

# Phénologies, mécanismes et perturbations anthropiques des dynamiques de migration dulçaquicoles des espèces amphidromes: cas des Sicydiinae de La Réunion

Raphaël Lagarde

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UNIVERSITÉ DE LA RÉUN





Phénologies, mécanismes et perturbations anthropiques des dynamiques de migration dulçaquicoles des espèces amphidromes : cas des Sicydiinae de La Réunion



Thèse pour l'obtention du titre de Docteur en biologie des populations de l'Université de La Réunion, école doctorale sciences, technologies et santé

par Raphaël Lagarde

Thèse dirigée par Dominique Ponton et soutenue le 25 juin 2018 devant un jury composé de :

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AGENCE FRANÇAISE POUR LA BIODIVERSITÉ ÉTABLISSEMENT PUBLIC DE L'ÉTAT



# Résumé

Les gobies amphidromes et, en particulier, ceux de la sous famille des Sicydiinae représentent une part importante de la diversité et de l'abondance des peuplements de poissons d'eau douce des îles tropicales. Ces espèces se reproduisent dans les rivières et ont une phase larvaire marine pendant plusieurs mois avant de retourner croitre et maturer en eau douce. L'objectif de cette thèse est d'acquérir des connaissances concernant la phénologie des dynamiques de migration en eau douce de deux espèces de Sicydiinae de La Réunion, Sicyopterus lagocephalus et Cotylopus acutipinnis et les mécanismes qui peuvent en être à l'origine. Ces études montrent que la dévalaison des larves vers la mer immédiatement après leur éclosion avait principalement lieu pendant l'été austral et en début de nuit dans les zones aval. Le débit des cours d'eau et ses fluctuations saisonnières et journalières jouent un rôle prépondérant dans cette dynamique de dévalaison en termes d'abondances de larves dérivant, de temps de dévalaison jusqu'à la mer et de survie des larves. Après leur arrivée en eau douce, les juvéniles vont coloniser l'ensemble des zones des bassins versants. Les plus fortes abondances de juvéniles en migration vers les zones amont sont observées en fin d'étiage et pendant l'aprèsmidi. Enfin, S. lagocephalus présente des performances locomotrices supérieures à celles de C. acutipinnis soutenues par des morphologies plus diverses. Ces meilleures performances, soutenues par des morphologies plus diverses, sont l'un des facteurs qui peuvent expliquer la large aire de répartition de S. lagocephalus, présent dans les océans Indien et Pacifique, par rapport à C. acutipinnis qui est endémique de l'archipel des Mascareignes. Des recommandations de gestion, permettant principalement de restaurer la continuité biologique au niveau des barrages, sont faites au regard des résultats obtenus durant cette thèse.

**Mots clefs :** amphidromie ; *Cotylopus acutipinnis* ; diadromie ; dispersiton ; dévalaison ; gestion ; Gobiidae ; montaison ; morphologie ; régime hydrologique ; structure peuplements ; *Sicyopterus lagocephalus* 

# Abstract

Amphidromous gobies, especially those of the Sicydiinae subfamily, represent most of the diversity and abundance of the freshwater fish assemblages in tropical islands. These species spawn in rivers, spend months in the ocean as pelagic larvae and return to freshwater to grow and reproduce. This doctoral thesis aims at describing the phenology and some mechanisms of the dynamics of migration in freshwater of two Sicydiinae species in Réunion Island: Sicyopterus lagocephalus and Cotylopus acutipinnis. These studies highlighted that larval downstream migration to the sea, immediately after hatching, occurs mainly during austral summer and a few hours after sunset in downstream reaches. Seasonal and daily fluctuations of the flow regime also greatly influence the abundances, the transport duration from spawning site to the sea and the survival of larvae during their downstream migration. After their return to the freshwater, juveniles settle in the watersheds from the estuary to the most upstream reaches. The highest abundances of juveniles migrating to upstream reaches are observed during low flow conditions at the end of the afternoon. Finally, locomotor performances are better for S. lagocephalus compared to C. acutipinnis. These better locomotor performances, supported by more diverse morphologies, are among the factors explaining the presence of S. lagocephalus from Eastern Pacific Ocean to Western Indian Ocean when C. acutipinnis is endemic to the Mascarenes Archipelago. Based on the results obtained in this doctoral thesis, management and conservation recommendations are suggested especially for the restoration of fish passage at several migration barriers such as dams and weirs.

**Key words :** amphidromy ; *Cotylopus acutipinnis* ; diadromy ; dispersal ; downstream migration ; flow varitions ; Gobiidae ; management ; morphology ; upstream migration ; populations structure ; *Sicyopterus lagocephalus* 

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# 1. Introduction générale

## **1.1 Diversité des types de déplacements et des modes de locomotion chez les poissons**<sup>1</sup>

Les déplacements de masses souvent saisonniers d'individus observés chez certaines espèces de poissons ont depuis longtemps fasciné le grand public et les scientifiques. Ce fort intérêt pour ce phénomène est principalement expliqué par trois spécificités. La première est le caractère spectaculaire des déplacements qui peuvent s'effectuer sur de très longues distances. C'est notamment le cas de l'Anguille européenne (Anguilla anguilla, Linné 1758) qui effectue un déplacement de plusieurs milliers de kilomètres entre sa zone de croissance et de maturation dans les eaux continentales européennes jusqu'à son aire de reproduction située dans la mer des Sargasses, au large des côtes de la Floride (Béguer-Pon et al., 2015). La deuxième caractéristique est liée aux intérêts culturaux et économiques que peuvent représenter la pêche de certaines espèces comme le Saumon Atlantique (Salmo salar, Linné 1758) en Europe (Peirson et al., 2001), ou les juvéniles de Galaxiidae, localement appelés « White bait », en Nouvelle Zélande (Haggerty, 2007). Enfin la dernière caractéristique pouvant expliquer la forte perception de ce phénomène par le public est liée aux effets indirects des déplacements des individus sur d'autres espèces et écosystèmes. Par exemple les Saumons Pacifique (Oncorhynchus ssp.) peuvent représenter une part importante du régime alimentaire des Ours (Ursus ssp.) qui les capturent lorsqu'ils remontent les rivières vers leurs zones de frayères (Hilderbrand et al., 2004). Après la ponte la décomposition des cadavres des Saumons Pacifique a aussi un rôle important de fertilisation pour la végétation riparienne (Ben-David et al., 1998).

Cependant les mouvements des poissons ne se limitent pas aux déplacements de masse saisonniers et sur de longues distances mais peuvent présenter une grande gamme d'amplitude spatiale et temporelle. En premier lieu les déplacements quotidiens entre les zones de repos et les zones d'alimentation (c'est-à-dire ce qui délimite le territoire quotidien) des poissons entrainent des mouvements à des échelles spatiales et temporelles beaucoup plus réduites. Harrison et al. (2013) ont démontré que la population de Lotte (*Lota lota*, Linné 1758) d'un lac canadien avait tendance à se déplacer de plusieurs mètres entre des zones profondes occupées pendant la journée et des zones peu profondes, proches des berges, la nuit vraisemblablement pour s'y nourrir. Les déplacements des organismes peuvent aussi être liés à l'ontogénie si leur territoire quotidien

<sup>&</sup>lt;sup>1</sup> Le terme « poissons » se réfère ici exclusivement aux poissons osseux ou Ostéichthyens

change entre les différents stades de développement. C'est notamment le cas du Vivaneau gibelot (Lutjanus fulviflamma, Forsskål 1775) dont les juvéniles se développent dans les mangroves avant de se déplacer vers les récifs coralliens à l'âge adulte (Paillon et al., 2014). Au sein d'un même stade de développement, des déplacements au-delà du territoire quotidien sont fréquents. Ces déplacements sont souvent expliqués par des changements de conditions locales d'habitat mais peuvent aussi être liés à un comportement exploratoire des individus. Les crues sont un exemple extrême de changement de conditions de l'habitat local. Lors de ces évènements David et Closs (2002) ont observé deux types de déplacements chez le Kokopu géant (Galaxias argenteus, Gmelin 1789). Certains individus se déplaçaient hors de leur habitat quotidien vers des zones de courant plus faible alors que d'autres étaient transportés en aval par les courants de crue. Deux comportements pouvaient suivre, la plupart des individus retournaient vers leur territoire quotidien occupé avant la crue alors que d'autres s'installaient dans un nouveau territoire quotidien. L'influence du comportement des individus sur la probabilité de changer de territoire quotidien a été décrite chez des jeunes juvéniles de Saumon de fontaine (Salvenilus fontinalis, Mitchill 1814) par Edelsparre et al. (2013). Ces auteurs ont montré que la probabilité de changement de territoire quotidien était fortement liée à la témérité des individus qui pouvait favoriser leur comportement exploratoire via leur tendance à sortir plus fréquemment et rapidement de leur refuge. Enfin les individus peuvent aussi se déplacer depuis leur territoire quotidien vers leur habitat de reproduction comme décrit pour l'Anguille européenne.

Pour effectuer ces déplacements les poissons utilisent différents modes de locomotions grâce à des mouvements actifs mais aussi à l'utilisation d'un moyen de transport qui, en général, est le courant. Un continuum de modes de locomotions est observé depuis un déplacement complètement actif lorsque les poissons se déplacent à contre-courant jusqu'à un déplacement quasi-exclusivement passif lorsque les individus dérivent avec le courant. Ce dernier cas concerne principalement les stades larvaires dont les capacités de locomotion sont limitées par leur faible capacité de nage liée principalement à leur petite taille (Lechner et al., 2016). Cependant malgré leurs capacités locomotrices limités, les larves peuvent activement augmenter la vitesse du mouvement en se déplaçant vers des zones de courant plus élevé et/ou en se déplaçant activement dans la direction du courant, ou au contraire la ralentir en se déplaçant vers des zones de courant faible et/ou en se déplaçant à contre-courant (Pavlov et al., 2008; Lechner et al., 2014). Lorsque les individus grandissent, la part de mouvement actif peut devenir plus importante. Cependant quand le déplacement s'effectue dans le sens du courant, ou que le courant est exceptionnellement élevé (cas des crues en rivière par exemple), la part de déplacement passif

peut rester prépondérante y compris pour des individus ayant de bonnes capacités de locomotion (Davidsen et al., 2005). Même lors des déplacements à contre-courant, les poissons peuvent mettre à profit les conditions locales d'hydraulique liées aux turbulences pour limiter l'effort de locomotion voire même brièvement profiter des turbulences comme moyen de locomotion passif (Liao et al., 2003). Lors de leurs déplacements actifs, les poissons peuvent utiliser plusieurs modes de locomotion en fonction des contraintes rencontrées lors du déplacement et de leurs adaptations morphologiques et physiologiques. Le mode de locomotion le plus rependu est la nage (Beamish, 1978). Cependant certaines espèces peuvent aussi utiliser leur capacité de saut (Mirzaei, 2017), de reptation (Legault, 1988), ou d'adhésion au substrat (Kemp et al., 2009; Carvajal-Quintero et al., 2015). Ces modes de locomotion particuliers sont en général utilisés lorsque les capacités de nage des individus ne permettent pas de franchir un obstacle comme, par exemple, une chute d'eau.

#### **1.2 Définition et enjeux écologiques de la migration**

La migration est un cas particulier de déplacement des poissons. Plusieurs définitions de la migration ont été formulées. Lucas et Baras (2001) ont proposé une définition très large de la migration comme étant un déplacement synchronisé d'individus d'une espèce à une échelle plus large que leur territoire quotidien et intervenant à un stade précis de leur cycle de vie. Cette définition est précisée par Dingle et Drake (2007) qui indiquent que la migration est un mouvement qui concerne une grande partie des individus d'une population, qui est unidirectionnel et peut se faire de manière active, en général via la nage dans le cas des poissons, ou en profitant d'un moyen de transport, par exemple le courant. Enfin, Alerstam et al. (2003) insistent sur l'importance de l'expression génique dans le contrôle de plusieurs fonctions nécessaires à la migration telles que les adaptations physiologiques et comportementales ou encore le déclenchement, la durée et l'orientation du mouvement.

La migration entre différents habitats présente plusieurs avantages qui peuvent avoir des répercussions sur le succès reproductif des individus. Tout d'abord l'exploitation de différents habitats peut engendrer des gains métaboliques lorsque la disponibilité des ressources alimentaires est hétérogène, dans l'espace ou dans le temps, entre ces habitats (Gross et al., 1988). Les gains métaboliques peuvent aussi être liés à la réduction de la compétition intra et inter spécifique pour les individus migrant vers un habitat où une nouvelle ressource alimentaire est présente (Chapman et al., 2011a). L'augmentation de taille résultant de cette migration peut alors directement influencer le succès reproductif. En effet les poissons de grande taille sont souvent

plus compétitifs par rapport à leur conspécifiques de plus petite taille. Ainsi, les femelles de grandes tailles ont, en général, une fécondité plus élevée et les réserves énergétiques investies dans les œufs puis larves sont plus importantes ce qui, in fine, augmente la probabilité de survie des larves (Pavlov & Savvaitova, 2008). La migration peut aussi augmenter le succès reproductif à travers la réduction du risque de mortalité des individus. La mortalité peut être due à un changement temporaire de conditions biotiques, par exemple à la présence de prédateurs (Skov et al. 2008), ou abiotiques (température, crue, sécheresse...) au sein d'un habitat particulier (McDowall, 2010).

Cependant le fait de se déplacer entre différents habitats engendre des coûts énergétiques pour les individus migrants, voire augmente leur risque de mortalité. Les coûts énergétiques peuvent être directement liés aux déplacements (McElroy et al., 2012) ou aux adaptations métaboliques liées au changement d'habitat (Bystriansky et al., 2007). Dans le cas extrême des Saumons rouges (Oncorhynchus nerka, Walbaum 1792), qui ne se nourrissent pas lorsqu'ils remontent les rivières vers leurs zones de frayères, plus de 50% des réserves énergétiques peuvent être utilisées pour migrer entre l'estuaire et les zones de frayère (Crossin et al., 2004). Pour cette même espèce, Rand et Hinch (1998) ont quant à eux estimé que des conditions de débit plus élevées que la moyenne pouvaient entrainer une dépense énergétique accrue lors de la migration vers les zones de frayère. Dans certaines conditions cette sur-dépense d'énergie pouvait même atteindre un niveau critique et engendrer des mortalités importantes. Lorsque le changement d'habitat est associé à une métamorphose des individus, une diminution de leur poids et condition peut aussi être observée. C'est en particulier le cas lors de la métamorphose après l'arrivée en rivière depuis l'océan des gobies du genre Sicyopterus. Schoenfuss (1997) et Taillebois et al. (2011) ont associé la diminution de poids, jusqu'à 15% en 36 heures, aux dépenses énergétiques liées à la métamorphose de deux espèces de ce genre. Enfin la migration s'effectue fréquemment le long de corridors ayant une faible emprise géographique. La concentration d'individus au sein de ces corridors peut ponctuellement augmenter le risque de prédation (Syväranta et al., 2009). Ce risque est particulièrement élevé lorsque qu'un obstacle à la migration des poissons entraine une accumulation de ces derniers en aval. La forte abondance de proies qui en résulte peut favoriser des abondances élevées de prédateurs et fortement augmenter le risque de prédation pour les espèces migrantes (Agostinho et al., 2012). Cet impact est d'autant plus marqué que la dépense d'énergie pour atteindre l'aval de l'obstacle et, éventuellement, celle liée aux tentatives de franchissement de ce dernier, peut augmenter la fatigue des individus et les rendre plus vulnérables à la prédation.

À l'échelle évolutive, la stratégie migratoire est sélectionnée si la différence entre succès reproductif et coût de la migration pour les individus migrants est supérieure au succès reproductif des individus résidents (Gross, 1987). Cependant la différence entre succès reproductif et coût de la migration n'est pas constante entre les individus d'une population, voire pendant la vie d'un individu. Cette variabilité explique en partie les phénomènes de migrations partielles de plus en plus décrits chez de nombreuses espèces. En particulier, Tsukamoto et Arai (2001) ont montré que certains individus d'Anguille japonaise (Anguilla japonica, Temmink & Schlegel 1846) ne migraient pas vers l'eau douce après leur arrivée près des côtes. Leur croissance et maturation s'effectuaient alors exclusivement en mer. De nombreuses études ont relié certains traits morphologiques, physiologiques ou comportementaux des individus au caractère migrant ou résident. Pour des populations de Cyprinidés d'eau douce, Skov et al. (2008) ont démontré que les plus grandes Brêmes bordelière (Blicca bjoerkna, Linné 1758) migraient moins que leurs conspécifiques de petite taille entre un lac et une rivière en hiver, probablement du fait de leur plus faible sensibilité au risque de prédation par les Brochets (Esox lucius, Linné 1758). Ces derniers ne migrent en effet pas entre le lac et la rivière où leur abondance est faible. À l'opposé, le caractère migratoire des Gardons (Rutilus rutilus, Linné 1758) présents dans le même système n'était pas relié à leur taille mais à la condition des individus et/ou à leur témérité : les individus en meilleure condition et les plus téméraires étant majoritairement migrants (Brodersen et al., 2008; Chapman et al., 2011b). En outre, une étude récente de Bond et al. (2015) concernant une population d'Omble du Pacifique (Salvenilus malma, Walbaum 1792) a démontré que les individus les plus vieux cessaient leur migration saisonnière entre la rivière et la mer. Ce résultat suggère que le caractère migrant ou résidant n'est pas seulement influencé par des différences de traits phénotypiques entre individus mais peut aussi varier en fonction de l'évolution des traits d'histoire de vie au cours de la vie des individus.

#### **1.3 Les différentes formes de diadromie**

Le cycle de vie diadrome implique une stratégie de migration très particulière. Les espèces diadromes migrent entre les milieux aquatiques d'eau douce et marins à un stade particulier de leur cycle de vie (Figure 1). Les individus de ces espèces effectuent donc des déplacements entre deux habitats aux caractéristiques extrêmement éloignées en termes d'abondance de proies et de prédateurs, de courantologie et de salinité. Trois catégories distinctes de diadromie ont été définies à partir des phases du cycle de vie de ces espèces se déroulant dans les milieux d'eau douce et marin (Myers, 1949). Les espèces anadromes croissent principalement en mer et migrent vers les eaux douces pour s'y reproduire. L'exemple le plus connu d'espèces anadromes est celui

des salmonidés en particulier les Saumons (Figure 1a) des genres Salmo et Oncorhynchus (Dodson et al., 2013) mais aussi de nombreuses autres espèces d'intérêt pour la pêche récréative telles que le Bar rayé (Morone saxatilis, Walbaum 1792) en Amérique du Nord (Secor et al., 1995) ou la grande Alose (Alosa alosa, Linné 1758) en Europe (Baglinière et al., 2003). Les espèces catadromes croissent principalement en eau douce et migrent en mer pour s'y reproduire. Après l'éclosion, les larves pélagiques retournent dans les rivières et les lacs. Le groupe le plus emblématique d'espèce catadromes est celui constitué par les Anguilles (Anguilla ssp. ; Figure 1b) mais certaines espèces d'intérêt pour la pêche récréative sont aussi catadromes telles que le Barramundi (Lates calcarifer, Bloch, 1790) en Australie (Crook et al., 2017). Enfin, les espèces amphidromes (Figure 1c) croissent principalement en eau douce et s'y reproduisent. Pour ces espèces, la phase marine de leur cycle de vie ne concerne que leur stade larvaire. Les gobies du genre Sicyopterus sont parmi les espèces amphidromes les plus emblématiques. Peu d'espèces amphidromes présentent un intérêt pour la pêche récréative du fait de leur petite taille. Cependant, des espèces atteignant plusieurs dizaines de centimètres de long tel que l'Ombre australien Prototroctes maraena (Günther 1864), ont pu être ciblées par les pêcheurs récréatifs dans le passé. La pêche de cette espèce est maintenant interdite du fait de sa raréfaction (Jenkins et al., 2007).



Figure 1 : Description des trois cycles de vie diadromes pour des espèces emblématiques : (a) anadromie chez le Saumon ; (b) catadromie chez l'Anguille et (c) amphidromie chez les gobies du genre *Sicyopterus*.

La reproduction des espèces amphidromes a lieu en eau douce (Delacroix, 1987, Teichert et al., 2013b). Immédiatement après l'éclosion, les larves dont la taille est généralement comprise entre 1 mm et 4 mm dérivent passivement jusqu'à la mer, c'est la migration de dévalaison (Iguchi & Mizuno, 1990; Bell, 2007). Suite à une phase de développement en mer qui peut durer

plusieurs mois (Radtke et al., 1988; Bell et al., 1995; Hoareau et al., 2007), les larves, mesurant alors quelques centimètres, reviennent dans les embouchures des rivières, puis colonisent les habitats d'eau douce sous la forme de juvéniles (Keith et al., 2008), c'est la migration de montaison.

Du fait de ses similitudes avec des caractéristiques propres aux cycles de vie anadrome et catadrome, la définition de l'amphidromie a fait l'objet de nombreux débats. Par exemple Gross (1987) et Bell (2009) considèrent que l'amphidromie n'est qu'un cas particulier d'anadromie pour lequel le retour en eau douce se fait au stade juvénile. Plus récemment, Augspurger et al. (2016) ont rapproché l'amphidromie de la catadromie du fait de la présence d'un stade larvaire pélagique pour les deux cycles de vie et que certaines espèces amphidromes peuvent effectuer des migrations de dévalaison pour la reproduction. La différence entre ces espèces et certaines espèces catadromes se reproduisant en milieu saumâtre ou côtier (Feutry et al., 2011) ne résiderait donc que dans le fait de franchir une certaine limite de salinité pour se reproduire. Malgré ces similarités entre le cycle de vie amphidrome et les cycles de vie catadrome et anadrome ; l'amphidromie est associée à des stratégies écologiques particulières (McDowall, 2007) ce qui justifie qu'elle soit considérée comme une catégorie à part entière. En particulier, la forte capacité de dispersion des larves des espèces amphidromes augmente leur probabilité de colonisation de nouveaux habitats d'eau douce (McDowall, 2010) par rapport aux espèces anadromes. Les espèces catadromes peuvent aussi avoir des capacités de dispersion élevées (Réveillac et al., 2009). Cependant, malgré les similitudes entre les cycles de vie catadrome et amphidrome soulignées par Augspurger et al. (2016) le fait que la reproduction dans deux milieux très différents justifie que ces deux cycles de vie soient différenciés.

# **1.4 Répartition géographique des espèces amphidromes et variabilité de leurs stratégies de migration**

Les espèces amphidromes sont principalement présentes dans les zones tropicales et subtropicales où elles peuvent représenter la majorité de la faune indigène de poissons et de crustacés d'eau douce (McDowall, 1997; Keith, 2003). Cependant l'amphidromie est aussi observée chez des espèces de zones tempérées telles que celles de la famille des Galaxiidae en Nouvelle-Zélande, Patagonie et dans les îles Falkland, ainsi que des Plecoglossidae et Gobiidae au Japon (McDowall, 1988). La plupart des espèces de poissons amphidromes, appartiennent à la famille des Gobiidae et en particulier à la sous famille des Sicydiinae. En effet, plus de 100 espèces de Sicydiinae sont actuellement connues (Taillebois et al., 2014) et de nouvelles espèces sont encore fréquemment décrites (Keith et al., 2015a, 2015b, 2016). Les espèces de Sicydiinae sont communes sur les petites îles tropicales et sub-tropicales, elles sont plus occasionnelles sur des îles de taille plus importante telles que Madagascar (Keith et al., 2011a), l'Australie (Ebner et al., 2012), ou dans les rivières continentales d'Afrique (Harrison, 1993), d'Amérique Centrale (Lyons, 2005) ou d'Asie (Abraham et al., 2011; Nip, 2010).

Les espèces de Sicydiinae sont probablement celles pour lesquelles l'appellation amphidrome apparait la plus appropriée. En effet, la migration diadrome des Sicydiinae est en général observée pour l'ensemble de la population alors que des stratégies alternatives de migration ont été décrites chez de nombreuses autres espèces considérées comme amphidromes. Ainsi, des études basées sur la microchimie des otolithes (Figure 2) menées sur des Gobiidae considérés comme amphidromes des genres Rhinogobius au Japon (Tsunagawa et al., 2009) et Awaous en Australie (Huey et al., 2014) ainsi qu'à Hawaii (Hogan et al., 2014) ont démontré que moins de la moitié des individus étudiés présentent une phase larvaire marine. Pour la majorité des individus, la phase larvaire se déroule dans des zones où la salinité est inférieure à celle de l'eau de mer. Par contre, pour la plupart des espèces Sicydiinae pour lesquelles des études similaires ont été menées (Lord et al., 2011; Tabouret et al., 2011; Taillebois et al., 2015; Teichert et al., 2018), l'ensemble des individus étudiés présentent une phase larvaire marine. La seule exception pour le moment est une étude menée à Puerto Rico par Smith et Kwak (2014a) dans laquelle ils estiment qu'environ 88% des individus de Sicydium spp. ont une phase larvaire marine, les autres 12% réalisant leur développement larvaire dans des zones où la salinité est inférieure à celle de l'eau de mer.



Figure 2 : Photo d'un otolithe d'un gobie du genre *Sicyopterus* de 43 mm de longueur totale capturé en eau douce. La flèche noire indique la position de la marque de métamorphose qui localise la période de transition entre la mer et l'eau douce.

Par contre, la migration de retour depuis les habitats marins, ou éventuellement saumâtres, vers l'eau douce semble être généralisée pour l'ensemble des espèces amphidromes. À ma connaissance, aucune étude n'a décrit une croissance et une maturation d'individus d'une espèce reconnue comme amphidrome sans un retour en eau douce de tous les individus. En résumé, les Sicydiinae ont quasiment tous un cycle de vie amphidrome impliquant une migration vers la mer après l'éclosion en eau douce des larves puis un retour des post-larves et juvéniles en eau douce (Figure 3a).





À une échelle spatiale plus fine, des stratégies de migration alternatives peuvent être observées entre les différents habitats des milieux d'eau douce et marins. En ce qui concerne la migration de dévalaison, des déplacements d'une partie ou de l'ensemble des adultes vers l'aval en période de reproduction ont été observés pour plusieurs espèces telles que *Prototroctes maraena* en Australie (Koster et al., 2013) ou *Galaxias maculatus* (Jenyns 1842) et *Cheimarrichthys fosteri* (Haast 1874) en Nouvelle Zélande (Hickford & Schiel, 2016;

Warburton & Closs, Université de l'Otago, Nouvelle-Zélande com. pers.). La reproduction de ces espèces a lieu dans des zones très proches de la mer, ce qui limite le temps mis par les larves pour atteindre la mer après leur éclosion. Le risque de mortalité des larves pendant la dévalaison pourrait ainsi être réduit. L'hypothèse d'une migration vers l'aval des adultes a été formulée pour certains Gobiidae amphidromes (Fitzsimons et al., 2007), y compris pour certains Sicydiinae (Lord et al., 2011). Cependant, des études plus récentes ciblées sur les mouvements des adultes de Sicydiinae ont démontré qu'aucune migration de reproduction vers l'aval n'était observée (Tabouret et al., 2015; Teichert et al., 2018). Bell (2009) a relié l'absence de migration de reproduction des adultes de Sicydiinae aux risques de blessures voire de mortalité encourus par ces derniers lorsque cette migration vers l'aval engendre le franchissement de chutes d'eau. L'absence de migration de reproduction des adultes peut aussi s'expliquer par le caractère très turbulent et les vitesses d'écoulement élevées dans les cours d'eau des îles peuplées par les Sicydiinae. Valade (2001) a estimé qu'un temps inférieur à une demi-journée était nécessaire pour que des larves de Sicydiinae atteignent la mer depuis des zones de reproduction situées en amont d'un bassin versant de La Réunion, à plus de 20 km de la mer. La réduction potentielle du temps de dévalaison des larves qu'entrainerait une migration de reproduction des adultes vers l'aval serait alors très faible. La migration de dévalaison des Sicydiinae se ferait donc uniquement au stade larvaire entre l'habitat de reproduction et la mer (Figure 3b). Du fait de la très faible taille des larves de Sicydiinae leur migration de dévalaison peut être considérée comme principalement passive.

Les déplacements de larves d'espèces amphidromes entre les milieux marins côtiers et pélagiques n'ont été que très peu étudiés. Les deux hypothèses généralement avancées concernant ces déplacements sont soit une dispersion de la plupart des larves vers le milieu pélagique, soit une rétention de ces dernières en milieu côtier, proche de l'embouchure (Closs et al., 2013). La première hypothèse s'appuie principalement sur les durées de vie en mer élevées et la faible taille des larves à leur arrivée en mer qui limite leur capacité à lutter contre les courants marins et de se maintenir proche des côtes. Cette large dispersion des larves pourrait en partie expliquer la faible structuration génétique généralement observée chez les populations de poissons amphidromes (Fitzsimons et al., 1990; Berrebi et al., 2005; Boseto et al., 2016). L'hypothèse d'une dispersion de la plupart des larves vers le milieu pélagique est aussi appuyée par la capture de deux larves de *Sicyopterus japonicus* (Tanaka, 1909) à environ 30 km des côtes du Japon (Watanabe et al., 2011). À l'opposé, un déplacement des larves vers le milieu pélagique augmenterait leur risque d'expatriation à chaque génération ce qui, à terme, pourrait diminuer le

succès reproducteur des adultes qui se trouve dans un bassin versant. L'hypothèse d'une rétention des larves en milieu côtier s'appuie sur les observations faites par Sorensen et Hobson (2005) qui attribuent au milieu côtier la signature isotopique observée dans les muscles de larves de *Lentipes concolor* (Gill 1860) lors de leur arrivée en eau douce. En résumé, en l'état actuel des connaissances, aucune observation directe ne permet de confirmer ou d'infirmer l'existence d'une migration entre les milieux marins côtiers et pélagiques chez les espèces amphidromes, y compris chez les Sicydiinae (Figure 3b).

Après leur arrivée en eau douce, les juvéniles des espèces amphidromes vont coloniser différents habitats. Le long d'un cours d'eau, une forte structuration des peuplements peut être observée en fonction des capacités de migration de chacune des espèces et de leurs préférences d'habitat (Nelson et al., 1997). Ainsi, de nombreuses espèces n'ayant pas d'adaptions spécifiques pour franchir des obstacles ne sont présentes que dans les secteurs situés en aval des premières chutes d'eau des cours d'eau des petites îles tropicales (McRae, 2007). Les Sicydiinae ayant généralement la capacité de franchir ces chutes d'eau (Schoenfuss & Blob, 2003) leurs adultes sont présents depuis la zone aval jusqu'aux zones amont des bassins versants (Kinzie, 1988; Jenkins & Jupiter, 2011; Teichert et al., 2014c). Les Sicydiinae peuvent donc s'installer, grandir et se reproduire dans l'ensemble des zones des bassins versants (Teichert et al., 2014b). La migration des Sicydiinae entre les différentes zones des bassins versants est donc partielle (Figure 3b). Cette migration à contre-courant est quasi exclusivement active et se fait soit par la nage soit en utilisant un mode de locomotion particulier lié à leur capacité d'adhésion au substrat, à l'aide de leur ventouse située en position ventrale voire de leur bouche, pour le franchissement des chutes d'eau.

# **1.5 Les dynamiques de migration en eau douce des espèces amphidromes tropicales et les enjeux de gestion associés**

Les dynamiques des migration de dévalaison et de montaison, c'est à dire les variations d'intensité des flux d'individus observées à différentes échelles spatio-temporelles, sont encore peu connues pour la plupart des espèces amphidromes tropicales. Or ces dynamiques influencent directement le ratio coûts/bénéfices des stratégies de migration et le succès d'installation des individus au sein des différentes zones des bassins versants (Smith & Kwak, 2014b). Les facteurs biotiques et abiotiques naturels pouvant influencer la dynamique de dévalaison ont été décrits chez plusieurs espèces de Gobies amphidromes, des genres *Awaous, Lentipes* et *Sicydium* aux Antilles et à Hawaii (Lindstrom, 1998; Way et al., 1998; Bell, 2007). Ces auteurs ont observé

une abondance plus élevée de larves dérivant après la tombée de la nuit. Cette dynamique est reliée à une stratégie de réduction du risque de prédation en lien avec l'incapacité des prédateurs à détecter visuellement les larves pendant la nuit. Way et al. (1998) ont aussi observé une augmentation de l'abondance des larves de Lentipes concolor dérivant avec le débit à une échelle saisonnière. La diminution du temps de dévalaison associée aux vitesses de courant plus élevées pendant les forts débits pourrait aussi réduire le risque de mortalité des larves pendant cette phase de leur cycle de vie. Les dynamiques de montaison des juvéniles des espèces amphidromes tropicales n'ont généralement été décrites qu'au niveau des estuaires pour les genres Rhinogobius, Sicydium et Sicyopterus (Delacroix, 1987; Bell et al., 1995; Shiao et al., 2015). Dans toutes ces études, la quantité de juvéniles capturés au niveau des estuaires fluctuait fortement avec la saison. Les abondances les plus élevées étant généralement observées lors du début (Delacroix, 1987; Shiao et al., 2015) ou de la fin de la saison chaude (Bell et al., 1995). Ces dynamiques peuvent en partie s'expliquer par la saisonnalité marquée de la reproduction (Teichert et al., 2014b) et la durée de vie en mer des différentes espèces (Bell et al., 1995; Shiao et al., 2015; Teichert et al., 2016b) qui induit un délai variable entre l'éclosion des larves et leur retour en eau douce. À l'échelle journalière, la montaison des juvéniles est plus importante durant l'après-midi pour Rhinogobius gigas (Aonuma & Chen 1996) et Sicyopterus japonicus au niveau des estuaires de Taiwan et du Japon (Iida et al., 2008; Shiao et al., 2015). L'abondance plus importante de juvéniles en migration pendant l'après-midi peut être liée à certains facteurs abiotiques, en particulier la température de l'eau. En effet les performances locomotrices des poissons sont en général meilleures dans les gammes de températures élevées de leur optimum thermique (Beamish, 1978; Larinier et al., 1992). Enfin, à l'échelle individuelle, Blob et al. (2010) ont suggéré que l'influence de la morphologie de Sicyopterus stimpsoni (Gill 1860) sur ses capacités de franchissement d'obstacle ou d'évitement de la prédation pouvait expliquer la dynamique de montaison des juvéniles. Cette hypothèse est en partie confirmée par les différences de morphologie observées entre adultes de cette même espèce capturés en aval et en amont de chutes d'eau. Les adultes présents dans les habitats amont ont globalement des morphologies associées aux fortes capacités de franchissement d'obstacles (Schoenfuss et al., 2013).

L'accroissement de la population humaine à l'échelle mondiale entraine un besoin grandissant de la demande en eau à des fins agricoles, énergétiques, industrielles ou domestiques (Postel, 2000), ainsi qu'une augmentation des espaces nécessaires aux activités humaines. Répondre à ces besoins passe généralement par de nombreux aménagements sur les cours d'eau tels que la construction d'ouvrages de prélèvement d'eau, l'endiguement des berges ou les rejets de substances polluantes chimiques ou organiques (Tabouret, 2013). Ces impacts ont un effet direct sur la qualité et la quantité des habitats disponibles pour les organismes vivants dans ces cours d'eau et, de ce fait, altèrent le fonctionnement de leurs populations (Karr, 1981). En particulier, les activités humaines peuvent artificiellement amplifier ou au contraire diminuer le rôle des facteurs biotiques et abiotiques naturels influençant les dynamiques des migrations de dévalaison et de montaison (Kinzie et al., 2006; Tabouret, 2012; Miles et al., 2013). L'endiguement des berges peut entrainer une uniformisation des habitats et des vitesses d'écoulement en réduisant les zones turbulentes. Cette uniformisation peut avoir des conséquences néfastes sur la dévalaison des larves d'espèces amphidromes en favorisant leur décantation lors des périodes de bas débits comme l'ont observé Worthington et al. (2014) pour les œufs semi flottants de cyprinidés dérivant dans une rivière d'Amérique du Nord. Les rejets de substances polluantes peuvent aussi altérer la migration des espèces amphidromes. Par exemple, Maes et al. (2008) ont démontré que les zones où la concentration en oxygène dissout était très faible agissaient comme des barrières de migration pour l'Alose feinte (Alosa fallax, Lacepède 1803) dans une rivière fortement polluée de Belgique. Il est probable que la détérioration de la qualité chimique de l'eau impacte de manière similaire la montaison des juvéniles d'espèces amphidromes (Jenkins et al., 2010). Les ouvrages de prélèvement d'eau peuvent avoir des effets particulièrement importants sur les dynamiques de migration des espèces amphidromes notamment à travers la diminution, voire la restriction de l'accessibilité des habitats en amont des seuils et barrages<sup>2</sup> (Holmquist et al., 1998; Cooney & Kwak, 2013), ou la réduction et la dégradation de l'habitat disponible en aval des prélèvements d'eau. La diminution de la disponibilité en habitats en aval d'un prélèvement d'eau peut amplifier les phénomènes de compétition pour l'accès aux ressources alimentaires et/ou aux habitats de refuge et reproduction et augmenter le nombre de juvéniles forcés à migrer vers l'amont. À l'inverse, un prélèvement d'eau peut diminuer la quantité de larves dévalant vers l'aval par piégeage des larves et le barrage associé à ce dernier peut aussi restreindre le nombre d'individus pouvant accéder aux habitats situés en amont. Le ratio coûts/bénéfices des stratégies de migration et le succès d'installation des individus au sein des différentes zones des bassins versants peuvent donc être fortement modifiés par les activités d'origine anthropique.

<sup>&</sup>lt;sup>2</sup> D'après le Service d'Administration Nationale des Données sur l'Eau un seuil est un ouvrage fixe ou mobile qui barre tout ou partie du lit mineur du cours d'eau alors qu'un barrage barre plus que le lit mineur.

#### 1.6 Les deux espèces de Sicydiinae de La Réunion

#### 1.6.1 Biologie et écologie de *Sicyopterus lagocephalus* et de *Cotylopus acutipinnis* à La Réunion

Les Cabots bouche-ronde, Sicyopterus lagocephalus (Pallas 1770 ; Figure 4a), espèce cosmopolite présente des Comores jusque dans l'est de l'Océan Pacifique (Keith et al., 2005a; Figure 4c) et Cotylopus acutipinnis (Guichenot 1863; Figure 4b), espèce endémique des Mascareignes (Keith et al., 2005b; Figure 4c), sont des Sicydiinae amphidromes. Ils constituent près de 90% des abondances de poissons observées dans les rivières de La Réunion (Olivier et al., 2004). Cette présence en sympatrie d'une ou plusieurs espèces endémiques et de S. lagocephalus est commune pour cette espèce au sein de son aire de répartition (Keith et al., 2005a; Lord et al., 2010). Jusqu'à présent, les études comparant les traits de vie d'espèces de Sicydiinae cosmopolites et endémiques se sont focalisées sur les durées de vie larvaire ou sur la comparaison de leur déplacement entre différentes zones des cours d'eau sur plusieurs îles. Ainsi, Lord et al., (2010) ont démontré que les durées de vie larvaire de S. lagocephalus étaient généralement plus élevées que celles de Sicyopterus aiensis (Keith, Watson & Marquet 2004), espèce endémique du Vanuatu, ou de Sicyopterus sarasini (Weber & de Beaufort 1915), espèce endémique de Nouvelle-Calédonie. À l'opposé, Taillebois et al. (2012) ont démontré que la durée de vie en mer de Sicyopus zosterophorum (Bleeker 1856), espèce cosmopolite de l'Océan Pacifique, n'était pas significativement différente de celles de Smilosicyopus chloe (Watson, Keith & Marquet 2001), espèce endémique du Vanuatu et de Nouvelle-Calédonie, et d'Akihito vanuatu (Watson, Keith & Marquet 2007), espèce endémique du Vanuatu. Pour ces six espèces, différents profils de variation des ratios de barium :calcium et strontium :calcium ont été observés dans les otolithes des adultes en eau douce (Lord et al., 2011; Taillebois et al., 2015). Ces auteurs ont interprété ces variations comme pouvant être liées à différentes stratégies de déplacement des individus en eau douce. Cependant aucune tendance marquée n'apparait entre espèces cosmopolites et endémiques, les différences observées sont plutôt reliées à des stratégies individuelles. Les connaissances acquises lors de travaux précédents sur la biologie et l'écologie des Cabots bouche-ronde (Teichert, 2012) sont plus exhaustives. En effet plusieurs traits d'histoire de vie de ces deux espèces peuvent être comparés. C'est en particulier le cas de la durée de vie en mer (Hoareau et al., 2007; Teichert et al., 2012, 2016b) et des stratégies de reproduction (Teichert et al., 2014b, 2016a) et d'utilisation de l'habitat (Teichert et al., 2013b, 2014c). A l'heure actuelle, le lien entre ces différents traits d'histoire de vie et les stratégies de déplacement et migration de ces deux espèces reste un sujet d'étude.



Figure 4 : Photographies de mâles de *S. lagocephalus* (a) et de *C. acutipinnis* (b). Aires de répartitions (c)
de *S. lagocephalus* (en bleu, d'après Lord et al., 2012) et *C. acutipinnis* (en orange, d'après Keith et al., 2005b). Crédits photos : Raphaël Lagarde.

Les Cabots bouche-ronde se reproduisent principalement dans les parties lotiques des cours d'eau (Teichert et al., 2013b). Lors de la reproduction, le mâle creuse un nid sous les blocs et galets où la femelle vient déposer ses œufs sous forme de patchs qui adhèrent au substrat. Le mâle féconde ensuite les œufs et garde le nid jusqu'à l'éclosion des larves (Teichert et al., 2013a). La fécondité des deux espèces est comparable avec environ 13 500 et 15 000 ovocytes par gramme de femelle respectivement pour *S. lagocephalus* et *C. acutipinnis*. Leur taille (longueur totale,  $L_T$ ) à première maturité varie selon les saisons de 43 à 55 mm  $L_T$  pour *S. lagocephalus* (Teichert et al., 2014b) et de 28 à 37 mm  $L_T$  pour *C. acutipinnis* (Teichert et al., 2016a). La période de reproduction est principalement contrôlée par la température et aucun développement ovarien n'a été observé pour des températures moyennes de l'eau inférieures à 18°C et 17°C respectivement pour *S. lagocephalus* et *C. acutipinnis* (Teichert et al., 2016a). Le contrôle de la période de reproduction par la température engendre une variabilité spatio-temporelle de la saison de reproduction au sein des bassins versants avec une reproduction tout au long de l'année dans les zones aval alors que la reproduction est limitée à l'été austral dans les zones situées audessus de 50 à 100 m d'altitude (Teichert et al., 2014b, 2016a).

Immédiatement après l'éclosion, les larves, mesurant environ 2 mm, dérivent passivement jusqu'à la mer. Leur capacité de nage est limitée par leur taille et leur comportement se limite à une alternance de nage active vers la surface suivie d'une décantation passive (Bell & Brown, 1995). Leur développement en eau douce est contraint et les larves meurent si elles n'atteignent pas la mer entre deux à sept jours après leur éclosion (Valade et al., 2009).

L'arrivée en eau douce des individus à la fin de leur stade larvaire a lieu toute l'année avec des périodes préférentielles allant d'octobre à janvier pour *S. lagocephalus* et de mai à septembre pour *C. acutipinnis* (ARDA, 2012; Teichert et al., 2012, Figure 5). Lors de leur arrivée en eau douce, les post larves ou juvéniles de *S. lagocephalus* sont âgés de trois à dix mois et mesurent entre 27 et 37 mm  $L_T$  (Teichert et al., 2016b) alors que ceux de *C. acutipinnis* sont âgés de deux à six mois et mesurent entre 17 et 23 mm  $L_T$  (Teichert et al., 2012). Ces variations de taille et d'âge lors de l'arrivée en eau douce sont saisonnières. Les individus qui passent le début de leur vie en mer lors de l'été austral retournent plus rapidement en eau douce et présentent une taille plus faible que ceux qui passent le début de leur vie en mer lors de l'hiver austral (Teichert et al., 2012, 2016b).



Figure 5 : Diagramme de distribution des périodes de fortes (en noire), moyennes (en gris) et faibles (en blanc) abondances de juvéniles arrivant en eau douce pour *S. lagocephalus* et *C. acutipinnis* (adapté d'après ARDA (2012) et Teichert et al. (2012)).

Outre la nage, les Cabots bouche-ronde ont des capacités de franchissement uniques qui leur permettent de franchir les chutes d'eau lors de leur migration de montaison (Voegtlé et al., 2002). Cette capacité de franchissement est principalement liée à la ventouse ventrale issue de la fusion des deux nageoires pelviennes. Deux modes de locomotion permettant le franchissement d'obstacles ont été décrits parmi les Sicydiinae : les modes « inching » et « power-burst » (Schoenfuss & Blob, 2003). Lors d'un franchissement d'obstacle un poisson utilisant le mode « inching» s'agrippe dans un premier temps au substrat à l'aide de sa bouche située en position inférieure. Dans un deuxième temps, il rapproche sa ventouse de la bouche et la fixe sur le substrat afin de pouvoir déplacer sa bouche vers l'avant. Lors de l'ensemble de ce cycle, des mouvements de faible amplitude du pédoncule caudal et des nageoires pectorales peuvent avoir lieu. Le mode « power-burst » consiste en une alternance de phases très actives où le poisson utilise des mouvements de forte amplitude de son pédoncule caudal et de ses nageoires pectorales

pour progresser, suivie de phases de repos pendant lesquelles ce dernier se maintient au substrat grâce à sa ventouse. Les premières observations réalisées sur les Sicydiinae de La Réunion ont montré que *S. lagocephalus* utilise le mode « inching » alors que *C. acutipinnis* utilise le mode « power-burst » (Keeffe et al., 2017).

Les Cabots bouche-ronde ont une sélectivité pour l'habitat de croissance peu marquée, des individus étant présents à la fois dans les parties lentiques et lotiques des cours d'eau (Teichert et al., 2014c). Le régime alimentaire de *S. lagocephalus* est principalement composé des microalgues composant le périphyton (Bielsa et al., 2003). Celui de *C. acutipinnis* est proche quoique plus diversifié, ces derniers pouvant occasionnellement se nourrir d'invertébrés benthiques (L. Faivre, Hydrô Réunion & G. Gassiole, MicPhyc; données non publiées).

### 1.6.2 Description des principales pressions d'origine naturelle s'exerçant sur S. lagocephalus et C. acutipinnis dans les cours d'eau de La Réunion

Comme de nombreuses îles volcaniques, La Réunion présente un relief abrupt et son climat est soumis à des variations extrêmes et relativement stochastiques. Le relief abrupt des massifs réunionnais est à l'origine de nombreuses chutes d'eau (Figure 6), appelées localement « cassés », dont certaines peuvent atteindre plus de 200 m de hauteur (DEAL, 2011). Ces chutes d'eau peuvent entrainer une fragmentation marquée des habitats d'eau douce, voire rendre certaines zones de cours d'eau inaccessibles pour la plupart des espèces de poissons indigènes à l'exception des Sicydiinae du fait de leurs capacités de franchissement des obstacles décrites précédemment. Cependant certaines chutes entravent de manière significative leur migration et peuvent avoir un impact marqué sur la structure des populations de Cabots bouche-ronde (Teichert et al., 2014a).



Figure 6 : Localisation des principales chutes naturelles sur les 13 rivières pérennes de l'île de La Réunion à partir de l'étude DEAL (2011).

Le climat de La Réunion présente une saisonnalité marquée avec l'alternance d'une saison sèche pendant l'hiver austral et d'une saison humide lors de l'été austral. Des évènements extrêmes peuvent survenir au sein de ces deux saisons. C'est en particulier le cas pour les précipitations qui peuvent être très faibles pendant de longues périodes lors de la saison sèche ou, au contraire, très intenses sur de courtes périodes lors des épisodes cycloniques de la saison humide. La pente élevée associée à la faible surface des bassins versants amplifient l'effet des crues liées à ces précipitations intenses. Ceci peut entrainer des détériorations majeures des habitats d'eau douce allant de l'asséchement total lors de la saison sèche (Figure 7a) à une forte déstructuration lors des crues cycloniques (Figure 7b). Ces crues peuvent atteindre des débits extrêmement élevés allant jusqu'à plus de 300 fois la valeur du débit moyen du cours d'eau (Robert, 1986). L'effet des crues cycloniques peut être très important sur les populations de poissons. Chen et al. (2015) ont décrit une diminution de l'abondance d'une espèce de Cyprinidae, Onychostoma barbatulum (Pellegrin 1908) après une crue cyclonique, en particulier pour les classes de taille les plus petites. Après le cyclone Iniki à Hawaii, Fitzsimons et Nishimoto (1995) ont observé un comportement territorial accru associé à une baisse du comportement de parade nuptiale des mâles de S. stimpsoni. Ces comportements peuvent sans doute être liés à la diminution des ressources alimentaires après le cyclone. La protection des ressources

alimentaires présentes sur leur territoire quotidien deviendrait alors prioritaire pour les individus par rapport à leur activité de reproduction.



Figure 7 : Illustrations d'une zone de cours d'eau asséchée (**a**) et d'une rivière en crue lors d'un épisode cyclonique (**b**). Crédits photos : a) Pierre Valade, Ocea Consult' ; b) Office de l'Eau Réunion.

Enfin les éruptions volcaniques peuvent aussi impacter les cours d'eau des îles volcaniques tropicales. Cependant pour que ces dernières atteignent les cours d'eau, il faut qu'elles soient d'intensité exceptionnelle ce qui est très peu fréquent actuellement à La Réunion. Par exemple, le dernier épisode volcanique intense, l'explosion de Bellecombe, date d'environ 4 500 ans (Gillot & Nativel, 1989).

À ces pressions abiotiques naturelles viennent s'ajouter des pressions biotiques liées à la compétition inter et intra spécifique et à la prédation. L'effet de la compétition intra spécifique sur les populations de Sicydiinae et leur dynamique de migration a été abordé pour *S. stimsoni* à Hawaii (Julius et al., 2005). Les adultes, en particulier les mâles, de cette espèce étant territoriaux, les juvéniles qui arrivent en rivière sont exclus des habitats de croissance et de reproduction les plus favorables (Fitzsimons et al., 1993, 2003). Cette compétition entre adultes et juvéniles entraine une augmentation du comportement de migration des juvéniles jusqu'à ce qu'ils atteignent des zones d'habitats propices non occupées par un adulte. Aucune étude n'a été menée à ce sujet à La Réunion cependant, étant données les abondances élevées de Cabots boucheronde, i.e. de un à plus de 10 individus par mètre carré (Olivier et al., 2004), il est possible que la compétition intra et inter spécifique joue un rôle important dans la structuration des populations et les dynamiques de migration. Pour comparaison, les abondances des espèces de Sicydiinae observées à Palau, à Puerto Rico et en Guadeloupe sont rarement supérieures à un individu par mètre carré (Nelson et al., 1997; Fièvet et al., 1999; Smith & Kwak, 2015). Dans les cours d'eau d'Hawaii, ces abondances peuvent toutefois atteindre quatre à huit individus par

mètre carré (Way et al., 1998). L'effet de la prédation a souvent été avancé pour expliquer la structure des peuplements de Sicydiinae sur plusieurs îles tropicales telles que la Micronésie (Nelson et al., 1997), Hawaii (McRae, 2007) ou Puerto Rico (Kwak et al., 2016). Selon cette hypothèse, les abondances plus importantes de Sicydiinae observées en amont des premiers obstacles s'expliqueraient par l'absence de pression de prédation sur ces populations, les principaux prédateurs des Sicydiinae n'ayant pas la capacité de franchir ces obstacles. Dans le cas de La Réunion, cette hypothèse est sans doute à nuancer car l'espèce piscivore la plus abondante, l'anguille marbrée *Anguilla marmorata* (Quoy & Gaimard 1824) a la capacité de franchir des chutes d'eau de plusieurs mètres de haut (Olivier et al., 2004; Lagarde et al., 2017) et se retrouve donc couramment jusqu'à plus de 600 m d'altitude.

## 1.6.3 États des lieux des pressions d'origine anthropique s'exerçant sur S. lagocephalus et C. acutipinnis dans les cours d'eau de La Réunion

La pêche traditionnelle des gobies amphidromes lors de leur arrivée en rivière est très largement répendue dans leur aire de répartition et a été décrite en Indonésie (Manacop, 1953), aux Philippines, à Hawaii, aux Antilles et Amérique centrale (Bell, 1999) ou encore à Taiwan (Shiao et al., 2015). À La Réunion, les Cabots bouche-ronde, alors appelés bichiques, font l'objet d'une pêcherie traditionnelle (Figure 8) lors de leur arrivée dans les rivières de l'île depuis plus de deux siècles (Vaillant, 1890; Aboussouan, 1969). Originellement, deux méthodes de pêche étaient utilisées : la capture des individus en mer à l'aide de filets fabriqués en toile et trainés par le pêcheur en marchant ou nageant, ou la capture des individus dans les premiers mètres de rivière à l'aide de nasses, ou « vouves », fabriquées à partir de fibres végétales et placées à l'extrémité amont d'un canal façonné par les pêcheurs à l'aide de galets et de plantes (Vaillant, 1890). Les méthodes de pêche ont peu évolué depuis (Barat, 1977; Schübel, 1998). Cependant de nouveaux matériaux ont été intégrés dans la construction des filets, vouves et canaux. Ainsi les filets des pêcheurs en mer sont actuellement fabriqués en filet à moustiquaires et les vouves peuvent être constituées d'une armature métallique recouverte de filet à moustiquaires (Schübel, 1998). Enfin l'intégration de matière plastique pour étanchéifier les canaux est de plus en plus commune (Schübel, 1998). Qui plus est, la mise en place d'équipes de pêche mobiles en mer se déplaçant entre plusieurs sites a été grandement facilitée depuis l'arrivée des téléphones cellulaires qui permettent une circulation rapide des informations concernant les quantités de bichiques au niveau de chaque embouchure (P. Valade; Ocea consult', communication personnelle). L'activité de pêche est réglementée par les arrêtés préfectoraux N°1742 du 15 juillet 2008 pour

la pêche professionnelle en mer et N°1743 du 15 juillet 2008 pour la pêche amateure en rivière. La pêche en mer ne doit pas se faire au droit de l'embouche et jusqu'à 100 m de part et d'autre des bras de rivières. Les filets utilisés ne doivent pas dépasser une surface de 25 m<sup>2</sup>. En rivière, la pêche ne peut se faire qu'avec des vouves construites en fibres végétales dont le diamètre d'ouverture ne dépasse pas 80 cm. Un canal situé au centre de l'embouchure doit être laissé libre de toute activité de pêche. La pêche est interdite entre la nouvelle et la pleine lune de mars. A l'heure actuelle cette réglementation n'est pas respectée sur la plupart des embouchures de l'île. Qui plus est, l'activité de pêche aux bichiques est partagée entre des pêcheurs professionnels, qui n'ont aucune obligation de déclarer leurs prises, et des pêcheurs « amateurs », qui revendent souvent illégalement les produits de leur pêche. De ce fait, aucune estimation fiable des quantités de bichiques pêchées n'est disponible (Barat, 1977; Hoareau, 2005).

Plus en amont, environ 70 obstacles anthropiques susceptibles d'entraver la migration des Sicydiinae ont été recensés sur les 13 principaux bassins versants de l'île (Figure 8, DEAL, 2011). Cette altération généralisée de la continuité biologique est supposée avoir un impact négatif sur l'abondance des populations d'espèces amphidromes et catadromes y compris celles de Sicydiinae (Mérigoux et al., 2012). Cet impact se traduit principalement par la réduction de l'abondance des Sicydiinae en amont des obstacles du fait des difficultés de leur franchissement. La présence d'obstacles d'origine anthropique est très fréquente au sein des différentes îles où les Sicydiinae sont présents (Benstead et al., 1999; Concepcion & Nelson, 1999; Brasher, 2003; March et al., 2003; Cooney & Kwak, 2013). La plupart des études décrivant l'impact des obstacles d'origine anthropique sur les populations de Sicydiinae ont été orientées sur la comparaison des abondances observées en aval et en amont des barrages. Ainsi, en fonction de la hauteur des ouvrages et de leur mode de gestion, ces derniers peuvent réduire de faiblement jusqu'à quasi-totalement le nombre d'individus accédant aux habitats amont (Holmquist et al., 1998; Cooney & Kwak, 2013). Cependant, pour que la restriction du nombre d'individus accédant aux habitats en amont soit quasi-totale, la dimension des ouvrages doit être très importante (i.e. hauteur supérieure à 30m; Cooney & Kwak, 2013) ou leur mode de gestion doit entrainer une absence chronique de débit de surverse sur le parement de ces derniers (Holmquist et al., 1998). Ces deux conditions ne sont, à l'heure actuelle, rencontrées sur aucun des ouvrages présents à La Réunion (DEAL, 2011).

Lorsqu'un prélèvement d'eau est associé au barrage, la structure des peuplements en aval peut aussi s'en trouver modifiée avec notamment une diminution de l'abondance et de la proportion relative de Sicydiinae dans les tronçons de cours d'eau situés en aval des prélèvements d'eau (March et al., 2003). Cette altération de la structure des peuplements en aval des prélèvements d'eau s'explique en partie par la modification des caractéristiques physiques de l'habitat et la réduction de la quantité d'habitat disponible. Dans certain cas, les prélèvements d'eau peuvent aussi contribuer à l'assèchement des tronçons de cours d'eau situés en aval. L'effet des prélèvements d'eau sur la migration de dévalaison des espèces amphidromes n'a été abordé que par Benstead et al. (1999). Cette étude, qui concernait des espèces de crustacés Atyidae et Palaemonidae, a conclu qu'une part importante des larves pouvait être entrainée avec l'eau prélevée. Cette eau étant destinée à des usages domestique et agricole, et aucun rejet dans la rivière n'ayant lieu, la mortalité des larves emportées dans le prélèvement était considérée comme totale. Ces résultats sont probablement extrapolables aux larves de Sicydiinae de la Réunion puisque qu'environ 130.10<sup>6</sup> m<sup>3</sup> d'eau sont prélevés chaque année dans les rivières (OLE, 2017).





Enfin, plusieurs espèces exotiques ont été introduites volontairement ou accidentellement dans les cours d'eau de La Réunion. Certaines de ces espèces comme le Guppy (Poecilia reticulata, Peters 1859) et le Porte épée (Xiphophorus hellerii, Heckel 1848), sont régulièrement observées dans les zones aval et intermédiaire de la plupart des bassins versants de La Réunion (Ocea Consult', 2014). D'autres sont observées plus occasionnellement et leur répartition entre et au sein des bassins versants est plus restreinte. C'est le cas notamment des Tilapias (Oreochromis ssp.), du Nigro (Amatitlania nigrofasciata, Günther 1867) ou de la Truite arc en ciel (Oncorhynchus mykiss, Walbaum 1792). Ces espèces exotiques peuvent potentiellement affecter les populations de Sicydiinae via la compétition pour l'accès à l'habitat et aux ressources alimentaires ou la prédation. A l'heure actuelle, aucune étude n'a montré qu'il existait des interactions compétitives ou de prédation entre les Sicydiinae et les espèces exotiques à La Réunion. La compétition entre les Sicydiinae et les espèces exotiques concerne probablement les espèces de petite taille (Guppy et Porte épée) et les stades juvéniles des espèces de plus grande taille. Les Truites arc en ciel et les Tilapias adultes peuvent aussi être des prédateurs potentiels des Sicydiinae. Dans une étude réalisée aux îles Fidji, Jenkins et al. (2010) ont montré que la présence de Tilapia avait un impact négatif sur la diversité d'espèces indigènes amphidromes. Ces auteurs ont principalement attribué cette observation à la prédation des Tilapias sur les individus de petite taille.

## 1.6.4 Prévision d'évolution de ces pressions dans un contexte d'accroissement démographique et de changements climatiques

En 2016, le nombre d'habitants à La Réunion s'élevait à environ 850 000 personnes (Insee, 2017) et il a été estimé que ce nombre devrait dépasser 1 000 000 de personnes d'ici 2030 (Sandron, 2013). A l'heure actuelle, les prélèvements d'eau superficielle représentent plus de 60% de l'eau consommée par les particuliers, l'agriculture et l'industrie (OLE, 2017). Qui plus est, environ 15% de l'énergie électrique produite à La Réunion provient de l'hydro-électricité (DEAL, 2013). Dans ce contexte, la croissance démographique de La Réunion devrait accroitre les pressions d'origine anthropique sur les milieux aquatiques d'eau douce. Même si aucune nouvelle construction de barrage n'est plannifiée, une augmentation des volumes d'eau prélevés au niveau de chaque aménagement devrait être observée. Cependant cette tendance est à nuancer. En effet sur la période 2013-2015, l'augmentation des volumes d'eau consommés n'a pas été aussi élevée que prévu. Ceci peut s'expliquer en partie par l'amélioration des rendements des réseaux d'adduction en eau potable et par une baisse de la consommation moyenne par habitant probablement liée à l'augmentation du prix de l'eau (OLE, 2017). De plus, l'application progressive des réglementations environnementales imposant la restitution d'un débit plus élevé
en aval des ouvrages de prélèvement d'eau et la restauration de la continuité biologique (montaison et dévalaison) au droit des ouvrages devrait permettre de limiter les impacts écologiques des prélèvements d'eau. En effet ces réglementations sont censées limiter la perte d'habitat liée à la diminution de débit en aval des prélèvements d'eau et restaurer l'accessibilité des habitats en amont pour les juvéniles et adultes ainsi que la dévalaison des larves vers l'aval. Ce dernier point reste à l'heure actuelle problématique du fait du manque de solutions techniques permettant d'empêcher l'entrainement des larves, en particulier celles de Sicydiinae, avec l'eau prélevée et du manque de connaissances fines de leur dynamique de dévalaison qui permettraient la mise en place d'arrêts de prélèvement ciblés sur les périodes de dévalaison principales. Des travaux expérimentaux de recherche appliquée, financés par l'Agence Française pour la Biodiversité (AFB), le Fond Européen de Développement Régional (FEDER) et le Parc National de La Réunion (PNR), ont été récemment initiés à Hydrô Réunion pour développer des solutions techniques permettant d'exclure physiquement les larves de la proportion d'eau prélevée. Les résultats préliminaires indiquent que l'efficacité de ces solutions est faible, le pourcentage de larves exlues de l'eau prélevée étant négligeable. Les résultats issus des études menées sur la dynamique de dévalaison des larves de Sicydiinae dans le cadre de cette thèse pourront permettre d'évaluer la faisabilité et la pertinence d'éventuels arrêts ciblés des prélèvements. Enfin des actions spécifiques visant à diminuer l'impact des pêcheries de bichiques sont en cours de développement par les associations de pêcheurs de bichiques de la rivière du Mât avec l'appui des services de l'état et du bureau d'étude Ocea Consult' (Ocea Consult' & FPTBRM, 2015; Ocea Consult' & PPEE-RDM, 2015). Ces actions ont pour but de limiter l'impact de l'aménagement des canaux de pêche sur les milieux aquatiques, de faire appliquer la réglementation en vigueur et, à terme, d'estimer l'efficacité des pêcheries à partir de la comparaison entre la quantité de bichiques pêchée et celle qui accède aux habitats en amont des pêcheries. Lorsque ces actions seront généralisées aux principales rivières de l'île, elles devraient favoriser l'accès des juvéniles aux habitats situés en amont des pêcheries ce qui a terme pourrait se traduire par une augmentation de la population d'adultes reproducteurs.

Depuis plusieurs décennies l'Océan Indien a connu une augmentation continue de la température à la surface de l'eau. Cette température a augmenté d'un à deux degrés dans le sudouest de l'Océan Indien entre 1960 et 1999 (Alory et al., 2007). Bien que les mécanismes à l'origine des différences d'intensité de ce réchauffement observées à l'échelle régionale soient encore controversés (Dong & McPhaden, 2016), ce dernier peut avoir des répercussions directes sur le fonctionnement des milieux aquatiques. En ce qui concerne le stade larvaire des Sicydiinae, l'augmentation de la température de l'eau de mer pourrait influencer la vitesse de croissance des larves et, in fine, pourrait se traduire par une diminution de la durée de la phase larvaire (Teichert et al., 2016b). Ceci pourrait limiter les risques de mortalité associés à ce stade. Cependant, l'augmentation de la température à la surface de l'eau peut entrainer une diminution des échanges de masses d'eau entre la surface et les zones plus profonde ce qui réduit la production planctonique (Roxy et al., 2016). La quantité de proies disponibles pour les larves de Sicydiinae pourrait ainsi être réduite alors que les besoins nutritionnels des larves augmentent avec la température (Houde, 1989). Qui plus est, la durée de la période de nourrissage mixte (i.e. période pendant laquelle les larves peuvent se nourrir à la fois à partir de proies exogènes et de leur réserves endogènes) diminue avec la température (Teichert et al., données non publiées). Ainsi, l'augmentation de la température de l'eau pourrait diminuer la probabilité de survie des larves lors de leurs premiers jours de vie en mer. Les larves auraient une période plus courte avant de trouver une source de nourriture exogène qui serait elle-même plus rare. En outre, Webster et al. (2005) ont montré que même si l'augmentation de la température de la surface des océans n'est pas corrélée à une augmentation de la fréquence des cyclones, les cyclones de très forte intensité pourraient être plus fréquents. Les crues d'intensité exceptionnelle associées aux cyclones très intenses, et pouvant significativement détériorer les habitats aquatiques, pourraient donc être plus fréquentes. Parallèlement une diminution des précipitations moyennes a été observée dans le sudouest de l'Océan Indien depuis 1961 (Vincent et al., 2011). Le déficit de précipitation pourrait être à l'origine d'étiages plus marqués et de l'augmentation de la fréquence et de l'emprise des assèchements de cours d'eau.

La prévision de l'évolution de l'impact que les espèces exotiques pourraient avoir sur les Sicydiinae est plus incertaine. L'augmentation démographique devrait accroitre le risque d'introduction accidentelle de nouvelles espèces. De nombreuses espèces exotiques présentes dans les cours d'eau comme le Nigro et plans d'eau de La Réunion comme le Néon du Pauvre (*Tanichthys albonubes*, Lin 1932) ou le Guapode tigre (*Parachromis managuensis*, Günther 1867) sont probablement issues d'introductions ponctuelles dans le milieu naturel par des aquariophiles amateurs. Le nombre d'aquariophiles devrait augmenter en même temps que la démographie entrainant un risque accru d'introductions accidentelles d'espèces exotiques. Cette tendance est illustrée par la récente découverte d'une espèce de crustacé exotique, la crevette « Red Cherry » (*Neocaridina davidi*, Bouvier 1904) sur le bassin versant de la rivière du Mât (Clicanoo.re, 2017). La présence de cette espèce très prisée des aquariophiles est en effet probablement due à une introduction. Qui plus est, l'augmentation de l'artificialisation des

milieux liée aux diverses pressions d'origine anthropique (i.e. prélèvement d'eau, aménagement des bassins versants, pollutions...) pourrait aussi être plus favorable aux espèces exotiques qu'aux espèces indigènes (Bunn & Arthington, 2002). Cependant l'augmentation de la fréquence des évènements catastrophiques tels que les crues ou les assèchements de cours d'eau pourrait avoir un impact fort sur les populations d'espèces exotiques. En effet ces espèces sont, jusqu'à présent, exclusivement d'eau douce. En cas de détérioration ponctuelle de leur habitat aucune recolonisation des cours d'eau par des individus présents en mer, comme c'est le cas pour les espèces indigènes diadromes, ne sera possible.

### 1.7 Objectifs et organisation de la thèse

L'objectif général de la thèse est d'acquérir des connaissances fondamentales sur l'écologie et les dynamiques de migration en eau douce de *S. lagocephalus* et *C. acutipinnis*. Plus précisément, il s'agit de relier les dynamiques de migration en eau douce aux différents traits d'histoire de vie et à la structure des peuplements décrits lors d'études précédentes. Ces études antérieures avaient permis de décrire des points clefs du cycle de vie de ces deux espèces, ponctuellement dans l'espace et le temps, mais sans intégrer les phases de migration des différents stades de développement et entre les habitats. Les dynamiques de migration lors de la dévalaison et de la montaison seront donc ici étudiées au regard des modes de locomotion particuliers utilisés par les Sicydiinae lors de ces déplacements. Ceci permettra de décrire certains mécanismes à l'origine des dynamiques de migration observées et d'émettre des hypothèses sur les stratégies écologiques sous-jacentes.

In fine, ces connaissances pourront être utilisées pour proposer des mesures de gestion spécifiques de ces populations ciblées sur pressions impactantes pour les migrations de montaison et de dévalaison (Figure 9). Il pourrait s'agir par exemple de définir des périodes de fonctionnement optimal des passes à poissons ou bien de développer des adaptations des passes à poissons existantes pour mieux répondre aux différentes exigences inter et intra spécifiques. Ces études pourraient aussi permettre de décrire la fraction de la population se présentant au pied des obstacles anthropiques n'ayant pas la capacité de les franchir. La description de la dynamique de dévalaison des larves pourrait permettre de proposer des mesures de gestion des ouvrages de prélèvement d'eau adaptées à cette étape du cycle de vie. Une attention particulière sera ainsi apportée, dans le présent travail, à l'évaluation de l'efficacité et à la faisabilité d'éventuels arrêts ciblés des prélèvements d'eau à l'échelle journalière et/ou saisonnière.



Figure 9 : Synthèse des différents impacts anthropiques s'exerçant sur les populations de Sicydiinae à La Réunion. Effets sur les dynamiques de montaison (**A**) et de dévalaison (**B**). Les flèches bleues représentent les déplacements de migration, les flèches rouges l'effet des impacts anthropiques et les flèches violettes l'accès des juvéniles à leurs habitats de croissance et de reproduction.

Le mémoire de thèse est articulé autour de trois chapitres. Le premier chapitre permet de replacer les communautés de poissons et de macro-crustacés indigènes de La Réunion dans un contexte régional. Il s'agit en particulier de comparer l'influence des facteurs environnementaux sur la structure des peuplements de poissons et de macro-crustacés de La Réunion et de Mayotte. Le deuxième et le troisième chapitre du mémoire de thèse concernent respectivement les dynamiques de dévalaison et de montaison en eau douce de *S. lagocephalus* et *C. acutipinnis.* Dans un premier temps, la phénologie de ces dynamiques sera décrite. Dans un deuxième temps l'effet des facteurs environnementaux, populationnels et individuels sur ces dynamiques de migration seront abordés au regard de la spécificité des modes de locomotion utilisés lors de ces déplacements.

Le manuscrit de thèse est principalement basé sur les articles scientifiques publiés, soumis ou en cours de préparation mais les chapitres 2 et 3 comprennent une partie en français visant à présenter de manière synthétique les principaux résultats des articles scientifiques. Seul le premier chapitre est intégralement rédigé en français.

## 2. Chapitre 1 : Effet des facteurs environnementaux sur la structure des peuplements de la macro-faune d'eau douce de Mayotte et de La Réunion.

Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif général de l'étude est de décrire les facteurs environnementaux et les interactions biologiques structurants les peuplements de poissons et de macro-crustacés à Mayotte et à La Réunion. Cette description est faite de l'échelle régionale, en comparant les peuplements des deux îles, jusqu'à l'échelle du bassin versant et du site. En termes de gestion, la description des facteurs structurants les peuplements permet de définir des unités de gestion homogènes qui pourront servir à l'évaluation de la qualité écologique des rivières de ces deux îles.

**Résultats :** La diversité taxinomique<sup>3</sup> est plus élevée à Mayotte (**A**) qu'à La Réunion (**B**). Pour les deux îles, les variables qui structurent le plus les peuplements de poissons et de macrocrustacés sont l'altitude à laquelle se trouve le site et la pente du site. Cet effet structurant de l'altitude et de la pente du site est particulièrement marqué pour les espèces de prédateurs pour les deux îles (**A2** ; **B2**), elle reste importante pour les espèces de consommateurs primaires à La Réunion (**B1**) mais pas à Mayotte (**A1**).



<sup>&</sup>lt;sup>3</sup> Le détail des noms scientifiques des différentes espèces schématisées est présenté dans l'annexe 2 du chapitre 1

Amélioration de la connaissance des espèces : La richesse taxinomique plus importante à Mayotte peut s'expliquer par la morphologie des cours d'eau de cette île qui présentent une diversité d'habitats à faible vitesse d'écoulement et proches de la mer plus élevée qu'à La Réunion. La proximité de Mayotte avec le continent africain et Madagascar pourrait aussi favoriser la colonisation des cours d'eau mahorais à partir de ces zones par les stade larvaires marins des espèces de poissons et de macro-crustacés indigènes.

Sur les deux îles, la forte structuration des peuplements de poissons et macro-crustacés le long des gradients d'altitude et de pente est cohérente avec le fait que les espèces indigènes présentent une phase larvaire marine. En effet, cette phase larvaire oblige chaque génération des espèces indigènes à coloniser les bassins versants à partir de leur embouchure.

La structuration des peuplements le long des gradients d'altitude et de pente est beaucoup plus importante pour les prédateurs que pour les consommateurs primaires. Les zones d'altitude élevée et à forte pente sont généralement associées à des vitesses de courant importantes. Les prédateurs ont globalement des capacités de franchissement d'obstacles inférieures à celles des consommateurs primaires ce qui peut leur limiter l'accès aux zones amont depuis la mer ou leur maintien dans ces zones.

Application à la gestion : Trois unités de gestions homogènes ont pu être délimitées à partir de l'altitude du site à Mayotte et quatre unités ont pu être délimitées à partir de l'altitude et de la pente du site à La Réunion. Le développement ou l'amélioration d'indices de qualité écologique des cours d'eau basés sur les poissons et les macro-crustacés devrait donc se faire au regard de ces unités de gestion uniformes. De plus ces indices devraient être particulièrement focalisés sur les espèces de prédateurs, les peuplements de prédateurs étant fortement structurés par les gradients d'altitude et de pente.

#### **2.1 Introduction**

Les facteurs environnementaux, naturels et anthropiques, peuvent agir à différentes échelles spatiales sur la structuration des peuplements aquatiques (Pool et al., 2010). À l'échelle du micro-habitat (de un à quelques m<sup>2</sup>) et du site (de quelques m<sup>2</sup> à plusieurs centaines de m<sup>2</sup>), la structure des peuplements aquatiques est influencée par la diversité des conditions abiotiques et par les interactions biotiques (Monti & Legendre, 2009; Donaldson et al., 2013). À l'échelle du bassin versant (de quelques km<sup>2</sup> à plusieurs centaines de km<sup>2</sup>), cette structure est influencée par

la répartition de facteurs abiotiques tels que le débit, la pente, l'oxygène dissous... et biotiques le long d'un gradient amont-aval (Schlosser, 1990). Enfin à l'échelle régionale (de quelque centaines de km<sup>2</sup> à plusieurs milliers de km<sup>2</sup>) la structure des peuplements aquatiques peut être influencée par les processus de dispersion et de spéciation (Angermeier & Winston, 1998). Ces différentes échelles interagissent aussi indirectement dans la structuration des facteurs biotiques et abiotiques. Par exemple, des différences de géologie à l'échelle régionale vont entrainer des morphologies de bassins versants différentes qui vont influencer la structuration des habitats le long du gradient amont-aval, et donc in fine la structure des habitats à l'échelle du site et du micro-habitat. La hiérarchisation de l'effet des facteurs agissant à chacune des échelles est indispensable si l'on veut comprendre la structuration et le fonctionnement des peuplements aquatiques (Menge & Olson, 1990).

La description de l'effet des facteurs biotiques et abiotiques sur la structuration des peuplements aquatiques est un aussi prérequis important pour la mise en place de mesures de gestion et de conservation ciblées sur certaines espèces ou groupes d'espèces (Leathwick et al., 2005). Il peut par exemple s'agir de définir l'échelle de gestion cohérente d'une population. En particulier, la directive cadre de l'union européenne sur l'eau (DCE, Directive 2000/60/CE, 2000), impose à tous ses pays membres une évaluation de la qualité écologique de ses cours d'eau basée sur les peuplements aquatiques. Cette démarche permet de définir des stratégies pour conserver les zones en bon état et pour restaurer celles dégradées. Pour la macrofaune vertébrée et invertébrée, l'évaluation consiste à mesurer l'écart entre la structure du peuplement d'un site à celle attendue lorsque les pressions d'origine anthropique sont minimales (Karr, 1991, 1999). La description de la structuration des peuplements en fonction des facteurs biotiques et abiotiques peut donc permettre de délimiter des unités de gestion au sein desquelles des sites de références homogènes peuvent être définis (Oberdorff et al., 2002).

Les poissons et macro-crustacés des petites îles tropicales sont des modèles intéressants pour étudier le lien entre les facteurs environnementaux et la structure des peuplements à différentes échelles. Tout d'abord chaque île est une entité discrète à l'échelle régionale pouvant avoir une histoire géologique et une diversité d'habitats aquatiques qui lui est propre (Fitzsimons et al., 2002). Ensuite, malgré la faible taille des bassins versants de ces îles, les gradients environnementaux observés au sein de ces derniers peuvent être très marqués (Strauch et al., 2017) que ce soit à l'échelle du bassin versant (i.e. gradient altitudinal important) ou du site et du micro-habitat (présence simultanée d'habitats très lotiques et lentiques). Enfin, les espèces indigènes peuplant ces milieux sont soit des espèces marines et estuariennes présentant de fortes tolérances aux variations de salinité soit, pour la plupart, des espèces diadromes (Keith et al., 2006). Deux sous-catégories de diadromie sont observées parmi les espèces peuplant ces îles (McDowall, 1988). Les espèces catadromes croissent principalement en eau douce et rejoignent la mer pour s'y reproduire. Après l'éclosion, les larves pélagiques retournent dans les rivières. Les espèces amphidromes croissent principalement en eau douce et s'y reproduisent. Pour ces espèces, la phase marine de leur cycle de vie ne concerne que leur stade larvaire. Quel que soit le cycle de vie des espèces indigènes, les individus présents dans les habitats d'eau douce les ont colonisés, à chaque génération, à partir de l'estuaire. Ceci souligne l'importance du gradient avalamont pour ces populations. Enfin la phase marine des espèces favorise une forte dispersion ce qui se traduit en général par un cortège d'espèces partagé entre plusieurs îles d'une même région (Kido, 2013).

Mayotte et La Réunion sont deux petites îles tropicales du sud-ouest de l'Océan Indien qui présentent des cortèges d'espèces indigènes de poissons et de macro-crustacés d'eau douce proches. En effet, de nombreuses espèces sont communes aux deux îles (Keith et al., 2006). Cependant l'âge géologique de ces deux îles est différent, i.e. environ 8 Ma pour Mayotte (Nougier et al., 1986) contre entre 2 et 3 Ma pour la Réunion (McDougall, 1971, V. Famin, université de La Réunion, com. pers.). Cette différence d'âge entraine de fortes différences dans la géomorphologie des cours d'eau entre les deux îles. Ainsi, le réseau hydrographique de Mayotte est caractérisé par de nombreux bassins versants de petite taille. Eberschweiler (1987) a dénombré 27 bassins versants dont l'exutoire est la mer avec une surface qui varie entre 2 et 23 km² (Figure 10). À l'opposé le réseau hydrographique de La Réunion se caractérise par un nombre plus limité de bassins versants, 13 seulement, dont l'exutoire est la mer et pour lesquels l'écoulement est pérenne. Les surfaces de ces bassins versants sont beaucoup plus importantes, elles varient entre 28 et 154 km² (Robert, 1986).



Figure 10 : Longueur du cours d'eau principal (km) en fonction de la surface du bassin versant (km<sup>2</sup>) des 27 bassins versants décrits par Eberschweiler (1987) pour Mayotte et des 13 décrits par Robert (1986) pour La Réunion.

Dans ce contexte, le but du chapitre 1 est de hiérarchiser les facteurs environnementaux qui structurent les peuplements de poissons et de macro-crustacés de Mayotte et de La Réunion. L'étude est principalement ciblée sur les facteurs abiotiques à l'échelle du bassin versant et à l'échelle du site. L'influence des facteurs agissant à l'échelle régionale ne sera considérée que qualitativement à travers la comparaison entre les deux îles. L'échelle du micro-habitat ne sera pas abordée, les données disponibles ne permettant pas de l'étudier. L'influence des facteurs biotiques sera abordée à partir de la comparaison de la structure des peuplements d'espèces de niveau trophique faible (i.e. les consommateurs primaires) et d'espèces à niveau trophique élevé (i.e. les prédateurs) le long des gradients de facteurs abiotiques et mis en relation avec la population de l'espèce exotique la plus commune sur chacune des îles. Enfin des unités de gestion homogènes seront proposées au sein de chacune des îles en fonction de ces résultats.

### 2.2 Matériel et méthodes

#### 2.2.1 Plan d'échantillonnage

Un total de 86 et 61 stations représentatives du gradient aval-amont de la plupart des bassins versants et facilement accessibles ont été inventoriées respectivement à Mayotte et à La Réunion entre 2004 et 2017. Les données sont issues principalement des réseaux de suivi des poissons et macro-crustacés réalisés depuis 2008 à Mayotte et depuis 2004 à La Réunion. En complément, des données issues d'inventaires ponctuels réalisés avec des méthodes identiques à celles des réseaux de suivi ont été intégrées en particulier les études menées par EDF sur les rivières des

Marsouins et de l'Est à La Réunion. Les données issues du réseau de suivi de La Réunion en 2015, 2016 et 2017 n'ont pas été prises en compte, les méthodes d'inventaire étant différentes de celles mises en place entre 2004 et 2014. Chaque station a été inventoriée entre une et sept fois à Mayotte (Figure 11b) et entre une et 12 fois à La Réunion (Figure 11c) ce qui représente un total de 161 inventaires à Mayotte et 366 à La Réunion.



Figure 11 : Localisation de Mayotte et de La Réunion dans le sud-ouest de l'Océan Indien (**a**) et positionnement des stations d'inventaires au sein des différents bassins versants de Mayotte (**b**) et de La Réunion (**c**). À Mayotte, les bassins versants correspondent à ceux identifiés par Eberschweiler (1987) ou ceux non identifiés par ce dernier mais sur lesquels des stations d'inventaire étaient présentes. À La Réunion les bassins versants correspondent à ceux identifiés par Robert (1986). Le nombre d'inventaires est précisé pour chaque station.

#### 2.2.2 Méthodes d'inventaire

Deux méthodes d'inventaire ont été utilisées selon les stations. Pour les stations dont la largeur mouillée moyenne était inférieure à 5 m, l'ensemble du linéaire de la station a été prospecté par pêche électrique avec un appareil portatif (Deka, 3000 ou Hans Grassl, IG 200). Le linéaire prospecté était supérieur ou égal à dix fois la largeur mouillée moyenne de la station (Olivier et al., 2004). Les extrémités amont et aval de la station étaient bloquées par un filet ou un obstacle (naturel ou anthropique) afin de limiter les émigrations et immigrations d'individus depuis ou vers la station pendant la durée de l'inventaire. Lorsque la largeur mouillée de la station était supérieure à 5 m une méthode d'inventaire stratifiée par type d'habitat a été mise en place. Une surface minimum de 200 m<sup>2</sup> a été échantillonnée au sein de la station dont le linéaire était supérieur ou égal à 20 fois la largeur mouillée moyenne (Olivier et al., 2004). Les différents habitats présents au sein de la station ont été décrits à partir des faciès d'écoulement selon la clé de Malavoi et Souchon (2002). Au sein des faciès des placettes d'échantillonnées au sein d'un type de faciès soit proche de la proportion de ce type de faciès dans la station. Les ambiances ont été prospectées par pêche électrique avec un appareil portatif (Deka, 3000 ou Hans Grassl, IG 200).

L'ensemble des individus capturés a été identifié à l'espèce à partir de Keith et al., (2006) à l'exception des genres *Eleotris* et *Anguilla* pour lesquels les plus petits individus ne sont pas identifiables et des genres *Ambassis*, *Glossogobius*, *Kuhlia*, *Agonostomus* et *Microphis*, des Carangidae et Mugilidae (autres qu'*Agonostomus*) pour lesquels l'identification des espèces est incertaine. Les abondances de chaque taxon (i.e. espèce, genre ou famille) ont été exprimées en nombre d'individus par 100 m<sup>2</sup>. Pour les échantillonnages de l'ensemble du linéaire, l'abondance d'un taxon a été estimée à partir du nombre d'individus divisé par la surface totale de la station. Pour les échantillonnages stratifiés, l'abondance d'un taxon dans chaque type de faciès, i.e. nombre d'individus capturés divisé par la somme de la surface des ambiances pour le type de faciès, a été pondérée par la proportion du type de faciès au sein de la station. L'abondance totale du taxon correspondait à la somme des abondances pondérées.

Les paramètres environnementaux de description de la station ont été mesurés directement lors des inventaires ou déterminés a postériori à partir de données cartographiques. Les paramètres relevés pendant les inventaires étaient : la température (°C), le pH, et la conductivité ( $\mu$ S.cm<sup>-1</sup>) mesurés à l'aide d'une sonde multi-paramètres (YSI, Professional Plus ou équivalent), l'oxygène dissout (O<sub>2</sub>, mg.l<sup>-1</sup>) mesuré à l'aide d'un capteur d'oxygène dissous (YSI PRO ODO ou équivalent) et le pourcentage de chaque type de faciès à partir des mesures de surfaces des différents faciès. Pour ce dernier paramètre les faciès profonds lentiques et lotiques ont été regroupés en un seul type de faciès (i.e. chenal) du fait de l'absence de faciès profonds lotiques à Mayotte. En outre, les coordonnées GPS de la limite aval de la station ont été relevées afin de la géolocaliser pour l'acquisition des données complémentaires à partir de traitement cartographique. Lors du traitement cartographique la distance de la limite aval de la station à la mer (distance à la mer, km) et l'altitude de cette limite aval (altitude, m) ont été mesurées à partir de carte IGN au 1/25000. De plus le nombre d'obstacles (N obstacles) au franchissement, naturels ou anthropiques (i.e. seuils, barrages...), en aval de la station, la hauteur maximum des chutes (H<sub>max</sub> chutes, m) correspondant à ces obstacles et leur hauteur de chute cumulée (H chutes, m) ont été renseignés. La localisation et les hauteurs de chutes des obstacles ont été estimées à partir d'études précédentes (DEAL, 2011, 2017) et de repérages ponctuels réalisés lors des campagnes de terrain. La pente de la station (pente, %) a été estimée à partir du ratio entre la différence d'altitude et la longueur du tronçon de cours d'eau sur lequel la station était localisée.

#### 2.2.3 Analyses des données

Une analyse des corrélations entre les paramètres environnementaux a été réalisée afin d'identifier les paramètres redondants. Lorsque plusieurs paramètres étaient corrélés entre eux avec un coefficient de corrélation de Kendal supérieur à 0,7 un seul paramètre a été conservé pour les analyses suivantes. Le paramètre choisi était soit celui dont l'effet observé sur les variations d'abondance des espèces lors d'une prévisualisation des données était le plus marqué soit un paramètre synthétisant plusieurs autres. Par exemple, la hauteur de chutes cumulée synthétise à la fois le nombre d'obstacles et leur hauteur de chute maximale.

La comparaison de l'hétérogénéité des paramètres environnementaux entre les îles a été réalisée qualitativement à partir d'une ACP interclasses basée sur les stations. Cette analyse permet de minimiser la variabilité interannuelle de certains paramètres (i.e. physico-chimie ou proportion des différents types de faciès...) pour les stations ayant été échantillonnées plus d'une fois.

L'effort d'échantillonnage pour les deux îles a été évalué à partir de courbes de richesse taxinomique cumulée (Ugland et al., 2003). Ces courbes ont été construites à partir de 1000 permutations aléatoires de la richesse taxinomique de chaque inventaire. Cette méthode permet d'évaluer visuellement si l'ensemble des inventaires réalisés sur chaque île a permis

d'échantillonner de manière exhaustive tous les taxons présents ou si, au contraire, la richesse taxinomique théorique maximale est supérieure à celle réellement observée.

La hiérarchisation des facteurs environnementaux qui structurent les peuplements de poissons et de macro-crustacés de Mayotte et de La Réunion a été réalisée à partir d'analyses de type « gradient forest » (Ellis et al., 2012). Cette méthode multivariée est basée, dans un premier temps, sur la modélisation de l'effet de chaque facteur environnemental sur l'abondance de chaque espèce. Cette modélisation se fait à partir de modèles de « random forest » (Breiman, 2001). Dans un deuxième temps, chaque modèle est agrégé par espèce ou par facteur environnemental. L'importance relative des espèces et facteurs environnementaux peut ensuite être hiérarchisée à partir de la valeur du coefficient de régression (R<sup>2</sup> pondéré) de chaque modèle agrégé (Ellis et al., 2012). Cette méthode conserve les avantages des analyses univariées basées sur les analyses de type random forest à savoir de ne pas être contrainte par les hypothèses de normalité et d'égalité des variances des données, de ne pas nécessiter de pré-transformation de ces dernières et d'intégrer des réponses non linéaires (Breiman, 2001). Ce dernier point apparait particulièrement important car des préanalyses ont confirmé la non linéarité des relations entre l'abondance de plusieurs espèces et certains paramètres environnementaux. Par ailleurs, l'effet des facteurs environnementaux sur les espèces très rares peut être biaisé par la faible probabilité d'échantillonnage de ces dernières et de leur présence limitée parfois à une station unique. Les analyses de type gradient forest n'ont donc été réalisées que pour les espèces dont l'occurrence était supérieure à 3%. L'analyse des ratios de densités de nœuds dans les modèles de gradient forest par rapport aux densités de données permet d'identifier des gammes de valeurs des variables environnementales dans lesquelles des changements marqués de structure des peuplements sont observés (Tang et al., 2017). Concrètement ces changements de structure des peuplements sont importants dans les gammes de valeurs des variables environnementales pour lesquelles le ratio entre la densité de nœud et la densité de données est supérieur à un.

Dans un second temps, la structure des peuplements des espèces de niveau trophique faible (i.e. les consommateurs primaires), des espèces à niveau trophique élevé (i.e. les prédateurs) ainsi que l'abondance de l'espèce exotique la plus commune sur chacune des îles ont été comparées le long des gradients des principaux facteurs environnementaux mis en évidence lors de l'étape précédente. Le régime alimentaire de chaque espèce indigène a été classé en trois catégories à partir des données bibliographiques existantes pour cette espèce ou à partir d'espèces du même genre (cf. tableau S1 en annexe de chapitre 1). Les espèces périphytophages, phytophages et saprophages ont été considérées comme des consommateurs primaires, les espèces invertivores et piscivores comme des prédateurs. Les espèces pouvant être à la fois consommateurs primaires et prédateurs (i.e. omnivores) n'ont pas été prises en compte du fait des interactions trophiques complexes qu'elles peuvent avoir avec les deux autres groupes. La structure des peuplements de consommateurs primaires, de prédateurs et de l'espèce exotique retenue a été modélisée à partir de random forest. La significativité de chaque facteur environnemental a été estimée à partir de l'indice de pureté des nœuds. Pour chaque facteur environnemental cet indice a été comparé à celui obtenu à partir d'une distribution nulle des facteurs environnementaux obtenue à partir de 1000 permutations aléatoires de ces derniers.

Toutes les analyses ont été réalisées à partir du logiciel R v. 3.3.1 (R Development Core Team, 2016) implémenté du package *vegan* (Oksanen et al., 2017) pour courbes de richesse taxinomique cumulée, du package *ade4* (Dray & Dufour, 2007) pour les analyses de composantes principales inter stations, du package *gradientForest* (Ellis et al., 2012) pour les analyses de gradient forest et des packages *randomForest* (Liaw & Wiener, 2002) et *rfPermute* (Archer, 2016) pour les analyses de random forest.

### 2.3 Résultats

#### 2.3.1 Caractéristiques environnementales des stations

Les stations inventoriées à Mayotte sont globalement caractérisées par des pourcentages plus élevés de faciès lentiques et peu profonds (i.e. plats lentiques) que celles de La Réunion (Tableau 1). Les stations de Mayotte sont aussi caractérisées par une altitude, une distance à la mer, une hauteur maximum et une hauteur cumulée d'obstacles en aval et une concentration en oxygène dissout plus faibles que les stations de La Réunion. À l'opposé, la température et la conductivité de l'eau sont généralement plus élevées à Mayotte. Les autres variables environnementales présentent des valeurs moyennes et des amplitudes proches entre les deux îles. Tableau 1 : Synthèse des paramètres environnementaux des différentes stations inventoriées à Mayotte et à La Réunion. Le nombre de stations à partir desquelles les moyennes et amplitudes de chaque paramètre ont été estimées est précisé (N).

|                                     | Mayotte |               |                      | La Réunion   |         |           |  |
|-------------------------------------|---------|---------------|----------------------|--------------|---------|-----------|--|
| Paramètre environnemental           | N       | Moyenne       | Amplitude            | N            | Moyenne | Amplitude |  |
| Pourcentage de cascades             | 86      | 1,7           | 0-44,5               | 61           | 10,5    | 0-84,0    |  |
| Pourcentage de rapide               | 86      | 1,0           | 1,0 0-54,5 61        |              | 17,2    | 0-75,4    |  |
| Pourcentage de radier               | 86      | 37,7 0-100 61 |                      | 61           | 22,6    | 2,6 0-100 |  |
| Pourcentage de plat courant         | 86      | 7,5           | 0-100                | -100 61 25,7 |         | 0-83,5    |  |
| Pourcentage de plat lentique        | 86      | 43,6          | 0-100                | 61           | 14,0    | 0-94,7    |  |
| Pourcentage de chenal               | 86      | 5,5           | 5,5 0-68,8 6         |              | 9,5     | 0-85,0    |  |
| Température (°C)                    | 86      | 24,3          | 24,3 20-30,7 61 19,4 |              | 19,4    | 13,6-29,5 |  |
| pH                                  | 79      | 7,8           | 5,9-9,6              | 61           | 8,0     | 6,0-10,0  |  |
| Conductivité (µS.cm <sup>-1</sup> ) | 85      | 253,0         | 85,0-1199            | 60           | 133,0   | 25,0-696  |  |
| $O_2 (mg.l^{-1})$                   | 86      | 6,9           | 1,0-12,6             | 59           | 9,2     | 3-12      |  |
| Altitude (m)                        | 86      | 67,0          | 2-220                | 61           | 284,0   | 5-890     |  |
| Distance à la mer (km)              | 86      | 3,2           | 0,1-13,9             | 61           | 12,2    | 0,1-30,5  |  |
| Pente (%)                           | 86      | 3,9           | 0,4-16               | 61           | 3,5     | 0,2-13,1  |  |
| Nombre d'obstacles                  | 86      | 1,6           | 0-9                  | 61           | 2,1     | 0-11      |  |
| H <sub>max</sub> chutes (m)         | 86      | 4,4           | 0-27                 | 61           | 11,6    | 0-200     |  |
| H chutes (m)                        | 86      | 4,7           | 0-29                 | 61           | 22,9    | 0-332     |  |

Cinq paramètres se sont avérés fortement corrélés (coefficient de corrélation de Kendal > 0,7). Il s'agit de la distance à la mer et de l'altitude ainsi que des trois paramètres descriptifs des obstacles (i.e. nombre d'obstacles, hauteur maximum de chute et hauteur de chute cumulée) Parmi ces trois dernières variables, la hauteur cumulée des obstacles, qui synthétise le nombre d'obstacles et leur hauteur de chute, a été conservée pour les analyses suivantes. L'altitude a été conservée plutôt que la distance à la mer du fait de son effet plus marqué sur les variations d'abondance des espèces observé lors de la prévisualisation des données. La température et le pH de l'eau ont aussi été exclus de ces analyses, la température n'étant pas comparable entre des deux îles du fait de leur situation latitudinale différente et de trop nombreuses mesures de pH étant manquantes à La Réunion (environ 30% des stations).

L'analyse multivariée (ACP inter stations) des 11 variables environnementales a été réalisée à partir de 153 inventaires à Mayotte et 262 à La Réunion, les inventaires contenant des données manquantes étant exclus (Figure 12). Les trois premiers axes représentent respectivement 30%, 20% et 13% de l'inertie totale. Le premier axe reflète principalement la proportion de facies lentiques et la conductivité. Le deuxième axe reflète principalement la position des stations au sein des bassins versant (i.e. leur altitude) et leurs caractéristiques morphologiques (i.e. la pente) alors que le troisième axe reflète principalement l'accessibilité de la station (i.e. la hauteur de chute cumulée en aval). Les stations d'inventaires de Mayotte et de

La Réunion sont plus discriminées les unes des autres le long de l'axe 1 que le long des axes 2 et 3.



Figure 12 : Comparaison des conditions environnementales des stations d'inventaires de Mayotte et de La Réunion à partir des deux premiers plans factoriels d'une ACP inter stations. Chaque point représente le barycentre des projections d'une station pour l'ensemble des années où elle a été inventoriée.

#### 2.3.2 Structure des peuplements de poissons et de macro-crustacés

Un total de 39 taxons indigènes a été capturé lors de l'ensemble des inventaires à Mayotte contre 21 à La Réunion. Cette richesse taxinomique est proche de la richesse taxinomique maximale à Mayotte. En effet la courbe de richesse taxinomique cumulée tend vers l'asymptote (Figure 13a). À La Réunion la courbe de richesse taxinomique cumulée atteint l'asymptote à partir d'environ 50 inventaires (Figure 13b). L'effort d'échantillonnage total de 264 inventaires pour lesquels l'ensemble des données étaient disponibles a donc permis d'observer la richesse taxinomique maximale de cette île.



Figure 13 : Courbes de richesses taxinomiques cumulées pour Mayotte (**a**) et La Réunion (**b**). Les zones grisées représentent les erreurs standards associées à chaque courbe.

Parmi les taxons indigènes capturés à Mayotte, 13 présentent une occurrence inférieure à 3% et sont donc considérés comme très rares. Aucun taxon indigène n'a été considéré comme très rare à La Réunion. Les espèces indigènes les plus fréquentes à Mayotte sont l'Anguille marbrée (*Anguilla marmorata*), les Caridines (*Caridina* ssp.), le Camaron (*Macrobrachium lar*), le Cabot noir (*Eleotris klunzingerii*) et la Chevaquine (*Atyoida serrata*; Figure 14a). À La Réunion, les espèces indigènes les plus fréquentes sont les Cabots bouche-ronde (*Sicyopterus lagocephalus* et *Cotylopus acutipinnis*), l'Anguille marbrée et la Chevaquine (Figure 14b). Les abondances moyennes des captures à Mayotte sont largement dominées par les Caridines (Figure 14c) alors qu'à La Réunion les captures sont dominées par les Cabots bouche-ronde et dans une moindre mesure la Chevaquine (Figure 14d).



Figure 14 : Fréquences d'occurrence et abondances moyennes des taxons indigènes capturés lors de l'ensemble des inventaires à Mayotte  $(\mathbf{a}, \mathbf{c})$  et à La Réunion  $(\mathbf{b}, \mathbf{d})$ . Les barres grises représentent les espèces de poissons et les noires celles de macro-crustacés. Le trait pointillé vertical  $(\mathbf{a})$  délimite les espèces considérées comme très rares puisque leur occurrence est inférieure à 3%. À noter la différence d'échelle des abondances moyennes entre Mayotte  $(\mathbf{c})$  et La Réunion  $(\mathbf{d})$ . Pour les noms complets des espèces, se référer au tableau S1 en annexe du chapitre 1.

Une seule espèce exotique a été capturée à Mayotte, le Guppy (*Poecilia reticulata*). Cette dernière a été observée dans près de 70% des inventaires. À La Réunion, le Guppy et, dans une moindre mesure le Porte épée (*Xiphophorus hellerii*), sont les espèces exotiques les plus fréquentes. Ces dernières ont été observées dans 28% et 17% des inventaires respectivement. Les autres espèces exotiques présentes à La Réunion que sont les Tilapias (*Oreochromis* ssp.), le Nigro (*Amatitlania nigrofasciata*) et la Truite arc en ciel (*Oncorhynchus mykiss*), sont beaucoup moins fréquentes, leur présence a été observée dans moins de 7% des inventaires. La structuration de l'abondance de Guppy le long des gradients de facteurs environnementaux a donc été détaillée pour les deux îles en relation avec les abondances de consommateurs primaires et de prédateurs.

## 2.3.3 Hiérarchisation des paramètres environnementaux structurants les peuplements de poissons et de macrocrustacés de Mayotte et de La Réunion

Deux analyses de gradient forest ont été réalisées séparément pour Mayotte et La Réunion à partir de 153 et 264 inventaires respectivement. Ces analyses ont été réalisées en retenant 26 taxons à Mayotte et 21 à La Réunion dont les abondances ont été modélisées en fonction des 11 variables environnementales retenues.



Figure 15 : Importance pondérée des R<sup>2</sup> agrégés en fonction des espèces (a, c) ou des variables environnementales (b, d) des analyses de gradient forest réalisées à partir des données de Mayotte (a, b) et de la Réunion (c, d). Seules les espèces pour lesquelles les R<sup>2</sup> sont supérieurs à 0,1 sont représentées. Les barres grises représentent les espèces de poissons et les noires celles de macrocrustacés (a, c). Pour les noms complets des espèces, se référer au tableau S1 en annexe du chapitre 1.

Les cinq taxons qui contribuent le plus à la description de l'effet des variables environnementales sur la structure des peuplements de poissons et de macro-crustacés sont *Ophieleotris* cf. *aporos*, *A. marmorata*, *Butis butis*, *Glossogobius* ssp. et *Eleotris mauritiana* à Mayotte (Figure 15a) et *E. klunzingerii*, *A. marmorata*, *Macrobrachium australe*, *Microphis* spp. et *S. lagocephalus* à La Réunion (Figure 15c). Les deux variables environnementales qui influencent le plus la structure des peuplements à Mayotte sont l'altitude et dans une moindre mesure la pente (Figure 15b). À La Réunion, ces variables sont les mêmes (Figure 15d) et leurs influences relatives sur la structuration des peuplements sont quasi identiques. La hauteur de chute cumulée en aval de la station a elle aussi une influence marquée bien que moins importante que les deux précédentes.

L'analyse des ratios de densités de nœuds par rapport aux densités de données dans les modèles de gradient forest a permis d'identifier des valeurs seuil dans la structure des peuplements. Le ratio de densités est maximum pour des altitudes d'environ 10m et 30m, il devient inférieur à un au-delà de 30m et 130m d'altitude respectivement à Mayotte et à La Réunion (Figure 16a, c). Le ratio de densités est supérieur à un pour des pentes inférieures à 2,2% à Mayotte (Figure 16b), pour des pentes inférieures à 1,4% et, ponctuellement, pour les pentes de 2,3-2,4% à La Réunion (Figure 16d).



Figure 16 : Densités de nœuds dans les modèles de gradient forest (lignes noires), densités de données (lignes rouges) et ratio de ces deux densités (lignes bleues) pour l'altitude (a, c) et la pente (b, d) à Mayotte (a, b) et à La Réunion (c, d). Les données brutes sont représentées par les barres grises. Les flèches noires identifient les seuils de ces deux variables qui influencent la structuration des peuplements de poissons et de macro-crustacés.

La représentation du premier plan factoriel de l'ACP réalisée à partir des prédictions du modèle de gradient forest à Mayotte (Figure 17a) met en évidence une structuration forte des assemblages modélisés le long du premier axe. Cette structuration est principalement liée à l'altitude. Le cluster II est peu séparé des clusters I et III. À La Réunion cette représentation met en évidence une structuration des assemblages modélisés le long des deux premiers axes de l'ACP (Figure 17b). Quatre clusters assez bien différentiés peuvent être identifiés : le cluster IA, composé de stations de moyenne à faible altitude ayant une pente moyenne à faible ; le cluster IB, composé de deux stations de faible altitude ayant une pente forte ; le cluster II, principalement composé de stations d'altitude moyenne et élevée ayant une pente faible et moyenne ; et enfin le cluster III composé exclusivement de stations ayant une pente forte la plupart d'altitude élevée, seulement deux stations de ce cluster étant à une altitude moyenne.



Figure 17 : Représentation des deux premiers axes d'une ACP basée sur les prédictions de structure des assemblages Mayotte (**a**) et de La Réunion (**b**). Les ellipses grises représentent les clusters de stations qui peuvent être reconnus visuellement à partir de l'altitude et de la pente.

# 2.3.4 Distribution des consommateurs primaires, des prédateurs et des Guppys le long des gradients de pente et d'altitude

La performance globale des modèles de random forest décrivant la structure d'abondance des prédateurs est correcte à Mayotte, le modèle explique 47% de la variance. Cette performance est bonne à La Réunion avec 65% de variance expliquée. Cette performance est mauvaise pour les consommateurs primaires à Mayotte avec seulement 12% de variance expliquée alors qu'elle est correcte à La Réunion avec 39% de variance expliquée. La réponse partielle de l'abondance des consommateurs primaires à Mayotte n'est significative pour aucune des variables environnementales (Tableau 2; Figure 18-1a-3a). À l'opposé, les réponses partielles de

l'abondance de consommateurs primaires à La Réunion et de prédateurs sur les deux îles en fonction de l'altitude, de la pente et de la hauteur de chutes cumulée sont toutes significatives (Tableau 2 ; Figure 18).

Tableau 2 : p-values associées à l'indice de pureté des nœuds pour les analyses de random forest modélisant la réponse de l'abondance des consommateurs primaires et des prédateurs à l'ensemble des paramètres environnementaux à Mayotte et à La Réunion. L'abondance de prédateurs ou de consommateurs primaires a été intégrée comme variable environnementale pour la modélisation de la réponse des consommateurs primaires ou des prédateurs respectivement.

|                              | Mayott                  | e          | La Réunion              |            |  |
|------------------------------|-------------------------|------------|-------------------------|------------|--|
| Paramètre environnementale   | Consommateurs primaires | Prédateurs | Consommateurs primaires | Prédateurs |  |
| Altitude                     | 0,07                    | 0,001      | 0,01                    | 0,001      |  |
| Pente                        | 0,30                    | 0,002      | 0,001                   | 0,001      |  |
| Conductivité                 | 0,36                    | 0,35       | 0,86                    | 1,00       |  |
| Pourcentage de plat lentique | 0,29                    | 1,00       | 0,65                    | 0,47       |  |
| Pourcentage de radier        | 0,72                    | 1,00       | 0,99                    | 1,00       |  |
| H chutes                     | 0,29                    | 0,001      | 0,005                   | 0,001      |  |
| $O_2$                        | 0,42                    | 1,00       | 0,96                    | 1,00       |  |
| Pourcentage de plat courant  | 0,16                    | 0,94       | 1,00                    | 1,00       |  |
| Pourcentage de chenal        | 0,66                    | 0,99       | 0,29                    | 1,00       |  |
| Pourcentage de cascades      | 0,83                    | 0,87       | 0,81                    | 0,96       |  |
| Pourcentage de rapide        | 0,68                    | 0,66       | 0,21                    | 1,00       |  |
| Prédateurs                   | 0,83                    | -          | 0,21                    | -          |  |
| Consommateurs primaires      | -                       | 1,00       | -                       | 1,00       |  |

À Mayotte et à La Réunion les abondances de prédateurs sont maximales pour les plus faibles valeurs d'altitudes et de pentes, elles diminuent fortement pour des altitudes supérieures à 50 m à Mayotte (Figure 18-1b) et 100 m à La Réunion (Figure 18-2b) et pour des pentes supérieures à 2% sur les deux îles (Figure 18-3b-4b). À La Réunion, les abondances de consommateurs primaires augmentent pour des altitudes supérieures à 100 m. Ces abondances sont maximales pour des pentes inférieures à 4% puis diminuent (Figure 18-4a). La forte augmentation ponctuelle des abondances de consommateurs primaires observée pour des pentes d'environ 3% s'explique par la contribution de deux stations en aval des rivières du Mât et de Saint Etienne où les abondances de Sicydiinae et d'Atyidae sont très importantes sur l'ensemble des années pour lesquelles ces stations ont été inventoriées (11 et 10 années respectivement).



Figure 18 : Réponses partielles des abondances de consommateurs primaires (1-4a) et de prédateurs (1-4b) en fonction de l'altitude et de la pente à Mayotte (1a-b ; 3a-b) et à La Réunion (2a-b ; 4a-b). La significativité des réponses partielles est évaluée à partir de l'indice de pureté des nœuds. Les courbes en traits pleins sont celles pour lesquelles la réponse partielle est significative alors que la réponse partielle des courbes en traits pointillés ne l'est pas. À noter la différence d'échelle des abondances entre Mayotte et La Réunion. Les espèces schématisées pour chaque groupe et chaque île le sont à titre illustratif et ne sont pas exhaustives, les noms scientifiques de ces espèces sont présentés dans l'annexe 2 du chapitre 1.

La performance globale des modèles de random forest décrivant la structure d'abondance des Guppys est mauvaise à Mayotte et à La Réunion avec respectivement 6% et 14% de variance expliquée. À Mayotte seule la réponse partielle de la hauteur de chutes cumulée en aval de la station est significative (Figure 19-1a). À La Réunion, les réponses partielles de l'altitude, la pente et la concentration en oxygène dissout sont toutes trois significatives (Figure 19-2a-3a). La réponse partielle de la concentration en oxygène dissout n'est pas représentée car elle n'était pas significative pour les consommateurs primaires et prédateurs indigènes (Tableau 2). À Mayotte, les abondances de Guppy sont minimales pour les stations où aucune chute n'est observée en aval et maximales lorsque la hauteur de chutes cumulée est supérieure à 30 m (Figure 19-1a). Les abondances de prédateurs sont maximales pour les stations où aucune chute n'est observée en aval, elles diminuent très vite lorsque cette hauteur est supérieure à deux mètres (Figure 19-1b). À La Réunion les Guppy sont surtout observés dans des zones où la pente est inférieure à 3% et de moins de 200 m d'altitude (Figure 19-2a-3a). La très forte abondance modélisée pour des pentes et altitude supérieures à 10% et 650 m est surement un artéfact du modèle due au fait que très peu de stations ayant ces caractéristiques ont été échantillonnées. Or une abondance de Guppy extrêmement élevée (près de 300 ind.100 m<sup>-2</sup>) a été observée dans l'une de ces stations.



Figure 19 : Réponses partielles des abondances de Guppy (*Poecilia reticulata*) (1-3a) et de prédateurs (1b) en fonction de la hauteur de chutes cumulée en aval de la station (H chutes) à Mayotte (1a-b) et de l'altitude et de la pente à La Réunion (2-3a). La p-value (p) associée aux réponses partielles est évaluée à partir de l'indice de pureté des nœuds. À noter la différence d'échelle des abondances entre Mayotte et La Réunion. Les espèces schématisées pour chaque groupe et chaque île le sont à titre illustratif et ne sont pas exhaustives, les noms scientifiques de ces espèces sont présentés dans l'annexe 2 du chapitre 1.

## 2.4 Discussion

# 2.4.1 Structuration des peuplements de poissons et macro-crustacés indigènes à l'échelle régionale

La richesse taxinomique de poissons et macro-crustacés indigènes est plus élevée dans les rivières de Mayotte (39 taxons) que dans les rivières de La Réunion (21 taxons). Ceci s'explique en partie par la présence de 13 taxons marins ou estuariens à Mayotte (tableau S1 en annexe du chapitre 1) alors que tous les taxons inventoriés à La Réunion sont diadromes (Keith et al., 2006). Les probabilités de captures plus élevées des espèces marines et estuariennes à Mayotte peuvent être liées à la fois au nombre de stations d'altitude inférieure à 5 m plus important qu'à la Réunion mais aussi à l'amplitudes plus forte des marées. Du fait de ces amplitudes importantes, les espèces marines et estuariennes peuvent pénétrer plus en amont dans les cours d'eau lors des marées hautes tout en restant à proximité de zones marines ou saumâtres. La richesse taxinomique des poissons et de macro-crustacés indigènes diadromes est elle aussi plus élevée à Mayotte avec 26 taxons alors qu'elle n'est que de 21 taxons à La Réunion. La différence d'habitat marquée entre les deux îles, avec en particulier la prépondérance des habitats lentiques à Mayotte, est probablement un facteur pouvant expliquer cette différence. En effet parmi les sept taxons de poissons et de macro-crustacés diadromes observés uniquement à Mayotte seul *Cotylopus rubripinnis* est considéré comme rhéophile, les autres sont tous limnophiles (tableau

S1 en annexe du chapitre 1). Enfin, la proximité de Mayotte avec le continent Africain et Madagascar peut aussi favoriser la dispersion au stade larvaire des espèces diadromes entre ces zones et Mayotte et non avec La Réunion (Crochelet et al., 2016). Cette hypothèse peut être appuyée par les observations de *Redigobius bikolakus* en Afrique du Sud (Whitfield, 1994) ou de *R. bikolakus, Hypseleotris cyprinoides, Ophiocara porocephala* à Madagascar (Fricke et al., 2018). Ces espèces, considérées comme diadromes, ont été recensées à Mayotte mais pas à La Réunion (Keith et al., 2006; cette étude). Toutefois, ces observations concernant les différences de diversité taxinomique entre les deux îles doivent être considérées avec précaution. En effet le statut taxinomique de nombreuses des espèces décrites dans ce chapitre est incertain et susceptible de changer comme cela a été le cas récemment pour le genre *Eleotris* (Mennesson & Keith, 2017). Ces auteurs se sont basés sur des analyses moléculaires du gène COI pour réviser le statut taxinomique d'*Eleotris fusca* (Forster 1801) dont l'aire de répartition présumée s'étendait des Comores jusque dans l'Océan Pacifique. Leurs résultats démontrent qu'*E. fusca* aurait une aire de répartition limitée à l'Océan Pacifique alors qu'une autre espèce, *E. klunzingerii* (anciennement identifiée comme *E. fusca*) serait endémique de l'Océan Indien.

## 2.4.2 Hiérarchisation des paramètres environnementaux structurants les peuplements de poissons et de macrocrustacés indigènes à l'échelle du bassin-versant et du site

Que ce soit à Mayotte ou à La Réunion, les paramètres environnementaux les plus structurants pour les peuplements de poissons et de macro-crustacés sont la pente et l'altitude de la station. Ces deux paramètres reflètent la position des sites d'inventaires au sein des bassins versants, les paramètres qui reflètent les conditions abiotiques et biotiques à l'échelle du site sont beaucoup moins structurants. Les peuplements de poissons et de macro-crustacés indigènes des deux îles étant diadromes, ou d'origine marine et estuarienne, la colonisation des habitats d'eau douce se fait, à chaque génération, de l'aval vers l'amont. La distribution des espèces d'origine marines et estuarienne va, en général, être limitée aux zones les plus proches des estuaires (i.e. zones de faibles altitude et pente). En ce qui concerne les espèces diadromes il est cohérent que les variables agissant à l'échelle du bassin versant soient les plus structurantes. En effet, les espèces n'ayant pas des capacités de nage élevées ou des modes de locomotion particuliers vont avoir des difficultés à franchir les premières zones de faciès aux vitesses de courant élevées voire les premières chutes. Ces zones difficiles à franchir sont plus fréquentes lorsque la pente du tronçon de cours d'eau est élevée (Malavoi, 1989). Par exemple, les espèces du genre *Eleotris*, qui sont parmi les espèces les plus structurantes pour les peuplements des deux îles, ont

probablement des performances de nage très limitées. Fitzsimons et al. (1997) ont montré qu'une espèce d'Hawaii, *Eleotris sandwicensis* (Vaillant & Sauvage 1875), ne pouvait pas résister à des vitesses de courants supérieures à 20 cm.s<sup>-1</sup> alors que les espèces sympatriques de Gobiidae pouvaient résister à des vitesses allant de 30 cm.s<sup>-1</sup> pour *Stenogobius hawaiiensis* (Watson 1991) jusqu'à près de 100 cm.s<sup>-1</sup> pour les Sicydiinae. Les performances de ces derniers peuvent sans doute être expliquées par l'utilisation de leur ventouse pelvienne (Maie et al., 2012) qui leur permet d'adhérer au substrat et de résister au courant voire de franchir des chutes de plusieurs dizaines de mètres (Schoenfuss et al., 2013). La faible structuration des peuplements à l'échelle du site est cohérente avec l'importance limitée des variables de profondeurs et de vitesses d'écoulement dans le choix de l'habitat quotidien observée pour certaines espèces que macrocrustacés et les Sicydiinae à La Réunion (Girard et al., 2014; Teichert et al., 2014). En effet les variables décrivant l'habitat à l'échelle du site lors de cette étude étaient les proportions des différents facies d'écoulement observés au sein des stations. Or cette description des faciès d'écoulement se base principalement sur les profondeurs d'eau et vitesses de courant moyennes (Malavoi & Souchon, 2002).

Malgré les abondances élevées et les occurrences fréquentes de consommateurs primaires à Mayotte, la modélisation de la distribution de ces espèces s'est avérée peu performante. Ce résultat met en évidence que certaines variables n'ayant pas été prises en compte dans cette étude sont probablement très structurantes pour ces espèces. À l'échelle du site les assemblages de consommateurs primaires peuvent être fortement structurés par l'état de colmatage du substrat, dû à des apports importants de matière en suspension sur les zones de bassins versants déforestées ou urbanisées, ou par la qualité physico-chimique de l'eau. Les Atyidae et Sicydiinae, principales espèces de consommateurs primaires de Mayotte, dépendent fortement des éléments granulométriques grossiers (i.e. galets, blocs). Les Sicydiinae se nourrissent en effet à partir du périphyton croissant à la surface des éléments granulométriques grossiers (Cullen et al., 2013). Les Sicydiinae et Atyidae peuvent aussi trouver refuge entre les interstices des blocs et galets (observations personnelles). Le colmatage important observé au niveau de nombreux sites des rivières mahoraises limite probablement le développement du périphyton à la surface des blocs et galets et en bouche les interstices. Les fonctions de nutrition et de refuge du substrat constitué d'éléments granulométriques grossiers pour ces espèces seront donc altérées. L'état physicochimique de l'eau de six des 10 stations de suivi des cours d'eau de Mayotte a récemment été considéré comme mauvais (PARETO et ASCONIT, 2013). Cette dégradation de l'état physicochimique, dû principalement aux faibles concentrations d'oxygène dissout, peut avoir des effets

directs sur les espèces les plus sensibles à la pollution. En outre Jenkins et al. (2010) ont émis l'hypothèse que la pollution de l'eau pouvait avoir un effet négatif sur les larves d'espèces diadromes lors de leur arrivée en rivière, ces dernières évitant les cours d'eau pollués. Dans ce cas, la structuration de l'abondance des espèces serait influencée principalement par la qualité physico-chimique des bassins versants. L'effet de la différence de qualité physico-chimique entre bassins versants serait donc prépondérant dans la structuration des peuplements de poissons et de macro-crustacés par rapport à celui des gradients de variables environnementales au sein des bassins versants analysés dans cette étude. Enfin, les interactions biotiques, en particulier l'évitement des prédateurs, ne sont pas apparues importantes pour ces espèces. Or, Monti et Legendre (2009) ont démontré que l'effet des interactions biotiques entre espèces pouvait jouer un rôle clefs dans la structuration des populations d'Atya innoculus en Guadeloupe. Les conclusions différentes entre notre étude et celle de Monti et Legendre (2009) peuvent s'expliquer par le fait que les interactions biotiques entre espèces, y compris entre consommateurs primaires et prédateurs, interviennent probablement à l'échelle du micro-habitat. McRae et al. (2013) ont montré qu'au sein des radiers, les micro-habitats occupés par trois espèces indigènes d'Hawaii ayant des niveaux trophiques différents sont bien discriminés les uns des autres.

# 2.4.3 Structuration des populations de Guppys à Mayotte et à La Réunion

Le Guppy est l'espèce exotique la plus fréquente et la plus abondante à Mayotte et à La Réunion. Cependant la modélisation de la distribution de sa population en fonction des variables abiotiques et biotiques s'est avérée peu performante avec moins de 13% de variance expliquée par les modèles. Ceci peut être dû, en premier lieu, au fait que la présence de cette espèce dépend de son introduction par l'homme dans la zone du bassin versant étudiée et/ou de la dispersion d'individus provenant de zones adjacentes. Du fait des introductions régulières, la colonisation des habitats d'eau douce par cette espèce n'est donc pas dépendante du gradient aval-amont. Enfin, comme pour le groupe des consommateurs primaires à Mayotte, il est possible que des variables non prises en compte dans cette étude, en particulier celles à l'échelle du micro-habitat, soient fortement structurantes pour les populations de Guppy. Hockley et al. (2014) ont ainsi démontré expérimentalement que les Guppy avaient des préférences marquées pour les zones peu turbulentes dont la vitesse d'écoulement était comprise entre 10 et 13 cm.s<sup>-1</sup>. Cette observation est cohérente avec les descriptions faites de l'habitat préférentiel du Guppy dans son habitat naturel (Reznick et al., 2001) et traduit une sélection marquée des vitesses d'écoulement

à l'échelle du micro-habitat. Enfin, Fitzsimons et al. (1997) ont estimé que les Poecilidae présents à Hawaii, y compris les Guppys, ne pouvaient pas résister à des vitesses de courant supérieures à 20 cm.s<sup>-1</sup>. Le régime de débit au sein des bassins versants et en particulier l'intensité des crues pourrait donc être un autre facteur structurant pour les populations de Guppys à Mayotte et à La Réunion.

#### 2.4.4 Applications à la gestion

Cette étude a permis de définir deux ou trois zones à Mayotte et quatre zones à La Réunion au sein desquelles la structure des peuplements de poissons et de macro-crustacés est relativement homogène. La définition de ces zones au sein des cours d'eau est un prérequis essentiel au développement d'indices de bio-indication (Karr, 1991). Qui plus est, les espèces les plus structurantes pour les peuplements de poissons et de macro-crustacés au sein des deux îles ont été mises en évidence. L'implication de ces résultats est différente pour Mayotte, où aucun indice de bio-indication basé sur les poissons et les macro-crustacés n'existe à l'heure actuelle, et pour La Réunion où un indice, basé sur les poissons uniquement, a été développé récemment (Mérigoux et al., 2012).

À Mayotte la démarche de développement d'un indice pourrait donc s'appuyer sur les résultats présentés dans cette étude. L'étape suivante de ce développement consisterait à définir, au sein des deux ou trois zones mises en évidence, la réponse des populations des espèces les plus structurantes aux gradients de pressions d'origine anthropique (Robinet et al., 2015). A ce stade, la démarche sera probablement limitée par la quantification précise de ces gradients. Toutefois, dans un premier temps l'état des différents sites vis-à-vis de ces pressions pourrait être qualifié à dires d'experts. Idéalement les espèces cibles retenues devraient être fortement structurantes pour le peuplement et avoir une réponse marquée à un seul type de pression. La structure des populations de l'ensemble des espèces cibles pour un site donné permettrait d'évaluer l'intégrité biotique globale de ce site, ou état écologique au sens de la DCE. La structure de population de chaque espèce cible pourrait permettre de cibler les principale pressions à l'origine de la dégradation de l'état écologique du site.

À La Réunion, l'indice existant a été développé à partir de cinq zones différentes définies à partir des caractéristiques morphologiques des cours d'eau et de deux ou trois zones altitudinales. L'intégration de nombreuses nouvelles données et la quantification de la réponse des peuplements aux gradients environnementaux réalisées lors de cette étude ont permis de redéfinir trois zones principales pour lesquelles les peuplements de poissons et de macrocrustacés sont homogènes. L'une des limites soulevées par Mérigoux et al. (2012) lors du développement de l'indice actuel était le faible nombre d'inventaires dans chacune des zones qu'ils avaient définies. Du fait de la réduction du nombre de zones et de l'intégration de nouveaux inventaires, l'étude présentée ici pourrait permettre d'améliorer ce point si de nouveau développements d'indices de bio-indication étaient prévus à La Réunion. Cependant le principal biais soulevé lors des travaux de Mérigoux et al. (2012), à savoir l'absence de sites pour lesquels les pressions d'origine anthropique sont très faibles, reste toujours d'actualité. Cette absence de sites faiblement impactés par les pressions d'origine anthropique limite les possibilités de quantification de la réponse des populations des espèces cibles aux gradients de pressions. Cette limite pourrait en partie être contournée en diversifiant le nombre de métriques pris en compte (Robinet et al., 2015). À l'heure actuelle, les métriques d'évaluation de l'intégrité biotique sont basées uniquement sur l'abondance de S. lagocephalus, de C. acutipinnis et de l'ensemble des espèces dites accompagnatrices. Ces dernières diffèrent en fonction de l'altitude. La diversification des métriques pourrait se faire en intégrant des métriques fonctionnelles basées sur des traits d'histoire de vie, comme l'abondance d'adultes matures de ces espèces ou encore l'abondance de l'ensemble des espèces des différents niveaux trophiques (Kido, 2013).

Enfin, même si des zones homogènes peuvent être définies à Mayotte et à La Réunion, la structuration des peuplements de poissons et de macro-crustacés, au sein et entre ces zones, en fonction de l'altitude et de la pente est plutôt graduelle que discrète. La structuration graduelle des peuplements en fonction de l'altitude est particulièrement visible au sein des sites de Mayotte. À La Réunion, les sites appartenant à la classe d'altitude moyenne (i.e. 30 à 130 m) sont fréquemment regroupés avec des sites d'altitude faible ou élevée. Ce regroupement est en parti expliqué par la présence de chutes d'eau en aval du site d'inventaire. Ceci entraine une structuration des peuplements principalement influencée par les espèces présentant des adaptations spécifiques au franchissement d'obstacles, structure caractéristique des sites qui se trouvent en amont. Il peut aussi être noté que certains sites d'altitude intermédiaire proche du seuil définit pour les différentes limites de classes peuvent être regroupés avec des sites amont ou aval. C'est en particulier le cas de deux sites « intermédiaires » des rivières des Marsouins et du Mât situés entre 30 m et 50 m d'altitude ou d'un site du Bras de La Plaine situé à 130 m d'altitude (i.e. le seuil d'altitude délimitant les sites intermédiaires et amont). Ces observations pourraient être à l'origine d'une adaptation de la démarche de développement des indices de bioindication. La démarche actuelle se base sur des comparaisons de métriques entre sites de

références et sites tests au sein d'une zone homogène. Dans le cas de Mayotte et dans une moindre mesure de La Réunion, il apparaitrait plus pertinent de comparer les métriques des sites tests à la réponse prédite des sites de référence dans des conditions d'altitude et de pente, voire d'accessibilité (hors obstacle d'origine anthropique) identiques. Cette démarche est semblable à celle mis en œuvre pour le développement d'indice de bio-indication dans les estuaires de France métropolitaine (Delpech et al., 2010).

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## Annexes du chapitre 1

Tableau S1 : Liste des taxons indigènes capturés dans les cours d'eau de Mayotte et La Réunion et de leurs principaux traits d'histoire de vie. Les chiffres entre crochets indiquent les références associées avec \* observation personnelle, pour les espèces diadromes : (A) taxon amphidrome et (C) taxon catadrome, - : donnée non renseignée car les préférences entre espèces du même taxon sont différentes. NA : donnée non disponible. Les tailles correspondent à des longueurs totales ou à la fourche pour les poissons et des longueurs du rostre à la queue ou de la carapace pour les macro-crustacés.

| Classe         | Famille     | Noms scientifique                                    | Guilde                         | Régime alimentaire                   | Préférences<br>hydrauliques | Gamme de<br>tailles (mm)<br>Mayotte | Gamme de<br>tailles (mm)<br>La Réunion |
|----------------|-------------|--|--------------------------------|--------------------------------------|-----------------------------|-------------------------------------|--|
| Actinopterygii | Anguillidae | Anguilla bicolor (McClelland 1844)                   | Diadrome (C) <sup>[29]</sup>   | Prédateur <sup>[20]</sup>            | Limnophile <sup>[20]</sup>  | 130-580                             | 127-546                                |
| Actinopterygii | Anguillidae | Anguilla marmorata (Quoy & Gaimard 1824)             | Diadrome (C) <sup>[29]</sup>   | Prédateur <sup>[28]</sup>            | Rhéophile <sup>[28]</sup>   | 130-1 520                           | 115-800                                |
| Actinopterygii | Anguillidae | Anguilla mossambica (Peters 1852)                    | Diadrome (C) <sup>[29]</sup>   | Prédateur <sup>[28]</sup>            | Rhéophile <sup>[20]</sup>   | NA                                  | 92-458                                 |
| Actinopterygii | Anguillidae | Anguilla sp.   | Diadrome (C) <sup>[29]</sup>   | Prédateur <sup>[33]</sup>            | NA                          | 53-120                              | 68-127                                 |
| Actinopterygii | Megalopidae | Megalops cyprinoides (Broussonet 1782)               | Marin-estuaire <sup>[34]</sup> | Prédateur <sup>[1]</sup>             | Limnophile <sup>[1]</sup>   | 92                                  | NA                                     |
| Actinopterygii | Mugilidae   | Agonostomus ssp.                                     | Diadrome (A) <sup>[31]</sup>   | Omnivore <sup>[27]</sup>             | Rhéophile <sup>[20]</sup>   | 40-72                               | 40-347                                 |
| Actinopterygii | Mugilidae   | <i>Mugillidae</i> sp.                                | Marin-estuaire*                | -                                    | Limnophile*                 | 60-140                              | NA                                     |
| Actinopterygii | Ambassidae  | Ambassis ssp.  | Marin-estuaire <sup>[20]</sup> | Prédateur <sup>[20]</sup>            | Limnophile <sup>[20]</sup>  | 39-99                               | NA                                     |
| Actinopterygii | Carangidae  | Carangidae ssp.                                      | Marin-estuaire <sup>[34]</sup> | Prédateur <sup>[5]</sup>             | Limnophile <sup>[34]</sup>  | 56                                  | NA                                     |
| Actinopterygii | Eleotridae  | Butis butis (Hamilton 1822)                          | Marin-estuaire <sup>[34]</sup> | Prédateur <sup>[35]</sup>            | Limnophile <sup>[20]</sup>  | 19-92                               | NA                                     |
| Actinopterygii | Eleotridae  | Eleotris klunzingerii <sup>[26]</sup> (Pfeffer 1893) | Diadrome (A) <sup>[25]</sup>   | Prédateur <sup>[23]</sup>            | Limnophile <sup>[13]</sup>  | 42-160                              | 38-192                                 |
| Actinopterygii | Eleotridae  | Eleotris mauritiana (Bennett 1832)                   | Diadrome (A) <sup>[25]</sup>   | Prédateur <sup>[23]</sup>            | Limnophile <sup>[13]</sup>  | 22-110                              | 27-190                                 |
| Actinopterygii | Eleotridae  | Eleotris ssp.  | Diadrome (A) <sup>[25]</sup>   | Prédateur <sup>[23]</sup>            | Limnophile <sup>[13]</sup>  | 18-60                               | 21-37                                  |
| Actinopterygii | Eleotridae  | Hypseleotris cyprinoides (Valenciennes 1837)         | Diadrome (A) <sup>[34]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 18-80                               | NA                                     |
| Actinopterygii | Eleotridae  | Ophieleotris cf. aporos                              | Diadrome (A) <sup>[11]</sup>   | Omnivore <sup>[8]</sup>              | Limnophile <sup>[20]</sup>  | 60-260                              | NA                                     |
| Actinopterygii | Eleotridae  | Ophiocara porocephala (Valenciennes 1837)            | Diadrome (A) <sup>[11]</sup>   | Omnivore <sup>[8]</sup>              | Limnophile <sup>[20]</sup>  | 52-300                              | NA                                     |
| Actinopterygii | Gobiidae    | Awaous commersoni (Schneider 1801)                   | Diadrome (A) <sup>[21]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 15-230                              | 28-155                                 |
| Actinopterygii | Gobiidae    | Cotylopus acutipinnis (Guichenot 1863)               | Diadrome (A) <sup>[19]</sup>   | Consomateur primaire <sup>[20]</sup> | Rhéophile <sup>[32]</sup>   | NA                                  | 24-133                                 |
| Actinopterygii | Gobiidae    | Cotylopus rubripinnis (Keith, Hoareau & Bosc 2005)   | Diadrome (A) <sup>[19]</sup>   | Consomateur primaire <sup>[20]</sup> | Rhéophile <sup>[20]</sup>   | 24-73                               | NA                                     |
| Classe         | Famille       | Noms scientifique                            | Guilde                         | Régime alimentaire                   | Préférences<br>hydrauliques | Gamme de<br>tailles (mm)<br>Mayotte | Gamme de<br>tailles (mm)<br>La Réunion |
|----------------|---------------|--|--------------------------------|--------------------------------------|-----------------------------|-------------------------------------|--|
| Actinopterygii | Gobiidae      | Glossogobius ssp.                            | Diadrome (A) <sup>[11]</sup>   | Prédateur <sup>[15]</sup>            | Limnophile <sup>[20]</sup>  | 20-130                              | NA                                     |
| Actinopterygii | Gobiidae      | Mugilogobius mertoni (Weber 1911)            | Marin-estuaire <sup>[20]</sup> | Prédateur <sup>[20]</sup>            | Limnophile <sup>[20]</sup>  | 15-32                               | NA                                     |
| Actinopterygii | Gobiidae      | Periophthalmus ssp.                          | Marin-estuaire <sup>[14]</sup> | Prédateur <sup>[14]</sup>            | Limnophile <sup>[14]</sup>  | 60-64                               | NA                                     |
| Actinopterygii | Gobiidae      | Redigobius bikolanus (Herre 1927)            | Diadrome (A) <sup>[11]</sup>   | Prédateur <sup>[20]</sup>            | Limnophile <sup>[20]</sup>  | 15-40                               | NA                                     |
| Actinopterygii | Gobiidae      | Sicyopterus lagocephalus (Pallas 1770)       | Diadrome (A) <sup>[10]</sup>   | Consomateur primaire <sup>[4]</sup>  | Rhéophile <sup>[32]</sup>   | 28-121                              | 28-137                                 |
| Actinopterygii | Gobiidae      | Stenogobius polyzona (Bleeker 1867)          | Diadrome (A) <sup>[20]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 30-90                               | 28-97                                  |
| Actinopterygii | Kuhliidae     | Kuhlia caudavittata (Lacepède 1802)          | Marin-estuaire <sup>[20]</sup> | Prédateur <sup>[20]</sup>            | Limnophile <sup>[20]</sup>  | 24-63                               | NA                                     |
| Actinopterygii | Kuhliidae     | Kuhlia ssp.                                  | Diadrome (C) <sup>[12]</sup>   | Prédateur <sup>[9]</sup>             | Limnophile <sup>[6]</sup>   | 29-330                              | 55-350                                 |
| Actinopterygii | Ludjanidae    | Lutjanus argentimaculatus (Forsskål 1775)    | Marin-estuaire <sup>[34]</sup> | Prédateur <sup>[30]</sup>            | Limnophile <sup>[34]</sup>  | 66-79                               | NA                                     |
| Actinopterygii | Syngnathidae  | Microphis ssp.                               | Diadrome (A) <sup>[20]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 84-180                              | 93-150                                 |
| Malacostraca   | Atyidae       | Atyoida serrata (Bate 1888)                  | Diadrome (A) <sup>[3]</sup>    | Consomateur primaire <sup>[7]</sup>  | Rhéophile <sup>[16]</sup>   | 6-44                                | 5-50                                   |
| Malacostraca   | Atyidae       | Caridina longirostris (Edwards 1837)         | Diadrome (A) <sup>[22]</sup>   | Consomateur primaire <sup>[20]</sup> | Limnophile <sup>[20]</sup>  | 10-40                               | NA                                     |
| Malacostraca   | Atyidae       | Caridina typus (Edwards 1837)                | Diadrome (A) <sup>[22]</sup>   | Consomateur primaire <sup>[20]</sup> | Limnophile <sup>[20]</sup>  | 5-30                                | 8-35                                   |
| Malacostraca   | Atyidae       | Caridina serratirostris (De Man 1892)        | Diadrome (A) <sup>[22]</sup>   | Consomateur primaire <sup>[20]</sup> | Limnophile <sup>[24]</sup>  | 23-32                               | 8-32                                   |
| Malacostraca   | Palaemonidae  | Macrobrachium australe (Méneville 1838)      | Diadrome (A) <sup>[20]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[16]</sup>  | 14-96                               | 20-110                                 |
| Malacostraca   | Palaemonidae  | Macrobrachium equidens (Dana 1852)           | Marin-estuaire <sup>[20]</sup> | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 10-70                               | NA                                     |
| Malacostraca   | Palaemonidae  | Macrobrachium lar (Fabricius 1798)           | Diadrome (A) <sup>[17]</sup>   | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 12-150                              | 21-140                                 |
| Malacostraca   | Palaemonidae  | Macrobrachium lepidactylus (Hilgendorf 1879) | Diadrome (A) <sup>[20]</sup>   | Omnivore <sup>[20]</sup>             | Rhéophile*                  | 11-80                               | 19-130                                 |
| Malacostraca   | Palaeomonidae | Palaemon concinnus (Dana 1852)               | Marin-estuaire <sup>[24]</sup> | Omnivore <sup>[20]</sup>             | Limnophile <sup>[20]</sup>  | 14-54                               | NA                                     |
| Malacostraca   | Portunidae    | Scylla serrata (Forsskål 1775 <b>)</b>       | Marin-estuaire <sup>[18]</sup> | Prédateur <sup>[2]</sup>             | Limnophile <sup>[2]</sup>   | 70-85                               | NA                                     |
| Malacostraca   | Sesarmidae    | Sesarmops impressum                          | Marin-estuaire <sup>[20]</sup> | NA                                   | Limnophile <sup>[20]</sup>  | 15-55                               | NA                                     |
| Malacostraca   | Varunidae     | Varuna literrata (Fabricius 1798)            | Diadrome (A) <sup>[20]</sup>   | Consomateur primaire <sup>[20]</sup> | Limnophile <sup>[24]</sup>  | 4-60                                | 7-47                                   |

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*Figure S2 : Correspondance entre les différentes espèces schématisées dans les figures du chapitre 1 et leurs noms scientifiques* 



### 3. Chapitre 2 : Phénologie et mécanisme de la dynamique de dévalaison des larves de Sicydiinae à La Réunion : impact des fluctuations naturelles et anthropiques du débit

### **3.1 Introduction**

Comme détaillé dans l'introduction générale, la migration de dévalaison des larves de Sicydiinae, immédiatement après leur éclosion est une étape clef du cycle de vie amphidrome de ces espèces (McDowall, 2010). Cette migration des milieux d'eau douce vers la mer peut être associée à plusieurs gains écologiques liées à l'utilisation d'habitats différents en fonction des stades de développement larvaires (McDowall, 2009, 2010; Burgess et al., 2015). Cependant le risque de mortalité des larves lors de leur dévalaison peut être très élevé du fait de leur faible de temps de survie en eau douce (Valade et al., 2009) ou de leur risque de piégeage dans les zones lentiques et de prédation (Bell 2009). Toutefois, les dynamiques de dévalaison peuvent réduire ce risque de mortalité. Par exemple, lorsque la dévalaison des larves est synchronisée avec les périodes de débits élevés, le temps de dévalaison et le risque de mortalité associé entre les zones d'éclosion et les habitats de nurserie peuvent être réduits (Næsje et al., 1995). De manière similaire, l'augmentation des abondances de larves dévalant après la tombée de la nuit est généralement associée à une stratégie de réduction du risque de prédation (March et al., 1998; Jarvis & Closs, 2015), les prédateurs potentiels des larves ne pouvant certainement pas les repérer visuellement dans l'obscurité.

De nombreuses pressions d'origine anthropique peuvent perturber la dévalaison des larves de Sicydiinae. Les prélèvements d'eau, en particulier, peuvent augmenter la mortalité des larves lorsque ces dernières sont entrainées avec l'eau prélevée (Benstead et al., 1999). Qui plus est, la réduction du débit en aval des prélèvements d'eau peut aussi avoir des conséquences sur la dévalaison des larves. Dans un premier temps, la réduction du débit est associée à une diminution des vitesses moyennes d'écoulement en aval (Girard et al., 2014a), et donc du temps de dévalaison des larves, ce qui peut augmenter leur risque de mortalité. Dans certains cas la diminution du débit en aval des prélèvements d'eau peut aussi amplifier le risque d'assèchement des rivières (Lill et al., 2013). Lorsque cet assèchement à lieu au niveau de l'embouchure il peut entrainer une mortalité totale des larves écloses sur tout le bassin versant (McDowall, 1995).

Tout ceci souligne l'importance de la prise en compte de la dévalaison des larves lors de mise en place de plans de gestion pour les espèces de Sicydiinae (Teichert et al., 2014a).

La petite taille des larves de Sicydiinae à l'éclosion (Bell & Brown, 1995; Valade et al., 2009) et leurs capacités de nage limitées (Bell & Brown, 1995; Iida et al., 2017) impliquent que leur migration de dévalaison se fait de manière passive, en profitant du courant comme moyen de transport. Qui plus est, leur petite taille limite la possibilité de mettre en place des dispositifs évitant qu'elles soient entrainées avec l'eau dérivée au niveau des prélèvements d'eau (Larinier et al., 1992; Valade et al., 2004; L Faivre, Hydrô Réunion, com. pers.). Il apparait donc important de trouver des solutions alternatives pour limiter la mortalité induite par les prélèvements d'eau lors de la dévalaison des larves. Une piste intéressante serait de mettre en place des arrêts de prélèvements d'eau ciblés sur les périodes pendant lesquelles l'abondance de larves en dévalaison est maximale.

Dans ce contexte, le chapitre 2 s'articule autour de trois objectifs principaux. Dans un premier temps il s'agit de décrire la phénologie des dynamiques de dévalaison des larves de *S. lagocephalus* et de *C. acutipinnis* et de l'expliquer au regard de certains facteurs environnementaux, en particulier le débit du cours d'eau. Dans un second temps, les dynamiques observées sont mises en lien avec les traits d'histoires de vie de ces deux espèces décrits lors d'études précédentes (Teichert, 2012). Une attention particulière a été apportée au lien entre les dynamiques de dévalaison observées et la biologie de la reproduction de ces deux espèces (Teichert et al., 2014b, 2016a). Enfin, dans un troisième temps, différentes mesures de gestion permettant de limiter la mortalité d'origine anthropique des larves lors de leur dévalaison sont proposées et leur pertinence est évaluée au regard des résultats précédents.

### 3.2 Variabilité spatiale et temporelle de la dynamique de dévalaison des larves de Sicydiinae le long du bassin versant de la rivière du Mât

Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif principal de cette étude est de comparer les abondances de larves de *S. lagocephalus* et de *C. acutipinnis* en dévalaison au niveau d'une zone amont et d'une zone aval du bassin versant de la rivière du Mât. Une attention particulière est portée aux variations saisonnières et journalières des abondances de larves entre les deux zones d'étude.

Cette comparaison a pour but d'émettre des hypothèses concernant les stratégies des espèces sensées réduire le risque naturel de mortalité des larves lors de leur dévalaison. Enfin le but ultime de ce travail est d'apporter des réflexions sur la pertinence d'éventuels arrêts ciblés des prélèvements d'eau dans le but de réduire le risque de mortalité des larves, lié aux prélèvements d'eau, lors de leur dévalaison.

**Résultats :** À l'échelle saisonnière, un pic marqué d'abondance de larves est observé pendant les mois de janvier et février au niveau des deux zones (**A1** ; **B1**). De plus, une synchronicité entre les pics d'abondances de larves et les périodes de fort débit (**C**) est décrite. À l'échelle journalière un pic d'abondance de larves est observé après la tombée de la nuit au niveau de la zone aval (**A2**) alors qu'aucun pic ne l'est au niveau de la zone amont (**B2**).



Amélioration de la connaissance des espèces : À l'échelle saisonnière, le pic d'abondance de larves observé au niveau de chacune des deux zones est beaucoup plus marqué que ce qui était attendu à partir des connaissances de la biologie de la reproduction des deux espèces. La synchronicité entre les pics d'abondances de larves et les périodes de fort débit laisse supposer que l'activité de reproduction est plus intense pendant ces périodes. Cette relation entre

l'activité de reproduction et les périodes de débit élevé peut être reliée à une stratégie de réduction du risque de mortalité des larves lors de la dévalaison. En effet, lors des périodes de débit élevé, les vitesses d'écoulement moyennes sont plus importantes ce qui réduit le temps mis par les larves pour parcourir la distance entre leur site d'éclosion et la mer. Cette dévalaison rapide diminue probablement leur risque de mortalité.

À l'échelle journalière, le pic d'abondance de larves observé après la tombée de la nuit au niveau de la zone aval peut être relié à une stratégie de réduction du risque de prédation : les prédateurs potentiels des larves ne pouvant certainement pas les repérer visuellement dans l'obscurité. L'absence de pic d'abondance de larves au niveau de la zone amont est cohérente avec cette hypothèse puisque les principaux prédateurs supposés des larves ne sont présents que dans les zones aval.

**Application à la gestion :** La plupart des ouvrages de prélèvement d'eau à La Réunion se situent dans les zones amont. L'absence de pic d'abondance de larves dans ces zones limite la possibilité de mettre en place des arrêts de prélèvement ciblés sur certaines heures de la journée afin de diminuer la mortalité des larves liée aux prélèvements d'eau. Cependant, étant donnée la saisonnalité marquée des abondances de larves en dévalaison, il apparait judicieux de suggérer de limiter les quantités d'eau prélevées pendant les mois de janvier et février. Cette proposition de gestion présente l'avantage, par rapport à des arrêts journaliers, de ne pas entrainer de modifications fréquentes de débit à l'échelle journalière en aval de l'ouvrage. En effet les variations anthropiques fréquentes de débits sont souvent pénalisantes pour les peuplements piscicoles.



## ARTICLE

1

# Temporal variability of larval drift of tropical amphidromous gobies along a watershed in Réunion Island<sup>1</sup>

Raphaël Lagarde, Nils Teichert, Henri Grondin, Hélène Magalon, Agathe Pirog, and Dominique Ponton

**Abstract:** Freshwater gobies of tropical islands are amphidromous: adults reproduce in rivers and larvae passively drift down to the sea immediately after hatching. Describing the phenology of this larval drift is essential to understanding the population dynamics of amphidromous gobies and to developing ecologically based recommendations for managing the watersheds. The larval drift patterns of two amphidromous gobies of Réunion Island, *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*, were studied on a monthly basis for 1 year using plankton nets at two sites on the Mât River, located 20 km and 7 km from the river mouth. Genetic analyses showed that larval assemblages were dominated at 90% by *S. lagocephalus*, although the proportion of *C. acutipinnis* increased during early summer. Our findings highlighted a marked larval drift peak in full austral summer. The diel larval drift dynamic was described using periodic linear models. A diel pattern was only observed downstream, peaking a few hours after sunset. Finally, this study presents a new approach that improves standard methods for sampling and analyzing larval drift of amphidromous species.

**Résumé** : Les gobies dulçaquicoles des îles tropicales sont amphidromes : les adultes se reproduisent dans les rivières et, immédiatement après l'éclosion, les larves dérivent passivement jusqu'à la mer. La description de la phénologie de la dérive des larves en eau douce est indispensable à la compréhension de la dynamique des populations de ces gobies amphidromes et pour préconiser des mesures de gestion des bassins versants adaptées à leur écologie. Les patrons de dérive des larves de deux espèces de gobies amphidromes de l'île de La Réunion, *Sicyopterus lagocephalus* et *Cotylopus acutipinnis*, ont été décrits mensuellement pendant une année à l'aide de filets planctoniques au niveau de deux sites de la rivière du Mât, situés respectivement à 20 km et 7 km de l'embouchure. Les analyses génétiques ont montré que les assemblages larvaires étaient dominés à 90 % par *S. lagocephalus*. Cependant, la proportion de *C. acutipinnis* était plus importante en début d'été. Nos résultats ont mis en évidence que la dérive des larves avait lieu principalement pendant l'été austral. La dynamique journalière de dérive des larves a été décrite à l'aide de modèles périodiques linéaires. Un patron journalier n'a été observé qu'en aval avec un pic quelques heures après la tombée de la nuit. Enfin, cette étude présente une approche originale, basée sur l'amélioration des méthodes standards d'échantillonnage et d'analyse des données de dérive des larves des espèces amphidromes.

#### Introduction

Diadromy is a life history strategy involving migrations between freshwater and marine biomes (Myers 1949). Within diadromy, amphidromy is a subcategory in which the longest part of the individual's growing period, as well as its reproduction, occurs in freshwater habitats (Manacop 1953). Newly hatched larvae of amphidromous species immediately drift down to the sea where they grow for months (Radtke et al. 1988; Bell et al. 1995). At the end of their larval stage, they return to estuaries and settle in rivers to complete their life cycle as juveniles and adults (McDowall 2007). Amphidromy is widespread among fish species (McDowall 1988), especially in tropical islands where most indigenous fishes are amphidromous (Keith 2003). The highly dispersive capacities of amphidromous fishes have been demonstrated for several species (Chubb et al. 1998; Berrebi et al. 2005). The drift of their larvae in rivers corresponds to the first part of this dispersal phase. Benefits of dispersal are numerous: avoiding the intergenerational competition, reducing the risks of inbreeding, and spreading larvae away from temporally unsuitable habitats (Burgess et al. 2015). The fact that rivers can become temporally unsuitable for fish species has been discussed particularly in the tropical context where cyclonic floods, droughts during the dry season, or even volcanic eruptions can occur and lead to temporary extirpation of fish populations (McDowall 2010). In the context of such unpredictable conditions, the dispersal stages of amphidromous species contribute to explaining the success of this life strategy in tropical islands (McDowall 2010). On the other hand, the risk of mortality during the larval stage is supposed to be huge. For example, Artzrouni et al. (2014) evaluated that the survival probability throughout the whole larval stage of *Sicyopterus lagocephalus* may

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range from  $10^{-4}$  to  $10^{-5}$ . Even during the short period of freshwater larval drift, Bell (2009) estimated that mortality could be as high as 50% per hour for *Sicydium* species. In this context, it is likely that amphidromous species have developed different strategies for reducing the mortality of their larvae when drifting in freshwater streams and rivers (McDowall 2009).

Superimposed on these natural risks of mortality, drifting larvae of amphidromous fishes also face numerous anthropogenic threats. Alteration of the river continuity and the hydrological regimes due to dams can reduce the access to growing-spawning habitats and (or) their availability (Brasher 2003; Cooney and Kwak 2013). Larval survival can also be severely impaired by dams because an important part of the drifting larvae can be entrained within the diverted waters (Benstead et al. 1999). Moreover, alteration of downstream flow regime can increase the risk of river droughts and the duration of these droughts and can also result in the closure of the river mouth (Lill et al. 2013). The consequences of these flow alterations can lead to a total loss of the larvae drifting downstream (McDowall 1995). Despite the fact that harmful effects of dams on drifting larvae have been documented for years, this critical period of the amphidromous fish life cycle has not received much attention from managers (Benstead et al. 1999; Lagarde et al. 2015). This may be due to the inefficiency of existing methods (i.e., intake screens, behavioral barriers, etc.) to avoid migrating small-sized larvae being entrained within diverted waters (Larinier et al. 1994).

In Réunion Island, a 2500 km<sup>2</sup> volcanic island in the southwestern Indian Ocean, the freshwater fish assemblages are dominated by two amphidromous gobies, Sicyopterus lagocephalus and Cotylopus acutipinnis. These two species are culturally important for local populations because the individuals entering estuaries at the end of their marine larval life are traditionally fished (Aboussouan 1969; Bell 1999). Once in freshwater, postlarvae transform into juveniles and colonize the watersheds up to the headwaters thanks to their efficient climbing abilities (Blob et al. 2006; Schoenfuss and Blob 2007). The abundance of S. lagocephalus adults gradually decreases from estuaries to upper habitats located approximately 30 km upstream and at more than 600 m above sea level (a.s.l.), whereas the abundance of C. acutipinnis adults is equally distributed throughout the rivers (Teichert et al. 2014a). Reproduction of both species occurs during the warmer months in the middle and upper reaches, but C. acutipinnis is capable of spawning at lower temperatures than S. lagocephalus (Teichert et al. 2014b, 2016). Thus, reproduction in upstream reaches extends from December to May when the temperature is higher than 19 °C, whereas reproduction can occur during the whole year in downstream reaches (Teichert et al. 2014b). Both species present similar fecundities, ranging from 13 500 to 14 900 oocytes per gram (wet mass) of female and can spawn several times during the reproductive season, with an interspawning interval of approximately 1 month (Teichert et al. 2014b, 2016). Females lay egg clutchs under pebbles and rocks in runs and riffles (Teichert et al. 2013a). After fertilizing the eggs, the male guards the nest until the larvae hatch (Teichert et al. 2013b). Immediately after hatching, larvae, which are at larval stage 1 according to Valade et al. (2009) and Ellien et al. (2016), passively drift down to the sea. Their only activity is a swim up – sink down behavior and they die if they do not reach the sea within few days after hatching (Valade et al. 2009).

The main objective of this study was to establish the spatiotemporal patterns in drifting larvae of *S. lagocephalus* and *C. acutipinnis*. As the number of drifting larvae should reflect both direct (i.e., on the larvae) and indirect (i.e., on the spawning population) disturbances, the ultimate aim was to evaluate the advantages of surveying drifting larvae for assessing the biotic integrity of tropical rivers. **Fig. 1.** Location of (*a*) Réunion Island in the southwestern Indian Ocean and (*b*) studied sites in the Mât River watershed, Réunion Island.



#### Material and methods

#### Sampling sites

This study was conducted in two sites along the watershed of the Mât River on the east side of Réunion Island (Fig. 1). This torrential river flows over 36.3 km from its spring at 2850 m above sea level (a.s.l.). Important hydrological variations are recorded between the dry and the rainy seasons, with the rainy season spanning from November to April, during which time short and intensive cyclonic floods with peak discharge up to 300 times the mean annual discharge can occur (Robert and Davy 1988). One sampling site (site 1; Fig. 1b) was located at 385 m a.s.l. and 20.1 km from the river mouth. The river width at this site was approximately 14 m. A dam is present immediately downstream, but the diversion of water was not operating during the sampling period. The other site (site 2; Fig. 1b) was located downstream to the main tributary (Fleurs Jaunes River), at 120 m a.s.l. and 6.7 km from the river mouth. The river width at this site was approximately 19 m. A dam is located 150 m upstream of site 2. Water diversion due to this dam has not been operative for years; however, the dam disturbs the upstream migration of most diadromous fish and crustacean species and only S. lagocephalus, C. acutipinnis, freshwater eels (Anguilla spp.), and "chevaquines" (shrimps) (Atyoida serrata) can usually reach upstream habitats thanks to their climbing capacities. The riverine habitat was very similar in both sites, with no canopy cover and running water over a substratum composed mainly of small boulders and cobbles. Such substratum composition is suitable for S. lagocephalus and C. acutipinnis to build their spawning nests (Teichert et al. 2013a), and egg clutches have been observed under boulders and cobbles in both sites (R. Lagarde, personal observations). This observation is consistent with a previous study in which egg clutches were observed in different places on the Mât River from 7 to 20 km to the sea (Teichert et al. 2013a). It is thus likely that spawning grounds of Sicydiinae are present from site 2 to the upper limit of presence of those species, which is several kilometres upstream to site 1.

#### Sampling plan

In total, 14 sampling sessions were performed from May 2013 to June 2014 at site 1 and 13 sampling sessions were performed from July 2013 to July 2014 at site 2. The frequency of the sampling sessions was approximately monthly, depending on meteorological conditions and staff availability. During the study, sunrise ranged from 0530 to 0655 and sunset ranged from 1745 to 1905. At the beginning of each sampling session, an estimate of the river discharge (Q<sub>river</sub>, m<sup>3</sup>·s<sup>-1</sup>) was performed. The river cross section was divided into a minimum of 10 vertical subsections. In each subsection, the water velocity was measured using a current meter (Mini Current Meter type M1, SEBA Hydrometrie GmbH, Kaufbeuren, Germany, at one to seven locations, depending on the water depth. The discharge of each subsection was estimated by multiplying the subsection area by its mean water velocity. The river discharge corresponded to the sum of the discharges of all subsections. The number of subsections, the position of each measurement, and the method used to calculate the mean velocity for each subsection were based on the recommendation of the standard NF EN ISO 748:2007 (International Organization for Standardization (ISO) 2007).

A gauging station located 3.8 km downstream of the junction of the Mât and the Fleurs Jaunes rivers (Fig. 1b) recorded the instantaneous discharge every 6 min during the entire study except during a cyclonic flood event on 2 January 2014 and for 45 days following the event. This flood presented a peak discharge of approximately 30 times the mean annual discharge (Julien Bonnier, Office de l'eau Réunion, personal communication). Data of this gauging station are available online (www.eaureunion.fr, accessed in October 2015). Due to this flood event, data of the gauging station were only available from May to December 2013 and from February to July 2014. For all of the sampling sessions during which the gauging station recorded data, the instantaneous flow estimated every 6 min at this station remained within 4% (SD = 1%) of the mean diel flow recorded. The only exception was on 27 November 2013, when a small flooding event started at approximately 1830. Sampling was stopped for safety reasons, and only the first three two-net samples obtained from 0922 to 1546 were kept for analyses. As a consequence, for all of the sampling sessions except one, the river discharge estimated manually at each sampling site was considered to be constant over the whole duration of the sampling session.

#### Sampling procedure

At each site, one sampling session consisted of two conical nets set every 2-4 h over a minimal period of 24 h. The nets were similar to those developed by Bell (1994, 2007) for quantitative drift sampling in small streams. Their mouth diameter was 0.12 m, cod end diameter was 0.06 m, length was 1 m, and mesh size was 80 µm. One of the two nets was fixed in the center of the stream flow, while the other one was randomly positioned along the river cross section. The distances between the two nets ranged between 0.3 m and 6.3 m (mean  $\pm$  SD = 2.1 m  $\pm$  1.3) in site 1 and between 0.2 m and 16.8 m (5.0 m  $\pm$  4.1) in site 2. Each net was set separately, but the second net was always set within a period never exceeding 10 min after setting of the first net. Using two nets quasi simultaneously, with one of the nets having a random position in the river, allowed us to take into account the eventual heterogeneity in the spatial distribution of larval flow along the cross section of the river. To save time, if no larvae were observed in the first two two-net samples, only two to five two-net samples were performed.

Each net was set facing upstream at about 50% of the water depth, held in place by a removable fitting attached to an iron rod hammered into the substratum. Each net was immersed between 1 and 20 min ( $D_{net}$ ), depending on the water velocity, to filter a volume of about 2 m<sup>3</sup> (mean ± SD = 2.4 ± 0.8). As the nets were not equipped with a current meter, two measures of water velocity ( $v_1$  and  $v_2$ ) were performed in front of the mouth of each net, immediately after being set and before being removed, with a current

meter (Mini Current Meter type M1, SEBA Hydrometrie GmbH). The sampled volume ( $V_{net}$ ) was estimated according to eq. 1:

(1) 
$$V_{\text{net}} = \frac{v_1 + v_2}{2} \times \pi \times r^2 \times D_{\text{net}}$$

where  $v_1$  and  $v_2$  are the instantaneous measures of water velocities (m·s<sup>-1</sup>) before and after the sampling, *r* is the radius of the net (i.e., 0.06 m), and  $D_{net}$  is the sampling duration (s).

After removing the net, the solid elements were immediately transferred from the cod end into a 2 L bottle filled with water from the river to keep the larvae alive. The larvae were counted alive as their movements facilitate their detection, sorting, and identification (Bell 2007). First, the sample was kept still for at least 2 h in the bottle to let vegetal and mineral debris to settle. Larvae remained in the water column thanks to their behavior of alternately actively swimming upward and passively sinking (Bell and Brown 1995; Valade et al. 2009). Larvae were then collected by carefully pouring the contents of the bottle on an 80 µm mesh sieve. The pouring was stopped before the overflow of vegetal and mineral debris. The water was returned to the bottle to repeat the decanting procedure twice. Larvae were transferred to a counting dish. All of the larvae in the counting dish were counted by removing each individual using a 15 µL micropipette (Bell 2007). The total number of larvae  $(N_{\text{larvae}})$  was the sum of all of the larvae captured at the end of the three-decant process. For each sample, the larvae were placed in a labeled 1 mL Eppendorf tube and fixed with 95% alcohol solution. This live counting procedure was performed within a period never exceeding 15 h after sampling. This delay was assumed to not affect the number of living larvae as the first mortality of Sicydiinae larvae usually occurs after approximately 24 h spent in freshwater (Valade et al. 2009; Iida et al. 2010). This assumption was confirmed by visual observations of active larvae 15 h after sampling.

The instantaneous larval flow ( $q_{\text{larvae}}$ , individuals (ind)·s<sup>-1</sup>), corresponding to the number of larvae per second drifting through the river cross section, was calculated. The use of larval flow instead of larval density (i.e., number of larvae per filtrated volume) was preferred because values of larval flow are not affected by dilution effect when the discharge increases (Barthem et al. 2014). Comparison of larval drift intensities between sites and seasons can thus be performed even if discharge varies. The instantaneous larval flow was calculated for each net according to eq. 2:

(2) 
$$q_{\text{larvae}} = \frac{N_{\text{larvae}}}{V_{\text{net}}} \times Q_{\text{river}}$$

where  $N_{\text{larvae}}$  is the number of larvae caught in the net,  $V_{\text{net}}$  is the sampled volume (m<sup>3</sup>), and  $Q_{\text{river}}$  is the river discharge (m<sup>3</sup>·s<sup>-1</sup>).

Differences in larval flow between each net of the two-net samples were tested for the whole data set using a paired Student's *t* test. When no significant difference was detected, the mean value of both nets was used as an estimate of the instantaneous larval flow.

#### Genetic identification of species

No morphological criteria discriminate the larvae of *S. lagocephalus* and *C. acutipinnis* (Teichert 2012). The larvae of both species present the same size, shape, color, and a similar repartition of their chromatophores. Criteria commonly used for morphological identification of amphidromous fish larvae (Lindstrom 1999; Bell 2007; Maeda and Tachihara 2010; Jarvis and Closs 2015) are thus not useful for *S. lagocephalus* and *C. acutipinnis*. Identification at the species level can only be based on DNA analysis.

A subsample of 768 larvae was randomly selected among the dates covering the whole period during which the number of

larvae caught was greater than 30. As a result, the number of larvae selected per date ranged from 33 to 57. Total genomic DNA was extracted from each whole larva using a DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Genotyping was performed using the microsatellite locus SIC122, which expresses specific alleles for each species (at 166 base pairs (bp) for C. acutipinnis and from 194 to 242 bp for S. lagocephalus; Hoareau et al. 2009). The forward primer was indirectly fluorochrome labeled (6-FAM) as described in Schuelke (2000), and polymerase chain reactions (PCR) were performed in a total volume of 10 µL: 5 µL of 2× MasterMix (Applied Biosystems, Foster City, California, USA), 2.25 µL of demineralized water, 0.25 µL (1 µmol·L<sup>-1</sup>) of forward primer to which a M13 tail was added at the 5' end, 0.25  $\mu$ L (10  $\mu$ mol·L<sup>-1</sup>) of reverse primer, 0.25  $\mu$ L (10 µmol·L<sup>-1</sup>) of a fluorophore-labeled universal M13 primer, and 2 µL of genomic DNA. The thermocycling program was as follow: 1 × 5 min at 94 °C; 7 × [30 s at 94 °C, 30 s at 62 °C (-1 °C each cycle), 30 s at 72 °C]; 40 × [30 s at 94 °C, 30 s at 55 °C, 30 s at 72 °C], 8 × [30 s at 95 °C, 30 s at 56 °C, 30 s at 72 °C]; and  $1 \times 5$  min at 72 °C. Amplicons were run on an ABI 3730 XL sequencer (Applied Biosystems), and allele size was determined using Genemapper ver. 4.0 (Applied Biosystems).

#### Diel variations of larval flow

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In each site, the diel variations of instantaneous larval flow were analyzed using periodic linear regressions as proposed by Bell (2007). Only the sampling sessions during which more than 100 larvae were caught and spanning over a minimum of 24 h were used to fit the regressions (four dates for site 1 and seven dates for site 2). With regard to the very low proportion of C. acutipinnis larvae captured during most of these dates (see Results), it appeared impossible to consider this species separately in the analyses. Indeed, the estimated number of C. acutipinnis larvae per sampling session was always less than 100 for all of the dates. Periodic linear regressions are frequently used to model predictable cyclical events and allow the use of time as a continuous variable rather than a series of arbitrary categories (Bliss 1958; Bell 2008). This is particularly appropriate for our study as the time interval between two successive two-net samples (from 2 to 4 h) and the number of two-net samples per sampling session (from nine to 12) were not constant between sampling sessions.

For each site, a mixed periodic model was adjusted with varying mesor and regression coefficients for each sampling session to integrate the variability of larval flow between dates (eq. 3):

(3) 
$$Y = \beta_0 + \beta_1 \sin(R_h) + \beta_2 \cos(R_h) + r(1 + \sin(R_h) + \cos(R_h)|Session)$$

where Y represents the instantaneous larval flow,  $R_h$  is the radiantransformed hour of the day (hour ×  $2\pi/24$ ),  $\beta_0$  is the mesor (i.e., mean response of the biological trait over cycles),  $\beta_1$  and  $\beta_2$  are the regression coefficients, and *r* is the matrix of individual effects for the sampling sessions. Residuals of regressions were plotted as a function of a theoretical normal distribution (quantile–quantile plot) to verify the assumption of normality. The significance of parameters was calculated based on the *F* statistic using Satterthwaite's approximation method for the fixed part and on likelihood ratio tests for the random part ( $\chi^2$  tests). The peak position (*P*, hour of the day) was determined for each periodic linear model according to eq. 4:

(4) 
$$P = 365 \times \frac{\arctan\left(\frac{\beta_1}{\beta_2}\right) + QC}{2\pi}$$

**Fig. 2.** Schematic representation of the method used for estimating the daily abundance of larvae ( $A_{\text{larvae}}$ ) from instantaneous larval flow ( $q_{\text{larvae}}$ );  $\bar{t}_n$  and  $\bar{q}_n$  represent the mean time and mean instantaneous larval flow of the two-net samples, respectively, and  $D_{\text{total}}$  represents the total duration of sampling (i.e., time between the first and the last two-net samples of the sampling session).



where QC is a quadrant correction (QC = 0 if  $\beta_1$  and  $\beta_2$  are both positive, QC =  $\pi$  if  $\beta_1$  is positive and  $\beta_2$  is negative or if both are negative, and QC =  $2\pi$  if  $\beta_1$  is negative and  $\beta_2$  positive). This peak was considered significant even if one part of the periodic model (i.e.,  $\beta_1$  or  $\beta_2$ ) was not significant because cycles cannot be expressed in less than two dimensions (Bell 2007).

As the random part appeared significant for each site (see Results), periodic linear models were adjusted for each of the 11 sampling sessions (four for site 1 and seven for site 2) according to eq. 5:

(5) 
$$Y = \beta_{n,0} + \beta_{n,1} \sin(R_h) + \beta_{n,2} \cos(R_h)$$

where Y represents the instantaneous larval flow,  $R_h$  is the radiantransformed hour of the day (hour × 2 $\pi$ /24), and  $\beta_{n,0}$ ,  $\beta_{n,1}$ , and  $\beta_{n,2}$ are the mesor and the regression coefficients for sampling session *n*, respectively. The significance of each of the parameters  $\beta_{n,1}$ and  $\beta_{n,2}$  was calculated based on the *F* statistic.

#### Diel abundance of larvae

The diel abundance of larvae corresponds to the number of larvae drifting through the river cross section during 24 h. Because the intervals between two-net samples within a sampling session were not constant and the larval flow varied with time during a sampling session, a simple arithmetic mean of larval instantaneous flow ( $q_{\text{larvae}}$ ) did not appear adequate to estimate the diel abundance of larvae. Diel abundances of larvae ( $A_{\text{larvae}}$ , ind·day<sup>-1</sup>) were thus obtained by integrating the instantaneous larval flow values obtained over 24 h (Fig. 2) according to eq. 6:

(6) 
$$A_{\text{larvae}} = \frac{\int_{\tilde{t}_1}^{t_n} \bar{q}_{\text{larvae}}(\bar{t}) dt}{D_{\text{total}}} \times 24 \times 3600$$

where *n* is the number of two-net samples obtained during a sampling session,  $\bar{t}$  is the mean time of sampling (s) of the two-net samples ( $(t_{net1} + t_{net2})/2$ , with  $t_{net1}$  and  $t_{net2}$  corresponding to the median times of sampling for net 1 and net 2, respectively) ranging from  $\bar{t}_1 = 0$  to  $\bar{t}_n = D_{\text{total}}$ ,  $D_{\text{total}}$  corresponds to the total sampling duration (s) of the sampling session, and  $\bar{q}_{\text{larvae}}$  is the mean value of instantaneous larval flow (ind·s<sup>-1</sup>) of the two-net sample (( $q_{\text{larvae_net1}} + q_{\text{larvae_net2}}/2$ ).

| Table 1. | Summary of | the sampling | effort and the | e number of successfi | illy identified ind | ividuals of each species | for site 1 and site 2. |
|----------|------------|--------------|----------------|-----------------------|---------------------|--------------------------|------------------------|
|----------|------------|--------------|----------------|-----------------------|---------------------|--------------------------|------------------------|

|                  | Time of the                 |                 | Total                    | Abundance   | Mean river                         | No. of      |                 |                |
|------------------|-----------------------------|-----------------|--------------------------|-------------|------------------------------------|-------------|-----------------|----------------|
| Date             | first two-net               | No. of          | filtrated                | of captured | discharge                          | genetically | No. of          | No. of         |
| (day/month/year) | sample (hours) <sup>a</sup> | nets            | volume (m <sup>3</sup> ) | larvae      | (m <sup>3</sup> ·s <sup>-1</sup> ) | identified  | S. lagocephalus | C. acutipinnis |
| Site 1           |                             |                 |                          |             |                                    |             |                 |                |
| 29/05/2013       | 0750                        | 10              | 31.9                     | 41          | 1.6                                | _           | _               | _              |
| 20/06/2013       | 1020                        | 4               | 14.4                     | 1           | 1.2                                | —           | —               | —              |
| 30/07/2013       | 1032                        | 4               | 10.5                     | 0           | 1.0                                | —           | —               | —              |
| 22/08/2013       | 1256                        | 4               | 8.0                      | 0           | 0.8                                | —           | —               | —              |
| 26/09/2013       | 1019                        | 4               | 11.2                     | 0           | 0.7                                | —           | —               | —              |
| 24/10/2013       | 0735                        | 14              | 37.6                     | 0           | 0.6                                | —           | —               | —              |
| 21/11/2013       | 0645                        | 16              | 43.1                     | 0           | 0.6                                | _           | —               | _              |
| 12/12/2013       | 0710                        | 20              | 42.9                     | 75          | 1.1                                | 42          | 33              | 9              |
| 28/01/2014       | 0748                        | 18              | 39.9                     | 1842        | 3.6                                | 50          | 48              | 2              |
| 20/02/2014       | 0745                        | 18              | 14.6                     | 436         | 3.1                                | 47          | 43              | 4              |
| 27/03/2014       | 0708                        | 20              | 49.7                     | 371         | 2.0                                | 47          | 43              | 4              |
| 23/04/2014       | 0735                        | 18              | 43.5                     | 420         | 1.9                                | 56          | 54              | 2              |
| 19/05/2014       | 0700                        | 18              | 50.1                     | 36          | 1.7                                | 33          | 33              | 0              |
| 18/06/2014       | 0737                        | 14              | 43.1                     | 0           | 1.1                                | —           | _               | _              |
| Site 2           |                             |                 |                          |             |                                    |             |                 |                |
| 01/07/2013       | 1204                        | 26              | 83.2                     | 65          | 4.8                                | —           | —               | —              |
| 22/07/2013       | 1153                        | 16              | 45.6                     | 2           | 3.9                                | —           | —               | —              |
| 19/08/2013       | 1023                        | 16              | 44.7                     | 0           | 3.6                                | —           | —               | —              |
| 16/09/2013       | 1058                        | 18              | 55.1                     | 1           | 3.2                                | —           | —               | —              |
| 28/10/2013       | 0907                        | 24              | 58.8                     | 139         | 2.7                                | 53          | 46              | 7              |
| 27/11/2013       | 0922                        | $6^b$           | 17.1                     | 77          | 5.9                                | 51          | 29              | 22             |
| 16/12/2013       | 0725                        | 20              | 49.3                     | 486         | 3.5                                | 54          | 54              | 0              |
| 04/02/2014       | 0808                        | 17 <sup>c</sup> | 16.4                     | 596         | 11.6                               | 51          | 47              | 4              |
| 23/02/2014       | 0732                        | 18              | 17.6                     | 736         | 8.7                                | 50          | 49              | 1              |
| 20/03/2014       | 0723                        | 20              | 42.3                     | 736         | 6.6                                | 54          | 53              | 1              |
| 05/05/2014       | 0723                        | 18              | 43.0                     | 598         | 6.0                                | 54          | 46              | 8              |
| 02/06/2014       | 0703                        | 22              | 71.4                     | 280         | 6.7                                | 54          | 42              | 12             |
| 02/07/2014       | 0713                        | 18              | 55.5                     | 80          | 4.1                                | 50          | 48              | 2              |

<sup>a</sup>Time is expressed in the 24-h system.

<sup>b</sup>Sampling stopped for safety reasons (see Material and methods).

'Technical issue with one net of the first two-net samples of the sampling session.

All statistical analyses were performed with the open-source R software (ver. 3.1.2; R Core Team 2013), implemented with the lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2015) packages for the mixed-model analyses and the tis package (Hallman 2014) for diel abundance estimation.

#### Results

#### Sampling effort and relative proportion of species

Drifting larvae were caught between 29 May and 20 June 2013 and between 12 December 2013 and 19 May 2014 in site 1 (Table 1). In site 2, drifting larvae were caught during the whole sampling period except on 19 August 2013. The nets set in site 1 (n = 182) and site 2 (n = 239) allowed us to collect a total of 3222 and 3796 larvae, respectively. The number of larvae captured per sampling session ranged from 0 to 1842 in site 1 and from 0 to 736 in site 2.

The measured river discharge ranged from 0.6 to  $3.6 \text{ m}^3 \cdot \text{s}^{-1}$  in site 1 and from 2.7 to 11.6 m<sup>3</sup> \cdot \text{s}^{-1} in site 2 (Table 1). Maximum values of river discharges were observed during the first sampling sessions after the cyclonic flood and then decreased in the following months.

The genetic identification of larvae at the species level was successfully achieved for 746 individuals (between 33 and 56 larvae per sampling session) among the 768 larvae randomly selected. A total of 668 larvae (90%) presented the alleles of *S. lagocephalus*, whereas 78 (10%) presented the allele 166 of *C. acutipinnis* (Table 1). In site 1, the mean proportion of *S. lagocephalus*, weighted by the diel abundance of larvae, was 94%. The lowest proportion of *S. lagocephalus* (79%) was observed on 12 December 2013. In site 2, the mean proportion of *S. lagocephalus*, weighted by the diel abundance of larvae, was 92%. The lowest proportion of *S. lagocephalus* (57%) was observed on 27 November 2013, and proportions of 85%

and 78% were observed on 5 May 2014 and 2 June 2014, respectively.

#### Diel variations of larval flow

For the two sites considered together, instantaneous larval flows ranged from 0 to 2 275 ind·s<sup>-1</sup> and did not significantly differ between each net of the two-net samples (paired Student's *t* test, n = 210,  $t_{208} = -1.40$ , P = 0.16). The orthogonal relationship of the log-transformed larval flow estimated from the fixed net (net 1) and from the randomly positioned net (net 2) illustrated that larval flow was similar across the river's section (Fig. 3). As a consequence, the mean value ( $\bar{q}_{larvae}$ ) of both nets was used for the following analyses.

The instantaneous larval flow ( $\bar{q}_{\text{larvae}}$ ) varied through the day, with diel coefficients of variation varying from 17.2% to 141.4% for site 1 and from 41.5% to 300.0% for site 2. The diel pattern of larval flow generally showed a unique peak, sometimes two peaks (Fig. 4).

In site 1, the part of variance explained by fixed periodic parameters  $\beta_1$  and  $\beta_2$  was not significant, reflecting the absence of consensual diel periodic effect (Table 2; Fig. 4*a*). In contrast, the fixed periodic parameters estimated for site 2 explained a significant part of larval flow variability and predicted a consensual peak of larval flow at 2230 (Table 2; Fig. 4*b*). The random periodic parameters included in each model explained a significant part of variance ( $\chi^2$  test, df = 3, *P* < 0.05 in both sites), reflecting that the hour of the day had an effect on the larval flow for some sampling sessions.

The periodic linear models adjusted separately for each sampling session were consistent with the observed values of larval flow (Fig. 4). For site 1, the part of variance explained by the parameters  $\beta_{n,1}$  and  $\beta_{n,2}$ , used to estimate the location of the peaks,

**Fig. 3.** Orthogonal regression of the estimated instantaneous larval flows (log + 1) between the fixed net (net 1) and the randomly positioned net (net 2). Data from both sampling sites and all sampling sessions are pooled (n = 210). The values of the intercept and slope are given with 95% confidence intervals, and  $r^2$  is the Pearson's correlation coefficient.



was only significant for two sampling sessions over the four. The two significant predicted peaks on 21 February and 28 March 2014 occurred during the afternoon (i.e., at 1230 and 1335; *F* test, P < 0.05; Fig. 4*a*). For site 2, predicted peaks occurred between 1955 and 0010, except on 16 December 2013 when the predicted peak occurred at 1230. The part of variance explained by the parameters  $\beta_{n,1}$  and  $\beta_{n,2}$ , used to estimate the location of the peaks, was significant (F test, p < 0.05; Fig. 4*b*), except on 28 October 2013.

#### Diel abundance of larvae

The diel abundance of larvae ranged between 0 and  $17 \times 10^{6}$  larvae·day<sup>-1</sup> for site 1 (Fig. 5*a*) and between 0 and 44 ×  $10^{6}$  larvae·day<sup>-1</sup> for site 2 (Fig. 5*b*). In both sites, a marked maximum was observed in January–February. A good concordance was observed in both sites between the highest diel abundances of larvae and the highest values of river discharge.

#### Discussion

#### Temporal and spatial dynamics of larval flow

A weak but significant diel pattern of larval drift was observed for both species of Sicydiinae in the downstream site, showing a consensual peak of larvae a few hours after sunset. The same pattern has been reported in similar tropical contexts for several amphidromous gobies (Lindstrom 1998), among them Sicydiinae species (Bell 2007), or for crustaceans (March et al. 1998; Benstead et al. 1999). Nocturnal drift may correspond to a strategy for reducing predation (Lucas and Baras 2001). The poor swimming abilities of Sicydiinae larvae (Bell and Brown 1995) suggest that drifting a few hours after sunset is more probably due to a synchronism of hatching instead of an active behavior of the larvae. Two hypotheses could explain this synchronism in hatching time. First, it could be the result of a preferred spawning time of adults during the day. The short incubation duration of Sicydiinae eggs, approximately 3 days according to Lindstrom (1998), makes plausible the hypothesis that spawning events over a short period of time can lead to the larvae hatching at a given time. For example, if adults spawn mainly at sunset, larvae could hatch approximately at sunset 3 days later. Synchronicity between diel spawning behavior of adults and diel larval drift has been observed in other species such as *Osmerus mordax* (Bradbury et al. 2004). These authors correlated hatching of eggs with the decrease of luminosity at sunset. However, the egg clutches of Sicydiinae are buried under cobles, so that luminosity in the nest is probably constantly low and makes this explanation less likely. The second hypothesis is that hatching could be provoked by the guarding male poking and fanning the eggs, as suggested by Maeda and Tachihara (2010).

Conversely, no clear diel pattern of larval drift was observed upstream. However, two significant peaks of larval drift, calculated for two different dates, were found to occur in the afternoon. The absence of clear diel larval drift pattern in upstream areas has already been observed for several amphidromous species, e.g., Rhinogobius brunneus by Iguchi and Mizuno (1990) or Palaemonidae and Atyidae shrimps by March et al. (1998). Two types of explanations were given for the lack of diel pattern of drifting larvae in upper reaches. First, Iguchi and Mizuno (1990) suggested that the higher complexity of hydrodynamics in upstream reaches could delay the drift of larvae due to their retention in eddies. Secondly, March et al. (1998) made the hypothesis that the absence of predators in upstream reaches could offset the advantage of nocturnal drift. The river sampled in Réunion Island presents a highly turbulent flow from head waters to the estuary; thus, it is unlikely that the different patterns of larval drift could be related to differences in hydraulic conditions between upstream and downstream sites. The hypothesis of March et al. (1998) seems more consistent regarding the structure of fish populations in the rivers of Réunion Island. Indeed, most indigenous predators such as Eleotris spp., Kuhlia spp., and Agonostomus sp. are present in downstream reaches only (Keith et al. 2006). Atyoida serrata, a common crustacean species of upstream reaches, is a detritivore species feeding mainly on organic matter and algae (Keith et al. 2006). So, the only predatory species commonly observed upstream are Anguilla spp., which are probably not predators of newly hatched larvae due to their very small size. Assuming that the mean flow velocity is 50 cm·s<sup>-1</sup> between the two studied sites, which are approximately 13 km apart, the time that larvae would take for passively drifting from site 1 to site 2 would be approximately 7 h. Thus, larvae caught in higher abundances during the afternoon at the upstream site would reach the downstream reaches of the river, where most of their predators are present, at night. However, estimation of the contribution of larvae from site 1 to the observed dynamics in site 2 is much more complicated due to the continuous presence of spawning grounds between both sites.

A very strong seasonal peak of larval drift, matching the period of highest flow, was observed in both studied sites. The period during which drifting larvae were observed corresponded to the reproductive season that was expected based on ovary maturation of S. lagocephalus (Teichert et al. 2014b) and C. acutipinnis (Teichert et al. 2016). However, the larval drift peaks were more intense than what could be speculated from these previous studies. High flow conditions thus appeared to strongly influence the larval drift of Sicydiinae in Réunion Island rivers, as observed for amphidromous gobies in Hawaiian rivers (Lindstrom 1998; Way et al. 1998). This synchronism between high flow and high larval drift could be a strategy to reduce the drifting time and thus the risk of mortality at this stage (Bell 2009) due to starvation (Moriyama et al. 1998; Iguchi and Mizuno 1999), developmental constraints (Bell and Brown 1995), or predation. Predation is probably also lower during high flow due to the increased turbidity limiting the detection of larvae by predators (Araujo-Lima et al. 2001).

#### **Relative proportion of species**

The relative proportion of larvae observed was only partially in agreement with the spatial repartition of adults of *S. lagocephalus* and *C. acutipinnis* and what is known about their reproductive biology. However, the overall proportion of *S. lagocephalus* larvae caught during this study (90%) was consistent with the common

**Fig. 4.** Instantaneous larval flow (log + 1) and predictions of the periodic linear mixed models (solid black line) according to the hour of the day for (*a*) site 1 and (*b*) site 2. The vertical dashed line represents the location of the consensual daily peak predicted by the periodic mixed model. The grey dashed lines and associated symbols represent the larval flow (log + 1) and the periodic linear model adjusted separately for each sampling session from (*a*) 28 January 2014 to 24 April 2014 and (*b*) 28 October 2013 to 2 June 2014. The significance of each model is indicated as follows: ns, nonsignificant; \*, P < 0.05; and \*\*, P < 0.01. The black arrows represent the locations of the predicted individual daily peaks.



**Table 2.** Summary of the mixed periodic models for site 1 and site 2 with the sampling session as random effect.

| Coefficient | Estimate | df   | F    | Р    |
|-------------|----------|------|------|------|
| Site 1      |          |      |      |      |
| βο          | 3.69     | _    | _    | _    |
| $\beta_1$   | -0.23    | 5.97 | 3.66 | 0.47 |
| $\beta_2$   | -0.27    | 2.99 | 0.67 | 0.11 |
| Site 2      |          |      |      |      |
| βο          | 4.14     | _    | _    | _    |
| $\beta_1$   | -0.21    | 5.47 | 3.94 | 0.09 |
| $\beta_2$   | 0.49     | 5.91 | 6.14 | 0.05 |

**Note:** The significance of fixed effects is based on Satterthwaite's method.

proportion of adults of this species in rivers of Réunion Island. Indeed, fish monitoring programs have demonstrated that this species generally represents more than 80% of the total abundance of Sicydiinae, whereas C. acutipinnis represents only 20% (Mérigoux et al. 2012). However, the proportion of S. lagocephalus adults is known to decrease from downstream to upstream reaches (Teichert et al. 2014a). Moreover, although the fecundity and interspawning intervals of both species are similar, C. acutipinnis is able to spawn at lower temperatures than S. lagocephalus (Teichert et al. 2014b, 2016). As a consequence, a lower proportion of S. lagocephalus larvae was expected upstream, as well as at the beginning and end of the reproductive season, when the mean diel water temperatures are below 19 °C. However, in this study, the proportions of S. lagocephalus larvae were approximately the same at both sites and were lower only at the beginning of the reproductive season (October-November). The only plausible explanation for this repartition of larvae would be a lower resilience of C. acutipinnis spawning population compared with S. lagocephalus after cyclonic flood events. A recent study in the same watershed highlighted important movements of adults of both species, probably due to the recolonization of upstream habitats after a cyclonic flood by washed-down individuals (Lagarde et al. 2015). As C. acutipinnis individuals are known to present slightly lesser climbing ability than S. lagocephalus (Voegtlé et al. 2002), they would probably take more time to return to their upstream spawning grounds after a cyclonic flood event. The lesser abilities of C. acutipinnis to recolonize upstream habitats could explain why the proportion of their larvae was lower than expected at the upstream site, especially after the cyclonic flood occurred.

### Is it possible to use larval drift for assessing the biotic integrity of tropical rivers?

Fishes have been used as indicators of the biotic integrity of riverine habitats for years in both temperate (Karr 1981) and, more recently, tropical areas (Mérigoux et al. 2012; Kido 2013), as they integrate the impact of natural and anthropogenic disturbances on riverine communities. In temperate streams, those indicators are generally based on estimations of the abundances of adult and juvenile fishes, as the numbers of adults and juveniles largely depend on the biotic integrity of growing and spawning habitats present in the watersheds. In rivers of tropical islands, the abundances of amphidromous fishes are strongly influenced by the number of juveniles returning in the watershed and by the biotic integrity of the habitats in which they will grow (McDowall and Taylor 2000). Thus, monitoring adults and juveniles of tropical amphidromous fishes does not directly reflect the biotic integrity of spawning habitat within a watershed because of the marine dispersal phase at the end of which no homing exists (Berrebi et al. 2005). In this context, the abundance of drifting larvae could be a good proxy of the biotic integrity of both growing and spawning habitats because it depends on the biomass of adults and their achievement of reproduction within the watershed. Monitoring larval drift could also represent an interesting complementary approach to classical fish monitoring methods based on electrofishing or visual counts and to adult habitat surveys. Indeed, it integrates the biotic integrity not only of habitats located in the sampling site, but also of all habitats up to several kilometres upstream to the sampling site. Monitoring larval drift could also allow evaluation of species richness (Luton et al. 2005) of rivers, especially as progress in genetic techniques will soon allow efficient larval identification and quantification at the species level (Loh et al. 2014). However, evaluation of species richness would be easier and more efficient using environmental DNA methods (Valentini et al. 2016). Anyway, the challenge will be to obtain unbiased estimation of numbers of larvae for several species to use monitoring larval data as complementary indicators of the biotic integrity of riverine habitats.

Before using larval drift for assessing the biotic integrity of riverine habitats, numerous gaps in the knowledge about the biology and ecology of amphidromous species have to be filled. Firstly, knowing how far each species is present upstream to a monitoring site is mandatory. Indeed, the absence of drifting larvae of one species in the samples could simply come from the fact that adults are absent upstream. Secondly, the localization of the **Fig. 5.** Seasonal fluctuation in total daily abundance of larvae (solid line and solid circles) and river discharge measured during the sampling session (dashed line and open circles) for (*a*) site 1 and (*b*) site 2. The discontinuity in the discharge curve (dashed line) gives the approximate date of the cyclonic flood.



growing and spawning habitats of each species (Teichert et al. 2013a, 2014a; Girard et al. 2014) appears essential. For example, Koster et al. (2013) observed that Prototroctes maraena, an amphidromous Osmeriformes from Australia, migrated downstream to their spawning grounds located 5 km up from the estuary, whereas adults were present up to 30 km upstream during the rest of year. In the case of this species, looking for drifting larvae in upstream reaches would be unsuccessful as growing and spawning habitats of adults were spatially separated. Finally, an estimate of the mortality of drifting larvae (Bell 2009) would be necessary to evaluate the spatial representativeness of the information obtained at each monitoring site. Indeed, Bell (2009) estimated that more than 99% of the drifting larvae that he caught had hatched in a 5 km section of river upstream from his sampling sites. In this situation, drift samples would be representative of the biotic integrity of riverine habitats located from the sampling site to less than 5 km upstream only. However, Bell's results varied over several orders of magnitude at a given sampling site and between sampling sites. It thus appears important to reevaluate how far upstream the larvae sampled at a given site are coming from in rivers presenting different biotic and abiotic conditions. Once this knowledge is obtained, determining relationships between larval drift and anthropogenic pressures would be possible and indicators of the biotic integrity of riverine habitats could be developed (Delpech et al. 2010; Kido 2013). In summary, before using larval drift for assessing the biotic integrity of riverine tropical habitats, future research programs should focus on the spatial distribution of adults of amphidromous fishes, localization of their growing and spawning habitats, and estimates of the mortality of their drifting larvae.

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### 3.3 Effet des variations anthropiques journalières de débit sur la dynamique de dévalaison et la survie des larves de Sicydiinae de la rivière Langevin

Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif général de l'étude est de décrire l'effet des variations journalières de débit d'origine anthropique dans la rivière Langevin sur l'abondance de larves dérivant et leur probabilité de survie. Plus précisément, le premier objectif de cette étude était de décrire plus finement la dynamique journalière naturelle de dévalaison dans une zone amont n'étant pas soumise à des variations anthropiques de débit. Au niveau de la zone aval, où des variations fréquentes et intenses du débit d'origine anthropique sont observées, l'objectif de l'étude est de quantifier l'effet de ces variations sur l'abondance des larves dérivant mais aussi sur leur temps de dévalaison et leur probabilité de survie. En termes de gestion, ces résultats permettent de proposer des mesures de gestion des ouvrages de prélèvements d'eau afin de réduire le risque de mortalité des larves dans les zones soumises à des variations anthropiques de débit.

**Résultats :** Au niveau de la zone amont, un faible pic d'abondance de larves est observé en milieu de journée (**A1**). Au niveau de la zone aval, plusieurs pics d'abondance de larves très marqués sont observés (**B1**). Ces pics sont concomitants aux augmentations de débit d'origine anthropique décrites dans cette zone (**B2**). Pendant les augmentations de débits (**B2**), les larves en dévalaison ont une probabilité de survie qui est réduite (**B3**) par rapport à celles dévalant pendant les périodes de débit stable (**A2-A3**). Enfin, la vitesse moyenne du courant augmente peu pendant les périodes de débit élevé en comparaison aux périodes de débit stable. La réduction du temps de dévalaison des larves entre la zone aval et la mer liée aux augmentations de débit n'est que de quelques dizaines de minutes.



Amélioration de la connaissance des espèces : Le faible pic d'abondance de larves observé en milieu de journée au niveau de la zone amont peut être relié au faible risque de prédation dans cette zone et confirme les résultats obtenus dans l'étude précédente au niveau de la zone amont de la rivière du Mât.

L'effet marqué des variations journalières de débit sur l'abondance de larves en dévalaison peut permettre de réduire le temps de dévalaison des larves. En effet, lors des crues mesurées pendant la saison des pluies, l'augmentation de débit peut être beaucoup plus importante que les augmentations d'origine anthropique observées lors de cette étude. Dans ce cas, le gain de temps de dévalaison associé au débit élevé pourrait compenser l'augmentation de la probabilité de mortalité des larves décrite pendant ces périodes. Ce gain pourrait être d'autant plus important que le site d'éclosion est éloigné de la mer.

**Application à la gestion :** Cette étude souligne l'importance d'une gestion raisonnée des variations de débit d'origine anthropique en aval des prélèvements d'eau. Il apparait important de limiter l'amplitude et la fréquence des variations de débit à l'échelle journalière afin de réduire l'impact de ces dernières sur la survie des larves. Des études complémentaires seraient toutefois nécessaires afin de définir les gammes d'amplitude de variations de débit pour lesquelles il n'y a pas d'impact sur la survie des larves.

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#### **ORIGINAL ARTICLE**

# Artificial daily fluctuations of river discharge affect the larval drift and survival of a tropical amphidromous goby

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#### Abstract

Amphidromous fish species reproduce in rivers, and their larvae immediately drift to the sea after hatching. Most of these larvae survive in freshwater for a few days only, rapidly reaching sea water is thus essential. Being of small size, especially among species of the Sicydiinae subfamily, the larvae possess poor swimming abilities; their drift dynamics is considered to be mainly passive and influenced by flow conditions. The influence of daily fluctuations in flow regime on Sicyopterus lagocephalus (Sicydiinae) larval drift patterns was studied using drift nets at three sites along the dammed Langevin River in Reunion Island. The river flow was stable at the upstream site when frequent anthropogenic river flow fluctuations were observed at the two sites downstream to the dam. Weak diel larval drift dynamics were detected at the upstream site and the first site under anthropogenic river flow conditions. In contrast, larval drift dynamics at the most downstream site was strongly influenced by anthropogenic daily fluctuations of discharge: the abundance of drifting larvae increased with peaks of discharge, regardless of the time. As higher mortality rates of drifting larvae were observed during discharge peaks, the benefit of a more rapid travel to the ocean associated with these peaks should be lower than expected. It is concluded that peaks of discharge increase the number of larvae drifting to the sea probably due to higher physical constraints on the egg clutches, but also decrease the chance of survival for larvae that may be nonfully developed.

#### KEYWORDS

diadromy, downstream migration, hydrology, mortality, Sicydiinae, Sicyopterus lagocephalus

#### 1 | INTRODUCTION

Flow regime is a major environmental driver of riverine fish ecology (Humphries, Serafini, & King, 2002; Winemiller, 1989). It notably influences the downstream movement, or drift, of fish larvae between their hatching and nursery habitats (Barthem, da Costa, Cassemiro, Leite, & Silva, 2014; Pavlov, Mikheev, Lupandin, & Skorobogatov, 2008). For example, high abundances of drifting larvae are frequently observed during periods of elevated river discharge (Charteris, Allibone, & Death, 2003; Næsje, Jonssons, & Skurdal, 1995). In addition to flow regime, larval behaviours may also, to some extent, influence larval drift (Lechner, Keckeis, & Humphries, 2016). Larvae of large size in low, steady flow conditions are either able to increase their downstream movements by swimming in the flow direction, or decrease it by swimming against the flow direction, or towards areas of low flow velocity (Lechner et al., 2014; Pavlov et al., 2008). In contrast, small larvae mostly drift passively as their swimming capacities are limited (Braaten et al., 2012; Lechner et al., 2016).

Amphidromous fish species spawn in rivers. Immediately after hatching, their larvae drift down to the sea and develop for months before returning to freshwater (Radtke, Kinzie, & Folsom, 1988; Teichert, Valade, Grondin, et al., 2016). The different hatching (i.e. river) and WILEY-

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nursery (i.e. sea) habitats highlight the importance of the larval drift in the amphidromous life cycle. Although some amphidromous species can spend their entire larval stage in freshwater (Closs, Smith, Barry, & Markwitz, 2003; Hogan, Blum, Gilliam, Bickford, & McIntyre, 2014), for many other species their survival time in freshwater varies from 1 to 7 days only (Iguchi & Mizuno, 1999; Valade et al., 2009). As these larvae must reach the sea within a constrained time window to successfully develop, reducing the period of drifting between their hatching habitats and the sea thus appears to be essential for limiting their mortality.

Among amphidromous species, the gobies of the Sicydiinae subfamily are a species-rich group of more than 100 described species (Taillebois et al., 2014). These species mainly occur in small tropical islands. The swimming abilities of their larvae are limited by their small size, which never exceeds 2 mm notochord length at hatching (lida, Watanabe, & Tsukamoto, 2013; Kinzie, 1993; Valade et al., 2009; Yamasaki & Tachihara, 2006). Once they hatch, the larvae present a single type of behaviour: "swim up-sink down" (Bell & Brown, 1995). The drifting mode of Sicydiinae larvae thus could be considered as mainly passive, and therefore, the flow regime and the eventual spawning strategies of adults are probably the only two factors affecting the time of larval freshwater drift.

For Sicydiinae species, a downstream spawning migration of adults has been hypothesised as one of the strategies aimed to reduce the time that larvae drift in freshwater environment. Indeed, the release of eggs in proximity to the estuary would reduce the distance between spawning grounds and sea. This hypothesis has been developed by Lord, Tabouret, Claverie, Pécheyran, and Keith (2011) based on the variations in otolith elemental composition in adults of Sicyopterus lagocephalus and S. aiensis in Vanuatu rivers. However, a recent study focused on the migration of adults and juveniles of two Sicydiinae species, including S. lagocephalus, in tropical rivers (Lagarde, Teichert, Boussarie, Grondin, & Valade, 2015), suggested that the downstream displacements of adults depend solely on hydrological disturbances during cyclonic floods. If spawning location is not intended to reduce the time spent by larvae in freshwater, the only strategy for reaching the ocean more rapidly would be that larvae drift faster, mainly during periods of elevated river discharge. Indeed, the increase in flow velocity associated with elevated discharge could significantly reduce the time larvae spend in rivers. This hypothesis of synchrony between larval drift peak and elevated discharge is supported by observations made by Way, Burky, Harding, Hau, and Puleloa (1998) and Lagarde et al. (2017). In both studies, a synchronicity between peaks of Sicydiinae larval drift in rivers and elevated discharge was demonstrated on a seasonal scale. However, the question of how daily fluctuations of rivers discharge influence the drift dynamics of Sicydiinae larvae in freshwater remains.

The first objective of this study was to confirm the previously observed diel variations of Sicydiinae larvae abundances in natural and stable flow conditions (Lagarde et al., 2017). The second objective was to test the hypothesis that daily anthropogenic fluctuations of river discharge strongly affect the larval drift dynamics of Sicydiinae (i.e. larval abundance, transport duration and larval survivorship). In other terms, the objective was to verify whether a benefit in terms of survival really exists when larval drifting time is reduced during periods of elevated discharge.

#### 2 | MATERIAL AND METHODS

#### 2.1 | Fish species studied

In Reunion Island, a small volcanic island in the south-western Indian Ocean (Figure 1a), two Sicydiinae gobies, Sicyopterus lagocephalus and Cotylopus acutipinnis, dominate the freshwater fish assemblages. These two species present an important cultural value as traditional fishermen mainly target them (Aboussouan, 1969; Bell, 1999). They are present from the estuaries to upstream reaches (Teichert, Valade, Lim, et al., 2014) as they can climb waterfalls tens of metres high due to their efficient climbing abilities (Blob, Rai, Julius, & Schoenfuss, 2006; Schoenfuss & Blob, 2007; Voegtlé, Larinier, & Bosc, 2002). Reproduction of both species occurs in middle and upper reaches of rivers during the warmer months, that is December to May (Teichert, Valade, Fostier, Grondin, & Gaudin, 2016; Teichert, Valade, Fostier, Lagarde, & Gaudin, 2014). Females lay eggs under pebbles and rocks in runs and riffles (Teichert, Valade, Bosc, Richarson, & Gaudin, 2013). After egg fertilisation, the male guards the eggs until the larvae hatch (Teichert, Keith, et al., 2013).

#### 2.2 | Sampling sites

The study was conducted at three sites along the watershed of Langevin River (Figure 1b). This torrential and very turbulent river flows southward from its source located on the south flank of the Piton de la Fournaise volcano. Approximately 500 m upstream to the estuary, a waterfall tens of metres high impedes the upstream migration of most amphidromous fish species. Due to their climbing capacities, only *S. lagocephalus* and *C. acutipinnis* can pass this waterfall and reach upstream river sections. Three intermittent sectors are present along the river due to the porosity of the bedrock (Figure 1c). Water flows through these sectors only a few days per year during flood conditions. In addition to natural flow variability within the Langevin River watershed, hydroelectric management of a dam, located at 6.5 km upstream to the estuary and 215 m above sea level (a.s.l.), results in diel fluctuations of river discharge.

The most upstream sampling site (site A, Figure 1c) was located immediately upstream of the dam at 215 m a.s.l. The river width at this site was approximately 20 m. The riverine habitats upstream to site A consisted of riffles and pools, several lotic areas being suitable for *S. lagocephalus* and *C. acutipinnis* to reproduce. A gauging station was located approximately 100 m upstream to site A.

Site B (Figure 1c) was located immediately downstream to the outlet channel of the hydropower plant. The river width at site B was approximately 5 m. The concrete-built channel presented no substratum suitable for *S. lagocephalus* and *C. acutipinnis* to reproduce, so it was assumed that no reproductive activity occurred in this channel during the study. On 17 February 2016, the dam was not operative and no

60°E



50°E

₄ <sup>|</sup>45°Ε

55°E

**FIGURE 1** Sampling sites along the Langevin River watershed (c), Reunion Island (b), Southwestern Indian Ocean (a). Discharge fluctuations on 22 January 2016, when the dam was in operation, and on 17 February 2016, when the dam was not in operation are presented as examples for each site. Water loss can be observed between sites A and B on 17 February 2016 due to the porosity of the bed rock

water was flowing in the channel upstream to the usual location of site B. The sampling site was thus moved to the river bed, approximately 50 m upstream to its usual location. At this occasion, the river width at site B was approximately 10 m.

(a)

4d°E

The most downstream sampling site (site C, Figure 1c) was located at 50 m a.s.l., 2 km downstream to site B and 2.5 km upstream to the estuary. The river width at this site was approximately 18 m. The riverine habitat between sites B and C consisted of riffles and pools, several lotic areas being suitable for *S. lagocephalus* and *C. acutipinnis* to reproduce. Egg clutches of Sicydiinae gobies had been observed in the river between both sites during a previous study (Teichert, Valade, et al., 2013).

During the study, data from site A (Figure 1c) were used to describe the daily variations of larval abundances in natural flow conditions. On 17 February 2016, when the dam was not operative, the river flowed between sites A, B and C without anthropogenic disturbances or natural input from tributaries (Figure 1c). During this sampling session only, data from sites B and C were also used to describe the variations of larval abundances in natural flow conditions. For all the other sampling sessions, the dam was operative and the whole river discharge was diverted into the hydropower plant. Consequently, the river section between the dam and site B was dried up. Larvae originating from upstream reaches situated nearby site A thus had to survive the passage through hydroelectric structures to reach site B. The diel fluctuations of discharge observed at sites B and C (Figure 1c) were due to hydropower management. When the dam was operative, data from site C were used to describe the effect of daily anthropogenic fluctuations of river discharge on larval drift dynamics. Data from site B were used for controlling that larvae coming from upstream to the dam, and observed at site A, did not significantly influence the larval drift dynamics observed at site C.

#### 2.3 | Sampling procedure

A total of six sampling sessions were performed simultaneously at the three sites every 2 weeks from January 2016 to March 2016. This period was selected as it corresponds to the main season of reproduction of Sicydiinae gobies in Reunion Island, especially in upstream sites (Teichert, Valade, Fostier, et al., 2014).

Each sampling covered an entire 24-hr cycle and consisted in immersing simultaneously two conical nets nine to ten times at each site. The first nine two-net samples were scheduled every 3 hr. The additional, tenth, two-net sample was performed during the first peak of discharge of the day if this peak did not occur during the scheduled samples. Peaks of discharge were detected based on constant visual observations of water height at site C. Synchronicity of sampling schedule among sites was maintained by regular communications among the teams working at each site using mobile phones. At each station, the two nets were immersed for 5–30 min ( $D_{nel}$ ) to filter a volume of 3–6 m<sup>3</sup>. This volume captures tens of larvae (Lagarde et al., 2017) and limits the quantity of organic and mineral debris in the net. The nets were similar to those used for quantitative

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drift sampling in small streams by Bell (1994, 2007). Their mouth diameter was 0.12 m, cod end diameter 0.06 m, length 1 m, and mesh size 80 um. One of the two nets was fixed in the centre of the stream flow, whereas the other one was randomly positioned along the lotic areas of the river cross-section. The distances between the two nets ranged between 1.2 and 8.7 m (mean ± standard deviation [SD] = 3.9 m ± 2.1) at site A, between 0.2 and 2.4 m (0.7 m ± 0.5) at site B and between 0.2 and 2.7 m (1.3 m ± 0.7) at site C. Each net was set separately, the second net being set within 10 min after the first net. Using two nets quasi simultaneously, homogeneity of larvae distribution across the river was quantified (Lagarde et al., 2017). Each net was placed facing upstream at about 50% of the water depth. It was attached to an iron rod hammered into the substratum. Two measures of water velocity ( $v_1$  and  $v_2$ ) were performed in front of the mouth of each net, immediately after being set and before being removed. Measures were performed with a FLO-MATE 2000 flow meter (Cometec) or a Z4000 current meter (OTT) at site A, a M1 current meter (SEBA Hydrometry) at site B, and a MF PRO flow meter (OTT) at site C. All these apparatuses gave values with the same precision.

The sampled volume  $(V_{net})$  was estimated with Equation (1):

$$V_{\rm net} = \frac{v_1 + v_2}{2} \times \pi \times r^2 \times D_{\rm net} \tag{1}$$

where  $v_1$  and  $v_2$  are the instantaneous water velocities measured in m/s before and at the end of the sampling respectively; *r*, the radius of the net mouth (i.e. 0.06 m); and  $D_{net}$ , the sampling duration (s).

#### 2.4 | Larvae sorting and counting

After recovering each net, the content of each cod end was immediately transferred into a 2-L bottle filled with water from the river. The sample was kept still for a minimum of 1 hr and a maximum of 11 hr in the bottle to let organic and mineral debris settle down. This delay was assumed not to affect the number of alive larvae as the first mortality of Sicydiinae larvae usually occurs after approximately 24 hr spent in freshwater (lida et al., 2010; Valade et al., 2009). This assumption was confirmed by visual observations of active larvae 11 hr after sampling. Larvae remained in the water column thanks to their "swim up-sink down" behaviour (Bell & Brown, 1995; Valade et al., 2009). Larvae were then collected by carefully pouring the contents of the bottle on an 80-µm-mesh sieve. The pouring was stopped before the overflow of vegetal and mineral debris. The water was returned to the bottle in order to repeat the decanting procedure twice. All larvae were transferred to a counting dish and counted by removing them one by one using a 15-µl micropipette. When the number of larvae appeared to be too high for direct count, the larvae were fixed with 95% alcohol solution, and their number was estimated later in the laboratory using a Dollfus tray. The total number of larvae  $(N_{larvae})$  corresponded to the sum of all the larvae removed at the end of the three decant process. For each sample, the larvae were placed in a labelled 1-ml Eppendorf<sup>®</sup> and fixed with 95% alcohol solution.

## 2.5 | Estimation of river discharge and fluctuations of water height

Data from the gauging station located upstream to site A were obtained online (www.eaureunion.fr, accessed in July 2016). The instantaneous river discharge ( $Q_{river}$ , m<sup>3</sup>/s) was recorded every 12 min.

At site B, the discharge at the outlet of the dam was estimated every hour by the hydroelectric company (Electricité de France) based on the mean hourly hydroelectric production. These data were used for estimating the river discharge during each two-net sample at this site, except on 17 February 2016 when the dam was not operative.

The river discharge at site C was estimated during each two-net sample using the velocity-area method. The river cross-section was divided into a minimum of ten vertical subsections. In each subsection, the water velocity was measured using a flow meter (type MF PRO, OTT) at up to three different water depths. The discharge of each subsection was estimated by multiplying the subsection area by its mean water velocity. The river discharge corresponded to the sum of the discharges of all subsections. The methods used for the measurement of flow velocities and for the estimation of discharge were based on the recommendation of the standard International Organization for Standardization (ISO, 2007).

The duration of the water height rising from base flow to the peak of discharge was identified based on measurements of water height at site C made every minute using a pressure sensor (Mini Diver SWS Technology) with an accuracy of  $\pm 1$  cm. The sensor was attached to an iron rod hammered into the substratum. As the position of the sensor varied between sampling sessions, only the relative variation in water height (i.e. difference between the water height at a given time and the minimum water height observed during the sampling session) was used.

#### 2.6 | Variations of larval abundance

Instantaneous larval abundance was approximated with larval density  $(D_{larvae}, ind/m^3)$  calculated for each net with Equation (2):

$$D_{\text{larvae}} = \frac{N_{\text{larvae}}}{V_{\text{net}}}$$
(2)

where  $N_{\text{larvae}}$  is the number of larvae caught in the net and  $V_{\text{net}}$  is the sampled volume (m<sup>3</sup>). Differences in the larval density between each net of the two-net samples were tested for the whole data set using a paired Student's *t* test. The homogeneity of the spatial distribution of larval density along the cross-section of the river was checked using orthogonal regressions between the larval densities estimated for each net of the two-net samples.

The daily variations in larval densities were analysed at each study site using periodic linear regressions as proposed by Bell (2007). Periodic linear regressions are frequently used for modelling predictable cyclical events, and allow the use of time as a continuous variable rather than a series of arbitrary categories (Bell, 2008; Bliss, 1958). This is particularly appropriate for this study as the time interval between two successive two-net samples (from 1 to 3 hr), and the

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number of two-net samples per sampling session (from 9 to 10), varied between sampling sessions.

A mixed periodic model was adjusted taking into account each sampling session in order to integrate the variability of larval density among dates (3):

$$D_{\text{larvae}} = \beta_0 + \beta_1 \sin(R_h) + \beta_2 \cos(R_h) + r(1 + \sin(R_h) + \cos(R_h)) \text{|Session|}$$
(3)

where  $D_{\text{larvae}}$  represents the instantaneous larval density;  $R_{\text{h}}$ , the radian transformed hour of the day (hour × 2 $\pi$ /24);  $\beta_0$ , the mesor (i.e. mean response of the biological trait over cycles);  $\beta_1$  and  $\beta_2$ , the regression coefficients; and r, the matrix of random individual effects for the sampling sessions. Residuals of regressions were plotted as a function of a theoretical normal distribution (quantile–quantile plot) to verify the assumption of normality. The significance of parameters was calculated based on the *F*-statistic using the Satterthwaite's approximation method for fixed part, and on likelihood ratio tests for random part (chi-square tests). The peak position (*P*, hour of the day) was determined for the mixed periodic linear model from Equation (4):

$$P = 24 \times \frac{\arctan\left(\frac{\beta_1}{\beta_2}\right) + QC}{2\pi}$$
(4)

where QC is a quadrant correction (QC = 0 if  $\beta_1$  and  $\beta_2$  are both positive, QC = $\pi$  if  $\beta_1$  is positive and  $\beta_2$  negative or if both are negative and QC =  $2\pi$  if  $\beta_1$  is negative and  $\beta_2$  positive). This peak was considered significant even if one part of the periodic model (i.e.  $\beta_1$  or  $\beta_2$ ) was not significant because cycles cannot be expressed in less than two dimensions (Bell, 2007). At site C, one outlier was excluded from this analysis to verify the assumption of normally distributed residuals.

## 2.7 | Estimation of larval drifting time and survival probability

The mean flow velocity of the river reaches downstream to site C was used to approximate the time taken by larvae drifting from site C to the sea. The estimation of mean flow velocity in this reach was performed twice: on a date when river discharge was low, and on a date when it was elevated. On each date, water velocity was measured at 40% of the water depth using a flow meter (type MF PRO, OTT) in several points along 12–14 transects following the protocol described by Girard, Lamouroux, and Mons (2014).

Estimations of survival probability were performed on larvae collected at sites A and C during three different sampling sessions when variations of river discharge were observed. These three dates were selected based on staff availability. For each of the three sampling sessions, survival probability was studied for larvae captured during the first two-net sample of the session, and for larvae captured during the additional two-net sample performed immediately after the first peak of discharge observed at site C. Larvae captured at site C were used to study the effect of discharge conditions on larval survival when those captured at site A were used for controlling the effect of the hour of the day on larval survival. A maximum of 60 larvae were subsampled per two-net sample. If the number of larvae captured in the two-net sample was lower than 60, all larvae were sampled. At site A, an additional third net was set immediately after the two-net sample in order to increase the number of larvae for this experiment.

Immediately after being captured, the larvae were transferred to the laboratory where they were sorted and counted following the protocol described above. They were placed in 500-ml beakers at 23.5  $\pm$  0.5°C, a temperature corresponding to the mean daily temperature observed in downstream reaches of the Langevin River during summer (Teichert, Valade, Fostier, et al., 2014). Every 6-8 hr, the dissolved oxygen (mg/L) in the beakers was measured using an oximeter (HQ30D; Hatch), and the dead larvae were removed using a 15-µl micropipette, and preserved in 95% alcohol solution. Larvae were considered dead when lying on the bottom of the beaker and not responding to a gentle stimulation using a soft paintbrush.

Estimations of larval survival probability with time were performed based on the Kaplan-Meier method. Due to the low number of larvae captured during some two-net samples, results of survival time from the three different sampling sessions were summed. Results were expressed for low and peak discharge at site C, and the corresponding time of sampling at site A, the station where hydrological conditions were not modified. Finally, the difference of survival probability with time among the four different groups was tested using a log-rank test.

All statistical analyses were performed with the open source R v. 3.3.1 software (R Development Core Team, 2016). The packages *Ime4* (Bates, Maechler, Bolker, & Walker, 2015) and *ImerTest* (Kuznetsova, Brockhoff, & Christensen, 2015) were used for the mixed periodic model analyses, and the package *survival* (Therneau, 2015) for the estimations of larval survival time.

#### 2.8 | Identification of the larvae to the species level

No morphological criteria allow to discriminate the larvae of *S. lago-cephalus* and *C. acutipinnis* (Teichert, 2012). The larvae of both species present similar size, shape, colour and repartition of their chromato-phores. Criteria commonly used for morphological identification of amphidromous fish larvae (Lindstrom, 1999) are thus not useful for identifying these two species.

Identification at the species level was thus based on DNA analyses. A sample of 480 larvae was selected, 288 being randomly subsampled among the 407 larvae used for survival experiments, and 78 and 114 being randomly subsampled among the two-net samples from sites A and C respectively. As no peak of discharge was observed on 17 February 2016, no larvae from this sampling session were sampled for DNA analysis.

Total genomic DNA was extracted from each whole larva using DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Following the same protocol as in Lagarde et al. (2017), genotyping was performed using the microsatellite locus SIC122, which expresses specific alleles for each species (at 166 bp for *C. acutipinnis*, and from 194 to 242 bp for *S. lagocephalus*; Hoareau, Barbisan, Dubois, Zane, & Berrebi, 2009). Amplicons were run on an ABI FRESHWATER FISH

**TABLE 1** Sampling dates at each site and corresponding number of two-net samples, number of samples (numbers in parentheses correspond to the use of a third net in parallel to some two-net samples in sites A and B for increasing the number of larvae caught, see text for details), filtrated volume (m<sup>3</sup>), number of Sicydiinae larvae captured, number of larvae used for DNA analyses and number of individuals successfully identified for each species. On 15 March 2016, peak of discharge occurred immediately after the second two-net sample of the day; therefore, no supplementary two-net sample was performed at site A. On the same date, one of the nets was still immersed at site B during the increase of discharge and the sample was thus lost

| Site  | Date       | Number of<br>two-net<br>samples | Number of samples | Filtered<br>volume<br>(m <sup>3</sup> ) | Number of<br>Sicydiinae<br>Iarvae | Number of larva<br>used for DNA<br>analyses | e Number of<br>Sicyopterus<br>lagocephalus | Number of<br>Cotylopus<br>acutipinnis |
|-------|------------|---------------------------------|-------------------|---|-----------------------------------|---|--|---------------------------------------|
| А     | 22/01/2016 | 9                               | 18                | 95                                      | 281                               | 10  | 10   | 0                                     |
|       | 03/02/2016 | 10                              | 20 (+2)           | 129                                     | 809                               | 59  | 58   | 1                                     |
|       | 17/02/2016 | 9                               | 18 (+1)           | 106                                     | 448                               | 16  | 11   | 0                                     |
|       | 02/03/2016 | 10                              | 20 (+2)           | 119                                     | 225                               | 19  | 19   | 0                                     |
|       | 15/03/2016 | 9                               | 18 (+1)           | 110                                     | 243                               | 64  | 49   | 1                                     |
|       | 30/03/2016 | 9                               | 18                | 90                                      | 521                               | 18  | 18   | 0                                     |
| В     | 22/01/2016 | 9                               | 18                | 79                                      | 42                                | -   | _  | _                                     |
|       | 03/02/2016 | 10                              | 20 (+2)           | 126                                     | 95                                | -   | _  | _                                     |
|       | 17/02/2016 | 9                               | 18                | 70                                      | 205                               | -   | _  | _                                     |
|       | 02/03/2016 | 10                              | 20 (+2)           | 96                                      | 189                               | _   | _  | _                                     |
|       | 15/03/2016 | 10                              | 18 (+1)           | 100                                     | 172                               | -   | -  | _                                     |
|       | 30/03/2016 | 9                               | 18                | 82                                      | 216                               | _   | _  | _                                     |
| С     | 22/01/2016 | 9                               | 18                | 53                                      | 8,829                             | 40  | 22   | 0                                     |
|       | 03/02/2016 | 10                              | 20                | 74                                      | 1,062                             | 46  | 43   | 0                                     |
|       | 17/02/2016 | 9                               | 18                | 82                                      | 1,061                             | _   | _  | _                                     |
|       | 02/03/2016 | 10                              | 20                | 98                                      | 2,319                             | 85  | 73   | 0                                     |
|       | 15/03/2016 | 10                              | 20                | 87                                      | 2,141                             | 83  | 64   | 0                                     |
|       | 30/03/2016 | 9                               | 18                | 75                                      | 788                               | 40  | 35   | 0                                     |
| Total | _          | 171                             | 349               | 1,671                                   | 19,646                            | 480   | 402  | 2                                     |

3730 XL sequencer (Applied Biosystems, Foster City, CA, USA), and allele size was determined using Genemapper v 4.0 (Applied Biosystems).

#### 3 | RESULTS

#### 3.1 | Sampling effort and relative proportion of species

Drifting larvae of Sicydiinae were present at all sampling sessions and each site (Table 1). At site A, a total of 2,527 larvae were collected in the 118 samples. Among the 186 larvae sampled for DNA analysis, 167 were successfully identified with 165 (99%) presenting the specific alleles of *S. lagocephalus* and two (1%) presenting the specific alleles of *C. acutipinnis*. At sites B and C, a total of 919 and 16,200 larvae were collected in the 118 and 114 samples respectively. Among the 294 larvae from site C sampled for DNA analysis, 237 were successfully identified as being *S. lagocephalus*. The unsuccessful identification of species was always due to a lack of DNA amplification that may be related to the low quantity of DNA per larva, or poor preservation of some samples. The total proportion of larvae at sites A and C presenting the specific alleles of *C. acutipinnis* was less than 0.5%. *Sicyopterus lagocephalus* and *C. acutipinnis* are the only two amphidromous fish species present in sampling sites, and the proportion of *C. acutipinnis* in samples appeared very low. The following results can thus be considered to mainly concern *S. lagocephalus* individuals.

All sites considered together, larval densities estimated for each sample of the two-net samples ranged from 0 to 1,346 ind/m<sup>3</sup>. They did not significantly differ between the fixed and the randomly positioned nets of the two-net samples (paired Student's *t* test, *n* = 169,  $t_{168} = 1.0$ , p = .31). The orthogonal relationship of the log-transformed larval density estimated from the fixed and the randomly positioned nets indicated that the larval density was similar across the river cross-section (*n* = 169; slope ± standard error [*SE*] = 0.99 ± 0.04; intercept ± *SE* = 0.01 ± 0.07;  $r^2 = .76$ ). As a consequence, the mean value ( $\bar{D}_{larvae}$ ) of all nets for each two-net sample was used for the following analyses. When, for technical reasons, the estimation of the larval density was available for only one net of the two-net sample (*N* = 2, i.e. 1.2% of the two-net samples), this unique value was used.

## 3.2 | Diel variations in larval density of *S. lagocephalus*

The larval density  $(\bar{D}_{larvae})$  of *S. lagocephalus* varied between 0.19 and 22 ind/m<sup>3</sup> (mean ± *SD* = 4.2 ± 4.2 ind/m<sup>3</sup>) at site A, between 0 and 5.8 ind/m<sup>3</sup> (1.8 ± 1.5 ind/m<sup>3</sup>) at site B and between 2.9 and 1,120 ind/



FIGURE 2 Log-transformed larval densities of Sicvopterus lagocephalus according to the hour of the day at sites A (a). B (b) and C (c). Open symbols differ for each date, the solid black line corresponds to the predictions for the fixed part of the periodic linear mixed models, and the black arrows correspond to the daily peak predicted for the fixed part of the periodic linear mixed model. The circled value at site C is an outlier which was excluded from the analysis to verify the assumption of normally distributed residuals. As no significant variation of discharge was observed on 17 February 2016, data from this sampling session were not included in the analysis at sites B and C

TABLE 2 Results of the periodic linear mixed models for sites A, B and C with the sampling session considered as a random effect. At site C, an outlier was excluded from the analysis to verify the assumption of normally distributed residuals (see Figure 2 for details). With  $\beta_{\alpha}$ : mesor, that is mean response of the biological trait over cycles,  $\beta_1$  and  $\beta_2$ : regression coefficients, df: degree of freedom estimated using the Satterthwaite's approximation method, F: F-statistic, and p: associated probability. As no significant variation of discharge was observed on 17 February 2016, data from this sampling session were not included in the analysis for sites B and C

|                | Coefficient    | Estimate       | df    | F     | р     |
|----------------|----------------|----------------|-------|-------|-------|
| Fixed effects  |                |                |       |       |       |
| Site A         | β <sub>0</sub> | 1.42           | -     | -     | _     |
|                | β1             | -0.01          | 4.82  | 0.00  | .96   |
|                | β <sub>2</sub> | -0.41          | 4.84  | 11.10 | .02   |
| Site B         | β <sub>o</sub> | 0.86           | -     | _     | _     |
|                | β              | -0.26          | 23.99 | 9.26  | < .01 |
|                | β <sub>2</sub> | -0.01          | 3.98  | 0.01  | .92   |
| Site C         | β <sub>0</sub> | 2.38           | -     | -     | _     |
|                | β1             | -0.33          | 13.71 | 1.60  | .27   |
|                | β <sub>2</sub> | -0.11          | 13.71 | 0.50  | .49   |
|                | Coefficient    | χ <sup>2</sup> |       | df    | р     |
| Random effects |                |                |       |       |       |
| Site A         | β1             | 0.66           |       | 3     | .90   |
|                | β2             | 1.44           |       | 3     | .70   |
| Site B         | β              | 0.12           |       | 3     | 1.00  |
|                | β <sub>2</sub> | 1.89           |       | 3     | .60   |
| Site C         | β1             | 4.86           |       | 3     | .90   |
|                | β <sub>2</sub> | 0.46           |       | 3     | .20   |

 $m^3$  (34.7 ± 146.2 ind/m<sup>3</sup>) at site C (Figure 2). The estimated fixed parameters,  $\beta_1$  and  $\beta_2$ , of the periodic models explained a significant part of larval densities variability at sites A and B, but not at site C (Table 2, Figure 2). As no significant variation of discharge was observed on 17 February 2016, data from this sampling session were excluded from the analysis at sites B and C. At sites A and B, the predicted peaks of larval densities were at 12:03 and 17:48 respectively. The variance explained by the random periodic parameters included in each model was never significant for the three sites (chi-square test, df = 3,  $p \ge .2$  in all sites). It means that the larval density dynamics considered separately for each sampling session were not different from the larval density dynamics described for all the sampling sessions considered altogether.



**FIGURE 3** Log-transformed larval densities of *Sicyopterus lagocephalus* at site B (open symbols) and site C (filled symbols), and relative fluctuations of water height at site C (dashed line) according to the hour of the day for each sampling session (from a to f)

# 3.3 | Effects of anthropogenic fluctuation of discharge on larval densities of *S. lagocephalus* at sites B and C

The larval densities observed at site C were always higher than those observed at site B with the exception of a single event at 23:00 on 17 February 2016 when the dam was not operating (Figure 3c). In addition, the maximum larval density at site C was at 20:00 on this day when the dam was not operating (Figure 3c). During the whole study, the relative fluctuations of water height at site C varied between 4 and 33 cm and the duration of the water height increase from base flow to the peak of discharge lasted from 12 to 17 min.

At site B, the discharge difference between two successive twonet samples ranged from -1.9 to +1.6 m<sup>3</sup>/s when the larval densities of *S. lagocephalus* difference ranged from -3.6 to +3.5 ind/m<sup>3</sup> (Figure 4a). At site C, the discharge difference between two successive two-net samples ranged from -2.1 to +1.9 m<sup>3</sup>/s when the difference in larval densities ranged from -1,110.9 to +1,114.9 ind/m<sup>3</sup> (Figure 4b). The log-transformed difference of larval density between two successive two-net samples was correlated to the difference of discharge between the same two-net samples at site C (n = 42;  $r^2 = .36$ ; p < .001, Figure 4), but not at site B (n = 41;  $r^2 = .01$ ; p = .6, Figure 4). As no significant variation of discharge was observed on 17 February 2016, data from this sampling session were excluded from the analysis.

### 3.4 | Estimation of larval drifting time and survival probability

The estimation of the mean flow velocity downstream to site C was performed on 7 April 2016 (118 measurements) and on 23 May 2016 (82 measurements). On 7 April 2016, the estimated discharge was  $1.0 \text{ m}^3$ /s for a mean flow velocity of 0.29 m/s while on 23 May 2016, discharge reached 1.6 m<sup>3</sup>/s and flow velocity 0.35 m/s. As a result, it would take 144 min for passive larvae to travel from site C to the estuary (distance = 2.5 km) on 7 April 2016, and 119 min on 23 May 2016. Thus, an increase in mean flow velocity from 0.29 to 0.35 m/s downstream to site C would result in an approximately 25-min reduction of larval drifting time.



FIGURE 4 Linear regression relating the difference of discharge to the difference of the log-transformed larval density of Sicyopterus lagocephalus between two successive two-net samples (a) at site B (open symbols) and (b) at site C (filled symbols). As no significant variation of discharge was observed on 17 February 2016, data from this sampling session were not included in the analysis

TABLE 3 Sampling conditions at sites A and C, and number of larvae used for the survival experiment. The sample obtained from site A on 2 March 2016 at 07:00 was lost during transportation to the laboratory. The number of larvae from these experiments used for DNA analyses is also indicated

| Site | Date       | Sampling time | River discharge<br>m <sup>3</sup> /s | Survival experiment treatment groups | Number of larvae used<br>in survival experiment | Number of larvae<br>subsampled for DNA<br>analyses |
|------|------------|---------------|--------------------------------------|--------------------------------------|---|--|
| А    | 03/02/2016 | 07:00         | 0.95                                 | Control_low                          | 25  | 20   |
|      | 03/02/2016 | 11:15         | 0.95                                 | Control_peak                         | 26  | 17   |
|      | 02/03/2016 | 07:00         | 1.68                                 | Control_low                          | -   | _  |
|      | 02/03/2016 | 14:30         | 1.68                                 | Control_peak                         | 23  | 15   |
|      | 15/03/2016 | 07:30         | 1.5                                  | Control_low                          | 26  | 18   |
|      | 15/03/2016 | 10:30         | 1.5                                  | Control_peak                         | 42  | 38   |
| С    | 03/02/2016 | 07:00         | 0.58                                 | Low                                  | 10  | 8  |
|      | 03/02/2016 | 11:15         | 1.14                                 | Peak                                 | 32  | 28   |
|      | 02/03/2016 | 07:00         | 1.78                                 | Low                                  | 43  | 24   |
|      | 02/03/2016 | 14:30         | 2.92                                 | Peak                                 | 65  | 50   |
|      | 15/03/2016 | 07:30         | 1.05                                 | Low                                  | 51  | 32   |
|      | 15/03/2016 | 11:00         | 1.52                                 | Peak                                 | 63  | 38   |

Estimations of S. lagocephalus larval survival probability with time were performed on a total of 406 larvae caught on 3 February, 2 March and 15 March 2016 (Table 3). Among these larvae, 105 were captured during low discharge conditions, later identified as "low," and 161 during peak discharge conditions, identified as "peak," in site C. This corresponded to 51 and 90 larvae captured at the same time at site A where stable conditions of discharge prevailed. Larvae captured at site A between 07:00 and 07:30 were identified as "control\_low" and larvae captured at the moment of the second sampling as "control peak". The mean dissolved oxygen concentrations in the beakers did not differ among the four groups of larvae "low," "peak," "control\_ low" and "control\_peak" (ANOVA, n = 206,  $F_{3,202} = 1.76$ ; p = .16). The maximum survival times for the four groups of larvae were similar and ranged between 130 and 140 hr (Figure 5). However, survival probabilities over time significantly differed among groups (log-rank test,  $df = 3, \chi^2 = 32, p < .001$ ), and the larvae captured during the peaks of discharge at site C had a lower survival probability, especially during the first 24 hr (Figure 5).

#### 4 DISCUSSION

#### 4.1 | Diel variations of larval abundances of Sicyopterus lagocephalus in natural flow conditions

Among the 404 larvae successfully identified by DNA analyses, 402 (99.5%) were identified as S. lagocephalus. The proportion of 10



**FIGURE 5** Mean larval survival probability over time based on the Kaplan–Meier method for the four groups of *Sicyopterus lagocephalus* larvae sampled on 3 February, 2 March and 15 March 2016. Larvae from the groups "low" and "control\_low" were captured between 07:00 and 07:30 when no peak of discharge was observed at site C. Larvae from the groups "peak" and "control\_peak" were captured during the peaks of discharge observed at site C, see Table 3 for details on sampling conditions. The origin of the *x*-axis is the time of capture of the larvae

*C. acutipinnis* larvae in this study can thus be considered as negligible, and the observed dynamics can be primarily attributed to *S. lagocephalus*. The very low proportion of *C. acutipinnis* larvae in Langevin River is not surprising as Teichert, Keith, et al. (2013) estimated that 99% of the mature adults present on the spawning grounds in this river were *S. lagocephalus* and that the number of *C. acutipinnis* eggs clutches was negligible. DNA-based identification of drifting larvae confirmed the observations made several years before, and demonstrated that larvae present in a river could be a good indicator of the adults present in upstream reaches.

Diel variations of abundances of S. lagocephalus larvae in natural and stable flow conditions were confirmed. The diel dynamics of abundances of S. lagocephalus larvae (i.e. larval density) captured in upstream site (site A) during all sampling sessions presented a weak but significant peak at around midday (precisely 12:03). The weak diel dynamics of larval drift in upstream reaches has already been documented for S. lagocephalus and C. acutipinnis in another watershed of Reunion Island (Lagarde et al., 2017). This observation has also been made for Rhinogobius brunneus, an amphidromous goby, in Japan (Iguchi & Mizuno, 1990), and for amphidromous shrimps in Puerto Rico (March, Benstead, Pringle, & Scatena, 1998). On 17 February 2016, the dam was not in operation, and the discharge remained stable in downstream reaches. At the most downstream site (site C), the peak of larval drift was observed few hours after night fall. This observation is consistent with the observations of larval drift dynamics made in downstream reaches of another watershed in Reunion Island for S. lagocephalus and C. acutipinnis (Lagarde et al., 2017). It is also consistent with observations made for other Sicydiinae species in Hawaii (Lindstrom, 1998; Luton, Brasher, Durkin, & Little, 2005).

## 4.2 | Effect of anthropogenic fluctuations of discharge on larval abundances of *Sicyopterus lagocephalus*

Larval abundances of *S. lagocephalus* were strongly affected by daily anthropogenic fluctuations of river discharge. The most elevated larval abundances observed at site C were clearly related to the rapid increases of discharge at this site. The number of larvae captured in site B was low compared to site C (919 larvae captured for a total filtered volume of 553 m<sup>3</sup> at site B vs. 16,200 larvae captured for a total filtered volume of 469 m<sup>3</sup> at site C). Larvae coming from upstream to the dam thus represented a negligible proportion of larvae caught at site C. Larval abundances at site C can be attributed to the spawning grounds present within the 2 km of the river between sites B and C.

Interestingly, when the dam was operative, a peak of drifting larvae was observed at the end of the afternoon (17:45) at site B. This peak was approximately 6 hr after the peak observed at site A. As no habitat appeared suitable for *S. lagocephalus* to reproduce between sites A and B, the larvae caught at site B probably originated from upstream reaches situated nearby site A. Thus, the 6 hr spent by larvae travelling between sites A and B reflected the time larvae took passing through the different hydroelectric structures between the water diversion at the dam and the outlet channel.

The variation of larval abundances at site C can be explained by the dynamics of hatching (Bradbury, Campana, Bentzen, & Snelgrove, 2004), or a coordinated and active swimming behaviour of larvae (lguchi & Mizuno, 1991; Jarvis & Closs, 2015). This latter hypothesis is very unlikely as Sicydiinae gobies are known to have very poor swimming abilities (Bell & Brown, 1995; Valade et al., 2009). Moreover, the torrential and very turbulent flow conditions in the Langevin River would impede any active displacement of tiny larvae. In addition, the mean flow velocity in the short length of the river section upstream to site C was elevated (approximately 30 cm/s). Larvae coming from upstream spawning grounds were thus rapidly transported to site C. So, the most probable explanation for the variation of larval abundances observed at site C is the dynamics of hatching.

# 4.3 | Effect of anthropogenic fluctuations of discharge on larval drifting time and survival probability of *Sicyopterus lagocephalus*

The larval transport duration of *S. lagocephalus* was slightly reduced during anthropogenic peaks of discharge. Oppositely, larval survival probability dropped during these peaks. The influence of river discharge on larval drift dynamics of Sicydiinae gobies has been described at the seasonal scale for *Lentipes concolor* in Hawaii (Way et al., 1998), and for *S. lagocephalus* and *C. acutipinnis* in another watershed in Reunion Island (Lagarde et al., 2017). At the seasonal scales, these authors hypothesised that elevated flow velocity induced by increase of discharge during rainy events reduced the drifting duration of Sicydiinae larvae, and could be a strategy to reduce the risk of mortality in freshwater. The present study demonstrates that, on a daily scale, the mortality of larvae drifting during

the short periods of elevated discharge may not be reduced but increased. Indeed, larvae survival probability was lower during peaks of discharge compared to low flow conditions. Consequently, the artificial increases in flow velocity probably do not counterbalance the increase in larval mortality as the time spent by larvae drifting to the estuary is not drastically reduced. The gain in time is only few minutes when discharge artificially increases from 1.0 to  $1.6 \text{ m}^3/\text{s}$ . Interestingly, the anthropogenic increases in discharge observed during this study were much less important than those associated with flash floods, which are frequent during the rainy season. The reduction of drifting time during natural flash floods is probably much greater than during artificial increases in flow velocity. For example, during a flood of low intensity recorded upstream to site A on 23 January 2016, the discharge increased of ca. 6 m<sup>3</sup>/s in less than 60 min. This value was much higher than the maximum increase of artificial discharge observed during this study  $(1.9 \text{ m}^3/\text{s in})$ 15 min). During natural flash floods, the reduction of drifting time, which may increase larvae survival by decreasing the time spent in freshwater, probably offsets the elevated probability of mortality. The positive effect of flash floods would be more important when the distance between spawning grounds and estuary increases.

## 4.4 | Influence of biological and environmental factors on larval drift dynamics of *Sicyopterus lagocephalus*

This study highlighted the direct relationship between increasing discharge and the quantity of drifting larvae of S. lagocephalus as well as their drifting time and survival probability in freshwater. These larval drift dynamics were related to hatching dynamics associated with peak of discharges in the downstream site (i.e. site C). Three factors can influence the dynamics of hatching: (i) the spawning strategy of adults, (ii) the behaviour of guarding males and/or (iii) the environmental factors (i.e. the river flow). Adults can influence the dynamics of hatching by spawning at a particular time. In unpredictable flow environment, some fish species can use the increase of discharge as a cue for spawning (Lytle & Poff, 2004). The guarding males of amphidromous gobies have also been suspected to actively provoke hatching. Indeed, Maeda and Tachihara (2010) suggested that the guarding males are poking and fanning the eggs more intensively to provoke hatching at a particular time of the day (i.e. at night). Similarly, males could also provoke hatching when sensing an increase of discharge. Finally, environmental factors such as the increase of shear stress on eggs clutches with river discharge (Lamouroux, Statzner, Fuchs, Kohmann, & Schmedtje, 1992; Statzner & Müller, 1989) can also promote hatching. Næsje et al. (1995) hypothesised that the increase of drifting larvae of two Coregonus species with increasing river discharge was due to the flow turbulence making the larvae hatch.

That the dynamics of hatching during this study was influenced by the spawning strategy of adults is very unlikely. Discharge peaks occurred unpredictably between 10:00 and 01:00 at site C, and no clear recurrent pattern was observed among sampling sessions. Moreover, Sicydiinae embryos develop in 3 days at temperatures ranging FRESHWATER FISH

between 19 and 21°C (Lindstrom, 1998). Adults are mostly likely unable to predict 3 days in advance when discharge peaks will occur.

Although a quantification of the influence of the guarding males' behaviour, or increase of shear stress on eggs clutches, was not performed during this study, it is likely that hatching was provoked by an increase of physical constraints. This increase of physical constraints on eggs clutches could force larvae that had not completed their embryonic development to hatch. The high proportion of incompletely developed larvae during the peaks of discharge may explain why their survival was lower.

This study demonstrated that larval abundance, larval transport duration and larval survivorship of Sicydiinae are strongly affected by daily anthropogenic fluctuations of river discharge. This strong relationship between environmental factors and larval drift dynamics of Sicydiinae in freshwater was largely expected for these small larvae released in highly turbulent flow conditions. However, more research remains needed to describe how larval drift dynamics varies with environmental factors regarding river morphology and flow conditions. As *S. lagocephalus* inhabits many tropical islands with varying river morphologies (Keith, Galewski, Cattaneo-Berrebi, Hoareau, & Berrebi, 2005), it will be interesting to study how the larval drift dynamics of this species adapts to different flow regimes.

#### 4.5 | Implication for management and conservation

This study demonstrated that anthropogenic fluctuations of river discharge can have harmful effects on larval drift dynamics when the associated decrease of larval transport duration is low compared to the increase of larval mortality. The harmful effect of erratic diurnal flow pattern due to hydropower operations is well recognised for several aquatic organisms (Bunn & Arthington, 2002) and especially for fish larvae (Weyers, Jennings, & Freeman, 2003). However, most of the management and conservation recommendations concerning the larvae of amphidromous species have been focused on the reduction of direct mortality associated with entrainment of larvae into the water intakes (Benstead, March, Pringle, & Scatena, 1999; Jarvis & Closs, 2015). The much lower larval survivorship of S. lagocephalus observed during the peaks of discharge in Langevin River suggests that the impact of daily anthropogenic fluctuations of discharge should be further considered when building management and conservation plans for amphidromous species. The strong correlation between the abundances of drifting larvae and the amplitude of the discharge peaks suggests that reducing the amplitude of these peaks would efficiently mitigate their harmful effect as already suggested by Nagrodski, Raby, Hasler, Taylor, and Cooke (2012) and Bruder et al. (2016). Such operational measures and their monitoring would bring crucial data to address the knowledge gaps concerning the impacts of hydropower operations on amphidromous species.

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# 4. Chapitre 3 : Phénologie et mécanisme de la dynamique de montaison des juvéniles de Sicydiinae à La Réunion : rôle des traits morphologiques

# **4.1 Introduction**

Comme détaillé dans l'introduction générale, les juvéniles de Sicydiinae vont coloniser l'ensemble des zones altitudinales des bassins versants depuis l'embouchure des rivières jusqu'à près de 900 m d'altitude (Teichert et al., 2014c, Chapitre 1 de cette thèse). La zone d'altitude dans laquelle les juvéniles de Sicydiinae s'installent joue un rôle prépondérant dans leur succès reproducteur une fois adulte de par son effet sur la saison de reproduction (Teichert et al., 2014b, 2016a) et/ou sur le risque de mortalité des individus due à la prédation (Blob et al., 2010; Maie et al., 2014). De plus, l'impact des crues sur les abondances de Sicydiinae est probablement plus limité dans les zones amont (Teichert et al., 2018). La migration de montaison vers les zones amont a donc certainement un rôle majeur dans la dynamique de population de ces espèces. De nombreux facteurs peuvent influencer les stratégies de migration des juvéniles au sein des bassins versants jusqu'à leur zone d'installation et de maturation. C'est en particulier le cas des capacités locomotrices (Blob et al., 2008; Kawano et al., 2013; Moody et al., 2017). En effet l'accès aux zones amont des bassins versants est en général restreint aux individus ayant les meilleurs capacités locomotrices (Schoenfuss et al., 2013). Cependant des facteurs environnementaux tels que le débit ou la vitesse de courant peuvent aussi influencer les dynamiques de montaison des juvéniles de Sicydiinae en augmentant ou, au contraire, diminuant les contraintes liées au déplacement. Les interactions entre le débit ou la vitesse d'écoulement et les dynamiques de montaison des juvéniles ont été décrites pour des espèces amphidromes de crustacés (Olivier et al., 2013) et de mollusques (Blanco & Scatena, 2005). Ces auteurs ont démontré que les abondances de juvéniles en migration de montaison étaient plus importantes lors des périodes de fort débit mais à proximité des zones de courant les plus faibles.

La migration de montaison des juvéniles de Sicydiinae peut être perturbée par de nombreux obstacles d'origine anthropique tels que les seuils et barrages (Cooney & Kwak, 2013). Ces derniers peuvent restreindre l'accès aux zones situées en amont pour les individus n'ayant pas les capacités locomotrices permettant de les franchir (Holmquist et al., 1998; Lin et al., 2017). En outre, lorsqu'un prélèvement d'eau est associé à un barrage, la diminution du débit peut amplifier la fréquence d'éventuels assèchements de la zone aval par rapport aux conditions naturelles (DEAL, 2011). Dans ce cas, l'accès aux zones amont devient temporairement impossible pour l'ensemble de la population de juvéniles. Ces impacts d'origine anthropique peuvent donc significativement modifier les stratégies de migration des juvéniles de Sicydiinae. Malgré cela, la qualification de l'effet des seuils ou barrages à l'échelle individuelle sur ces espèces n'a, à ma connaissance, jamais été abordée.

La migration de montaison des juvéniles de Sicydiinae s'effectue à contre-courant de l'aval des cours d'eau vers l'amont et, est donc principalement active. La ventouse issue de la fusion des deux nageoires pelviennes des Sicydiinae joue un rôle prépondérant dans leur capacités locomotrices (Maie et al., 2012; Cullen et al., 2013) en leur permettant d'adhérer au substrat et de résister au courant (Fitzsimons et al., 1997) ou de lutter contre la gravité lors du franchissement des chutes d'eau (Schoenfuss & Blob, 2003). Deux modes de franchissement des substrats à forte pente ont été détaillés chez les Sicydiinae : le mode « inching » chez les espèces du genre Sicyopterus et le mode « power-burst » chez les espèces des genres Lentipes, Sicydium et Cotylopus (Schoenfuss & Blob, 2003; Schoenfuss et al., 2011; Keeffe et al., 2017). De nombreux facteurs ont été reliés aux performances locomotrices des Sicydiinae en fonction de leur mode de franchissement. Par exemple, Blob et al. (2008) ont montré que les individus de S. stimpsoni, utilisant le mode « inching », ayant une morphologie hydrodynamique et une ventouse de taille élevée avaient de meilleures performances de franchissement que leur conspécifique. En outre, Kawano et al., (2013) ont démontré que les individus de Sicydium punctatum (Perugia 1896), utilisant le mode « powerburst », avant un poids plus élevé pour une taille donnée avaient de meilleures performances de franchissement probablement en lien avec une puissance musculaire accrue. La rugosité du substrat sur lequel les Sicydiinae se déplacent semble aussi affecter leurs performances locomotrices. Ainsi, Blob et al. (2006) ont montré que les performances locomotrices de deux espèces de Gobiidae utilisant le mode « power-burst » (i.e. L. concolor et Awaous guamensis; Valenciennes 1837) étaient significativement meilleures lorsque la rugosité du substrat augmentait alors que les performances de S. stimpsoni variaient peu. Cependant, Voegtlé et al. (2002) ont observé que les performances de S. lagocephalus et de C. acutipinnis diminuaient sur les supports où des rugosités de plusieurs centimètres de diamètre étaient présentes par rapport aux supports plus lisses où les rugosités ne dépassaient pas l'échelle du centimètre. Ce résultat est cohérent avec ceux de Blob et al. (2006) qui ont effectué leurs expériences avec des rugosités ne dépassant pas 3 mm de diamètre.

Les capacités locomotrices particulières des Sicydiinae ont été utilisées pour proposer des méthodes de dimensionnement de passes à poissons spécifiques leur permettant de franchir les

seuils et barrages (Fièvet et al., 2000; Voegtlé et al., 2002). Ces dispositifs consistent en une rampe avec une pente longitudinale maximale de 50°, généralement construite en béton et sur laquelle s'écoule un faible débit d'eau (Voegtlé et al., 2002). La fonctionnalité des premières passes à poissons spécifiquement dimensionnées pour les Sicydiinae à La Réunion a déjà été démontrée (Lagarde et al., 2015). Cependant aucune étude, jusqu'à présent n'a permis d'évaluer, même qualitativement, leur efficacité.

Dans ce contexte, le chapitre 3 s'articule autour de trois objectifs principaux. Dans un premier temps il s'agit de décrire la phénologie des dynamiques de montaison vers les zones amont des juvéniles de *S. lagocephalus* et de *C. acutipinnis* et de la relier à leur saison principale d'arrivée en eau douce et/ou à certains facteurs environnementaux, en particulier le débit du cours d'eau. Dans un second temps, l'effet de la morphologie des individus de ces deux espèces sur leurs capacités à franchir les obstacles sera évalué expérimentalement. Enfin, les résultats expérimentaux obtenus seront transposés à une étude en milieux naturel afin de qualifier l'impact que peuvent avoir des obstacles d'origine anthropique sur la migration de montaison de *S. lagocephalus* et de *C. acutipinnis*.

# 4.2 Variabilité temporelle de la dynamique de montaison des juvéniles de Sicydiinae dans le bassin versant de la rivière du Mât

# Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif principal de cette étude est de décrire les variabilités saisonnière et journalière des abondances de *S. lagocephalus* et de *C. acutipinnis* en montaison vers une zone amont du bassin versant de la rivière du Mât. Les dynamiques de montaison de ces deux espèces, déduites de ces observations, sont reliées à des facteurs biotiques, tels que la période d'arrivée en eau douce des juvéniles, ou abiotiques, tels que l'hydrologie du cours d'eau. Enfin, en termes de gestion, des préconisations de mesures de gestion des barrages permettant de limiter leur impact sur les dynamiques de montaison des Sicydiinae sont proposées. Il peut par exemple s'agir de préciser la période durant laquelle le fonctionnement des passes à poissons doit être optimal.

**Résultats :** À l'échelle saisonnière, un pic d'abondance des juvéniles *S. lagocephalus* (A1) et de *C. acutipinnis* (B1) en montaison est observé entre les mois de septembre et décembre.

Aucune corrélation entre les abondances de juvéniles et le débit du cours d'eau n'est détectée, cependant après les premières crues de la saison cyclonique, une forte diminution de l'abondance des juvéniles parallèlement à une augmentation de l'abondance d'adultes en montaison sont décrites pour les deux espèces. À l'échelle journalière un pic d'abondance de juvéniles des deux espèces en montaison est observé en fin d'après-midi (**A2, B2**).



**Amélioration de la connaissance des espèces :** À l'échelle saisonnière, les abondances de juvéniles des deux espèces en montaison peuvent être reliées à leurs périodes d'arrivée en eau douce. En effet, il est estimé que les juvéniles de *S. lagocephalus* mettent au minimum un mois pour atteindre la passe à poissons après leur arrivée en eau douce alors que ceux de *C. acutipinnis* mettent au minimum deux mois et demi. Dans ce cas les pics d'abondances de juvéniles de ces espèces, observés entre les mois de septembre et de décembre, peuvent être reliés aux périodes où les abondances de juvéniles arrivant en eau douce sont les plus élevées : de septembre à décembre/janvier pour *S. lagocephalus* et de mai à septembre pour *C. acutipinnis*. L'effet du débit sur la dynamique de montaison des juvéniles de ces deux espèces se limite à une altération marquée de cette dynamique suite aux crues cycloniques.

A l'échelle journalière, le pic d'abondance de juvéniles des deux espèces en migration pendant l'après-midi peut être expliqué par un compromis entre orientation visuelle de la migration, évitement des prédateurs nocturnes, en particulier les anguilles, et maximisation des capacités locomotrices. En effet, de nombreuses espèces de poissons ont des capacités locomotrices maximales dans les gammes les plus élevées de leur optimum thermique, et les températures journalières les plus élevées sont observées en fin de journée et début de nuit dans la rivière du Mât.

Application à la gestion : Cette étude permet de souligner l'importance du maintien d'une continuité hydraulique entre la mer et les zones situées à l'amont et d'une fonctionnalité optimale des passes à poissons pendant les mois de septembre à décembre. La continuité hydraulique peut être assurée en diminuant la part de débit prélevée ce qui permet de limiter les risques d'assèchement en aval. En ce qui concerne la fonctionnalité des passes à poissons, il faudrait réduire le nombre et l'importance des zones d'écoulements parasites de débit qui peuvent attirer les poissons ailleurs que vers l'entrée de la passe à poissons. Il est aussi important de veiller à ce que la passe à poissons ne soit pas obstruée par des sédiments pendant cette période. Immédiatement après les crues cycloniques il faut aussi rapidement rétablir la fonctionnalité de la passe à poissons afin de permettre aux adultes des deux espèces, probablement déplacés accidentellement en aval par la crue, de regagner les habitats de croissance et reproduction situés en amont des barrages.

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# Upstream migration of amphidromous gobies of La Réunion Island: implication for management

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**Abstract** Diadromous species of tropical islands face numerous anthropogenic disturbances. Understanding how these disturbances affect the population dynamic of these species is important to develop ecologically based management measures. The upstream migration dynamics of two amphidromous gobies, *Sicyopterus lagocephalus* (Pallas) and *Cotylopus acutipinnis* (Guichenot), was described using intensive fishway monitoring (28 sampling dates over 1.5 years, 13 000 *S. lagocephalus*, 23 000 *C. acutipinnis* captured). Migration peak occurred for both species during the afternoon at the end of austral winter/beginning of austral summer. Abundance and size of fish caught in the river showed a marked impact of a dam (six sampling dates approximately 4000 individuals of each species captured). This study provides critical data for better management of fishways used by tropical amphidromous gobies. It appears especially important to reduce unwanted rheotactic sources that attract the fish away from the fishway's entrance.

KEYWORDS: amphidromy, dams, fishway, Gobiidae, river continuum, tropical islands.

#### Introduction

Worldwide, human population growth has resulted in a steady increase in the demands on fresh water (Postel 2000) for dinking, irrigation, hydropower or industrial needs. The unequal global and regional repartition of

water resources leads to various constraints among localities. In tropical islands, freshwater supplies are characterized by scarce and over exploited groundwater resources and important but spatially and temporally non-homogeneous surface water supplies (Join *et al.* 1997). The usual strategy of local authorities is to divert

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surface water (Tabouret 2012) using structures that stabilise the head of water and allow varying diversion of water. These structures are usually small dams or weirs (Pringle *et al.* 2000) that alter the downstream hydrological cycle and break the river continuum (Dynesius & Nilsson 1994; Benstead *et al.* 1999; Kinzie *et al.* 2006). This river fragmentation severely impacts life cycles of fish and crustaceans by impeding their downstream dispersion or upstream migratory movements. Given this situation, the restoration and preservation of the river continuity is one of the main aims of the European Water Framework Directive (Directive 2000/60/EC, Anonymous 2000).

In tropical islands, most of the indigenous fish and crustacean species exhibit a diadromous life cvcle (McDowall 1997). Amphidromous gobies are important in terms of abundance and diversity (Keith 2003). Adults of amphidromous gobies spawn in rivers (Manacop 1953). After hatching, free embryos drift down to the sea where they grow during several months (Radtke et al. 1988; Hoareau et al. 2007; Lord et al. 2009; Teichert et al. 2012). At the end of their larval stage, they return into rivers, transform into juveniles and migrate upstream (Teichert et al. 2014a). As soon as they enter rivers, amphidromous gobies face numerous anthropogenic impact such as traditional fisheries in the estuaries (Aboussouan 1969; Delacroix & Champeau 1992; Bell 1999), poaching in rivers and habitat fragmentation caused by dams and weirs.

In several tropical islands, local authorities have underlined the urgent need for ecologically based management and conservation policies of these amphidroof mous gobies. However, upstream migrations amphidromous gobies have been studied close to the estuaries only (Bell et al. 1995; Iida et al. 2008; Shiao et al. 2014). Information about migration peaks in the upstream reaches are lacking although they are fundamental for mitigating the effects of fish habitat fragmentation by adapting released discharge and maintenance schedules (McDowall 1995). Moreover, although several types of fishways are commonly used to allow fish to pass dams and weirs (Larinier et al. 1992), until recently those built in tropical rivers were based on recommendations made for temperate species (Benstead et al. 1999). These fishways were not adapted to the extreme hydrological events occurring in tropical rivers or to the biology of tropical species (March et al. 2003). It is only recently that the impressive climbing abilities of some tropical taxa have been considered resulting in fishways comprising a climbing ramp above which a thin layer of water flows (Hamano et al. 1995; Fièvet et al. 2000; Voegtle et al. 2002; Olivier et al. 2013). The type of substratum and the slope angle of these fishways as well as hydraulic recommendations are adapted to the specific requirements of local species based on laboratory experiments (Hamano *et al.* 1995; Voegtle *et al.* 2002). However, evaluation of the performances of fishways and description of fish migration dynamics to suggest improvements of structure engineering, attraction discharge management and maintenance (Santos *et al.* 2002) requires *in situ* studies (Benstead *et al.* 1999; Crivelli *et al.* 2008). To date, monitoring of fishways specially designed for amphidromous gobies has not yet been conducted in field conditions.

In La Réunion Island, two amphidromous Gobiidae dominate the freshwater fish assemblages: Sicyopterus lagocephalus (Pallas) and Cotylopus acutipinnis (Guichenot). The arrival of their larvae in estuaries occurs all year round but maximum abundances are observed between September and February for S. lagocephalus (Delacroix & Champeau 1992) and May to July and September to October for C. acutipinnis (Teichert et al. 2012). Once in rivers, juveniles colonise the whole watersheds up to the headwaters (Fièvet et al. 2001) thanks to their strong climbing abilities (Blob et al. 2006; Schoenfuss & Blob 2007) due to the ventral sucker made by the fusion of pelvic fins. Juvenile abundances of both species gradually decrease along a downstream-upstream gradient, from estuaries to upper habitats located more than 20 km upstream (Teichert et al. 2014a). The same pattern was observed for S. lagocephalus adults, whereas the abundances of C. acutipinnis adults were equally distributed throughout the longitudinal gradient. Both species show weak preferences within the available habitat in the rivers of La Réunion (Teichert et al. 2014a) except for spawning which occurs mainly in runs and riffles (Teichert et al. 2013). Reproduction happens during the warmer months, i.e. from November to May, in the middle and upper reaches (Teichert et al. 2014b, in press).

The aim of this study was to examine daily and seasonal variations in abundances of two indigenous gobies, *S. lagocephalus* and *C. acutipinnis*, using a fishway. The ultimate goal was to give guidance for fishway monitoring and for better environmental management of dams in tropical islands.

#### Material and methods

#### Study site

La Réunion Island is located in the Mascarenes Archipelago, Western Indian Ocean. The island is characterised by a tropical climate with a dry and cold austral winter from May to October and a warm and wet austral summer from November to April. Cyclones mainly occur



Figure 1. Location of studied fish-way on the Fleurs Jaunes River, Mât River watershed, La Réunion Island, Western Indian Ocean.

during the austral summer. The dominant wind direction is from east to west, and the high elevation of the summits leads to more precipitations (Robert 1988) and a higher number of perennial rivers on the eastern side of the island (Fig. 1). In 2006, a tunnel diverting water from the Mât and the Fleurs Jaunes rivers on the eastern side of the island to the western coast was initiated.

The Fleurs Jaunes River is the main tributary of the Mât River. The area of its watershed is approximately 45 km<sup>2</sup>. The junction between the two rivers is situated 13 km from the river mouth. The 9.5 m high dam on the Fleurs Jaunes River is located 1 km upstream of the junction at 385 m above sea level (Fig. 1). During the study, the water diversion was not effective since the building of all the infrastructure associated with the dam was not completed. The diverted water was returned to the river using a sluice gate located on the right side of the dam, 2 m to the left of the downstream entrance of the fishway. The fishway is situated on the right bank and comprised three elements (Fig. 2): a downstream 3-m wide and 6-m long concrete apron, a  $4-m^3$  energy dissipation pond and a 14.25-m long, 50° longitudinal slope, climbing ramp. This ramp had been designed following the recommendation of Voegtle et al. (2002). The ramp is made of smooth concrete to facilitate the progression of gobies with their ventral sucker. However other species have been recorded on the ramp, such as eels, Anguilla spp. and atyids shrimps, Atyoida serrata (Bate). Along with Sicydiinae gobies, these species are the only two indigenous species commonly found in the Fleurs Jaunes River although rare observations of Macrobrachium lar (Fabricius) have been made.



Figure 2. Schematic representation the fish-way of the dam on the Fleurs Jaunes River. The scale is not respected.

A gauging station is located 3.8 km downstream of the junction of the Mât and the Fleurs Jaunes Rivers (Fig. 1). The instantaneous and mean daily discharges were recorded during the entire study except during important flood events (data are available online, www.eaureunion.fr, accessed in June 2014). During the monitoring period, the mean daily discharge was approximately 4 m<sup>3</sup> s<sup>-1</sup> and the maximum discharge was estimated at approximately 70 m<sup>3</sup> s<sup>-1</sup>, 80 m<sup>3</sup> s<sup>-1</sup> and 160 m<sup>3</sup> s<sup>-1</sup> (eau Réunion pers. comm.) respectively for the three cyclonic floods observed during the study period (Dumile on 3 January 2013, Felleng on 1 February 2013 and Bejisa on 2 January 2014). Before these three climatic events, the latest recorded cyclone in La Réunion was Gamède in 2007.

#### Fish sampling in river

The abundance and size frequency of fish were described at two stations in the river to highlight the dam effect. One station was located immediately downstream to the energy dissipation pool of the dam and the other was located approximately 150 m upstream to the dam. Samplings were performed on six occasions between October 2012 and December 2013 (12 October 2012; 16 November 2012; 14 December 2012; 21 June 2013; 25 October 2013; 12 December 2013). A stratified sampling design was achieved to estimate the fish abundance using portable electrofishing equipment (Hans Grassel IG 200-2, pulsed current 50 pulses per second, output voltage pulse of 500 V). Each sampling station was divided into hydromorphic units, which were considered uniform in terms of water velocity, depth and substratum composition (Malavoi & Souchon 2002). Seven habitat units ranging from 8 m<sup>2</sup> to 13.2 m<sup>2</sup> were delimited within the hydromorphic units (Pouilly 1994; Girard et al. 2013) and sampled by one operator moving upstream with the portable electrofishing gear. Three persons collected the stunned fish with hand nets (1 mm mesh size, 50 cm of diameter) immediately downstream of this operator. A minimum total area of habitat units of 70 m<sup>2</sup> was sampled on each date and at each station. The delimitation of habitat units was performed the day before the sampling to reduce the effect of disturbance on fishing efficiency. During the study period, water conductivity remained stable (from 202 to 247  $\mu$ S cm<sup>-1</sup>) and the water was clear enough to see the river bottom in both fishing stations. These parameters were assumed to be stable enough to not bias electrofishing efficiency. Vadas and Orth (1993) used comparable sampling strategies for small temperate rivers and demonstrated that the number of catches was concordant with more exhaustive strategies, such as two or three pass removal methods. Vadas and Orth's (1993) results are especially consistent in fast flowing habitats (i.e. runs and riffles), which are the only habitats sampled in both stations in the present study. In similar tropical context, Fièvet et al. (1999) showed that electrofishing efficiency was not influenced by the sampling conditions for Sicydiinae species (i.e. Sicydium ssp). Catch abundances of S. lagocephalus and C. acutipinnis can thus be compared between sites and dates in this study.

Captured fish were anesthetised with clove oil, identified, measured (total length, TL nearest mm) using an ichtyometer, placed in a bucket of fresh water and released in their capture site once recovered. Estimation of the number of fish captured per effort unit (CPUE, ind.  $m^{-2}$ ) was made in two successive steps. The first step consisted on estimating the average catches per square meter for each hydromorphic unit (mean of catches per square meter of all the habitat units present in the hydromorphic unit). Then, the CPUE was estimated by the mean of catches by square meter of each hydromorphic unit weighted by the relative area (proportion of the station area) of these units in the station (Pouilly 1994). Adults were separated from juveniles according to size thresholds of 38 mm for C. acutipinnis (Teichert et al. in press) and 55 mm for S. lagocephalus (Teichert et al. 2014b).

#### Sampling in the fishway

Sampling in the fishway aimed at describing the seasonal and daily migratory dynamics of the two species. The sampling was performed once per month from 25 March 2013 to 22 August 2013 and from 28 January 2014 to 19 May 2014, but increased to once per week from 30 November 2012 to 28 December 2012 and from 26 September 2013 to 27 December 2013. The two periods for weekly sampling were chosen in expectation of peak upstream migration for both species based on the main season of arrival in the estuaries (Delacroix & Champeau 1992; Teichert *et al.* 2012). For each sampling date, discharge in the fishway ( $Q_{\text{fw}}$  in m<sup>3</sup> s<sup>-1</sup>) was estimated using:  $Q_{\text{fw}} = C \frac{\sqrt[3]{2 \times g}}{2 \times tan(\alpha)} h^{2.5}$  where g = 9.81 m s<sup>-2</sup>, C is a positive constant depending on the roughness of the gauging section (i.e. here estimated as equal to 0.33),  $\alpha$ the angle in radians of the lateral slope of the ramp and *h* the head in metres upstream to the climbing ramp (see Fig. 2).

During each sampling day, a minimum of five samples, rarely seven, were taken, the first between 06:15 and 07:30 am, and the next every 2 h ( $\pm$  5 min). Sample#1 to sample#5 were spread over a period of approximately 10 h (Table 1) and thus covered most of the daytime duration (approximately from 06:30 to 18:00 in winter and from 05:30 to 19:00 in summer). The two last samples (i.e. sample#6 at dusk and sample#7 at night) were performed on eight occasions only. Two complementary sampling methods were used to catch fish present in the fishway. Firstly, fish present on the ramp were swept down with a foam scraper and captured in hand nets at the bottom of the ramp. Secondly, the dissipation pond was sampled by electrofishing using a two passes removal method. Captured fish were anesthetised with clove-oil, identified measured, placed in a bucket of fresh water, and released upstream to the dam once they had recovered. The estimated number of fish captured in the fishway  $(\hat{N})$  was determined using the Carle and Strub (1978) removal method. Success of sampling was estimated from capture efficiency  $(E_s)$ using:  $E_s = \frac{C_1 + C_2}{\hat{N}} \times 100$ , where  $C_1$  and  $C_2$  are respectively the number of fish captured during the first and the second passes.

Probability of capture between the first and the second pass (P) was also estimated for each sample. The number of fish captured per hour (CPUE, ind.  $h^{-1}$ ) was estimated as the ratio of  $\hat{N}$  over the time separating the sample to the previous one. The first sample of the day was excluded from analyses because it comprised individuals that have accumulated in the pond over an unknown period of time. Proportions of juveniles versus adults were calculated only when more than 30 individuals were caught per day. Daily abundance was estimated by summing the estimated number of fish captured in the four samples from Sample#2 to sample#5.

The number of captured fish per hour was estimated as a function of the hour of the day using generalized additive mixed models (GAMM), an approach that accounts for non-linear dynamics of fish abundances.

|            | Sample #1          | Sample #2          | Sample #3          | Sample #4          | Sample #5          | Sample #6         | Sample #7         |  |  |  |
|------------|--------------------|--------------------|--------------------|--------------------|--------------------|-------------------|-------------------|--|--|--|
|            | $N_{\rm day} = 28$ | $N_{\rm day} = 8$ | $N_{\rm day} = 8$ |  |  |  |
| Mean (±SD) | 06 h31             | 09 h02             | 11 h24             | 13 h50             | 16 h17             | 18 h42            | 21 h07            |  |  |  |
| start time | (±11 min)          | (±10 min)          | (±10 min)          | (±12 min)          | (±12 min)          | (±14 min)         | (±18 min)         |  |  |  |
| Mean (±SD) | 07 h04             | 09 h28             | 11 h48             | 14 h13             | 16 h41             | 19 h10            | 21 h34            |  |  |  |
| end time   | (±14 min)          | (±11 min)          | (±12 min)          | (±12 min)          | (±13 min)          | (±18 min)         | (±21 min)         |  |  |  |
| Mean (±SD) | 33 min             | 24 min             | 24 min             | 23 min             | 25 min             | 27 min            | 28 min            |  |  |  |
| duration   | (±6 min)           | (±5 min)           | (±5 min)           | (±4 min)           | (±4 min)           | (±5 min)          | (±4 min)          |  |  |  |

**Table 1.** Mean ( $\pm$  SD) sampling start time, end time, and duration for each the seven samples performed in the fishway of the dam on the FleursJaunes River, La Réunion Island

The day of sampling was included as a random effect to take into account the high variability of fish abundances between dates. The amount of variation explained by the hour of the day was tested by comparing the reduction of residual deviance with a model integrating the sampling day as a random effect only. The level of significance was  $\alpha = 0.05$ . A significant effect indicates a preferred period of migration during the day.

Statistical analyses were performed using the open source R software (R Development Core Team 2013).

#### Periodic linear regression

The seasonal fluctuations of fish abundance in the fishway were described using a periodic linear regression. Periodic linear regression allows a better description of cyclic effects, such as seasonal and lunar cycle, than classic linear models (Bliss 1958; de Bruyn & Meeuwig 2001; Bell 2007). Using this approach, time is not considered as discrete values but described as an ellipse based on two independent functions (sin, cos). Bell et al. (1995) suggested using this method to describe the seasonal variability in number of larvae of two Sicydium species in an estuary. In addition, the mean daily discharge in the fishway was integrated to the model to estimate the potential effect of this variable on the migration dynamic. The migration dynamics of S. lagocephalus and C. acutipinnis were described by:  $A = \beta_0 + \beta_1 \sin(R_{day}) + \beta_2 \cos(R_{day}) + \beta_3 Q_{fw}$ , where A is the estimated daily abundance of S. lagocephalus or C. acutipinnis,  $R_{day}$  is the radian transformation of the day (1–365) of the year (day  $\times 2\pi/365$ ),  $Q_{\rm fw}$  is the estimated discharge (m<sup>3</sup> s<sup>-1</sup>) in the fishway,  $\tilde{\beta}_0^{11}$  is the intercept and  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are coefficients. The positioning of the maximum of the curve was determined by:

 $M = 365 \times \frac{\arctan\left(\frac{\beta_1}{\beta_2}\right) + QC}{2\pi}$  where *M* is the day of the year of the maximum and QC the quadrant correction (QC = 0 if  $\beta_1$  and  $\beta_2$  are both positive, QC =  $\pi$  if  $\beta_1$  is positive and  $\beta_2$  negative or if both are negative and QC =  $2\pi$  if  $\beta_1$  is negative and  $\beta_2$  positive). Each variable (i.e.  $\sin(R_{day})$ ,  $\cos(R_{day})$  and  $Q_{fw}$ ) was tested to explained significant amounts of independent variation, based on the significant reduction of residual deviance compared with the previous model (Chi square test; Dobson 2001). Significant effects of explanatory variables reflect temporal variation of daily abundance of *S. lagocephalus* or *C. acutipinnis* among dates and discharges.

#### Results

#### Abundance and size frequency distribution in river

The minimum sampled area in the river ranged from 71.3 to 77.5 m<sup>2</sup> for the downstream station and from 70.6 to 77.2 m<sup>2</sup> for the upstream station. A total of 4069 S. lagocephalus (2012 downstream and 2057 upstream) and 4229 C. acutipinnis (2103 downstream and 2126 upstream) were captured. The size range of captured S. lagocephalus was between 30 and 120 mm TL (Fig. 3a). At the downstream station S. lagocephalus <40 mm TL represented more than 45% of the individuals while fish larger than 90 mm TL represented <5%. The size distribution of the S. lagocephalus caught at the upstream station was less skewed with more than 40% of the fish between 55 and 75 mm TL. The size range of C. acutipinnis was between 25 and 105 mm TL (Fig. 3b), both stations being dominated by small individuals. However, the overall size distribution in the upstream station was greatly influenced by a huge number of individuals <35 mm TL caught on one occasion (Fig. 4b).

The mean CPUE of *S. lagocephalus* (adult and juvenile) was 4.5 ind. m<sup>-2</sup> downstream to the dam and 5.1 ind. m<sup>-2</sup> upstream. The CPUE of juveniles was higher downstream than upstream for all the sampling dates, whereas the CPUE of adults was always higher upstream except on 21 June 2013 (Fig. 4a). This date corresponded to the first sample after the two cyclonic floods. The mean CPUE of *C. acutipinnis* (adult and juvenile) was 4.7 ind. m<sup>-2</sup> downstream to the dam and 50.1 ind. m<sup>-2</sup> upstream (Fig. 4b). The CPUE of juveniles



**Figure 3.** Size distribution (total length in mm) (a) for *Sicy*opterus lagocephalus and (b) for *Cotylopus acutipinnis*. With grey bars: individuals caught downstream to the dam on the Fleurs Jaunes River and white bars: individuals caught upstream.

was higher downstream than upstream for all the sampling dates except on 25 October 2013 where more than 13.0 ind.  $m^{-2}$  were observed upstream. On the first sampling date after the cyclonic floods (i.e. 21 June 2013), the CPUE of juveniles dropped to 0.3 ind.  $m^{-2}$  downstream of the dam and no juveniles were caught upstream. After the cyclonic floods, the CPUE of adults slightly decreased to 0.9 ind.  $m^{-2}$  upstream but did not vary notably downstream.

#### Daily catches fluctuations

A total of 13 422 *S. lagocephalus* and 23 235 *C. acutipinnis* from 28 samples were captured on the fishway. The total daily catches ranged between 0 and 1413 *S. lagocephalus* and 0 and 3305 *C. acutipinnis*. Catches usually consisted of more than 90% of juveniles except for the two sampling dates following Bejisa's (2 January 2014) cyclonic flood, when these values decreased to 40% of *S. lagocephalus* juveniles and 35% of *C. acutipinnis* juveniles (Fig. 6).

The probability of capture in the fishway estimated by Carle and Strub (1978) removal method was  $0.6 \pm 0.2$  for both species. The capture efficiency was  $84\% \pm 15$  for *S. lagocephalus* and  $86\% \pm 13$  for *C. acutipinnis*. The lowest values of probability of capture and capture efficiency were mainly obtained when the number of individuals caught in the fishway was very low. The estimated CPUE per sample ranged from 0 to 239 ind. h<sup>-1</sup> for *S. lagocephalus*, and from 0 to 482 ind. h<sup>-1</sup> for *C. acutipinnis*.

The daily variation in the number of individuals using the fishway followed the same trend for *S. lagocephalus* (Fig. 5a) and *C. acutipinnis* (Fig. 5b). The hour of the day had a significant effect on the estimated number of individuals using the fishway for both species (ANOVA, P = 0.001). For both species, the migration peak occurred at approximately 15:00 and the estimated number of fish using the fishway dropped during dusk and night.

#### Seasonal catches fluctuations

The number of fish caught daily in the fishway ranged between 3 and 1441 for S. lagocephalus and between 0 and 2572 for C. acutipinnis. These values fluctuated over seasons for both species with the highest abundances in December 2012, and between September 2013 and February 2014, for S. lagocephalus (Fig. 6a) and in December 2012, and between September and December 2013, for C. acutipinnis (Fig. 6b). Over the studied period, the flow discharge in the fishway ranged from 0.02 to  $0.5 \text{ m}^3 \text{ s}^{-1}$ . The effect of the flow discharge in the fishway on the number of fish was not significant for S. lagocephalus (deviance reduction test, P = 0.14) and for *C. acutipinnis* (deviance reduction test, P = 0.65) and this factor was not considered further and only the periodic effects (i.e.  $sin(R_{day})$  and  $cos(R_{day})$ ) were kept in the models. The periodic linear models explained 24.4% of the total deviance for S. lagocephalus (deviance reduction test, P = 0.02, Table 2) and 33.7% for C. acutipinnis (deviance reduction test, P < 0.002, Table 2). The predicted maximum corresponded to 18



**Figure 4.** Capture per unit of effort (CPUE, individuals per  $m^2$ ) of (a) *Sicyopterus lagocephalus* and (b) *Cotylopus acutipinnis* caught downstream (left column) and upstream (right column) of the dam on the Fleurs Jaunes River on the six sampling dates. Shaded bars correspond to juveniles and filled bars to adults. The two arrows correspond to the floods during the Dumile and Felleng cyclonic events.

October for *S. lagocephalus* and 4 October for *C. acutipinnis*.

On the four dates when sampling was performed on both the fishway and the river, good concordance was found between the number of juveniles caught in the fishway and in the river downstream and upstream to the dam (Fig. 7). Regressions have not been fitted because of lack of data (n = 4).

#### Discussion

# Using fishways for studying the upstream migration of fishes

Fishways are commonly used to assess diadromous and potamodromous fish migrations (Laine *et al.* 1998;

Santos et al. 2002; Crivelli et al. 2008) along with several others methods such as surveying fishing catches (Aprahamian et al. 2008; Maes et al. 2008), fish telemetry (Chanseau et al. 1999a; Lundqvist et al. 2008) or mark and recapture studies (Chanseau et al. 1999b; Smith & Kwak 2014). In La Réunion Island, fishing for S. lagocephalus and C. acutipinnis upstream of the estuaries is officially forbidden. Even if poaching is common, information about the catches of poachers is scarce. Fish telemetry cannot be used for fish <55 mm TL (Cooke & Thorstad 2012; Pursche et al. 2014). Marking individuals seems difficult to implement as the marking effort would be huge regarding the high number of fish captured daily in the fishway (more than 3000 fish). Fishway monitoring thus appears to be best method to describe the upstream migration of tropical amphidromous gobies in La



**Figure 5.** Daily variations in the capture per unit of effort (CPUE, individuals per hour) in the fish-way (a) for *Sicyopterus lagocephalus* and (b) for *Cotylopus acutipinnis*. The solid line represents the fixed effect of the hour of the day. The shaded areas represent the confidence interval ( $\pm$  2 standard error). The dots correspond to the estimated CPUE in the fish way over the whole sampling period. The grey arrows correspond to the estimated time of migration peak.

Réunion Island. However, description of fish migration patterns based on fishways monitoring is site dependent as it strongly depends on the efficiency of the fishway. Analysing the number of individuals using a fishway cannot be performed without taking into account the quantity of individuals downstream of the dam as it is the only way to explain presence or absence of fish in the fishway (Thorstad et al. 2008). In this study, good concordance was found between the number of juveniles present downstream of the dam and the quantity of fish (mainly juveniles) captured in the fishway. Good concordance was also found between the quantity of fish captured in the fishway and number of juveniles present upstream of the dam. These results mean that fish downstream of the dam are finding the fishway and passing the dam thanks to this fishway. As both species are able to climb a ramp with a slope up to  $90^{\circ}$  (Voegtle *et al.* 2002), the effects of the hydraulic conditions of the fishway may not be as important as those for mainland Europe fish species (Larinier et al. 1992).

#### Seasonal and daily migration patterns

Describing the patterns of migration of amphidromous gobies is a key point for understanding their population



**Figure 6.** Seasonal variations in the number of individuals using the fish-way (a) for *Sicyopterus lagocephalus* and (b) for *Cotylopus acutipinnis*. With solid line: periodic linear regression fitted for each species and black dots: proportion of juveniles (calculated when number of individuals >30). The three arrows correspond to the floods during the Dumile, Felleng and Bejisa cyclonic events.

dynamic and proposing ecologically based management policies. Most studies concerning the colonization of watersheds by these species focused on their arrival in estuaries (Delacroix 1987; Bell et al. 1995; Iida et al. 2008; Teichert et al. 2012; Shiao et al. 2014). In all these studies, arrivals in estuaries were more important during a 5-6 months period but remained globally highly variable. Migration of other amphidromous species such as shrimps (Benstead et al. 1999; Olivier et al. 2013) or snails (Blanco & Scatena 2005) has been surveyed in streams and abiotic factors such as discharge, water velocity and water temperature have been found to be critical for their migration dynamic. During this study, both S. lagocephalus and C. acutipinnis showed similar seasonal patterns with a main upstream migration period from September to December and an observed peak in migration in October. This peak of upstream migration is consistent with the migration delay in the river after the main period of arrival of the larvae in the estuaries for both species (Delacroix & Champeau 1992; Teichert et al. 2012). Indeed, the minimum time required for moving from the estuary to the dam on the Fleurs Jaunes River was

**Table 2.** Summary of the results of the two periodic linear models for *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*. A<sub>Sic</sub> and A<sub>Coa</sub> are the estimated abundances of *S. lagocephalus* and *C. acutipinnis*; Rday is the radian transformation of the day (1–365) of the year (day  $\times 2\pi/365$ ). M<sub>Sic</sub> and M<sub>Coa</sub> are the days of the year of the maxima

|                 | Periodic linear model  | Explained deviance | Maximum day                           |
|-----------------|--|--------------------|---------------------------------------|
| S. lagocephalus | $\begin{split} A_{Sic} &= 256.9 - 177.4 \times sin(Rday) + 184.7 \times cos(Rday) \\ A_{Coa} &= 407.5 - 577.2 \times sin(Rday) + 126.2 \times cos(Rday) \end{split}$ | 24.4%              | $M_{Sic} = 320 (15 \text{ November})$ |
| C. acutipinnis  |  | 33.7%              | $M_{Coa} = 286 (12 \text{ October})$  |



Figure 7. Relationship between the number of juveniles captured in the fish way and the CPUE of juveniles upstream and downstream to the dam for *Sicyopterus lagocephalus* (triangles) and *Cotylopus acutipinnis* (circles). With filled symbols: downstream and open symbols: upstream.

estimated to be one month for S. lagocephalus and at 2.5 months for C. acutipinnis using otolith increments analysis (Lagarde, unpublished data). Given this observation, the main upstream migration period at the dam should occur between October and March for S. lagocephalus and between August and February for C. acutipinnis (respectively one and 2.5 months after the main period of arrival of the larvae in the estuaries). Nevertheless, the period larvae enter the estuaries is probably one factor among others explaining the pattern of upstream migration observed in the fishway. Other factors such as discharge (Delacroix 1987; Blanco & Scatena 2005; Olivier et al. 2013), intra-specific densities (Gorbach et al. 2012) or densities of predators (Blob et al. 2010) can also interfere with the dynamic of fish migrating upstream.

Some authors have described the daily patterns of upstream migration of amphidromous fishes. Iida *et al.* (2008) observed that a higher number of larvae of *Sicyopterus japonicus* (Tanaka) entered the estuary of the Ota River, Japan, during the afternoon. The same observation was made by Shiao *et al.* (2014) for juveniles of *Rhinogobius gigas* (Aonuma & Chen) and *S. japonicus* in the Hsiukuluan River, Taiwan. The highest catch rate during the afternoon for *S. lagocephalus* and *C. acutipinnis* is consistent with the

observations made by those authors suggesting a similar daily dynamic of migration for the different amphidromous gobies species and development stages. Afternoon migration could result in a balance between sight orientation (Chanseau *et al.* 1999a; Shiao *et al.* 2014) and the increased swimming and climbing performances induced by the rise of water temperature (Beamish 1978; Larinier *et al.* 1992).

# Effects of cyclonic floods on upstream migration dynamic

Increases in river discharge, i.e. floods, have largely been described as stimulating upstream migration of diadromous fishes in both temperate (Erkinaro et al. 1999; Crivelli et al. 2008) and tropical areas (Delacroix 1987; Fièvet et al. 2000). The effects of small floods on upstream migration of tropical amphidromous gobies remain to be described. This would require a monitoring method to estimate the number of individuals migrating upstream daily and continuous monitoring of the discharge at several locations upstream and downstream to the studied dam. The effect of exceptional flood event, such as cyclonic floods, is also poorly documented. Robinet (2004) observed a decrease in the diversity of fish species along a tropical watercourse after a major cyclonic flood. Smith and Kwak (2014) explained the higher displacement rate of the freshwater mullet, Agonostomus monticola (Bancroft) as an effect of cyclonic flood. This study identifies the effect of cyclonic floods on migration of S. lagocephalus and C. acutipinnis. Indeed, the number of individuals migrating upstream dropped drastically after the three cyclonic floods. The most likely explanation is that juveniles were more sensitive to flood disturbance due to their weaker swimming performances compared with older fish (Beamish 1978). This hypothesis would explain the decrease in the total catches and in the proportion of juveniles in the fishway observed after cyclonic floods. The higher proportion of adults caught in the fishway during the months following the floods is probably due to recolonisation of upstream habitats. This observation is consistent with those made by Smith and Kwak (2014) for A. monticola.

#### Management implications

The effects of dams on tropical amphidromous species are numerous (March et al. 2003). The most common effect is a diminution of the density of individuals of several species upstream of a dam compared with downstream (Brasher 2003; Olivier et al. 2013). Some species may even disappear from upstream reaches (Gorbach et al. 2012). The high number of juveniles of the two species studied using the fishway and captured upstream of the dam suggest that the fishway is functioning. However, the higher number juveniles generally observed downstream to the dam is inconsistent with variability in abundance usually observed between two stations that are <1 km from each other (Teichert et al. 2014a). This higher number of juveniles downstream to the dam probably indicates a delay in the upstream migration of the juveniles of both species. This delay is probably due to some other rheotactic characteristics that attract the juveniles away from the fishway entrance (Fièvet & Le Guennec 1998). Indeed, during this study some fish have regularly been observed trying to climb along a perennial runoff on the side of the dam. However, the lack of water continuity on the wall of the dam does not allow the fish to pass the dam when they follow these paths. The major recommendation concerning the management of fishways is thus to minimise the importance of other rheotactic sources by maximising the proportion of the flow discharged through the fishway (Larinier et al. 1992). This study has also highlighted the periods during which higher numbers of amphidromous gobies migrating upstream are observed. During these periods, the fishway (discharge management, cleaning clogging by gravels, reparation of damaged structures) must be very careful maintained and managed. Finally, it also appears important to restore the fishway functionality quickly after cyclonic floods to allow recolonisation of upstream habitats by adults.

This study allowed suggestions for several 'best practices' in the management of fishways on tropical rivers to enable efficient upstream migration by amphidromous gobies, although the downstream migration of free embryos also has to be taken in account when managing dams (Fièvet & Le Guennec 1998; Valade *et al.* 2009). Indeed, during this phase, the natural mortality of amphidromous fishes can be very high (Bell 2009). The sensitivity of free embryos to anthropogenic pressures is also important since free embryos are barely able to swim and thus can be easily entrained with diverted water. The development and management of hydraulic structures taking into account downstream migration of free embryos is probably the next challenge for ensuring the conservation and restoration of amphidromous fish species.

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# 4.3 Influence des traits morphologiques individuels sur les performances locomotrices des juvéniles de Sicydiinae en milieu expérimental

Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif principal de cette étude est d'évaluer les différences de morphologie entre les individus capables de franchir une rampe expérimentale de 2,5 m de long, c'est-à-dire les individus avec des performances de franchissement élevées, et ceux incapables de le faire. Dans le détail il est attendu que les jeunes juvéniles de *Sicyopterus lagocephalus* capables de franchir la rampe aient des morphologies proches de celles des *Sicyopterus stimpsoni* capables de franchir une rampe similaire à Hawaii. Ces deux espèces utilisent en effet toutes deux le mode « inching ». À l'opposé des morphologies différentes entre les jeunes juvéniles de *S. lagocephalus* et de *Cotylopus acutipinnis* capables de franchir la rampe sont attendues. *Cotylopus acutipinnis* utilisant un mode « powerburst » différent de celui utilisé par *S. lagocephalus*.

**Résultats :** Globalement les taux de succès de franchissement des jeunes juvéniles de *S. lagocephalus* (**A**) sont supérieurs à ceux de *C. acutipinnis* (**B**). Les individus de *S. lagocephalus* capables de franchir la rampe ont soit une morphologie hydrodynamique, due à une faible largeur de la tête et une faible hauteur du corps (**A1**), soit un périmètre de la bouche important associé à une largeur de la tête élevée (**A2**). Les individus de *C. acutipinnis* capables de franchir la rampe ont une ventouse de dimension supérieure à ceux incapables de la franchir (**B**).



**Amélioration de la connaissance des espèces :** Pour les deux espèces, les morphologies des individus ayant les meilleures performances de franchissement peuvent être reliées à leur mode de déplacement. *Sicyopterus lagocephalus* utilise alternativement sa ventouse et sa bouche pour adhérer au substrat lorsqu'il franchit des obstacles. Dans ce contexte, un individu avec une bouche plus grande voit sa force d'adhérence au substrat augmenter ce qui lui permet de mieux résister à la gravité. De manière similaire, les individus ayant une morphologie plus hydrodynamique sont moins sujets aux forces de friction de l'eau. En ce qui concerne *C. acutipinnis*, le lien positif entre une dimension élevée de la ventouse et la performance de franchissement est cohérent avec le mode « powerburst ». En effet, dans ce mode les phases de mouvement sont plus courtes que les phases de repos durant lesquelles les individus doivent se maintenir au substrat grâce à leur ventouse.

Les meilleures performances de franchissement d'obstacles de *S. lagocephalus* leur confèrent probablement un avantage compétitif par rapport à *C. acutipinnis*. Après leur arrivée en eaux douce, une plus grande proportion des juvéniles de *S. lagocephalus* sont en effet probablement capables de franchir les obstacles présents au sein des bassins versants et ainsi d'accéder aux habitats de croissance et de reproduction situés en amont.

**Application à la gestion :** Malgré la faible longueur des rampes expérimentales, ces dernières se sont avérées difficilement franchissables pour les jeunes juvéniles de *S. lagocephalus* et très difficilement franchissables pour ceux de *C. acutipinnis*. Ce résultat souligne l'importance d'aménager tous les obstacles d'origine anthropique, même ceux de faible hauteur, afin de faciliter leur franchissement pour les deux espèces de Sicydiinae et en particulier pour *C. acutipinnis*.

# Intra and inter-specific morphological diversity of amphidromous gobies influences waterfall-climbing performances

Running title: Morphological diversity influences waterfall-climbing performance

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## Abstract

The morphology of an individual can affect functional performance and, ultimately, survival and fitness. To study these links, a first step is to evaluate the relationship between morphology and performance. Sicydiine fishes are an interesting model for such studies, because successful completion of their life cycle depends on a functionally demanding task: climbing waterfalls when they return to freshwater from the ocean. Previous studies identified two different climbing modes among sicydiines: "inching" and "powerburst". Relationships between morphology and climbing performance have been found for inching and powerburst species present on different islands from distant oceans (Pacific and Caribbean), but species from the same island have not been compared. In this study, we challenged two different sicydiine species from Reunion Island to an artificial climbing ramp: the inching climber Sicyopterus lagocephalus and the powerburst climber Cotylopus acutipinnis. For each species, we evaluated differences in morphology between successful and unsuccessful climbers. We predicted that species with similar climbing styles (S. lagocephalus and S. stimpsoni) would show differences between successful and unsuccessful climbers that more closely resembled each other than differences between successful and unsuccessful climbers across species from the same island (S. lagocephalus and C. acutipinnis). This prediction was only partially met. S. lagocephalus individuals with a streamlined body showed better climbing performance, as observed for S. stimpsoni. However, the size of the pelvic sucker, which fish use to attach to the substrate while resting, appeared less important for S. lagocephalus than for S. stimpsoni and C. acutipinnis. Instead, the size of the mouth, which inching species use to attach to the substrate while moving up, seemed important for S. lagocephalus but not for other species. Thus, differences in the morphology-performance relationship among sicydiines may relate not only to differences in climbing mode, but also to species-specific specializations within each climbing mode.

Key words: Fish, Diadromy, Locomotion, Phenotype, Selection, Shape, Tropical Islands.

# Introduction

The ability of animals to perform functional tasks can be critical to their survival (Arnold, 1983). Among many factors that can influence functional performance is the morphology of the body and its component anatomical structures (Irschick, 2002). This relationship can be complicated by a number of factors (Irschick et al., 2005; Wainwright, 2007), including the evaluation of which aspects of performance are most critical to consider (Domenici, 2001). Nonetheless, physical principles provide a foundation for predicting how well animals that exhibit different morphologies would be expected to perform different tasks (Vogel, 2013). Thus, despite complications, consideration of morphological variation can facilitate understanding of the mechanisms underpinning variation in performance.

Gobies of the subfamily Sicydiinae, a diverse group of fishes inhabiting rivers of tropical and subtropical islands, provide novel opportunities for gaining insight into how functional performance may be influenced by morphology because they include several species that face severe, distinctive locomotor demands. Sicydiines are amphidromous: after a larval stage in the ocean, they return to rivers where they grow to maturity and spawn (Teichert et al., 2013b, 2014c). However, in addition to common hazards such as predators (Blob et al., 2010), most rivers in mountainous tropical islands are also punctuated by tall waterfalls. For several species, re-colonization and, therefore, survival and reproduction, depend on climbing up such waterfalls that can be tens of meters high (Schoenfuss & Blob, 2003). During recent decades, the increased abundance of dams and weirs in tropical islands has further increased the number of barriers that sicydiine fishes need to climb to reach their freshwater habitat (March et al., 2003). These artificial obstacles have thus amplified the importance of waterfall-climbing function for sicydiine species and may adversely affect their sustainability.

Previous studies on the locomotion of sicydiines from Hawai'i and Dominica described two different modes of waterfall climbing behavior (Schoenfuss & Blob, 2003; Schoenfuss et al., 2011). "Inching" climbers alternately use their pelvic sucker, formed by the fusion of their pelvic fins, and their oral sucker to attach to the substrate while axial movements remain limited during prolonged bouts of climbing. In contrast, "power burst" climbers lack an oral sucker, and their climbing mode consists of rapid bursts powered by the pectoral fins and axial movements, followed by long resting periods while attached to the substrate with their pelvic sucker. Previous studies that performed climbing trials up artificial ramps (Blob et al., 2008, 2010; Kawano et al., 2013; Moody et al., 2017) have identified relationships between fish morphology and waterfall-climbing performance in the inching species *Sicyopterus stimpsoni* from the Pacific Island of Hawai'i, and the powerburst species *Sicydium punctatum* from the Caribbean island of Dominica. In those studies, the best performing inching climbers generally had a narrow and flat, streamlined body that minimized drag, and a large pelvic sucker to improve adhesion to the substrate. In contrast, the best performing powerburst climbers generally had larger body masses, but fewer distinct anatomical differences from unsuccessful climbers, a result attributed to the greater integration of body movements required for this style of climbing (Kawano et al., 2013). Although these studies provide some expectations for how morphology might influence performance in different climbing behaviors, they were performed on species from widely separated geographic locations, with potentially idiosyncratic differences in the selective regimes to which each species was exposed. Comparisons of climbing performance between inching and powerburst species living in the same stream, which have been subject to similar selective conditions, could help to better evaluate whether different structural factors are advantageous between the climbing styles.

Oceanic larval life history of sicydiines might affect the morphology of juveniles and in term their waterfall-climbing performance. Indeed pelagic larval duration (PLD), a proxy of larval life history, is highly variable among sicydiines, ranging from two to ten months and significantly influences size at settlement in freshwater (Teichert et al., 2012, 2016b). As size can influence morphology via allometric growth of anatomical variables (Maie et al., 2007), PLD may indirectly influences waterfall-climbing performance for either species from Réunion.

In this context, our first aim was to compare how waterfall climbing performance is influenced by morphology for two sicydiine species from Reunion Island (Western Indian Ocean): *Sicyopterus lagocephalus*, a cosmopolitan (Keith et al., 2005a), inching (Keeffe et al., 2017) species present from the Eastern Pacific Ocean to the Western Indian Ocean; and *Cotylopus acutipinnis*, a powerburst climber (Keeffe et al., 2017) endemic to Reunion and Mauritius islands (Keith et al., 2005b). We hypothesized that the relationship between waterfall-climbing performance and morphology would be more similar between inching species (*S. lagocephalus* and *S. stimpsoni*) and between powerburst species (*C. acutipinnis* and *S. punctatum*) than it would be between the two species found together on Réunion (*S. lagocephalus* and *C. acutipinnis*). The second aim of the study was to evaluate whether

pelagic larval duration (PLD) influenced waterfall-climbing performance for either species from Réunion.

## Materials and methods

### Fish capture and climbing experiments

Juveniles of *S. lagocephalus* (N= 616) and *C. acutipinnis* (N= 655) were collected immediately after their return to freshwater at the mouth of the Saint Etienne River (South-Western Reunion Island  $21.0^{\circ}$ S–55.5°E, supplementary material Fig. S1) using a Hans Grassel IG 200-2 (Germany) portable electro-shocker. *Sicyopterus lagocephalus* were collected during three periods (i.e. March-April, July and November 2015) and *C. acutipinnis* during two periods (June and November 2015). These periods were selected in order to sample the whole range of individual size and PLD each species can express when returning to freshwater (Teichert et al., 2012, 2016b). Fish were transferred to the lab in aerated buckets containing stream water within four hours after capture, and acclimated overnight in the lower tank of the experimental arena (Fig. 1).



Fig. 1: Schematic representation of the experimental arena used for selection experiments on climbing in juvenile *S. lagocephalus* and *C. acutipinnis*. The trapping system placed in the upper tank at the outlet of the climbing ramp in not represented.

The experimental arena was similar to the one used by Blob et al. (2008). It consisted of a 2.40 m ramp made with a semicircular plastic rain gutter linking two identical tanks (Fig. 1). To improve traction, the surface of the ramp was roughened using sandpaper, and rinsed with stream water prior to use. The ramp angle was set to 70° for *S. lagocephalus* (i.e. the ramp angle used by Blob et al. (2008)) but only to 45° for *C. acutipinnis* as preliminary tests demonstrated that individuals of this species were unable to climb the ramp at a more acute angle. The experimental arena was set in a temperature-regulated room at approximately 24°C, a temperature frequently observed in Reunionese rivers (Teichert et al., 2014b). The room was maintained at a constant photoperiod to match natural conditions and lighted from 6:00 to 18:00 hours.

The climbing experiments were performed on three consecutive days, from 8:00 to 18:00 hours, during which fish had no access to food. During each experiment, between 34 and 336 fish were placed simultaneously in the lower tank depending of the number of individuals captured in the field. The climbing behavior was stimulated by a 2.7 L.mn<sup>-1</sup> discharge of stream water pumped from the lower tank to the upper tank, which was allowed to flow down the ramp. The upper tank was fitted with a trapping system to prevent fish from moving back down the climbing ramp after reaching the top. At the end of each experimental day, all fish that had successfully climbed the ramp (referred as "climbers") were removed from the trap in the upper tank and maintained in aerated stream water until the end of the three-day experiment. At the end of the of the three-day experiment, all of the fish that did not climb the ramp (referred as "non-climbers") were removed from the ramp) were considered as non-climbers.

## Measurement of anatomical variables and estimation of pelagic larval duration

The day after the conclusion of each three-day experiment, all climbers, and an equivalent number of randomly sampled non-climbers, were euthanatized with an overdose of eugenol. Each individual was first weighted (fresh weight, Fw) to the closest 0.001g, after which lateral and ventral view pictures were taken with an Epson perfection V750 PRO scanner using an improved procedure based on Steinke et al. (2009). A total of 15 anatomical variables were measured from these images using IMAGE J v1.47 (Rasband, 2015). These anatomical variables were similar to those measured by Blob et al. (2010), except for the length of the two

dorsal and the anal fins which were difficult to measure on scanned images (Fig. 2A and B). We also measured a supplementary anatomical variable, the perimeter of the inner margin of the mouth lip (MOU), because of the importance of the oral sucker for inching climbers.



Fig. 2: Lateral (**A**) and ventral (**B**) views illustrating the linear measurements performed on *S. lagocephalus* and *C. acutipinnis.* (**A**) *Ls* : Standard length; HH : Head heigth, PBL : Basal length of the pectoral fin, MBH : Heigth at mid body, CPH : Heigth of th caudal peduncle. (**B**) HL : Head length, TrL : Trunk length, TaL : Tail length, SuL : Sucker length, PL : Length of the margin of the pectoral fin, HW : Head width, SuW : Sucker width, TrW : Trunk width, ABW : Width of the body at the location of the anal pore, MOU : Perimeter of the inner margin of the mouth lip.

To evaluate the relationship between PLD and waterfall climbing performance, paired sagittal otoliths were extracted under binocular microscope magnification for randomly subsampled individuals: 100 climbers and 97 non-climbers of *S. lagocephalus* and 60 climbers and 59 non-climbers of *C. acutipinnis*. One otolith (randomly left or right) was placed in a drop of immersion oil and photographed at X400 with a transmitted light microscope following the protocol described by Teichert et al. (2016). The microstructures of the otolith were blindly enumerated (without prior knowledge of the capture period or the fish length) by an experienced operator. When more than 15% of the microstructures were indistinguishable, the fish was removed from analysis. In addition, the microstructures were blindly examined by a second experienced operator for 57 and 40 randomly sampled otoliths of *S. lagocephalus* and *C. acutipinnis* respectively in order to verify the similarities in PLD estimations by the two operators.

## Analysis of the influence of anatomical variables and PLD on waterfall-climbing performance

Size (standard length, *Ls*) can directly influence other anatomical variable due to allometric growth. In particular, Maie et al. (2007) observed an allometric growth of anatomical variables

expected to be important for the waterfall-climbing behavior (i.e. the pelvic sucker length and caudal peduncle height) in *S. stimpsoni*. To minimize the effect of size on analyses, size frequency distributions were first compared between climbers and non-climbers for the two species using kernel density estimates (Langlois et al., 2012). When no significant difference in the two size frequency distributions was detected, analysis of the influence of anatomical variables on the waterfall-climbing performance was performed without size correction.

The importance of the measured variables for the climbing performance of both species was analyzed using the random forest approach (Breiman, 2001). This method does not depend on the hypothesis of normality or homoscedasticity of the data, and no previous transformation of the data is required (Breiman, 2001). For these analyses, climbers were assigned a performance of one (success) and non-climbers a performance of zero (failure). Two different random forest analyses were performed for each species. The first one was performed on the whole data set, whereas the second one was performed only on individuals for which PLD was estimated. For each random forest analysis, the goodness of fit was based on the estimation of out-of-bag data error rate, and the relative contribution of each variable was ranked based on the estimated mean decrease of the Gini index (Liaw & Wiener, 2002). Finally, the significance of the mean decrease of Gini index for each variable was estimated by comparing the predicted values with a null distribution. The null distribution was obtained based on 1,000 random permutations of the values.

All statistical analyses were performed with the open source R v. 3.3.1 software (R Development Core Team, 2016). It was implemented with the packages *Kernsmooth* (Wand, 2015) and *sm* (Bowman & Azzalini, 2014) for the comparison of size frequency distribution, *Hmisc* (Harrel Jr., 2016) for correlation analyses, and *randomForest* (Liaw & Wiener, 2002) and *rfPermute* (Archer, 2016) for random forest analyses.

## Results

Anatomical variables were measured on a total of 401 *S. lagocephalus* and 244 *C. acutipinnis.* For *S. lagocephalus* the percentages of climbers were 42%, 27%, and 40% for fish captured in March-April, July, and November respectively. Climbers accounted for 19% and 17% of *C. acutipinnis* captured in June and November respectively.

The PLD estimated by the two operators on a subset of otoliths were not significantly different for both species (paired test of student, p = 0.59 for *S. lagocephalus* and p = 0.32 for *C. acutipinnis*). The microstructures of the remaining otoliths were consequently interpreted based on observations of just the first operator.

The *Ls* frequency distribution for *S. lagocephalus* climbers was bimodal with one mode at 2.8 cm *Ls* and the other at 3.1 cm *Ls*; in contrast, the distribution was unimodal for nonclimbers with a mode at 2.8 cm *Ls* (Fig. 3A). The *Ls* frequency distributions were unimodal for both climbers and non-climbers *C. acutipinnis* with modes between 1.8 and 1.9 cm *Ls* (Fig. 3B). *Ls* frequency distributions of *S. lagocephalus* climbers and non-climbers were significantly different (Kernel density estimate, band width = 0.05 cm, p = 0.01) with most fish with a *Ls* greater than 3.0 cm being climbers. The *Ls* frequency distributions of *C. acutipinnis* climbers and non-climbers were not significantly different (Kernel density estimate, band width = 0.05 cm, p = 0.40). When considering only the main mode of sizes for *S. lagocephalus* (i.e. from 2.4 cm to 3.0 cm *Ls*) and for *C. acutipinnis* (i.e. from 1.7 cm to 2.0 cm *Ls*), the size frequency distributions of climbers and non-climbers were not significantly different for both species (Kernel density estimate, band width = 0.05 cm for *S. lagocephalus* and 0.02 cm for *C. acutipinnis*, p> 0.30). Subsequent analyses were thus performed on these size ranges only, resulting in the suppression of 70 *S. lagocephalus* (comprising 48 climbers) and 10 *C. acutipinnis* (comprising five climbers) from the original data set.



Fig. 3: Standard length (*Ls*) frequency distribution of fish that successfully climbed the ramp (i.e. "climbers") and those that did not (i.e. "non-climbers") for *S. lagocephalus* (**A** and **B**) and *C. acutipinnis* (**D** and **E**). The band width (i.e. 0.05 cm for both species) of the histograms was chosen using the R package "KernSmooth" (Wand, 2015) and rounded to the closest 0.02 cm. Comparison of Kernel density estimated for the same groups (**C** and **F**) was performed using the previously selected bandwidth. The gray shaded area represents the standard error of the null model considering both distributions are equal. The vertical dashed lines on Fig 3. **A**, **B**, **D** and **E** illustrate the size range retained for further analysis.

The first random forest analysis was performed for each species separately and on all the individuals within their respective selected size range. For both species, the fresh weight, *Ls*, trunk width (TrW) and width of the body at the location of the anal pore (ABW), appeared correlated to more than one variable with a coefficient of correlation > 0.80. As a consequence, they were not considered in the random forest models. The random forest models fitted on the remaining 12 anatomical variables (Table 1) had an out-of-bag error rate of 25% for *S. lagocephalus* and 29% for *C. acutipinnis*, indicating a reasonable overall performance of the models. For *S. lagocephalus*, the partial response of each anatomical measurement, evaluated based on a permutation test, only appeared significant for head width (HW), perimeter of the inner margin of the mouth lip (MOU), and mid-body height (MBH, Table 1). For *C. acutipinnis*, only sucker width (SuW) and length (SuL, Table 1) appeared significant. Interestingly, *S. lagocephalus* with small and large HW were better climbers, but those with intermediate HW were not (Fig. 4A). Good climbers had also a large MOU and a small MHB (Fig. 4A). For *C. acutipinnis*, individuals with large SuW and SuL were better climbers (Fig. 4B).



Fig. 4: Partial response plots of the three most important anatomical variables influencing climbing performance for *S. lagocephalus* (**A**) and *C. acutipinnis* (**B**). Higher partial responses indicate better climbing performances associated with the range of values of the anatomical variable. Evaluations of the partial response were based on random forest of 3000 trees for both species within their respective selected *Ls* ranges. The solid lines represent significant partial responses (p<0.05) when the dashed line represents non-significant partial responses (p>0.05). HW : Head width (**A1**); MOU : Perimeter of the inner margin of the mouth lip (**A1-B3**); MBH : Heigth at mid body (**A3**); SuW : Sucker width (**B1**) and SuL : Sucker length (**B2**).

The second random forest analyses were performed using the same 12 anatomical variables along with the PLD using the 149 *S lagocephalus* and 96 *C. acutipinnis* for which PLD had been estimated. None of these 13 variables were correlated to other variables with a correlation coefficient greater than 0.80. The random forest models fitted with these 13 variables had an out-of-bag error rate of 26% for *S. lagocephalus* and 29% for *C. acutipinnis*. For *S. lagocephalus* the two most important variables explaining the climbing performance were HW (mean decrease of Gini = 9.0) and MOU (mean decrease of Gini = 7.3), with the shape of their partial response plots remaining the same compared to the first random forest analysis (supplementary material Fig. S2). The third most important variable was PLD (mean decrease of Gini = 7.2). Its partial response indicated that PLD from 100 to 120 days were negatively associated with waterfall-climbing performances. However only the partial response of HW was significant (p = 0.001), with partial responses of MOU and PLD only

marginally significant (p = 0.09 and 0.07 respectively). For *C. acutipinnis* SuL and SuW were the two most important variables explaining climbing performance, and the shapes and significance of their partial response plots remained similar to those of the original analysis. The third most important variable for *C. acutipinnis* was head height (HH), with a partial response indicating that waterfall-climbing performance was negatively associated with small HH, and positively associated with large HH. However, the effect of HH was only marginally significant (p = 0.07). Table 1: Mean decrease of Gini index and associated p-values (p) based on random forest analysis for *S. lagocephalus* 2.40 cm to 3.00 cm *Ls* and *C. acutipinnis* 1.70 cm to 2.00 cm *Ls*.

| S. lagocephalus   | C. acutipinnis              |       |                        |                                |       |
|---|-----------------------------|-------|------------------------|--------------------------------|-------|
| Anatomical<br>measurement                                     | Mean decrease of Gini index | р     | Anatomical measurement | Mean decrease<br>of Gini index | р     |
| Head width ( <b>HW</b> )                                      | 18.164                      | 0.001 | SuW                    | 15.137                         | 0.001 |
| Perimeter of the inner margin of the mouth lip ( <b>MOU</b> ) | 17.274                      | 0.004 | SuL                    | 12.543                         | 0.001 |
| Heigth at mid body ( <b>MBH</b> )                             | 16.528                      | 0.002 | MOU                    | 9.924                          | 0.138 |
| Length of the margin of the pectoral fin (PL)                 | 14.330                      | 0.231 | HL                     | 8.259                          | 0.778 |
| Basal length of the pectoral fin ( <b>PBL</b> )               | 13.519                      | 0.188 | TrL                    | 8.249                          | 0.839 |
| Sucker width (SuW)  | 12.555                      | 0.778 | HH                     | 8.040                          | 0.683 |
| Head heigth ( <b>HH</b> )                                     | 12.089                      | 0.881 | PL                     | 7.704                          | 0.992 |
| Trunk length ( <b>TrL</b> )                                   | 11.943                      | 0.997 | TaL                    | 7.421                          | 1.000 |
| Tail length ( <b>TaL</b> )                                    | 11.421                      | 1.000 | HW                     | 7.155                          | 0.997 |
| Heigth of th caudal peduncle (CPH)                            | 11.411                      | 0.979 | MBH                    | 7.015                          | 0.996 |
| Head length (HL)  | 11.009                      | 1.000 | СРН                    | 6.263                          | 1.000 |
| Sucker length (SuL)   | 10.240                      | 1.000 | PBL                    | 5.688                          | 1.000 |
#### Discussion

Immediately after they return to freshwater, juveniles of *S. lagocephalus* appear to be better waterfall climbers than *C. acutipinnis*. Indeed, approximately 37% of *S. lagocephalus* 2.4 to 3.0 cm *Ls* were able to climb an experimental ramp angled at 70° when only 18% of *C. acutipinnis* 1.7 to 2.0 cm *Ls* were able to climb the same ramp angled at a less steep 45°. The discrepancy in climbing abilities between these two species is consistent with differences in their respective climbing speeds (Keeffe et al., 2017). When expressed as body length per second (BL.s<sup>-1</sup>), *C. acutipinnis* juveniles have a lower net climbing speed of approximately 0.06 BL.s<sup>-1</sup> compared to approximately 0.10 BL.s<sup>-1</sup> for *S. lagocephalus*.

Predictions for expected relationships between fish morphology, waterfall-climbing mode, and waterfall-climbing performance were only partially met. The positive relationship observed for S. lagocephalus between narrow head, slim body and waterfall-climbing performance appeared consistent with results of Blob et al. (2008) for inching S. stimpsoni, for which fish with more streamlined bodies had higher rates of waterfall climbing success. This supports the conclusion that body shapes that can reduce drag (Webb, 1984) encountered during waterfall climbing should enhance performance for inching species. Surprisingly, size of the oral sucker (MOU) was found to influence waterfall-climbing performance of S. lagocephalus, but the size of the pelvic sucker (i.e. SuL or SuW) was not. Although comparative data on oral sucker size are not available for S. stimpsoni (Blob et al., 2008), this result is of particular interest for S. lagocephalus because, as an inching climber, it alternates attachment between the oral and pelvic sucker while in motion (Maie et al., 2012). Waterfall-climbing occurs at the interface between air and water as the individuals generally use a water layer that is only a few mm thick. While climbing, fish thus encounter both the constraints of drag from flowing water, and the force of gravity (Maie et al., 2007, 2012). As juvenile S. lagocephalus returning to freshwaters are generally bigger and heavier than the other sicydiine species previously studied, both of these forces should be relatively greater than in smaller taxa, because gravitational force scales with animal mass and drag scales with surface area (Maie et al., 2007, 2012). A larger perimeter of the inner margin of the mouth lip (MOU) might provide an increase in attachment force that would help to maintain a streamlined shape, with a bulbous leading edge that tapers continuously toward the tail. Similarly, such benefits could also account for the positive effect of a wider head (HW) on climbing performances.

*Cotylopus acutipinnis* individuals displaying better waterfall-climbing performance showed morphological features that enhanced adhesion to the substrate (i.e. a large pelvic sucker) but did not show features that would enhance thrust (i.e. long and deep caudal peduncle and pectorals fins). Among the three powerbursting, sicydiine species for which climbing speeds have been measured, *C. acutipinnis* is the slowest (Keeffe et al., 2017). This slow climbing speed is mainly explained by the lower proportion of time *C. acutipinnis* spends in motion compared to other powerburst species. As *C. acutipinnis* uses a climbing mode involving long rest periods, it is not surprising that the size of the pelvic sucker, which is used to adhere to the substrate during resting periods, significantly influenced its waterfall climbing performance.

The better climbing performance of S. lagocephalus may be among the factors explaining its successful colonization of many tropical island rivers compared to its endemic conspecific, C. acutipinnis. Indeed, as the proportion of returning S. lagocephalus juveniles that can climb the first waterfalls encountered in rivers is higher than C. acutipinnis, the probability of successful settlement in many riverine habitats located upstream to waterfalls is greater for S. lagocephalus. Moreover, cohorts of juvenile sicydiines returning to rivers may have different morphologies, as observed in S. stimpsoni (Moody et al., 2015). The diversity of morphologies associated with waterfall-climbing performance for S. lagocephalus increases the probability that individuals that perform sufficiently well to facilitate successful settlement may be present within each cohort. Moreover, the ecological advantage of the better climbing performance of S. lagocephalus compared to C. acutipinnis is probably exacerbated by the dams and weirs that have been during the past decades in Réunion Island. Most of these barriers are much higher than the experimental ramps of this study and/or with a longitudinal slope steeper than 45° (DEAL, 2011; R. Lagarde et al., 2015). The selective pressure of these anthropogenic barriers can consequently be beyond the climbing performances of most C. acutipinnis juveniles and as a result, add a threat to the sustainability of this endemic species population.

PLD was among the three variables associated with successful waterfall-climbing performance in the second random forest analysis for *S. lagocephalus*. The longest PLD had a marginally significant effect indicating improved waterfall-climbing performance. In contrast, PLD showed little influence on climbing success in *C. acutipinnis*. *Sicyopterus lagocephalus* also generally have longer PLD than *C. acutipinnis* (Teichert et al., 2012, 2016b). In this context, longer PLD was recently shown to enhance the reproductive performance of

*S. lagocephalus* strategy after returning to rivers (Lagarde et al. unpublished data). Thus, our present results confirm the importance of longer PLD for *S. lagocephalus* for success in its ecological strategy.

This study was the first step to understand the relationship between morphology and performance for the waterfall-climbing function of these two sympatric sicydiine species. However, in natural conditions, additional selective pressures such as predation (Blob et al., 2010; Maie et al., 2014; Diamond et al., 2016) may also affect morphological selection, especially in rivers where the first waterfall is located farther inland. A more comprehensive evaluation of the factors influencing individual fitness in these species will, therefore, require field verification of the relationship between the anatomical variables highlighted experimentally during this study, across climbing and other functional demands. Nonetheless, our data show the strong potential for climbing performance to be one of the major factors influencing morphology both within and across sicydiine species.

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#### Supplementary material



Fig. S1: Location of Reunion Island within the Mascarene Archipelago (Western Indian Ocean)



Fig. S2: Partial response plots of the three most important anatomical variables influencing climbing performance for *S. lagocephalus* (**A**) and *C. acutipinnis* (**B**) for which PLD had been estimated. Higher partial responses indicate better climbing performances associated with the range of values of the anatomical variable. Evaluations of the partial response were based on random forest of 3000 trees for both species within their respective selected *Ls* ranges. The solid lines represent significant partial responses (p<0.05) when the dashed lines represent non-significant partial responses (p>0.05). HW : Head width (**A1**); MOU : Perimeter of the inner margin of the mouth lip (**A2**); PLD : Pelagic larval duration (**A3**); SuL : Sucker length (**B1**); SuW : Sucker width (**B2**) and HH : Head heigth (**B3**).

## 4.4 Influence de la pression de sélection des barrages sur les traits morphologiques individuels et vitesses de migration des juvéniles de Sicydiinae dans le bassin versant de la rivière du Mât

Résumé graphique étendu :

**Objectifs de l'étude :** L'objectif principal de cette étude est de vérifier en milieu naturel la cohérence des relations décrites expérimentalement entre les performances de franchissement d'obstacles et la morphologie des juvéniles de *S. lagocephalus* et de *C. acutipinnis*. Plus précisément deux hypothèses sont testées : 1) les juvéniles de *S. lagocephalus*, comparativement à ceux de *C. acutipinnis*, ont des vitesses de migration plus élevées et sont moins impactés par les deux barrages situés à 7 et 20 km de l'embouchure de la rivière du Mât; 2) les juvéniles de *S. lagocephalus* capables de franchir les barrages ont soit une morphologie plus hydrodynamique soit une dimension de la bouche plus élevée par rapport aux juvéniles incapables de franchir les barrages et les juvéniles de *C. acutipinnis* capables de franchir les barrages ont une dimension de la ventouse plus élevée. En termes de gestion, ces résultats permettent de qualifier l'impact des barrages sur la migration des deux espèces à l'échelle individuelle.

**Résultats :** Les vitesses de migration des deux espèces sont apparues plus importantes pour les individus capturés au niveau du barrage amont que pour ceux capturés au niveau du barrage aval. Globalement, les juvéniles de *S. lagocephalus* (**A**) ont des vitesses de migration plus élevées que *C. acutipinnis* (**B**) entre l'embouchure et chacun des barrages. Aucune différence de morphologie entre les juvéniles de *S. lagocephalus* capturés en aval et en amont des deux barrages n'est mise en évidence (**A1, A3**). Cependant, les juvéniles capturés en aval du barrage amont ont une bouche plus grande et une hauteur du corps plus faible que ceux capturés en amont du barrage aval (**A2**). Les juvéniles de *C. acutipinnis* capturés en amont des deux barrages ont une ventouse plus grande que ceux capturés en aval chacun de ces barrages (**B1, B3**). Aucune différence de morphologie n'est observée entre les juvéniles capturés en aval du barrage amont ceux capturés en amont du barrage aval (**B2**). Pour les deux espèces les morphologies associées aux performances de franchissement des barrages sont cohérentes avec les observations expérimentales précédentes.



Amélioration de la connaissance des espèces : Les juvéniles de *S. lagocephalus* ont une vitesse de migration en rivière plus importante que ceux de *C. acutipinnis* et leur migration semble moins impactée par les barrages. En effet, le fait qu'aucune différence de morphologie ne soit observée entre les juvéniles de *S. lagocephalus* capturés en aval et en amont des barrages

suggère que la majorité de ces individus ont des performances de franchissement d'obstacles suffisamment élevées pour franchir les barrages, indépendamment de leur morphologie, ce qui n'est pas le cas des juvéniles de *C. acutipinnis*. Cependant, des différences de morphologie sont observées entre les juvéniles de *S. lagocephalus* capturés en amont du barrage aval et ceux capturés en aval du barrage amont. Ceci laisse présumer qu'une sélection de la morphologie des individus, en lien avec leurs performances locomotrices, a lieu pendant leur migration entre les deux barrages.

Enfin, les vitesses de migration plus élevées pour les individus capturés au niveau du barrage amont par rapport à ceux capturés au niveau du barrage aval peuvent être reliées à des stratégies individuelles de migration différentes au sein des populations de ces deux espèces. Les individus colonisant les zones amont des bassins versants auraient tendance à migrer plus vite que ceux restant dans les zones intermédiaire et aval. Cette hypothèse peut être expliquée par des différences individuelles de performances locomotrices au sein des populations des deux espèces : les individus les plus performants migreraient plus vite et plus en amont.

**Application à la gestion :** Malgré la hauteur modérée des deux barrages étudiés (i.e. entre 9 et 10 m) et le fait que le barrage amont soit équipé d'une passe à poissons spécifiquement dimensionnée pour *S. lagocephalus*, ces obstacles se sont avérés difficiles à franchir pour *C. acutipinnis*. Ce résultat souligne l'importance d'adapter les passes à poissons existantes ou d'en construire de nouvelles, en prenant en compte les plus faibles capacités de franchissement de *C. acutipinnis*. Il pourrait par exemple être judicieux de construire des bassins intermédiaires séparées par des rampes de quelques mètres afin de permettre aux individus empruntant une passe à poisson de s'y reposer. Une autre solution serait d'équiper les passes à poissons de supports mieux adaptés au franchissement par les Sicydiinae que le béton lisse actuellement utilisé.

### Individual morphological selection and migration speed of two amphidromous gobies along an anthropogenically altered watershed

## Running title: Individual morphological selection and migration speed of amphidromous gobies

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#### Abstract :

Individual locomotor performances of migrating fish are affected by inter-individual morphological differences and influence the response of the population to anthropogenic impacts. Amphidromous gobies, Sicyopterus lagocephalus (SIL) and Cotylopus acutipinnis (COA), can climb-up migration obstacles tens of meters high, after their arrival in rivers from the ocean. A previous study demonstrated that juveniles of SIL performed better than COA when challenged with an artificial climbing ramp and that individual morphology explained climbing performances for both species. This present study was focused on the effects of two 10 m high dams along a watershed in La Réunion Island on the individual morphological selection of these species. We hypothesized that, compared to COA, 1) SIL juveniles will reach the dams faster after they arrive in freshwater and 2) their morphology will play a lesser role in their capacity to climb-up the dams. Anatomical traits were measured for 186 and 201 SIL and 179 and 221 COA captured downstream and upstream to the dams respectively. The time they spent in freshwater was estimated by examining the microstructures of their otoliths. As expected, SIL individuals reached the dams faster than COA and their morphology upstream and downstream to the dams did not differ. These results seem to indicate that juveniles of the cosmopolite SIL have strongest migration capacities than the endemic COA. Moreover, the assessment the impact of dams on

fish individuals' morphologies appears as an efficient tool to quantify the disruptions of freshwater upstream migration of amphidromous species due to anthropogenic obstacles.

**Key words :** *Cotylopus acutipinnis*, Dam, Diadromy, Fish-ways, Locomotor performance, River continuum, *Sicyopterus lagocephalus*, Tropical Island

#### Introduction

Individual variability of performances is of major importance for the ecological strategies of fish species and their responses to anthropogenically altered habitat conditions (Schoenfuss & Blob, 2007). In natural habitats, locomotor performances can be linked to habitat use (Fulton et al., 2001), predator avoidance (Domenici, 2001), or access to food resources (Rincón et al., 2007). For alleviating the effects of dams, the design of many fishways is based on the evaluation of individual swimming, or leaping, capacities (Larinier et al., 1992). As a result, the probability for an individual to successfully pass a fishway, and reach upstream habitats, greatly depends on its own performances. Understanding the factors affecting the locomotor performances of an individual is thus mandatory when we want to increase our understanding of fish species ecological strategies, or to evaluate the potential impact of human obstacles.

Morphology is one of the most critical biotic factors affecting individual performance (Arnold, 1983) and many studies experimentally linked the morphology of individual fish to their locomotor performance (Plaut, 2000; Laborde et al., 2016). This link between morphology and locomotor performance is particularly well described for the climbing function of the tropical gobies of the Sicydiinae subfamily (Blob et al., 2008; Kawano et al., 2013; Lagarde et al. submitted). This climbing function allows juveniles of these amphidromous species to climb-up steep waterfalls (Schoenfuss & Blob, 2003) and reach their riverine growing and spawning habitats once they complete their larval stage in the ocean (Radtke et al., 1988; Teichert et al., 2013b, 2014c). Differences in morphologies have been observed between adult populations of *Sicyopterus stimpsoni* located downstream and upstream to natural waterfalls (Schoenfuss et al., 2013); however, the question of how morphology of juveniles affects their capacity to climb-up anthropogenic obstacles during their upstream migration still remains.

Sicyopterus lagocephalus and Cotylopus acutipinnis, two Sicydiinae gobies, dominate the freshwater fish assemblage in Réunion Island (Olivier et al., 2004). They occur from the

estuaries to more than 20 km upstream and 600 m above sea level (a.s.l) in Réunionese rivers (Teichert et al., 2014c). Their pelvic sucker, formed by the fusion of their pelvic fins, and the oral sucker for *S. lagocephalus*, allow them to climb up natural and anthropogenic obstacles (Voegtlé et al., 2002). However, differences of climbing performances were observed in experimental conditions between the two species. *Sicyopterus lagocephalus* climbed faster and was able to successfully pass steeper experimental climbing ramps than *C. acutipinnis* (Keeffe et al., 2017; Lagarde et al. submitted). Moreover, within each species, *S. lagocephalus* individuals with a narrow and flat streamlined body, or a flat body and a large oral sucker, and *C. acutipinnis* individuals with a large pelvic sucker performed better when challenged to the experimental ramps (Lagarde et al. submitted).

In this context, our aim was to verify if the differences of climbing performances, and associated morphologies, between *S. lagocephalus* and *C. acutipinnis* observed in natural conditions were consistent with those described experimentally. More precisely our first hypothesis was that the migration speed will be faster for *S. lagocephalus* compared to that of *C. acutipinnis* in relation with their respective climbing speed highlighted experimentally. Our second hypothesis was that individuals with a morphology correlated to better climbing performances in experimental conditions will also perform better in natural conditions. Finally, we hypothesized that the impact of anthropogenic obstacles will be stronger for *C. acutipinnis* juveniles compared to *S. lagocephalus* due to their weaker climbing performances.

#### Material and methods

#### Fish sampling

The study was conducted in two sites along the Mât River watershed in Reunion Island (Fig. 1a-b). Site 1 was located at 7 km from the river mouth and 120 m a.s.l (Fig 1b). The dam located at Site 1 was 10 m high with a longitudinal slope of 80° (Fig 1c) and was not equipped with a fishway. This dam impairs the upstream migration of most diadromous indigenous species but *S. lagocephalus*, *C. acutipinnis* and few other species including fresh water eels (*Anguilla* ssp.), palaemonids (*Macrobrachium* ssp.) and atyids shrimps (*Atyoida serrata*) are present in upstream habitats. Site 2 was located at 20 km from the river mouth and 380 m a.s.l. The dam located at Site 2 was 9.5 m high (Fig 1d). It was equipped with a fishway located on the right bank. The fishway consists on a 14 m concrete ramp angled at 50° as described by Lagarde et al. (2015).



Fig. 1: Location of sites 1 and 2 in the Mât River watershed (Fig. 1b), La Réunion Island, Western Indian Ocean (Fig. 1a). Photography of the dams at Site 1 (Fig. 1c) and Site 2 (Fig. 1d) that act as obstacles to fish upstream migration.

At each site, *S. lagocephalus* and *C. acutipinnis* were captured downstream and upstream to the dams. Individuals who successfully climbed the dams (referred as "climbers") were captured using a passive trap similar to this described by Bell et al. (1995). Briefly, this passive trap consisted in a 30 cm conical funnel entrance, with a 22 cm entrance diameter and

a 6 cm exit diameter, leading to a 70 cm trapping chamber. Net lateral wings (3 m long) were set up at the entrance to enhance the trapping efficiency. All structures were covered with 1 mm mesh size mosquito net. At Site 1, fish were previously observed to climb mainly on the left bank of the dam. The trap was thus set in the river on the left bank approx. three meters upstream to the dam. At Site 2, the trap was set immediately upstream to the exit of the fish way on the right bank. Downstream to the dams, fish were captured in riffles within 200 m to the dams using a portable electro-shocker (Hans Grassl IG 200-2, Germany). Sicyopterus lagocephalus smaller than 4.0 cm standard length (Ls) and C. acutipinnis smaller than 3.0 cm (Ls) which are the maximum sizes of migrating fish previously observed (Lagarde et al. 2015) were collected. This procedure allowed to capture fish (referred as "non-climbers") which were either future successful climbers, unsuccessful climbers, or freshly settled juveniles. The whole range of individual life history and morphological traits was thus sampled. Sampling was performed from September to November 2016, which is the main upstream migration period of Sicydiinae in the Mât River ((R. Lagarde et al., 2015). The exact dates were 6 and 13 September and 19 October at Site 1, and 11 October and 29 November at Site 2. Immediately after capture fish were transported to the lab in aerated buckets containing stream water.

#### Anatomical variables measurement and estimation of migration speed

Fish were preserved alive overnight in the lab in aerated water. For each date and species, up to 60 fish were randomly sampled within the climbers and non-climbers groups and euthanized with an overdose of eugenol. The number of fish sampled was selected regarding to the total number of fish captured in order to roughly balance the number of individuals in the climbers and non-climbers groups. A lateral and ventral picture of all euthanized individuals were taken with an Epson perfection V750 PRO scanner using a procedure improved from Steinke et al. (2009). First, a 2 cm deep water pool was built on the scanner glass surface using Plastiline®. Individuals were placed in the pool and maintained on the scanner glass surface in lateral and ventral view using fine needles placed in the Plastiline®. The 15 anatomical variables measured (Fig. 2) were the same as these measured by Lagarde et al. (submitted). All individuals were euthanized within 24 h to 36 h after capture in order to limit the effects of prolonged captivity on fish condition and thus measurements.



Fig. 2: Lateral (A) and ventral (B) views illustrating the location of linear anatomical variables measured on *S. lagocephalus* and *C. acutipinnis*. (A) *Ls* : Standard length; HH : Head heigth, PBL : Basal length of the pectoral fin, MBH : Heigth at mid body, CPH : Heigth of the caudal peduncle. (B) HL : Head length, TrL : Trunk length, TaL : Tail length, SuL : Sucker length, PL : Length of the margin of the pectoral fin, HW : Head width, SuW : Sucker width, TrW : Trunk width, ABW : Width of the body at the location of the anal pore, MOU : Perimeter of the inner side of the mouth lip.

In order to estimate migration speed, the freshwater duration (FD) was estimated for at least 80 climbers and 80 non-climbers of each species haphazardly sub-sampled at each site. These individuals were collected proportionally to their abundance in 1 mm size class of Ls. Shen and Tzeng (2002) observed that the transition between sea and freshwater is characterized by a metamorphosis check mark in the otoliths of Sicyopterus japonicus. Moreover, Lagarde et al. (submitted) demonstrated the daily rhythm of increment deposition from the check mark to the edge of the otolith, i.e. the period corresponding to the FD, in S. lagocephalus and C. acutipinnis. Paired sagittal otoliths of each subsampled individual were extracted and one whole otolith was placed in a drop of immersion oil, examined at X400 and photographed with a transmitted light microscope (Olympus CX41) equipped with a camera (Olympus C-5060). The number of increments between the check mark and the otolith edge was estimated on the pictures using IMAGE J 1.47 software (Rasband, 2015) by an experimented operator (R. Lagarde). All otoliths were analyzed twice by the same operator at an interval superior to one month. When the coefficient of variation (Panfili et al., 2002) between the two analyses did not exceed 10%, FD was evaluated based on the mean of the two estimations (Dodson et al., 2013), otherwise the sample was excluded from the analyses. The migration speed corresponded to the ratio between FD and the distance between each site and the river mouth.

#### Statistical analysis

For each species, the *Ls* and FD frequency distribution climbers and non-climbers at each site were compared using kernel density estimations (Langlois et al., 2012). The same comparison was performed between individuals of Site 1 and Site 2. The bandwidth of *Ls* and FD were selected based on the procedure described by Sheather and Jones (1991). The statistical difference between groups was tested with a permutation test comparing the kernel frequency distributions to a null model of no difference (Langlois et al., 2012).

Most anatomical variables were strongly correlated to each other (coefficient of correlation > 0.8) due to scaling relationship with size (Maie et al., 2007). A size correction procedure was thus performed on the selected anatomical variables following Berner (2011). The selected anatomical variables were HW, MOU and MBH for *S. lagocephalus* and on SuW and SuL for *C. acutipinnis* which were the only anatomical variables significantly linked to climbing performances in a previous experimental study (Lagarde et al. submitted). The size correction procedure consists on estimating the residuals from a generalized linear regression (GLM) between each selected morphological variable and a size metric. The size metric was expressed as the first axis (PC1) of a principal component analysis (PCA) performed on all anatomical variables (Berner, 2011). Finally, the residuals of the GLM between each selected anatomical variable and the PC1 (i.e. size corrected measurements) were compared between climbers and non-climbers, for each species and each site using an ANOVA followed by a post test of Tukey.

All statistical analyses were performed with the open source R v. 3.3.1 software (R Development Core Team, 2016) implemented with the packages *Kernsmooth* (Wand, 2015) and *sm* (Bowman & Azzalini, 2014) for the comparison of *Ls* and FD frequency distributions and *ade4* (Dray & Dufour, 2007) for PCA analysis.

#### Results

#### Size frequency distributions

Anatomical variables, including *Ls*, were measured on 204 and 193 *S. lagocephalus* (including 100 and 91 climbers) and on 205 and 211 *C. acutipinnis* (including 86 and 98 climbers) captured at Site 1 and Site 2 respectively (Table 1). Most individuals were smaller

than 4.0 cm *Ls* for *S. lagocephalus* and 3.0 cm *Ls* for *C. acutipinnis* (Fig. 3). Individuals larger than these threshold values were not considered in the following analyses. It resulted on the suppression of 10 *S. lagocephalus* (comprising five climbers) and 16 *C. acutipinnis* (comprising five climbers) from the original data set. The *Ls* frequency distributions were not significantly different between climbers and non-climbers at each site for the two species (kernel density estimate; h band = 0.07 cm for *S. lagocephalus* and h band = 0.06 cm for *C. acutipinnis*; p>0.10; Fig. 3e-f-k-l). As expected, the *Ls* frequency distribution of all individuals, climbers and non-climbers, captured at Site 1 were significantly smaller than those of individuals captured at Site 2 for the two species (kernel density estimate; h band = 0.06 cm for *S. lagocephalus* and 0.05 cm for *C. acutipinnis*; p<0.001).

Table 1: Numbers (N) of juveniles of *Sicyopterus lagocephalus* and *Cotylopus acutipinnis* captured (capt) between September and November 2016, and sub-sampled (ssamp) for the measurement of anatomical variables among climbers and non-climbers (see text for definition) at each date for sites 1 and 2 (see Fig. 1). When more than 100 individuals were captured, the exact N was not evaluated.

|        | Sicyopterus lagocephalus |          |         |              |         | Cotylopus acutipinnis |         |              |         |
|--------|--------------------------|----------|---------|--------------|---------|-----------------------|---------|--------------|---------|
|        |                          | Climbers |         | Non-climbers |         | Climbers              |         | Non-climbers |         |
| Site   | Date                     | N capt   | N ssamp | N capt       | N ssamp | N capt                | N ssamp | N capt       | N ssamp |
| Site 1 | 06 Sept.                 | 35       | 35      | 25           | 25      | >100                  | 35      | 35           | 35      |
|        | 13 Sept.                 | >100     | 22      | 28           | 28      | 9                     | 9       | 31           | 31      |
|        | 19 Oct.                  | 95       | 43      | 51           | 51      | 69                    | 42      | >100         | 53      |
| Site 2 | 11 Oct.                  | 38       | 38      | 47           | 47      | >100                  | 42      | >100         | 53      |
|        | 29 Nov.                  | >100     | 53      | >100         | 55      | >100                  | 56      | >100         | 60      |



Fig. 3: Standard length (*Ls*) frequency distribution and kernel density estimation (Langlois et al., 2012) of fish captured upstream to each dam (i.e. "climbers") located at Site 1 and Site 2 and fish captured downstream to the same dam (i.e. "non-climbers") for *S. lagocephalus* (Fig. 2a-c-e and Fig. 2g-i-k) and *C. acutipinnis* (Fig. 2b-d-f and Fig. 2h-j-l). The grey shaded area (Fig. 2e-f and Fig. 2k-l) represents the standard error of the null model considering both distributions are equal. The vertical dashed lines illustrate the upper *Ls* range selected for the analyses.

#### Freshwater duration and estimation of migration speed

Freshwater duration (FD) was estimated on a subsample of 81 and 80 *S. lagocephalus* (including 40 and 40 climbers) and on 81 and 81 *C. acutipinnis* (including 41 and 40 climbers) captured at Site 1 and Site 2 respectively. The CV between the two estimations of FD was superior to 10% for 29 individuals which were thus not considered in the following analyses. It resulted on the suppression of 19 FD values for *S. lagocephalus* and 10 for *C. acutipinnis* from the original data set. At Site 1, the FD frequency distributions of climbers were unimodal for the two species (Fig. 3a-b) with a mode at 60 days for *S. lagocephalus* and 70 days for *C. acutipinnis* when no clear mode was observed for non-climbers (Fig. 3b-d). At Site 2, the FD frequency distributions were unimodal for *S. lagocephalus* with a mode at 50 days (Fig. 3g-i) and bimodal for *C. acutipinnis* with one mode at 70 days and the other at 90 days (Fig. 3h-j).

The FD frequency distributions were not significantly different between climbers and nonclimbers at Site 2 for *S. lagocephalus* and at both sites for *C. acutipinnis* (kernel density estimate; h band = 8 days for both species; p>0.10; Fig. 4f-k-l). The FD frequency distributions were significantly different between *S. lagocephalus* climbers and non-climbers at Site 1 (kernel density estimate; h band = 8 days; p=0.05; Fig. 4e). At both sites, most individuals had a FD ranging from 40 days to 80 days for *S. lagocephalus*, and from 50 days to 100 days for *C. acutipinnis*. It resulted on an estimated migration speed between the river mouth and Site 1 ranging from 90 m.day<sup>-1</sup> to 180 m.day<sup>-1</sup> for *S. lagocephalus* and from 70 m.day<sup>-1</sup> to 140 m.day<sup>-1</sup> for *C. acutipinnis*. The estimated migration speed between the river mouth and Site 2 was much higher: from 250 m.day<sup>-1</sup> to 500 m.day<sup>-1</sup> for *S. lagocephalus*, and from 200 m.day<sup>-1</sup> to 400 m.day<sup>-1</sup> for *C. acutipinnis*. The FD frequency distribution of all individuals, climbers and non-climbers, captured at Site 1 were not significantly different to the frequency distribution of all individuals captured at Site 2 for the two species (kernel density estimate; h band = 7 days for *S. lagocephalus* and h band = 6 days for *C. acutipinnis*; p>0.1).



Fig. 4: Freshwater duration (FD) frequency distribution and kernel density estimation (Langlois et al., 2012) of fish captured upstream to each dam (i.e. "climbers") located at Site 1 and Site 2 and fish captured downstream to the same dam (i.e. "non-climbers") for *S. lagocephalus* (Fig. 2a-c-e and Fig. 2g-i-k) and *C. acutipinnis* (Fig. 2b-d-f and Fig. 2h-j-l). The grey shaded area (Fig. 2e-f and Fig. 2k-l) represents the standard error of the null model considering both distributions are equal.

#### Selective pressure of the dams on fish morphology

The first axis of the PCA performed on all anatomical variables represented 93% of the total inertia for *S. lagocephalus* and 83% for *C. acutipinnis* (supplementary material Fig. S1). For *S. lagocephalus*, the size corrected measurements for the head width (HW), the perimeter of the inner side of the mouth lip (MOU), and height at mid body (MBH), which are the three selected variables, were not significantly different between climbers and non-climbers at each site (post test of Tukey; p>0.28; Fig.5a-b-c). It means that no difference in morphology was observed, for the selected variables, between climbers and non-climbers. Oppositely these size corrected measurements were significantly different between climbers captured at Site 1 and non-

climbers captured at Site 2 for MOU and MBH (post test of Tukey; p<0.001; Fig.5b-c) but not for HW (post test of Tukey; p=0.06; Fig.5a). The size corrected MOU were smaller when the size corrected MBH were larger for climbers captured at Site 1 compared to non-climbers captured at Site 2 (Fig.5b-c). For *C. acutipinnis*, the size corrected sucker width (SuW) of climbers was significantly larger compared to non-climbers at both site (post test of Tukey; p<0.02; Fig.5d). The size corrected sucker length (SuL) significantly larger for climbers compared to non-climbers at Site 1 (post test of Tukey; p<0.001, Fig.5e) but not at Site 2 (post test of Tukey; p=0.12, Fig.5e). These size-corrected measurements were not significantly different for climbers captured at Site 1 compared to non-climbers captured at Site 2 (post test of Tukey; p>0.34, Fig.5d-e).



Fig. 5: Size corrected head width (HW, Fig4a), perimeter of the inner side of the mouth lip (MOU, Fig4b) and height at mid body (MBH, Fig4c) for *S. lagocephalus* and sucker width (SuW, Fig4d) and length (SuL, Fig4e) for *C. acutipinnis*. Differences of size corrected measurements of each anatomical variables are presented between fish captured downstream (i.e. "non-climbers") and upstream (i.e. "climbers") to the dams at Site 1 and Site 2. The significance of the difference of size corrected measurements of each anatomical variables between group were tested using a post-hoc test of Tukey. n.s : non significant; \* p<0.05,\*\* p<0.01; \*\*\* p<0.001.

#### Discussion

Migration strategies of S. lagocephalus and C. acutipinnis

Sicyopterus lagocephalus juveniles had a faster upstream migration speed than C. acutipinnis juveniles. Indeed, the fastest individuals of S. lagocephalus migrated at approximately

180 m.day<sup>-1</sup> between the river mouth and Site 1 and 500 m.day<sup>-1</sup> between the river mouth and Site 2 when the fastest C. acutipinnis migrated at 140 m.day<sup>-1</sup> and 400 m.day<sup>-1</sup> respectively. This difference in migration speed is consistent with the instantaneous climbing speed estimated experimentally for each species (Keeffe et al., 2017). The net climbing speed on a 20 cm long experimental ramp angled at 70° was 0.10 body length per second (BL.s<sup>-1</sup>) for *S. lagocephalus* when it was only 0.06 BL.s<sup>-1</sup> for *C. acutipinnis*. Interestingly, individuals captured at Site 2 spent the same time traveling along the 20 km from the river mouth than individuals captured Site 1, 7 km from the river mouth. This observation is consistent with the recent finding of Teichert et al. (2018) who hypothesized that individuals present in upstream reaches traveled along the downstream section too fast to have the chemical signature of this portion of river recorded in their otoliths. In addition, S. lagocephalus and C. acutipinnis juveniles captured at Site 2 were 0.2 cm Ls larger than those captured at Site 1 (i.e. 7% and 8% larger for each species respectively). Two hypotheses can explain the observed size difference between the two sites when no difference in age was observed between the two populations. The first hypothesis is that individuals who have a larger size when they arrive in freshwater migrate faster, and more upstream, than those with a smaller size. The size range of S. lagocephalus and C. acutipinnis returning in freshwater is quite important ((Teichert et al., 2012, 2016b) and the largest young juveniles of S. lagocephalus present better climbing performances (Lagarde et al. submitted). This may explain the larger size at age (FD) and the faster colonization speed of individuals observed at Site 2. The second hypothesis is that individuals who grew faster after they arrived in freshwater had better climbing performances and faster migration speed. Faster growing individuals are known to perform better for different functions in many fish species. For example, Takasuka et al. (2003) described a lower predation rate on faster growing larval Japanese anchovy (Engraulis japonicus) which was associated to better predation avoidance performances of these individuals. This second hypothesis is supported by the observation of older S. lagocephalus individuals downstream to the dam at Site 1 compared to upstream when the size frequency distributions were the same. In this situation, these slower growing individuals, i.e. older at an identical size, may not have been performant enough to climb up the dam and remained downstream. In order to disentangle these two hypotheses, further otoliths analyses are required. They will allow back calculating size of individuals when they arrive in freshwater and estimating their freshwater growth trajectories.

Morphological selection of anthropogenic obstacles on S. lagocephalus and C. acutipinnis populations

The selected anatomical variables were not significantly different between climbers and nonclimbers for S. lagocephalus at each site when they were for C. acutipinnis. The absence of difference of the selected anatomical variables between S. lagocephalus climbers and nonclimbers is probably explained by the individuals climbing performances which are probably sufficient to easily pass each dam. Another explanation may be that morphology alone is not sufficient to explain the differences in climbing performances between climbers and nonclimbers. Indeed, other individual traits such physiological profiles (Schoenfuss et al., 2013) or individual behavior (Kemp et al., 2009) can also influence climbing performances. However, a significant selection of fish based on their morphology occurred while they were migrating from Site 1 to Site 2. Sicyopterus lagocephalus non-climbers captured at Site 2 had a larger oral sucker (MOU) and smaller mid body height (MBH) than climbers captured at Site 1. This result is consistent with the observation made experimentally on young juveniles of this species by Lagarde et al. (submitted). These authors observed that larger young juveniles of S. lagocephalus with a large MOU and a small MBH performed better when challenged with an experimental climbing ramp. They hypothesized that a large MOU increases attachment forces, as the oral sucker is used by S. lagocephalus to attach the substratum while moving up, while a small MBH, i.e. a narrow and flat streamlined body, minimizes drag. In this study, juveniles S. lagocephalus were older and bigger than in the study of Lagarde et al. (submitted). In this context, it is not surprising to observe differences in morphologies between non-climbers captured at Site 2 compared to climbers captured at Site 1 similar to these experimentally associated with the successful biggest climbers in Lagarde et al. (submitted).

The selected anatomical variables were significantly different between climbers and nonclimbers for *Cotylopus acutipinnis*. Climbers had a bigger pelvic sucker compared to nonclimbers at both sites as expected based on experimental observations (Lagarde et al. submitted). Interestingly the size corrected sucker length (SuL) was only significantly different between climbers and non-climbers at Site 1. This observation may be explained by the strong selective pressure of the dam at Site 1 which is not equipped with a fish-way and consequently more difficult to pass. This strong selective pressure of the dam at Site 1 may also explain the absence of difference of size corrected sucker width (SuW) and sucker length between *C. acutipinnis* climbers captured at Site 1 and non-climbers captured at Site 2. Indeed, climbers captured at Site 1 already had a morphology associated with better climbing performance. These strong climbing performances were probably sufficient to allow most individuals to migrate from Site 1 to Site 2 without experiencing further significant selective pressure.

#### Implication for management

Previous studies quantifying the impact of anthropogenic obstacles on tropical amphidromous species mainly focused on quantitative comparisons of fish and crustaceans populations between undisturbed and disturbed locations (Holmquist et al., 1998; Cooney and Kwak, 2013; R. Lagarde et al., 2015; Lin et al., 2017). However, this quantification is particularly difficult for Sicydiinae gobies due to their climbing performances which allow individuals to pass waterfalls hundreds meters high (Englund & Filbert, 1997). Due to the climbing performances of Sicydiinae, the impact of anthropogenic obstacles smaller than 10 m on their population is supposed to be weak (Cooney & Kwak, 2013). The assessment of obstacles impacts at the individual level is traditionally performed with telemetry (Lundqvist et al., 2008), or mark recapture studies (Smith and Kwak, 2014). However these methods are difficult or impossible to efficiently use due to the small size of Sicydiinae juveniles (Cooke & Thorstad, 2012), and to the difficulties to efficiently recapture marked individuals (L. Faivre & R. Lagarde, Hydro Reunion, unpublished data). Nevertheless, this study confirmed that the selective pressure of a ca. 10 m high anthropogenic obstacles on individual fish morphology can be qualified. Similar studies may be an efficient alternative to telemetry, or mark recapture, to evaluate the effect of anthropogenic obstacles on small-sized Sicydiinae upstream migration at the individual level (Schoenfuss & Blob, 2007).

Despite the careful design of the fishway located at Site 2, the selective pressure of this obstacle appeared significant on *C. acutipinnis*. The design of the fishway was based on an experiment performed by Voegtlé et al. (2002) who concluded that a 50° longitudinal ramp made of fine concrete was adapted to Sicydiinae. Their experiment was based on evaluation of the climbing success of Sicydiinae on a 4 m long experimental ramp. The integration of fish fatigue during climbing was not taken into account when building the 14 m long ramp at Site 2. Fatigue may explain why the fishway was less efficient for *C. acutipinnis*. One solution to limit fatigue of climbing individuals would be to build a fishway consisting of several ramps, with a maximum length of 4 m, separated by pools allowing fish to recover from the climbing effort. Another solution would be to equip the ramp with a more adapted substrate. A recent experimental study demonstrated that the climbing success of *S. lagocephalus* and *C. acutipinnis* was better on a substrate specially developed for freshwater eels compared to fine concrete (Lagarde et al., 2017). The equipment of existing fishways with these substrates may reduce their selective pressure on migrating juveniles Sicydiinae.

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Fig. S1. Projections of all individuals on the first factorial plan of the principal component analyses performed on the 15 anatomical variables for *S. lagocephalus* (Fig S1. a, b) and *C. acutipinnis* (Fig S1. c, d). PBL : Basal length of the pectoral fin, TaL : Tail length, *Ls* : Standard length, PL : Length of the margin of the pectoral fin, SuW : Sucker width, SuL : Sucker length, HL : Head length, HW : Head width, TrW : Trunk width, HH : Head height, CPH : Height of the caudal peduncle, TrL : Trunk length, MBH : Height at mid body, ABW : Width of the body at the location of the anal pore, MOU : Perimeter of the inner side of the mouth lip

## **5. Discussion générale et perspectives**

# 5.1 Les migrations en eau douce des Sicydiinae, des phases clefs de leur cycle de vie amphidrome ?

Les dynamiques de migration en eau douce des Sicydiinae peuvent réduire le risque de mortalité des individus lors de ces déplacements et, à terme, assurer leur succès reproducteur. Les dynamiques de dévalaison décrites dans le chapitre 2 permettent sans doute de minimiser le temps de dérive des larves et leur risque de mortalité par prédation. La mortalité des larves reste tout de même particulièrement élevée lors de la dévalaison. En effet, Bell (2009) a évalué que le taux de survie des larves de Sicydium punctatum dans trois rivières de La Dominique était de l'ordre de 50% par heure et kilomètre de cours d'eau. Ces mortalités peuvent être imputées aux contraintes liées au développement ontogénique des larves (Bell & Brown, 1995), à d'éventuels piégeages dans des zones lentiques (Valade et al., 2009) ou à la prédation (Lindstrom, 1998). Cependant, des données récemment acquises sur la rivière Langevin, le long d'un tronçon dépourvu de prédateurs potentiels des larves, laissent penser que les taux de mortalités liés à d'autres facteurs que la prédation sont beaucoup plus faibles (Lagarde, 2016; Lagarde & Valade données non publiées). Ces données ont en effet permis d'estimer qu'entre 30% et 50% des larves de Sicydiinae mourraient lors de la dévalaison d'un tronçon de 2,2 km. Le temps mis par les larves pour franchir ce tronçon peut être grossièrement estimé à deux heures. Ceci implique une mortalité des larves entre 15% et 25% par heure et entre 14% et 23% par kilomètre de cours d'eau, soit approximativement la moitié de la valeur avancée par Bell (2009).

Cependant, il est possible que la phase du développement larvaire pendant laquelle le risque de mortalité est le plus important se situe après l'arrivée en mer et non pendant la dévalaison en rivière (McDowall, 2010). Les principales sources de mortalité des larves après leur arrivée en mer peuvent être liées à la prédation et à la disponibilité de leurs proies potentielles. Les abondances de prédateurs potentiels des larves (i.e. petits poisson pélagiques omnivores, petits invertébrés planctonivores...) sont probablement beaucoup plus élevées en milieux côtiers que dans les rivières. Le risque de mortalité des larves due à la prédation y serait donc plus important (McDowall, 2009). Les abondances élevées de larves en dévalaison après la tombée de la nuit observées dans les zones aval des cours d'eau se traduisent sans doute aussi par des abondances plus élevées de larves atteignant la mer pendant la nuit. Le risque de prédation serait alors réduit à court terme, au moins pour ce qui est des prédateurs visuels. Qui plus est, la période du développement larvaire située entre le moment de l'ouverture de la bouche et la résorption des

réserves énergétiques endogènes est une phase critique de la vie larvaire de toutes les espèces de poissons. À ce moment, les taux de mortalités sont particulièrement élevés et, au final, ils peuvent entrainer de fortes fluctuations des abondances de juvéniles (Houde, 2008). En effet, si les larves ne trouvent pas rapidement une source de nourriture exogène pendant cette période, elles risquent d'atteindre un stade de jeûne irréversible (Cushing, 1990; Nunn et al., 2012; Iida et al., 2017). L'ouverture de la bouche et l'essentiel de la résorption des réserves endogènes des Sicydiinae n'ont lieu que lorsque les larves atteignent la mer ou des zones saumâtres (Ellien et al., 2011). Ainsi, la période critique pendant laquelle les larves de Sicydiinae doivent trouver une source de nourriture exogène se déroule en mer.

Les dynamiques de migration et les performances de franchissement d'obstacles des juvéniles après leur arrivée en eau douce ont pour but d'assurer leur succès reproducteur lorsqu'ils seront adultes. La principale période de migration en eau douce se situe pendant l'étiage. Durant cette période, les contraintes liées au déplacement vers l'amont sont sans doute limitées du fait des vitesses moyennes d'écoulement plus faibles. La migration des juvéniles vers les zones intermédiaire et amont présente plusieurs avantages écologiques pour ces espèces. En premier lieu, les abondances de prédateurs et de compétiteurs potentiels accédant à ces zones sont limitées même en l'absence d'obstacles (chapitre 1, Figure 20-1A). Le risque de prédation et la compétition pour l'habitat de croissance devraient donc être plus faibles dans ces zones par rapport à la zone aval. De plus, l'effet des crues sur les populations de Sicydiinae est probablement moindre en amont (Teichert et al., 2018; Figure 20-2A). Mais, d'un autre côté, la saison de reproduction est beaucoup plus étendue dans les zones aval ce qui peut entrainer un nombre d'évènements de reproduction plus élevé pour les individus présents dans ces zones (Teichert et al., 2014b, 2016a; Figure 20-2A). Dans les cours d'eau où un obstacle est situé dans la zone aval, les capacités de franchissement d'obstacles des Sicydiinae leurs permettent d'accéder à la majorité des habitats disponibles pour leur maturation et reproduction (Figure 20B). Les abondances de prédateurs et de compétiteurs potentiels étant plus importantes dans les zones situées en aval des obstacles à la migration (chapitre 1, Figure 20-1A-1B), les risques de prédation et la compétition pour les habitats de croissance sont réduits en amont de ces derniers. Une fois l'obstacle franchi, les avantages pour les Sicydiinae devraient donc être importants. Lorsque les obstacles sont situés dans les zones intermédiaire et amont des cours d'eau (Figure 20C), le lien entre les capacités de franchissement des Sicydiinae et leur succès reproductif n'est pas direct. En effet dans ces zones, les abondances de prédateurs et de compétiteurs potentiels sont limitées même en l'absence d'obstacles (chapitre 1, Figure 20-1A-1C). Pour les individus

de Sicydiinae franchissant un obstacle dans les zones intermédiaire et amont, la réduction du risque de prédation et de la compétition pour l'habitat de croissance n'est donc pas aussi importante que lorsque cet obstacle est situé dans la zone aval.



Figure 20 : Schéma théorique de l'impact des gradients de l'aval vers l'amont des facteurs biotiques (gradients rouges, 1) et abiotiques (gradient vert, 2) sur l'installation, la croissance et la survie des juvéniles et adultes de Sicydiinae ainsi que la reproduction des adultes. Ces impacts sont présentés dans un contexte de bassins versants sans obstacle à la migration (A), de bassins versants où l'obstacle à la migration est situé dans la zone aval (**B**) ou dans la zone intermédiaire **(C)**. Le gradient vert représente l'impact positif de la température à travers son effet sur la saison de reproduction. Les limites des trois zones sont définies à partir des caractéristiques de pente et d'altitude issues du chapitre 1.
La Figure 21 permet de proposer des pistes de réflexions intéressantes concernant les facteurs qui peuvent affecter les populations de Sicydiinae de La Réunion pendant leur phase larvaire en mer et après leur arrivée en eau douce. Les abondances de juvéniles de C. acutipinnis arrivant en eau douce semblent cohérentes avec les abondances de larves en dévalaison trois mois auparavant (Figure 21 B1-B2a-b). A l'opposé, les abondances observées de juvéniles de S. lagocephalus arrivant en eau douce ne correspondent pas aux abondances de larves en dévalaison cinq à sept mois auparavant (Figure 21 A1-A2a-b). Après l'arrivée des juvéniles en eau douce, les abondances d'individus des deux espèces en montaison vers les zones amont (Figure 21 A3, B3) sont globalement cohérentes avec les abondances observées de juvéniles arrivant en eau douce (Figure 21 A2b, B2b). Ceci est particulièrement vraie pour C. acutipinnis puisque les plus fortes abondances de juvéniles en migration vers les zones amont correspondent aux plus fortes abondances de juvéniles qui arrivent en eau douce trois mois plus tôt. En ce qui concerne S. lagocephalus, le lien entre les abondances de juvéniles en migration vers les zones amont et les abondances de juvéniles qui arrivent en eau douce deux mois plus tôt est moins marqué. Les éléments discutés à partir de la Figure 21 doivent tout de même être considérés avec prudence car la variabilité spatiale et temporelle des dynamiques de migration n'est pas ou peu prise en compte dans ce schéma. En effet, la saisonnalité de la dévalaison des larves et de leur arrivée en mer n'a été estimée qu'à partir des observations faites sur la rivière du Mât entre mai 2013 et juillet 2014. Or, la saisonnalité des pics d'abondances de larves en dévalaison peut varier d'une année à l'autre. En effet, les fluctuations interannuelles de température et du débit des rivières peuvent influencer la période de reproduction des Sicydiinae (Teichert et al., 2014b, 2016a, chapitre 2). Comme les abondances de juvéniles arrivant en eau douce ont été estimées à partir d'observation faites entre 2006 et 2011, le lien entre les abondances de larves en dévalaison et celles de juvéniles arrivant en eau douce n'intègre pas cette variabilité temporelle. De plus, d'autres rivières de La Réunion peuvent contribuer à la production larvaire et donc aux abondances de juvéniles qui arrivent dans les rivières de La Réunion (Lord et al., 2012; Teichert et al., 2014a). Il est par contre peu probable que les populations de Sicydiinae de Maurice contribuent significativement aux abondances de juvéniles qui arrivent dans les rivières de La Réunion. En effet, les occurences et abondances de Sicydiinae dans les rivières de cette île sont beaucoup plus faibles qu'à La Réunion (ARDA, 2003). De même, il est possible que les fluctuations temporelles des abondances de juvéniles arrivant aux embouchures (Hoareau, 2005) influencent les abondances de juvéniles qui migrent vers les zones amont. Or, les abondances de juvéniles en migration vers les zones amont ont été uniquement estimées sur le bassin versant de la rivière du Mât et sur une période de 18 mois, entre novembre 2012 et mai 2014.



Figure 21 : Représentation schématique des périodes de fortes (en noire), moyennes (en gris) et faibles (en blanc) abondances de larves dévalaison (1), de juvéniles arrivant en eau douce (2) et de juvénile en montaison (3) vers les zones amont pour *S. lagocephalus* (A) et *C. acutipinnis* (B). Les abondances des larves en dévalaison (1) et des juvéniles qui accèdent aux zones amont (3) sont estimées à partir des résultats des chapitres 2 et 3. Les abondances des juvéniles qui arrivent en eaux douces ont été estimées : à partir des abondances de larves en dévalaison et de la durée de vie en mer des deux espèces (Teichert et al., 2012, 2016b) pour les arrivées en eau douce théoriques (2a), et à partir des observations d'abondances réalisées directement au niveau des embouchures pour les arrivées en eau douce observées (ARDA, 2012 ; 2b). Les temps de vie en mer des larves sont estimés à partir des résultats de Teichert et al. (2012, 2016b). Les temps de vie en rivière des juvéniles avant qu'ils n'atteignent les zones amont sont déterminés à partir des valeurs médianes de durées de vie en rivière estimées dans la troisième étude du chapitre 3. Il doit être noté que ces durées diffèrent des valeurs présentées lors de la première étude du chapitre 3 qui correspondaient à des durées de vie en rivière minimales.

Outre l'effet discuté ci-dessus des variabilités spatiales et temporelles des différentes dynamiques, la diminution de la survie des larves avec l'augmentation de la température de l'eau de mer pourrait expliquer le décalage entre les abondances observées de juvéniles de S. lagocephalus arrivant en eau douce et les abondances maximales de larves en dévalaison de cinq à sept mois auparavant. En effet, la durée qui sépare le moment de l'ouverture de la bouche et celui de la résorption des réserves endogènes, c'est-à-dire la période pendant laquelle les larves doivent trouver une source de nourriture exogène, diminue de manière importante avec l'augmentation de la température chez S. lagocephalus (Figure 22). Ainsi, à 24°C cette durée est de 43 heures alors qu'elle n'est plus que de 33 heures à 30°C ce qui pourrait diminuer leur probabilité de survie. Ces températures sont dans la gamme de températures estimées à partir des analyses des images prises par le satellite NOAA au niveau de La Réunion qui varient de 22 à 30°C sur la période 2000-2018 (NOAA Coral Reef Watch 2000). Qui plus est, Roxy et al. (2016) ont décrit une corrélation négative entre les températures moyennes de surface de l'Océan Indien en été et la concentration en Chlorophylle a entre 1950 et 2012. Ces auteurs ont émis l'hypothèse que des températures de surface de l'océan plus élevées pourraient augmenter la stratification entre les différentes masses d'eau et diminuer les échanges de masses d'eau entre la surface et les zones plus profondes ce qui réduirait la production planctonique. La possibilité pour les larves de trouver une source de nourriture exogène pendant cette phase critique en serait alors d'autant plus réduite.



Figure 22 : Résumé synthétique de l'effet de la température de l'eau de mer sur les durées pour aboutir à l'ouverture de la bouche (**a**), à la résorption des réserves endogènes (**a** et **b**) et à la mort en l'absence de toute nutrition (**c**) chez les larves de *S. lagocephalus* en conditions expérimentales. Adapté à partir du poster présenté par Lagarde et al. lors des 7èmes rencontres de l'ichtyologie en France, Paris, mars 2018 (annexe 5).

Plusieurs hypothèses peuvent expliquer le fait que les plus fortes abondances de juvéniles de S. lagocephalus observées en migration vers les zones amont ne correspondent pas exactement aux plus fortes abondances observés aux embouchures deux mois plus tôt (ARDA, 2012, chapitre 3). Tout d'abord lors des 18 mois de suivi des abondances de juvéniles en montaison vers les zones amont (chapitre 3), des crues cycloniques ont eu lieu au début du mois de janvier. Ces crues ont entrainé une diminution marquée des abondances de juvéniles en montaison, ces derniers n'ayant probablement pas des capacités locomotrices suffisantes pour résister aux courants de crues. Cette hypothèse est cohérente avec les observations de Chen et al. (2015) qui ont décrit une forte diminution des abondances d'une espèce de Cyprinidae, Onychostoma barbatulum, après un typhon dans des rivières de Taiwan. Cette diminution était plus importante pour les individus dont la longueur totale était inférieure à 9,0 cm. Ainsi, la plupart des juvéniles de S. lagocephalus arrivés en rivière après le mois d'octobre n'ont probablement pas pu atteindre la zone amont avant que la première crue cyclonique ne survienne, le temps passé en rivière pour atteindre la zone amont depuis l'embouchure étant généralement supérieur à deux mois. Ceci expliquerait que peu de juvéniles en migration de montaison ont été observés après les crues lors des études du chapitre 3. Un autre élément pouvant expliquer le décalage temporel entre les fortes abondances de S. lagocephalus arrivant en rivière et celles des juvéniles observées en migration vers les zones amont est en lien avec la biologie de la reproduction de cette espèce. En effet, il a récemment été montré (Lagarde et al. soumis, annexe 4) que le temps passé en rivière avant que les femelles de S. lagocephalus ne soient matures est d'environ 4,5 mois celles arrivées en rivière pendant l'hiver austral contre 2,5 à 3,0 mois pour celles arrivées en rivière pendant le reste de l'année. Cette différence de temps de maturation pourrait être la conséquence d'un compromis pour l'allocation des réserves énergétiques à la maturation ou à la migration (McBride et al., 2015). Les individus arrivant en rivière pendant les périodes où leur maturation est rapide, c'està-dire pendant l'été austral, pourraient favoriser l'allocation de leurs réserves énergétique à la reproduction au dépend de leurs déplacements migratoires. Cette hypothèse est cohérente avec les observations de Kinnison et al. (2001, 2003) qui ont démontré que la quantité d'énergie allouée par œuf, ou au développement de caractères sexuels secondaires, était plus faible pour les Saumons Chinook (Oncorhynchus tshawytscha, Walbaum 1792) migrant en amont des rivières par rapport à ceux se reproduisant dans les zones plus en aval. La compétition inter et intra spécifique pour l'accès à l'habitat peut aussi expliquer les dynamiques de migration vers les zones amont des juvéniles de S. lagocephalus. Pendant l'étiage, c'est-à-dire de juillet à décembre, la disponibilité en habitats de croissance et/ou de reproduction est plus faible que pendant les périodes de hautes eaux (Girard et al., 2014a; Teichert et al., 2013b, 2014c). Les

individus arrivant en rivière pendant l'étiage sont donc probablement soumis à une compétition plus intense en particulier dans les zones aval où les abondances de compétiteurs potentiels sont les plus importantes (chapitre 1). De manière similaire, Louca et al. (2009) ont démontré expérimentalement pour le Tilapia de Guinée (*Coptodon guineensis*, Günther 1862) que plus la densité de compétiteurs intra spécifique était élevée dans un bassin, plus les individus avaient tendance à se déplacer vers un autre bassin dépourvu de compétiteurs. En dernier lieu, il est aussi possible que lors des périodes de fortes arrivées en eau douce des juvéniles de *S. lagocephalus* la pression de pêche au niveau des embouchures soit maximale. La proportion d'individus capturés par rapport à ceux accédant aux cours d'eau serait ainsi plus élevée ce qui limiterait les abondances de juvéniles de *S. lagocephalus* pouvant accéder aux zones intermédiaire et amont des cours d'eau pendant ces périodes.

# 5.2 Les capacités de migration en eau douce de *S. lagocephalus*, un avantage compétitif par rapport à *C. acutipinnis* ?

Les abondances de *S. lagocephalus* observées dans les rivières de La Réunion sont beaucoup plus élevées que celles de *C. acutipinnis* (chapitre 1) ce qui semble indiquer une meilleure adaptation de *S. lagocephalus* aux conditions biotiques et abiotiques de ces milieux. L'aire de répartition de *S. lagocephalus* s'étend depuis l'ouest de l'Océan Indien jusqu'à l'est de l'Océan Pacifique (Keith et al., 2005a) alors que *C. acutipinnis* est endémique des îles Maurice et de La Réunion (Keith et al., 2005b). Le succès de la récente expansion de *S. lagocephalus*, il y a moins de 3,5 millions d'années, depuis un centre de spéciation situé à l'ouest de l'Océan Pacifique (Keith et al., 201b) peut en partie être expliqué par la durée élevée de sa période larvaire en mer qui varie de 96 à 296 jours (Hoareau et al., 2007; Teichert et al., 2016b). Cette longue durée de vie en mer contribue probablement à augmenter les capacités de dispersion de l'espèce au stade larvaire et donc la probabilité d'atteindre de nouveaux habitats d'eau douce (Lord et al., 2010). Cependant, la persistance d'une population dans un nouvel habitat est aussi dépendante de la capacité des individus à s'y installer, s'y maintenir, s'y reproduire, puis à y retourner après la phase larvaire en mer (McDowall, 2010). Ces derniers points dépendent fortement des traits d'histoire de vie de l'espèce (Agrawal, 2001; Karjalainen et al., 2016).

Jusqu'à présent, la comparaison des traits d'histoire de vie de *S. lagocephalus* et de *C. acutipinnis* ne permettait pas toujours de mettre en évidence une meilleure adaptation de *S. lagocephalus* aux conditions locales d'habitat par rapport à *C. acutipinnis* (Tableau 3). En

effet, après leur arrivée en eau douce, les deux espèces présentent une faible sélectivité dans le choix de leur habitat de croissance et peuvent donc s'installer dans la plupart des habitats disponibles dans les cours d'eau (Teichert et al., 2014c). Qui plus est, le régime alimentaire de C. acutipinnis semble être plus diversifié que celui de S. lagocephalus (L. Faivre, Hydrô Réunion & G. Gassiole, MicPhyc; données non publiées). Or, la diversité du régime alimentaire peut augmenter la résilience d'une espèce suite aux perturbations d'origines naturelle ou anthropique (Lisi et al., 2018) ce qui devrait donc avantager C. acutipinnis par rapport à S. lagocephalus. De manière similaire, les traits d'histoire de vie concernant la biologie de la reproduction semblent présenter un avantage en faveur de C. acutipinnis : les deux espèces ont des fécondités similaires mais la saison de reproduction de C. acutipinnis, dans une zone donnée, est plus étendue (Teichert et al., 2014b, 2016a) et sa fréquence de ponte probablement plus élevée (Teichert, 2012). Ainsi, dans chaque zone et pendant chaque saison de reproduction, les femelles de C. acutipinnis devraient produire plus d'œufs et de larves que celles de S. lagocephalus. Cependant, la taille à première maturité des femelles de S. lagocephalus est supérieure à celle des femelles de C. acutipinnis (Teichert et al., 2014b, 2016a) et leur temps de maturation après leur arrivée en eau douce est plus court (Lagarde et al. soumis, annexe 4). Ceci permet sans doute aux femelles de S. lagocephalus de s'installer plus vite dans les premiers habitats de reproduction disponibles pour lesquels la sélectivité est marquée (Teichert et al., 2013b). Qui plus est, le temps de maturation plus court des femelles de S. lagocephalus après leur arrivée en eau douce peut aussi leur permettre minimiser leur risque de mortalité à chaque génération lié à des évènements catastrophiques comme les crues cycloniques (Lagarde et al. soumis, annexe 4).

Tableau 3 : Résumé des traits d'histoire de vie en rivière à La Réunion chez *S. lagocephalus* et *C. acutipinnis* issu des études antérieures à mon travail de thèse. Les valeurs en gras sont censées représenter un avantage compétitif d'une espèce par rapport à l'autre.

|              | Traits d'histoire de vie en rivière                  | S. lagocephalus             | C. acutipinnis                |
|--------------|--|-----------------------------|-------------------------------|
| Croissance   | Selectivité de l'habitat                             | Faible                      | Faible                        |
|              | Régime alimentaire                                   | Périphyton                  | Périphyton +<br>invertébrés ? |
| Reproduction | Sélectivité de l'habitat                             | Forte                       | Forte ?                       |
|              | Fécondité  | 13 000 œufs.g <sup>-1</sup> | 15 000 œufs.g <sup>-1</sup>   |
|              | Températures permettant le développement<br>ovarien  | >19 °C                      | >18 °C                        |
|              | Intervalle minimum entre deux évènements<br>de ponte | Un à deux mois ?            | < à un mois ?                 |
|              | Taille à première maturité                           | 44 mm                       | 29 mm                         |
|              | Temps passé en eau douce avant maturation            | <b>2,5</b> à 4,5 mois       | 3,0 à 4,5 mois                |

Les différences de performances locomotrices entre les deux espèces, en particulier pour le franchissement d'obstacles (chapitre 3), peuvent aussi être un avantage compétitif de S. lagocephalus par rapport à C. acutipinnis. Les études du chapitre 3 ont permis de mettre en évidence des similitudes entre les dynamiques de montaison de S. lagocephalus et de C. acutipinnis à l'échelle journalière et saisonnière. Cependant, des différences de performances de franchissement entre les deux espèces ont été observées au laboratoire et en milieu naturel (chapitre 3). Il a ainsi été démontré que S. lagocephalus a des performances de franchissement généralement plus élevées que C. acutipinnis, ce qui peut lui procurer un avantage compétitif marqué. En effet, la colonisation des bassins versants s'effectue à la même saison et au même moment de la journée pour les deux espèces. Les juvéniles des deux espèces se retrouvent donc dans des conditions de température et de débit similaires et les contraintes abiotiques liées au déplacement vers l'amont sont donc semblables pour les deux espèces. De plus, les rivières de La Réunion sont ponctuées de nombreuses chutes d'eau naturelles et/ou d'obstacles anthropiques (DEAL, 2011). Les meilleures performances de franchissement de S. lagocephalus peuvent permettre à une plus grande partie de sa population d'accéder aux habitats de croissance et de reproduction situés immédiatement en amont de ces obstacles par rapport à C. acutipinnis. Même en l'absence d'obstacle à franchir, les vitesses de migration plus élevées des juvéniles de S. lagocephalus peuvent permettre à ces derniers d'atteindre les premiers habitats de croissance

et de reproduction disponibles et de s'y installer avant les juvéniles de *C. acutipinnis*. Qui plus est, la plus grande taille des juvéniles de *S. lagocephalus* après leur arrivée en eau douce les rend sans doute plus compétitifs que les juvéniles de *C. acutipinnis* pour l'accès aux premiers habitats de croissance rencontrés (Teichert, 2012). Si les juvéniles de *S. lagocephalus* atteignent les premiers habitats de croissance plus rapidement que les juvéniles de *C. acutipinnis* et sont plus compétitifs une fois installés dans ces habitats (Figure 23a), les juvéniles de *C. acutipinnis* se retrouvent forcés à migrer plus en amont (Figure 23b). Il ne s'agit que d'hypothèses mais cellesci pourraient expliquer les abondances plus élevées de juvéniles de *C. acutipinnis* en migration vers les zones amont et les biomasses plus importantes d'adultes de cette espèce dans ces zones.



Figure 23 : Schéma théorique de l'effet de la compétition inter spécifique entre les juvéniles de *S. lagocephalus* (**a**) et de *C. acutipinnis* (**b**) sur leurs possibilités d'installation dans les habitats disponibles au sein des bassins versants. Les cercles bleus représentent les habitats de croissance déjà occupés par des adultes d'une des deux espèces, les cercles verts les habitats disponibles pour les juvéniles au sein des bassins versants. Les flèches bleues représentent les déplacements de migration, la flèche rouge l'effet de la compétition inter spécifique et les flèches violettes l'accès des juvéniles à leurs habitats de croissance.

La survie larvaire, que ce soit en eau douce ou après leur arrivée en mer, pourrait être un autre élément pouvant expliquer les différences d'abondances de juvéniles puis d'adultes des deux espèces de Sicydiinae dans les rivières de La Réunion. Cependant, l'impossibilité d'identifier l'espèce des larves à partir de critères morphologiques (Teichert 2012) et la faible proportion de *C. acutipinnis* observée lorsque l'identification de l'espèce a été réalisée à partir d'analyses moléculaires n'a pas permis d'étudier d'éventuelles différences inter spécifiques de dynamique de dévalaison (chapitre 2). A l'heure actuelle, seule l'observation d'un temps de survie en eau douce plus faible des larves de *C. acutipinnis* par rapport à celles de *S. lagocephalus* dans les mêmes conditions de température permet d'émettre l'hypothèse que la mortalité lors de la dévalaison pourrait être plus faible pour *S. lagocephalus* (Teichert, 2012). Toutefois, cette observation a été réalisée à partir d'une seule ponte de *C. acutipinnis*, elle doit donc être considérée avec prudence.

## 5.3 Vers la mise en place de mesures de gestions adaptées aux populations de Sicydiinae de La Réunion

Comme détaillé dans chacun des trois chapitres de cette thèse, plusieurs mesures de gestion adaptées aux populations de Sicydiinae de La Réunion peuvent être préconisées à partir des résultats de mon travail de thèse. Tout d'abord, quatre unités de gestion homogènes des peuplements indigènes de La Réunion, toutes comprenant des Sicydiinae, ont été délimitées. Pour chacune de ces unités de gestion, l'impact des principales pressions d'origine anthropique et donc les préconisations de gestion associées peuvent être différentes (Figure 24).



Figure 24 : Bilan synthétique de (I) l'effet des pêcheries aux embouchures (A1), des réductions de débits dans les zones aval (A2, B2) et des barrages (A3, B1) sur les abondances de juvéniles en montaison (A) et de larves en dévalaison (B) et de (II) l'effet attendu sur ces mêmes abondances des mesures de gestion préconisées sur ces mêmes stades. Les différentes mesures de gestion préconisées sont : l'application de la règlementation existante concernant les pêcheries aux embouchures (II A1), l'augmentation des débits réservés en aval des prélèvements d'eau (II A2 et B2) et la restauration de la continuité biologique au niveau des barrages à la montaison (II A3) et à la dévalaison (II B1). Les flèches bleues représentent les déplacements de migration, les flèches rouges l'effet des impacts anthropiques et les flèches violettes l'accès des juvéniles à leurs habitats de croissance et de reproduction.

Dans les zones des cours d'eau d'altitude et de pente à faibles à intermédiaires (i.e., zones aval et intermédiaire, unités de gestion IA et II du chapitre 1), le nombre d'obstacles physiques à la continuité écologique, en particulier les barrages, est plus faible que dans les zones amont.

Cependant, dans les zones aval et intermédiaires, les effets des prélèvements d'eau en amont, des pollutions diffuses sur l'ensemble du bassin versant (Buttermore et al., 2018) et des interactions entre espèces exotiques et indigènes peuvent être plus marqués (DEAL, 2011, chapitre 1). Dans ces zones, il apparait donc important de favoriser des mesures de restauration physique de l'habitat (Figure 24 A2, B2). Il pourrait par exemple s'agir de restituer un débit plus élevé au niveau des ouvrages de prélèvement d'eau situés en amont, voire de mettre en place des régimes de restitution du débit (Lamouroux et al., 2016). Cette dernière solution présente à la fois l'avantage d'augmenter la disponibilité en habitats en aval des barrages pendant des périodes clefs du cycle de vie amphidrome comme la reproduction et la dévalaison, mais aussi de réguler les populations des petites espèces exotiques telles que les Guppys. En effet, Fitzsimons et al. (1997) ont démontré expérimentalement que les Guppys n'ont pas les capacités de nage suffisantes pour résister aux vitesses de courant élevées, contrairement aux Sicydiinae. Malgré le fait qu'aucune interaction n'ait été observée à l'échelle du bassin versant ou du site entre les abondances de Guppy et celles de juvéniles et adultes d'espèces indigènes (chapitre 1), il est possible, comme suggéré par Walter et al. (2012), que la prédation des Guppys sur les larves des espèces amphidromes indigènes en dévalaison soit importante. Peu d'études portant sur l'impact de la prédation par les Guppys dans les petites îles tropicales existent, seuls Englund (1999) et Englund et Polhemus (2001) ont décrit leur impact négatif sur des populations de libellules endémiques d'Hawaii. Or, la faible taille des larves de Sicydiinae et leur comportement de nage leur permettant de se maintenir proche de la surface (Valade et al., 2009) les rendent probablement encore plus sensibles à la prédation par les Guppys et les autres Poeciliidae que le sont les larves d'insectes.

Dans les zones d'altitude et de pente élevées des cours d'eau (i.e. zones amont, unité de gestion III du chapitre 1) l'effet des prélèvements d'eau est moins marqué, les barrages sont en effet généralement situés en aval ou au sein de ces zones. Par contre, comme les abondances d'adultes de Sicydiinae sont parfois élevées dans les zones amont (chapitres 1 et 3), il semble nécessaire de mettre en place des mesures de gestion permettant de limiter les quantités de larves emportées avec l'eau prélevée (Figure 24 B1). La mesure qui est apparue la plus pertinente jusqu'à présent est de réduire les débits prélevés pendant les mois de janvier et février (chapitre 2). Cette recommandation présente aussi l'avantage d'augmenter le débit dans les tronçons situés en aval des barrages et ainsi d'accroitre la disponibilité en habitat pendant la saison de reproduction (Girard et al., 2014a). Cependant, cette recommandation se base sur des observations faites pendant une seule saison de reproduction, de mai 2013 à juillet 2014, et sur

le seul bassin versant de la rivière du Mât. L'efficacité d'une réduction des prélèvements d'eau pendant les mois de janvier et février sur différentes rivières de l'île, et sur plusieurs années doit donc encore être évaluée. Quoiqu'il en soit, la prise en compte de la dévalaison des larves dans les projets de restauration de la continuité écologique au niveau des barrages apparait prioritaire. Jusqu'à présent la restauration de la dévalaison des larves n'était pas prise en compte faute de recommandations techniques permettant la mise en place de mesures cohérentes (Valade et al., 2004, arrêté préfectoral N°2015-2624/SG/DRCTCV définissant les tronçons de cours d'eau pour lesquels la continuité écologique doit être restaurée). Dans ce contexte, la démarche qui parait être la plus pragmatique est de préconiser, dans un premier temps, la mise en place d'arrêts ciblés des prélèvements d'eau sur les barrages identifiés comme étant les plus impactant pour la dévalaison des larves (Teichert et al., 2014a). Dans un deuxième temps, des suivis de l'efficacité de cette mesure de gestion pourront permettre d'affiner les périodes des arrêts ciblés de prélèvement d'eau, voire de proposer d'autres mesures de gestion. Ces mesures pourraient par exemple consister à la mise en place de barrières physiques, comme des grilles à espacement inter barreaux inférieur à 0,25 mm ou des cloisons de surface, permettant de rediriger les larves présentes dans les décanteurs vers un exutoire de dévalaison. Des tests préalables d'efficacité et de faisabilité de ces mesures devront tout de même être réalisés. Enfin, les suivis de l'efficacité des arrêts ciblés de prélèvement d'eau permettront d'améliorer la connaissance de la variabilité spatiale et temporelle de la dynamique de dévalaison des larves ainsi que des facteurs pouvant l'influencer. C'est cette démarche qui est en cours à l'heure actuelle au niveau du barrage hydroélectrique de la rivière Langevin (Lagarde, 2016; Lagarde & Valade données non publiées). Il est possible que la mortalité des larves lors du passage au travers des installations de cet aménagement (barrage de prélèvement, décanteurs, conduites d'amenées et turbines) ne soit pas plus élevée que la mortalité naturelle en rivière entre le barrage et la zone de restitution de l'eau. Pour ce barrage, il apparaitrait donc plus pertinent de développer d'autres mesures de gestion de l'eau prélevée mieux adaptés à la restauration de la dévalaison des larves. Il pourrait ainsi être préconisé de limiter les temps de séjours dans les décanteurs et/ou de réduire les vitesses de rotation des turbines plutôt que d'arrêter les prélèvements d'eau. Enfin, malgré les abondances élevées de Sicydiinae, en particulier C. acutipinnis, observées en amont des barrages (chapitres 1 et 3), les études menées lors du chapitre 3 ont démontré l'impact négatif des deux barrages, situés à 7 et 22 km de l'embouchure de La Rivière du Mât, sur la dynamique de migration de C. acutipinnis (Figure 24 A3). Pour ces barrages, il apparait indispensable d'adapter les passes à poissons existantes, ou d'en construire de nouvelles mieux dimensionnées pour permettre leur franchissement par l'ensemble ou, à minima par une majorité, des juvéniles de C. acutipinnis en

montaison. Il pourrait par exemple être envisagé de réduire la pente des rampes spécifiques pour les Sicydiinae, de les équiper de substrats plus efficaces que le béton lisse (Lagarde et al., 2017) ou encore d'installer des bassins de repos intermédiaires permettant aux juvéniles de fractionner l'effort nécessaire au franchissement des rampes. Enfin, tout comme pour la dévalaison des larves, des suivis de passes à poissons similaires à ceux réalisés dans le chapitre 3 devraient permettre d'améliorer les connaissances de la phénologie de la montaison des juvéniles, d'évaluer l'efficacité des nouvelles passes à poissons et, le cas échéant, d'affiner les recommandations de gestion ou de dimensionnement de ces dernières.

En ce qui concerne la quatrième unité de gestion homogène, c'est-à-dire les zones aval à forte pente (unité IB du chapitre 1), il est difficile de préconiser des mesures de gestions adaptées à l'ensemble de l'unité de gestion. Seul un site sur la rivière Langevin et un sur la ravine Saint Gilles sont inclus dans cette unité de gestion et il apparait donc plus pertinent de réfléchir à des mesures de gestion pour chacun de ces sites. Ainsi, si la limitation de la fréquence et de l'amplitude des variations de débit d'origine anthropique apparait adaptée pour améliorer la gestion de la dévalaison des larves au niveau du site de la rivière Langevin (chapitre 2), cette mesure n'est absolument pas adaptée au site de la ravine Saint Gilles puisque les variations de débit d'origine anthropique sont faibles voire inexistantes.

Enfin, les zones d'embouchures apparaissent comme une priorité pour la gestion des espèces amphidromes en général et des Sicydiinae en particulier. En effet, toutes les larves écloses au sein de l'ensemble des unités de gestion doivent franchir une embouchure avant d'arriver en mer. De manière similaire, les juvéniles devant accéder aux différentes zones des bassins versants sont dépendants d'un franchissement aisé de l'embouchure. La gestion des débits prélevés sur le bassin versant est un point clef pouvant affecter à la fois les quantités de larves atteignant la mer et celles de juvéniles retournant dans les cours d'eau. Sur de nombreuses rivières de La Réunion, des infiltrations d'eau importantes peuvent être observées au niveau des embouchures. Dans certains cas, ces infiltrations peuvent entrainer des périodes d'assèchement total des cours d'eau (DEAL, 2011). Ces périodes d'assèchement sont plus ou moins étendues en fonction des bassins versants et de l'hydrologie annuelle. Lorsque cet assèchement est proche de l'embouchure voire à l'embouchure, aucune larve ne peut rejoindre la mer et aucun juvénile ne peut accéder au cours d'eau ce qui a un impact majeur sur les dynamiques de migration de ces stades. Il apparait donc primordial de restituer un débit suffisant au niveau des barrages afin de supprimer, ou, tout au moins, de limiter la durée d'assèchement des embouchures. En outre,

Delacroix (1987) a décrit une relation positive entre le débit des cours d'eau et les abondances de juvéniles arrivant en eau douce. Cette relation pourrait être due à une plus grande emprise spatiale de la plume d'eau douce en mer qui faciliterait l'orientation des individus ayant terminé leur phase larvaire vers les embouchures de cours d'eau (Crivelli et al., 2008). Enfin, la généralisation à l'ensemble des bassins versants d'actions visant à diminuer l'impact des pêcheries de bichiques, comme celles entreprises au niveau de la rivière du Mât (Ocea Consult' & FPTBRM, 2015; Ocea Consult' & PPEE-RDM, 2015), pourrait permettre d'augmenter significativement les abondances de juvéniles accédant aux bassins versants (Figure 24 A1). Toujours au niveau des pêcheries, il pourrait aussi être intéressant d'évaluer leur sélectivité en fonction de la morphologie des juvéniles. Il est par exemple possible, que seuls les individus *S. lagocephalus* les plus fins puissent passer à travers les mailles des engins de capture utilisés (vouves). Or, les individus ayant une largeur de la tête élevée présentent des fortes performances de franchissement. Ainsi, la sélectivité de la morphologie des individus par les pêcheries aux embouchures pourrait affecter les dynamiques de migration en eau douce des juvéniles.

### 5.4 Intérêts de la mise en place de suivis long terme des flux migratoires des Sicydiinae

La généralisation du suivi des abondances de larves en dévalaison et de juvéniles arrivant en rivière pourrait permettre de mieux décrire les facteurs biotiques et abiotiques pouvant influencer les populations de Sicydiinae de La Réunion (Figure 25). Les estimations d'abondances de larves en dévalaison pourraient se faire au niveau des embouchures selon les mêmes méthodes que celles décrites dans le chapitre 2. Idéalement plusieurs embouchures des principaux cours d'eau de La Réunion devraient être suivies avec une fréquence mensuelle voire hebdomadaire pendant les mois de janvier et février. Les observations d'abondances de juvéniles arrivant dans les rivières devraient se faire en dénombrant les quantités prélevées par les pêcheurs traditionnels aux embouchures (Bell, 1999). La comparaison des distributions d'abondances de larves en dévalaison et de juvéniles revenant en eau douce (Figure 25-1-2), pourrait permettre de mettre en évidence les sources de mortalités lors du développement larvaire jouant un rôle prépondérant sur les abondances de juvéniles arrivant en rivière. Par exemple, il serait intéressant de vérifier si les larves arrivant en mer lors des périodes de fortes abondances de leurs proies potentielles ont un taux de survie plus élevé et donc participent de manière plus importante aux quantités de juvéniles arrivant en rivière, comme discuté lors du premier paragraphe de la discussion générale. Pour ce faire, il faudrait aussi mettre en place des suivis d'abondances de Chlorophylle a et de proies planctoniques dans les zones côtières de La Réunion. En ce qui

concerne l'abondance de Chlorophylle a et la composition du phytoplancton, ces paramètres sont déjà suivis trois fois par an (en juillet/août, novembre/décembre et février/mars) dans le cadre du Réseau Hydrologique Littorale de La Réunion (RHLR, Duval et al. (2015)). Ces suivis pourraient donc aisément être complétés, en profitant des moyens de navigation du RHLR, afin de mieux cibler les zones proches des embouchures des principales rivières. Des campagnes complémentaires pourraient aussi être mises en place en janvier et février afin de décrire plus précisément les fluctuations d'abondances de Chlorophylle a et de composition du phytoplancton pendant la période principale d'arrivée des larves en mer. En ce qui concerne les suivis d'abondances et de composition du zooplancton, des moyens spécifiques seraient à mettre en œuvre (Mackas & Beaugrand, 2010), aucun échantillonnage spécifique du zooplancton n'étant réalisé dans le cadre du RHLR. Ces suivis d'abondances de Chlorophylle a et de proies planctoniques apparaissent particulièrement importants car la synchronicité entre la période d'éclosion des larves de plusieurs espèces de poissons dont les larves se développent en mer et l'abondance de leur proies (phyto et/ou zooplancton) a souvent été reliée à leur taux de survie et, in fine, aux abondances de juvéniles et d'adultes (Cushing, 1990; Fortier et al., 1995; Brander et al., 2001). Cependant à ma connaissance aucune étude n'a démontré ce lien pour des espèces amphidromes tropicales. L'intégration de modèles de courantologie marine (Crochelet et al., 2016) pourrait être une piste complémentaire pour interpréter les éventuels décalages entre les abondances de larves arrivant en mer et celles de juvéniles en eau douce. En effet les courants marins peuvent être une source importante d'expatriation des larves loin de leurs rivières natales, en particulier pour les premières étapes du développement larvaire chez lesquelles les capacités de nage sont très limitées (McDowall, 2010). Ainsi, des changements de courantologie marine pourraient entrainer une absence de relation entre les abondances de larves arrivant en mer et celles de juvéniles arrivant en eau douce alors que la disponibilité des proies pour les larves est optimale.



Figure 25 : Préconisations de suivi des flux migratoires des Sicydiinae de La Réunion. 1) Suivi des abondances de larves en dévalaison ; 2) suivi des abondances de juvéniles arrivant aux embouchures et 3) suivi des abondances de juvéniles en migration vers les zones intermédiaire et amont. Le nombre de bassins versants et la localisation des lieux de suivi des abondances de juvéniles en migration vers les zones intermédiaire et amont ne sont présentés qu'à titre illustratif.

La mise en place de suivis des abondances de juvéniles en montaison au niveau de quelques passes à poissons pilotes réparties parmi différents bassins versants pourraient permettre de confirmer la robustesse des résultats présentés au chapitre 3 (Figure 25-3). Idéalement, ces suivis devraient se faire à partir de piégeage d'individus ou de suivis vidéos (Boussarie et al., 2016). Cependant la faible taille des juvéniles de Sicydiinae implique que les mailles des pièges doivent être très fines (i.e, de l'ordre du mm) et le colmatage de ces derniers impose une fréquence de relève élevée (L. Faivre, Hydrô Réunion, données non publiées). Les moyens humains à mettre en place seraient donc importants. Les suivi vidéos peuvent se faire à faibles moyens humains, cependant, à l'heure actuelle l'identification de l'espèce à partir de vidéos reste impossible pour les juvéniles de Sicydiinae (G. Boussarie, Ecole Normale Supérieure de Lyon, données non publiées). La méthode d'estimation des abondances de juvéniles de Sicydiinae dans une passe à poissons décrite dans le chapitre 3 présente une alternative intéressante pour évaluer ces abondances de manière plus ponctuelle. La fréquence de mise en place de ces suivis de passes à poissons devrait être à minima mensuelle. La comparaison des distributions d'abondances de juvéniles arrivant en rivière et celles observées en migration vers les zones intermédiaire et amont quelques mois plus tard pourrait en particulier permettre de mieux décrire le rôle des fluctuations du régime hydrologique dans la dynamique de montaison des juvéniles de Sicydiinae.

Sur le long terme, la mise en place de tous ces suivis devrait aussi permettre de décrire les effets potentiels du réchauffement climatique sur les populations des Sicydiinae. La poursuite de l'augmentation de un à deux degrés de la température du sud-ouest de l'Océan Indien observée entre 1960 et 2010 et liée au réchauffement climatique (Alory et al., 2007; Dong & McPhaden, 2016) pourrait avoir des impacts contrastés sur le développement larvaire et les taux de mortalités à ce stade. Par exemple, Teichert et al. (2016b) ont décrit une augmentation des taux de croissance en mer des larves de S. lagocephalus d'environ 0.07 mm.jour<sup>-1</sup> et une diminution de leurs durées de vie en mer d'environ 70 jours lorsque la température moyenne rencontrée pendant l'ensemble de la phase larvaire augmentait de 24 à 28°C. L'augmentation des taux de croissance en mer et la diminution de la durée de la phase larvaire marine liées à l'augmentation des températures pourrait réduire leur risque de mortalité pendant ce stade. En effet, les taux de mortalité des larves de poissons se développant en mer sont en général plus faibles lorsque leur croissance est élevée et bien que ces taux diminuent avec l'âge des larves ils restent généralement non nuls pendant l'ensemble de la phase larvaire (Houde, 1989). Des études pluriannuelles de durées de vie et de la croissance en mer des larves, basées sur l'interprétation des microstructures des otolithes, en relation avec les abondances de juvéniles arrivant en eau douce pourraient permettre de confirmer ou au contraire d'infirmer cette hypothèse. Cependant, l'augmentation de la température des océans pourrait aussi diminuer les taux de survie des larves au début de leur développement en mer. En effet les températures des océans plus élevées peuvent réduire la durée de la phase critique pendant laquelle les larves doivent trouver une source de nourriture exogène. Le réchauffement de un à deux degré des températures moyennes de l'air observé depuis 1960 à La Réunion (Vincent et al., 2011) pourrait se traduire par une augmentation de la température des cours d'eau. Cette augmentation de la température des cours d'eau pourrait avoir un effet direct sur la biologie de la reproduction des Sicydiinae. Les individus devraient ainsi trouver des conditions favorables à la reproduction dans la zone intermédiaire une majeure partie de l'année (Teichert et al., 2014b, 2016a). Cette extension de la saison de reproduction dans la zone intermédiaire pourrait entrainer une modification des dynamiques de dévalaison des larves. Les proportions de larves dévalant avant et après les mois de janvier et février dans les zones intermédiaire et aval seraient sans doute plus élevées. Enfin, Webster et al. (2005) ont observé que le nombre de cyclones d'intensité forte et très forte (i.e, catégories 4 et 5) avait doublé dans

le sud-ouest de l'Océan Indien entre les années 1975-1989 et 1990-2005 ce qui devrait accroitre le risque de crues exceptionnelles lié au réchauffement climatique à La Réunion. Vincent et al. (2011) ont quant à eux décrit une augmentation du nombre maximum de jours consécutifs sans précipitation de deux jours par décade sur certaines stations météorologiques de La Réunion entre 1961 et 2008 ce qui peut se traduire par des d'étiages plus marqués. L'augmentation de la fréquence et de l'intensité des crues et des étiages pourrait affecter les dynamiques de dévalaison des larves et de montaison des juvéniles vers les zones intermédiaire et amont. Toutes ces hypothèses ne pourront être confirmées que si les changements de température et du régime hydrologique des cours d'eau, induits par le réchauffement climatique, peuvent être mis en relation avec les dynamiques de migration des Sicydiinae sur plusieurs années voire dizaines d'années.

#### 5.5 Perspectives de recherche

Les études de ma thèse ont permis de mettre en évidence la phénologie et certains mécanismes à l'origine des dynamiques de migration en eau douce des Sicydiinae de La Réunion. Ces résultats apportent des éléments de compréhension concernant les stratégies de déplacement sous-jacentes et permettent ainsi de mieux décrire leur cycle de vie amphidrome. Cependant afin d'avoir une vision plus précise du lien entre ces dynamiques et le succès reproducteur des espèces voire des individus au sein d'une même espèce, plusieurs points doivent encore être éclaircis.

Dans un premier temps, les études de ma thèse n'ont pas permis de comparer les dynamiques de dévalaison inter spécifique en eau douce (chapitre 2). Étant données les fortes proportions de larves de *S. lagocephalus* identifiées à partir de méthodes moléculaires, il est probable que la phénologie de la dynamique de dévalaison de cette espèce soit proche de celle observée. Ainsi, il apparaitrait important de focaliser les études à venir concernant la dynamique de dévalaison des larves de Sicydiinae de La Réunion sur *C. acutipinnis*. Pour se faire, il faudrait cibler des cours d'eau dans lesquels la proportion d'adultes de *C. acutipinnis* est importante, comme la rivière des Marsouins, et/ou accentuer l'effort d'identification à partir de méthodes moléculaires afin d'identifier des effectifs de *C. acutipinnis* suffisamment élevés. Ces études pourraient permettre de comparer les dynamiques saisonnière et journalière de dévalaison des larves de Sicydiinae. De plus il serait intéressant de confirmer les observations faites par Teichert (2012) concernant les temps de survie en eau douce plus faibles des larves *C. acutipinnis* par rapport à *S. lagocephalus*. Idéalement il faudrait aussi étendre ces études à la durée des

différents stades de développement après l'arrivée des larves de *C. acutipinnis* en mer comme présenté Figure 22 pour *S. lagocephalus*.

Un autre élément indispensable pour comprendre les fluctuations des abondances de juvéniles arrivant en rivière est de décrire le caractère obligatoire ou facultatif de la migration des larves de Sicydiinae entre l'eau douce et la mer. Plusieurs études ont démontré qu'une partie de la populations de certaines espèces de gobies amphidromes pouvaient réaliser leur développement larvaire dans des zones où la salinité est inférieure à celle de l'eau de mer voire en eau douce (Hogan et al., 2014; Huey et al., 2014). Dans le cas particulier des Sicydiinae, Smith et Kwak (2014a) ont estimé, à partir d'analyse de microchimie des otolithes, que 12% des 70 Sicydium spp. étudiés avaient réalisé leur développement larvaire uniquement en eau douce. Chez S. lagocephalus, le développement larvaire ne peut se faire que si les larves sont dans des milieux où la salinité est comprise entre plus de deux et 35 (Ellien et al., 2011). Ainsi dans les rivières sans zone d'estuaire, la migration des larves en mer serait obligatoire. Teichert et al. (2018) ont démontré, à partir d'analyse de microchimie des otolithes, que l'ensemble des 176 individus de S. lagocephalus échantillonnés dans la rivière Saint Etienne, une rivière sans zone d'estuaire (Figure 26), avaient réalisé leur développement larvaire en mer. Cependant des populations de Sicydiinae se reproduisent dans des rivières possédant une zone d'estuaire voire dans les affluents des étangs côtiers. Dans ces étangs la salinité peut varier de un à six (ANTEA, 2001; ARDA, 2007). Il est possible que les larves puissent réaliser l'intégralité de leur développement dans ces zones lentiques d'embouchure sans avoir besoin de migrer en mer. Des études de microchimie des otolithes d'individus capturés dans ces rivières et étangs pourraient permettre de vérifier cette hypothèse. Dans le cas où tout ou partie des larves peuvent réaliser leur développement dans les zones d'estuaires ou dans les étangs, les mesures de gestion prises pour restaurer et préserver les populations d'espèces amphidromes devront être spécifiques à chaque rivière ou étang.



Figure 26 : Photographie de l'embouchure de la rivière Saint Etienne en août 2012. Crédits photos : Raphaël Lagarde.

La question de la migration des larves entre les milieux côtiers et pélagiques reste non résolue (Closs et al., 2013). Ceci est en partie due à la difficulté de capturer des larves d'espèces amphidromes en milieu pélagique (Watanabe et al., 2011). Une méthode pour échantillonner des larves, alternative aux engins de capture de différents types généralement utilisés en milieux pélagique, serait l'étude des contenus stomacaux des petits prédateurs pélagiques. Étant donné que les larves de Sicydiinae mesurent entre 2 et 37 mm pendant leur phase marine (Valade et al., 2009; Teichert et al., 2012, 2016b) elles ne seront probablement pas identifiables visuellement dans les contenus stomacaux et il sera alors nécessaire de recourir à des méthodes d'identification moléculaire. L'observation de larves de Sicydiinae dans les contenus stomacaux des petits prédateurs pélagiques pourrait permettre de localiser des zones où la présence de ces larves est la plus fréquente. Ces zones pourraient alors être interprétées comme les lieux de croissance larvaire en mer. Plus proche des côtes, il pourrait être judicieux de réaliser des échantillonnages de méso-planctons dans les plumes d'eau douce pendant les périodes principales de dévalaison des larves. Ces échantillonnages pourraient être réalisés à partir des mois de janvier/février et jusqu'à ce que les plumes d'eau douce ne soient plus détectables visuellement avec une fréquence hebdomadaire le premier mois puis mensuelle. Cependant un effort important de calibration des méthodes d'échantillonnage devra être réalisé, ce type d'échantillonnage n'ayant, à ma connaissance, jamais été réalisé pour des espèces amphidromes. L'observation de larves de Sicydiinae dans les plumes d'eau douce pourrait permettre de décrire les étapes du développement larvaire qui peuvent se dérouler à proximité des côtes.

Après leur arrivée en rivière, les juvéniles de Sicydiinae vont avoir différents comportements migratoires qui peuvent en partie s'expliquer par leurs performances locomotrices. Seuls les individus ayant les meilleures performances locomotrices vont pouvoir accéder aux zones amont (chapitre 3). La qualification des impacts liés aux obstacles d'origine anthropique n'a pas pu être réalisée dans les études du chapitre 3. Les différences significatives de morphologies observées entre les juvéniles de *C. acutipinnis* qui ont réussi à franchir les barrages étudiés et ceux présents en aval peuvent s'interpréter par une sélectivité marquée des barrages. Ainsi, seuls les individus ayant une morphologie associée à des fortes performances de franchissement d'obstacles ont pu franchir les barrages. Cependant la proportion de ces individus par rapport au nombre total de juvéniles se présentant en aval des barrages n'a pas pu être estimée ce qui ne permet pas de qualifier leurs impacts. La qualification de l'impact des obstacles pourrait se faire à partir de deux approches complémentaires. La première consisterait à utiliser des méthodes d'estimation directe de la proportion d'individus réussissant à les franchir. Ce type

d'étude peut être réalisé à partir de captures et marquages d'individus en migration en aval des obstacles et de recaptures des individus marqués immédiatement en amont. Une seconde solution pourrait être de mesurer d'autres traits fonctionnels que les traits morphologiques pouvant être liés au comportement de franchissement d'obstacles. Il pourrait par exemple s'agir de comparer des marqueurs écophysiologiques (quantités de réserves énergétiques, de métabolites...) entre les individus présents en aval de l'obstacle et ceux l'aillant tout juste franchi. Ainsi, en théorie, pour un obstacle ayant un impact fort, la majorité des traits fonctionnels mesurés différera entre les individus ayant les capacités de franchissement nécessaires pour le franchir et ceux présents en aval (Tableau 4). A l'opposé, seuls quelques traits fonctionnels différeront entre les individus de ces mêmes groupes pour un obstacle d'impact modéré voire aucuns pour un obstacle d'impact faible (Tableau 4).

Tableau 4 : Exemple théorique des différences de certains traits fonctionnels entre les individus ayant réussi à franchir un obstacle et ceux présents en aval chez *C. acutipinnis* en fonction du niveau d'impact de l'obstacle. + trait de valeur plus élevée pour les individus ayant réussi à franchir l'obstacle par rapport à ceux présents en aval ; - trait de valeur moins élevée et = aucune différence de trait

| Trait fonctionnel |  | Obstacle à impact<br>faible | Obstacle à impact<br>modéré | Obstacle à impact<br>fort |
|-------------------|--|-----------------------------|-----------------------------|---------------------------|
| Morphologie       | Longueur de la ventouse                      | =                           | =                           | +                         |
|                   | Largeur de la ventouse                       | =                           | +                           | +                         |
| Physiologie       | Quantité de glycogène<br>dans les tissus     | =                           | =                           | -                         |
|                   | Concentration de lactate<br>dans les muscles | =                           | +                           | +                         |

Cependant la question de l'intérêt écologique de la migration vers les zones amont reste entière. En effet, à l'heure actuelle les connaissances sur les espèces de Sicydiinae de La Réunion sont insuffisantes pour évaluer finement le succès reproducteur des individus présents dans différentes zones des bassins versants. Dans un modèle théorique de dynamique des populations de *S. lagocephalus*, Artzrouni et al. (2014) ont évalué que l'un des paramètres clefs dans la démographie de cette espèce est l'espérance de vie. En effet, plus les individus sont âgés plus le nombre de fois où ils auront pu se reproduire est grand et plus leur biomasse et fécondité seront élevées (Teichert et al., 2014b). Or, comme discuté précédemment, les risques de mortalité par prédation ou liés aux crues sont plus faibles dans les zones amont ce qui devrait se traduire par une espérance de vie plus élevée dans ces zones (chapitre 1, Teichert et al. (2018)). Cependant la saison de reproduction est plus étendue dans les zones aval (Teichert et al., 2014b) et donc pour un âge donné, les individus des zones aval auront eu l'occasion de se reproduire plus fréquemment. Afin d'évaluer finement l'effort de reproduction des individus présents dans différentes zones il faudrait pouvoir évaluer le nombre d'évènements de reproduction au cours de leur vie afin de calculer la fécondité réelle. Ceci nécessite de pouvoir estimer l'âge des individus adultes, or à l'heure actuelle, la détermination de l'âge n'a pu être réalisée que pour des individus n'ayant que quelques mois de vie en rivière (Lagarde et al. soumis, annexe 4). Au-delà de ces premiers mois les marques de croissances journalières ne sont plus distinguables sur les structures calcifiées et les différences de croissance saisonnières sont difficilement interprétables (Teichert & Lagarde, données non publiées). Des efforts importants de développements méthodologiques restent donc à faire pour résoudre ce problème. Il pourrait par exemple être intéressant d'utiliser des méthodes directes d'estimations de l'âge des individus basées sur un premier marquage des poissons et des otolithes puis sur des recaptures des individus et marquages successifs des otolithes (Panfili et al., 2002). Le marquage des poissons pourrait se faire à l'aide de tags alphanumériques pour les jeunes adultes. Celui des otolithes pourrait se faire à partir de marqueurs fluorescents (Lagarde et al. soumis, annexe 4). Cette méthode nécessite cependant un effort de terrain très important afin de marquer une quantité d'individus suffisante pour assurer une probabilité élevée de recapture. Une deuxième méthode pourrait être basée sur d'éventuelles variations saisonnières de la concentration de certains éléments chimiques dans l'eau. Dans ce cas, une analyse de la variation de la concentration de ces mêmes éléments dans les otolithes pourrait mettre en évidence des patrons saisonniers et ainsi permettre d'estimer l'âge des poissons. Cependant cette méthode nécessiterait aussi un effort de terrain très important pour caractériser les variations saisonnières des concentrations des éléments cibles dans l'eau en plusieurs points du ou des bassins versants cibles et sur plusieurs années.

Pour finir, les éléments discutés dans ma thèse sont issus principalement des connaissances acquises sur les traits d'histoire de vie et les stratégies écologiques des Sicydiinae de La Réunion. La très large aire de répartition de *S. lagocephalus* (Keith et al., 2005a) associée à des différences marquées de structure génétique entre les populations de l'ouest de l'océan Pacifique, de la Polynésie, des Comores et des Mascareignes (Lord et al., 2012) pourrait permettre de vérifier la variabilité locale des traits d'histoire de vie de cette espèce. En effet, il est probable que les traits

d'histoire de vie de *S. lagocephalus* aient évolué différemment pour chacune de ces populations en réponse aux spécificités des habitats marins et d'eau douce des différentes îles (Winemiller & Rose, 1992). Il apparait ainsi très intéressant de réaliser, en différents points de la zone de répartition de cette espèce, des études similaires à celles qui ont été faites à La Réunion concernant la variabilité des traits d'histoire de vie en mer (Teichert et al., 2012, 2016b), les préférences d'habitat de croissance (Teichert et al., 2014c) ou de reproduction (Teichert et al., 2013b), la biologie de la reproduction (Teichert et al., 2014b, 2016a) et les stratégies de migration (chapitres 2 et 3). Il serait aussi intéressant d'acquérir les mêmes connaissances simultanément pour les espèces de Sicydiinae endémiques vivant en sympatrie avec *S. lagocephalus* dans ces différentes localités. La comparaison des traits d'histoire de vie entre les espèces endémiques et *S. lagocephalus* pourrait permettre de mettre en évidence quels facteurs peuvent expliquer le succès écologique de *S. lagocephalus* à large échelle. Ceci devrait aussi apporter des éléments de compréhension des mécanismes à l'origine de l'endémisme pour les espèces amphidromes tropicales.

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# Annexes

## Annexes 1 :

Teichert N, Valade P, Fostier A, Lagarde R & Gaudin P (2014). Reproductive biology of an amphidromous goby, Sicyopterus lagocephalus, in La Réunion Island. Hydrobiologia. 726: 123–141. PRIMARY RESEARCH PAPER

## Reproductive biology of an amphidromous goby, *Sicyopterus lagocephalus*, in La Réunion Island

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**Abstract** In the Indo-Pacific region, rivers are inhabited by amphidromous gobies. They are often subjected to a heavy fishing pressure, highlighting the urgent need to acquire knowledge on their biology for management purposes. This study investigated the reproductive strategy of *Sicyopterus lagocephalus*, a widespread amphidromous goby, in two rivers of La Réunion Island. Histological observations of ovarian samples and oocyte-size frequency distributions revealed that females had a group-synchronous ovarian follicle development (i.e., two cohorts of oocytes were distinguished simultaneously in ovaries). Females laid an entire clutch in a unique event (from 14,304 to 232,475 eggs) and then another batch of oocytes was recruited, showing that the annual fecundity is indeterminate.

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N. Teichert · P. Gaudin INRA, UMR ECOBIOP, INRA/UPPA, Pôle d'Hydrobiologie de l'INRA, Quartier Ibarron 64 310, St Pée sur Nivelle, France Ovarian growth was isometric at all oocyte development stages showing that the gonadosomatic index (GSI) is a good proxy of reproductive condition. The main reproductive season of *S. lagocephalus* spanned from early February to May with a narrower range upstream and a wider one downstream. Reproduction activity is mainly restricted by water temperatures in upstream areas, whereas it is likely influenced by female body condition and competition in downstream areas. The variability of reproductive traits leads to size structure variation in stocks of spawning females throughout the year.

**Keywords** Amphidromy · Gobiidae · Ovarian development · Reproductive strategy · *Sicyopterus lagocephalus* · Spawning pattern

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#### Introduction

In tropical and sub-tropical islands of the Indo-Pacific region, the short and oligotrophic rivers are inhabited by fish assemblages exhibiting singular life histories (McDowall, 1997), such as amphidromous gobies (Keith, 2003; McDowall, 2004, 2010). These fish spawn in rivers, then immediately after hatching, larvae drift down to the sea where they grow as pelagic larvae. After a few months, they return into rivers where they complete their growth and sexual maturation until reproduction (McDowall, 2007; Keith et al., 2008). Some amphidromous gobies are able to colonize mid- to upper-reaches of rivers thanks to strong climbing abilities, as described in Hawaiian gobies (e.g., Blob et al., 2006; Schoenfuss & Blob, 2007; Keith et al., 2008). However, they are likely to be affected by habitat modifications due to human activities (e.g., Lord & Keith, 2008; Jenkins et al., 2009; Ramírez et al., 2012) and post-larvae are often subjected to massive fisheries at the river mouths, as observed in La Réunion, Philippines, Hawaii, Dominica, or French Polynesia (e.g., Aboussouan, 1969; Delacroix & Champeau, 1992; Bell, 1999). Given these threats, developing the knowledge about the biology and ecology of amphidromous gobies is urgently needed for management requirements. Life history traits are still poorly understood in many amphidromous gobies, despite the economic importance of some species (e.g., 30-40 €/kg for Sicyopterus lagocephalus fry on La Réunion Island). Knowledge on reproductive traits is essential to improve conservation approaches based on direct (i.e., identification of critical sizes or seasons) and indirect ways (e.g., estimation of annual egg production).

According to life history theory, the species traits, shaped by natural selection, tend to optimize the reproductive success of individuals depending on the environmental conditions encountered by populations (Stearns, 1992; Andersson, 1994). Murua & Saborido-Rey (2003) define the reproductive strategy of a species as "the overall pattern of reproduction common to individuals, whereas the reproductive tactics are those variations in response to fluctuations in the environment". Fish reproductive strategies are greatly different depending on the species and can be described by the association of multiple life history traits, such as mating system, sexual preferences,

parental care, fecundity, spawning patterns, and others (e.g., Balon, 1984; Murua & Saborido-Rey, 2003; Teletchea et al., 2009). Some amphidromous gobies are semelparous (i.e., spawn once and die; Caputo et al., 2003; Keith, 2003) but the majority are iteroparous (i.e., show several sexual cycles) (e.g., Manacop, 1953; Daoulas et al., 1993; Ha & Kinzie, 1996; Yamasaki et al., 2011; Iida et al., 2013). Freshwater gobies inhabiting tropical and sub-tropical islands usually show an extended reproductive season, as observed in Sicyopterus lagocephalus (Manacop, 1953), Lentipes concolor (Kinzie, 1993), Sicydium punctatum (Bell et al., 1995), or Awaous guamensis (Ha & Kinzie, 1996). Conversely, Sicyopterus japonicus living at temperate latitudes of Japan shows a relatively short-spawning season, suggesting that temperature is a determining factor in the reproduction timing and duration (Iida et al., 2011, 2013). Iteroparous species display either a group-synchronous or an asynchronous ovarian follicle development (Murua & Saborido-Rey, 2003), which is a major component of the spawning strategy of each fish species (Murua et al., 2003). Group-synchronous oocyte development is often exhibited by species with determinate fecundity, i.e., species for which the number of oocytes destined to be matured in a reproductive season is decided prior to the onset of spawning (Hunter et al., 1992; Murua & Saborido-Rey, 2003). Conversely, asynchronous oogenesis (i.e., oocytes at all development stages exist in the ovary without a majority of any group of oocytes at a specific stage of oogenesis) is often observed in females with indeterminate fecundity (Murua & Saborido-Rey, 2003). This supposes that unyolked oocytes from the standing stock can continue to be recruited for vitellogenesis, then are spawned during the whole spawning season, mainly depending on individual physiological conditions and environmental cues (Alonso-Fernández et al., 2008; Gordo et al., 2008; Wootton & Fletcher, 2009).

A good knowledge of major reproductive traits such as ovarian development and spawning pattern is required for a proper estimation of fecundity (Murua et al., 2003). Similarly, demographic traits, such as size-at-first-maturity, spawning frequency, or the organization of spawning groups are essential components to evaluate the spawning stock biomass which strongly affects population dynamics (Lowerre-Barbieri et al., 2009, 2011). Traditional methods to describe the reproductive cycle of fish are based on histological observation or on indices established to estimate gonadal maturation (e.g., Brown-Peterson et al., 2007; Lowerre-Barbieri et al., 2011; Nunes et al., 2011). The gonadosomatic index (GSI) is commonly used because of ease of use. However, the use of GSI requires a preliminary validation due to fish size-dependence and changes in ovarian allometry depending on the species (see, e.g., Somarakis et al., 2004; Plaza et al., 2007). Therefore, for management purpose, an accurate description of a species reproductive strategy often requires several approaches.

Sicyopterus lagocephalus is the most widespread amphidromous goby, living from the Western Indian Ocean to the Eastern Pacific (Berrebi et al., 2005; Lord et al., 2009, 2012). Adults measure between 4 and 13 cm. They inhabit the short and oligotrophic coastal streams of continents and islands where they feed on micro-algae that cover the river substratum (Bielsa et al., 2003). The spawning season extends over most of the year, with a short pause in reproductive activity during the cooler months, as observed in the Philippines (Manacop, 1953). In La Réunion Island (southwest Indian Ocean), this goby dominates the fish assemblages and represents a major economic activity for local fishermen (e.g., Aboussouan, 1969; Delacroix, 1987; Delacroix & Champeau, 1992). Reproductive biology of this species remains poorly documented (Delacroix, 1987; Bielsa et al., 2003; Teichert et al., 2013a), especially concerning its oogenesis and spawning patterns, type of fecundity and spatial variation of reproductive activity. Such knowledge is essential to develop accurate management plans, especially those based on spawning stock biomass estimates or on models of population

dynamics. The purpose of this study was to provide an exhaustive framework of knowledge about reproductive strategy of females of Sicyopterus lagocephalus. Though male investment in reproduction is generally underestimated (Dewsbury, 1982), we chose to focus only on female reproductive traits, because they are assumed to be a major limitation in egg production for most fishery management studies (Murua & Saborido-Rey, 2003; Murua et al., 2003). Fecundity, size-atfirst-maturation, ovarian organization, and development index were investigated, based on histological observation of ovary of females collected in La Réunion Island's rivers. Then, the temporal and spatial variability of reproductive activity and of spawning populations were investigated based on GSI after a validation process.

#### Materials and methods

Sample collection and biological parameters

Samples were collected during two different field campaigns in two rivers of La Réunion Island (Fig. 1). Fish caught in Marsouins River were used to estimate



Fig. 1 Map of La Réunion Island located Southwest Indian Ocean and geographical distribution of fishing sites (stations) for *Sicyopterus lagocephalus* along Langevin and Marsouins rivers

| River     | Location               | Sampling design   | Specifications    | Number of females | Purpose of sample   |
|-----------|------------------------|---|-------------------|-------------------|---|
| Marsouins | Station A              | Once a month between Jan. 2011<br>and Jan. 2012 (13 sampling dates) | Total sample      | 557               | Length-at-maturity  |
|           |                        |   | Histological obs. | 482               | Ovarian organization  |
|           |                        |   | OW > 0.01 g       | 371               | Ovarian allometry   |
|           |                        |   | Mature gonad      | 390               | Reproductive timing   |
|           |                        |   | GSI > 7           | 78                | Batch fecundity   |
|           |                        |   | April excluded    | 66                | Batch fecundity   |
|           |                        | Jan. 2011   | Histological obs. | 20                | Homogeneous<br>development<br>between gonad parts                           |
|           | Station B              | Jan. 2012   | GSI > 7           | 33                | Batch fecundity   |
| Langevin  | Station 1              | Twice a month between Jan 1999<br>and Feb 2000 (27 sampling dates)  | Total sample      | 888               | Spatial variability of<br>reproductive timing<br>and spawning<br>population |
|           | Station 2              |   | Total sample      | 864               |   |
|           | Station 3<br>Station 4 |   | Total sample      | 868               |   |
|           |                        |   | Total sample      | 747               |   |

Table 1 Fishing sites and sampling effort for Sicyopterus lagocephalus in Marsouins and Langevin rivers

OW wet ovary weight

length-at-maturity and fecundity. Histological observation of gonads was used to describe the ovarian allometry and organization (Table 1). After checking the relevance of taking GSI for a proper estimation of the ovarian development, we used historical unpublished data on GSI collected in Langevin River to describe the spatial variability of reproductive timing and of the spawning populations, only based on GSI.

In Marsouins River, fish were collected every month between January 2011 and January 2012 (Table 1), on a mid-stream zone (Station A) located at 2.2 km from the river mouth (Fig. 1). The water temperature was continuously recorded (Tinytag Aquatic 2, precision <0.2°C). A minimum of 50 samples of about 1 m<sup>2</sup> following the Point Abundance Sampling method (PAS, Persat & Copp, 1990) were performed by electrofishing (portable electrofisher IG200/2D, HANS GRASSL GmbH, Germany), randomly distributed in the station in order to take into account the available habitat diversity (Scholten, 2003). After fishing, a length-stratified sampling procedure was performed to collect 30 mature females (all sizes available,  $\geq$ 45 mm, based on Delacroix (1987) observations) and 10-immature females (<45 mm). Sampling took place in the morning (7:30-10:00 am) and fish were kept alive till their euthanasia, 3-6 h after fishing, and dissection in the laboratory. Due to logistical constraints, fish caught in April 2011 were anesthetized and euthanatized with eugenol immediately after sampling prior to fixation in 4% formaldehyde. As formalin treatment causes mass alteration, these females were excluded from analyses based on weight. In January 2011, another sample of 20 females was randomly caught in Station A to confirm that stages of development of oocytes were homogeneous within the ovary after histological observation of various ovarian parts. In January 2012, a complementary fishing was performed in the upper reaches at 16.5 km from the river mouth (Station B, Fig. 1) to collect 30 mature females for estimating their fecundity (Table 1).

For each fish, total length (TL  $\pm 1$  mm), wet total body weight (BW  $\pm 1$  mg), wet ovary weight (OW  $\pm 1$  mg), and wet liver weight (LW  $\pm 1$  mg) were recorded. Condition factors *K* were calculated as follows:  $K = BW TL^{-3}$ . Gonadosomatic and hepatosomatic indices were calculated as the ratio of gonad (OW) or liver (LW) weight to body weight (BW), respectively, according to the following formula: index = (W BW<sup>-1</sup>) × 100, where index = gonadosomatic index (GSI) or hepatosomatic index (HSI) and W = weight of the respective variable (i.e., OW and LW). In fish, the HSI is often considered as a good proxy of lipid reserves, which may influence the gonad maturation of females (Yoneda et al., 1998).

In Langevin River, fish were sampled twice a month by electrofishing (Portable DEKA 3000, Germany) between January 1999 and February 2000, on four stations located throughout the upstream–downstream gradient (i.e., 0.01, 1.0, 3.0, 6.5 km from the river mouth; Fig. 1). Water temperature was continuously recorded in stations located in the highest and lowest altitudes, i.e., stations 1 and 4, respectively (Tinytag Transit Aquatic TG-3100, precision <0.2°C). Fishing was performed until about 30 mature females ( $\geq$ 45 mm) were caught per station. Fish were kept alive till the day after fishing for anesthesia with a lethal dose of eugenol (clove oil), because dissection on fresh biological material could not be performed on the fishing spot. For each fish captured in Langevin River, total length (TL ± 1 mm), wet total body weight (BW ± 1 mg), wet ovary weight (OW ± 1 mg) were recorded, and GSI was calculated.

#### Histological classification of females

Histological observation of ovary tissues was only performed for fish sampled in the Marsouins River (Table 1). Ovarian tissues were fixed in Dietrich solution (30 ml 95% ethanol, 10 ml formalin, 2 ml glacial acetic acid, 58 ml distilled water) during 7 days minimum (i.e., between 7 and 15 days), then embedded in paraffin, sectioned to 7 µm thickness, and stained with hematoxylin and eosin Y, following standard histological procedures. Histological sections were photographed under microscope (×100) at random positions. In a first step, sections from six parts of the ovary (anterior, middle, and posterior part of both right and left ovaries) of 20 females were observed (i.e., fish randomly caught in Marsouins River, station A, January 2011). No difference could be found in maturation stage within each ovary and between the right and left gonad, thus only sections of the mid-part of the left or right ovary were used for histology. Four development stages of oocytes have been identified (Brown-Peterson et al., 2007): primary growth (PG, chromatin nucleolar, and perinucleolar stages-small size oocyte with large nucleus and many nucleoli at the periphery), cortical alveoli (CA, cortical alveoli in the periphery of nucleus and cytoplasm), early vitellogenic (EVO, yolk is incorporated form small yolk globules within the peripheral ooplasm), and vitellogenic oocytes (VO, yolk globules, and droplets increase in number and size and fill the entire ooplasm). Other ovarian components, such as hydrated oocyte (characterizing final oocyte maturation before ovulation), postovulatory follicles (POF) and attretic oocytes were looked for and recorded when present. Histological classification of the ovaries was performed according to the maturation stage of the most advanced batch of oocytes, the presence of POF or other post-spawning evidence (e.g., Ganias et al., 2004; Alonso-Fernández et al., 2008; Brown-Peterson et al., 2011). Six reproductive phases were identified on females, according to the Brown-Peterson et al. (2007) classification revised for S. lagocephalus (Fig. 2). The immature phase corresponds to females that have never spawned (Fig. 2a). The developing phase is the period of gonadal growth prior to the beginning of the spawning season, characterized by the production of vitellogenic oocytes (Fig. 2b). The spawning capable phase is marked by the presence of advanced oocyte development and refers to females being capable of spawning within the current reproductive cycle (Fig. 2c). At the spent phase, late hydrated oocytes or post-ovulatory follicles are present in ovaries and suggest a recent spawning (Fig. 2d). The regressing phase is characterized by high prevalence of atresia in ovaries and indicates the end of the reproductive cycle (Fig. 2e). The regenerating phase is defined as the fish sexually mature but reproductively inactive and is characterized by presence of primary growth oocytes, late-stage atresia, and a thicker ovarian wall than is seen in immature fish (Fig. 2f). Gonad of early recruited stages were too small to perform histological sections (i.e., post-larval stages 2 and juvenile stage 1, see Keith et al. (2008) for detailed features of these stages), so they were directly observed under microscope for sex checking and fish were classified as immature.

#### Ovarian organization analysis

The statistical analyses were performed using the R software (R Development Core Team, 2011). The oocyte size measurements were performed on photographs of histological section of fish from Marsouins River, using the ImageJ 1.42 software (Rasband, 2012). In order to test the homogeneity of oocyte size between the six parts of 20 fish gonads previously used to check the maturation stage similarity (Table 1), a random sample of 30 most advanced stage oocytes per ovarian part was measured ( $\pm 0.1 \mu m$ ), based on the Feret's diameter (i.e., longest distance between any two points along the selection boundary). Since two-way analysis of variance (ANOVA) showed no significant differences between ovaries ( $F_{(1, 3594)} = 0.383, P = 0.53$ ) or between ovarian parts ( $F_{(2, 3594)} = 0.034, P = 0.96$ ) and no significant interaction  $(F_{(2, 3594)} = 0.169)$ ,



PG : Primary growth oocyte, CA : Cortical alveolar oocyte, EVO : Early vitellogenic oocyte, VO : Vitellogenic oocyte, POF : Post-ovulatory follicles, ATS : Atresia stages

| Reproductive phases  | Histological features  |    |  |
|--|--|----|--|
| Immature<br>Never spawned  | Primary growth oocytes only, including chromatin nucleolus stage (small cells with large nucleus), and initial perinucleolar stage (larger oocytes). No evidence of prior spawning (no atresia). Well-organized gonad.               |    |  |
| Developing<br>Gonads beginning to<br>develop, will no spawn soon | Following oocytes stages may be present in gonad : primary growth, cortical alveolar, and/or early vitellogenic. No evidence of POFs.  | b) |  |
| Spawning Capable<br>Fish will spawn in this cycle                | Vitellogenic oocytes present. Some atresia may be present. Mid and late vitellogenic oocytes prevalent without evidence of previous spawning. Less-developed oocytes often present.  | c) |  |
| Spent<br>Recent spawning   | Late hydrated oocytes or post-ovulatory follicles present. Less developed oocytes often present.   | d) |  |
| Regressing<br>Cessation of spawning                              | Atresia present (any stage). Vitellogenic oocytes undergoing alpha or beta atresia comon. Less developed oocytes often present.  | e) |  |
| Regenerating<br>Sexually mature,<br>reproductively inactive      | Primary growth oocytes present, including chromatin nucleolar and perinucleolar stage. Some cortical alveolar may be present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma, delta atresia may be present. | f) |  |

Fig. 2 Ovarian histology showing the features and oocytes stages used to discriminate six reproductive phases in *Sicyopterus* lagocephalus female:  $\mathbf{a}$  immature,  $\mathbf{b}$  developing,  $\mathbf{c}$  spawning capable,  $\mathbf{d}$  spent,  $\mathbf{e}$  regressing, and  $\mathbf{f}$  regenerating

P = 0.84), measurements were routinely performed on sections of the mid-part of the ovaries. The Feret's diameters of all oocytes with a visible nucleus contained within a quadrat (500  $\times$  500  $\mu$ m) randomly placed on micrograph were measured ( $\pm 0.1 \mu m$ ). This process was repeated until a minimum of 30 oocytes measured per fish was reached. When counting a quadrat was started, all oocytes within the quadrat were measured to respect the relative occurrence of oocyte size in ovaries. The relative size frequency distribution of oocytes was examined by 25-µm interval classes and calculated according to the following equation:  $Freq_i = N_i / N_{tot}$ , where  $Freq_i$  = relative oocyte size occurrence of the class i,  $N_{\text{tot}} = \text{total number of oocytes } (N_{\text{tot}} = \sum N_i)$ , and  $N_i$  = corrected number of oocytes of the class i. The number of oocytes  $(N_i)$  was corrected to account for the overcount due to the presence of split particles in multiple sections (Abercrombie, 1946; Von Bartheld, 2002; Kopiejewska & Kozlowski, 2007), as follows:  $N_i = n_i$ .Th/(Th +  $D_i$ ), where  $N_i$  = corrected number of oocytes of the class i, Th = section thickness,  $D_{\rm i}$  = arithmetic mean of 30 random nucleus diameters of oocytes of the class i, and  $n_i$  = number of crosssections of oocytes of the class i. This correction factor was related to the nucleus diameters of oocytes (i.e., Di) because the measured oocytes were sampled according to their nucleus position within the quadrat (inside or outside) and because the nucleus diameter increased with the oocyte diameter. For each developmental stage of oocytes, 150 oocyte diameters were measured randomly to define the range of variation.

#### GSI and ovarian allometry

We examined whether GSI and body weight were independent from females caught in Marsouins River (Table 1). The traditional assumption for a valid GSI is that the slope of the relationship  $\log(BW) = \log(a) + b \log(OW)$  is not significantly different from 1 in the different maturity stages (e.g., Somarakis et al., 2004). Individuals were ranged by 75 µm intervals of mean diameters of the five largest oocytes measured in the ovaries (i.e., <75, 75–150, 150–225, >225 µm), which can be considered as proxies of oocyte development stages (West, 1990; Plaza et al., 2007). Then, *t* tests were used to test for isometry (*b* = 1) and analysis of covariance (ANCOVA) to test for homogeneity of slopes among oocyte-size classes (Somarakis et al., 2004; Plaza et al., 2007). The relationship between the log-transformed GSI and average diameters of the five largest oocytes in the ovaries was examined using linear regression (F test). For these analyses, females with ovary weight <0.01 g were excluded due to imprecision of measurements.

#### Length at first maturation

Length-at-maturity was defined for females caught in Marsouins River because histological observations provided accurate information on reproductive phases (Table 1). Nonparametric Kruskal–Wallis test (KW) was used to compare the body size of females between the sampling months. Females were considered immature when only primary growth oocytes were present in ovaries and there was no evidence of prior spawning activity (Fig. 2). After attained sexual maturity, a fish never can exit the reproductive cycle and return to the immature phase. A logistic generalized linear model (GLM) was used to examine female maturity according to the total length and sampling month (Alonso-Fernández et al., 2008; Lowerre-Barbieri et al., 2011). Mature females were categorized as 1, whereas the other females were categorized as 0. Significant effects of month and its interaction with total length (i.e., based on sequential analysis of deviance, Chi square test) denote that size at first maturation was not constant throughout the year. Length-at-maturity  $(L_{50})$ was considered as the length at which 50% of females (P = 0.5) were mature according to the logistic model (Lowerre-Barbieri et al., 2009).

#### Batch fecundity estimation

Fecundity was estimated using a gravimetric method (Murua et al., 2003) for Marsouins River females with GSI > 7 (Table 1). This threshold was chosen because at this developmental stage the oocytes of a spawning batch can be undoubtedly segregated from unyolked oocytes according to their sizes (see "Results" section). Fixed ovaries used for counting were weighted ( $\pm 0.01$  mg) and three 3–5 mg subsamples ( $\pm 0.01$  mg) were randomly removed from the right or left ovaries (the other gonad being kept for histology). Subsamples were placed in a Petri dish with distilled water, and then oocytes were manually segregated and photographed under binocular microscope with an attached camera. A semi-automated particle counting procedure was used to estimate the number of oocytes,

based on a standard binary-image-analysis (e.g., Klibansky & Juanes, 2008; Ganias et al., 2010, 2011). A size-threshold was applied to exclude the batch of non-spawning oocytes from counting. It corresponded to the critical size at which a gap between the more advanced oocytes and the smaller oocytes was clearly evident (Ganias et al., 2010). The automated counting procedure was completed by visual check of micrographs to detect potential mistakes. For each female, the coefficient of variation (CV) was calculated. ANCOVAs were used to test for relationships between batch fecundity, sampled station (mid-stream/upstream), and body weight (BW), or total length (TL, log-transformed). The relative number of maturing oocytes per gram of body weight was compared between the first (Oct, Nov, Dec, Jan, Feb) and the second (Mar, Apr, May, June, July) parts of the spawning season, using a t test of Student. The grouping was chosen to ensure a sufficiently large number in each group for a reliable analysis (n > 30). As fish sampled in April were fixed in formaldehyde, they were excluded from analyses based on weight.

#### Spawning females and their reproductive timing

In Marsouins River, the reproductive timing was only estimated from mature females (immature females were excluded, because their number was dependent on the sampling design). Nonparametric Kruskal–Wallis tests (KW) were used to analyze the fluctuations of GSI, HSI, and *K* according to sampling dates. Pearson's correlation coefficients were used to examine the relationships between the GSI and HSI and mean water temperatures prior to samplings. Logistic regressions were used to test the relationship between the probability for an ovarian cycle initiation (i.e., female at developing, spawning capable, or spent reproductive stages in Marsouins River) and water temperature.

In Langevin River, since ovarian histology was not performed, a threshold value of GSI was defined to segregate the spawning females from the inactive ones. We considered that females with a GSI higher than 2 had initiated an ovarian growth (see "Results"). To test the hypothesis of ovarian growth synchronism according to the stations and the sampling dates, we modeled the probability that a female initiated an ovarian spawning cycle (i.e., active female) using a logistic GLM (Lowerre-Barbieri et al., 2009, 2011). This approach allowed analyzing the relationship between a binary response variable (in this case active/inactive females) as a function of a set of explanatory variables (Dobson, 2001). Spawning females (GSI  $\geq$  2) were categorized as 1, whereas other females were categorized as 0. We tested whether each variable (i.e., date, station) and their interaction (date × station) explained a significant amount of independent variation, based on the significant reduction of residual deviance compared to the previous model (Chi square test; Dobson, 2001). Significant effects of explanatory variables reflect temporal and/or spatial variation of ovarian growth probabilities among mature females. The sizes of females caught in Langevin River were compared between stations using a Kruskal-Wallis test and post hoc pairwise comparisons were performed using a Steel-Dwass-Chritchlow-Fligner test (Hollander & Wolfe, 1999).

#### Results

In Marsouins River, 557 females were collected (from 36 to 48 fish per month) and ovarian histology was performed on 482 of them (Table 1). A complementary sampling in the upstream station (Station B) allowed to collect 33 matures females for fecundity estimation. In Langevin River, 3,367 matures females of *S. lagocephalus* were sampled in the four stations (19–66 fish per site and sampling date).

#### Ovarian allometry

For females caught in Marsouins River, ovary weight was significantly related to body weight (ANCOVA,  $F_{(1, 363)} = 165.35, P < 0.001$ ) with a high coefficient of determination  $(r^2)$  in all advanced-oocyte-size classes (Table 2, n = 371, ovaries weighing <0.01 g excluded). The intercepts were significantly different among oocyte size classes (ANCOVA,  $F_{(3, 363)} =$ 835.48, P < 0.001). The slopes b were homogeneous for all classes (ANCOVA,  $F_{(3, 363)} = 0.35$ , P > 0.05) and did not differ significantly from 1 (Table 2, all P < 0.05), showing an isometric relationship between BW and OW. The log-GSI was strongly related to the mean diameter of the five largest oocytes measured  $(F_{(1, 369)} = 3,245.6, P < 0.001)$ , reflecting that the GSI was a great proxy of oocyte development stage in the S. lagocephalus ovaries (Fig. 3).

**Table 2** Summary of allometric relationships [log (BW) = log  $(a) + b \log$  (OW)] between ovary weight (OW) and body weight (BW) for each size-class of the five largest oocytes in the ovaries of *Sicyopterus lagocephalus* collected in Marsouins River (N = 371)

| Oocyte-size classes<br>(µm) | Log<br>(a) | b    | п   | r <sup>2</sup> | t    | Р    |
|-----------------------------|------------|------|-----|----------------|------|------|
| <75                         | -4.65      | 1.00 | 98  | 0.78           | 0.07 | 0.95 |
| 75–150                      | -4.06      | 1.00 | 102 | 0.85           | 0.08 | 0.94 |
| 150-225                     | -2.92      | 0.94 | 98  | 0.76           | 1.07 | 0.29 |
| >225                        | -2.14      | 0.98 | 73  | 0.92           | 0.45 | 0.65 |

Probabilities (P) and t statistics for the isometry hypothesis are shown. n Sample size,  $r^2$  coefficient of determination



**Fig. 3** Linear relationship between the Gonadosomatic index (GSI, log-transformed) and the mean diameter of the five largest oocytes (DLO,  $\mu$ m) in the ovaries of *Sicyopterus lagocephalus* collected in the Marsouins River. The equation of linear relation is presented with their associated coefficient of determination ( $r^2$ ) (female number = 371)

#### Ovarian organization

Primary-growth oocytes were found in all ovarian histology of females caught in Marsouins River and their diameters ranged from 11 to 69  $\mu$ m (random sample of PG oocytes, n = 150, Fig. 4). Cortical alveolar oocytes ranged from 49 to 122  $\mu$ m (random sample, n = 150) and were also present in all ovaries, except in those of immature females. Early vitellogenic oocytes (diameters ranging from 78 to 182  $\mu$ m, random sample, n = 150) were present in all ovaries, except in both immature and regenerating females, whereas vitellogenic oocytes (diameters ranging from



**Fig. 4** Oocytes size frequency distribution (25- $\mu$ m intervals) in ovaries according to the gonadosomatic index (GSI) class by 1-step, for *Sicyopterus lagocephalus* collected in the Marsouins River (female number = 482). Only size-classes with frequencies >0.01 are plotted. *Boxplots* present the median, the lower and upper quartile, and the minimum and maximum values of oocyte diameter ( $\mu$ m) related to the four developmental stages of oocytes: *PG* primary growth, *CA* cortical alveoli, *EVO* early vitellogenic, *VO* vitellogenic (*n* = random sample of 150 oocytes for each stage)

119 to 325  $\mu$ m, random sample, n = 150) were observed only in spawning-capable and several regressing females. Early vitellogenic oocytes were detected in 60% of spent ovaries, which suggests that several oocyte cohorts could successively grow during the reproductive season. No vitellogenic oocytes remain in regenerating females showing that growing oocyte cohorts were not conserved for the next season.

For females caught in Marsouins River, the frequency distribution of oocyte size according to the GSI revealed that *S. lagocephalus* exhibits a group-synchronous ovarian follicle development (female number = 482, Table 1). Two cohorts of oocytes were distinguished in the ovaries: a synchronous population of larger oocytes and a population of smaller oocytes from which the maturing batch was recruited (Fig. 4). At the beginning of a new ovarian spawning cycle, the recruitment of a new batch of oocytes to the stage of final growth started at the cortical alveolar stage (oocyte diameter > 75 µm) and for a GSI ranging between 1 and 4 (Fig. 4). Moreover in this study, we considered that a value of GSI  $\geq$  2 was a satisfactory threshold to discriminate females that have initiated an ovarian

| 1 0               | · · · ·           | •           |        |
|-------------------|-------------------|-------------|--------|
| Factor            | Residual deviance | df residual | Р      |
| nul               | 680.33            | 556         | -      |
| month             | 654.54            | 544         | 0.01   |
| TL                | 62.68             | 543         | <0.001 |
| $TL \times month$ | 36.34             | 531         | 0.01   |

**Table 3** Results of length-at-maturity analysis for *Sicyopterus lagocephalus*, based on logistic GLM with total length (TL) and sampling month (month) as explanatory variables

 $\chi^2$  probabilities were calculated compared to the previous model. Values in bold are significant *P* values

growth from the inactive ones. From oocyte size > 125  $\mu$ m (GSI > 4), the oocyte size-frequency distribution was interrupted by a distinct hiatus, which clearly separated the batch of growing oocytes from the other ones. As ovary ripening progressed, the size of yolked oocytes increased (i.e., vitellogenic oocytes), whereas the smaller oocytes (i.e., PG and CA) temporally remained <100 µm. Among the most developed ovaries (GSI > 14), the relative frequencies of oocytes at both a cortical alveolar and an early vitellogenic stage (i.e., 75-125 µm) increased, suggesting that a new process of recruitment was initiated (Fig. 4). Hydrated oocytes were never observed among females sampled in the Marsouins River, except for a few non-ovulated hydrated oocytes in some spent ovaries. Females seemed to lay the entire clutch of developed oocytes only once, since no advanced yolked or even mature oocytes remained in spent ovaries (Fig. 2d). The incidence of atresia in ovaries was very low throughout the reproductive season, and then, increased at the end of the season (i.e., June–July, see below).

#### Length at first maturation

All *S. lagocephalus* females sampled in the Marsouins River (station A) were used to estimate the length-atmaturity (n = 557, Table 1). There was no significant differences in the body size of females among sampling months (KW test, df = 12, K = 5.95, P = 0.91). The L<sub>50</sub> varied significantly between the sampling months (Table 3): values ranged between 43.6 mm TL in March and 55 mm TL in August (Fig. 5).

#### Fecundity



**Fig. 5** Length-at-maturity ( $L_{50}$ , mm) of *Sicyopterus lagocephalus* female according to the sampling month in Marsouins River between January 2011 and January 2012, based on a logistic regression analysis (female number = 557)

spawning batch is clearly segregated from smaller oocytes (Fig. 4). We only counted the oocytes larger than 150 µm to exclude the less developed oocytes (i.e., PG and CA stages). The fecundity was estimated for 111 females of S. lagocephalus in the Marsouins River (n = 78 for station A and n = 33 for station B, Table 1); it ranged from 14,304 to 232,475 eggs. The mean coefficient of variation between subsamples was 0.047 (range 0.006–0.122). The fecundity (Fig. 6) was strongly related to both female total body length  $(ANCOVA, n = 111, F_{(1, 107)} = 1,998.91, P < 0.001)$ and female body weight (ANCOVA,  $n = 99, F_{(1, 95)} =$ 2,088.45, P < 0.001; females sampled in April being excluded from the analysis) and was not significantly different between stations (ANCOVAs,  $F_{(1, 107 \text{ or } 95)}$ ranged from 0.01 to 2.73, all P > 0.05 for the main effect of station and its interaction with TL or BW). The relative number of maturing oocytes per gram of BW (13,509  $\pm$  434 oocytes g<sup>-1</sup>) was not significantly different between the first (Oct, Nov, Dec, Jan, Feb, n = 57 females) and the second (Mar, Apr, May, June, July, n = 42 females) part of the spawning season, suggesting that fecundity did not vary throughout the year (t test, n = 99, t = 1.40, P = 0.16; females sampled in April being excluded from the analysis).

#### Reproductive timing in Marsouins River

In Station A of the Marsouins River, temperature values were the lowest in July–August (around 18°C), then increased to reach a maximum in February–March (around 22°C, Fig. 7a). Photoperiod followed the same



**Fig. 6** Sicyopterus lagocephalus batch fecundity (BF,  $\times 10^3$  eggs) in relation to **a** the total body length (TL, mm) and **b** the body weight (BW, g) of females sampled either in mid-stream (Station A, circle) or upstream (Station B, triangle) of the Marsouins River between January 2011 and January 2012. The

seasonal pattern with a lag of about one month, the longest days being observed in December and the shortest days in June. The reproductive timing was examined on mature females (n = 390, see Table 1). The GSI fluctuated monthly (KW test, df = 11, K = 146.2, P < 0.001; females sampled in April being excluded from the analysis) with higher values observed between February and May (Fig. 7b), which corresponded to the period during which more than 55% of mature females were spawning capable (Fig. 7d). Previous spawning evidence (i.e., occurrence of POFs) were observed in about 4% of mature females between December and July, except in January 2011 when ovaries were mainly still developing. The proportion of females in both regressing and regenerating stages increased from the end of the spawning season in June, and was associated with a decrease in GSI. During August and September, the median of GSI values remained low (GSI < 1) and the mature females were reproductively inactive (except a few females in vitellogenic phases). From October-November, GSI increased again showing that ovaries had entered the developing stage (Fig. 7b, d).

In Station A, the monthly mean of GSI was positively related with the water-temperature (Fig. 7a, b), especially with the mean temperature of the preceding month (Pearson's correlation coefficient, r = 0.95, df = 9, t = 9.51, P < 0.001). The probability to have initiated an ovarian cycle ( $P_{\text{growth}}$ , i.e.,



equations of linear regressions between BF and TL or BF and BW are also presented with their associated coefficient of determination  $(r^2)$  (female number = 111 for total length and 99 for body weight analysis)

developing, spawning capable, or spent) at any given time is strongly influenced by the temperature of the previous month (Logistic regression,  $Logit(P_{growth}) =$ Temp × 1.706–32.585, n = 390, explained deviance = 46.1%, P < 0.001). This probability reached 0.5 for a water temperature of 19.2°C. The drop of the photoperiod observed at the beginning of the southern winter (i.e., May–July) matched with the decrease of reproductive activity of S. lagocephalus (Fig. 7a, b). Both condition factor K and HSI also varied significantly throughout the sampling period (Fig. 7c, KW tests, df = 11, K = 56.8, and 183.7, all P < 0.001) with relatively similar patterns (Pearson's correlation coefficient, r = 0.82, df = 10, t = 4.62, P < 0.001). The monthly average of HSI was negatively correlated with the GSI mean (Pearson's correlation coefficient, r = -0.88, df = 10, t = -6.02, P < 0.001). Its highest values were observed at the end of the nonreproductive period (HIS > 5 and K > 1), then decreased during the spawning season until a minimum in March (HIS < 2 and K < 1). After the end of the main spawning activity, the HSI and K values increased again progressively during austral winter.

Spawning females in Langevin River

Between January 1999 and February 2000 in Langevin River, temperature values were lower upstream



Fig. 7 Seasonal fluctuations of environmental conditions and both reproductive and condition variables of *Sicyopterus lagocephalus* mature females collected in the Marsouins River between January 2011 and January 2012 (female number = 390). **a** Monthly changes in water-temperature mean (°C) and in photoperiod. 95% confidence interval is represented by *vertical bars*. **b** *Boxplot* of gonadosomatic index values (GSI) according to the month. **c** Monthly mean variation of hepatosomatic index (HIS) and of condition factor (K). 95% Confidence interval is represented by vertical bars. **d** Monthly frequencies of females at the six reproductive phases identified by ovarian histology: developing, spawning capable, spent, regressing, and regenerating, n = number of females

(station 1, from 17.8 to  $19.5^{\circ}$ C) than close to the river mouth (station 4, from 18.3 to 24.0°C, Fig. 8c). Minimal values were observed in July–August, whereas maximal ones were reached in February 2000. The longest days were observed in December and the shortest in June (Fig. 8c).

In Langevin River, the spawning females were defined upward from the GSI threshold value of 2. We considered that this value differentiated the females that have initiated an ovarian spawning cycle  $(GSI \ge 2)$  from the inactive ones (GSI < 2); see Fig. 4). The probabilities to have initiated an ovarian growth varied significantly throughout the year (Table 4), highlighting a slow reproductive period during austral winter. The location of the station in the river significantly influenced both initiation and duration of the spawning season (Table 4, Station, Station  $\times$  Date, P < 0.001). In females living upstream, ovarian growth began in January-February and reproduction stopped in May (Station 1, Fig. 8a), whereas the reproductive season was extended from December to June in the mid-stream areas (Station 2 and 3, Fig. 8a, b), as observed in the Marsouins site. In station 1, the 15 day means of water temperature prior to samplings (Fig. 8c) were strongly related with the female probabilities to have begun an ovarian growth  $(P_{\text{growth}})$  (Logistic regression, Logit( $P_{\text{growth}}$ ) = Temp  $\times$  5.575 - 104.311, n = 888, explained deviance = 54.1%, P < 0.001). This probability reached 0.5 for a water temperature of 18.8°C on the station. The drop of reproductive activity substantially coincided with the shorter days of the photoperiodic cycle in stations 1, 2, and 3 (Fig. 8a, b). By contrast, females living close to the river mouth (Station 4) showed high probabilities to have initiated an ovarian growth throughout the year, with a small decrease between July and September corresponding to the coolest water temperatures (Fig. 8b, c). However, the 15-day means of water temperature and the probabilities to have initiated an ovarian growth  $(P_{\text{growth}})$  were not significantly related in this station (Logistic regression,  $Logit(P_{growth}) = Temp \times 0.082 - 0.168, n = 747,$ explained deviance = 54.1%, P = 0.119). In stations 1 and 2 the probabilities remained close to 1 during the short and intensive windows of spawning (Fig. 8a), showing that all females have initiated an ovarian growth cycle. In stations 3 and 4 probabilities were high, but fluctuated over the sampling dates during the spawning season (Fig. 8b), suggesting that all females did not reproduce synchronously (i.e., for the same date, some females had initiated an ovarian cycle while others did not).

Fig. 8 Probabilities for Sicyopterus lagocephalus females to have initiated their ovarian growth and oocyte development a in stations 1 (full square) and 2 (open diamond), and b in stations 3 (open triangle) and 4 (full circle) of Langevin River between January 1999 and February 2000 (female number = 3,367). c 15 Days mean of water temperature prior to samplings in Station 1 (full square) and Station 4 (full circle) of Langevin River and photoperiod changes during the study



**Table 4** Summary of deviance reduction tests on logistic GLM analysis with spawning level (based on GSI  $\geq$ 2) of *Sicyopterus lagocephalus* female as dependent variable, and with station and date as explanatory variables

| Factor                | df<br>residual | Residual deviance | Р      | ED<br>(%) |
|-----------------------|----------------|-------------------|--------|-----------|
| Null                  | 3,366          | 4664.0            | _      | _         |
| Station               | 3,363          | 4175.7            | <0.001 | 17.2      |
| Date                  | 3,337          | 2619.3            | <0.001 | 54.7      |
| Station $\times$ date | 3,259          | 1817.5            | <0.001 | 28.2      |

 $\chi^2$  probabilities were calculated compared to the previous model. The proportion of explained deviance (ED) was specified. Values in bold are significant *P* values

In Langevin River, the size structure of females varied significantly between the sampled stations (KW test, df = 3, K = 1,237.1, P < 0.001). Post hoc tests of Steel–Dwass confirmed these significant differences for all pairwise of stations (all P < 0.001).

Although females caught in station 2 are slightly larger than those caught in station 1, the general pattern was an increasing female size from the river mouth to upstream (Fig. 9).

#### Discussion

#### Ovarian growth dynamics and fecundity

Data based on ovarian histology showed that *Sicy-opterus lagocephalus* is a multiple spawner with a group-synchronous ovarian follicle development and an indeterminate fecundity. Oocyte size-frequency distribution revealed a distinct gap between the less developed oocytes and the advanced yolk oocytes, corresponding to a clutch which is going to be spawned in mature females. Although this type of oocyte development is commonly associated with an



**Fig. 9** Size class distributions of *Sicyopterus lagocephalus* females (TL, mm) caught in **a** station 1, **b** station 2, **c** station 3 and **d** station 4 of the river Langevin between January 1999 and February 2000 (female number = 3,367). Highest values included in intervals

annual determinate fecundity (see, e.g., Hunter et al. 1992; Murua & Saborido-Rey, 2003; Murua et al., 2003), several studies found opposed results (Ganias et al., 2004; Plaza et al., 2007). It seems to be the case for S. lagocephalus, for which our study provided multiple lines of evidence suggesting an indeterminate fecundity: (1) a prolonged reproductive season of females showing various ovarian development stages throughout the season, (2) a generalized prevalence of atresia and resorption of mature oocytes at the end of the spawning season (Hunter et al., 1992; Murua & Saborido-Rey, 2003), (3) a fecundity remaining constant from the beginning to the end of the spawning season (e.g., Alonso-Fernández et al., 2008; Gordo et al., 2008), (4) a new process of oocyte recruitment is initiated among the most mature ovaries and early vitellogenic oocytes are observed in spent ovaries, highlighting a de novo vitellogenesis. The finding of an indeterminate fecundity suggests that successive batches of oocytes can grow over a prolonged reproductive season. This type of reproductive strategy is generally favored in unpredictable environments inducing a high juvenile mortality (Winemiller & Rose, 1992). In amphidromous species, larval survival is very low due to predation, starvation and random oceanic dispersal (McDowall, 2010). Production of a great number of small eggs at several times during the year is possibly a response to a stochastic environment which increases the chances of larvae to encounter favorable marine conditions and compensates for a high mortality rate.

The spawning frequency is poorly known in amphidromous species. Bell (2009) relates that Sicydium punctatum could spawn every 14 days throughout the reproductive season. In S. lagocephalus, we can expect that the spawning interval was around 1-2 months, as the first signs of ovarian growth appeared in October-November after the non-reproductive season when the first spent females were observed in December. Nevertheless, the spawning frequency is susceptible to vary according to environmental cues and over the spawning period, as demonstrated for several species (Bapary et al., 2009; Wootton & Fletcher, 2009; Bapary & Takemura, 2010; Lowerre-Barbieri et al., 2011). Manacop (1953) suggests that the spawning frequency of Sicyopterus lagocephalus is certainly higher during the peak of reproduction than at the beginning and at the end of the reproductive season.

The spawning pattern refers to the rate at which oocytes are ovulated (Murua & Saborido-Rey, 2003). In S. lagocephalus, we showed that the entire clutch of yolked oocytes is ovulated and laid in a unique event, since no late vitellogenic or hydrated oocytes remained in spent ovaries. For this species, the occurrence of atresia was very low during the spawning season; thus we suggest that almost all the advanced yolk oocytes observed in an ovary will be spawned in the corresponding batch. We confirmed that S. lagocephalus produced a great number of eggs per batch, from 14,304 to 232,475 small oocytes depending on female size (see also Delacroix, 1987), as observed in other amphidromous Sicydiinae (e.g., Ha & Kinzie, 1996; Yamasaki & Tachihara, 2006; Iida et al., 2011; Yamasaki et al., 2011). This high fecundity probably contributes to offset the high larval mortality due to environmental unpredictability (McDowall, 2007). In S. lagocephalus, the relative batch fecundity remained constant throughout the reproductive season and between sites, suggesting that it was not affected by environmental factors and body condition of females, as reported in other fish species (Yamada et al., 1998; Murua et al., 2006; Wootton & Fletcher, 2009). However, reproductive dynamics and total fecundity for a spawning season can be influenced by these factors as discussed below.

#### Dynamics and spatial distribution of reproduction

Sexual maturity and spawning periods are crucial components of population dynamics (Lowerre-Barbieri et al., 2011). The unpredictable flow conditions of tropical insular rivers (i.e., cyclonic flood, temporary streams, extremely low-flow winter periods, etc.) are expected to promote early maturation and shortgeneration time (Winemiller, 1989; Winemiller & Rose, 1992). Throughout the year, S. lagocephalus post-larvae recruit in the rivers at various age and size (i.e., 26.5-37 mm TL, Hoareau et al., 2007; Teichert 2012), as observed in some other amphidromous gobies (e.g., Bell et al., 1995; Radtke et al., 2001; Iida et al., 2008; Teichert et al., 2012). Delacroix (1987) reported that morphological dimorphism appeared from 42 mm TL. We showed that the size-at-first maturation was larger (from  $\sim$  44 to 55 mm TL) and varied significantly throughout the year. Young gobies entering in river at the beginning of the reproductive period (Delacroix, 1987) likely initiate an ovarian growth and spawn in this first period, whereas the others entering later continued their somatic growth and could not reproduce directly due to cool water temperature.

Fish with indeterminate fecundity can repeatedly recruit batches of oocytes and thus increase their ability to spawn a large number of eggs over a prolonged season (Ganias et al., 2003; Lowerre-Barbieri et al., 2011). For these species, the reproductive dynamics is mainly related to the female physiological conditions and to environmental cues. As we showed for S. lagocephalus, amphidromous gobies inhabiting tropical regions often exhibit an extended and plastic reproductive season related to the environmental conditions and localities (e.g., Manacop, 1953; Kinzie, 1993; Ha & Kinzie, 1996). The main reproductive season of S. lagocephalus spanned from early February to May with a narrower range upstream and a wider one downstream. In January 2011, spent ovaries were not observed probably related to flooding events recorded in the river prior to sampling in Marsouins River. Photoperiod and temperature are potent factors regulating the reproductive cycle of temperate and tropical fish (e.g., Bapary et al., 2009, 2012; Bapary & Takemura, 2010; Lowerre-Barbieri et al., 2011). For example, Iida et al. (2011, 2013) observed a seasonal rhythm of reproduction in females of Sicyopterus japonicus and reported changes in spawning season depending on latitude. In S. lagocephalus, we showed that the ovarian growth process was positively related with water temperature and that 50% of females were reproductively inactive below 18.8-19.2°C, which can explain the extended nonspawning period in upstream areas. Although annual fluctuations of photoperiod are low in tropical regions (i.e., from 10.5 to 13.2 h in La Réunion Island), the drop of daylight duration could also influence the inhibition of oogenesis in S. lagocephalus.

Lipid reserves and fish body condition may also affect gonad maturation of females (Yoneda et al., 1998; Nunes et al., 2011; Bapary et al., 2012). In S. lagocephalus, we showed that the GSI annual fluctuations were inversely linked to those of HSI. This is consistent with the fact that energy and lipids stored in liver, muscles and fat decreased in fish because of their mobilization for the synthesis of vitellogenin which accumulates in oocyte yolk (Bielsa et al., 2003; Murua et al., 2006; Alonso-Fernández et al., 2008; Nunes et al., 2011). In downstream areas, the reproductive activity of S. lagocephalus seemed weakly limited by hot water temperatures (often >19°C) and photoperiod variations, suggesting that other factors could play a role. In these areas, the proportion of females that had initiated an ovarian growth was fluctuant throughout the spawning season, reflecting the fact that all the females were not active at the same time (Lowerre-Barbieri et al., 2011). This pattern might result from differences in female reserves which are available for gonadal development during the year and which control the reproductive dynamics. Therefore, it may be that factors regulating the reproductive process (i.e., duration of reproductive period and spawning frequency) diverge throughout the river gradient. In upstream areas, we can expect that the reproductive activity of females was mainly restricted by water temperature (all females reproduce during a short favorable window), whereas in downstream areas it was essentially limited by other factors, such as physiological condition (e.g., Bapary et al., 2012), food availability (e.g., Bielsa et al., 2003; Plaza et al., 2007; Bapary et al., 2012) or competition for available habitat (e.g., Teichert et al., 2013b). Indeed, Bielsa et al. (2003) have shown that the lipid reserves and the female body condition of *S. lagocephalus* were overall lower downstream. These areas were often characterized by higher competition (e.g., Schoenfuss & Blob 2007; Iida et al., 2013) and predation (e.g., Blob et al., 2010).

In tropical island streams, spatial distribution of species is significantly influenced by the downstreamupstream gradient (e.g., Fièvet et al., 2001; Fitzsimons et al., 2002; Ebner et al., 2011; Teichert et al., 2013c). In amphidromous species, fish living in the upper reaches are often older and larger than those observed downstream (e.g., Yuma et al., 2000; McDowall, 2007; Tamada, 2009, 2011; Iida et al., 2013), as we showed in Langevin River for S. lagocephalus. As a result, the size structure of spawning females in the river varied throughout the year, due to spatial disparities of reproductive activity. During the austral winter, only small females inhabiting downstream were reproducing, whereas during the main spawning season all females were reproducing independently of their size.

Future studies should focus on the demographic process (e.g., age, growth, and longevity) influencing population organization, which could contribute to explain the spatial repartition along the river course. To date, knowledge of reproductive traits gained from the present study can be used to improve management and conservation of Sicyopterus lagocephalus populations. The intensive reproductive period (i.e., February-May) should be considered for the management of hydraulic structures. Maintenance and restoration of ecological continuity during this period is crucial to enhance the chances of amphidromous larvae to reach the sea and continue their development. Moreover, the egg production of La Réunion Island can be estimated by combining the reproductive traits identified in this study with the characteristics of the rivers systems (i.e., wetted area, altitude, temperature, etc.) and of fish populations (i.e., mature female biomass). This approach could provide a suitable estimation of annual changes in egg production and an identification of highly productive areas (relative contribution of different watersheds and of upstream-downstream gradient). Conservation measures or restoration efforts could then be undertaken in these critical areas for maintaining ecological continuity and habitat quality.

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### Annexes 2 :

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# BICHICAM, AN UNDERWATER AUTOMATED VIDEO TRACKING SYSTEM FOR THE STUDY OF MIGRATORY DYNAMICS OF BENTHIC DIADROMOUS SPECIES IN STREAMS

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### ABSTRACT

Conventional methods for surveying diadromous fish migration from marine coastal waters to freshwater habitats are mainly based on electrofishing, a non-optimal technique for the study of fish migrations in rivers, and fishermen catch data. Underwater video has been recognized for a long time as a good alternative, but those approaches usually require intensive labour for retrieving the information from the video sequences. To overcome these problems, an underwater video system specifically designed for field work (low-weight, low-cost and autonomous) named *BichiCAM* has been developed for automatically counting, measuring and tracking fish observed in video sequences. The efficiency and precision of the *BichiCAM* system were tested by filming *Sicyopterus lagocephalus* juveniles passing through the camera field of vision in the Saint-Etienne River, Reunion Island, Western Indian Ocean. The *BichiCAM* system accurately measured fish length of the observed individuals when lens distortion of the camera was corrected, and the error percentages on the measurements presented a standard deviation of 5.1% of the total length. The *BichiCAM* system provides a powerful tool that will not only facilitate research on migrating fishes and invertebrates' communities but also allow studies of the effectiveness of fishways associated to dams or the impacts of fishery activities. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: image processing; migration; rivers; amphidromy; recruitment; fish; invertebrates

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### INTRODUCTION

Migration strategies can be considered as an adaptive response of animals for optimizing the use of the spatial heterogeneity of the environment (Dingle, 1996). Indeed, animals maximize their fitness when the benefit for travelling to favourable areas in terms of resource availability and abundance oversteps the energy costs engendered by the migration (Metcalfe *et al.*, 2002). For many fishes, mature individuals migrate to a place more suitable in terms of reproductive success. Migration can thus directly advantage genitors (e.g. greater food abundance and lower risk of predation) or indirectly improve the survival of their offspring (e.g. better conditions for growth and survival) (Jørgensen *et al.*, 2008). Using different habitats depending on the ontogenetic stage may also contribute to the reduction of intraspecific competition for food (Metcalfe *et al.*, 2002).

Diadromy is an extreme example of the optimization of habitat use, as this strategy implies a transition between freshwater and saltwater, two drastically different environments. Diadromy is widespread in tropical fishes, with about 250 species (Dadswell et al., 1987) migrating at precise life stages between freshwater and saltwater (Myers, 1949; McDowall, 2008a). Studying these migrations and the different habitats used throughout the life history of diadromous species provides fundamental knowledge on the ecology of these populations. The return in stream systems requires an upstream migration from estuaries to freshwater habitats. Determining the parameters influencing these essential migrations is a necessary step to the conservation of diadromous species through the study of spatial population dynamics. This is especially important in tropical islands where increasing human population directly threatens freshwater ecosystems (Brasher, 2003; Jenkins et al., 2009; Ramírez et al., 2012).

Sampling upstream migrating organisms is not an easy task. Attempts have been made to improve capture methods in rivers (e.g. Benbow *et al.*, 2004; Iida *et al.*, 2008; Bell, 2009), but nets and traps remain difficult to use in this environment. These gears are poorly efficient because of (i) the small size of juveniles migrating upstream; (ii) the filamentous algae that can rapidly clog the nets; (iii)

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significant current modifications when using fish net and traps, which can be detected by migrating fish. Visual counts are possible only for large fish (Borcherding et al., 2002), and even considering the recent steps forward towards the miniaturization of acoustic tags (Pursche et al., 2014), this technique still remains limited by subject size (Brown et al., 2010). The sampling method for estimating size classes and abundances of many freshwater fish species remains to be electrofishing, which can be considered as a potentially harmful sampling method (Ellender et al., 2012). Moreover, electrofishing does not allow making the difference between installed and migrating fish. Precise and accurate estimations of fish sizes and abundances can also be obtained using underwater video (UWV) (Shortis, 2007). This approach is generally based on expensive and heavy material and/or often requires long hours of processing (Ebner et al., 2008). UWV has been considerably improved by computer-based automatic recognition of aquatic organisms: it is now widely used in aquaculture (Lines et al., 2001; Hufschmied et al., 2011; Sadoul et al., 2014) or for surveying fish pathways (Negrea et al., 2014). As UWV necessarily requires a fixed position and lightings (Negrea et al., 2014), and/or implies the use of expensive software for fish tracking (Noldus et al., 2001; Pérez-Escudero et al., 2014), Ellender et al. (2012) underlined the need to develop mobile video systems for studying fish populations in river streams.

In this context, our objective was to develop a video system aimed at estimating the abundances and sizes of fishes (or invertebrates) that swim close to the substrate. This system had to be compact and mobile in order to be used from estuaries up to the headwater streams, or to be punctually associated to fishways. We named this system 'BichiCAM'<sup>1</sup> from the local name 'bichiques', which is used for the late larval stages of amphidromous Gobiidae (Sicydiinae) entering the rivers of Reunion Island, Western Indian Ocean. Sicydiinae are amphidromous species (ranging from 2 to 15 cm in total length at juvenile and adult stages) that spawn in rivers and in which larvae migrate passively downstream following hatching (McDowall, 2008b). Larvae grow during a planktonic marine phase before returning to estuaries and migrating upstream as juveniles. The arrival of Sicydiinae in estuaries and their migration upstream are not well known, especially in the Mascarene Islands, although some progress in the knowledge of the biology of these species has been made (Bell et al., 1995; Radtke et al., 2001; Lord, 2009; Teichert, 2012). In this study, we chose Sicyopterus lagocephalus (Sicydiinae) as a biological model for testing the BichiCAM system, focusing on the evaluation of the number of individuals, the estimation of their size and the record of their trajectories.

### MATERIAL AND METHODS

### The 'BichiCAM' system

The BichiCAM system is composed of three polyvinyl chloride (PVC) panels assembled with a metallic armature and forming a U-shaped canal parallel to the water flow above in which a GoPro® camera is placed (Figure 1). An access ramp is composed of brown fabric upon which substratum is disposed at the downstream entrance of the canal in order to facilitate fish entry. A bottom 50 \* 50 cm white panel constitutes the background. The metallic armature is resistant to strong water currents but can be easily dismantled for transportation. The whole system is fixed to the riverbed with four stakes placed at each angle. A sunshade can be added above the system to reduce parasite reflection of sun rays. One-metre or 2-m-long net wings parallel to the flow can be set at the downstream entrance in order to insure that fish do not avoid the entrance of the BichiCAM system. Indeed, a fish moving upstream in the channel formed by the net wings will less likely turn back to avoid the BichiCAM system. The GoPro® camera is fixed on the adjustable vertical part of the armature, underwater and at a distance of 30 cm from the white panel. In this study, we used a GoPro® 3 White Edition, with data acquisition adjusted to 1280\*960 pixels and 30 frames per second at the widest field of vision.



Figure 1. Schematic diagram of the *BichiCAM* system. (1) White panel (50 \* 50 cm), with a calibration scale. (2) metal frame. (3) GoPro® camera. Grey arrow represents water flow. Black arrows represent the general direction of fish movements through the canal

<sup>&</sup>lt;sup>1</sup>Patent pending



Figure 2. Flow chart of the basic steps applied during the processing. Input is a video file (.mp4), output a number of fish with their length and recorded trajectory. Black boxes correspond to processing steps performed using Photoshop (or VirtualDub), white boxes to processing steps performed using R performed using R

### Video sequences acquisition and analyses

Operating conditions of *BichiCAM* are limited by the characteristics of the river. First, the water level has to be greater than 30 cm in order to allow the GoPro® camera to be underwater and its field of vision covering the whole surface of the bottom panel. Secondly, turbidity must be low enough to insure that the bottom panel is visible when the camera is placed at 30 cm above it. GoPro® camera battery and extension (GoPro® Battery BacPac<sup>TM</sup>) allows uninterrupted recording for approximately 3 h (Letessier *et al.*, 2013; Thomson and Heithaus, 2014). However, the GoPro® camera camera can be easily replaced by another one in the field.

The analysis of digital images follows three successive steps (Figure 2). First, video sequences are converted to series of Tagged Image File Format (TIF) images using Photoshop or VirtualDub.<sup>2</sup> The images are then processed using Fiji (Schindelin *et al.*, 2012). Data are finally analysed using R (R Core Team, 2014).

*Image processing: frame selection.* To minimize calculation time, two steps are first applied: each TIF image extracted from the video sequence is submitted to a Gaussian function for smoothing with a radius of three pixels (Figure 2), and then local maxima of grey values are detected. If no local maximum is detected, the frame is ignored, and the same steps are applied on the next frame of the image sequence. If however at least one local maximum is detected, the current frame is submitted to the following processing steps.

Image processing: distortion correction. Lens distortion had to be corrected in order to obtain accurate length measurements of fish migrating on the bottom of the device (fish never use the sidewalls—personal observations of the authors). A calibration of the video camera was realized by calculating the intrinsic distortion parameters of the camera's lens when underwater using the plugin *Optic\_Calib* on Fiji by following the method described by Zhang (2000). Five pictures of a calibration panel were taken at different distances underwater and oriented with an approximate angle of 45° relative to the optical axis. The estimated values of the intrinsic camera parameters of the GoPro® 3 White Edition at the widest field of vision (1280 \* 960 px) showed a significant radial distortion with  $k_1 = -0.190675$  and  $k_2 = 0.124536$ , following Zhang (2000).

A correction of the optical lens distortion is applied to each TIF image extracted from the video sequence using the *Undistort\_Image* plugin modified to accept highresolution pictures. Each TIF image is then converted into an eight-bit picture (Figure 2).

*Image processing: fish detection.* After correction of lens distortion, fish detection is performed on each TIF image extracted from the video sequence and selected following the method previously described (see section on image processing: frame selection). For this purpose, several operations are needed. First, a Gaussian function for smoothing with a radius of three pixels is applied (Figure 2). Local maxima are detected and a noise tolerance of 50 of their grey values applied. This way, adjacent pixels showing a grey value superior to each detected local maximum minus the noise tolerance are considered as belonging to the

<sup>&</sup>lt;sup>2</sup>Available freely at http://www.virtualdub.sourceforge.net/

foreground and the others are considered as belonging to the background. This thresholding operation creates binary images in which each pixel is either 1 or 0. A threshold is then applied on the size of the detected objects in order to reduce noise and eliminate small particles (<3 pixels  $\approx$  12 mm) that are passively carried by water stream.

In order to test for the influence of turbidity on fish detection, 14 dead *Sicyopterus lagocephalus* (total length between 3.1 and 7.6 cm) were installed on the white panel in the camera field of vision and immerged in an experimental tank. The tank was filled with turbid water of 14.9 NTU measured with a Hanna HI 93703 turbidimeter. The turbid water was regularly diluted with clear water, and a short video sequence was recorded at each step. In total, 11 short video sequences were obtained from 14.9 to 0.2 NTU. As fish were not moving, 10 images were extracted from each video sequence, and the number of fish was detected using the procedure described in the following.

*Image processing: fish length estimation.* Fish length estimation is based on skeletonization, distance mapping and particles analysing (Figure 3). The combination of these three procedures allows the determination of the length of each individual independently of its shape, orientation or curvature as long as this individual is separated from others by at least

a single pixel. The BichiCAM system in its present form, as all the other automatic systems used in the field, cannot estimate the size of individuals within aggregations. The first step is to skeletonize the binary image (Figure 3b) using the thinning algorithm developed by Zhang and Suen (1984). Their method consists in sequentially removing pixels from the edges of the foreground objects except pixels for which removal would produce the separation of the object into two different entities (Figure 3d). Skeletonization of an almond-shaped 2D object, that is, presenting pointy extremities, creates a segment corresponding to the longest axis of the shape. On the contrary, the skeletonization of an ellipse 2D object creates a segment shorter than the longest axis of the ellipse. Depending on the 2D shape of a fish, skeletonization may therefore cause a loss of information in its head and tail parts as a few pixels at each end may be eroded during the process. The skeletonization process appears to be an efficient tool for length estimations but consequently has to be associated to Euclidian distance mapping procedure (EDM) and erosion. Skeletonization alone can be applied, but only for estimating the length of animals with pointy ends such as Cænorhabditis elegans (Geng et al., 2004). When considering animals with curved extremities, such as fish, skeletonization alone will induce an underestimation of their size.



Figure 3. Schematic representation of fish length estimation (in order to improve readability, only one fish is presented and the resolution of the image was decreased). With (a) 8-bit picture; (b) binary image obtained after binary conversion; (c) visual representation of Euclidian Distance Map (EDM) in which the grey value of each pixel is proportional to its distance to the nearest background pixel in the binary image; (d) binary image obtained after skeletonization using Zhang and Suen (1984) algorithm, the two end-point pixels correspond to the crossed boxes; (e) binary image obtained after erosion of the two end-point pixels; (f) visual representation of the integrated density corresponding to the EDM values of all the pixel constituting the skeleton after erosion This figure is available in colour online at wileyonlinelibrary.com/ journal/rra

In order to estimate the total fish length, the EDM (Leymarie and Levine, 1992) is applied on each binary image (Figure 3b). EDM generates a matrix, or distance map, that corresponds to the distance between each foreground pixel and the nearest background pixel (Figure 3c; distances are converted to grey values in the graphic representation). In this distance map, the information corresponding to the pixels present in the skeleton image is retained. The result is an EDM value for each pixel of the skeleton (Figure 3f). At this stage, the skeleton is untransformed (Figure 3d), and a copy is eroded in order to remove the two end-point pixels (Figure 3e). EDM values for each pixel of the skeleton are then summed, and the result is called 'Integrated Density'. The integrated density is calculated for the skeleton before (Figure 3f) and after (Figure 3g) erosion. The value of the total length of the fish is finally estimated from Equation (1).

Length = 
$$(N - 2)$$
+Integrated density<sub>before erosion</sub> (1)  
-Integrated density<sub>after erosion</sub>

with

$$(N-2)$$
 = number of pixels of the skeleton image after erosion  
Integrated density<sub>before erosion</sub> =  $\sum_{i=1}^{N}$  (EDM value of pixel  $n^{\circ}i$  of the  
skeleton image before erosion)  
Integrated density<sub>after erosion</sub> =  $\sum_{i=1}^{N}$  (EDM value of pixel  $n^{\circ}i$  of the  
skeleton image after erosion)

### Data analysis: individual tracking

An identification number is automatically attributed to each fish entering the field of vision of the camera. Tracking is realized by comparing the positions of all the fish at time (t+1) with the positions at time (t). For every fish on image (t+1) and for every fish on image (t), the value of  $(x_{t+1}-x_t)^2 + (y_{t+1}-y_t)^2$  is calculated and stored into a matrix of squared-distances, x and y being the coordinates of the centre of mass of the object on the white background. The lowest value in the matrix of squared-distances, that is, the smallest displacement of a fish in two consecutive images is retained. The corresponding fish is identified on image (t+1), and the associated line and column are removed. The procedure is repeated on the matrix of squared-distances until the last fish at frame (t+1) is identified. A threshold on the distance between fish observed in two consecutive images is added in order to avoid identification mismatches. This threshold corresponds to a maximum displacement of 350 pixels ( $\approx$ 14 cm) between two frames. This distance would correspond to a swimming speed of ca 30 body length per second for a 14-cm-long Sicvopterus lagocephalus, a value far greater than the maximum velocity

(fast-start swimming) of benthic species (Domenici and Blake, 1997). Using this procedure, each fish is detected and tracked for the entire duration of its presence in the field of vision of the camera. Its size is also estimated on each picture in which it is observed. The length estimations obtained for each fish are averaged when it leaves the field of observation. Fish that are detected in less than five frames are not counted in order to remove objects such as air bubbles passing through the camera field of vision in turbulent streams. Individual tracking stops when occlusions occur. Objects not moving more than 40 mm during the whole sequence are not taken into account as they may correspond to inert objects if water current speed is low. This 40-mm distance defined for the whole video sequence allows the recognition of fish showing discontinuous displacement, which is the most frequent case for migrating juveniles. Finally, inert objects (woody debris or floating algae) pass through the field of vision of the camera in the downstream direction when the fish are going upstream. A filter on the directionality of the movement of the detected objects is therefore applied to retain those moving upstream only.

### Field test

Sicyopterus lagocephalus (29-90 mm total length-TL, N=58) were sampled in the Saint-Etienne River (Reunion Island) using electrofishing (portable electrofisher IG200/2D, Hans Grassl GmbH, Germany). The BichiCAM system was installed in the riverbed, and the fish were regularly released in front of the downstream opening of BichiCAM. The mean values of length estimations obtained with BichiCAM were calculated for each detected fish, either without or with correcting the lens distortion. The real size (TL) of each fish was first estimated by selecting an image corrected for lens distortion in which its body was observed without any curvature. Then the number of pixels from the top of its head to the end of its tail was counted using Fiji, and the obtained number of pixels was transformed to millimetre. Tracked individuals were visually identified in order to associate the measures obtained by BichiCAM (LengthBichiCAM thereafter) with fish length measured manually (Length<sub>reference</sub> thereafter). Linear regressions were then calculated between Length<sub>BichiCAM</sub> and Length<sub>reference</sub> for values obtained on images corrected, or not corrected, for lens distortion. Three types of measurement errors were assessed: invariable errors on TL (in millimetre), invariable relative errors depending on total length (in percentage of TL) and random errors.

Error percentages were calculated following Equation (2).

$$EP = \frac{Length_{BichiCAM} - Length_{reference}}{Length_{reference}} \times 100$$
(2)

with EP as error percentage,  $Length_{BichiCAM}$  as length obtained by the *BichiCAM* system (mean value for each

individual) and  $Length_{reference}$  as length measure obtained manually (single measure).

### RESULTS

For the 58 fishes measured, fish lengths obtained with the *BichiCAM* system (*Length*<sub>*BichiCAM*</sub>) were highly correlated to the fish lengths measured manually (*Length*<sub>*reference*</sub>), either for images uncorrected for lens distortion (Figure 4a) or for images corrected for lens distortion (Figure 4b). The intercept was not significantly different from 0 for both regressions (Student's *t*-tests, *p*-value = 0.182 and 0.459 for images uncorrected and corrected for lens distortion, respectively). This means that no invariable error on TL was induced by the *BichiCAM* system.

The slope of the regression for measures obtained from images uncorrected for lens distortion was significantly different from 1 (Student's *t*-test, *p*-value = 0.008, Figure 4a). The error percentages calculated following Equation (2) for the measures based on images uncorrected for lens distortion followed a normal distribution (Shapiro–Wilk test, *p*-value = 0.87, Figure 5a), which was not centred on 0 (Kolmogorov–Smirnov test, *p*-value < 0.001, Figure 5a). The mean percentage error was -3.0%, with a standard deviation of 5.2%. Length measurements obtained with the *BichiCAM* system were thus underestimated by 3%, the real TL of observed fish when images uncorrected for lens distortion were processed.

With images corrected for lens distortion, the slope of the regression became not significantly different from 1 (Student's *t*-test, *p*-value = 0.84, Figure 4b), and the error percentages remained normally distributed (Shapiro–Wilk test, *p*-value = 0.99, Figure 5b), but were now centred on 0 (Kolmogorov–Smirnov test, *p*-value = 0.132, Figure 5.b). This means that the *BichiCAM* system induced no invariable relative errors on TL estimates when the images were corrected for lens distortion. The error percentages on the length estimates obtained with images corrected for lens distortion were characterized by a standard deviation of 5.1%. This deviation corresponds to the remaining random errors that cannot be corrected.

The *BichiCAM* system allows recording the trajectories of each detected individual and can represent graphically the consecutive positions of their centre of masses (Figure 6a). When fish densities are high and/or some individuals group together and swim close together, occlusions may occur (Figure 6b), and the identities of individuals may not be maintained. Post-occlusion length measurements are not taken into account to minimize the consequences of such occlusion on the estimations of the number and the size of the individuals.

Automatic fish detection performed well at turbidity lower than 3 NTU as the mean proportion of fish detected



Figure 4. Relationship (solid line) between length measurements obtained with the *BichiCAM* system (*Length*<sub>BichiCAM</sub>, mean value for each individual) and the length measurements obtained manually (*Length*<sub>reference</sub>, single measure for each individual) for 58 *Sicyopterus* lagocephalus (a) for images uncorrected for distortion, (b) for images corrected for distortion. The dotted line corresponds to a linear model with a regression coefficient equal to 1 and with a null intercept

was 100% (Supporting Information 1). However, this proportion decreased drastically when turbidity was greater than 5 NTU.

### DISCUSSION

Automatic estimation of fish length based on pictures has considerably improved in recent years. White *et al.* (2006)





Figure 5. Distributions of error percentages of the length estimations performed with the *BichiCAM* system (a) for images uncorrected for distortion and (b) for images corrected for distortion

proposed a method for individually measuring fishes placed on a conveyor belt. Their method consisted in plotting a line joining eight points distributed along the central axis of each fish in order to take into account the curvature of its body. Their system was based on high-resolution pictures of the lateral view of fishes. They obtained accurate measurements of fish body length using this method (standard deviation of 1.2 mm for a 413-mm fish). Unfortunately, their approach cannot be applied for most diadromous species as eight points are not sufficient for precisely following the central axis of the body of species that can present high degrees of curvature of their body.

One of the issues raised by automatic fish multitracking was the loss of detection of individuals resulting from fish occlusion. Physical contact between two or several tracked objects leads to the detection of a single object instead of distinct objects, preventing the tracking algorithm from identifying correctly the distinct individuals on the next frames. Delcourt *et al.* (2009, 2013), and more recently Dell *et al.* (2014), underlined this issue and proposed various solutions and software, as tracking continuity is of major concern in behavioural studies. Several software are now available for automatically tracking individuals without tagging (reviewed by Dell *et al.*, 2014), but most are expensive and require high-end computers in order to process the video sequences. Moreover, they are developed for behavioural studies, thus based on a limited number of individuals



Figure 6. Examples of graphical representation of trajectories of *Sicyopterus lagocephalus* swimming upstream obtained with the *BichiCAM* system, with (a) trajectories of 10 individuals without occlusion and (b) trajectories of three individuals showing different occlusion events (arrows). Three fishes were detected at the beginning of the sequence, but only one over the entire field of view of the camera. Detection of the two individuals in grey stopped at the moment of the first occlusion, whereas the second occlusion is silent, because occurring between one individual (in black) and one or two individuals for which detection had previously stopped

in a closed and controlled area; none can be used to study animals on the field with an accuracy allowing the resolution of occlusion events (Dell *et al.*, 2014). The system developed by Delcourt *et al.* (2009) is based on statistical observations and predictions of trajectories. Their system takes into account previous positions of fish in order to predict their future trajectories by assuming that fish display uninterrupted movements. Yet, the swimming behaviour of amphidromous gobiids is far from being continuous. It consists of an alternation of stop-and-goes, made possible by their pelvic-sucking disc (Schoenfuss and Blob, 2003). The recent idTracker software developed by Pérez-Escudero *et al.* (2014) maintains the identities of animals indefinitely without bio-logging or marking, even in complex habitats, but needs an evenly distributed and consistent lighting in the camera field of vision. Such lightning conditions are difficult to obtain in the field.

With the BichiCAM system, some fish were taken into account from their entrance in the field of view of the camera to the moment they entered in contact with one or several other fish. At this time, their loss of detection during several frames could not be resolved. The loss of information consecutive to isolated occlusion events (lower number of measures on the same individual) will have only a low impact on the studies involving generally high numbers of individuals. However, when fish aggregate, as a result of important densities for instance, other indices of fish quantification can be used. Calibration tests are still required to identify the fish density threshold beyond which the current procedure of the BichiCAM system no longer allows an accurate estimation of the number of individuals passing through the camera field of vision. Beyond this threshold, a mean number of detections for a given period of time (number of detections by time unit) can be calculated as a proxy of fish density. Combined with an estimation of fish relative speed, this approach should be a suitable alternative when identification mismatches (i.e. occlusions) become higher than a threshold value determined by the user. Estimations of fish length still can be obtained from detections prior to occlusion, thus giving an estimate of the fish sizes, although based on a lower number of images. Even when fish densities are high, the BichiCAM system should remain a powerful tool for estimating relative abundances and size distributions of migrating fishes. Otherwise, manually sorting the fish from the images (Delcourt et al., 2013) is the ultimate solution, but this operation is more time-consuming.

Water turbidity is a limiting factor for visual or videobased fish detection methods. Our laboratory tests demonstrated that all the fish present were automatically detected by the *BichiCAM* system when the water turbidity was lower than 3 NTU. In order to evaluate how the system would have performed during our past field sampling sessions in the Saint-Etienne River (between 2007 and 2015), we used the records for turbidity available online for this river (www.eaureunion.fr, accessed July 2015). Our conclusions are that the *BichiCAM* system would have been efficient 27 times over 49 of our sampling sessions (55%).

The low cost of the *BichiCAM* system and the reproducibility of the obtained measurements allow to simultaneously deploy several video systems at different sites in order to fully assess migration events. Indeed, the different processes leading to the dispersal of juveniles in river basins are still unknown for many amphidromous species. This aspect could be more easily studied with the *BichiCAM* system as the video monitoring approach would easily help in characterizing migrating patterns. However, adequate sampling strategies (i.e. the number and positioning of

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*BichiCAMs* on the riverbed; duration and intervals of video sampling) remain to be determined in order to precisely evaluate fish relative migrating intensity in rivers. These sampling strategies will need to take into account the artificial nature of the white PVC panel on the bottom of the *BichiCAM* system. This panel allows fish detection and tracking but cannot be used for behavioural and physiological studies: fish climbing movements and speed on the PVC panel may reveal differently in the *BichiCAM* system than on natural substrates.

The BichiCAM system also has various applications on the management field. Restoration of the ecological continuity in rivers is a major concern for migratory species with a dispersal stage. The equipment of river dams with fish ladders is one of the solutions to this issue, but requires recurrent monitoring in order to evaluate the efficiency of such structures for fish passage and to assess periods of abundant migrations. BichiCAM is an adapted tool for monitoring fishways, as it can be easily placed at different strategic points (i.e. downstream entrance, fishway's upstream exit) without any adjustment of the dam structure. A second interest of BichiCAM is its potential of assessment of diadromous species' post-larvae recruitments at river mouths. Fisheries are widely present in the estuaries of many tropical Indo-Pacific islands, but actual catch data are scarce because of the lack, or the lack of implementation, of a regulatory framework for these fishing activities. The non-extractive nature of BichiCAM may be more acceptable by fishermen and would allow managers to place them downstream and upstream to the fishing gears for studying the abundance and size structure of post-larvae at river mouths. This approach would lead to some estimation of the catches without impacting the resource. However, the use of BichiCAM for these applications will require an important calibration effort: further research will focus on the quantification of fish flow in different biotic (i.e. number of migrating fish and development stage of individuals and species) and abiotic (i.e. flow velocity and location along river transect) conditions.

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### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

# Annexes 3 :

Teichert N, Tabouret H, **Lagarde R**, Grondin H, Ponton D, Pécheyran C & Bareille G (2018). Site fidelity and movement of an amphidromous goby revealed by otolith multi-elemental signatures along a tropical watershed. *Ecology of Freshwater Fish.* Publié en line. **ORIGINAL ARTICLE** 



WILEY FRESHWATER FISH

# Site fidelity and movements of an amphidromous goby revealed by otolith multi-elemental signatures along a tropical watershed

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# Abstract

Otolith microchemistry can provide crucial information to address gaps of knowledge in spatio-temporal ecology of fish species. However, understanding the seasonal variability of water chemistry and its effect on otolith signatures is needed to interpret fish movements. Otolith multi-elemental signatures were used to examine the diadromous migration and small-scale movements of a tropical goby (Sicyopterus lagocephalus) within a watershed in La Réunion Island, Indian Ocean. The elemental ratios Sr:Ca, Ba:Ca and Sr:Ba recorded monthly in the water of nine sampling sites varied between localities and were correlated with otolith signatures, whereas the Mg:Ca signature was not. The incorporation of some trace elements in otoliths was influenced by the size of fish and site where they were caught, reflecting an effect of endogenous and exogenous factors. Despite these sources of variation, the elemental signatures did not overlap for three river sections distributed along the 26-km-long watershed. The diadromous migration and fish lifetime movements between these river sections were reconstructed using an original process based on random forest analysis. This approach revealed distinct migratory behaviours after fish entered in the river, with some individuals progressing slowly in the watershed whereas other rapidly reached the upper localities. As adults, S. lagocephalus showed a restricted exploratory behaviour and a strong site fidelity to a particular part of the watershed. The detection of adult movement was typically only between adjacent locations and is possibly explained by shifts in local intraspecific hierarchies and/or displacement during extreme discharge caused by cyclones.

### KEYWORDS

habitat discrimination, individual life histories, movement patterns, otolith chemistry, random forest, river networks, water chemistry

# 1 | INTRODUCTION

Several methods have been developed to investigate fish movements in their natural environment: electronic tags (e.g. Arnold & Dewar, 2001), DNA markers (e.g. Manel, Gaggiotti, & Waples, 2005), stable isotopes (e.g. Hobson, 1999) or otolith chemical signature (e.g. Campana, Chouinard, Hanson, Frechet, & Brattey, 2000). Thanks to their structural and chemical properties, the otoliths are an efficient tool to reconstruct the movement patterns over the entire individual life history of fishes, even those of small size (Secor, Henderson-Arzapalo, & Piccoli, 1995). When fish move between habitats of different chemical signatures, some elements present in the water are incorporated in the matrix of their otoliths. Hence, elemental profiles along otoliths transect can record how fish move between └-WILEY-

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these habitats (Campana, 1999). For example, the Sr:Ca ratio has been widely used to reveal the migration of diadromous fish, relying that the Sr:Ca ratio is generally much elevated in the marine environment than in freshwater (e.g. Lord, Tabouret, Claverie, Pécheyran, & Keith, 2011; Radtke, 1989). However, the incorporation processes of trace elements can be influenced by several exogenous and endogenous factors (Elsdon et al., 2008) that should be factored into any interpretation of fish movement (Walther, Kingsford, O'Callaghan, & McCulloch, 2010). For instance, the temperature regime, food availability, growth rate or life history stage has been reported to affect the incorporation rate of several elements in fish otoliths (e.g. Bath et al., 2000; Elsdon & Gillanders, 2002; Tabouret et al., 2011; Walther et al., 2010). Understanding the relationship between water chemistry and otolith signatures is thus mandatory to avoid misinterpretation related to environmental variability or physiological effects.

Indigenous fish species living in freshwater of tropical islands are mainly diadromous. Among them, amphidromous fish species, which represent an important part of the fish diversity in insular tropical streams (Keith, 2003), grow and spawn in freshwater (McDowall, 1988; Myers, 1949). Immediately after hatching, larvae drift to the sea where they grow before returning to rivers (Manacop, 1953). Once in freshwater, juveniles migrate upstream and settle in various locations along the river to grow and reproduce (Keith, 2003). Some species are able to climb waterfalls, and reach upstream reaches where predation and competition are generally reduced (Blob et al., 2010; Schoenfuss & Blob, 2007). Amphidromous species can be threatened by a range of anthropogenic stressors that currently impact the river systems, such as habitat loss and alteration (Cooney & Kwak, 2013), pollution (Ramírez, De Jesús-Crespo, Martinó-Cardona, Martínez-Rivera, & Burgos-Caraballo, 2009) or introduction of exotic species (Jenkins, Jupiter, Qaugau, & Atherton, 2010). However, the alteration of migratory pathways is probably one of the main threats related to the loss of the ocean-stream connectivity (Walter et al., 2012).

By definition, amphidromous species move between the marine and freshwater environments; however, there is scope for considerable movement with the stream network during the juvenile and adult phase. Partial or facultative migration is also possible as demonstrated by recent research for species that are classified as amphidromous such as Awaous stamineus or Gobiomorus dormitor (e.g. Hogan, Blum, Gilliam, Bickford, & McIntyre, 2014; Smith & Kwak, 2014b). This flexibility in behaviour was assumed to be related to some landscape characteristics (river flow intensity, distance from the sea, longitudinal slope of the river, etc.) that can allow larval retention and survival in freshwater (Closs, Hicks, & Jellyman, 2013; Huey et al., 2014). Otolith microchemistry has been used for investigating migrations of a large number of taxa between marine and freshwater environments (e.g. Huey et al., 2014; Shen, Lee, & Tzeng, 1998; Tabouret et al., 2014). Oppositely, the patterns of fish movements within river systems remain largely unknown (Bell, 2009). Several studies have detected variations in otolith microchemistry of some amphidromous fish that could be interpreted as movements

from the upper river reaches to downstream areas or to the estuaries (Lord et al., 2011; Smith & Kwak, 2014b). Downstream migration can be related to movement of adult fish towards spawning grounds close to the marine environment. This behaviour has been reported in several species, such as Prototroctes maraena (Koster, Dawson, & Crook. 2013), and is believed to reduce the time larvae spend in freshwater, and thus their mortality (McDowall, 2009). However, fish movements between river reaches are not exclusively linked to reproduction, but can also be related to foraging behaviour or competition for food and/or territory, or caused by involuntary displacement due to periodic disturbances, such as cyclonic floods (Lord et al., 2011). For instance, Lagarde, Teichert, Boussarie, Grondin, and Valade (2015) documented upstream movements of Sicyopterus lagocephalus adults that were probably recolonising their initial habitats after having been washed down during flood events. Given the high diversity in movement patterns observed among amphidromous species, insights on the successive habitats crossed by individuals in both marine and freshwater environments are essential to understand populations dynamic and improve conservation efforts.

Sicyopterus lagocephalus is one of the most widespread amphidromous gobies, distributed from the Western Indian Ocean to the Eastern Pacific (Lord et al., 2012). This small-sized species measures from 4 cm to 12 cm standard length. Postlarvae recruit in the oligotrophic coastal streams where juveniles and adults settle and feed on microalgae that cover the river substratum (Bielsa, Francisco, Mastrorillo, & Parent, 2003). In La Réunion Island, S. lagocephalus dominates the freshwater fish assemblages from the estuaries to upper river habitats, more than 20 km upstream (Teichert, Valade, Lim, et al., 2014). The species shows weak preference for specific habitats in rivers, excepting during the reproductive period when the males select specific spawning habitats (Teichert, Valade, Bosc, Richarson, & Gaudin, 2013). The reproduction can happen throughout the year in downstream reaches, but is restricted to the warmer months, that is from February to May, in the middle and upper reaches (Teichert, Valade, Fostier, Lagarde, & Gaudin, 2014).

In this study, we investigated how variations in otoliths multielemental signatures can help to reconstruct individual lifetime movements of *S. lagocephalus* within a small-scale watershed of La Réunion Island. The spatial congruence between otolith elemental signatures and ambient water chemistry was first assessed during an annual hydrological cycle, aiming to identify river localities with distinct elemental signatures. Then, the diadromous migration and fish lifetime movements between river sections were reconstructed. Sources of variability related to annual hydrological cycle, sitespecific incorporation rate and fish size were carefully taken into account.

### 2 | MATERIALS AND METHODS

### 2.1 | Study sites

Fish sampling and water sampling were carried out in nine sites distributed within the St-Etienne River watershed, La Réunion Island, **FIGURE 1** Location of sampling sites within the St-Etienne River watershed, La Réunion Island, south-western Indian Ocean. The nine river sites, from A to I, were distributed along the St-Etienne River and its two main tributaries, that is Bras de la Plaine and Bras de Cilaos. The bar plot indicates the mean standard length of fish sampled in each site, and bars represent the range of measures. The dashed horizontal line indicates the mean size of the 176 fish collected. n: number of individuals per site



south-western Indian Ocean (21°5'S, 55°3'E; Figure 1). The river flows over approximately 26 km from the sources of its two main tributaries, Bras de la Plaine and Bras de Cilaos, to the sea. The mean annual discharge of the Bras de la Plaine is about twice the discharge of Bras de Cilaos, that is 4 m<sup>3</sup>/s versus 2 m<sup>3</sup>/s (DEAL, 2011). To cover most of the spatial repartition of the species, the sampling sites were located from 1.9 to 22.7 km from the river mouth, the corresponding elevation varying from 46 to 650 m. Sampling was designed to capture the individual signature of several tributaries and river reaches (Figure 1). The riverine habitats were overall homogenous across the nine sites. They consisted in torrential and turbulent flow conditions (i.e. succession of riffles and pools). The substratum was dominated by pebbles and boulders, which can be used by S. lagocephalus for reproduction (Teichert, Valade, Lim, et al., 2014). The salinity remained null in all river sites. Indeed, no transition area with brackish water is present at the mouth of this river: the freshwater flow directly enters into the sea along a coastal dune of cobbles.

### 2.2 | Water sampling and chemical analysis

Water samples (50 ml) were collected monthly at the subsurface from April 2013 to April 2014 and were processed using ultraclean protocol. Samples were filtered with syringes through a PVDF filter (0.45  $\mu$ m; Millipore) into acid-washed polyethylene bottles, fixed with nitric acid 2% (JT Baker Ultrex; Germany) and then stored at 4°C. Samples were diluted four times with nitric acid 2% immediately before being analysed. The elemental composition was analysed using an inductively coupled plasma mass spectrometer (ICP-MS; Aurora Elite; Bruker, Germany). Internal standard of indium (1 ppb) was used to correct for the instrumental drift. The general performance of the procedure was checked using the certified reference freshwater SLRS-5 (NRCC, Canada). Although the concentrations of 20 elements were initially tracked (i.e. Mg, K, Ca, Be, Al, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Sr, Mo, Ag, Cd, Ba, Pb, U), we thereafter restricted the analyses to Mg, Ca, Ba and Sr because concentrations of other elements in the otoliths were below detection limits. Accepted recovery of reference materials ranged from 93% to 103%. Sr, Ba and Mg were standardised to Ca (i.e. Sr:Ca and Mg:Ca in mg/g and Ba:Ca in  $\mu$ g/g) for comparison with otolith ratios. External precision for the laboratory standard was 0.7% for Sr:Ca, 1.1% for Ba:Ca and 2.1% for Mg:Ca. For each elemental ratio, an ANOVA was conducted to compare the concentrations in water samples between the nine river sites, and then, pairwise comparisons were conducted using Tukey's HSD tests at a significance level  $\alpha$  = .05.

### 2.3 | Fish sampling and otolith preparation

Fish were sampled by electrofishing (portable electrofisher IG200/2D; HANS GRASSL GmbH, Germany) in October 2013. On each site, sampling was focused on the largest adults of S. lagocephalus, independently of their sex, to reconstruct fish movements over long periods. Selected fish were anaesthetised and euthanised with an overdose of eugenol prior to fixation in 90% ethanol. An ANOVA was conducted on the standard lengths (SL, mm) of fish to test for differences between sampling sites. Pairwise comparisons were then conducted based on Tukey's HSD test to determine homogeneous groups. In the laboratory, both sagittal otoliths were extracted from the fish under a binocular magnifier, carefully cleaned with ultrapure water and stored dry in 5-ml Eppendorf<sup>®</sup> tubes. One otolith per fish (randomly left or right) was embedded in epoxy resin (Araldite 2020; Escil, Chassieu, France), sectioned transversely with a low-speed saw, ground to the core using sandpaper (from 400 to 2000 grains per inch) and polished with diamond-tipped polishing powder. Lastly, it was carefully rinsed with ultrapure water and dried prior to storage.

### 2.4 | Otolith microchemistry analysis

The elemental composition (Mg, Ca, Sr, Ba) of the otoliths was guantified using a femtosecond laser ablation (LA, IR 1030 nm; Alfamet-Novalase, France) coupled to an ICP-MS (DRCII; Perkin Elmer, Shelton, CT). The ablation was performed from one edge of the otolith to the other through the core with a raster scan strategy previously described by Tabouret et al. (2011) at a 50 Hz frequency, with a 25  $\mu$ m laser beam diameter and a 5  $\mu$ m/s speed. The resulting elemental profile consists of successive measures (hereafter referred to as laser spots) distributed each 5 µm along the otolith. This strategy represents the best compromise to ablate enough material to detect the elements while keeping a fine spatial resolution (Tabouret et al., 2011). The analysis of three certified reference glasses NIST614, NIST612 and NIST610 (National Institute of Standards and Technology, USA) ensured the quantification. Calcium was used as an internal standard to account for any variations in the amount of ablated material and laser energy in the ablation yield. Analytical accuracy was measured with the fish certified otolith reference materials NIES22 (National Institute for Environmental Studies, Japan; Yoshinaga, Nakama, Morita, & Edmonds, 2000) and FEBS-1 (National Research Council Canada, Canada). Strontium, barium and magnesium compositions were expressed as mass elemental ratios (i.e. Sr:Ca, Ba:Ca and Mg:Ca) on the basis of the stoichiometry of Ca carbonate (380,000 µgCa/g otolith) (Campana, 1999). The average detection limits based on three standard deviations of the blank gas were 0.97  $\mu$ g/g for <sup>25</sup>Mg, that is 2.53 × 10<sup>-6</sup> for Mg:Ca ratio; 6.62  $\mu$ g/g for <sup>86</sup>Sr, that is 1.73 × 10<sup>-5</sup> for Sr:Ca ratio; and 0.22  $\mu$ g/g for  $^{138}$ Ba, that is 5.74 × 10<sup>-7</sup> for Ba:Ca. Accepted recovery of reference materials ranged from 95% to 110%.

## 2.5 | Congruence between water and otolith chemistry

We assumed that the otolith signature at the otolith edge, that is the last period of the fish life, indicates the chemical signature of the site where the fish was living at the moment it was caught. A number of six consecutive laser spots from the edge of each otolith was selected to determine the site-specific signatures, and for verifying the congruence between otolith and water signatures. Six laser spots, corresponding distance of  $30 \,\mu\text{m}$  (6 x 5  $\mu\text{m}$ ), were selected because they provided the best discrimination of sites according to several principal component analyses on Mg:Ca, Sr:Ca, Ba:Ca and Sr:Ba ratios, integrating from 1 to 15 successive laser spots from the edges (Supplementary Material Appendix A: Table S1).

The congruence between otolith elemental signatures and ambient water chemistry was verified using linear regressions. For each elemental ratio, the mean value recorded in the six laser spots at the otolith edge was regressed against the mean value recorded in the water samples collected before fish sampling, that is from April to September. The otolith elemental ratios that were significantly related to water chemistry were conserved in following analyses to determine the site-specific signatures. The partition coefficient of elemental ratios (D<sub>ratio</sub>) for each fish was also determined to assess the influence of local environment and fish size on elemental incorporation in otoliths. These coefficients describe the proportion of trace elements in water that are incorporated in otoliths (Campana, 1999) and can therefore be used to detect changes in incorporation rates between sites or according to fish size (Walther et al., 2010). For each elemental ratio, a linear model (i.e. two-way ANOVA) was conducted with the partition coefficient as response variable, whereas the sampling site and fish size (SL mm) were integrated as explanatory variables, along with their interaction. Tukey's HSD tests were then conducted to compare the partition coefficients among the nine river sites. During this study, samples of coastal seawater were not collected; therefore, the partition coefficients for the larval phase were calculated using elemental concentrations reported in a previous study (Riou, 2016). Kruskal-Wallis nonparametric tests were used to compare the partition confidents between the marine and the freshwater phase.

#### Analysis of site-specific signatures 2.6

To assess the spatial variability in water chemistry across the watershed, a principal component analysis (PCA) on the elemental ratios, that is Sr:Ca, Ba:Ca and Sr:Ba, was conducted using all monthly samples collected during 1 year, that is from April 2013 to April 2014. Nevertheless, spatial differences in otolith composition can substantially differ from differences in water chemistry because of variations in the incorporation rate according to sites and fish size. Therefore, to identify clusters of sites with distinct elemental signatures, estimates of elemental concentrations in otoliths were inferred from partition coefficients predicted by the linear models adjusted previously. Partition coefficients were predicted for each date and site using 100 body sizes randomly generated following a uniform distribution on the interval from 40 to 110 mm, that is the range of fish size collected during the study. Then, these modelled partition coefficients were applied to monthly records of water chemistry to obtain expected elemental signatures in otoliths for each site during an annual cycle, integrating the variability related to fish size. A PCA was conducted on these expected signatures to determine the sites, or clusters of sites, presenting distinct elemental signatures over the year. These sites, or clusters of sites, were then used to reconstruct the individual movements.

#### 2.7 Random forest classifier and site attribution

The reconstruction of individual movements was achieved using a random forest classifier (Breiman, 2001), as suggested by Mercier, Mouillot, Bruguier, Vigliola, and Darnaude (2011). Random forest is a machine learning method, which allows freedom from normality and homoscedasticity assumptions and does not require data transformation (Mercier, Darnaude, et al., 2011). The random forest algorithm generates a great number of decision trees. The model prediction (i.e. site attribution) is then commonly obtained by taking the majority vote from all the individual classification trees of the

forest. In this study, we also considered the site that got the secondlargest number of votes to enhance accuracy of model predictions (see Supplementary Material Appendix B). A forest of 500 regression trees was built to predict a site for each laser spot according to the elemental ratios recorded along to the otoliths, that is Sr:Ca, Ba:Ca and Sr:Ba. To identify the signature of marine environment. we randomly selected six laser spots distributed in the central area of each otolith. The limit of this central area was defined by the presence of visible metamorphosis check mark that is formed when the postlarvae return to the rivers (Shen & Tzeng, 2002). The laser spots corresponding to the marine larval stage were combined with the six laser spots of otolith edge to form the matrix used to train the random forest algorithm and evaluate model accuracy. The model was trained using a random selection of four edge spots and four central spots from each individual. The remaining four laser spots of each fish, two at the edge spots and two in the central area, were used to provide estimates of the prediction errors.

Along each transect on the otoliths, the random forest model was used to predict which site corresponded to each spot by taking the majority vote from all the classification trees. However, this classical procedure sometimes results in sporadic isolated predictions within homogeneous sequences as sites are attributed independently of each other (Fablet, Daverat, & Pontual, 2007). These errors in site attribution can cause an overestimation in the number of sites crossed by an individual during its life. In the context of this study, we developed a procedure for correcting this problem (see Appendix SB for detailed explanations of the process and R code). The main idea is to produce sequences consisting in a minimum of three successive similar attributions to ensure the chronological coherence of continuous sequences. In a final step, the effectiveness of attribution process was evaluated by estimating the prediction FRESHWATER FISH

error before and after the sequence corrections using the remaining four laser spots of each fish not used for training the model.

The statistical analyses were performed using the R software, version 3.2.1 (R Core Team, 2014), supplemented by the package "agricolae" for the post hoc Tukey's HSD tests (De Mendiburu, 2014), "ade4" for the multivariate analyses (Chessel, Dufour, & Thioulouse, 2004) and "randomForestSRC" for the random forest algorithm (Ishwaran & Kogalur, 2014).

### 3 | RESULTS

A total of 176 individuals were collected, their number varying between 16 and 23 per sampling site. The mean total length was 74.4 mm (range 41–110 mm SL), and it varied significantly between sites (ANOVA, n = 176, F = 40.1, p < .001). Overall, the pairwise comparisons based on Tukey's HSD test revealed that individuals from the lower reaches (sites A and B) were smaller than those from the other sites, individuals from the upper reaches (sites I and E) being larger (Figure 1; Appendix A: Table S2).

# 3.1 | Congruence between water and otolith chemistry

The water chemistry varied significantly between the nine river sites regarding the four elemental ratios (ANOVAs, n = 108; F = 91.17, p < .001 for Sr:Ca; F = 19.22, p < .001 for Ba:Ca; F = 23.43, p < .001 for Sr:Ba; and F = 11.04, p < .001 for Mg:Ca). The highest Sr:Ca concentrations were recorded in water samples of the sites C, D and I, whereas the lowest were observed in site H (Figure 2). Overall, the sites located in the Bras de Cilaos tributary (sites F, G, H and I)

**FIGURE 2** Concentration of elemental ratios of Sr:Ca (a), Ba:Ca (b), Sr:Ba (c) and Mg:Ca (d) recorded in the water samples collected in the nine river sites (from A to I) along the St-Etienne River watershed. Samples were collected monthly from April 2013 to April 2014. The dashed lines represent the concentrations of Sr:Ca, Ba:Ca and Sr:Ba reported in coastal waters of La Réunion Island by Riou (2016). Among the nine river sites, the letters above the boxes represent homogeneous groups resulting from multiple comparisons based on Tukey's HSD test (Appendix A: Table S3)



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**FIGURE 3** Linear relationships between elemental ratios recorded in water samples and otolith edge of *Sicyopterus lagocephalus*. The mean elemental ratios of Sr:Ca (a), Ba:Ca (b), Sr:Ba (c) and Mg:Ca (d) were calculated for the nine river sites (from A to I) along the St-Etienne River watershed. The vertical and horizontal bars represent the standard deviation

**TABLE 1** Summary of the ANOVAs investigating the effect of fish size (SL mm) and site on the partition coefficient of elemental ratios: (a)  $D_{Sr:Ca}$ , (b)  $D_{Ba:Ca}$  and (c)  $D_{Sr:Ba}$ 

| Variable               | Sum of squares | df  | Mean squares | F-value | p-value |
|------------------------|----------------|-----|--------------|---------|---------|
| (a) D <sub>Sr:Ca</sub> |                |     |              |         |         |
| Fish size              | 0.026          | 1   | 0.026        | 0.77    | .382    |
| Site                   | 32.779         | 8   | 4.097        | 119.81  | <.001   |
| Fish size x Site       | 0.524          | 8   | 0.066        | 1.92    | .061    |
| Residuals              | 5.403          | 158 | 0.034        |         |         |
| (b) D <sub>Ba:Ca</sub> |                |     |              |         |         |
| Fish size              | 0.020          | 1   | 0.020        | 8.02    | .005    |
| Site                   | 0.175          | 8   | 0.022        | 8.80    | <.001   |
| Fish size x Site       | 0.013          | 8   | 0.002        | 0.63    | .748    |
| Residuals              | 0.382          | 154 | 0.002        |         |         |
| (c) D <sub>Sr:Ba</sub> |                |     |              |         |         |
| Fish size              | 106.890        | 1   | 106.894      | 15.64   | <.001   |
| Site                   | 478.190        | 8   | 59.774       | 8.74    | <.001   |
| Fish size x Site       | 9.510          | 8   | 1.189        | 0.17    | .994    |
| Residuals              | 1073.180       | 157 | 6.836        |         |         |

Value in bold indicates *p*-value <.05.

showed lower Ba:Ca values than the other sites (Figure 2b), while an inverse trend was observed for the Sr:Ba concentrations (Figure 2c). The highest Mg:Ca values were recorded in the site H (Figure 2d; Appendix A: Table S3). The elemental ratios recorded in the otolith edges were linearly related to the water composition of sampling sites for the 6 months preceding the fish sampling for Sr:Ca (Figure 3a; n = 9,  $R^2 = .81$ , F = 29.4, p < .001), Ba:Ca (Figure 3b; n = 9,  $R^2 = .71$ , F = 17.1, p < .001) and Sr:Ba (Figure 3c; n = 9,  $R^2 = .82$ , F = 30.9, p < .001). The relationship was not significant for Mg:Ca (Figure 3d; n = 9,  $R^2 = .05$ , F = 0.40, p = .54); therefore, this elemental ratio was excluded from the following analyses because concentrations recorded in otoliths were not directly related to the local environment.

For Sr:Ca, Ba:Ca and Sr:Ba, the partition coefficients were significantly affected by the site where fish were caught (Table 1). The partition coefficient of Sr:Ca was lower than 1 for all sites except site H where it reached a value of 2, which indicates that Sr is being concentrated in otoliths at this site (Figure 4a). The variation of partition coefficients of Ba:Ca and Sr:Ba presented an inverse trend between sites, revealing a gradient in incorporation rate of Ba from downstream to upstream sites, especially from site A to site E (Figure 4b,c). The partition coefficient of Sr:Ca was not affected by fish size (Table 1; Figure 4d), but the incorporation rate of Ba:Ca slightly decreased, whereas that of Sr:Ba increased, with the standard length of fish (Table 1; Figure 4e,f). Although remaining in the same order of magnitude, the partition coefficients of the three elemental ratios for the marine environment differed significantly from those recorded in freshwater sites (Figure 4a-c), even if the site H was excluded from analysis (Kruskal-Wallis tests, all p < .001).

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**FIGURE 4** Partition coefficients of elemental ratios ( $D_{Sr:Ca}$ ,  $D_{Ba:Ca}$  and  $D_{Sr:Ba}$ ) determined for *Sicyopterus lagocephalus* in the nine sites distributed along the St-Etienne River watershed (a,b,c) and according to the standard length of fish (d,e,f). Among the nine river sites, the letters above the boxes represent homogeneous groups resulting from multiple comparisons based on Tukey's HSD test (Appendix A: Table S4). The partition coefficients estimated for the marine environment are also presented. The average trends in the relationships between partition coefficient and fish size are indicated by dashed lines. Outliers excluded from the analysis are represented in the graphs



**FIGURE 5** Multivariate analysis of spatial changes in water chemistry during an annual hydrological cycle along the St-Etienne River watershed (a) and the expected elemental signatures in otolith of *Sicyopterus lagocephalus* (b). The correlation circles reflect the association of elemental ratios (Sr:Ca, Ba:Ca and Sr:Ba) with the two-first axes of the PCAs. Otolith elemental ratios were inferred from water chemistry using the partition coefficients derived from the linear models integrating the effects of site and fish size. The vertical and horizontal bars represent the standard deviance. The dashed circles in colours indicate the site and clusters of sites with distinct elemental signatures used to reconstruct the fish movements

### 3.2 | Insights on site-specific signatures

The first factorial plan of the PCA performed on the water chemistry during an annual hydrological cycle explained 93.5% of the total variation (axis 1: 58.6% and axis 2: 34.9% of explained variation) and revealed spatial variations of water chemistry within the watershed (Figure 5a). Distinct geochemical signatures were identified for two sites (H and I) and two clusters of sites (cluster of sites A-B-C-D-E and cluster F-G). For these sites, or clusters of sites, the annual variability in water chemistry did not induce substantial overlap **TABLE 2** Classification accuracy obtained from the attribution process (a) before and (b) after the sequences were corrected (see text and Appendix SA for details)

|   | Percentages of correct | Localities attributed for each laser spot |               |        |     |
|---|------------------------|---|---------------|--------|-----|
| Sampling locality                       | classification         | Cluster A-B-C-D-E                         | Cluster F-G-H | Site I | Sea |
| (a) Before the sequences were corrected |                        |   |               |        |     |
| Cluster A-B-C-D-E                       | 95.59                  | 195                                       | 7             | 2      | 0   |
| Cluster F-G-H                           | 92.59                  | 6   | 100           | 2      | 0   |
| Site I                                  | 92.5                   | 1   | 2             | 37     | 0   |
| Sea                                     | 99.72                  | 0   | 0             | 1      | 351 |
| (b) After the sequences were corrected  |                        |   |               |        |     |
| Cluster A-B-C-D-E                       | 97.06                  | 198                                       | 4             | 2      | 0   |
| Cluster F-G-H                           | 94.44                  | 5   | 102           | 1      | 0   |
| Site I                                  | 100                    | 0   | 0             | 39     | 0   |
| Sea                                     | 100                    | 0   | 0             | 0      | 352 |

The percentages of correct attributions are presented for each locality with the associated classification matrix.

between localities. The first factorial plan of PCA conducted on otolith elemental ratios inferred from water chemistry explained 90.0% of the total variation (axis 1: 64.2% and axis 2: 25.8% of explained variation). Although the general trends were similar to those reported for the water chemistry, the elemental signature of site H overlapped with that of cluster F-G (Figure 5b). This change is essentially related to the high rate of incorporation observed for Sr:Ca in site H which buffers the variation in water chemistry. Consequently, sites F, G and H were merged to form a single cluster (cluster F-G-H). The final clustering allowed to clearly separate the St-Etienne River and Bras de la Plaine tributary (cluster A-B-C-D-E) from the Bras de Cilaos tributary (cluster F-G-H), which also differed from the upper site I (Figure 5b). The elemental signatures of these localities were assumed stable enough to support robust interpretation of fish movement patterns. Indeed, inferences about otolith composition integrated sources of variability related to annual hydrological cycle, site-specific incorporation rate and fish size.

### 3.3 | Model training and attribution accuracy

The attribution process was achieved using four localities: sea, cluster A-B-C-D-E, cluster F-G-H and site I. The random forest classifier was trained using 1,408 laser spots, 704 from the central area of the otoliths and 704 from their edge (i.e. four spots by otolith area for each individual, the total number of individuals being 176). The percentage of correct classification was on average 97.0% before the sequences were corrected, values ranging from 92.5% to 99.7% depending on localities (Table 2). After the sequences were corrected, 3.1% of the whole initial attributions were modified (1,107 laser spots). A total of 42 laser spots (0.1% of the total attributions) were suppressed because they remained isolated after the sequences were corrected. When sequences were corrected, the percentage of correct classification raised to an average of 98.3% (Table 2), and the spots corresponding to the marine period of life became clearly segregated from freshwater signatures (100% of correct classification).

Similarly, the river localities were also well discriminated, the percentages of correct classification ranging from 94.4% to 100.0%. The number of movements estimated for fish was reduced by suppressing the short transitions caused by isolated predictions (i.e.  $7.4 \pm 5.9$  [mean  $\pm$  *SD*] before corrections and  $3.5 \pm 2.3$  after applying the correcting process).

### 3.4 | Reconstruction of lifetime movements

All analysed specimens had experienced a marine phase before recruiting in the St-Etienne watershed where they settled for the rest of their life. The overview of individual sequences emphasised a settlement phase once entering the river during which most of the fish were briefly assigned to downstream reaches, that is cluster A-B-C-D-E (Figure 6). Although the elemental signature of this cluster was observed for 84.8% of fish after the marine signature, some individuals were directly assigned to the cluster F-G-H, or the upstream site I (10.1% and 5.2% respectively). For fish caught at site I, 13.9% were directly assigned to the cluster F-G-H and 27.7% to site I. Moreover, most of individuals firstly assigned to the downstream reaches rapidly reached the upstream site I, without being assigned to the middle location (i.e. cluster F-G-H). This indicates that an important proportion of *S. lagocephalus* progress rapidly through the watershed.

After the settlement phase, the fish assignations were more stable over the time and frequently corresponded to the sampling sites where the fish were caught (Figure 6). Overall patterns of lifetime movements suggested very few displacements between distant localities, especially between the two main tributaries of the watershed (i.e. Bras de la Plaine versus Bras de Cilaos). These movements between the two main tributaries were essentially observed for individuals caught at sites B, C and F, that is close to the tributaries' junction and <5 km distant from each other. In contrast, small-scale movements appeared more frequent within the Bras de Cilaos tributary, for which the spatial dissimilarity in elemental signatures allowed discriminating sites along the longitudinal gradient. For instance, 83.3% and 81.2%



FIGURE 6 Overview of the individual sequences for both sides of the otolith of Sicyopterus lagocephalus after entering in the St-Etienne River, La Réunion. Fish caught in the nine sampling sites (from site A to site I) were used to reconstruct the movements across three localities (cluster A-B-C-D-E, cluster F-G-H and site I). Sites in blue colour are located in the St-Etienne River or in the Bras de la Plaine tributary, whereas sites in orange and red are located in the Bras de Cilaos tributary

of fish caught respectively in middle sites F and G were assigned at least once to the upstream site I throughout their lifetime. Similarly, all fish caught in the site I completed at least one round trip to the middle reaches (cluster F-G-H), but these downstream movements were not related to periodic trends. Such downstream movements cannot be examined for fish caught at site H because of signature overlap with the sites F and G, but the stability of attributions to the site H indicated that fish movements between upstream sites H and I were extremely rare. This result suggests that once S. lagocephalus completed their first upstream migration, they tended to use the same migration route and did not explore other tributaries.

#### DISCUSSION 4

# 4.1 | Otolith signatures and relationship with water chemistry

The reconstruction of fish movements based on otolith signatures is challenged by the ability to detect and interpret elemental differences relating to water chemistry (Elsdon et al., 2008). Several studies have been conducted in tropical streams, but most of them focused on large-scale variations among river basins, or along coarse estuarine gradients (Hogan et al., 2014; Lord et al., 2011; Smith & Kwak, 2014b; Tabouret et al., 2011). Among these studies, few considered the relationship between elemental signatures of water and otoliths (Huey et al., 2014; Pouilly, Point, Sondag, Henry, & Santos, 2014). Low concentrations of trace elements are commonly expected in coastal rivers of tropical regions where water chemistry is closely related to the substratum composition (Louvat & Allègre, 1997).

In the present study, although 20 trace elements were initially tracked, only Mg, Ba, Sr and Ca overstepped the analytic detection limits in otoliths, and Sr:Ca, Ba:Ca and Sr:Ba elemental ratios revealed a strong congruence with water chemistry. As reported in previous studies (e.g. Elsdon & Gillanders, 2002), the Mg:Ca signature recorded in otoliths was not directly related to ambient water chemistry. The Mg concentration in otoliths is influenced by other factors, such as physiological processes; therefore, this trace element appears unlikely to reflect spatial patterns in the watershed (Elsdon et al., 2008). For the three other elemental ratios, the results indicated significant effects of fish size and sampling site on partition coefficients. These differences in incorporation rates between river sites may have been influenced by endogenous processes and local environmental conditions, including temperature, type of sediment or food availability (e.g. Bath et al., 2000; Elsdon & Gillanders, 2002; Tabouret et al., 2011; Walther et al., 2010). The most obvious effect was observed for the site H where Sr concentration in water was the lowest of all the river sites and where the partition coefficient of Sr:Ca was greater than 1. This indicates that Sr is being concentrated in otoliths and suggests that complex mechanisms are involved in regulating elemental deposition when some elements are in low concentrations in water. Further laboratory experiments are required to confirm whether the relationship between water and otolith concentration can become nonlinear when a species-specific threshold of concentration in water is reached (Bath et al., 2000). Although the Ba:Ca partition Ecology of FRESHWATER FISH

coefficients varied between sites, the amplitude of variations was less noticeable than for the Sr:Ca and essentially reflected a longitudinal gradient along the watershed. A similar, but inverse, pattern was observed for Sr:Ba partition coefficients. Both patterns are probably related to the decrease in water temperature from downstream to upstream sites. Temperature is known to have an impact on the incorporation of Ba in otoliths (Elsdon & Gillanders, 2002), although the effect of temperature on Sr and Ba incorporation may vary between species (Bath et al., 2000; Walther et al., 2010). Alternatively, Tabouret et al. (2011) suggested that differences in biofilm composition consumed by grazing fish, such as *S. lagocephalus*, may induce variation in Ba otolith concentration.

An additional source of variability in otolith composition can be related to fish body size and developmental stage, which are generally correlated with the growth rate (Chittaro, Hogan, Gagnon, Fryer, & Sale, 2006; Elsdon et al., 2008; Walther et al., 2010). Despite significant differences between marine and freshwater life stages, the partition coefficients of the three elemental ratios remained relatively similar for S. lagocephalus in comparison with findings previously reported between life stages of other species, such as the bicolour damselfish, Stegastes partitus (Chittaro et al., 2006). This result confirms that the change in otolith elemental signatures of S. lagocephalus between the marine larval phase and the juvenile/adult freshwater phase indicates a habitat shift rather than an ontogenetic artefact (Lord et al., 2011). On the other hand, our results revealed that the Ba incorporation was weakly, but significantly, influenced by fish size during the freshwater phase, whereas the Sr partition coefficient remained unaffected. It is likely that the Ba partition coefficient decreased progressively in response to the decrease in the growth rate over the fish life. Although a progressive diet shift could also explain the relationship (Walther et al., 2010), this hypothesis is unconvincing because juveniles and adults of S. lagocephalus feed on biofilm as soon as they enter freshwater (Bielsa et al., 2003).

Ontogenetic and site-specific effects on otolith deposition are important factors to consider for reconstructing fish movements across river locations because otolith signatures can substantially differ from the direct records of water chemistry. Accounting for these sources of variations, three localities within the small watershed of St-Etienne River were segregated on the basis of their water chemical signatures, which were reflected in otoliths. The elemental signatures of the downstream sites (A and B) were comparable to those recorded in sites located in the Bras de la Plaine (sites C, D and E) certainly because water inputs of this tributary are much greater. The upstream site I was clearly segregated from the other sites (F, G and H) located in the Bras de Cilaos, allowing disentangling smallscale movements of fish along this part of the watershed. Despite substantial fluctuations during the annual hydrological cycle, the spatial structure was stable enough over the year to avoid signatures overlapping between the different localities. The changes in otolith signatures are thus assumed to reflect fish movements between localities, rather than the temporal variability of the elemental composition for a given locality.

### 4.2 | Reconstruction of fish movements

Several methods have been proposed to assign localities from otolith elemental composition, but random forest classifier is particularly efficient for multi-elemental data (Mercier, Darnaude, et al., 2011). The high prediction accuracies reached in our study were comparable to those obtained with similar methods for fish in mangrove areas (Paillon, Wantiez, Kulbicki, Labonne, & Vigliola, 2014). However, the attribution process frequently generates isolated unlikely predictions because sites are attributed independently of each other. To limit the overestimation in the number of fish movements between localities, a simple correcting process focusing on the doubtful parts of individual sequences (i.e. isolated attributions) was developed. The temporal dimension of otolith sequences has also been considered in other studies, for instance using a signal-processing procedure embedded in a Bayesian framework (Fablet et al., 2007). Overall, such quantitative approaches enable a nonsubjective reconstruction of fish movements when compared to visual interpretations of otolith elemental composition (Vignon, 2015).

The final clustering properly discriminated a larval period in the ocean for all the *S. lagocephalus* specimens. This result supports previous studies that demonstrated the amphidromous behaviour of this species, without evidence of facultative marine migration (Lord et al., 2011). As for most of Sicydiinae, larvae die after three or four days in freshwater (Ellien et al., 2011; Valade et al., 2009). Moreover, the steep rivers with high flow velocity of La Réunion Island rapidly flush fish larvae into the marine environment as they cannot resist the strong river currents (Lagarde et al., 2017). Steep flowing streams do not provide suitable habitats for larval retention in freshwater (e.g. Huey et al., 2013). It can be safely concluded that larvae of *S. lagocephalus* experience a mandatory marine phase lasting four to ten months (Teichert et al., 2016).

The upstream migration of amphidromous gobies has mainly been described using conventional methods based on sampling nets or electrofishing in few sites (e.g. Bell, Brown, & Pepin, 1995; Lagarde et al., 2015). These approaches provided a partial view of fish movements at the watershed scale. In contrast, otolith microchemistry used in this study allowed focusing on the successive habitats occupied by fish over their entire life after they recruit in rivers. In this study, the first freshwater habitats attributed to most juveniles of S. lagocephalus were generally those of downstream localities (cluster of sites A-B-C-D-E). This probably suggests that most fish need some time to complete their metamorphosis into juveniles (Keith et al., 2008). However, a fast progression to the upper reaches was the strategy undertaken by some individuals, especially for those collected in the upstream site I located at least 18 km from the river mouth. These contrasted migratory patterns may originate from differences in the individual condition or from exogenous factors, such as habitat availability or biotic interactions, that are known to affect the ability of juveniles to settle in adults' habitats (Keith et al., 2008; Schoenfuss et al., 2013). Nevertheless, it is important to note that the movement patterns were reconstructed only from fish

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that survived and reached a large size. Some type of movements may thus be underrepresented in our study, especially those associated with higher rates of mortality during juvenile or young adult stage.

Movements of adult fishes within river continuum have been reported for several amphidromous species (Fitzsimons, McRae, & Nishimoto, 2007; Koster et al., 2013; Smith & Kwak, 2014a), including S. lagocephalus (Lagarde et al., 2015; Lord et al., 2011). However, the results of this study indicate that individuals did not appear to move much between the two main tributaries and that most showed a strong site fidelity to a particular part of the watershed during their entire lifetime. This limited dispersion of adults appears in accordance with the territorial lifestyles commonly reported in Sicydiinae species (Fitzsimons & Nishimoto, 1990; Keith, 2003). Moreover, the results indicated a restricted exploratory behaviour across tributaries of the watershed because fish tend to use the same tributary when completing longitudinal movements. It is likely that males are more territorial than females because they need to select a place where they take care alone for the eggs until hatching (Teichert, Keith, et al., 2013). However, the assumption that the males travel less frequently and/ or far than the females should be addressed by future investigations because the sex of individuals was not recorded in this present study.

Overall, fish movements along the longitudinal gradient appeared to be constrained between adjacent localities, although scarce distant displacements were observed. The hypotheses explaining these displacements are generally related to fish competition for habitat (Fitzsimons & Nishimoto, 1990), extreme climatic events that induce fish flushing (Lagarde et al., 2015; Smith & Kwak, 2014a), or reproduction (Koster et al., 2013; Lord et al., 2011). Adults of some amphidromous species move to downstream spawning grounds probably for shortening the distance larvae must travel to the sea (McDowall, 2009) and thus reducing the risk of mortality due to predation or starvation (Bell, 2009; Closs & Warburton, 2016). However, the current study did not reveal any periodic trends in S. lagocephalus movements. Moreover, field surveys conducted on different rivers of La Réunion Island demonstrated that egg clutches and larvae of S. lagocephalus can be found more than 20 km from the river mouth (Lagarde et al., 2017; Teichert, Valade, et al., 2013). It is thus unlikely that fish movements observed in this study were related to reproduction. Once settled, adults of Sicydiinae species are known to have a small territory (Fitzsimons, Nishimoto, & Yuen, 1993), and to show a strong fidelity to their territory over the years (Fitzsimons & Nishimoto, 1990). Displacements due to foraging behaviour are thus unlikely to explain most of the movements reported during this study. On the other hand, tropical rivers are regularly subjected to extreme cyclonic floods that induce sudden increases in river discharge and strongly affect the structure of fish communities (Chen, Wen, Meng, Cherh, & Shao, 2015; Fitzsimons & Nishimoto, 1995; Monti & Legendre, 2009; Smith & Kwak, 2015). For instance, Smith and Kwak (2014a) explained the higher displacement rate of the freshwater mullet, Agonostomus monticola, in rivers of Puerto Rico as a result of cyclonic floods. Floods may thus explain the movement patterns of S. lagocephalus observed

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in La Réunion Island, where Lagarde et al. (2015) reported adults recolonising upper reaches after flood events. Despite the recurrence of extreme floods in tropical streams, their impact on the spatial structure of aquatic fauna remains poorly documented (Chen et al., 2015; Fitzsimons & Nishimoto, 1995; Smith & Kwak, 2015) and deserves further investigation.

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### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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# Annexes 4 :

Lagarde R, Teichert N, Grondin H, Gaudin P & Ponton D. Influence of larval and juvenile life history on age at first maturity in two amphidromous fish species. *Soumis à Marine and Freshwater Research en décember 2017*.



# Influence of larval and juvenile life history on age at first maturity in two tropical amphidromous fish species

| Journal:                      | Marine and Freshwater Research  |
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| Keyword:                      | ecology, freshwater, otoliths, population dynamics, reproductive biology, saltwater   |
|                               |   |



- Influence of larval and juvenile life history on age at first maturity in two 1
- 2 tropical amphidromous fish species
- Running headline: Age at first maturity of amphidromous fish 3
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## 16 Abstract

17 Age at first maturity is of major importance for understanding fish ecological strategies. This 18 study investigates how age at first maturity of two tropical amphidromous species 19 Sicvopterus lagocephalus and Cotylopus acutipinnis varies regarding to their larval and juvenile life history. Reproductive stage was estimated based on histological observation of 20 ovaries of more than 200 females of each species caught monthly over a year. The age of all 21 fish was estimated by interpreting the daily increments deposed on otoliths during the oceanic 22 23 larval phase, and the juvenile phase in the river. The age at first maturity was approximately 9 24 months for S. lagocephalus and 7 months for C. acutipinnis, i.e. 2.5 to 4.5 and 3.0 to 4.5 months after they returned in freshwater respectively. For both species, the time spent in 25 26 freshwater before maturity was significantly influenced by the duration of the larval stage in 27 sea (PLD) and the season of return in freshwater. Individuals with a long PLD, or returning in freshwater during the warmer season, maturated faster once in freshwater. This reproductive 28 strategy may minimize the risk of extirpation due to catastrophic events at each generation 29 30 and thus probably benefit to amphidromous species living in very unpredictable tropical 31 rivers.

32 Keywords : *Cotylopus acutipinnis*, Diadromy, Gobiidae, Reproductive strategy,

33 Sicyopterus lagocephalus

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# Introduction

36 Age at first maturity (AFM) is one of the four major life-history traits describing fish species 37 strategies (He and Stewart, 2001), the way AFM varies indicating how species react to natural 38 and anthropogenic disturbances (Winemiller and Rose, 1992). Fish species with an opportunistic strategy (sensu Winemiller and Rose, 1992) are characterized by a low AFM 39 and a continuous reproductive effort. These opportunistic species have strong (re)colonizing 40 41 capacities and are expected to be less sensitive to frequent and stochastic disturbances (Winemiller and Rose, 1992). However, within a given species, AFM can vary among 42 43 individuals as it strongly depends to individuals' life history traits. For example, Nile tilapia, Oreochromis niloticus (Linnaeus, 1758) growing rapidly during their juvenile stage reach 44 maturity at a younger age than individuals that grew slower (Duponchelle and Panfili, 1998). 45 Describing the variability of AFM regarding to different parameters of individual life history 46 47 thus appears crucial to better understand the whole range of strategies fish species can 48 develop.

The fish fauna inhabiting the rivers of small tropical islands is mainly composed of species 49 50 migrating between the freshwater and sea (McDowall, 1997). Most of these species are amphidromous (Keith, 2003): they reproduce in freshwater, their larvae drift to the sea where 51 52 they grow during several months before returning in freshwater as post-larvae or young 53 juveniles (McDowall, 1988). Then, their juveniles grow and become adults in freshwater. 54 Amphidromous fish successively inhabit two different environments where seasonal 55 variations of different parameters, especially temperature, impact their biology. For example, 56 Teichert et al. (2012, 2016a) demonstrated that larval growth of Sicyopterus lagocephalus 57 (Pallas, 1770) and Cotylopus acutipinnis (Guichenot, 1863), two amphidromous gobies, was positively correlated to sea water temperature. After they returned in freshwater, seasonal 58

variation of the size at first maturity was observed for both species, individuals maturing at a
smaller size during the summer months (Teichert et al., 2014a, 2016b).

In Reunion Island, S. lagocephalus and C. acutipinnis dominate the freshwater fish 61 62 assemblages. These two species grow and reproduce in sympatry from the estuary to more than 600 m above sea level (Teichert et al., 2013, 2014b). Sicyopterus lagocephalus is a 63 cosmopolite species that recently colonized numerous islands from eastern Pacific Ocean to 64 western Indian Ocean (Keith et al., 2005a). Oppositely, C. acutipinnis is endemic to the 65 Mascarenes Archipelago (Keith et al., 2005b). Females of both species are multiple spawners 66 and present similar fecundity of 13,000 to 15,000 eggs per gram of female (Teichert et al., 67 2014a, 2016b). However, the AFM of both species, and its eventual variations in regard to 68 other parameters of individual life history, has never been described. 69

In this context, the present study first aimed at describing the AFM of *S. lagocephalus* and *C. acutipinnis* based on histological observation of ovarian samples, and interpretation of otoliths daily increments. The second objective was to determine how the duration of the larval and the juvenile stages influenced the AFM of each species. To achieve these objectives, the feasibility of aging fish using the daily increments deposition on otoliths after they return in freshwater had first to be validated.

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# Materials and methods

# 77 Validation of daily rhythm of increments deposition on otoliths

Post-larvae of *S. lagocephalus* (N>30) and *C. acutipinnis* (N>30) were collected immediately
after their returned in freshwater, in December 2012 and March 2014 respectively, at the
mouth of Saint Etienne River (Fig. 1) using a portable electro-shocker (Hans Grassel IG 2002). Fish were immediately transported to the lab in two aerated 101 buckets fill with water

82 from the river. Individuals of both species were reared separately in a 1000 l and 200 l tank respectively. They were fed with periphyton covered cobbles that were collected in the same 83 river. The cobbles were renewed every three days to provide sufficient food. 84 85 Sicyopterus lagocephalus were reared for 70 days whereas C. acutipinnis were reared for 40 days regarding to the increasing difficulty to feed individuals as they grow larger. The water 86 87 temperature during the rearing period was kept at 25±1°C, a temperature regularly observed 88 in Reunionese rivers (Teichert et al., 2014a), and the lightning conditions were 12 h light and 89 12 h dark.

When arrived at the lab, all individuals were immersed in a 301 aerated tank containing a 100 mg.1<sup>-1</sup> solution of alizarin Red-S (ARS) during 12 h. This immersion produced the initial mark before fish rearing (M0) in the otoliths. A second mark (M1) was produced using the same protocol after 14 and 12 days of rearing, and the third mark (M2) after 28 and 29 days of rearing for *S. lagocephalus* and *C. acutipinnis* respectively. A fourth mark (M3) was only produced for *S. lagocephalus* after 62 days of rearing. At the end of their rearing period, fish were all euthanatized with an overdose of eugenol and preserved in 95% ethanol.

Among reared individuals, 28 S. lagocephalus and 33 C. acutipinnis were randomly selected 97 and their pair of sagittal otoliths was extracted under a binocular microscope. Two technics 98 99 can be used for aging fish based on otoliths microstructures: interpreting the microstructures 100 of the whole otolith, or after sectioning the otoliths. Interpreting the microstructures of the 101 whole otolith is much faster, and has been proven accurate for larvae and small juveniles 102 including Sicydiinae gobies (Teichert et al. 2012, 2016a). However, this technic may become 103 inaccurate when fish become older, in this case, interpreting the structure of sectioned otolith is necessary (Sponaugle, 2009). The two different technics were used to verify that the daily 104 105 rhythm of increments deposition on otoliths was validated whatever the technic was used. For 106 Interpreting the structure of the whole otolith, 23 otoliths of S. lagocephalus and 27 otoliths of 107 C. acutipinnis (randomly left or right) were placed in a drop of immersion oil, examined at 400X trough transmitted light microscope (Olympus CX41) and photographed with a 108 microscope camera (Olympus C-5060). The locations of the marks were determined by 109 examining and photographing the otoliths under UV light with the same microscope fitted 110 111 with a fluorescent attachment (Olympus U-RFLT50). Estimation of the number of increments 112 between each mark was performed with IMAGE J 1.47 software (Rasband, 2015). For 113 interpreting the structure of sectioned otoliths, an additional 5 otoliths for S. lagocephalus and 114 7 for C. acutipinnis were embedded in Crystal-Bond and grinded using grinding discs of 115 decreasing grades (800 and 1200) to expose the otolith core. Sectioned otoliths were examined, photographed and analyzed as described previously. 116

The validation of the daily rhythm of increments deposition on the otoliths was performed using linear regression between the estimated number of increments and the known number of rearing days. If the slope and intercept of the regression were not significantly different from 1 and 0 respectively, the daily deposition of increments was validated (Panfili et al., 2002). The technics for interpreting the structure of the otolith (i.e. whole or sectioned otolith) was included as qualitative factor to the regression, and its significance tested with a test of deviance reduction using the *F* statistic.

# 124 Estimation of age at first maturity

Fish were collected on a mid-stream reach of Marsouins River located at 2.2 km from the river mouth (Fig. 1) every month between January and December 2011. The water temperature was continuously recorded every 20 mn with Gemini Data Loggers Tinytag Aquatic 2 (precision 0.5 °C). A minimum of 50 point-abundance samples (Persat and Copp 1990) randomly distributed in the station were performed by electrofishing (portable electroshocker, Hans Grassel IG 200-2). Females smaller than 54 mm total length ( $L_T$ ) and 39 mm
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131  $(L_{\rm T})$ , which are the maximum sizes at first maturity observed over a year for *S. lagocephalus* 132 and *C. acutipinnis* respectively (Teichert et al., 2014a, 2016b), were collected. In the field, 133 females were identified based on the form of their urogenital papilla. In the laboratory, each 134 female was classified as immature or mature (i.e. in one of the following reproductive phase: 135 developing, spawning capable, spent, regressing and regenerating) based on histological 136 observations of its ovarian tissues performed following Teichert et al. (2014).

137 Paired sagittal otoliths of each female were extracted, and one otolith (randomly left or right) was embedded in Crystal-Bond and grinded using grinding discs of decreasing grades (800 138 139 and 1200) to expose the otolith core. Otoliths were examined, photographed and analyzed following the protocol described in the experiment of validation of daily rhythm of increments 140 141 deposition on otoliths. In Sicydiinae, the transition between sea and freshwater is 142 characterized by a metamorphosis check mark, i.e. a structural discontinuity on the otolith 143 (Shen and Tzeng, 2002). On otoliths of fish captured in freshwater, the pelagic larval duration 144 (PLD) can be estimated by counting the number of increments from the core to the check mark. Identically, the freshwater duration (FD) corresponds to the number of increments 145 located from the check mark up to the edge of the otolith. As the date of capture for each 146 147 individual is known, FD allows to estimate the date of return in freshwater, when the sum of PLD and FD, i.e. the age of the individual, allows to calculate the date of hatching. 148

Estimation of PLD and FD were performed without knowing the sampling date or the fish length by an experimented operator (Operator A, N. Teichert). A subsample of 60 otoliths for each species was also blindly examined (without knowing the results of the first operator, the sampling date, or the fish length) by another experimented operator (Operator B, H. Grondin). The PLD and FD estimated by each operator were compared using orthogonal regressions. If the slope and intercept of the regression between the estimations made by operators A and B were not significantly different from 1 and 0 respectively, it was assumed that estimations ofPLD and FD were consistent between the two operators.

#### 157 Statistical analysis

The age at first maturity was estimated using logistic general linear models (GLM). Maturity was considered as a binary variable (immature/mature), the age of the females being the explanatory variable. Age at first maturity was considered as the age when 50% of the females were mature ( $A_{50}$ ).

To investigate if the date of return in freshwater influenced the moment females became 162 163 mature, the duration of the period in freshwater when 50% of the females were mature (FD<sub>50</sub>) 164 was estimated for different periods. According to their date of return in freshwater, females were grouped in three periods. These four-month periods were defined according to the 165 166 variations of the mean water temperature observed at the sampling site during the 30 days 167 before sampling (Table 1). The three periods also correspond to the maximum reproductive 168 season, the minimum reproductive season and the beginning of the reproductive season based 169 on observations made on ovaries and drifting larvae (Teichert et al., 2014a, 2016b; Lagarde et 170 al., 2017). Maturity of females, considered as a binary variable (immature/mature), was 171 explained using logistic GLM with FD, the period of return in freshwater and the interaction between FD and the period of return in freshwater as explanatory variables. 172

Finally, the effect of individual PLD on  $FD_{50}$  was described using logistic GLM with FD, and the interaction between FD and PLD, as explanatory variables. For all GLMs the significance of explanatory variables was tested with a test of deviance reduction using the *Chi*<sup>2</sup> statistic. All statistical analyses were performed with the open source R v. 3.3.1 software (R Development Core Team, 2016) 178

#### Results

#### 179 Validation of daily increments

For all observed otoliths (N= 61), the location of the metamorphosis check mark 180 superimposed on the initial ARS mark M0. The technic for interpreting the structure of the 181 otoliths (i.e. whole or sectioned otolith) did not influence the estimated FD ( $F_{1,58} = 0.25$ ; 182 183 P = 0.62 for *S. lagocephalus* and  $F_{1,60} = 0.58$ ; P = 0.45 for *C. acutipinnis*). For S. lagocephalus the mean ( $\pm$  standard deviation) estimated number of increments 184 185 corresponded to the number of rearing days between M0 and M1  $(13.9 \pm 0.3 \text{ and } 14 \text{ days})$ 186 respectively) and between M0 and M2 ( $27.8 \pm 1.0$  and 28 days respectively). However, the 187 mean estimated number of increments was slightly lower than the number of rearing days between M0 and M3 ( $60.0 \pm 1.7$  and 62 days respectively). The intercept of the regression 188 between the estimated number of increments and the number of rearing days (from M0 to M3) 189 was not significantly different from 0 (intercept = -0.61;  $t_{58} = -1.3$ , P = 0.11) whereas the slope 190 was significantly different from 1 (slope = 1.04;  $t_{58} = 4.2$ , P < 0.001; adjusted R<sup>2</sup> = 0.99). 191 192 When only considering the rearing period between M0 and M2, the intercept and slope of this regression were not significantly different from 0 and 1 respectively (intercept = -0.24;  $t_{32} = -$ 193 0.4, P = 0.69; slope = 1.00;  $t_{32} = 0.1$ , P = 0.91; adjusted  $R^2 = 0.98$ ). For *C. acutipinnis* the 194 195 mean estimated number of increments corresponded to the number of rearing days between 196 M0 and M1 (15.4  $\pm$  1.4 and 15 days respectively) and between M0 and M2 (29.0  $\pm$  1.4 and 29 days respectively). The linear regression between the estimated number of increment and the 197 198 number of rearing days confirmed these results. The intercept and the slope of the regression were not significantly different from 0 and 1 respectively (intercept = 0.89;  $t_{60} = 1.4$ , P = 0.16; 199 200 slope = 0.97;  $t_{60}$  = 1.0, P = 0.31; adjusted R<sup>2</sup> = 0.95).

#### 201 Estimation of age at first maturity

202 Between 18 January 2011 and 14 December 2011, the mean water temperature during the 203 30 days before the sampling ranged between 18.1 and 22.0 °C. A total of 205 S. lagocephalus ranging from 29 to 54 mm  $L_{\rm T}$ , and 223 C. acutipinnis ranging from 22 to 39 mm  $L_{\rm T}$ , were 204 205 captured (Table 1). For each species, the slope and intercept of the orthogonal regressions between the estimations of PLD and FD made by operators A and B were not significantly 206 207 different from 1 and 0 respectively (Table 2). Moreover, the Pearson correlation coefficients 208 of these regressions  $(R^2)$  ranged for 0.95 to 0.98 traducing high estimation consistency 209 between the two operators. It was safely concluded that the values of PLD and FD estimated 210 by the two independent operators were not significantly different, and operator A analyzed the 308 remaining otoliths. 211

The estimated age (PLD+FD) of the analyzed females ranged from 124 to 392 days for *S. lagocephalus*, and from 123 to 316 days for *C. acutipinnis* (Fig. 2). The age at first maturity (A<sub>50</sub>)  $\pm$  standard error (SE) estimated by the logistic GLMs was 276  $\pm$  8 days (df = 203, Chi<sup>2</sup> test p < 0.001), i.e. approximately 9 months, for *S. lagocephalus* (Fig. 2a) and 219 days  $\pm$  2 days (df = 221, Chi<sup>2</sup> test p < 0.001), i.e. approximately 7 months, for *C. acutipinnis* (Fig. 2b).

217 The estimated FD of the analyzed females ranged from 8 to 196 days for S. lagocephalus, and from 16 to 216 days for C. acutipinnis. The FD as well as the period of return in freshwater 218 219 significantly influenced the moment the females became mature for the two species (Table 3). 220 The lowest FD<sub>50</sub> ( $\pm$  SE) was observed for females of S. lagocephalus returning in freshwater 221 between January and April (FD<sub>50</sub> =  $70 \pm 5$  days, i.e. approximately 2.5 months, Fig. 4a). For C. acutipinnis, the lowest FD<sub>50</sub> was observed for females returning in freshwater between 222 September and December (FD<sub>50</sub> =  $90 \pm 7$  days i.e. approximately three months Fig. 4b). The 223 highest values of FD<sub>50</sub> (130 ± 8 days for S. lagocephalus and 130 ± 6 days for C. acutipinnis, 224 225 i.e. approximately 4.5 months) were observed for females of both species returning in fresh 226 water between May and August. Sicyopterus lagocephalus females returning in freshwater

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between September and December had a  $FD_{50}$  of  $90 \pm 10$  days when *C. acutipinnis* females returning in fresh water between January and April had a  $FD_{50}$  of  $120 \pm 9$  days, i.e. approximately three and four months respectively.

230 The estimated PLD of the analyzed females ranged between 86 and 289 days for S. lagocephalus, and between 66 and 171 days for C. acutipinnis (Fig. 4). For each species, 231 the FD<sub>50</sub> decreased significantly with PLD (Table 4, Fig. 4). This result indicates that the 232 233 longer the fish stayed in the ocean as larvae, the faster they matured once returned in freshwater. For example, *S. lagocephalus* with a PLD of 100 days had a FD<sub>50</sub> of 150 days but 234 235 when their PLD reached 250 days, their  $FD_{50}$  decreased to 70 days. In a similar way, 236 C. acutipinnis with a PLD of 70 days had a  $FD_{50}$  of 140 days when their PLD reached 160 237 days, their FD<sub>50</sub> decreased to 100 days. In other terms, for S. lagocephalus a decrease by 53%238 of the FD<sub>50</sub> is observed when the PLD increases of 150%, these values are respectively 29% 239 and 129% for C. acutipinnis.

To summarize the results of this study, when reaching their age at first maturity, females of 240 241 S. lagocephalus had always a PLD at least equal to, or greater than, their  $FD_{50}$ : PLD was between 4.4 and 6.7 months when  $FD_{50}$  was between 2.5 and 4.5 months (Fig. 5a). 242 Oppositely, for females of C. acutipinnis, the relative length of their PLD and FD varied 243 244 depending on the period they returned in freshwater. Females retuning in freshwater earlier in the year had a PLD shorter than  $FD_{50}$ . When returning later in the year, their PLD became 245 246 longer, and their  $FD_{50}$  became shorter (Fig. 5b). As a result, for each period of return in freshwater considered, the ratio between PLD and  $FD_{50}$  was more elevated for 247 248 S. lagocephalus, ranging between 1.0 and 2.7, than for C. acutipinnis, ranging between 0.7 and 1.2 only. 249

#### 250

#### Discussion

#### 251 Otolith daily increments in freshwater

252 This study confirmed the expected daily rhythm of increment deposition in otoliths of 253 S. lagocephalus and C. acutipinnis after they returned in freshwater. This observation is 254 consistent with two other studies that validated the daily rhythm of increment deposition 255 during the larval period of *Sicyopterus* species (Iida et al. 2010; Hoareau et al., 2007). For S. lagocephalus, a slightly lower estimated number of increments compared to the known 256 257 number of days reared in aquaria was observed for individuals kept more than 30 days in captivity. This discrepancy may be explained by the decrease in the fish growth rate that made 258 259 increments more difficult to detect. The reduced growth rate of individuals kept in aquaria 260 during similar experiments has been explained by the difficulties to feed the fish in the 261 laboratory (Siegfried and Weinstein, 1989), the stress caused by handling, or by ARS marking 262 (lida et al., 2010). In natural environment, it can safely be assumed that the growth rate is 263 more elevated than in captivity. As a consequence, the daily increments are easier to detect 264 over a longer period in freshwater.

#### 265 Influence of individual life history on age at first maturity

266 The time spent by females of S. lagocephalus and C. acutipinnis in freshwater before they 267 become mature  $(FD_{50})$  varied depending on the period they returned in freshwater. These 268 differences can be explained by environmental conditions, and particularly water temperature, they encountered in freshwater. Indeed, the probability of both species to initiate their ovarian 269 270 growth is positively correlated to water temperature (Teichert et al., 2014a, 2016b). Fish 271 returning in rivers at the beginning or during the reproductive season, i.e. between September 272 and April, had enough time to initiate ovarian growth during the current spawning season 273 (Fig. 5). Oppositely, fish returning in freshwater between May and August did not have 274 enough time to initiate ovarian growth before the water temperature decreased below. Indeed,

275 Teichert et al. (2014a and 2016b) demonstrated that S. lagocephalus and C. acutipinnis do not reproduce below 19 °C and 18 °C respectively. Females returning in freshwater when 276 temperature was low had to pursue their growth until water warmed up at the beginning of the 277 278 next austral summer. The role played by the freshwater temperature regime on age at first maturity may explain why S. lagocephalus and C. acutipinnis reach maturity much earlier, 9 279 280 and 7 months respectively, than Sicyopterus japonicus (Tanaka 1909) which reach maturity 281 after 2 years (Iida et al., 2013). The temperate S. japonicus reproduces in summer only (Iida et 282 al., 2013, 2015) and the juveniles return in freshwater seven to nine months after hatching (Iida et al., 2015). These juveniles do not have enough time to mature before water 283 284 temperature drops. As a consequence, their maturation is delayed until the next summer, when 285 environmental conditions become more favorable.

286 Independently to seasonal variations previously described, females of both species that 287 experienced a longer PLD matured earlier in freshwater (i.e. had a shorter  $FD_{50}$ ). The dynamic 288 of maturation for both species spans a continuous gradient from spending a long period of 289 time at sea, and maturing quickly after returning in the river, to spending less time at sea, and waiting for a longer period of time in the river before maturing. The energetic storage 290 291 accumulated by fish before maturation is usually allocated to growth and/or maturation 292 (Martin et al., 2017). Sicyopterus lagocephalus and C. acutipinnis display a large range of 293 PLD; the individuals with a longer PLD generally return in freshwater at larger size (Teichert 294 et al., 2012, 2016a). Moreover, the Fulton condition factor tends to increase with PLD, especially for S. lagocephalus (R. Lagarde, unpublished data). The energetic storage of fish 295 296 with a longer PLD is thus probably higher, explaining their more rapid maturation once they 297 return in freshwater.

#### 298 Interspecific differences in reproductive strategy

299 The S. lagocephalus spawning strategy consisting of spending a longer period in the ocean 300 and a shorter period of maturation in freshwater may be an explanation of its success in Reunionese rivers compared to C. acutipinnis. In Reunionese rivers, the abundance of 301 S. lagocephalus is estimated to be twice that of C. acutipinnis (Teichert et al., 2014b). After 302 303 returning in freshwater, juvenile of Sicydiinae gobies are subjected to competitive interaction 304 with adults and juveniles of their own species, and of other species. These interactions are 305 exacerbated by the territorial behavior of the males (Fitzsimons and Nishimoto, 1990) as they 306 need to select their spawning habitat (Teichert et al., 2013). The longer PLD of 307 S. lagocephalus is associated with a larger size of larvae when they return in freshwater, i.e. from 26.5 and 37 mm  $L_{\rm T}$ , compared to C. acutipinnis, i.e. from 17 to 23 mm  $L_{\rm T}$  (Teichert et 308 309 al., 2012, 2016a). As they are larger when they return in freshwater, S. lagocephalus 310 individuals are probably more competitive, and are thus more likely to spawn in the first 311 spawning habitats encountered after their return in freshwater. The spawning habitats that are closer to the estuary are supposed to produce more eggs and larvae per  $m^2$  as they allow the 312 313 fish to have a longer reproductive season, and probably higher number of spawning events per individual compared to upstream reaches (Teichert et al., 2014a). Moreover, the proximity of 314 315 the lower reaches to the sea greatly reduces the drifting time of larvae after hatching, and thus 316 the associated risk of mortality (Bell, 2009). Interestingly, the shortest  $FD_{50}$  of 317 S. lagocephalus, i.e. 2.5 months, was observed during the maximum of the reproductive 318 season which is also the period when the risk of cyclonic flood is higher. A rapid maturation 319 of the females during this period of the year may limit the risk of being entrained by cyclonic floods. 320

The successful colonization of new environment by amphidromous species depends mainly on their capacity to disperse widely and on the competitive effectiveness of their strategies, including their reproductive strategy, when reaching new environments (McDowall, 2010). 324 The longer PLD of *S. lagocephalus* is usually associated with a high dispersal ability (Lord et 325 al., 2010). This hypothesis was used to explain the relatively recent colonization by this species of numerous islands from eastern Pacific Ocean to western Indian Ocean (Keith et al., 326 327 2005a). The results of this study suggest that the longer PLD of S. lagocephalus also influences its reproductive strategy due 1) a larger size when returning to freshwater, and 2) a 328 329 faster maturation compared to the endemic C. acutipinnis. The long PLD of S. lagocephalus 330 thus appears pivotal in its recent and widespread colonization enhancing both its dispersal 331 capacity and reproductive strategy.

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341

#### **Conflict of Interest**

342 The authors declare no conflicts of interest.

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Location of the Saint Etienne and Marsouins Rivers, Reunion Island, Western Indian Ocean.

734x313mm (120 x 120 DPI)

34x31.



Logistic GLM estimating the probability of maturity regarding to the age for females of a) Sicyopterus lagocephalus and b) Cotylopus acutipinnis. The grey dashed lines represent the age when 50% of the females were mature ( $A_{50}$ ),  $N_m$  and  $N_i$  the number of mature and immature females respectively. The gray shaded area represents the range of the predictions ± standard error.

265x429mm (120 x 120 DPI)



Logistic GLM estimating the probability of maturity regarding to the freshwater duration (FD) and the period of return in freshwater (i.e. September to December, January to April and May to August) for females of a) *Sicyopterus lagocephalus* and b) *Cotylopus acutipinnis*. The grey dashed lines represent the freshwater duration when 50% of the females were mature (FD<sub>50</sub>) for each period, N<sub>m</sub> and N<sub>i</sub> the number of mature and immature females for each period respectively. The gray shaded area represents the range of the predictions  $\pm$  standard error.

496x341mm (120 x 120 DPI)



Freshwater duration when 50% of the females were mature (FD<sub>50</sub>, black lines) on which are superimposed the pelagic larval duration (PLD) and freshwater duration (FD) of matures (black dots) and immatures (open dots) females of a) *Sicyopterus lagocephalus* and b) *Cotylopus acutipinnis*. The FD<sub>50</sub> was estimated with a logistic GLM describing the probability of maturity regarding to the FD and the interaction between the FD and the PLD.

826x352mm (120 x 120 DPI)

### Fig. 5

a) S. lagocephalus



Schematic diagram representing the life history of a) *S. lagocephalus* and b) *C. acutipinnis* from hatching to the first reproductive event based on three periods of return in freshwater: May to August (open symbols), September to December (greys symbols) and January to April (black symbols). The period of hatching (square symbols) is estimated based on the median PLD when the period of the first reproductive event (circular symbols) is estimated based on the FD<sub>50</sub> for each periods of return in freshwater (triangular symbols). The horizontal black lines represent the estimated ranges.

157x161mm (120 x 120 DPI)

Table 1: Sampling dates, corresponding mean daily water temperature (and range) during the 30 days before sampling ( $T_{30}$ , °C), number of fish sampled (N) and range of total length ( $L_T$ , mm) for each species. The three periods of return in freshwater which were used for grouping the fish in the analyses are specified.

| Compling data     | T (ranga)               | Period of return | S. lagocephalus |                  | C. acutipinnis |                  |
|-------------------|-------------------------|------------------|-----------------|------------------|----------------|------------------|
| Sampling date     | 1 <sub>30</sub> (1ange) | in freshwater    | Ν               | Range of $L_{T}$ | Ν              | Range of $L_{T}$ |
| 18 January 2011   | 21.6 (20.2-22.5)        | Maximum          | 10              | 32-52            | 14             | 26-39            |
| 16 February 2011  | 21.6 (20.9-22.6)        | temperature –    | 18              | 33-50            | 19             | 25-39            |
| 18 March 2011     | 22.0 (21.3-22.9)        | maximum of       | 12              | 36-52            | 31             | 25-39            |
| 20 April 2011     | 21.2 (20.6-22)          | season           | 16              | 35-54            | 29             | 26-39            |
|                   | Total period #1         |                  | 56              | 32-54            | 93             | 25-39            |
| 18 May 2011       | 20.1 (19.2-21.2)        | Decreasing       | 21              | 34-54            | 24             | 26-38            |
| 15 June 2011      | 18.9 (18.3-19.4)        | temperature –    | 21              | 29-54            | 16             | 28-39            |
| 13 July 2011      | 18.4 (16.9-19.3)        | minimum          | 15              | 32-53            | 11             | 23-39            |
| 17 August 2011    | 18.1 (17.6-18.8)        | season           | 19              | 31-54            | 10             | 26-39            |
|                   | Total period #2         |                  | 76              | 29-54            | 61             | 23-39            |
| 14 September 2011 | 18.5 (17.7-19.2)        | Increasing       | 19              | 31-53            | 15             | 27-39            |
| 12 October 2011   | 18.7 (18.1-19.3)        | temperature –    | 15              | 33-52            | 17             | 27-37            |
| 16 November 2011  | 20.2 (19.2-21.7)        | beginning of the | 21              | 32-53            | 22             | 22-39            |
| 14 December 2011  | 21.2 (19.9-21.9)        | season           | 18              | 33-52            | 15             | 24-38            |
|                   | Total period #3         |                  | 73              | 31-53            | 69             | 22-39            |
|                   | Total                   |                  | 205             | 29-54            | 223            | 22-39            |
|                   |                         |                  |                 |                  |                |                  |
|                   |                         |                  |                 |                  |                |                  |
|                   |                         |                  |                 |                  |                |                  |
|                   |                         |                  |                 |                  |                |                  |
|                   |                         |                  |                 |                  |                |                  |
|                   |                         |                  |                 |                  |                |                  |

Table 2: Intercept and slopes of the orthogonal regressions of the values of PLD and FD estimated by operators A and B. The values in brackets are the lower and upper limit of the 95% confidence intervals.

| Species           | Ν  | Period | Intercept        | Slope            | R²   |
|-------------------|----|--------|------------------|------------------|------|
| C. In a comb alwa | 60 | PLD    | 1.5 (-6.4-9.4)   | 0.99 (0.94-1.04) | 0.96 |
| S. lagocephalus   | 60 | FD     | 2.8 (-0.1-5.7)   | 0.99 (0.96-1.03) | 0.98 |
| C. acatininain    | 60 | PLD    | 3.1 (-2.4-8.6)   | 0.98 (0.94-1.03) | 0.96 |
| C. acutipinnis    | 60 | FD     | -3.6 (-14.0-6.7) | 1.03 (0.98-1.09) | 0.95 |

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Table 3: Summary of deviance reduction on logistic GLM estimating the probability of maturity with individual freshwater duration (FD), period of return in freshwater (F\_return) and the interaction of FD and F\_return as explanatory variables. The significance of explanatory variables was tested with a test of deviance reduction using the Chi<sup>2</sup> statistic.

| Species         | Variable      | Deviance | d.f | P-value |
|-----------------|---------------|----------|-----|---------|
|                 | Null          | 246      | 204 | -       |
| C. I            | FD            | 178      | 203 | <0.001  |
| S. Iugocephalus | F_return      | 130      | 201 | <0.001  |
|                 | FD x F_return | 129      | 199 | 0.7     |
|                 | Null          | 297      | 222 | -       |
| C acutininnic   | FD            | 157      | 221 | <0.001  |
| C. acatipininis | F_return      | 124      | 219 | 0.001   |
|                 | FD x F_return | 121      | 217 | 0.2     |
|                 |               |          |     |         |

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Table 4 : Summary of deviance reduction on logistic GLM estimating the probability of maturity with the freshwater duration (FD) and the interaction between FD and pelagic larval duration (PLD) as explanatory variables. The significance of explanatory variables was tested with a test of deviance reduction using the Chi<sup>2</sup> statistic.

| Species         | Variable | Deviance | d.f | P-value |
|-----------------|----------|----------|-----|---------|
|                 | Null     | 246      | 204 | -       |
| S. lagocephalus | FD       | 178      | 203 | < 0.001 |
|                 | FD x PLD | 151      | 202 | <0.001  |
|                 | Null     | 297      | 222 | -       |
| C. acutipinnis  | FD       | 162      | 221 | <0.001  |
|                 | FD x PLD | 150      | 220 | <0.001  |
|                 |          |          |     |         |
|                 |          |          |     |         |
|                 |          |          |     |         |

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## Annexes 5 :

**Lagarde R**, Teichert N, Occelli N. H, Gaudin P & Ponton D. Effet de la temperature sur la survie et le développement larvaire d'une espèce amphidrome tropicale. *Poster présenté lors des 7ème rencontres de l'ichtyologie en France. Mars 2018.* 

# Effet de la température sur la survie et le développement larvaire d'une espèce amphidrome tropicale

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#### Contexte

Les poissons des rivières insulaires de la région Indo-pacifique sont majoritairement amphidromes. Les adultes de ces espèces vivent et se reproduisent en rivière. A l'éclosion, les larves dérivent passivement jusqu'à la mer où elles poursuivent leur croissance pendant plusieurs mois, avant de retourner en rivière. L'ontogénie est bloquée à un stade précoce durant la dérive larvaire, si bien qu'un accroissement du temps de résidence en eau douce et/ou une augmentation de la température liés à la présence d'obstacles peut affecter la survie des larves. En mer, le développement larvaire se poursuit avec notamment la formation de la bouche qui conditionne la première prise de nourriture et marque le début de la période de nourrissage mixte. Cependant, l'augmentation de la température des océans pourrait influencer la phénologie du développement larvaire et, à terme, affecter la survie des larves amphidromes.



#### Conclusion

Au-delà de l'**impact direct sur la survie larvaire en eau douce et en mer**, la température **influence le début de la période de nourrissage mixte et sa durée**. Durant cette période, la larve peut s'alimenter mais profite également de réserves endogènes. En absence de prise de nourriture pendant cette période, l'état physiologique des larves se dégrade rapidement. Ainsi, une augmentation de la température de l'éau est susceptible d'affecter la survie des larves amphidromes et, *in fine*, affecter les abondances de juvéniles retournant en rivière.

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