 2008
A. b. bicolor	Indonesia	1996	49.4 ± 2.4	139.0 ± 15.9	18.0 ± 4.2	177.0 ± 16.4	-	Arai et al., 1999b
A. b. bicolor	Reunion	2001	54.0 ± 2.1	46.2 ± 5.8	33.6 ± 7.5	79.8 ± 7.7	0.90 ± 0.20	Robinet et al., 2003
A. b. bicolor	Mauritius	2005	52.6 ± 2.0	110.6 ± 16.7	32.0 ± 9.9	142.6 ± 19.2	0.59 ± 0.06	Robinet et al., 2008
A. b. bicolor	Mayotte	2005	54.8 ± 3.0	101.8 ± 9.2	36.3 ± 6.8	138.3 ± 11.3	0.69 ± 0.07	Robinet et al., 2008
A. b. bicolor	Seychelles	2005	-	110.9 ± 13.8	28.0 ± 7.3	138.9 ± 14.4	0.68 ± 0.06	Robinet et al., 2008
A. reinhardtii	Australia	1996	52.2 ± 1.5	146.4 ± 9.8	-	181.4 ± 13.6	-	Shiao et al., 2002
A. mossambica	Reunion	2001	51.2 ± 2.7	102.1 ± 17.2	21.5 ± 4.5	123.6 ± 17.0	0.70 ± 0.10	Robinet et al., 2003
A. mossambica	Madagascar	2005	48.6 ± 1.7	82.5 ± 8.2	22.4 ± 3.7	105 ± 8.1	0.95 ± 0.10	Réveillac et al., *in prep*
A. mossambica	Madagascar	2005	48.3 ± 2.1	84.8 ± 10.8	21.9 ± 4.6	106.7 ± 13.0	1.00 ± 0.14	Réveillac et al., *in prep*
A. mossambica	Madagascar	2005	50.0 ± 1.7	92.5 ± 18.8	22.5 ± 3.4	115.0 ± 17.5	0.90 ± 0.19	Réveillac et al., *in prep*
A. mossambica	Madagascar	2005	52.3 ± 1.4	103.0 ± 20.3	27.2 ± 4.3	130.2 ± 21.7	0.86 ± 0.10	Réveillac et al., *in prep*
A. mossambica	Madagascar	2005	53.5 ± 1.5	96.6 ± 14.5	22.4 ± 2.9	119.0 ± 14.8	0.90 ± 0.17	Réveillac et al., *in prep*

CONCLUSIONS ET PERSPECTIVES

CONCLUSIONS ET PERSPECTIVES

"Il est un besoin impérieux d'acquérir quelques notions des énigmes de l'Univers et d'essayer de contribuer à les résoudre". C'est peut-être motivé par ses propres paroles que Freud fût l'un des nombreux chercheurs à se confronter au mystère du cycle de vie des anguilles (Freud 1877). Tandis qu'il cherchait, en vain, un appareil reproducteur mâle sur des individus de rivière, on ignorait encore qu'il existait une phase larvaire, objet de cette thèse. Et avant de conclure cette étude par des perspectives de recherche, il semble intéressant de revenir sur l'origine de:

LA PHASE LARVAIRE EN MILIEU MARIN

Pourquoi un stade larvaire?

Le développement indirect via une phase larvaire est un caractère apparu secondairement chez les ostéichtyens (Hadfield et al. 2001). Les questions sont de savoir "Pourquoi avoir développé cette phase? Quels avantages procurent-elle?".

L'une des premières réponses rencontrées dans la littérature fait référence à la capacité de dispersion (importante ou non) que confère cette phase (Doherty et al. 1985). Grâce à cette propriété, les organismes ont la possibilité de se soustraire à la prédation et à la compétition en s'éloignant des habitats très peuplés (Johannes 1978 in Doherty et al. 1995), et de traverser plusieurs habitats défavorables jusqu'à atteindre ceux propices à leur établissement et au déroulement du cycle de vie (Clobert et al. 2003).

Se disperser, mais pour aller où?

Avoir la capacité de se disperser, ne signifie pas obligatoirement qu'elle est exploitée (Kudenov 1975, Roff et Fairbairn 2003). Les zones de recrutement peuvent en effet être celles des géniteurs. Ainsi les larves de certains poissons de récifs se dispersent pendant une dizaine de jours avant de recruter étonnamment près de leurs géniteurs (Jones et al. 2005). Pour les mêmes poissons, le recrutement peut également se faire, a contrario, loin des habitats parentaux (recrutement allochtone). Dans ce cas, l'établissement peut avoir lieu dans des habitats où l'espèce est déjà présente, sur des aires perturbées où l'espèce avait disparue (Covich 2006), ou encore sur de

nouvelles zones jusque là inexplorées par l'espèce (*e.g. Anguilla reinhardtii*, Jellyman et al. 1996).

Étendre l'aire de distribution mais à quels risques?

Grâce à la dispersion larvaire, l'aire de distribution peut s'élargir à chaque nouvelle génération par colonisation saltatoire d'habitats adjacents connectés seulement via la phase larvaire. Dès lors, si une barrière à cette dispersion émerge entre deux unités géographiques, elles peuvent diverger en évoluant séparément au risque de s'éteindre si leur effectif est trop faible.

Quid des anguilles?

Dans le cas des anguilles, la colonisation saltatoire ne peut avoir lieu puisque les géniteurs migrent pour se reproduire sur une aire *a priori* fixe et unique par système océanique. Dès lors, l'expansion de l'aire de distribution géographique des anguilles ne peut se faire que part augmentation des capacités de dispersion larvaire ou par fondation de nouvelles boucles migratoires par émigration dans de nouveaux systèmes océaniques.

Les objectifs de cette thèse étaient de caractériser les mécanismes de la dispersion larvaire des Anguillidae, et d'examiner leur incidence sur la biogéographie et l'évolution du genre.

LA PHASE LARVAIRE DES ANGUILLES. Conclusions et perspectives

Déterminismes de la dispersion

La dispersion est contrôlée par de nombreux facteurs interdépendants qui l'affectent à différentes échelles (Ronce et al. 2003). Dans cette thèse, les capacités de dispersion des larves d'anguilles ont été définies comme principalement dépendantes de la durée de la phase larvaire et de la distance parcourue par une larve pour un temps donné.

D'une part, la durée de vie larvaire est fonction du métabolisme individuel qui régule les dépenses énergétiques, la vitesse de développement et donc les capacités de la larve à se maintenir dans le milieu avant d'acquérir la compétence à se métamorphoser. S'il est probable que ce métabolisme soit en partie génétiquement déterminé, il semble également modulé par les conditions environnementales, en

particulier la température. De la combinaison de ces déterminismes, il résulte que la diversité spécifique des histoires de vie larvaire observée est la conséquence de la plasticité des traits de vie qui les composent.

D'autre part, la distance parcourue est fonction de la vitesse et de la complexité des courants de transport. Néanmoins, la dispersion (processus passif) n'est pas obligatoirement de mise chez les larves d'anguille. En effet, certains auteurs rapportent qu'elles possèderaient d'importantes capacités à s'orienter et à nager activement (migration). Ce comportement de nage n'a pas été explicitement qualifié ni quantifié chez les leptocéphales et devrait faire l'objet d'investigations tant en milieu naturel qu'en milieu contrôlé. La mise au point de l'élevage expérimental de leptocéphales d'anguille japonaise *A. japonica* permet d'envisager cette perspective pour *A. anguilla* même si certaines étapes restent à maîtriser. L'étude du comportement de nage pourrait notamment faire la lumière sur la différence des estimations des durées de vie larvaire réalisées par otolithométrie et par modélisation de la dispersion chez l'anguille Européenne. Cette discordance est imputée d'une part, au biais introduit par les modèles de dispersion lorsqu'ils ne prennent pas en compte une potentielle nage active des larves, et d'autre part, au biais lié à la lecture des otolithes dont le rythme d'incrémentation et l'influence des paramètres environnementaux n'ont pas été validés ou quantifiés sur la totalité de la phase larvaire. Néanmoins, en ce qui concerne l'otolithométrie, ces travaux de thèse ont montré (1) que les durées de vie larvaire estimées étaient cohérentes avec la géographie des habitats colonisés, et (2) que le taux de croissance de l'otolithe, proxy du métabolisme larvaire, pouvait refléter les variations de température de l'environnement.

Caractérisation de la géographie de la dispersion

L'examen des histoires de vie larvaire et de leurs variations au sein des espèces a permis de supporter les hypothèses sur l'emplacement des zones de ponte des espèces du sud-ouest de l'Océan Indien par identification de gradients géographiques d'arrivée des larves. Cette étude a également permis d'avancer de nouvelles hypothèses sur les routes de dispersion larvaire. Ainsi, il est notamment apparu que plusieurs voies pourraient alimenter les zones de croissance continentales d'*A.*

anguilla. Afin de tester et d'affiner ces hypothèses, d'autres études pourraient être envisagées.

Une première approche serait d'intégrer les données des durées de vie larvaire acquises dans cette thèse à des modèles courantologiques pour simuler la dispersion larvaire. Cette perspective est en cours de réalisation sur les trois espèces du sud-ouest de l'Océan Indien *A. mossambica*, *A. marmorata* et *A. bicolor bicolor* pour tenter de quadriller plus précisément leurs zones de ponte respectives et d'en évaluer la stabilité temporelle. Les premiers résultats sur *A. marmorata* semblent conforter l'hypothèse de l'existence d'au moins une zone de ponte régionale à l'Est de Madagascar. Néanmoins, les seuls paramètres hydrologiques ne suffisent pas à simuler précisément les dispersions et à les faire remonter à des zones de ponte précises. Il est donc nécessaire d'introduire dans les modèles d'autres paramètres liés aux caractéristiques de la dispersion larvaire.

Dans cette optique, une deuxième approche, complémentaire, viserait à étudier la composition chimique des différentes zones de l'otolithe qui incorpore les éléments chimiques des masses d'eau de transport. D'une part, l'étude du nucleus, supposé refléter les caractéristiques des masses d'eau au tout début de la vie larvaire (Campana et al. 1994, Ashford et al. 2006), pourrait indiquer le nombre de zones de ponte qui alimentent une région et leur contribution respective à la colonisation des habitats de croissance. D'autre part, l'examen de la zone de l'otolithe formée pendant la vie leptocéphale pourrait renseigner sur les conditions de température, par analyse des ratios des isotopes stables de l'oxygène $^{18}O/^{16}O$. Cette information, par référence aux profils de variations bathymétrique de température, permettrait également de connaître les profondeurs moyennes de dispersion des larves. De plus, en se référant aux distributions océaniques connues de certains éléments traces (*e.g.* cadmium, cuivre, aluminium; Van der Loeff et al. 1997), les voies de dispersion pourraient être identifiées (Campana et al. 2000). Néanmoins, préalablement à certaines de ces études, l'analyse des facteurs d'incorporation des éléments cibles dans les otolithes devrait être réalisée.

Les hypothèses concernant les zones de ponte et les voies de dispersion issues de ces approches pourraient ensuite être testées en étudiant la structure génétique et ainsi confirmer le fonctionnement des boucles de migration. C'est, par exemple, ce qui a

été réalisé sur l'anguille marbrée *A. marmorata*. Parmi les six populations génétiques qui la composent (Ishikawa et al. 2004), les populations Est et Ouest Indienne semblent avoir récemment renoué contact par le biais supposé de la dispersion larvaire (Gagnaire et al. in prep). Ce contact secondaire par introgression de la population Est dans la population Ouest a pu être favorisé (1) par suppression des barrières physiques/temporelles qui avaient conduit à leur séparation, et/ou (2) par augmentation des capacités de dispersion des larves de l'Est à la faveur (*i*) d'une augmentation de la vitesse du courant Sud-Équatorial qui circule vers l'Ouest ou (*ii*) d'un retardement de la compétence des larves à se métamorphoser. Ce type d'investigation sera prochainement mené sur des civelles d'anguille Européenne dont les traits de vie larvaire ont été examinés, pour réviser les hypothèses de panmixie et de structuration génétique de l'espèce alternativement proposées au cours de la dernière décennie.

Connaître pour mieux gérer

En termes de gestion, le couplage des approches proposées et des informations qui en résultent est crucial. En effet, à l'heure où les anguilles tempérées déclinent de façon dramatique si bien que l'anguille Européenne est citée à l'Annexe II de la Convention sur le Commerce International de la Flore et de la Faune Sauvage Menacées d'Extinction (CITES 2007), la mise en place de plans de gestion basés sur les connaissances du cycle de vie est fortement préconisée. Cette mesure concerne également les espèces tropicales, comparativement moins exploitées, qui font l'objet d'un intérêt commercial croissant. Aussi, s'il semble primordial d'approfondir, au moyen des études proposées dans cette conclusion, les connaissances de la phase de vie larvaire qui conditionne le succès et la géographie du recrutement, il semble également essentiel d'identifier les régions productrices de géniteurs efficaces (géniteurs qui atteignent la zone de reproduction, se reproduisent et engendrent des larves qui recruteront avec succès). Dans cette perspective, il serait intéressant de définir l'existence d'un transfert maternel des éléments remobilisés lors de l'ovogénèse dans le nucleus des otolithes. Si ce transfert était avéré et que les éléments traces transmis étaient caractéristiques des zones continentales de croissance des génitrices, il pourrait être possible d'identifier ces zones et donc de les définir comme prioritaires dans la mise en place de plans de gestion.

La stratégie dispersive soumise à l'épreuve du changement global

Quantifier la part de déterminisme génétique et d'héritabilité de la durée de vie larvaire est un objectif crucial dans la perspective d'étudier les capacités de résilience et la vitesse d'adaptation des espèces aux changements environnementaux. En effet, si la part de déterminisme génétique et donc d'héritabilité des traits de vie larvaire est importante, la réponse des anguilles aux changements nécessiterait plusieurs générations pour s'exprimer (longues chez les anguilles, environ dix ans) et impliquerait donc une forte inertie. Dès lors, le caractère soudain du changement global s'avèrerait dramatique pour le maintien des boucles de migration. A l'inverse, si la durée de vie larvaire se révèle être fortement influencée par les paramètres environnementaux, la rapidité d'adaptation pourra peut être permettre aux populations de déplacer leurs boucles de migration vers des zones refuges tel qu'elles l'ont probablement fait lors des dernières glaciations.

GLOSSAIRE
GLOSSARY

Attribut - *Attribute*: valeur ou modalité prise par un trait sur un point d'un gradient de variation. *Value or modality taken by a trait at a point of a gradient* (Violle et al. 2007).

Compétence à se métamorphoser - *Metamorphic competence*: capacité à subir la métamorphose lorsqu'elle est déclenchée par des facteurs intrinsèques ou extrinsèques. *Developmental capacity to undergo metamorphosis when triggered by internal or external factors* (Hadfield et al. 2001).

Dispersion - *Dispersal*: mouvement définitif d'un organisme d'un lieu à un autre. *Permanent movement of an organism from one location to another* (Roff et Fairbairn 2003).

Espèces naissantes - *Incipient species*: deux ou plusieurs populations divergentes qui sont de façon substantielle mais pas totalement isolées lors de la reproduction. *Two or more diverged populations that are substantially, but not completely, reproductively isolated* (Trends in Ecology & Evolution, Speciation Glossary, 2001).

Évolution - *Evolution*: modification au fil des descendances (Darwin 1859); changements opérés entre les générations d'une même lignée. *Changes operated between generations in the same lineage* (Ridley 2004).

Histoire de vie - *Life history*: déroulement du cycle de vie. *Life-cycle and its events* (Stearns 1992).

Métamorphose - *Metamorphosis*: processus du développement précédé par une phase larvaire fonctionnelle, libre et qui produit une phase juvénile fonctionnelle. *Developmental process preceded by a functional, free-living larval stage and results in a functional juvenile stage* (Hadfield et al. 2001).

Plasticité phénotypique individuelle - *Individual phenotypic plasticity*: response génétiquement déterminée à l'environnement expérimenté par l'individu. *Genetically controlled response to the environment* (Murren et al. 2003).

Polymorphisme génétique - *Genetic polymorphism*: histoires de vie génétiquement déterminées formant un réservoir de diversité dans lequel l'environnement sélectionne certaines histoires. *Genetically determined life histories*

forming a reservoir of diversity in which environment can select some histories (d'après Murren et al. 2003).

Résilience - *Resilience*: mesure de la persistance des systèmes ou des populations et de leur capacité à absorber les changements et les perturbations tout en maintenant la même relation entre les populations ou les variables d'état. *Measure of the persistence of systems or populations and their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables* (Holling 1973).

Rythme circadien - *Circadian rythm*: rythme d'une période d'environ 24h (latin - circa : environ; dies: jour).

Sclérochronologie - *Schlerochronology*: science qui étudie les pièces calcifiées des êtres vivants pour reconstituer leur histoire de vie. *Science studying calcified structures of animals and plants to reconstruct their life-history* (Panfili et al. 2002).

Sélection disruptive - *Disruptive selection*: sélection naturelle au sein d'une même population envers différents phénotypes. *Natural selection within a single population towards two different phenotypes.* (Trends in Ecology & Evolution, Speciation Glossary, 2001).

Spéciation écologique - *Ecological speciation*: Evolution de l'isolation reproductive causée par sélection disruptive entre phénotype d'une même population dans des environnements différents. *Evolution of reproductive isolation caused by disruptive selection between phenotypes of a single population in different environments* (Trends in Ecology & Evolution, Speciation Glossary, 2001).

Trait - *Trait*: tout paramètre morphologique, physiologique, ou phenologique mesurable au niveau individuel sans référence à l'environnement. *Any morphological, physiological or phenological feature measurable at the individual level, without reference to the environment* (Violle et al. 2007).

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ANNEXES

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ORIGINAL PAPER

Eel community structure, fluvial recruitment of *Anguilla marmorata* and indication for a weak local production of spawners from rivers of Réunion and Mauritius islands

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Abstract Anguillid eels were sampled from permanent rivers in the Réunion and Mauritius islands, western Indian Ocean, with a standardized electrofishing method. *A. marmorata* was very dominant, corresponding to 91.7 and 90.7% of all the eels collected in Réunion and Mauritius, respectively. Three other species (*A. mossambica*, *A. bicolor bicolor* and *A. nebulosa labiata*) were also present in both islands. *A. marmorata* showed a strong altitudinal gradient of densities from the lower to upper zones, especially in the younger stages (TL <250 mm), while *A. mossambica* was only found in the upper zones and *A. bicolor bicolor* occurred only in the lower zones (*A. nebulosa labiata* was rare). The eel species composition in freshwaters of both islands is very similar because these two adjoining islands are located in the same trail of drifting marine larvae. Mean estimated eel biomasses were noticeably low (11.1 and 22.2 kg ha^{-1} in Réunion and Mauritius islands, respectively), especially when compared to those of other tropical insular systems without any eel fishery (Comoros or Polynesia, more than 100 kg ha^{-1}). Nevertheless, the fluvial recruitment of *A. marmorata* seemed to be regular during the surveyed period, staggering from October to April. The obvious lack of large eels in Mauritius but more significantly in Réunion suggests a high pressure from traditional fishery, and the local reproductive turnover is uncertain. Because sexual maturation seems to occur at a large body size for *A. marmorata*, as for temperate species, the Réunion and Mauritius rivers may only have a weak contribution to the regional production of spawners. However, the

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giant mottled eel population in the western Indian Ocean is believed to be panmictic at the regional scale, and may not rely exclusively on these islands' contribution. A comparison is made with those of freshwater systems in other tropical islands.

Keywords Tropical eels · Indian Ocean · Fluvial recruitment · Reproductive turnover · Conservation

Introduction

Four Anguillid eel species (*Anguilla bicolor bicolor* McClelland 1844, *A. marmorata* Quoy & Gaymard 1824, *A. mossambica* Peters 1852 and *A. nebulosa labiata* Peters 1852) occur in the western Indian Ocean (Ege 1939). The spawning area of these catadromous fishes is believed to be somewhere in the northeastern waters of Madagascar (Jubb 1961; Miller 2003; Robinet et al. 2003a). In the continental and insular freshwaters surrounding this region, the composition of eels communities are more or less contrasted, due to different drifting routes of marine eel larvae before their estuarine recruitment. *Anguilla mossambica* largely dominates in South Africa (Jubb 1960; Bruton et al. 1987), whereas *A. nebulosa labiata* is reported as the dominant eel species in Kenya rivers (Frost 1954), but seems relatively rare in Madagascar (Moreau 1987). Conversely, *A. marmorata* is well represented in this large island. *A. bicolor bicolor* is exclusively distributed in the northern part of the area, and is the only eel species occurring in the Seychelles archipelago (Valade and Feunteun, unpublished data).

At about 600 km east from Madagascar, the Réunion and Mauritius twin islands are orientated south-southeastern from the hypothetical spawning areas, and 200 km apart. It is not known whether the eel species assemblages of Réunion and Mauritius are similar. Kiener and Duchochois (1981), Marquet et al. (1997) and Keith et al. (1999) reported the presence of four eel species in the Réunion freshwaters, without describing species proportion or their local population structure. In Mauritius rivers, the different eel species were reported by Gudger (1929), Blanc and Postel (1958), Starmülhner (1979) and Baissac (1990), but no information about the populations structure has been published yet.

Anguilla marmorata, the giant mottled eel, is the Anguillid eel species with the widest distribution in the world. Its Indo-Pacific distribution ranges from the East African coast (Ege 1939; Jubb 1961), Indonesia and Philippines (Budimawan 1997), Southeastern Asia and North Pacific (Nishi and Imai 1969; Williamson and Boëtius 1993; Tzeng et al. 1995) to South Pacific (Jellyman 1987; Marquet et al. 1997) and French Polynesia (Marquet and Galzin 1991). Moreover, *A. marmorata* is the only eel species for which five distinct populations are known (Ishikawa et al. 2004), one of them surrounding Madagascar. Most studies on *A. marmorata* have focused on its early life history (Tabeta et al. 1976; Aoyama et al. 1999; Arai et al. 1999; Robinet et al. 2003a). In contrast, its inland freshwater life (i.e. fluvial recruitment, feeding ecology, growth dynamics, dwelling or nomadic behavior, insular and continental production of breeders) remains largely unknown. Only Marquet (1987) and Marquet and Galzin (1991) studied *A. marmorata* ecology in South-Pacific islands, whereas Robinet et al. (2003b) described the upstream migration dynamics in the Réunion Island.

In this study, we analyze and compare the eel community structure in Réunion and Mauritius islands. We particularly focus on the dominant species *A. marmorata*, by analyzing the fluvial recruitment rhythm in the Réunion Island, based on the relatively high mean growth rate for yellow eels and on length-frequency diagrams decomposition. This fluvial population structure is then compared with those of freshwater systems in other tropical islands.

Material and methods

Study sites

The Réunion and Mauritius islands (21.0°S–55.5°E and 20.0°S–57.0°E) are recent volcanic formations in the southwest Indian Ocean. These islands were formed 10 Ma (Mauritius) and 2.1 Ma ago (Réunion; Dercourt 1997). Réunion

(2,507 km^2) is the highest island and hosts 13 permanent rivers, with surfaces ranging from 15 km^2 (River Bras-Panon) to 145 km^2 (River du Mat) (Fig. 1). Headwaters all originate in one of the three volcanic cirques, 700–1,000 m above sea level, or in the altitudinal forests that cover mountains slopes. The water flow is usually low between May and October (0.10–0.25 m^3 s^{-1} km^{-2}), but it can suddenly rise up to more than 10–20 m^3 s^{-1} km^{-2} during the cyclonic season from December to April (2,500 m^3 s^{-1} recorded in the River du Mat, Hyacinth cyclone in 1980). Mauritius (1,860 km^2) is an older island, more eroded (highest point 828 m, 3070 m in Réunion), surrounded by large lagoons, which shelters 11 permanent rivers. Between these two islands, the Réunion rivers presents the steeper slopes (for the 13 rivers from the source to the sea, mean slope is 6.5 ± 3.0%, from 2.5% to 12%). Abrupt slopes are mostly confined in the highest altitudes, above waterfalls (500–600 m). The lower courses (< 100 m) usually have a smoother slope (for the last 4 km before the sea, mean slope is 2.4 ± 2.2%, from 0.2 to 7.5%). Sampling stations staggered in altitude up to 600 m for the Réunion rivers, and until 310 m in Mauritius.

Sampling protocol

All the Réunion data were extracted from the Réunion Fish Network survey (‘‘Réseau Piscicole

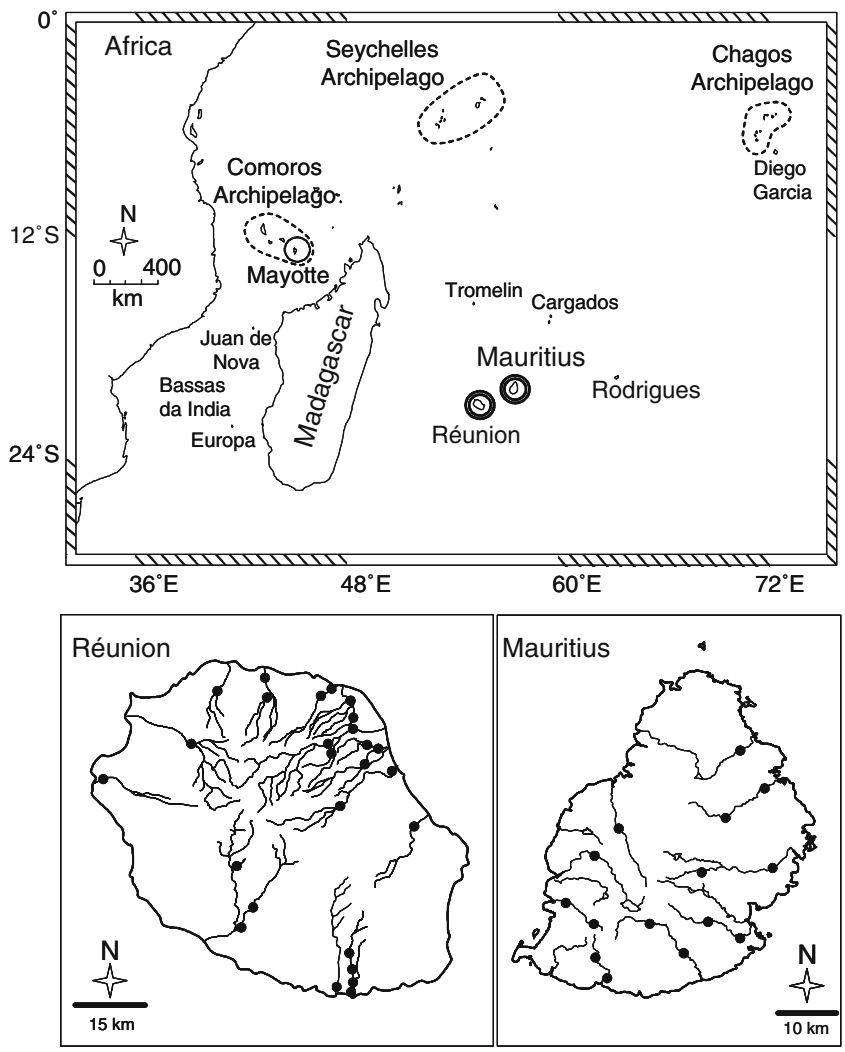

Fig. 1 Location of the Réunion and Mauritius islands in the western Indian Ocean. Sampling stations are designated by black dots

Réunionnais''), lead by the Association Réunionnaise de Développement de l'Aquaculture (ARDA 1999, 2000, 2001, 2002), except in the River du Mat (Robinet et al. 2003b). In different seasons, the 13 permanent rivers (from 100 to 500 m in length) in Réunion were sampled at one to four stations (Fig. 1). Stations were sampled at exactly the same location every year. Eels were collected during low water periods using a portative electroshocker (DEKA 3000 from EFKO manufacturer), delivering electric impulses (30 impulses s^{-1}, 350 V and 4 A). Sampling was completed by one of two methods; with a standardized sampling effort of 30 s for each sampling point (corresponding to a 5 m^2 water surface area, with a minimum 3 m between sampling points), or with a continuous sampling throughout the whole station. Mauritius rivers were sampled with the sampling points protocol during an inventory mission in November 2002.

Data from other fish inventory campaigns were used for comparisons with those of Réunion and Mauritius. They were lead by the ARDA in Comoros (Mayotte Island, Mozambique Channel, 12°S–46°E, November 2003), by the National Museum of Natural History (NMNH, Paris, France) and the Symbiose Association in New Caledonia (South Pacific 21°S–165°E, March–April 1999), and the NMNH in Marquesas (South Pacific 7°S–140°W, Hiva Oa, Tahuata and Nuku Hiva islands, February 2000). Eels were collected using the same type of portative electroshocker and standard sampling protocol, but only data concerning *A. marmorata* are presented here.

All collected eels were anesthetized with clove oil in ethanol (Peake 1998), total length (TL) was measured to the nearest mm, weighted to the nearest g, and examined tail pigmentation and dorsal coloration. Specimens were returned to the same station in which they were caught. We used morphometric keys (Ege 1939) for species determination, crossing the back coloration, or the tail pigmentation for the youngest eels (Robinet et al. 2003ab), and the A–D ratio (ratio between anal and dorsal fins in relation to the body length). With this A–D ratio, distinction can be made between *A. bicolor bicolor* (short-finned, A–D ratio <2%) and the other species (long-finned, A–D ratio >14% for *A. marmorata*, around 14% for *A. mossambica*, <14% for *A. nebulosa labiata*, see Ege 1939 for details). *A. marmorata* shows a mottled brown and black back, and *A. nebulosa labiata* shows a similar pattern in dark green, *A. mossambica* does not have a mottled or marbled back, and *A. bicolor bicolor* a plain dark grey back. It was not possible to determine the species of some long-finned juveniles in the field with classical morphological characteristics, because the adult dorsal coloration only appears around 100–120 mm, and were designated as ''undetermined long-finned specimens''.

The fishing efficiency of the sampling method was tested in July 2001 in the River du Mât (largest river of Réunion Island), with three successive passes at the same station, consisting of 30 sampling points, with eels removal at each pass. The numbers of eels collected in each pass (20, 11 and 3, respectively) were used in a multi-pass estimator program (Carle and Strub 1978). The total number of eels was estimated to be of 36. The fishing efficiency for the 1st pass represented 55.5% of the total eels estimated for all sizes (Carle and Strub 1978), and this efficiency was not affected by the eel size (57% for eels <200 mm and 55% for eels >200 mm). Similar hydrological conditions (low water level with no turbidity) were encountered during this efficiency test and the sampling campaigns. Relative densities (CPUE – for relative densities calculated from a single pass) were expressed in individual ha^{-1} or in individual 100 m^{-2} of water surface. Relative biomasses, (i.e. biomass collected during the single pass), were expressed in kg ha^{-1}. Estimated densities and biomasses were expressed after the efficiency correction.

Coefficients of variation (*CV*) were calculated based on the relative densities of three size classes (<250 mm, 251–400 mm, >401 mm). Sampling of at least two consecutive years, during the same season and at the same station, makes a CV calculation possible (Freeman et al. 1988; Grossman et al. 1990; Taylor and Warren 2001): with d_n the linear relative density at the year n, $CV_{(d1...dn)}$ = [SD ($d1...dn$)/mean ($d1...dn$)] 100.

Condition factor and length-frequency decomposition

Individual condition factors (CF, Ricker 1975) were calculated for *A. marmorata* in Réunion as follows: CF = 100 000 (W/L^b), where L is total length (mm), W is body weight (g) and b is the slope from the (log length–log weight) regression for all *A. marmorata* specimens. We used multiple regression (Sokal and Rohlf 1995) to analyze the effects of the river, the sampling date and the altitude of the station on condition factors.

In the Réunion data set, length-frequency histograms were made for each station and each year, using a class-interval of 15 mm. Polynomial decompositions were adjusted on these time-series of length-frequency using the Bhattacharya's method (Bhattacharya 1967), that fits normal distributions on each modal-class of the length-frequency histograms. Graphic analyses were performed with the FISAT II software (Gayanilo and Pauly 1997). Means and standard deviations of each mod were calculated. Growth rate of *A. marmorata* yellow eels was previously estimated (17.4 ± 3.4 mm month^{-1}; Robinet et al. 2003b). We used this growth estimation to link the modal-class in the length-frequency histograms, like the time-size spectra diagrams of ICES (2005) and Kristensen et al. (2006), and characterize the newly recruited fraction every year.

The modal classes extinction rate was defined as the slope (z) of the regression line between modal classes on each length-frequency diagram ($y = z\ x + b$). To avoid incomplete recruitments inherent to the sampling date, the first modal class retained has been defined as the higher bar of the diagram. Such local extinction rates for *A. marmorata* modal classes were compared between these insular systems.

Results

Eel community composition

Among a total of 1978 eels sampled in Réunion and 128 in Mauritius, the majority were *A. marmorata* (Table 1). Undetermined long-finned specimens were not reported in this table. *A. marmorata* represented 91.7 and 90.7% of all the eels determined in Réunion and Mauritius, respectively. The mean A–D ratio for *A. marmorata* was 16.7 ± 1.0% (range 14.2–20.6), and was positively correlated with the total body length (adj. $r^2 = 0.141$, $P < 0.001$). Other eel species collected were *A. bicolor bicolor* (short-finned), *A. mossambica* (mean A–D ratio 14.0 ± 2.2%, range 8.6–17.7) and *A. nebulosa labiata* (mean A–D ratio 12.2 ± 1.7%, range 8.5–13.6).

Relative densities and biomasses

The mean densities and biomasses of all species, relative and estimated, are reported in Table 2 for both Réunion and Mauritius. *A. bicolor bicolor*, and *A. nebulosa labiata* were found to be confined to the lower sections (altitude < 300 m, Table 3), whereas *A. mossambica* was found in upper

Table 1 Relative proportions of the four Anguillid species in freshwaters of some locations around Madagascar (yellow eels collected upper the freshwater limit)

Location	Source	*A. bicolor bicolor*	*A. marmorata*	*A. mossambica*	*A. nebulosa labiata*
Réunion[1]	This study	2.0%	**91.7%**	5.6%	0.7%
Mauritius[2]	This study	0.8%	**90.7%**	6.2%	2.3%
Seychelles (Mahé)[3]	Valade et al. (unpublished)	**100%**	–	–	–
Comoros (Mayotte)[4]	Valade et al. (unpublished)	3.2%	**96.1%**	0.6%	–
South Africa	(Bruton et al. 1987)	0.6%	9.7%	**86%**	3.7%

Sources:

[1] Réunion Fish Network survey (1999–2002, N determined = 1978)

[2] Inventory mission in Mauritius (November 2002, N determined = 128)

[3,4] Inventory campaigns in November 2003 (see the Acknowledgements section for the details). For the Réunion, Mauritius and Mayotte Islands, undetermined longfinned eels were not included in these proportions

Table 2 Mean relative and estimated densities and biomasses of eels in Réunion and Mauritius rivers

	A. bicolor bicolor	*A. marmorata*	*A. mossambica*	*A. nebulosa labiata*	Undet. longfin. Eels	Total eels
Réunion Island						
Relative density in rivers (ind. ha^{-1}, mean ± sd, max.)						
Single pass (CPUE)	2.8 (±16.5, 183.1)	162.7 (±432.5, 5158.7)	11.4 (±45.1, 404.0)	1.6 (±17.6, 276.5)	67.0 (±261.0, 3759.4)	245.5 (±773.0, 9781.8)
Estimated	5.1 (±29.6, 329.9)	293.2 (±779.4, 9295.0)	20.5 (±81.3, 728.0)	2.8 (±31.7, 498.2)	120.7 (±470.8, 6773.7)	442.2 (±1392.9, 17624.8)
Relative biomass in rivers (kg ha^{-1}, mean ± sd, max.)						
Single pass (CPUE)	<0.1 (−1.8)	5.5 (±16.8, 228.3)	0.4 (±2.4,31.9)	<0.1 (−3.7)	0.1 (±0.4,4.8)	6.1 (±20.1, 270.5)
Estimated	<0.1 (−3.3)	10.0 (±30.3, 411.3)	0.8 (±4.3,57.5)	<0.1 (−6.6)	0.2 (±0.7,8.7)	11.1 (±36.2, 487.3)
Mauritius Island						
Relative density in rivers (ind. ha^{-1}, mean ± sd, max.)						
Single pass (CPUE)	0.2 (±0.9, 3.5)	146.8 (±244.8, 933.3)	9.3 (±19.8, 66.3)	1.0 (±3.3, 13.0)	2.3 (±5.1, 15.9)	159.6 (±243.7, 933.3)
Estimated	0.4 (±1.6, 6.3)	264.4 (±441.0, 1681.7)	16.8 (±35.6, 119.4)	1.9 (±6.0, 23.4)	4.1 (±9.1, 28.7)	287.6 (±439.0, 1681.7)
Relative biomass in rivers (kg ha^{-1}, mean ± sd, max.)						
Single pass (CPUE)	<0.1	10.7 (±13.9, 50.6)	0.8 (±2.5, 9.2)	<0.1	–	11.6 (±13.8,50.6)
Estimated	<0.1	20.5 (±25.3,91.2)	1.6 (±4.5,16.7)	<0.1	–	22.2 (±25.0,91.2)

Relative density is the no. eels collected during the single electrofishing pass, reported to the surface unit (i.e. CPUE), whereas estimated density was corrected by a Carle and Strub (1978) estimator of efficiency. Undet. longfin. eels: undetermined longfinned eels

zones. Since *A. nebulosa labiata* was very rare in Réunion, no altitudinal preference can be given for this species; same observation in Mauritus, but with much less sampling stations. *A. marmorata* dominated in both communities. It showed a strong altitudinal gradient from the lower to the medium and upper zones, especially for the younger stages (<250 mm, Fig. 2). CV values were logically higher for the lower mean densities. CV stayed below 100% for the smaller and medium length (<400 mm, relatively stable densities), but were amplified for larger eels (>401 mm, unstable densities).

In the Réunion Island, the mean condition factor was 0.112 (±0.017, range 0.026–0.225) for *A. marmorata*, 0.105 (±0.015, range 0.077–0.127) for *A. bicolor bicolor*, and 0.043 (±0.007, range 0.022–0.070) for *A. mossambica*. There were not sufficient individuals of *A. nebulosa labiata* to give an estimate. The condition factor of *A. marmorata* in Réunion showed a slight positive correlation with the altitude (r^2 and *P*-value both <0.05), whereas no significant differences were found among rivers nor among sampling dates.

Structure of *A. marmorata* local populations

For Réunion rivers, mean length (±sd) of each modal class was reported on a time-axis, corresponding to the successive sampling dates for the 1999–2002 period. Assuming that growth is uninterrupted in tropical areas, modes were linked between successive modal classes for the River des Roches (Fig. 3). With these linkages, the mean growth rate for yellow eels in the River des Roches was 14.5 ± 3.2 mm month^{-1} (range 10.7–19.7), in accordance with the rate estimated by otolith analysis (Robinet et al. 2003b). Successive fluvial recruitments can then be visualized (three modal classes in July 2000, three in May 2001, two in April 2002 and one in October 2002). Based on this method, yearly fluvial recruitments were pointed out in six other rivers (Fig. 4), showing every year from one to four new modal classes. No new recruits were observed from May to August (River des Roches, Fig. 3), or from May to July (River Bras-Panon, Fig. 4), whereas the first new recruits were observed in October (River des Roches). The fluvial recruitment

Table 3 Distribution of eel species with altitude in the Réunion rivers (mean relative densities in stations ± standard deviation ind. per 100 m^2, Réunion Fish Network survey 1999–2002)

Altitude (m)	*A. marmorata* (n = 1250)	*A. mossambica* (n = 79)	*A. bicolor bicolor* (n = 28)	*A. nebulosa labiata* (n = 5)
< 100	23.0 (±22.9)	1.8 (±3.1)	0.6 (±1.3)	0.1 (±0.6)
>100– < 200	10.3 (±11.6)	0.4 (±1.0)	0.1 (±0.3)	0
>200– < 300	10.9 (±11.5)	0.1 (±0.3)	0.1 (±0.4)	0
>300– < 400	58.9 (±40.5)	0.4 (±0.7)	0	0
>400– < 600	0	0	0	0
>600	28.0 (±19.9)	0.6 (±1.0)	0	0

seemed to stagger every year from at least October to approximately April.

On the length-frequency diagrams for other insular freshwater-systems (Fig. 5), the A. *marmorata* from Réunion and Mauritius showed a much higher cohorts extinction rate (mean 5.34% and 3.13%, respectively) than those of Marquesas (1.56%), Comoros (1.28%) and New Caledonia (1.47%).

Discussion

Composition of the eel community in southwestern Indian Ocean freshwaters

Compositions of the eel community are very similar between these two adjoining islands. *A. marmorata* largely dominates and can reach high altitude areas, whereas *A. mossambica*, *A. bicolor*

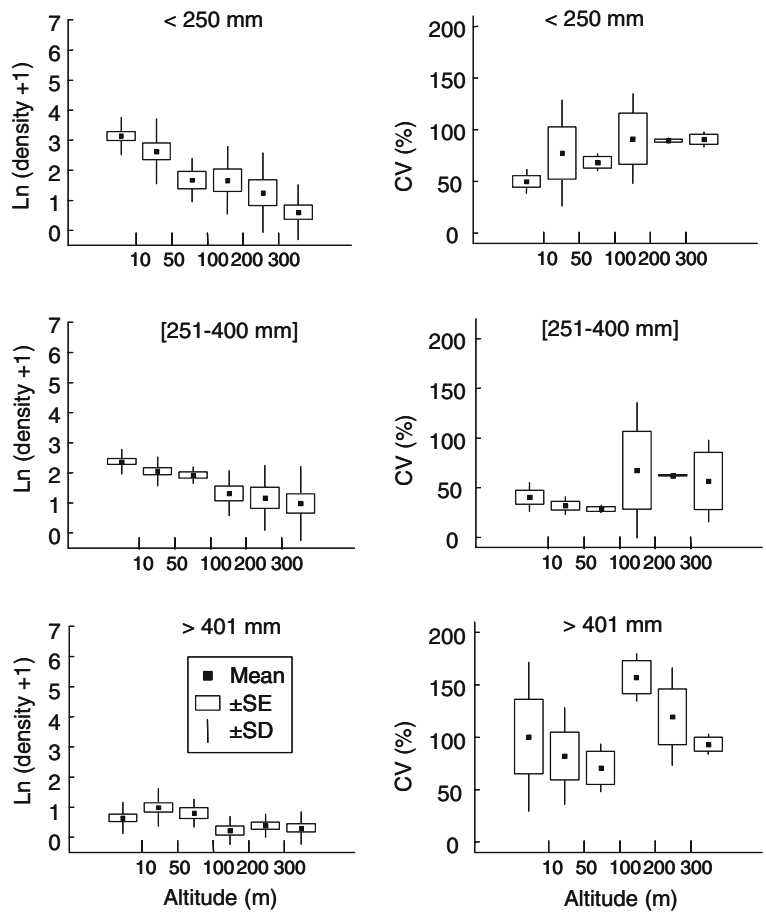

Fig. 2 Mean relative densities (Ln [densities +1], ind. per 100 m^2, left diagrams) and corresponding variation coefficients (right diagrams) of three length classes of *A. marmorata* with altitude in the Réunion rivers, based on 1,250 eels collected during the Réunion Fish Network survey 1999–2002

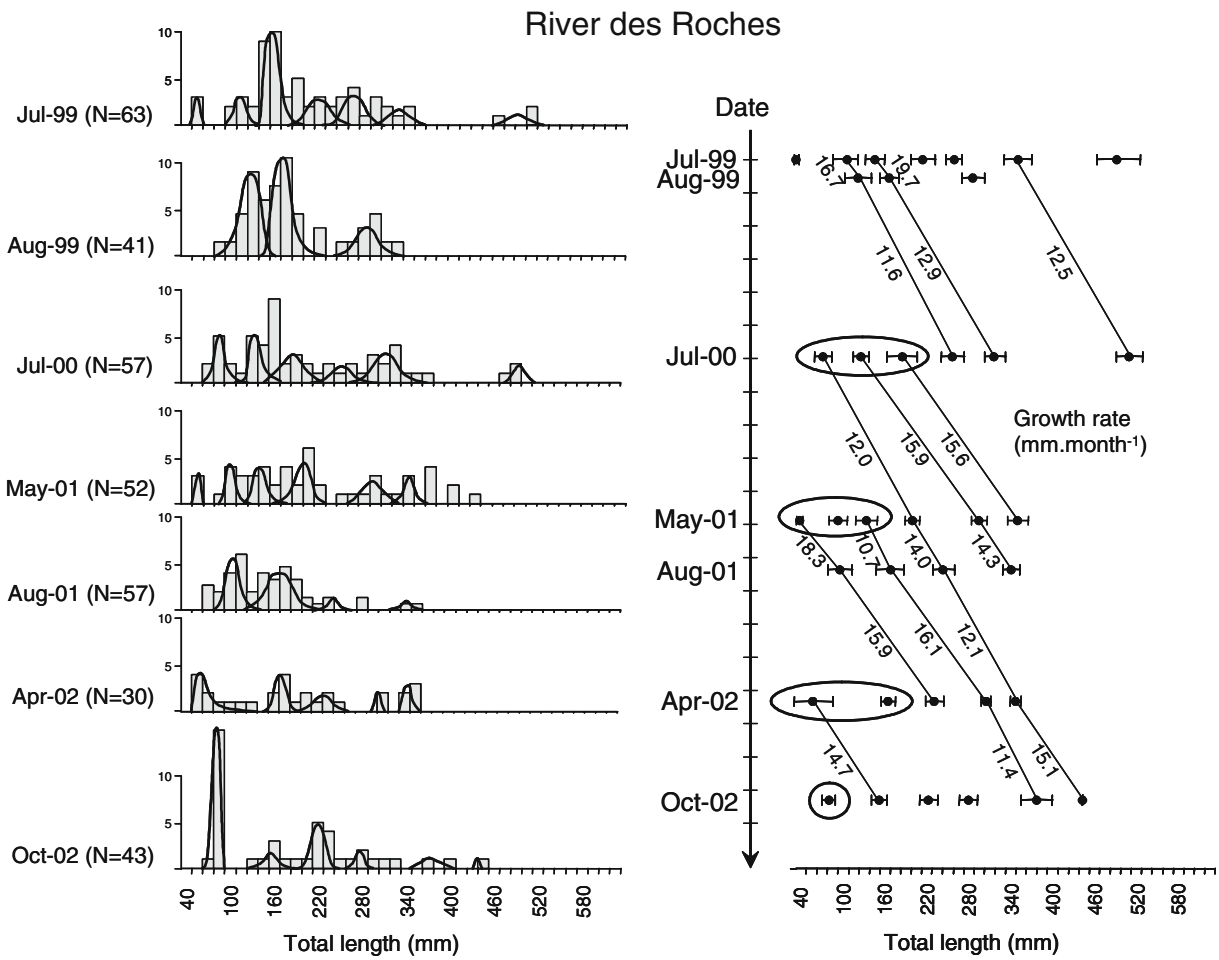

Fig. 3 Length-frenquency decomposition of *A. marmorata* in the River des Roches (Réunion Island) from July 1999 to October 2002, assessed by the Bhattacharya's method (left diagram); links were established between the supposed identical modal-classes (mean ± sd), according to growth rate and time between samplings (right diagram). Growth rates out of the estimated range (Robinet et al. 2003b, i.e. lower than 10 mm month^{-1} or higher than 20 mm month^{-1}) are not figured. New fluvial recruits are encircled

bicolor and *A. nebulosa labiata* are much less abundant. If the actual composition of eel communities in the western Indian Ocean rivers are examined, two contrasted communities occur around Madagascar: one northern, dominated by *A. bicolor bicolor* and *A. nebulosa labiata*; and one southern, dominated by *A. marmorata* and *A. mossambica* (Jespersen 1942; Jubb 1961; Tesch 1977; Bruton et al. 1987; Watanabe 2003). These differences in the riverine species composition reflect those of the estuarine recruitment, a consequence of the marine routes of the leptocephalus larvae.

Given the similar species compositions in the eel communities, the Réunion and Mauritius islands are obviously located in the same trail of drifting larvae. Moreover, they may be located on the southern migration route (south-east of Madagascar), because *A. bicolor bicolor* and *A. nebulosa labiata* are poorly represented there, as in the southeastern African coast (Jubb 1961). However, the dominant species is not *A.*

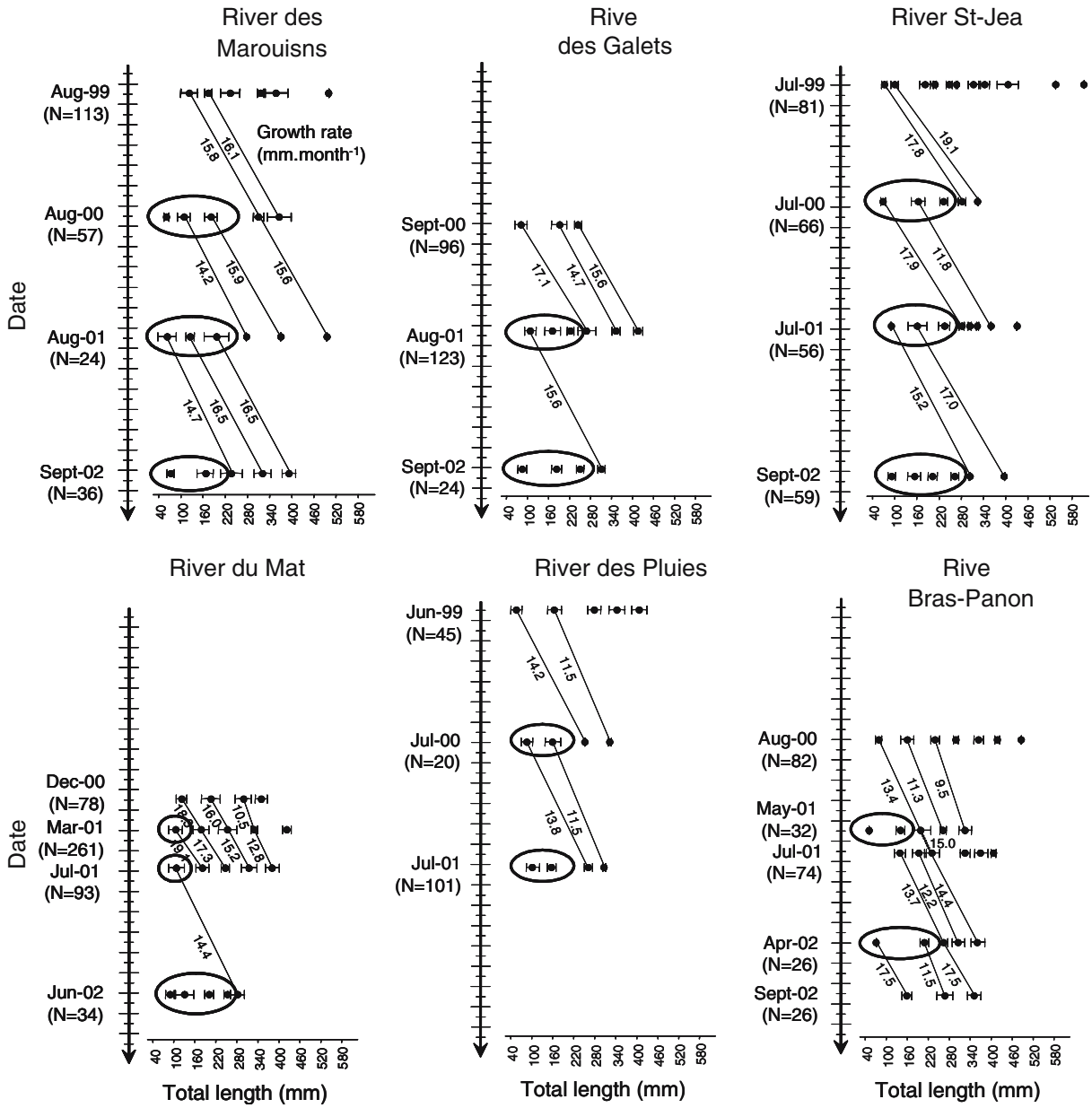

Fig. 4 Supposed identical modal-classes (mean ± sd) of *A. marmorata* linked for six rivers in the Réunion Island, according to growth rate and time between samplings. Out-ranged growth rates are not figured. In every river, 2, 3 or 4 new cohorts can recruit every year (encircled)

mossambica, as in rivers of the southeastern African coast (Bruton et al. 1987). This could be a consequence of the 2-months interval between *A. mossambica* and *A. marmorata* hatching dates and arrival to Réunion Island (Robinet et al. 2003a). Changes in the current configuration during this 2 months interval can induce a shift in the drifting routes, inducing that most of the drifting *A. mossambica* might miss these islands, but not those of *A. marmorata*.

Dynamics of *A. marmorata* local populations

The survey of eel local populations by electrofishing can be considered a useful way to monitor the estuarine recruitment patterns. This

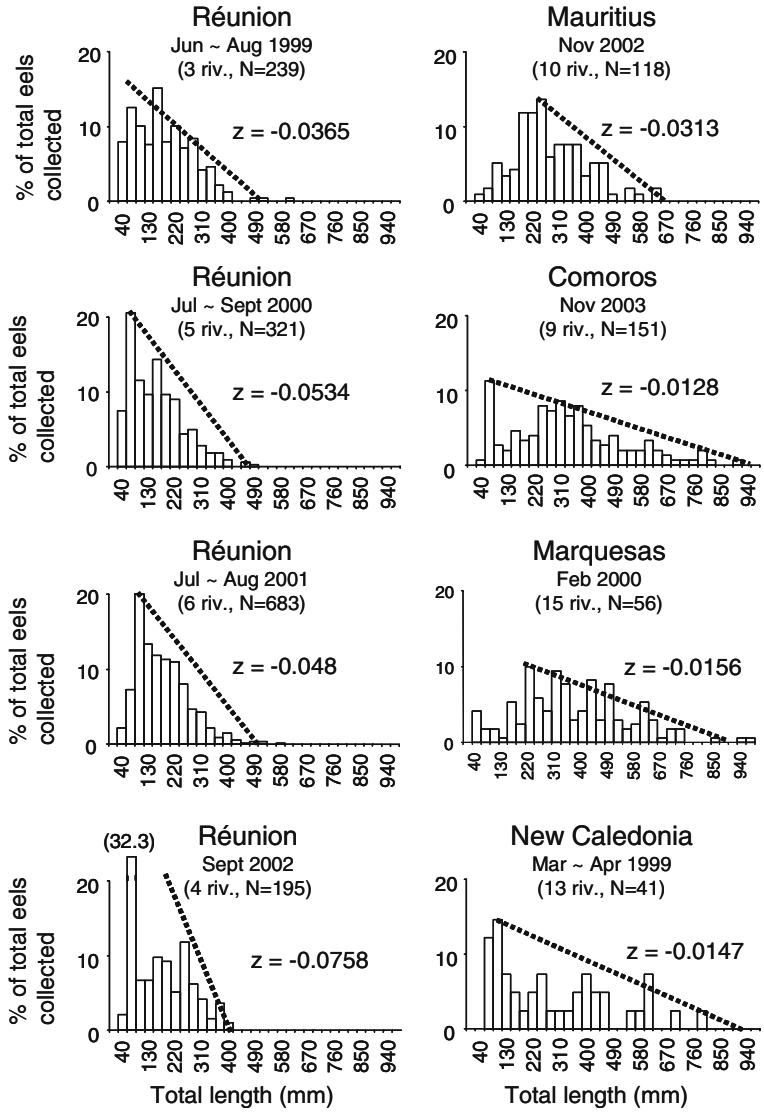

Fig. 5 Length-frequency diagrams of *A. marmorata* for the Réunion, Mauritius, Comoros, Marquesas and New Caledonia rivers, in percent of the total eels collected. For the Réunion Island, rivers were grouped within a limited time-interval of sampling (<3 months). Large *A. marmorata* (TL >450 mm) are lacking in the Réunion rivers, and, in a less proportion, in Mauritius, whereas they are well represented in other islands. Comparing the modal classes extinction rate (z), the Réunion and Mauritius Islands *A. marmorata* show a much steeper one (mean 5.34% and 3.13%, respectively) than those of Marquesas (mean 1.56%), Comoros (1.28%) and New Caledonia (1.47%) islands

was not an attempt to link size-classes to ages (we do not have any size-age key) but to visualize rhythms and periods of the annual fluvial recruitment in each river. With this aim, a low number of eels in each modal class is not a problem, because in these tropical rivers elvers have a high growth rate, making the new recruits, easily visible in diagrams. However, these fluvial recruitments do not necessarily reflect *exactly* the estuarine recruitments, and such links between them must be investigated further. Particularly, the exact succession of estuarine recruitments cannot be surely identified without a complementary otolith microstructure analysis.

Nevertheless, this study clearly shows the amount of *A.marmorata* yearly recruited in rivers, and can lead to formulate reasonable inferences relative to the fluvial recruitment period. In the Réunion rivers, between 1999 and 2002, the fluvial recruitment of *A. marmorata* staggered from October to April, during the whole cyclonic season. There was no perceptible fluvial recruitment from April to October. These patterns coincide almost exactly with the estuarine recruitment patterns observed in the River des

Roches (Réunion), from November 2000 to April 2001 (Robinet et al. 2003b). They are also very similar with those observed for *A. marmorata*, *A. megastoma* and *A. obscura* in Tahiti (estuarine and fluvial recruitment staggered from October to April; Le Belle et al. 1987; Marquet 1987, 1992), and *A. mossambica* in the Eastern Cape, South Africa (estuarine recruitment from September to April; Bruton et al. 1987). Conversely, in the estuaries of Sumatra (Indonesia), the recruitment has been showed to occur all the year long, with considerable interannual variation (Sugeha et al. 2001). Tahiti, in the Société archipelago (18°S), the Réunion and Mauritius islands (around 20°S) and the Eastern Cape (around 35°S) are under contrasted hydroclimatic regime, composed of a dry and wet (cyclonic) season, whereas Sumatra (0°) is located in an equatorial zone, without such contrasted seasons. These differences might influence the timing of spawning migration for maturing ''silver'' eels, inducing the observed patterns in the subsequent estuarine recruitment.

Eel mean relative densities and biomasses were weaker in Réunion (relative biomasses 6.1 kg ha^{-1}, range 0–270.5) than in Mauritius rivers (11.6 kg ha^{-1}, range 0–50.6), with a high variability between stations. To compare with other tropical insular systems, we calculated the estimated densities and biomasses in relation to the fishing efficiency (mean 11.1 kg ha^{-1}, range 0–487.3 for Réunion; mean 22.2 kg ha^{-1}, range 0–91.2 for Mauritius). These estimated biomass values are comparable to those estimated by Balon (1975) in the Lake Kariba (7.5 kg ha^{-1}, eels maybe inhabiting only the lake edges), but both are low compared with those in the Comoros rivers (Mayotte, mean 233 kg ha^{-1}, range 16–1032, November 2003, Valade and Feunteun unpublished data), French Polynesian rivers (mean 538.5 kg ha^{-1} in the Society Islands, from 207 to 485 in the Austral Islands, from 267 to 742 in the Gambier Islands, from 94 to 291 in the Marquesas Islands; Marquet and Galzin 1991). This difference may be induced by the lack of large eels (TL >400 mm) in Réunion and Mauritius rivers, which might have been caused by subsistence fisheries (field observations, no data available). The disappearance of *A. marmorata* modal classes seems to be very quick, maybe less than 3 years, as shown by the steep extinction rates, particularly when compared to other tropical insular systems where there is no traditional eel fishery (Comoros, New Caledonia and Marquesas Islands; Fig. 5).

Local lack of future spawners and the regional panmixia hypothesis

Sexual maturation in *A. marmorata*, is thought to be slow (Sugeha 2003), the single maturing male captured in Réunion Island was 10 years old and 708 mm long (Robinet and Feunteun 2002; Robinet et al. 2003c). Therefore, due to the lack of such large eels in Réunion and Mauritius rivers, the local reproductive turnover is uncertain. These rivers may only have a weak contribution to the regional production of breeders of *A. marmorata*, except if there are some non-freshwater local populations in brackish systems (coastal lakes) or in coastal areas, as observed for *A. japonica* (Tsukamoto et al. 1998; Kotake et al. 2004, 2005). Nevertheless, this deficit in local production of spawners may not interfere with local recruitment patterns that appeared to occur regularly throughout the cyclonic period. This observation reinforces the panmixia hypothesis at the regional scale, at least for *A. marmorata*, and pleads for a regionally mixed origin of the local recruitment.

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RESEARCH ARTICLE

New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands

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Abstract A total of 4,172 freshwater eels have been collected by electrofishing in upper estuaries from Madagascar (East coast), Mascarene (Réunion and Mauritius Is.), Comoros (Mayotte Is.) and Seychelles (Mahé and Praslin Is.) Archipelagos, between October 2003 and February 2006. Eel species composition in the sampling stations was contrasted between eastern Madagascar (*Anguilla mossambica* 96.0%, *A. marmorata* 3.9% and *A. bicolor bicolor* 0.2%), the Comoros (*A. marmorata* 56.1% and *A. bicolor bicolor* 43.9%), the Mascarene (*A. marmorata* 91.4%, *A. bicolor bicolor* 5.4% and *A. mossambica* 3.2%) and the Seychelles Archipelagos (*A. bicolor bicolor* 100.0%). This gradient in species composition, even concerning the short time-range of our sampling, argued for separate migration routes between species. A total of 168 eels were aged by reading their otolith microstructure, and otolith growth rates were calculated from pre-leptocephalus stage (post-hatching) to metamorphosis, until freshwater check. For all species, mean otolith growth rate (OGR) was related to specific migration routes: *A. bicolor bicolor* is distributed in the lowest latitudes and showed the highest OGR during leptocephalus stage, whereas *A. mossambica*, endemic of the Malagasy area, has the most southern distribution and showed the lowest OGR. OGR during leptocephalus stage was negatively correlated to the leptocephalus stage duration, showing a decrease of global metabolism with time, classical in leptocephali. This relationship was found significant for *A. marmorata* and *A. mossambica*, probably because all these larvae crossed successively the same environments, but not for *A. bicolor bicolor*, probably because their larvae crossed different pelagic environments, opening the hypothesis of larvae from different origins.

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Introduction

Freshwater eels are represented by a single genus, *Anguilla* Schrank 1798, and 15 species distributed in the Atlantic, Indian and Pacific oceans (Castle 1984, 1986, Watanabe 2003; Lecomte-Finiger 2003). *Anguilla* sp. spawn in the ocean and grow in coastal, estuarine or continental areas (Tsukamoto et al. 2002). To link these two zones that compose lifecycle, eels disperse first from their oceanic hatching area to coastal areas as pelagic, flattened and transparent leptocephalus larvae (Mochioka 2003). Leptocephali, when they approach the continental shelf, metamorphose into glass eels that will settle in the continental system to grow for years as yellow eels. The marine dispersal of leptocephali drives the continental distribution of freshwater eel species, but also their evolution and the phylogeography of the genus (Tsukamoto and Aoyama 1998).

In the south-western Indian Ocean (SWIO), four eel species occur: *Anguilla mossambica* and *A. nebulosa labiata* are endemic of the Madagascar area, *A. bicolor bicolor* is present along the coasts from Western to Eastern Indian Ocean, and the marbled eel *A. marmorata* spreads widely from the East African coast, through the Indo-Pacific area, far to the Mid-Pacific Islands (Ege 1939; Jubb 1961; Nishi and Imai 1969; Marquet and Lamarque 1986; Jellyman 1987; Marquet and Galzin 1991; Williamson and Boëtius 1993; Budimawan 1997; Marquet et al. 1997; Robinet et al. 2007). Eels in the SWIO are facing a growing interest from the fisheries international markets in Madagascar and South Africa. Knowing their patterns of larval dispersal would be of prime importance for managing this resource. However, freshwater eels spawning location and migration routes in the Indian Ocean are still unknown, as whether there is a single or several spawning places per species. In parallel with population genetic studies, description of species local assemblages and analysis of larval life-histories would provide useful information on species dispersal patterns on one hand, and on the ontogenic metabolism of these tropical species on the other.

Among the few studies available on larval life history of tropical eels, most of them concern the Indo-Pacific (Indonesia, Philippines and Sulawesi; Arai et al. 1999a, 2001a) and western Pacific regions (Taiwan and Japan; Arai et al. 2001b, 2002a, 2002b; Miller et al. 2002). In the Indian Ocean, early life-histories of freshwater eels were studied on the eastern part (Java Is., Arai et al. 1999b; Aoyama et al. 2007; Budimawan and Lecomte-Finiger 2008) and on the western part (Réunion Is., Robinet et al. 2003a), but both were limited in time and space. Since Jespersen (1942) and Jubb (1961) suggested a single large spawning area in SWIO, common to all the freshwater eel species somewhere in the NE waters of Madagascar, there has been no real progress concerning the western spawning area(s) location. Based on local species composition and larval life-histories, the present study proposes new information for migration routes of freshwater eels that recruit in estuaries of eastern Madagascar and surrounding islands.

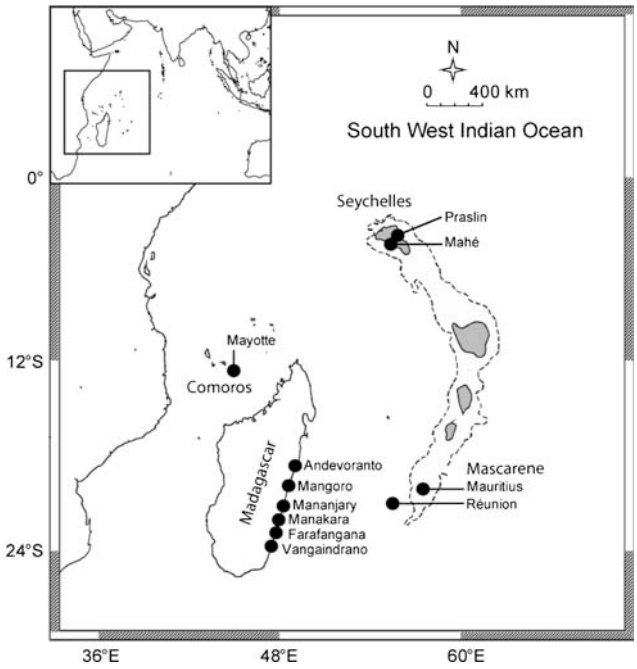

Fig. 1 Location of sampling sites (*black circles*) in SWIO. *Hashed line* represents the 1,200 m depth isobaths, sand beds of the Mascarene ridge are in *plain grey* (isobaths 200 m, after Padfield and Coward 1998)

Materials and methods

Sites and sampling protocol

Eels were sampled in estuaries of Réunion Is. (21°S 56°E), Mauritius Is. (20°S 57°E), Mayotte Is. (Comoros, 12°S 45°E), Mahé and Praslin Is. (Seychelles, 4°S 55°E), Mananjary and Vangaindrano (Madagascar, 22°S 48°E and 24°S 48°E, respectively, Fig. 1). For all the sites except those of Madagascar, sampling was conducted with a portable electroshocker delivering electric impulses (DEKA 3000, EFKO manufacturer, DC 30 i.s-1, 350 V, 4 A). Glass eels were sampled at the tidal limit of the permanent rivers in Mauritius (5–7 April 2005), Réunion (11–12 April 2005), and Mayotte (15–19 April 2005). In Madagascar, glass eels were collected in traditional fyke-nets with the collaboration of local fishermen, from September 2005 to February 2006. Because no glass eels were present during the sampling campaign in Mahé and Praslin Is. (Seychelles, October 2003), only riverine yellow eels were sampled.

Species determination

After fixation in 90% ethanol, eels were measured and identified using Ege's determination key (Ege 1939), based on the caudal pigmentation (for glass eels), the skin colour (for yellow eels), and the distance between the origins of the dorsal and anal fins as percent of the fish total length (Robinet et al. 2003a). Undetermined specimens were identified using semi-multiplex PCR (Gagnaire et al. 2007).

Otoliths preparation and reading

To sub-sample according to species and sites, in a maximum of 15–30 specimens by species and by site, 168 eels were selected for aging, regarding to their otolith microstructure (160 glass eels or elvers of less than 120 mm total length (TL): Réunion, Mauritius, Mayotte and Madagascar; and 8 yellow eels: Seychelles). In Réunion Is., elvers reach a TL = 120 mm 2–4 months after their freshwater entrance (Robinet et al. 2003b), so eels of TL < 120 mm entered estuaries at the same season than sampling. For microstructure analysis, otoliths were extracted and embedded in epoxy resin (Epofix Struers), ground with 1,000 and 5 µm grit paper, or using a Struers Discoplan with a grit stone, until the nucleus was visible, and polished with 1 µm grit paper (Rotopol 35, Struers) and colloidal silica suspension (OP-S, Struers). Then the otoliths were etched with 5% EDTA solution, and coated with gold (10 nm) before examination with a scanning electron microscope (SEM, Hitachi S-520) at various magnifications.

Using SEM microphotographs of otolith sections, different patterns were identified in accordance with conventional characteristics established for other eel species (primordium and core, first feeding-check, leptocephalus zone, metamorphosis zone, and transition mark to freshwater: Castonguay 1987; Tabeta et al. 1987; Tsukamoto 1989; Umezawa et al. 1989; Tsukamoto and Umezawa 1990; Lecomte-Finiger 1992; Tzeng and Tsai 1992). Wider growth increments that have been interpreted by previous authors to occur in association with metamorphosis were used to separate the leptocephalus zone from the metamorphosis zone. Since Umezawa et al. (1989), Arai et al. (2000a) and Sugeha et al. (2001) established that otolith increment-deposition occurs daily in *Anguilla japonica*, *A. celebesensis* and *A. marmorata*, the number of these increments for the oceanic larval stages were counted from the hatching check (HC) to the freshwater recruitment-check (FWC). The beginning of metamorphosis was identified by the sudden increase of the increments width (Arai et al. 2001a). The number of increments from the HC to the beginning of metamorphosis represented the leptocephalus stage duration (LD), and those from the beginning of metamorphosis to the FWC represented the marine life duration after metamorphosis (MD). The number of increments counted between HC and FWC was interpreted as the age at recruitment (AR, Lecomte-Finiger 1992). General patterns of otolith microstructure are presented in Fig. 2. Hatching dates were back-calculated based on AR and sampling dates. LD and MD were counted for each otolith, AR and hatching date calculated, and means (±SD) were calculated for each species. After testing that the basic assumptions of normality of each sample were verified (Kolmogorov-Smirnov and Liliefors tests), a pairwise comparison (Student's *t* test) was used to compare LD of each species and each site.

Otolith growth

The mean increment width was calculated by measuring the width of every 10 increments, from HC to FWC. This measure was considered as the instantaneous growth rate of

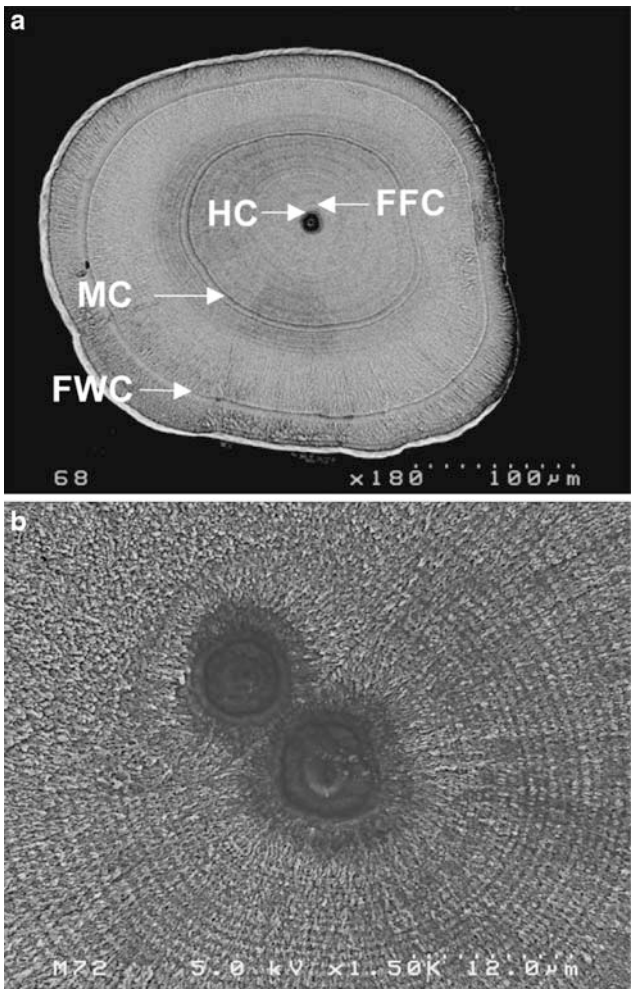

Fig. 2 **a** Otolith section from a glass-eel of *A. bicolor bicolor* (Mayotte), viewed with Scanning Electron Microscope. *FFC* First feed check; *FWC* freshwater check; *HC* hatching check; *MC* metamorphosis check. **b** Detail of an otolith section from a glass-eel of *A. bicolor bicolor* (Mayotte), showing an atypical double-core

the otolith (OGR), pooled by groups of 10 days. A linear regression was used to test the correlation between LD (days) and the mean OGR (μm days^{-1}) during the leptocephalus stage of each species.

Results

Specimens collected

A total of 4,172 eels were collected in the sites sampled. The species composition was very heterogeneous between sites (Table 1). *A. bicolor bicolor* was the only species in the Seychelles, and was fairly present in Mayotte (43.9% of the eels sampled). Elsewhere, 1–3 species occurred, with *A. marmorata* as dominant species in Mauritius (93.3%), Réunion (89.5%) and Mayotte (56.1%), and *A. mossambica* in Madagascar (96.0 %). The eels collected sized from 43 up to 1140 mm, but 60% were glass eels (total length < 60 mm, newly recruited), and 10% elvers (total length up to 150 mm, recruited at the same season than sampling).

Early-life histories

The duration of larval stages, otolith growth rates, ages at recruitment and hatching dates are listed in Table 2 and compared in Table 3. For each species and locality, LD was normally distributed (Kolmogorov-Smirnov and Liliefors tests, $p > 0.05$ for both). Among the three species, *A. mossambica* had the shortest LD (all sites 95.1 ± 16.7 days), especially those recruited in Madagascar (94.5± 16.6 days), which were significantly shorter than those of *A. marmorata* in the same island (115.6± 13.9 days). *A. marmorata* was the species with the longest leptocephalus mean duration (all sites 123.0 ± 20.3 days), and showed significant differences with *A. bicolor bicolor* in sites where both species coexisted (Mauritius and Mayotte). Between site comparisons showed different patterns according to the species. In *A. bicolor bicolor*, mean leptocephalus stage was shorter in Mayotte (100.9 ± 8.5 days, 87–117 for all specimens) than any sampling sites, but not significantly (paired t test $p > 0.05$, excluding Réunion—151 days, the single LD could not be tested). In *A. marmorata*, leptocephalus stage was shorter in Réunion (111.1 ± 15.9 days and Farafangana (108.8 ± 8.4 days) than in Mayotte (119.9± 13.2 days), Mananjary (122.5 ± 15.2 days) and Mauritius (139.2± 24.0 days). *A. marmorata* from Mauritius showed the highest mean LD with a twice higher standard deviation than the other localities. *A. mossambica* had a similar duration of leptocephalus stage whether they recruited in the Malagasy sites (Mananjary and Vangaindrano, 92.5± 18.8 and 96.6 ± 14.5 days, respectively, paired t test $p = 0.506$), or in Réunion (75 days, the single LD could not be tested).

Otolith growth

Otolith growth patterns are represented for all the specimens analysed in Fig. 3. All showed general patterns

Table 1 Species composition of eel [post-larvae (glass-eels) and juveniles eels (yellow eels)] samples collected in prospected estuaries

Site	River	Date	*N*	*A. mossambica* (%)	*A. marmorata* (%)	*A. bicolor bicolor* (%)
Seychelles	All rivers	October 2003	8	–	–	100.0
Mauritius	All rivers	April 2005	80	1.1	93.3	5.6
Réunion	All rivers	April 2005	19	5.3	89.5	5.3
Mayotte	All rivers	April 2005	98	–	56.1	43.9
Madagascar	Andevoranto	September 2005	72	98.6	–	1.4
		November 2005	27	100.0	–	–
	Mananjary	November 2005	693	99.4	0.3	0.3
		November 2005	621	99.5	–	0.5
	Manakara	December 2005	50	100.0	–	–
	Mangoro	December 2005	50	100.0	–	–
	Andevoranto	December 2005	50	100.0	–	–
	Vangaindrano	December 2005	56	100.0	–	–
	Mananjary	December 2005	989	99.2	0.7	0.1
	Farafangana	January 2006	211	77.3	22.7	–
	Manakara	January 2006	175	99.4	0.6	–
	Mananjary	January 2006	227	98.7	1.3	–
		February 2006	337	98.8	0.9	0.3
		February 2006	409	72.4	27.6	–

N Number of eels collected

Table 2 Early-life history of *A. bicolor bicolor*, *A. marmorata* and *A. mossambica* based on the otolith microstructure of eels collected in estuaries of different locations of the SWIO

	N	TL (mm)	LD (days)	OGR (μm days^{-1})	MD (days)	AR (days)	HP
A. bicolor bicolor							
All sites	33	158.4 ± 174.7 50–644	158.4 ± 174.7 50–644	0.67 ± 0.08 0.50–0.83	32.8 ± 8.1 15–49	138.9 ± 14.1 108–179	March 1–December12 2004*
Mauritius	9	52.6 ± 2.0 50–56	110.6 ± 16.7 87–139	0.59 ± 0.06 0.50–0.66	32.0 ± 9.9 15–44	142.6 ± 19.2 108–179	October 7–December12 2004
Mayotte (1)	12	54.8 ± 3.0 51–62	101.8 ± 9.2 87–117	0.69 ± 0.07 0.59–0.81	36.3 ± 6.8 24–49	138.3 ± 11.3 120–157	October 8–December12 2004
Mayotte (2)	3	169.7 ± 32.5 163–205	97.0 ± 4.4 92–100	0.76 ± 0.07 0.71–0.83	33.3 ± 5.0 28–38	130.3 ± 3.5 127–134	March 1–August14 2004
Réunion	1	53	151	0.60	32	183	September 10 2004
Seychelles	8	452.4 ± 98.9 364–644	110.9 ± 13.8 87–128	0.68 ± 0.06 0.61–0.79	28.0 ± 7.3 20–38	138.9 ± 14.4 117–158	Nc**
A. marmorata							
All sites	104	55.6 ± 14.6 46–178	123.0 ± 20.3 91–180	0.61 ± 0.08 0.47–0.76	26.7 ± 4.2 18–39	149.6 ± 22.2 114–211	August 25–November 8 2005
Mauritius	30	52.1 ± 2.6 46–58	139.2 ± 24.0 91–180	0.61 ± 0.07 0.47–0.76	28.1 ± 3.5 21–35	167.3 ± 25.6 117–211	August 28–December 5 2004
Mayotte	29	59.8 ± 8.9 47–79	119.9 ± 13.2 104–151	0.63 ± 0.08 0.49–0.82	23.7 ± 3.2 18–29	143.7 ± 15.0 126–180	September 21–December 21 2004
Réunion	15	67.5 ± 33.0 50–178	111.1 ± 15.9 94–142	0.56 ± 0.07 0.48–0.71	25.5 ± 3.2 21–32	136.6 ± 17.7 121–173	August 25–December 4 2004
Madagascar (Farafangana)	15	49.4 ± 1.3 48–52	108.8 ± 8.4 94–120	0.62 ± 0.04 0.56–0.59	28.5 ± 3.7 20–34	129.6 ± 10.8 113–145	August 15–September 16 2005
Madagascar (Mananjary)	15	48.9 ± 1.0 47–50	122.5 ± 15.2 92–145	0.60 ± 0.05 0.52–0.69	28.8 ± 5.4 22–39	143.8 ± 17.1 108–167	September 14–November 8 2005
A. mossambica							
All sites	31	52.5 ± 4.8 48–75	95.1 ± 16.7 73–131	0.47 ± 0.09 0.34–0.76	22.6 ± 3.2 18–29	117.7 ± 16.3 99–152	June 28–August 29 2005
Madagascar (Mananjary)	15	50.0 ± 1.7 48–53	92.5 ± 18.8 73–131	0.47 ± 0.08 0.38–0.65	22.5 ± 3.4 18–29	115.0 ± 17.5 99–152	June 28–August 29 2005
Madagascar (Vangaindrano)	15	53.5 ± 1.6 51–56	96.6 ± 14.5 78–127	0.48 ± 0.10 0.34–0.76	22.4 ± 2.9 18–29	119.0 ± 14.8 100–149	June 29–August 20 2005
Réunion	1	75	113	0.51	27	140	October 2 2004

N Number of eels analysed; *TL* total length; *LD* leptocephalus duration; *OGR* otolith growth rate during the leptocephalus stage; *MD* marine life duration after metamorphosis; *AR* age at recruitment in estuary; *HP* hatching period

* Without specimens from Seychelles, ** Nc not calculated (hatching dates were not calculated for eels from the Seychelles because they were 4–8 years old at sampling)

Table 3 *T* test pairwise comparisons of LD (mean ± SD in brackets) between sites

	A. bicolor bicolor				*A. marmorata*					*A. mossambica*		
	Mau (110.6 ± 16.7)	May (100.9 ± 8.5)	Réu (151)	Sey (110.9 ± 13.8)	Mau (139.2 ± 24.0)	May (119.9 ± 13.2)	Réu (111.1 ± 15.9)	Fara (108.8 ± 8.4)	Man (122.5 ± 15.2)	Man (92.5 ± 18.8)	Van (96.6 ± 14.5)	Réu (113)
A. bicolor bicolor												
Mau (110.6 ± 16.7)		Ns	–	Ns	***	**	Ns	Ns	*	Ns	Ns	–
May (100.9 ± 8.5)	Ns		–	Ns	***	***	**	**	***	Ns	Ns	–
Réu (151)	–	–		–	–	–	–	–	–	–	–	–
Sey (110.9 ± 13.8)	Ns	Ns	–		***	*	Ns	Ns	*	Ns	Ns	–
A. marmorata												
Mau (139.2 ± 24.0)	***	***	–	***		***	***	***	*	***	***	–
May (119.9 ± 13.2)	**	***	–	*	***		Ns	**	Ns	***	***	–
Réu (111.1 ± 15.9)	Ns	**	–	Ns	***	Ns		Ns	Ns	**	*	–
Fara (108.8 ± 8.4)	Ns	**	–	Ns	***	**	Ns		**	**	**	–
Man (122.5 ± 15.2)	*	***	–	*	*	Ns	Ns	**		***	***	–
A. mossambica												
Man (92.5 ± 18.8)	Ns	Ns	–	Ns	***	***	**	**	***		Ns	-
Van (96.6 ± 14.5)	Ns	Ns	–	Ns	***	***	*	**	***	Ns		–
Réu (113)	–	–	–	–	–	–	–	–	–	–	–	

Far Farafangana; *Man* Mananjary; *Mau* Mauritius; *May* Mayotte; *Réu* Réunion; *Sey* Seychelles; *Van* Vangaindrano

Ns Not significant (*t* test $p > 0.05$). LD of *A. bicolor bicolor* and *A. mossambica* from Réunion Is. could not be tested because only one specimen in each. Significant differences: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

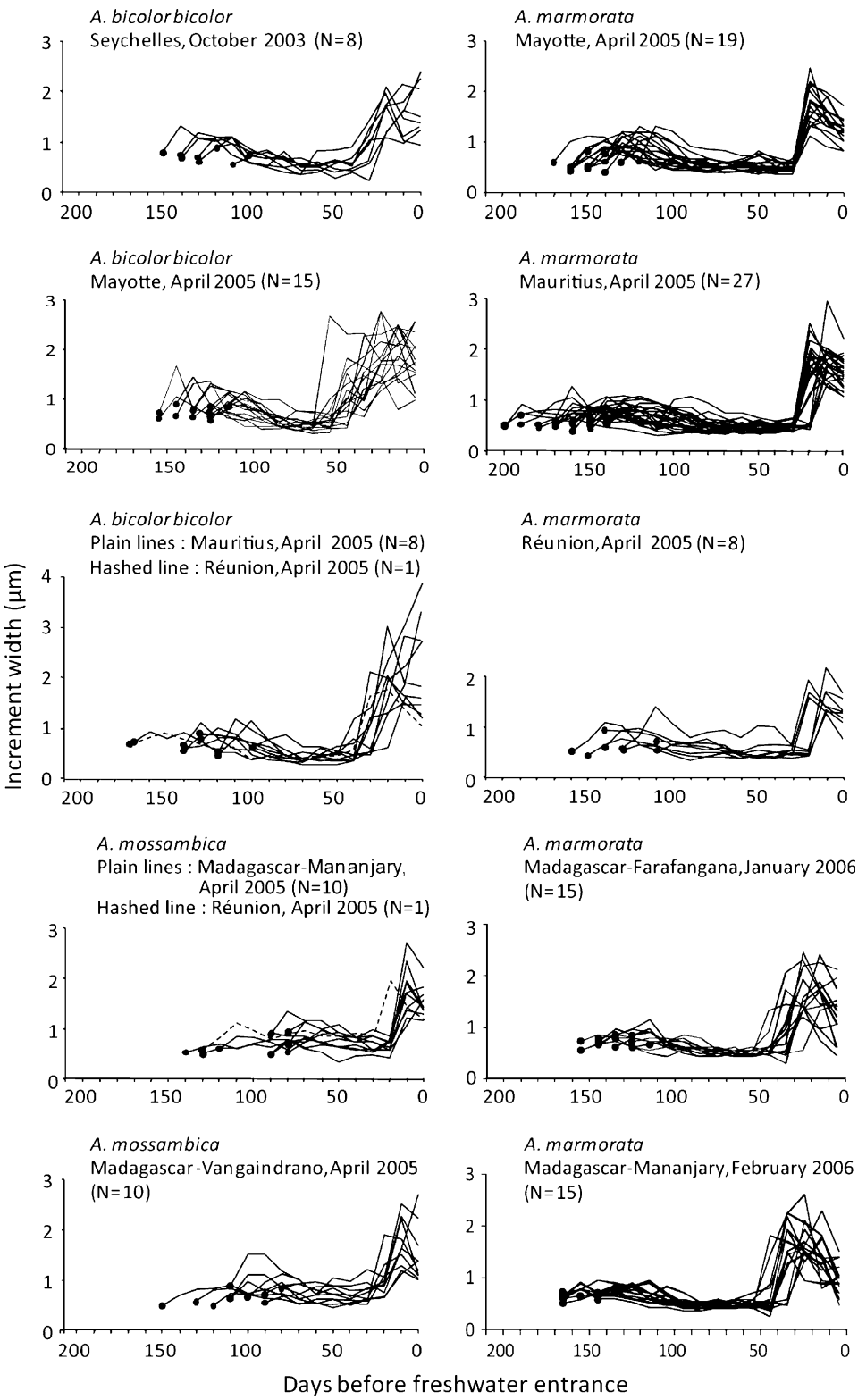

Fig. 3 Otolith growth history, from HC (*black dot* on the left end of the curves) to FWC (right end of the curves), for the 168 specimens analysed

described in Arai et al. (2001a) and Kuroki et al. (2007): a slight increase during the first 15 days, then a continuous decrease until the end of the leptocephalus stage, followed by a drastic increase corresponding to the metamorphosis of the leptocephalus into glass eel. Glass eels of *A. mossambica* seemed to enter in estuaries less than 10 days after metamorphosis, whereas *A. bicolor bicolor* and A. *marmorata* glass eels recruited in estuaries 10–30 days after metamorphosis was completed. LD was negatively correlated to OGR in *A. marmorata* ($r^2 = 0.113$,

$p = 0.003$) and *A. mossambica* ($r^2 = 0.208$, $p = 0.014$), but not in *A. bicolor bicolor* ($r^2 = 0.025$, $p = 0.376$, Fig. 4).

Discussion

Otolith growth

Otolith microstructures showed growth patterns usually observed in anguillid eels (Arai et al. 2001b; Kuroki et al. 2007): just after FFC, the increment width increased until a first peak at *c.* 10–15 days after HC (up to *c.* 1.0–1.5 µm days^{-1}), after what the increment width decreased to a minimum value (*c.* 0.4–0.5 µm days^{-1}) until metamorphosis. The metamorphosis began with a drastic growth increase, usually up to 2 µm days^{-1} and with a maximum of 3.88 µm days^{-1} for a specimen of *A. bicolor bicolor* in Mauritius.

OGRs during leptocephalus stage of *A. bicolor bicolor* (mean 0.67 ± 0.08) were comparable to those described for the same sub-species in North eastern Indian Ocean during the year 2003 (mean 0.78 ± 0.12 from core to the first peak, 1.13 ± 0.16 at the peak, 0.52 ± 0.05 after the peak and before metamorphosis, Kuroki et al. 2007). Mean OGRs of *A. bicolor bicolor* in the present study (Seychelles 2003, other sites 2005–2006) were lower than that observed in 2001 in Réunion Is. (mean 0.90 ± 0.20 µm days^{-1}, Robinet et al. 2003a). This could reflect changes in pelagic environments, that is known to have an influence on natural larval growth (Sponaugle and Pinkard 2004). OGR of *A. bicolor bicolor* in the present study was a bit lower than those of the other sub-species in western Pacific (*A. bicolor pacifica*, mean 0.79 ± 0.11, Arai et al. 2001b). *A. marmorata* OGRs (mean 0.61 ± 0.08) were similar to those of *A. bicolor bicolor*, but lower than those of the same species in western Pacific (mean 0.96 ± 0.07, Arai et al. 2001b). *A. mossambica* showed relatively low OGR (mean 0.47 ± 0.09) compared to other species. For all the SWIO species, it is likely that the mean OGR is related to specific migration routes: *A. bicolor bicolor* is distributed in the

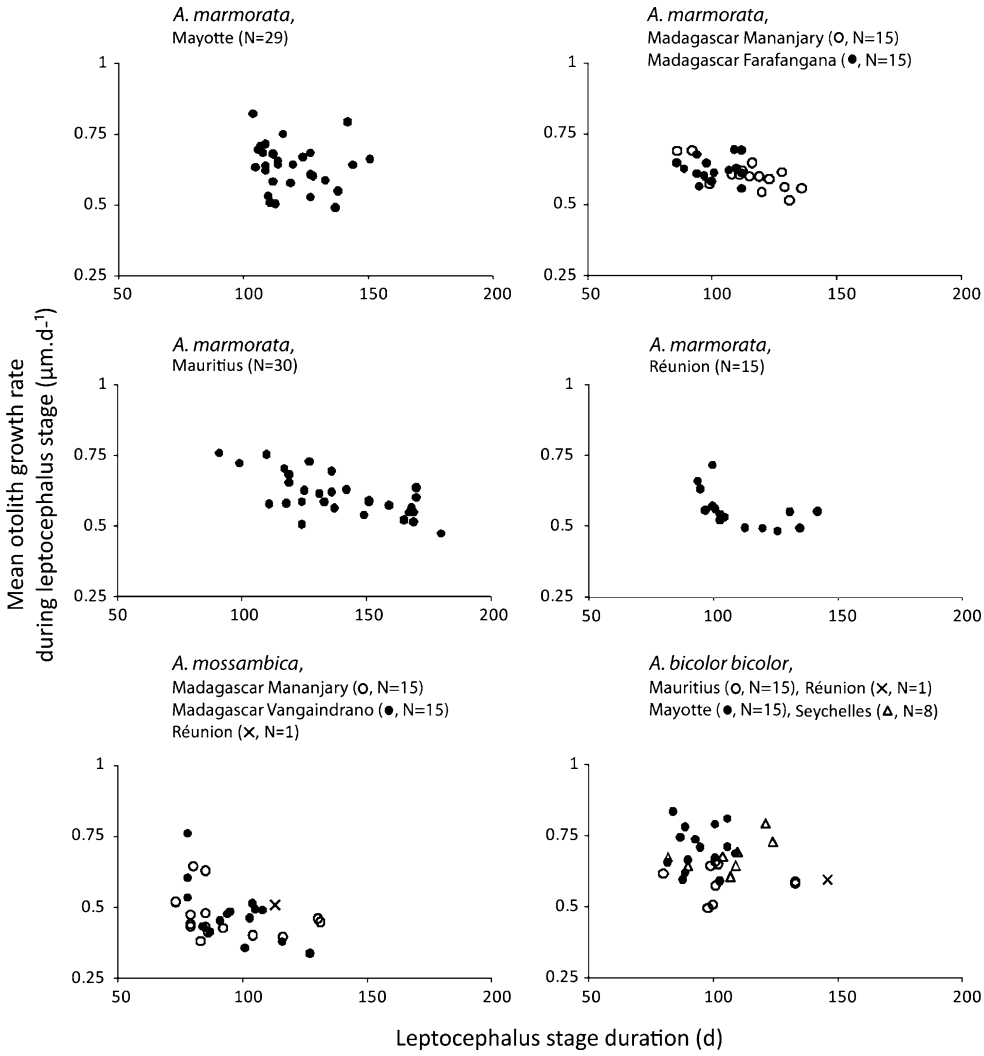

Fig. 4 Representation of OGR (µm days^{-1}, *y*-axis) in function of LD (days, *x*-axis) for the 168 eels analysed

lowest latitudes and showed the highest OGR during leptocephalus stage, whereas *A. mossambica*, endemic of the Malagasy area, has the most southern distribution and showed the lowest OGR.

Leptocephali metabolism as revealed by otolith growth

Through the analysis of the otolith growth patterns, the present study retraces the very singular ontogenic metabolism of eel leptocephali in the SWIO. The pre-metamorphic OGR of analysed eels decreased with age, until metamorphosis. This pattern clearly appeared for *A. marmorata* and *A. mossambica*. Though many studies showed that, for eel leptocephali, TL follows age in a classical Gompertz growth curve (Castonguay 1987; Tsukamoto and Umezawa 1990; Tanaka et al. 2001; Kuroki et al. 2006), this relationship does not relate the ontogenic metabolism of leptocephali, that is conversely observed through OGR analysis. In the present study, the growth patterns observed are similar to those described in other families of Anguilliforms (Congridae, Muraenidae, Ophichthidae, Bishop and Torres 1999): the more the leptocephalus body weight increases, the more its metabolism per unit of wet weight slows down (O_2 consumption, enzymatic activity, osmoregulation and excretion, Pfeiler and Govoni 1993; Bishop and Torres 1999; Bishop et al. 2000). This trend, that seems to be common to all elopomorph fishes, is not a true metabolic dormancy: metabolically inert glycosaminoglycans (GAGs) replace progressively the actively metabolizing tissues in the larvae (Bishop and Torres 1999), allowing leptocephali to reach a large size with a minimal metabolic penalty. This growth strategy, singular among fishes, probably reduces the spectrum of potential predators and maximizes the lift ability (Bishop and Torres 1999; Pfeiler 1999).

A slackening growth rate of leptocephali, waiting for favourable conditions to metamorphose, allows anguillid larvae to survive to long dispersals and to reach growing areas far away from the hatching zone. Same patterns were observed in temperate species: a longer duration of the leptocephalus stage in *A. Anguilla*, compared to *A. rostrata* (European and American eel, respectively), has been attributed to a slower growth rate during the leptocephalus stage (Arai et al. 2000b; Wang and Tzeng 2000; Kuroki et al. 2007). These considerations has lead some authors to develop the hypothesis that the timing of metamorphosis, triggered by the larval growth rate, was accounting for larval segregation between two species that spawns in close areas (e.g. the Atlantic eels species). This "Timing of Metamorphosis" hypothesis, as proposed by Kuroki et al. (2008), is probably also accounting in the Indian Ocean eels that would spawn in adjoining areas, and for whose different growth rates would control different dispersal ranges.

Larval migration routes in the Indian Ocean

During sampling period in the prospected estuaries, eel species composition was contrasted between sites. This gradient in species composition argued for separate migration routes between species, as suggested by Jubb (1961). However, we combined data from the few historical oceanographic cruises in the Indian Ocean with the LD of the different species analysed in the present study to synthesize the present information concerning these migration routes of eels that reach the SWIO.

A. marmorata is present in the Indian Ocean, but the number and location of its spawning places in this ocean remain unclear. The Dana expedition collected 1,225 leptocephali off Sumatra (September–December 1929, Jespersen 1942), but without genetic identification, it was impossible to distinguish species for the smallest ones (<20 mm, $N = 408$). Among the large leptocephali collected (>20 mm), 696 were *A. bicolor bicolor* (short-finned), and the 121 others, all long-finned, could be *A. marmorata* as well as *A. nebulosa nebulosa*. Thus, even if they were mostly *A. marmorata*, these larvae were too large to come with certainty from south-western Sumatra area, and could have come from elsewhere. Moreover, a recent oceanographic cruise off Sumatra only collected a single specimen (June 2003, Aoyama et al. 2007). In the northern waters of Madagascar, also prospected during the Dana expedition (December 1929–September 1930), only a few large *A. marmorata* leptocephali were collected (Jespersen 1942). On the other hand, *A. marmorata* glass eels collected in eastern Madagascar and surrounding islands in 2001 (Robinet et al. 2003a) and 2005–2006 (this study) showed ages at metamorphosis that make possible any hypothesis for reproduction places (60–135 days in Réunion in 2001, 94–142 days in Réunion in 2005, 104–151 days in Mayotte in 2005, 91–180 days in Mauritius in 2005, and 92–145 days in eastern Madagascar in 2005). It is worth noting that the high standard deviation in *A. marmorata* LD from Mauritius, twice higher than those from the other localities, could be a consequence of heterogeneous origins of larvae recruiting there. The probable explanation is separated spawning areas (completely distinct or slightly overlapping) for the *A. marmorata* matured eels coming from SWIO and western Indonesian areas. This has to be explored by molecular analysis.

Anguilla bicolor bicolor extends all along the Indian Ocean coasts, from South-Africa (Bruton et al. 1987), Arabian peninsula (Attaala and Rubaia 2005), Sri Lanka (Wicktröm and Enderlein 1988), to western Indonesia and north-western Australia (Ege 1939). This species probably spawns in the eastern Indian Ocean, *c.* south-western Sumatra, because small leptocephali (20–40 mm) were collected there during the Dana expedition (1929–1930, lead

by Johannes Schmidt; Jespersen 1942; Miller 2003). However, recent analysis argued for a spawning area not directly located above the Mentawei trench as Jespersen (1942) proposed: leptocephali trawled in June 2003 during the Baruna Jaya VII expedition off Sumatra were large (TL > 40 mm, Indonesian Institute of Science RV, Aoyama et al. 2007; Kuroki et al. 2007). A western spawning place was also suspected by several authors in the eastern Malagasy region (Jespersen 1942; Jubb 1961; Robinet et al. 2003a), but remains to be validated because only a few large leptocephali were collected there (Jespersen 1942). Otolith microstructures showed that ages at metamorphosis of *A. bicolor bicolor* recruited in various places around Madagascar were quite variable: 39–57 days (in Réunion in 2001), 87–139 days (in Mauritius in 2005), 87–125 days (in Mayotte in 2005), and 87–128 days (in Seychelles in 2005, Robinet et al. 2003a, this study). However, a spawning place in north-eastern Madagascar is highly probable because (1) these ages at metamorphosis were similar to those of the endemic species (*A. mossambica*), except in Réunion in 2001 where they were much shorter, and (2) *A. bicolor bicolor* silver eel sexual maturity is quite advanced at the onset of their spawning migration in Réunion Is., supplying the hypothesis of a rather close spawning place (Robinet and Feunteun 2002; Robinet et al. 2003b). Recent population genetics works in *A. bicolor bicolor* did not show evidence of genetic structure between East and West Indian Ocean samples (Minegishi 2006). Glass eels of *A. bicolor bicolor* arriving in SWIO could therefore originate from the same spawning area as those recruiting in Sumatra.

Anguilla mossambica is endemic of the SWIO, so its spawning area must be in this region. However, the Dana expedition only collected a few large specimens in the northern Malagasy waters (Jespersen 1942). Age at metamorphosis recorded for this species ranged 72–130 days in Réunion Is. (2001, Robinet et al. 2003a), and 73–131 days in Madagascar (2005, this study). *A. mossambica* was dominant in eastern Madagascar estuaries but less dominant in Mayotte (Comoros), and rare in Mascarene Archipelago. Among the three eel species studied here, *A. mossambica* had the shortest leptocephalus duration (95.1 ± 16.7 days). Because the South Equatorial Current sweeps the SWIO westwards (Schott and McCreary 2001), the origin of *A. mossambica* larvae should lay in the Madagascar eastern waters, between Madagascar and the Mascarene Archipelago.

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Anguilla marmorata larval migration plasticity as revealed by otolith microstructural analysis

Elodie Réveillac, Eric Feunteun, Patrick Berrebi, Pierre-Alexandre Gagnaire, Raymonde Lecomte-Finiger, Pierre Bosc, and Tony Robinet

Abstract: The oceanic early-life history of *Anguilla marmorata* was examined in the southwestern Indian Ocean in Mayotte, Mauritius, and Réunion islands through otolith microstructural analysis. The study of the hatching dates, the first feeding check diameter (FFD), the leptocephalus (LD) and metamorphosis (MD) durations, the age at recruitment (AR), and the leptocephalus otolith growth rate (OGR) of glass eels revealed great variations in early-life traits and relationships between them. An agglomerative nesting analysis discriminated three early-life histories, differently represented according to the locality: (*i*) fast migrants with short LD, short MD, young AR, large FFD, and high OGR dominated in Réunion and Mayotte; (*ii*) midspeed migrants with intermediate LD, MD, AR, FFD, and OGR dominated in Mauritius; (*iii*) slow migrants with long LD, long MD, old AR, small FFD, and low OGR were recorded only in Mauritius. All possible strategies were not observed and therefore not successful at the sampling time. However, several were simultaneously expressed, which suggests larval migration plasticity at the population level. This evidence is crucial information regarding both the species dispersal capabilities and the evolution from short-migratory tropical species towards long-migratory temperate ones in the genus *Anguilla*.

Résumé : L'histoire de vie larvaire d'*Anguilla marmorata* a été examinée dans le sud-ouest de l'Océan Indien à Mayotte, Maurice et La Réunion, par analyse de la microstructure des otolithes des civelles. Les traits de vie tels les dates d'éclosion, la marque de première prise de nourriture (FFD), les durées de vie leptocéphale (LD) et de métamorphose (MD), l'âge au recrutement (AR) et les taux de croissance de l'otolithe (OGR), se sont montrés variables et diversement corrélés. Trois types d'histoires de vie larvaire, discriminés par analyse de groupement agglomératif hiérarchique, ont été observés à l'échelle géographique : (*i*) migrateurs rapides à LD et MD courtes, AR jeunes, et FFD et OGR importants, dominants à La Réunion et à Mayotte; (*ii*) migrateurs intermédiaires à LD, MD, AR, FFD et OGR intermédiaires, dominants à Maurice; (*iii*) migrateurs lents à LD et MD longues, AR avancés, et FFD et OGR faibles, observés seulement à Maurice. Toutes les stratégies possibles n'ont pas été observées et ont donc été inefficaces pendent la période étudiée. L'expression simultanée de plusieurs stratégies laisse supposer, à l'échelle de la population, une plasticité de la migration larvaire chez *A. marmorata*. L'information est cruciale au regard des capacités de dispersion et du scénario d'évolution du genre *Anguilla* qui suppose une émergence des espèces tempérées aux migrations larvaires longues à partir des espèces tropicales aux migrations larvaires courtes.

Introduction

The duration of a fish larval stage, and therefore, its metamorphosis timing, might be key factors determining distances of dispersal and species distribution range (Arai et al. 2001*a*; Hoareau et al. 2007). Variation in oceanic migration duration of successfully recruited larvae probably reflects the species capabilities to delay metamorphosis and therefore the ability to maximize chances of finding suitable growth areas (Victor 1986). This delay has been observed to be very flexible in some fish groups and mostly for those composing the monophyletic group of the Elopomorpha

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Table 1. Duration (mean ± standard deviation, SD) of the leptocephalus stage of *Anguilla marmorata* reported in literature for glass eels sampled throughout the species distribution range from 1994 to 2005.

Locality	Year	*N*	Leptocephalus duration (days)	SD (days)	Min. (days)	Max. (days)	Range (days)	Source
Indonesia	1996	18	120	15.6	96	147	51	Arai et al. 1999
	1996	1	162	14.0	—	—	—	Marui et al. 2001
	1997	68	128	15.2	114	158	44	Arai et al. 2001*b*
	1999	23	79	11.2	—	—	—	Budimawan and Lecomte-Finiger 2005
Philippines	1994	10	120	13.0	105	140	35	Arai et al. 1999
	1998	16	146	19.5	112	183	71	Marui et al. 2001
Taiwan	1999	15	114	13.8	92	141	49	Arai et al. 2002
Japan	1999	15	123	13.9	100	155	55	Arai et al. 2002
Réunion	2001	9	97	26.4	60	135	75	Robinet et al. 2003
	2005	15	111	15.8	94	142	48	Present study
Mauritius	2005	30	139	24.0	91	180	89	Present study
Mayotte	2005	29	120	13.1	104	151	47	Present study

(i.e., Elopiformes, Albuliformes, Saccopharyngiformes, and Anguilliformes; Inoue et al. 2004).

In the complex catadromous anguillid eel life cycle, the duration of the leptocephalus stage, which undergoes an oceanic migration from spawning areas to growth coastal or inland waters, can vary widely among species. In eels, this larval phase is known to be shorter in tropical ancestral species than in the most recent temperate ones (Kuroki et al. 2006). Migration loops made by tropical species from intertropical spawning areas seem to have enlarged during evolution, offering the emergence of new species with large migration loops, with spawning areas still located in tropical waters while growth areas shifted toward temperate waters (Tsukamoto et al. 2002). This evolution could be consecutive to an intraspecific variability in the oceanic larval life duration, found in a number of recent studies, as for *Anguilla marmorata* (Marui et al. 2001; Arai et al. 2002; Robinet et al. 2003; Table 1), which is the most widespread species of the genus (Jubb 1961; Ishikawa et al. 2004; Robinet et al. 2007). This plasticity in the duration of the larval migration at the population scale might be the expression of selected strategies, which are defined here as genetically determined life histories or behaviours. Each individual will not show the whole strategy, but rather one of several tactics that the strategy may be composed of. The selection of strategies might occur according to environmental conditions (currents, water physico-chemical characteristics, trophic resource, etc.) and distance of the recruitment areas from the spawning location, maximizing the number of larvae that reach growth zones.

In the southwestern Indian Ocean (SWIO), *A. marmorata* spawning area was proposed to be unique and roughly localized northeast off the Mascarene Ridge by Jespersen (1942), Jubb (1961), and Robinet et al. (2008) (Fig. 1). In the present paper, we compare, through otolith microstructural analysis, the early-life traits (ELT: hatching dates, timing and duration of metamorphosis, age at recruitment, and otolith growth rate) of *A. marmorata* glass eels, sampled within the same month in three localities of the SWIO. On the one hand, Jespersen's hypothesis about a single regional spawning area is discussed in the light of the regional current circulation. On the other hand, variability of ELT is discussed in terms of response to variations of the pelagic environment and in terms of intra- and inter-specific dispersal capabilities.

Materials and methods

Study area and sampling

Réunion (21°S, 56°E; 2507 km^2) and Mauritius (20°S, 57°E; 1865 km^2) islands belong to the Mascarene Archipelago and are the most southern islands of the Mascarene Ridge (Fig. 1). Mayotte (12°S, 45°E, 374 km^2) is a part of the Comoros Archipelago located 1300 km northwest of the Mascarene Islands at the northern entry of the Mozambique Channel. These two archipelagos are bathed, respectively, by the southern and the northern bifurcation of the main regional current, the South Equatorial Current (SEC), flowing westward and splitting on the Mascarene Ridge and on the east coast of Madagascar (Schott and McCreary 2001).

74 glass eels and young elvers of *A. marmorata* were sampled in April 2005 in Mauritius (30 individuals), Réunion (15 individuals), and Mayotte (29 individuals) islands in the SWIO, with a portable electroshocker delivering electric impulses (DEKA 3000, EFKO manufacturer, DC 30 impulses·s^{-1}, 350 V, 4 A). Sampling occurred in the estuary of 26 permanent rivers as follow: eight rivers in Mauritius (5–7 April), four in Réunion (11–12 April), and 14 in Mayotte (15–19 April).

Species identification

After fixation in 90% ethanol, eels were measured and identified using Ege's glass eel determination key (Ege 1939). Criteria used were caudal pigmentation and the distance between the origins of the dorsal and anal fins as a percentage of the fish total length: A–D (%) = [(LD – LA)/LT] × 100, where LD is dorsal length, LA is anal length, and LT is total length (Ege 1939; E. Réveillac, P.A. Gagnaire, R. Lecomte-Finiger, P. Berrebi, T. Robinet, P. Valade, and E. Feunteun, unpublished data). Identifications were confirmed through molecular analysis using semimultiplex PCR (Gagnaire et al. 2007). The pigmentation stage was determined according to Elie et al. (1982).

Otolith microstructural analysis

Otoliths can be regarded as a reliable record of early-life

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Fig. 1. Location of Mayotte, Mauritius, and Réunion islands in the southwestern Indian Ocean. The presumed spawning area of *Anguilla marmorata* by Jespersen (1942) is shown in grey; the Mascarene Ridge (thin dotted line) and main regional currents (solid and dotted lines with arrows) are also indicated: SEC, South Equatorial Current (dividing into the NEMC (Northeast Madagascar Current) and SEMC (Southeast Madagascar Current)).

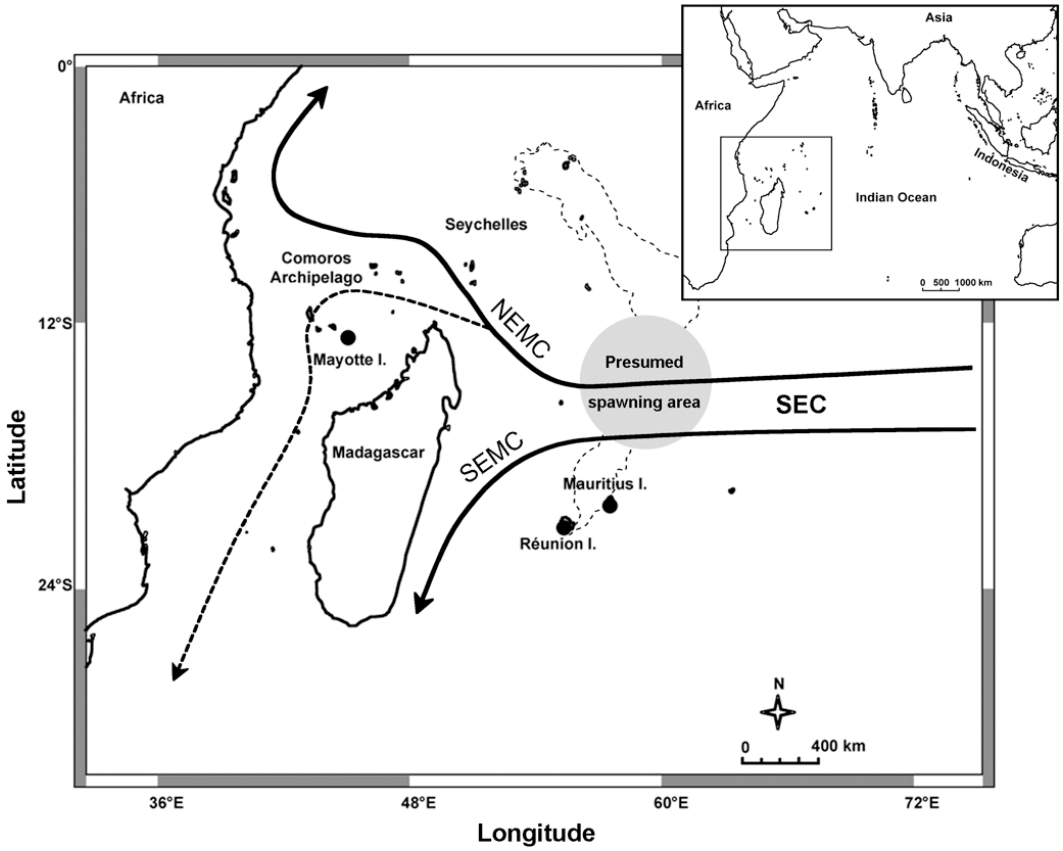
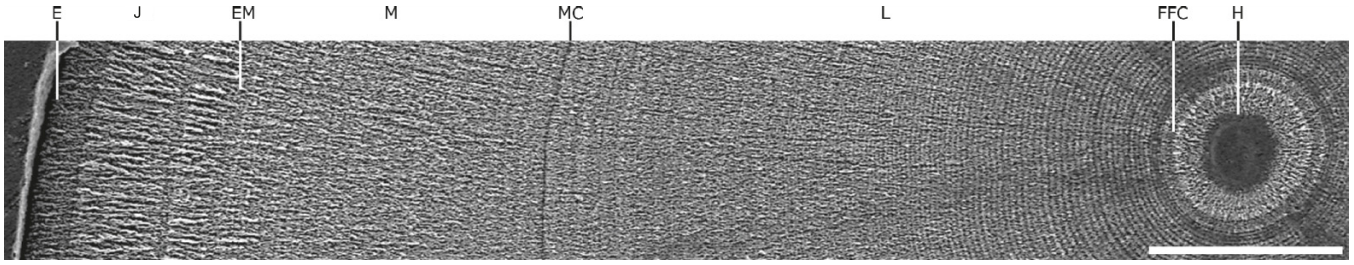


Fig. 2. Scanning electron microscope (SEM) photograph of the microstructure of an etched otolith of *Anguilla marmorata* with marks of developmental events. H, hatch check; FFC, first feeding check; L, leptocephalus stage; MC, metamorphosis check; M, metamorphosis; EM, end of metamorphosis; J, juvenile stage; E, edge of otolith. Scale bar = 20 μm.



history (ELH) (Lecomte-Finiger 1992; Campana 2001). Previous works on eel otolith microstructure revealed by scanning electron microscope (SEM) concluded that growth increment–deposition occurs daily with a low error margin (Martin 1995; Sugeha et al. 2001; Shinoda et al. 2004). Moreover, remarkable checks are thought to correspond to shifts between the different ontogenetic stages and, if increment–deposition is clear, enable the determination of the age of the individual at every shift (Wang and Tzeng 2000; Campana and Thorrold 2001; Jessop et al. 2006; Fig. 2). The otolith core can be observed as a deep hole in the centre of the etched otolith, with a surrounding ring described as the hatch check. The first feeding check, which is thought to correspond to the end of the preleptocephalus stage and to the complete absorption of the yolk reserve, is in the vicinity of the crystalline crown surrounding the core (Marui et al. 2001; Kuroki et al. 2005). The metamorphosis check, which marks the transition from the leptocephalus stage to the metamorphosis stage, is usually observed when increment widths start to increase suddenly (Lecomte-Finiger 1992). The end of metamorphosis, and therefore the onset of the glass eel stage, is represented by one or two successive annuli from which increment widths start to decrease towards the otolith edge (Lecomte-Finiger 1992). A total of 74 left sagittae of *A. marmorata* (30 from Mauritius, 15 from Réunion, and 29 from Mayotte) were extracted under binocular microscope, cleaned, embedded in metacrylate resin, and ground with 150, 9, and 3 μm

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grit paper until the nucleus was visible. Once polished, etched with 9% EDTA solution, and coated with gold, they were examined with an SEM (JEOL JSM 5410 LV). The age at first feeding could not be precisely determined because layers deposited within the crystalline crown surrounding the otolith core are not always well visible. Therefore, to characterize the preleptocephalus stage, we measured the diameter of the first feeding check (FFD in μm). This parameter and the duration of the leptocephalus (LD) and the metamorphosis (MD) stages, the larval otolith growth rates during the leptocephalus stage (OGR), the age at recruitment (AR) and, by back-calculation, the hatching date (HD) were determined for each individual. Otolith average growth rates (μm·day^{-1}) were calculated by the average thickness of every 10 increments from the FFD to the margin of each otolith, along the measurement axis.

Statistical analysis

Agglomerative nesting (“agnes”; hierarchical clustering), developed for R (R Development Core Team 2007; Kaufman and Rousseeuw 1990), was performed on the regional sample for FFD, LD, OGR, MD, and AR variables. The Euclidean metric system and the average method of linkage were used after the variables were standardized. A bootstrap analysis was performed to test the strength of the structure. An analysis of variance (ANOVA) was performed to test the differences for each variable between groups computed by the cluster analysis. The shape of the LD frequencies distribution was tested with MCLUST density test analysis of data aggregation (MCLUST: model-based clustering – normal mixture modeling) (Fraley and Raftery 2003, 2007), developed for R (R Development Core Team 2007). Means (± standard deviation, SD) of each variable were calculated for groups of individuals computed by the cluster analysis. Comparisons were made after performing Anderson–Darling normality tests and verifying variance equality with Student’s *t* test or Kruskal–Wallis (KW) test. Correlation tests between variables were performed with the Spearman test for nonparametric data.

Results

Pigmentation and size at recruitment

The pigmentation of the 30 individuals caught in Mauritius was only developed on the caudal and rostral regions of the body (stages V_A to VI_{A0}), classifying them all as glass eels (Elie et al. 1982). Among the 15 individuals sampled in Réunion, four eels were at a more advanced pigmentation stage (VI_{A1} to VI_B), and one was classified as a stage VII (elver). In Mayotte, 14 eels were classified as stages VI_{A1} to VI_B.

Mean body length of all eels (i.e., all stages included) and only glass eels (V_A to VI_{A0}) were, respectively, 67.53 ± 32.97 mm (range: 50–178 mm) and 52.40 ± 1.07 mm (range: 50–54 mm) in Réunion Island and 59.76 ± 8.86 mm (range: 47–79 mm) and 52.53 ± 3.74 mm (range: 47–55 mm) in Mayotte Island. Mean body length of glass eels caught in Mauritius was 52.13 ± 2.60 mm (range: 46–56 mm). No significant variability in the size of glass eels occurred between the sites (KW test, $p > 0.05$).

Oceanic life

Anguilla marmorata glass eels sampled simultaneously in April 2005 showed a wide distribution range of HD from late August to late December 2004 (Fig. 3). The glass eels from Mauritius hatched significantly earlier (hatching date: 8 October 2004 ± 26.70 days) than those of Réunion and Mayotte, which showed quite similar distributions and mean HD (5 November 2004 ± 36.21 days and 6 November 2004 ± 23.11 days, respectively; KW test, $p > 0.05$).

The other ELT showed wide ranges of values at insular and regional scales (Fig. 3). They also exhibited interrelationships (Fig. 4), with LD being negatively correlated to FFD (Spearman, $R^2 = 0.746$, $p < 0.0001$) and to OGR (Spearman, $R^2 = 0.142$, $p < 0.01$) and positively correlated to MD (Spearman, $R^2 = 0.284$, $p < 0.0001$) and to AR (Spearman, $R^2 = 0.982$, $p < 0.0001$).

Three main clusters of individuals were computed by the agnes hierarchical cluster analysis (agglomerative coefficient = 0.88, bootstrap values > 98%; Fig. 5). They showed statistically different ELT values (ANOVA, $p < 0.05$) and corresponded to three modes of LD distribution frequencies observed at the regional scale (MCLUST density test, $E = 3$). The first group was composed of 30 individuals sampled in all three islands ($N = 10$ in Réunion, $N = 4$ in Mauritius, and $N = 16$ in Mayotte). Their life history was characterized by large FFD (mean 20.4 ± 0.5 μm), short LD (mean 104.6 ± 6.2 days, range 91–116 days), high OGR (mean 0.64 ± 0.08 μm·day^{-1}), short MD (mean 22.9 ± 2.5 days), and young AR (mean 127.5 ± 5.7 days). They were qualified as fast migrants. The second group (midspeed migrants) included 34 individuals also sampled in the three islands ($N = 5$ in Réunion, $N = 16$ in Mauritius, and $N = 13$ in Mayotte). They had intermediate values of FFD (mean 19.3 ± 0.4 μm), LD (mean 129.4 ± 10.3 days, range 117–151 days), OGR (mean 0.59 ± 0.06 μm·day^{-1}), MD (mean 26.7 ± 2.8 days), and AR (mean 156.1 ± 11.8 days). The third group (slow migrants) was composed of 10 individuals only sampled in Mauritius. They had small FFD (mean 18.1 ± 0.8 μm), long LD (mean 166.8 ± 47.6 days, range 159–180 days), low OGR (mean 0.55 ± 0.05 μm·day^{-1}), long MD (mean 29.3 ± 3.5 days), and old AR (mean 196.1 ± 8.0 days).

Geographical differences were observed, as each type of ELT combinations (i.e., ELH) was not similarly represented among islands. Indeed, fast migrants were dominant in Réunion and Mayotte, while midspeed migrants were the most represented in Mauritius recruitment. Slow migrants only occurred in Mauritius, where they were more abundant than fast migrants. The three types of ELH were therefore different in terms of ELT values and in terms of geographical occurrence.

OGR pattern

The OGR pattern from the centre to the edge of the otolith is shown (Fig. 6). It comprised four phases as described for *Anguilla japonica* (Arai et al. 1997); *Anguilla rostrata* (Arai et al. 2000); *Anguilla australis*, *Anguilla dieffenbachii*, and *Anguilla bicolor pacifica* (Marui et al. 2001); *Anguilla celebesensis*, *A. marmorata*, and *Anguilla bicolor bicolor* (Arai et al. 1999); and *Anguilla anguilla* (Lecomte-Finiger 1992). High individual variations were re-

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Fig. 3. Hatching date (*a*), first feeding check diameter (FFD, µm) (*b*), leptocephalus duration (days) (*c*), and metamorphosis duration (days) (*d*) frequencies distribution, determined by otolith microstructural analysis of 74 glass eels (*Anguilla marmorata*) sampled in the southwestern Indian Ocean in Réunion (N = 15), Mauritius (N = 30), and Mayotte (N = 29) islands in April 2005.

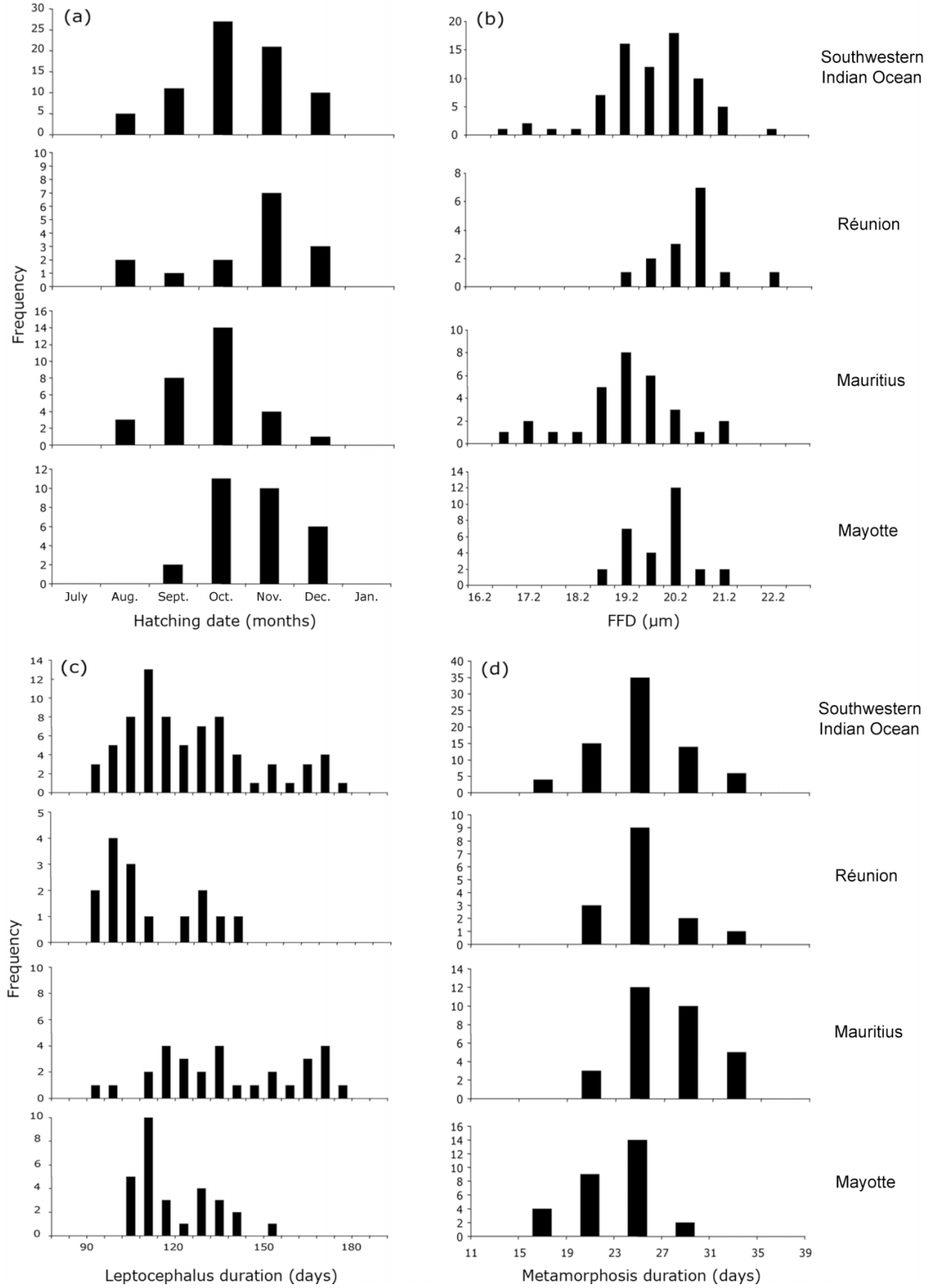

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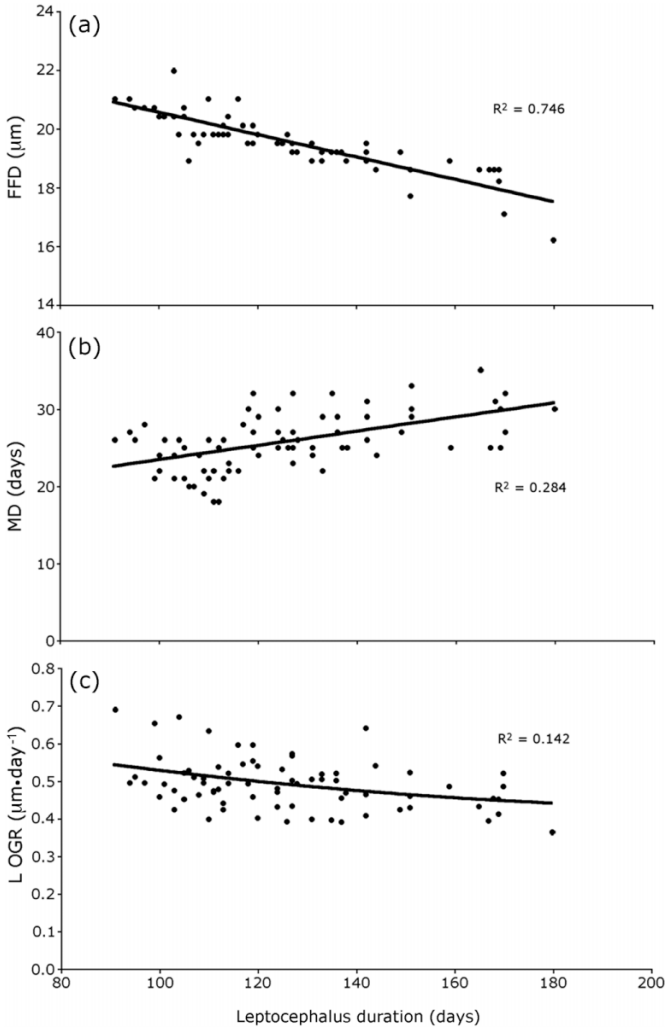
Fig. 4. Relationship between the first feed check diameter (FFD, μm) (*a*), the metamorphosis duration (days) (*b*), the leptocephalus daily otolith growth rate (L OGR) (μm·day^{-1}) (*c*), and the leptocephalus duration (days) in glass eels (*Anguilla marmorata*) caught in the southwestern Indian Ocean (N = 74) in April 2005.



corded within each phase, independently from the general pattern (Fig. 6). During the first phase, otolith increment widths increased between the hatch check and age 20–40 days (maximum peak average 0.94 ± 0.15 μm·day^{-1}, range: 0.68–1.30 μm·day^{-1}) and then gradually decreased until almost constant during the second growth phase (mean values 0.49 ± 0.08 μm·day^{-1}, range: 0.29–0.80 μm·day^{-1}). At the end of the steady growth phase, a sudden increase of the OGR occurred, corresponding to the third phase (maximum peak average 1.73 ± 0.35 μm·day^{-1}, range: 1.08–2.99 μm·day^{-1}). Increment widths then decreased afterward (fourth growth phase).

Discussion

Size at recruitment

In the present study, the body size at recruitment of *A. marmorata* (i.e., for juveniles at stages V_A to VI_{A0}) was poorly correlated to the migration duration, indicating no clear correspondence between these parameters at the intraspecific level. Nevertheless, mean sizes observed in each island (52.13 ± 2.60 mm in Mauritius, 52.40 ± 1.07 mm in Réunion, and 52.53 ± 3.74 mm in Mayotte) were close to those previously recorded for the same species recruiting into Indonesia (Arai et al. 1999, 2001*b*), into Taiwanese and Japanese coastal waters (Arai et al. 2002), and into Réunion estuaries (Robinet et al. 2003). Also, as observed in previous studies, these mean values were smaller than for temperate species at the same pigmentation stages, such as *A. anguilla* (68 mm) (Lecomte-Finiger 1992), *A. japonica* (57 mm) (Arai et al. 1997), *A. rostrata* (58 mm) (Arai et al. 2000), *A. dieffenbachii* (64 mm) (Marui et al. 2001), and *A. australis* (59 mm) (Shiao et al. 2001). Therefore, there is an obvious difference in length at recruitment between temperate and tropical species.

As temperate eels undergo much longer migrations than tropical ones (Lecomte-Finiger 1992, 1994; Kuroki et al. 2006), the size at recruitment seems, at the interspecific level, to be influenced by the LD, as suggested by Marui et al. (2001).

Clues for a single, regional spawning area

In the years 1928–1930, leptocephalus larvae were sampled in the Indian Ocean during the Carlsberg Foundation's Oceanographic Expedition Around the World. The results enabled Jespersen (1942) to locate a regional spawning area for anguillid eels at the northeast of Madagascar on the Mascarene Ridge (discussed by Robinet et al. 2008). However, further studies should be conducted to test Jespersen's hypothesis. Indeed, a model combining life history traits and oceanic circulation would help to simulate larval transport under various conditions. The global model NEMO (simulation DRAKKAR ORCA025-G70 over years 1959 to 2004, resolution 1/4°; Penduff et al. 2007) computed 45 years of currents speeds and directions in the SWIO (Fig. 7). This model, roughly combined with migration durations we recorded in this study, seems to support the spawning area proposed by Jespersen (1942) and supported by Robinet et al. (2008). From this area, indeed, the SEC and the North Equatorial Madagascar Current could have transported larvae to Mayotte at the speed of about 20 cm·s^{-1} (Fig. 7). In that case, larvae would have crossed 1500 km in about 90 days, which roughly corresponds to the LD recorded for larvae recruited in this island. As well, from the Mascarene Ridge, the SEC and the South-Equatorial Madagascar Current could have carried larvae first to Mauritius and then to Réunion at the speed of about 10 cm·s^{-1}. Thus, those larvae would have crossed 1000 km in about 110 days, which is also consistent with the mean LD registered in those two islands.

Variability of ELH traits

Developmental variability was clearly expressed through obvious variations of early-life stages durations. The sum of these durations resulted in variations of ages at recruitment. This variability seemed to be also related to fluctuations of the OGR, which reflects individual somatic metabolic rates (Wright 1991). Relationship between developmental stages duration and OGR has already been described in other anguilliform larvae such as Anguillidae (Tzeng 1990; Robinet et al. 2008) and the American conger eel *Conger oceanicus*

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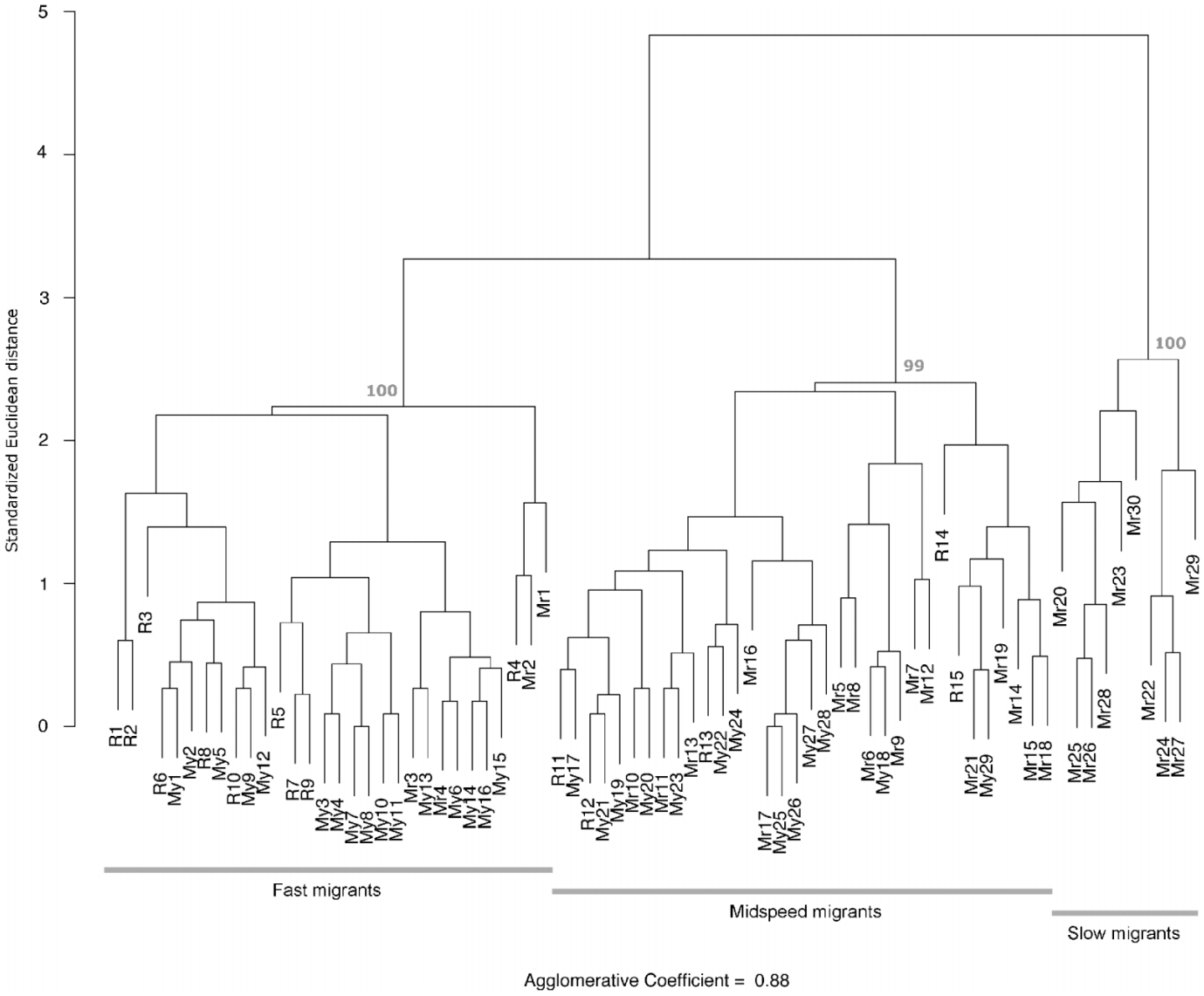
Fig. 5. Dendrogram computed by agglomerative nesting analysis (agnes; hierarchical clustering) of 74 individual glass eels (*Anguilla marmorata*) characterized by five early-life traits: first feed check diameter, leptocephalus duration, metamorphosis duration, otolith growth rate, and age at recruitment. Variables were standardized before the analysis of Euclidean distances. Bootstrap values are reported for the three identified strategies of larval migration: fast, midspeed, and slow migrants. R plus sample number, Mr plus sample number, and My plus sample number represent glass eels collected in Réunion, Mauritius, and Mayotte islands, respectively.



(Correia et al. 2004), but also in Pleuronectiformes with *Limanda ferruginea* (synonym *Pleuronectes ferrugineus*, in Benoit and Pepin 1999) or in some reef fishes (Wellington and Victor 1992). This study goes further, demonstrating correlations between more than two ELTs. These complex relationships discriminated individuals into three groups and revealed the existence of at least three ELHs (Fig. 8).

Observed ELT variations may be explained by two alternative or complementary hypotheses: (*i*) the intrinsic metabolism hypothesis and (*ii*) the environmental conditions hypothesis. Indeed, both may govern modalities of energy expense and may have repercussions on ELT and then on ELH. Environmental conditions such as water temperature (Høie et al. 1999; Otterlei et al. 2002; Bang et al. 2006) and food availability (Takasuka and Aoki 2006) are thought to be the primary determinant of larval growth rate and subsequent larval duration (Anderson 1988; Jenkins and King 2006). Then, their variations are thought to have mainly produced the different ELH recorded. As the HD was not related to the other ELT, observations of several different ELHs might not be related to temporal heterogeneity, but rather to spatial heterogeneity of environmental conditions. As the hypothesis of a single spawning area seemed plausible, it is likely that heterogeneous conditions in this spawning area and (or) several migration routes have produced the different ELH observed. The global NEMO model showed that migrations were possible within the mean durations recorded through otolith microstructural analysis. However, complexity of currents was undervalued because this model calculated the mean circulation over several decades. Over shorter periods of time, like a season, those currents are indeed reported to have more complex trajectories (Schott

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Fig. 6. Otolith increment widths along the preleptocephalus, leptocephalus, and metamorphosis stages of 74 glass eels (*Anguilla marmorata*) sampled in the southwestern Indian Ocean in April 2005.

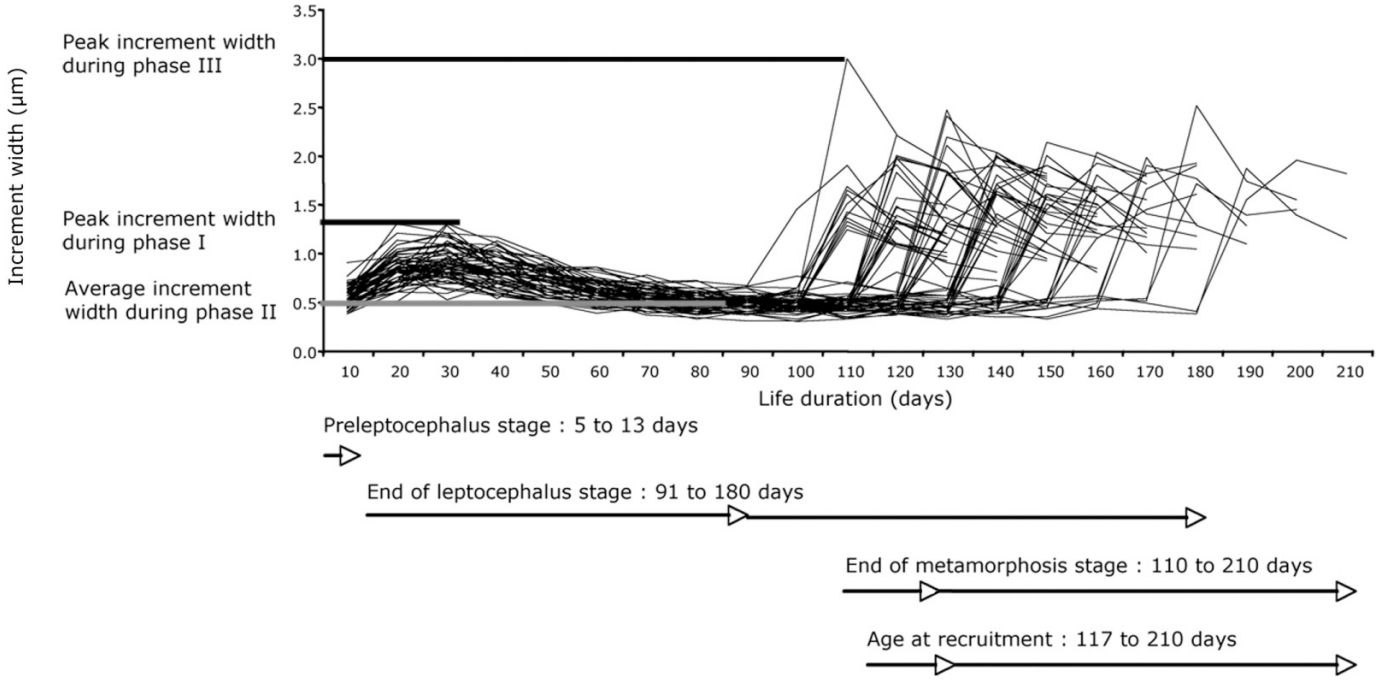
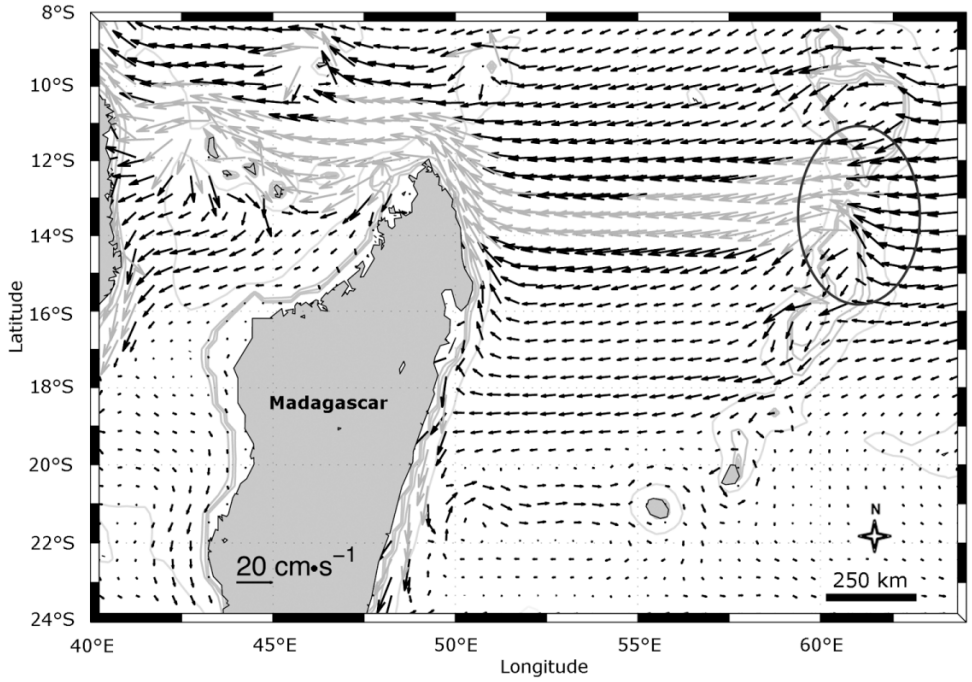


Fig. 7. Southwestern Indian Ocean mean currents speeds and directions (0 to 100 m depth) computed over years 1959 to 2004 by the global oceanographic model NEMO (simulation DRAKKAR ORCA025-G70, resolution 1/4°; Penduff et al. 2007). The spawning area of *Anguilla marmorata* proposed by Jespersen (1942) is delimited by a black ellipse on the Mascarene Ridge. Grey-shaded current vectors correspond to current velocities higher than 20 cm·s^{-1}.



and McCreary 2001; S. Pous, Université Pierre et Marie Curie, LOCEAN/IPSL, 4 place Jussieu, F-75252 Paris, CEDEX 5, France, unpublished data). As they encounter islands or shallow waters like the Mascarene Ridge, gyres are created (Padfield and Coward 1998). The turbulence of this system could partly explain how different migration routes could have transported larvae to different localities in different environmental conditions, inducing disparities in ages at recruitment and delays of arrival between localities.

In light of these results, more precise modeling is required to test hypotheses on *A. marmorata* migration routes in the SWIO. Active swimming, diffusion mechanisms, larval mor-

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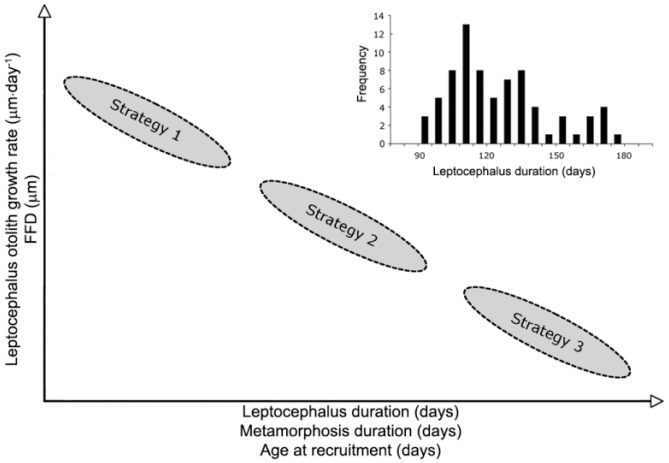
Fig. 8. Schematic representation of the three strategies (1, fast; 2, midspeed; and 3, slow migrants) discriminated by cluster analysis based on early-life trait combinations of glass eels (*Anguilla marmorata*) caught in April 2005 in the southwestern Indian Ocean. Frequencies of each strategy occurrence are shown in the top right corner. Other possible strategies were not observed. FFD, first feeding check diameter.



tality, and water temperature are some of the parameters that would have to be introduced in the model. In parallel, growth dynamic, which seemed to influence and (or) be influenced by the developmental rhythm at every stage of the oceanic life, has to be further examined to analyze the contribution of environmental and intrinsic factors to the anguillid eel larval life course.

A plasticity of larval migration in the anguillid eel?

As previously mentioned, variability of migration traits led to the observation of three ELH patterns, which respond to the following trend: the migration duration is inversely proportional to OGR and the associated metabolic rate. This variability demonstrates that *A. marmorata* larval migration can be achieved at various times. This might be a key in the migratory anguillid eel life cycle success. Indeed, several ELH patterns, qualified here as strategies, were expressed in variable proportions according to the recruitment place, while other strategies were not expressed. There is a possible trade-off between these various strategies. On the one hand, fast migration (linked to high metabolic rate) probably reduces mortality (Takasuka and Aoki 2006) while it also reduces the probability to find growth habitats. On the other hand, slow migration (low metabolic rate) might reduce larval survival while it might increase the probability to find suitable growth habitats. The existence of such a range of larval migratory strategies might globally increase the fitness of the population. It might also represent a strong selective advantage for *A. marmorata*, because it sustains an extraordinary dispersion capacity among fish species. Indeed, a short duration of the leptocephalus stage might favour geographical retention, while a long migration duration might favour both emigration (Correia et al. 2004) and connectivity between populations separated during their growth phase in continental systems.

The fact that no other strategies were observed could reflect unsuccessful or inexistent combinations of ELT. As McCormick (1999) proposed, larval duration of a fish is a product of its genotype, its larval environment, and the capacity of the species to delay metamorphosis. The lower age limit for settlement is governed by the rate of larval development, while the upper age limit is determined by the extent to which a delay of metamorphosis is possible, both also linked to the timing of finding suitable places to settle. On the one hand, short migration with low growth rate might be lethal because larvae that reach rapidly coastal shelves are not ready to undergo metamorphosis (i.e., are not competent for recruitment; Victor 1986; Hickford and Schiel 2003). On the other hand, long migration with high growth rate might induce rapid consumption of energy reserves, leading to body depletion and therefore death before coastal waters are reached.

Regarding the evolution of the genus *Anguilla*, short migration with high metabolic rate could be seen as the ancestrally successful strategy in tropical waters wherein the genus seems to have originated (Aoyama et al. 2001; Lin et al. 2001). Long migration with low growth rate could then be regarded as the strategy that has generated large migration loops leading to the emergence and establishment of temperate species. This strategy could have started to be profitable and widely represented when oceans opened, allowing larger dispersal toward temperate waters. This possibility of extending the dispersal range could have been supported by a lower temperature of migration, which, by decreasing the larval metabolic rate, led to viable migration strategies establishment (Gillooly et al. 2002; O'Connor et al. 2007). This scenario hypothesis must be examined in anguillid eels to deepen the knowledge on their evolution.

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Résumé: Parmi les processus qui contribuent à la diversité des histoires de vie, la dispersion est probablement le plus impliqué dans la persistance et l'évolution des espèces. Elle permet de se soustraire à la compétition et aux conditions de vie défavorables, de maintenir la connectivité entre des unités géographiquement isolées, et de déplacer et d'étendre l'aire de distribution par exploration de nouveaux habitats. A ce titre, les anguilles sont parmi les animaux les plus remarquables en terme de capacité de dispersion de leurs larves. Ces leptocéphales peuvent en effet parcourir de plusieurs centaines à plusieurs milliers de kilomètres jusqu'à atteindre les aires de croissance côtières, estuariennes ou dulcicoles, d'où les adultes s'échappent pour rejoindre les zones de pontes océaniques tropicales, se reproduire et mourir. Cette boucle de migration est supposée avoir d'abord eu lieu en milieu tropical et s'être progressivement élargie jusqu'aux habitats tempérés pour la croissance. Ce travail de thèse a examiné les capacités de dispersion larvaire des anguilles au travers de l'étude des traits d'histoire de vie (*e. g.* durée de vie larvaire, métabolisme), et leur contribution à l'évolution du genre dont la radiation s'est faite au cours de l'expansion géographique. Trois espèces ont été particulièrement étudiées : l'anguille tropicale mozambicaine *A. mossambica*, la plus ancienne, se distribue uniquement dans le sud-ouest de l'Océan Indien; l'anguille tropicale *A. marmorata* la plus récente, possède la plus vaste aire de répartition et est la plus fortement structurée; l'anguille tempérée Européenne *A. anguilla,* la plus récente, réalise les plus grandes dispersions. La plasticité des traits de vie, en réponse aux variations de l'environnement, est supposée avoir généré la diversité d'histoires de vie larvaire observée à l'échelle spécifique. Néanmoins, l'élasticité intra-spécifique de la dispersion a montré des limites qui ont possiblement ségrégé spatialement et/ou temporellement des boucles de migration, probablement à l'origine de nouvelles espèces. La grande diversité des histoires de vie a permis de mettre en évidence un fort potentiel de résilience des larves d'anguilles face aux changements de leur environnement. Il est proposé que ce potentiel ait pu promouvoir la persistance des espèces, particulièrement les espèces tempérées, lors des changements climatiques et océaniques passés. Néanmoins, la réactivité de la plasticité des traits de vie, dépendante de la proportion prise par le déterminisme génétique, est questionnée au regard de la soudaineté du changement global annoncé.

Abstract: Among life-history processes that contribute to life-histories diversity, dispersal is probably the most important one involved in both species persistence and evolution. It grants escapement from competition and unfavourable conditions, permits to keep connections between isolated populations, and enlarges or displace distribution areas by exploration of the environment. Anguillid eels are famous fish species for the huge dispersal capacities of their leaf-like transparent larvae. These leptocephali can indeed cross thousands to hundreds of kilometres to reach coastal, estuarine or freshwater growth habitats from which adults escape to return to natal waters in tropical areas to spawn and die. This migration loop is thought to have first occurred entirely in tropical marine waters and progressively enlarged toward temperate areas for growth. This work examined the larval dispersal capacities of eels through the study of larval traits (*e.g.* larval duration, metabolic rate) and their contribution to the evolution of the genus through speciation along with range expansion. Emphasis was made on three species among which the tropical Mozambican eel *Anguilla mossambica* is the most ancient species and is endemic to the southwestern Indian Ocean; the giant mottled eel *A. marmorata* is the most widespread species but also the most genetically structured one; and the temperate European eel *A. anguilla* is the youngest species and displays the highest dispersal capacities. Plasticity of traits was proposed to have generated the observed larval life-histories diversity, which, supported by environmental conditions could have favoured specific range expansion. However, intraspecific dispersal elasticity displayed limits that might have induced temporal and/or spatial segregation of migration loops that subsequently formed new species. Nevertheless, the huge variability of dispersal capacities recorded in each species evidenced a high potential of resilience in face of environmental changes. This is proposed to have supported species, particularly temperate species, persistence during past climate and oceanic changes. However, the unknown reactivity of the dispersal plasticity, dependent on the proportions of genetic and environmental determinism, is questioned in regard to the suddenness of the forthcoming global change.