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Variabilité intraspécifique chez les espèces invasives et ses conséquences sur le fonctionnement des écosystèmes aquatiques

Charlotte Evangelista

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Charlotte Evangelista. Variabilité intraspécifique chez les espèces invasives et ses conséquences sur le fonctionnement des écosystèmes aquatiques. Ecologie, Environnement. Université Paul Sabatier - Toulouse III, 2016. Français. NNT : 2016TOU30233 . tel-01688161

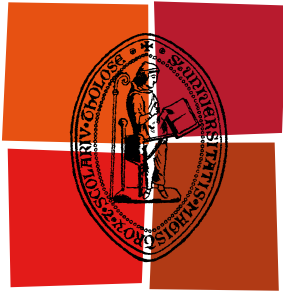
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Université
de Toulouse

THÈSE

En vue de l'obtention du
DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par :

Université Toulouse III Paul Sabatier (UT3 Paul Sabatier)

Discipline ou spécialité :

Ecologie

Présentée et soutenue par :

Charlotte EVANGELISTA

le : 8 Décembre 2016

Titre :

Variabilité intraspécifique chez les espèces invasives et ses conséquences sur
le fonctionnement des écosystèmes aquatiques

Ecole doctorale :

Sciences Ecologiques, Vétérinaires, Agronomiques et Bioingénieries (SEVAB)

Unité de recherche :

Laboratoire Evolution & Diversité Biologique (EDB) - UMR 5174 (CNRS/UPS)

Directeur(s) de Thèse :

Julien CUCHEROUSET (Chargé de recherche, CNRS Toulouse)

Antoine LECERF (Maître de conférence, Université de Toulouse III)

Rapporteurs :

Damien BANAS (Professeur, Université de Lorraine)

Emili GARCIA-BERTHOU (Professeur, Université de Gérone, Espagne)

Membre(s) du jury :

Géraldine LOOT (Professeur, Université de Toulouse III)

Sébastien VILLEGGER (Chargé de recherche, CNRS Montpellier)



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Avant propos

Ce travail de thèse de l'école doctorale SEVAB de l'Université Toulouse III a été réalisée au sein des laboratoires Evolution et Diversité Biologique et Ecologie Fonctionnelle et Environnement. Elle a été financée par une bourse doctorale de l'Université Fédérale Toulouse Midi-Pyrénées. Le fonctionnement de la thèse a été financée par l'ERG Marie Curie de Julien Cucherousset (PERG08-GA-2010-276969), l'Office Nationale de l'Eau et des Milieux Aquatiques dans le cadre du projet ISOLAC (ISOLAC-Convention 13-V5-28), un financement obtenu par la Fisheries Society of the British Isles Research, un Projet International de Coopération Scientifique (Ind_Eco_Evo_Inva) ainsi que par le "Laboratoire d'Excellence" TULIP (ANR-10-LABX-41). Ce manuscrit de thèse est composé d'une introduction générale (*Chap. I*), d'un matériel et méthodes (*Chap. II*), de cinq chapitres rédigés en anglais sous forme d'articles (*Chap. III à VII*) et d'une discussion générale (*Chap. VIII*). Un article a été publié dans la revue *Ecology and Evolution* (*Chap. III*), un est en révision majeure dans la revue *Oikos* (*Chap. VII*) et les trois autres sont en préparation (*Chap. IV, V et VI*).

Remerciements

En premier lieu, je tiens à remercier Julien Cucherousset et Antoine Lecerf, mes encadrants, de m'avoir offert l'opportunité de réaliser cette thèse. Merci à vous deux pour votre soutien, vos conseils avisés, la confiance que vous m'avez accordée et pour le temps que vous m'avez consacré tout au long de ces trois années.

Je tiens à remercier les membres du jury d'avoir accepté d'évaluer ce travail. Je remercie les rapporteurs de cette thèse, Damien Banas, Professeur à l'Université de Lorraine, et Emili Garcia-Berthou, Professeur à l'Université de Gérone. Je remercie Sébastien Villéger, Chargé de recherche au CNRS de Montpellier, qui a accepté d'être examinateur de cette thèse. Un grand merci à Géraldine Loot, Professeure à l'Université de Toulouse III, pour avoir accepté de présider le jury de cette thèse. Merci beaucoup pour l'intérêt que vous avez porté à mes travaux de recherches et pour vos conseils.

Je souhaite remercier les différents propriétaires des gravières pour nous avoir donné accès à leurs plans d'eau, ainsi que Serge Boutes et ses collègues pour m'avoir laissé conduire une expérimentation en mésocosme au Golf de Téoula.

Mes remerciements vont également à tous les membres de l'équipe Aquaeco et de l'équipe Bioref qui ont participé de près ou de loin à cette thèse, que se soit dans le cadre du travail ou de la vie. Je remercie en particulier Tian Zhao, Nicolas Charpin, Thomas Pool, Rémy Lassus, Maria Alp, Carine Rigolet et Libor Zavorka pour tous les bons moments passés ensemble sur le terrain. Merci Nico pour ta bonne humeur et tes "charpinades", attends toi à voir débarquer un jour la grognasse en NC. Merci Carine, Libor et Jan Hackel pour leurs encouragements pendant les derniers jours de rédaction. Carine je te remercie chaleureusement pour ton écoute attentive et pour tous les conseils que tu as pu m'apporter.

Je souhaite remercier Alexandre Carpentier, Rob Britton, Michelle Jackson et Julian Olden. Merci Alex de m'avoir fait découvrir le monde aquatique alors que j'étais étudiante à Rennes. Merci beaucoup Rob, Michelle et Julian pour votre accueil à Bournemouth et Seattle, j'ai beaucoup apprécié de collaborer avec vous.

Je remercie chaleureusement les amis et les soutiens qui m'entourent depuis plusieurs années, qui sont essentiels à ma vie et sans qui cette thèse n'aurait pas été la même. Un grand merci à Zineb Brissel, Loubna Bouroukba et Leila Jmouhi pour être à mes côtés depuis les bancs de Guynemer et Poinca, merci les filles d'être des amies formidables. Merci à Sonia Bichalon d'avoir été mon binôme de TP, j'ai adoré nos discussions et les moments qu'on a passé ensemble. Tu me manques ma biche et j'espère qu'on se verra bientôt au Canada ou ailleurs. Merci Hélène Cristofari pour les pâtisseries, tes encouragements et nos discussions toujours très agréables, dans un an c'est ton tour! Merci à Matthieu Friadt, Jules Fontaine et Pierre Berthelot de m'avoir accueillie dans cette belle coloc' du 48 Matabiau! Merci à Claire Bordenave de ne pas avoir été sur le bail. Merci à tous les Toulousains et Toulousaines qui ont rendu ma vie à Toulouse agréable: Virginie Roulland, Marie Rougié, Daphnée Pélissier, Romain Couffignant, Mathieu & Astrid Jamin, Olivier Durand, Coraline Koleczkiw, Sébastien Peron, Karima El Hadjjam, Céline Mathieu, Frédéric Ferchaud, Maria-Rosa Velardo, Nicolas Voyer, Manon Larousse, sans oublier les petits derniers, Manel et Noah. Merci pour tous les bons moments partagés ensemble. Un très grand merci à Julien pour son soutien et son aide. Enfin je remercie ma famille, mes parents Marc et Marie, et mes frères, Stanislas et Briec. Merci de m'avoir toujours soutenu dans mes choix, je n'en serai jamais arrivé là sans vous.

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Introduction générale

I.1 - Biodiversité et fonctionnement des écosystèmes

I.1.1 - Evaluer la biodiversité pour mieux appréhender le fonctionnement des écosystèmes

Un des objectifs majeurs de l'écologie est de comprendre le rôle de la biodiversité dans la dynamique de l'énergie et de la matière et dans les cycles des éléments au sein des écosystèmes. Les organismes régulent les processus écologiques (e.g., cycle des nutriments, production de biomasse, décomposition de la matière, flux trophiques) et contribuent à la stabilité des écosystèmes (e.g., résistance aux perturbations). Traditionnellement, la biodiversité est évaluée selon une approche « espèce-centrée » basée sur le calcul d'indices de diversité prenant en compte la richesse spécifique et l'abondance relative des espèces au sein des communautés (Fig. I.1). Cette diversité peut contrôler le fonctionnement des écosystèmes au travers d'effets de sélection d'espèces importantes et l'établissement de complémentarité entre espèces dans l'utilisation des ressources et de l'espace (Loreau & Hector 2001). Cependant, un nombre grandissant d'études a révélé que les changements de richesse spécifique n'ont pas toujours d'impacts forts sur les processus fonctionnels étudiés (Hooper et al. 2005, Reiss et al. 2009). Ceci s'explique par le fait que, au sein de communautés riches, plusieurs d'espèces peuvent jouer le même rôle, l'une pouvant se substituer à l'autre en cas d'extinction (Walker 1992). Cette redondance fonctionnelle ainsi que l'importance des espèces dans les écosystèmes sont largement déterminés par les caractéristiques biologiques (e.g., taille du corps, morphologie, régime trophique, mode de locomotion) et l'écologie des organismes (niche écologique) (Tilman et al. 1997, Loreau et al. 2001, Hooper et al. 2005, Griffin et al. 2009; Fig. I.1). Par conséquent, notre compréhension du fonctionnement d'un écosystème doit se baser sur l'utilisation d'approches « trait-centré » qui permettent une meilleure évaluation des fonctions remplies par les espèces constituant le système (Mouillot et al. 2013).

Les approches « trait-centré » sont basées sur l'étude des traits fonctionnels, c'est-à-dire des caractéristiques phénotypiques (e.g., morphologie, physiologie, comportement, phénologie) mesurable à l'échelle de l'individu et qui influence de manière indirecte sa fitness par des effets sur les performances individuelles (e.g., croissance, survie, reproduction) (Violle et al. 2007). Un trait fonctionnel peut traduire simultanément la réponse d'un organisme face aux changements de conditions environnementales (*traits de réponse*) et ses effets sur l'écosystème (*traits d'effets*) (Díaz & Cabido 2001). Par exemple, la taille du corps détermine la sensibilité d'une espèce aux perturbations ainsi que l'intensité de son effet sur l'écosystème (Woodward et al. 2005). L'utilisation des traits fonctionnels permet d'étudier conjointement comment les gradients environnementaux modulent les caractéristiques phénotypiques des espèces et quelles en sont les conséquences pour le fonctionnement des écosystèmes. Cette approche a donc été principalement utilisée à l'échelle des communautés, bien que sa nature individu-centrée suggère qu'elle pourrait être extrapolée à l'échelle des populations, et ainsi permettre d'étudier la composante intraspécifique de la diversité fonctionnelle (Fig. I.1).

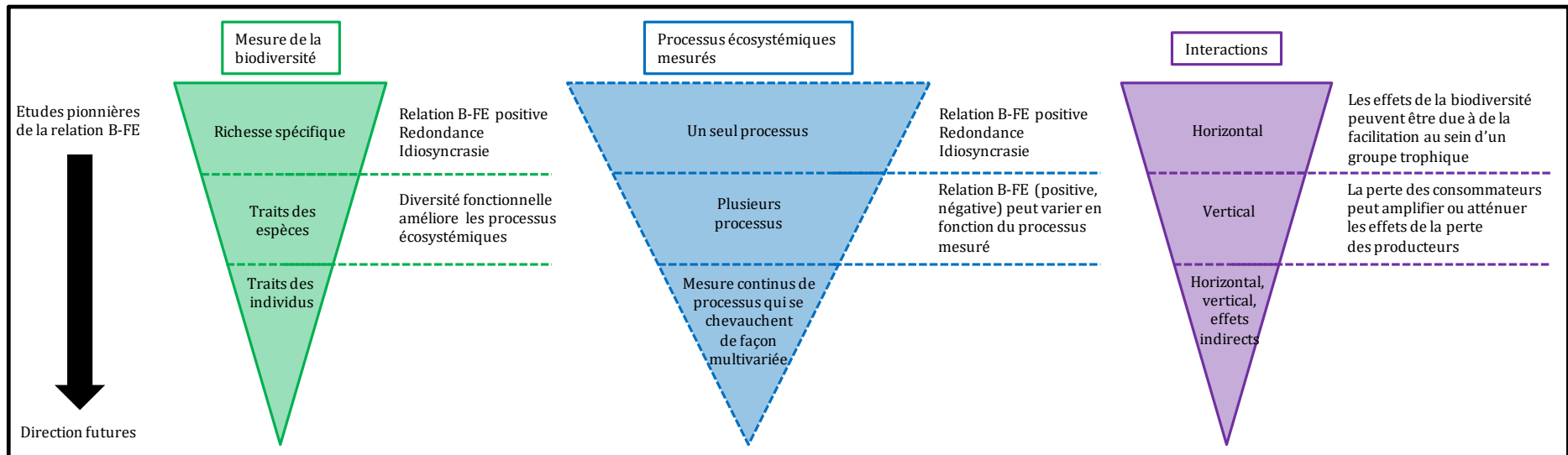


Figure I.1 Description générale de l'évolution historique et des directions de recherche future concernant l'étude des relations entre la biodiversité et le fonctionnement des écosystèmes (B-EF). Adaptée à partir de Reiss et al. 2009.

Les relations trophiques sont au cœur du fonctionnement de l'écosystème (Lindeman 1942). La quantification des flux d'énergie établis lors des interactions trophiques entre les organismes, qui constituent la structure du réseau trophique, permet de mieux appréhender le fonctionnement global de l'écosystème (Thompson et al. 2012a). Un réseau trophique peut être caractérisé par deux dimensions: l'une verticale correspondant au niveau trophique occupé par chaque individu au sein de la chaîne alimentaire et l'autre horizontale représentant l'occupation des niches écologiques au sein des groupes trophiques (Duffy et al. 2007). Ces dimensions sont définies au niveau des espèces (longueur de la chaîne trophique et nombre d'espèce au sein d'un même niveau trophique) mais sont également pertinentes pour décrire les variations de traits trophiques au niveau intra-spécifique. Par exemple, des variations du degré d'omnivorie (propension à s'alimenter à plusieurs niveaux trophiques) au sein d'une espèce peut conduire à des changements de niveau trophique (dimension verticale) mais également le degré de généralisme dans l'utilisation des ressources (dimension horizontale) au sein de populations. De plus, des études ont mis en évidence des conséquences de modifications de la structure verticale (e.g., perte des prédateurs; Pace et al. 1999, Estes et al. 2011) et/ou horizontale (e.g., augmentation de la richesse spécifique au sein d'un niveau trophique; Cardinale et al. 2002) des réseaux trophiques sur le fonctionnement des écosystèmes en se focalisant sur les effets directs des consommateurs et les effets en cascade qui en découlent (Suraci et al. 2016). Cependant les consommateurs peuvent également intervenir indirectement dans la dynamique du cycle des nutriments (Schmitz et al. 2010) et l'étude des relations trophiques pourraient permettre de renforcer nos connaissances sur les mécanismes indirects impliqués dans la régulation des processus écosystémiques par les consommateurs.

Le fonctionnement d'un écosystème est contrôlé par des mécanismes descendants (« top-down »; Fig. I.2A) initiés par les prédateurs qui régulent l'abondance des consommateurs primaires (Shurin et al. 2006). Cet effet direct des prédateurs régule ensuite de manière indirecte les stocks de biomasses et nécromasses végétales via le phénomène de cascade trophique (Shurin et al. 2006). En parallèle, le fonctionnement de l'écosystème est contrôlé par des mécanismes ascendants (« bottom-up »; Fig. I.2A) via les phénomènes de limitation des ressources (énergie, nutriments, etc.) pour les consommateurs et leurs prédateurs (Lindeman 1942). Les consommateurs, en agissant sur la régénération et la distribution des ressources pour les niveaux trophiques

inférieurs, peuvent aussi opérer un contrôle ascendant sur la dynamique trophique (Taylor et al. 2015; Fig. I.2B). En effet, les consommateurs peuvent moduler le cycle des nutriments (notamment l'azote et le phosphore) via différents mécanismes incluant le transport de nutriments au sein et entre les écosystèmes, l'excrétion et l'égestion de nutriments, la séquestration de nutriments (e.g., le phosphore dans le squelette) par l'organisme ou encore la décomposition de carcasses (Sturner & Elser 2002, Vanni 2002, Schmitz et al. 2010). Les nutriments ainsi apportés par les consommateurs vont être utilisés par les producteurs primaires et les microorganismes décomposeurs pour leur croissance, en particulier dans les milieux aquatiques d'eau douce pauvres en nutriments (Sturner & Elser 2002; Fig. I.2B). Dans certains cas, les organismes aquatiques tels que les poissons peuvent s'agréger localement en forte biomasses et constituer des « hot spots » biogéochimiques via l'excrétion de nutriments (McIntyre et al. 2008, Boulêtreau et al. 2011, Capps & Flecker 2013a), c'est-à-dire des endroits où les concentrations en nutriments sont supérieures à celles que requièrent les producteurs primaires (McIntyre et al. 2008). Par conséquent, les consommateurs via leurs produits d'excrétion, jouent un rôle important dans le cycle des nutriments, et ce même dans des milieux anthropisés recevant des apports non négligeables de nutriments (Vanni et al. 2006, Wilson et al. 2011). Ils participent donc à la régulation des processus écosystémiques (Allgeier et al. 2013, Taylor et al. 2015) et il apparaît nécessaire d'étudier les mécanismes impliqués dans la régulation du cycle du nutriment par les consommateurs afin de mieux évaluer leur rôle indirect dans le fonctionnement des écosystèmes (Vanni 2002).

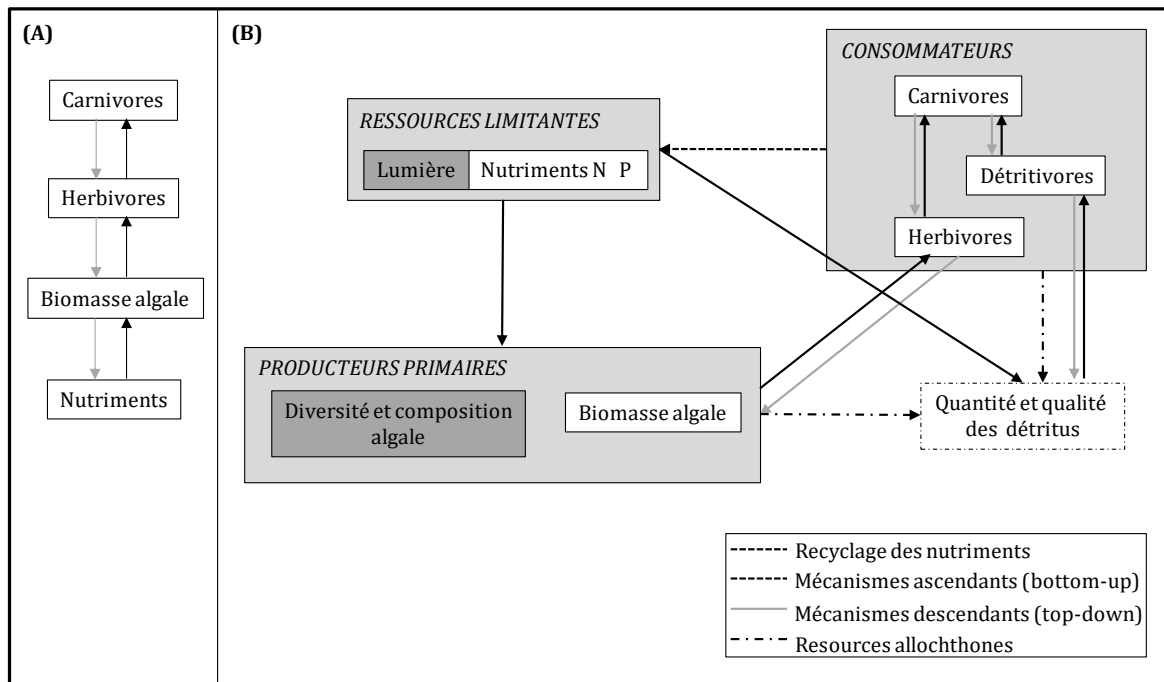


Figure 1.2 Dynamique trophique (A) Conception traditionnelle où s'opposent les mécanismes de contrôle ascendants (« bottom-up ») et descendants (« top-down ») au sein d'un réseau trophique linéaire. **(B)** Conception actualisée intégrant les phénomènes de recyclage des nutriments par les consommateurs et la matière organique inerte (débris). Adaptée de Taylor et al. 2015.

1.1.2 - Composante intraspécifique de la biodiversité

Les études se référant à la diversité fonctionnelle comme mesure de la biodiversité se sont principalement focalisées sur la valeur moyenne des traits des espèces ou au mieux des populations. Ces études ont donc considéré les individus d'une même espèce comme étant écologiquement similaires, négligeant ainsi la présence de variabilité phénotypique au sein ou entre les populations d'une même espèce (Bolnick et al. 2011, Violle et al. 2012; Fig. 1.3). En effet, des individus peuvent diverger selon de nombreux aspects comme leur génétique (Pauls et al. 2013), leur morphologie (Quevedo et al. 2009), leur comportement (Dall et al. 2012), leur physiologie (Bouwhuis et al. 2014), la composition élémentaire de leur corps (El-Sabaawi et al. 2016), leur régime alimentaire (Bolnick et al. 2003) ou bien encore leurs traits d'histoire de vie (Biro & Stamps 2008). Cette variabilité phénotypique intraspécifique peut s'avérer supérieure à la variabilité existant entre les espèces (Bolnick et al. 2003, Woodward & Hildrew 2005) et pourrait ainsi moduler les effets des espèces sur le fonctionnement des écosystèmes. Par exemple, de nombreuses espèces expérimentent au cours de leur développement ontogénique des changements écologiques qui se traduisent généralement par un changement de régime alimentaire (Werner & Gilliam 1984). Les individus appartenant

à des stades de développement différents sont donc fonctionnellement différents et des changements de la structure en taille des populations peut modifier le fonctionnement de l'écosystème (Rudolf & Rasmussen 2013a). Par conséquent, bien qu'il se soit opéré un véritable bouleversement dans l'étude des relations entre biodiversité et fonctionnement des écosystèmes (i.e., intégration de multiple processus écosystémiques, utilisation d'approche fonctionnelle, incorporation des dimensions horizontale et verticale du réseau trophique), il est de plus en plus reconnu qu'intégrer la variabilité intraspécifique en tant que source potentielle de modification des processus écosystémiques permettrait d'obtenir une vision plus complète des mécanismes par lesquels la biodiversité module la fonctionnement des écosystèmes. Enfin, puisque le régime alimentaire d'un individu décrit sa fonction au sein du système, tenir compte de la variabilité trophique intraspécifique devrait permettre de tester les effets des changements de structure et de fonctionnalité des populations sur le fonctionnement des écosystèmes (Luck et al. 2003) et ainsi apporter une vision plus précise des relations entre biodiversité et fonctionnement.

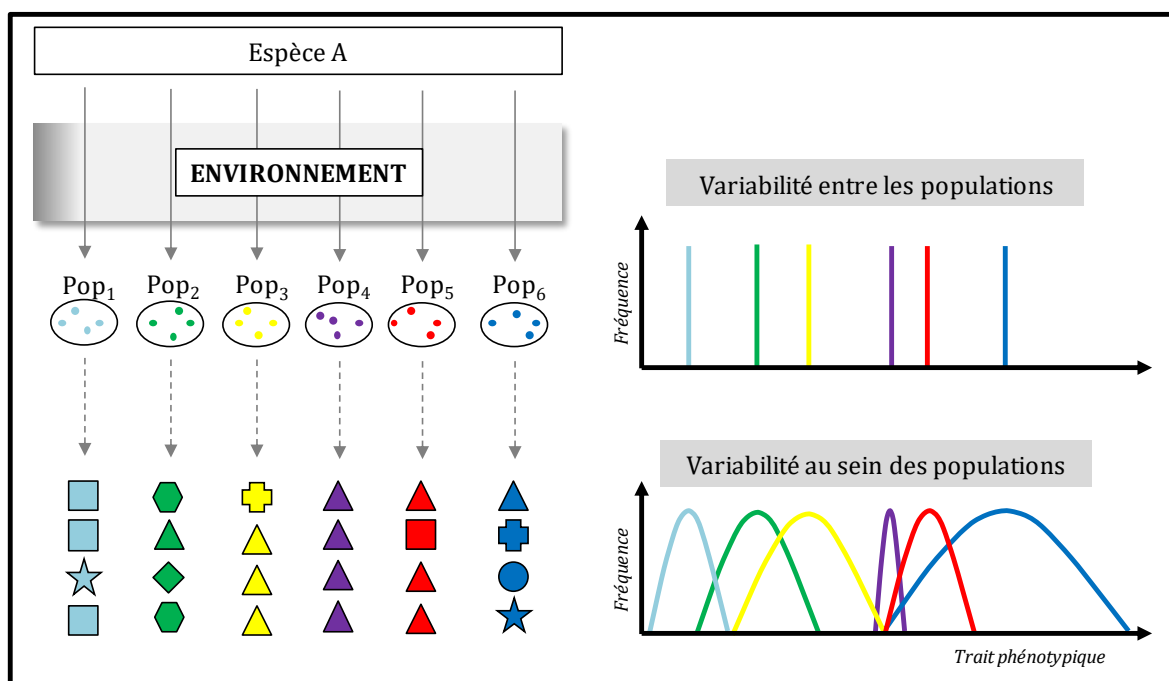


Figure I.3 Illustration des deux facettes de la variabilité intraspécifique (i.e., entre les populations d'une même espèce et au sein de chacune de ces populations) en réponse à différentes conditions environnementales. Adaptée de Violle et al. 2012.

La variabilité trophique intraspécifique correspond à une différenciation de la niche trophique des individus d'une même espèce à travers l'utilisation de différentes ressources alimentaires (Bolnick et al. 2003). Elle a été largement mise en évidence ces

dernières années (e.g., Araújo et al. 2009, Darimont et al. 2009a, Matich et al. 2011, Layman & Allgeier 2012, Vander Zanden et al. 2013, Newsome et al. 2015) et trouve en partie ses bases théoriques dans la théorie de l'approvisionnement optimal (OFT: « *Optimal Foraging Theory* »; Charnov 1976). L'OFT prédit qu'un individu sélectionne sa ressource afin d'optimiser le gain d'énergie entre les coûts associés à l'acquisition des ressources alimentaires et les bénéfices énergétiques apportés par ces ressources. Par conséquent, la balance énergétique dépend des caractéristiques de la ressource, des capacités phénotypiques de l'individu à capturer, manipuler et digérer sa ressource mais également des risques associés à l'acquisition des ressources alimentaires (e.g., présence de prédateurs). L'OFT prédit que les individus sélectionnent les ressources qui leur rapportent le plus d'énergie. Toutefois, lorsque l'abondance des ressources les plus profitables diminue, les individus devraient élargir leur niche en utilisant des ressources inutilisées jusque là. La niche trophique des individus est donc fonction de l'abondance et de la diversité des ressources disponibles ainsi que des traits phénotypiques des individus. Les facteurs environnementaux biotiques et abiotiques se révèlent primordiaux dans la mise en place de la variabilité intraspécifique et témoignent de l'adaptation (plastique ou génétique) de l'individu à son environnement. Généralement, la prédation, la compétition (intra-et interspécifique) et la disponibilité des ressources trophiques sont les principaux facteurs favorisant des variations de la taille de la niche trophique des individus (Araújo et al. 2011). Par exemple, la compétition intraspécifique peut favoriser l'expansion de la niche trophique de la population par le biais d'une augmentation de la divergence de niche trophique entre les individus (Bolnick et al. 2010). A l'inverse, la prédation peut conduire à une convergence des niches trophiques des proies si la présence d'un prédateur entraîne le déplacement de tous les individus vers l'habitat le plus sûr et qui présentant un choix restreint de ressources (Eklöv & Svanbäck 2006). De plus, la disponibilité de la ressource trophique (diversité et abondance) interfère avec ces interactions écologiques et influence l'intensité de la variabilité trophique intraspécifique (Araújo et al. 2011). Cependant de nombreuses études se résument à tester l'effet d'un nombre restreint de facteurs environnementaux à la fois, conduisant à un déficit de connaissances concernant les effets cumulés de plusieurs facteurs sur cette variabilité intraspécifique.

La variabilité intraspécifique trophique peut être associée à des différences morphologiques entre individus reflétant l'existence de compromis dans l'efficacité de

consommation de différentes ressources. Dans de nombreux cas, les différents morphes peuvent constituer des entités très distinctes et on parle alors de polymorphisme de ressource (Skúlason & Smith 1995, Smith & Skúlason 1996). Ce phénomène est également associé à des divergences d'utilisation de l'habitat, traduisant une ségrégation spatiale, plus ou moins fine, des individus pouvant conduire à long terme à de la spéciation (Smith & Skúlason 1996). De nombreux exemples de polymorphisme de ressources ont été mis en évidence chez différentes espèces de poissons et sont principalement associés au gradient littoral-pélagique dans les lacs (e.g., Malmquist et al. 1992, Svanbäck & Eklöv 2002, Jastrebski & Robinson 2004, Harold et al. 2010, Matthews et al. 2010). Généralement, les morphes qui occupent et se nourrissent dans la zone littorale sont caractérisés par un corps robuste facilitant la manœuvrabilité dans les habitats dont la structure est complexe. En parallèle, les morphes qui utilisent et se nourrissent dans la zone pélagique possèdent un corps plus allongé leur permettant d'augmenter leur vitesse pour capturer les proies plus mobiles du milieu pélagique (Smith & Skúlason 1996). Par conséquent, ces corrélations entre régime alimentaire et morphologie sont particulièrement intéressantes à étudier de manière à déterminer la stabilité temporelle de la variabilité et les potentielles conséquences évolutives de la variabilité intraspécifique (Bolnick et al. 2003).

La variabilité trophique intraspécifique est donc une composante primordiale de la biodiversité et des études récentes ont révélé ses effets à différents niveaux d'organisations biologiques. Ainsi, elle peut avoir des effets sur la fitness des individus (Bolnick & Araujo 2011, Darimont et al. 2007) et sur la dynamique des populations via notamment la transmission sélective de pathogènes (Johnson et al. 2009), ces effets pouvant alors se répercuter sur la structure des communautés (Matich et al. 2011, Svanbäck et al. 2008, Svanbäck et al. 2015). A l'échelle de l'écosystème, les effets de la variabilité trophique sur les processus écosystémiques ont principalement été explorés par l'étude des mécanismes descendants et de leurs effets cascades sur les niveaux inférieurs (Harmon et al. 2009). Plus récemment, les effets du régime alimentaire sur le recyclage des nutriments par les consommateurs via l'excrétion et ses conséquences sur le fonctionnement de l'écosystème ont été mis en évidence. En particulier, il a été montré chez les guppy de Trinidad (*Poecilia reticulata*) que les individus se nourrissant principalement de matière animale (i.e., invertébrés aquatiques) excrétaient l'azote à un plus fort taux que les individus se nourrissant principalement de matière végétale (i.e.,

algues). Cet apport de nutriment pouvait favoriser la production primaire au sein de l'écosystème, traduisant une amplification du contrôle ascendant par les consommateurs (Bassar et al. 2010). Cependant, les effets de la composition du régime alimentaire sur les taux d'excrétion des nutriments présentent des résultats contradictoires dans les études en milieu naturel (Higgins et al. 2006, Torres & Vanni 2007, McManamay et al. 2011), potentiellement parce que la variabilité trophique intraspécifique n'a pas été prise en compte. Par conséquent, il serait intéressant d'intégrer la composition des ressources consommées mais également le degré de spécialisation trophique afin de mieux évaluer les effets du régime alimentaire sur les taux d'excrétion des consommateurs.

I.2 - Invasions biologiques

I.2.1 - De l'introduction des espèces au phénomène d'invasion

Les invasions biologiques sont actuellement reconnues comme une cause majeure de perte de biodiversité pouvant conduire à une homogénéisation globale des communautés et des habitats (McKinney & Lockwood 1999). Une espèce invasive est une espèce introduite par l'Homme en dehors de son aire de répartition géographique naturelle, qui s'établit de manière durable dans son aire d'introduction, se disperse à partir de son point d'introduction et impacte les espèces natives et les écosystèmes où elle est introduite (Lockwood et al. 2007; Fig. I.4). Les invasions biologiques se sont considérablement accélérées sous l'intensification des activités humaines, plus particulièrement du développement des transports et des échanges internationaux (Mooney & Cleland 2001). En parallèle de ces introductions fortuites, de nombreuses espèces ont été introduites volontairement par l'Homme à des fins ludiques (pêche, aquariophilie) ou commerciales (agriculture, aquaculture, production de fourrure). Pour ces raisons, les invasions biologiques peuvent intervenir rapidement et à large échelle géographique, modifiant ainsi la dynamique de colonisation naturelle des habitats (Lockwood et al. 2007).

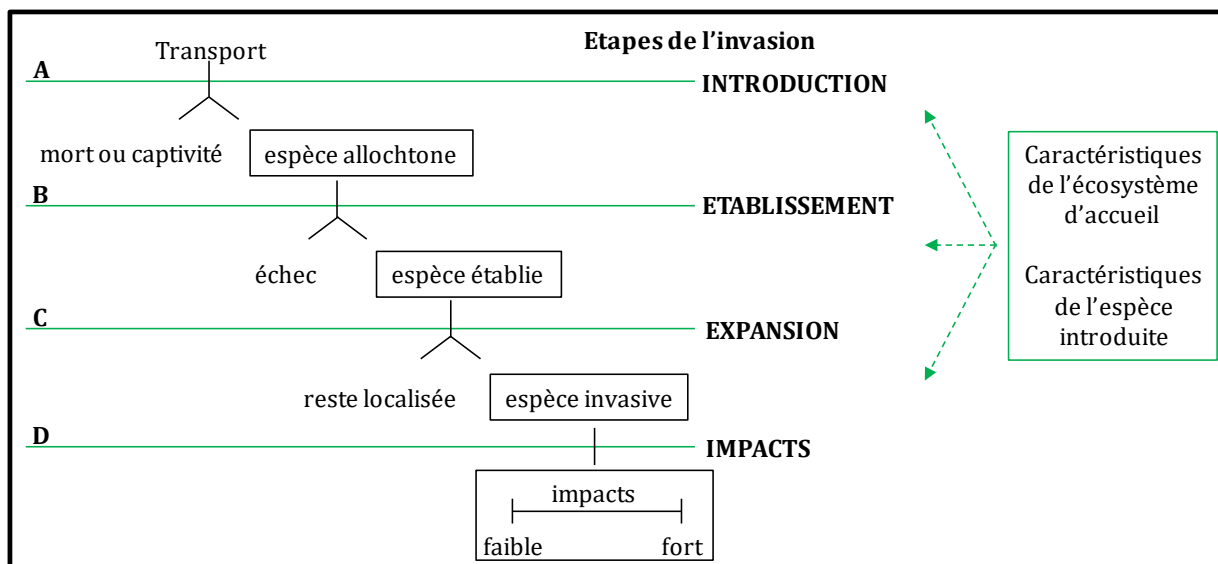


Figure I.4 Le processus d'invasion biologique est composé de quatre étapes majeures: i) l'introduction, ii) l'établissement, iii) l'expansion de l'espèce allochtone introduite et iv) les impacts écologiques. Le passage entre ces différentes étapes nécessite le franchissement de plusieurs barrières: (A) géographiques (inter- ou intracontinentale), (B) environnementales (biotiques et abiotiques), (C) de reproduction et (D) de dispersion (locales et régionales). Le franchissement de ces barrières dépend donc des caractéristique de l'écosystème envahi (e.g., présence de prédateurs, conditions climatiques) et des caractéristiques de l'espèce introduite (e.g., capacité de dispersion, stratégie r de survie). Adaptée de Lockwood et al. 2007.

Le succès d'une espèce invasive dépend des capacités des individus issus de la population introduite à franchir différentes barrières géographiques, de reproductions et environnementales (Fig. I.4). Il apparait donc que certains caractères biologiques puissent expliquer le succès invasif de certaines espèces (Facon et al. 2006). En effet, le degré d'affinité de l'espèce avec l'Homme (e.g., comestibilité, qualités sportives ou esthétiques) et la pression de propagule (i.e., le nombre d'individus introduits et la fréquence de ces introductions) sont des facteurs prépondérants à son introduction et à son établissement (Kolar & Lodge 2001, Lockwood et al. 2007). Les traits d'histoire de vie vont également déterminer le potentiel invasif et il est généralement admis que des espèces à stratégie r (i.e., temps de génération court, croissance rapide, forte fécondité) ont un potentiel invasif plus important (Sakai et al. 2001, Facon et al. 2006). De plus une forte plasticité phénotypique, traduisant une forte tolérance aux conditions environnementales, combinée à un potentiel adaptatif rapide (Lee 2002), favorisent la survie et la reproduction des individus introduits, et donc le succès d'invasion. Finalement, le succès invasif d'une espèce découle d'une bonne adéquation entre les caractéristiques de l'espèce introduite et l'environnement d'accueil. Par conséquent, la compréhension des interactions établies entre les facteurs environnementaux biotiques

(e.g., prédation, compétition) et abiotiques (e.g., disponibilité en ressource trophique, morphologie du milieu) et les caractéristiques des espèces introduites (e.g., structure des populations, régime alimentaire, morphologie) est d'un intérêt majeur et fait l'objet d'un vaste domaine de recherche en écologie.

1.2.2 - Conséquences écologiques des invasions biologiques en milieu aquatique: du gène à l'écosystème

Les conséquences écologiques des invasions biologiques peuvent être importante et s'étendent à l'ensemble des niveaux d'organisations écologiques (Simberloff et al. 2013). Par exemple, les phénomènes d'hybridation génétique sont fréquentes chez les espèces invasives (Ellstrand & Schierenbeck 2006) et peuvent parfois engendrer l'extinction de l'espèce native (Huxel 1999). Les impacts des espèces invasives sur les populations et les communautés natives ont largement été étudiés probablement parce qu'ils sont immédiatement visibles et relativement simple à mesurer. En effet, via des interactions directs (compétition, prédation, parasitisme) ou indirectes (modifications des habitats, introduction de pathogène), les espèces invasives conduisent généralement à une diminution de l'abondance et de la diversité ainsi qu'à une modification de la structure des populations natives (Kaufman 1992, Sakai et al. 2001, Blackburn et al. 2004). Bien qu'il semble implicite que les effets des espèces invasives sur les niveaux inférieurs d'organisation biologiques vont se répercuter aux niveaux supérieurs, leurs impacts sur le fonctionnement de l'écosystème et les mécanismes impliqués demeurent relativement peu étudiés (Cucherousset & Olden 2011, Strayer et al. 2012). Plus précisément, les invasions biologiques perturbent les relations trophiques précédemment établis entre les espèce autochtones, modifiant ainsi les mécanismes ascendants et descendants régulateurs du fonctionnement de l'écosystème (Ehrenfeld 2010). En parallèle, les invasions biologiques peuvent également impacter le fonctionnement de l'écosystème par le biais de modifications chimiques et physiques de l'habitat comme par exemple lors de la formation de "hot-spot" biogéochimique (Boulêtreau et al. 2011, Capps & Flecker 2013a). Cependant, puisque les conditions environnementales interviennent dans le succès d'invasion des populations, les impacts écologiques des populations invasives devraient varier en fonctions des conditions locales. Par exemple, il est généralement admis que les impacts seront d'autant plus sévères que les milieux seront pauvres en diversité spécifique et limités en nombre d'interactions biotiques (e.g.,

compétition et prédation) (Ricciardi & MacIssac 2011). Par conséquent, mieux comprendre les caractéristiques des populations invasives le long des gradients environnementaux se révèle d'un enjeu crucial afin de mieux prédire leurs impacts potentiels sur l'ensemble des niveaux d'organisation biologiques.

1.2.3 - Gestion des invasions biologiques en milieu aquatique

Des changements de traits phénotypiques induits par les activités humaines ont été largement documentés dans les écosystèmes terrestres et aquatiques (Kettlewell 1958, Allendorf & Hard 2009). De plus, l'Homme exploite les populations naturelles de manière non-aléatoire en sélectionnant préférentiellement certains individus de la population (Coltman et al. 2003, Festa-Bianchet & Lee 2009). Cette sélection se base sur les traits phénotypiques des individus (Biro & Post 2008, Biro & Sampson 2015) et peut conduire à des changements évolutifs rapides et parfois drastiques (Conover & Munch 2002, Darimont et al. 2009b). Par exemple, la pêche industrielle ou récréative vise à capturer préférentiellement les individus d'intérêts, c'est-à-dire ceux avec la plus grande taille, ce qui peut altérer les traits d'histoire de vie (e.g., maturité précoce à taille réduite, diminution de la croissance), se répercuter sur les paramètres démographiques et potentiellement conduire au déclin de la population (Jørgensen et al. 2007, Laugen et al. 2014).

Les milieux aquatiques d'eau douce sont particulièrement vulnérables aux invasions biologiques (van der Velde et al. 2006). Les poissons sont parmi les organismes les plus introduits dans les milieux aquatiques du fait de leur forte attractivité pour l'aquaculture et la pêche, qu'elle soit récréative ou professionnelle (García-Berthou et al. 2005a). La gestion des espèces invasives en milieu aquatique se base principalement sur des méthodes visant à éradiquer l'espèce invasive ou réguler son abondance par des moyens de lutte mécaniques, chimiques ou biologiques. Toutefois, l'éradication totale et définitive d'une espèce invasive n'est souvent possible que dans les premiers stades d'invasion (Britton et al. 2011). Lorsque l'établissement d'une espèce invasive est considéré comme irréversible, des mesures de contrôle sont mise en place de façon à réduire l'importance des populations. Ainsi, la lutte mécanique est une méthode de contrôle largement préconisée ayant pour avantage d'être spécifique à l'espèce ciblée, mais qui requiert une main d'œuvre importante et une répétition des campagnes de contrôle. Par conséquent, cette approche est privilégiée

dans de petites zones d'intervention et peut s'effectuer sous différentes formes telles que la collecte à la main des individus, la mise en place de pièges ou encore la pêche, et a donc pour avantage de faire intervenir un grand nombre d'opérateurs. Par conséquent, comprendre comment l'action de l'Homme peut moduler les traits phénotypiques des individus au sein des populations invasives et quelles en sont les conséquences sur l'écosystème s'avère être un enjeu crucial afin notamment de déterminer l'efficacité des méthodes de régulation mises en place.

1.2.4 - Variabilité intraspécifique et invasion biologique

Au cours de ces dernières décennies, de réels progrès ont été réalisés dans le domaine des invasions biologiques et ont abouti au développement d'un cadre conceptuel général permettant d'expliquer quels sont les caractères biologiques des espèces introduites impliqués dans leur succès invasif et leurs impacts écologiques (Kolar & Lodge 2001, Facon et al. 2006, Gurevitch et al. 2011). En parallèle, le concept de variabilité intraspécifique s'est appliqué à une large gamme de taxon mais demeure relativement peu étudié dans le contexte des invasions biologiques. Les populations invasives sont un choix intéressant pour étudier la variabilité intraspécifique puisque les individus sont souvent caractérisés par une forte plasticité phénotypique (Davidson et al. 2011) et sont donc susceptible de présenter des caractéristiques variables le long du front d'invasion. De plus, les capacités d'invasion et les impacts écologiques des individus introduits dépendent de leurs traits phénotypiques. Par exemple, l'expansion de l'espèce au sein de la zone géographique d'introduction va être favorisée par le caractère dispersant de l'espèce, lui même biaisé par le comportement de chaque individu (Cote et al. 2010a, Juette et al. 2014). Ensuite, les individus mâles et femelles d'une espèce étant souvent différents sur de nombreux traits phénotypiques, ceci permettrait d'expliquer que des populations invasives de *Gambusia affinis* de sex-ratio différent affectent différemment les processus écosystémiques (Fryxell et al. 2015). Par conséquent, bien que la variabilité intraspécifique est été relativement peu étudiée chez les espèces invasives, il s'avère important de quantifier son ampleur en milieux naturels afin de mieux prédire les conséquences écologiques des espèces invasives. C'est dans ce contexte qu'il serait également intéressant comparer les impacts écologiques induits par l'introduction de l'espèce à ceux causés par la variabilité intraspécifique elle-même.

I.3 - Objectifs

L'objectif général de cette thèse a été d'abord de quantifier la variabilité intraspécifique chez des espèces invasives puis d'évaluer son rôle dans la modulation des impacts de ces espèces sur le fonctionnement des écosystèmes aquatiques (Fig. I.5). Ce projet s'est basé sur des suivis de populations invasives présentes dans des écosystèmes aquatiques et des approches expérimentales qui ont permis de tester les effets de la variabilité intraspécifique sur les processus écosystémiques. La perche soleil *Lepomis gibbosus* (Linnaeus 1758) et l'écrevisse de Louisiane *Procambarus clarkii* (Girard 1852) ont été choisies comme espèces modèles du fait de leur caractère invasif dans une vaste aire géographique. L'utilisation de ces deux espèces modèles taxonomiquement et trophiquement distinctes, avait pour intérêt de pouvoir appréhender les effets de la variabilité intraspécifique sur un large panel de processus écosystémiques dépendants des caractéristiques écologiques et biologiques de chaque espèce.

La première partie de cette thèse avait pour objectif de mettre en évidence l'existence et de quantifier l'amplitude de la variabilité phénotypique chez les espèces invasives à différentes échelles d'organisation (i.e., entre et au sein des populations). Cette partie visait également à examiner le rôle des conditions environnementales dans la modulation de cette variabilité, en se focalisant plus particulièrement sur leur interaction. Ainsi, cette partie reposait sur des études comparatives des caractères structurels et fonctionnels de populations invasives sauvages établies le long de gradient environnementaux. Dans un premier temps, les effets de la gestion de l'invasion par la pêche récréative sur les traits d'histoire de vie et la structure des populations ont été examinés (*Chap. III*). Des analyses des niches trophiques ont permis de révéler la variabilité trophique entre populations invasives et par la suite d'examiner les effets complexes des facteurs environnementaux agissant en interaction dans la mise en place de cette variabilité (*Chap. IV*). Pour finir, une analyse à large échelle des divergences morphologiques entre des populations invasives établies sur le continent Nord Américain et Européen a été réalisée de façon à évaluer l'unicité des déterminants environnementaux et des mécanismes écologiques de la variabilité (*Chap. V*).

La deuxième partie de cette thèse s'est principalement focalisée sur les conséquences écologiques de la variabilité intraspécifique. Plus précisément, après avoir discriminé morphologiquement différentes populations invasives, une étude

expérimentale en mésocosmes a permis de tester les effets de la variabilité interpopulationnelle sur le taux de consommations et ses potentiels effets cascades sur le fonctionnement de l'écosystème (*Chap. VI*). Pour finir, après avoir quantifier des différences de régime alimentaire au sein des populations, une expérience en laboratoire a été mise en place pour appréhender le rôle de la variabilité trophique dans la modulation des taux d'excrétion de nutriments des consommateurs. L'utilisation de microcosmes a ensuite permis de comprendre comment cette variation du recyclage des nutriments pouvait moduler les effets indirects des consommateurs sur le fonctionnement de l'écosystème (*Chap. VII*).

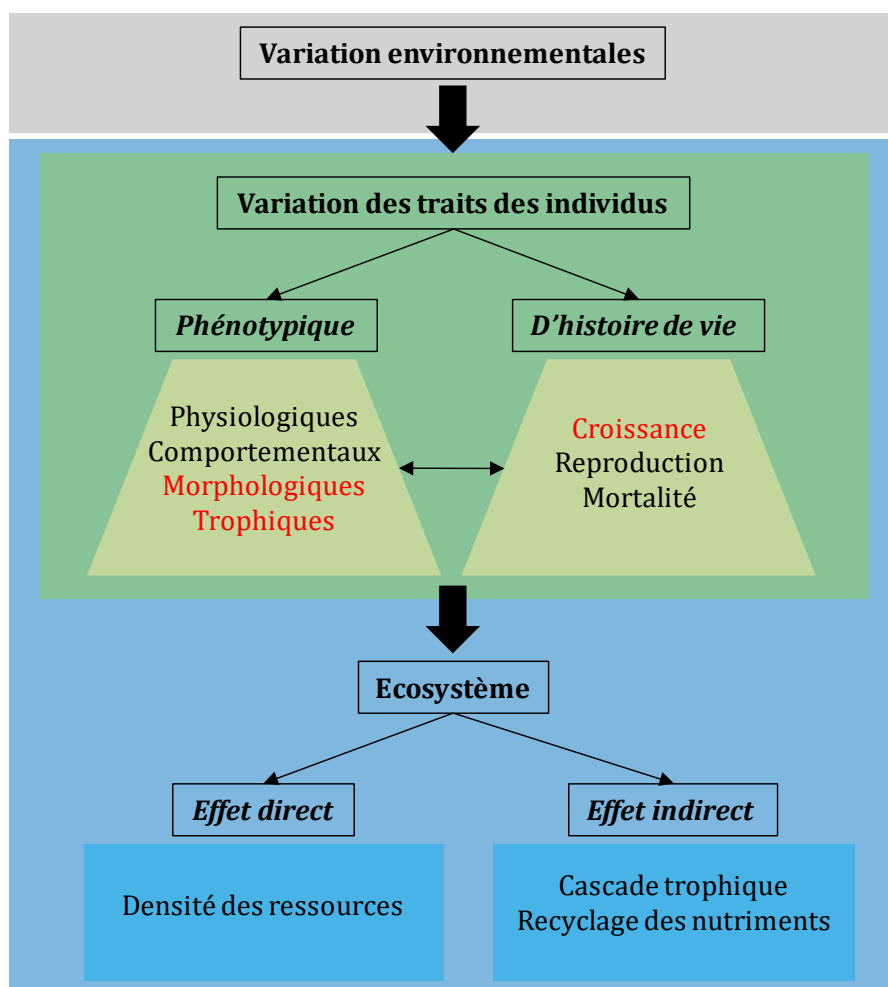


Figure I.5 Schéma de l'objectif général de cette thèse. Dans un premier temps, les effets des conditions environnementales dans la modulation de la variabilité des traits (i.e., phénotypiques et d'histoire de vie) au sein des espèces ont été déterminés. Puis, les conséquences de la variabilité intraspécifique sur le fonctionnement de l'écosystème ont été quantifiées par l'intermédiaire de l'étude des effets directs et indirects des consommateurs. En rouge, les traits principalement étudiés au cours de ce travail de thèse.

II.1- Sites d'étude

Ce travail de thèse a été conduit dans des plans d'eau artificiels situés le long de la plaine d'inondation de la Garonne dans le sud-ouest de la France. Ces plans d'eau artificiels sont des lacs de gravières, dont la formation est directement causée par l'extraction de granulats en zones de plaines alluviales ou de terrasse. En effet, pendant leur exploitation, les gravières se remplissent naturellement d'eau provenant de la nappe phréatique pour former des écosystèmes artificiels propices au développement de la vie aquatique (Zhao et al. 2016). Au cours de ces dernières décennies, la production de granulat s'est largement développée en Europe, en particulier à proximité des grandes agglomérations pour lesquelles les besoins en granulat pour la construction sont très importants. Ainsi, environ 400 millions de tonnes de granulat sont produites en moyenne chaque année en France depuis 1995 (données UNICEM - UNPG) pour satisfaire les besoins de la construction à l'échelle nationale, plaçant la France en 4ème producteur européen de granulat (données UEPG pour l'année 2013). La région Midi-Pyrénées est fortement sollicitée pour la production de granulat et représente 5.9 % de la production nationale, cette production étant principalement concentrée dans le département de la Haute-Garonne qui englobe 33 % de la production régionale (données UNICEM - UNPG pour l'année 2014). De plus, la production de granulat en Midi-Pyrénées est majoritairement d'origine alluviale et se concentre principalement dans le bassin de la Garonne, conduisant à la formation d'un vaste réseau de petits lacs peu profond et relativement jeunes. Ces lacs de gravières possèdent également la particularité d'être, pour la plupart, totalement déconnectés des autres systèmes aquatiques permanents du réseau hydrographique adjacent. De plus, l'attractivité de ces milieux pour les activités humaines est importante de part leur proximité avec les grandes agglomérations et ils font l'objet d'usages multiples tels que la pêche récréative, la promenade ou les activités nautiques. Par conséquent, ces milieux artificiels rendent de nombreux services écosystémiques (e.g., production alimentaire, support à la

biodiversité, régulation du climat) mais favorisent également l'introduction volontaire ou accidentelle d'espèces aquatiques non-natives.

Ce travail de thèse s'est concentré sur 19 gravières situées au sud-ouest de la ville de Toulouse et dans un rayon allant de 15 à 60 km du centre de la ville (Fig. II.1). Les gravières sélectionnées étaient situées le long d'un gradient d'âge de formation allant de quelques années pour les plus jeunes et jusqu'à plus d'une cinquantaine d'années pour les plus anciennes. Ce gradient d'âge a conféré aux sites étudiés des caractéristiques environnementales contrastées, principalement associées aux niveaux de maturité des écosystèmes et aux pratiques de gestion mises en place (Zhao et al. 2016). Plus précisément, les sites âgés étaient souvent caractérisés par une forte eutrophisation, accentuée par le développement des activités humaines (urbanisation, pêche récréative) du fait de leur proximité avec l'agglomération Toulousaine. Le fort contraste écologique entre les lacs était perceptible au niveau de nombreux attributs biotiques (e.g., productivité, richesse spécifique et biomasse de poisson, densité des populations invasives, intensité de la pêche) et abiotiques (i.e., turbidité, concentration en nutriments, périmètre du lac). Cette hétérogénéité parmi ces lacs localisés pourtant dans un périmètre relativement restreint offre une occasion unique pour l'étude des relations entre les populations invasives et le fonctionnement des écosystèmes (Fig. II.1).

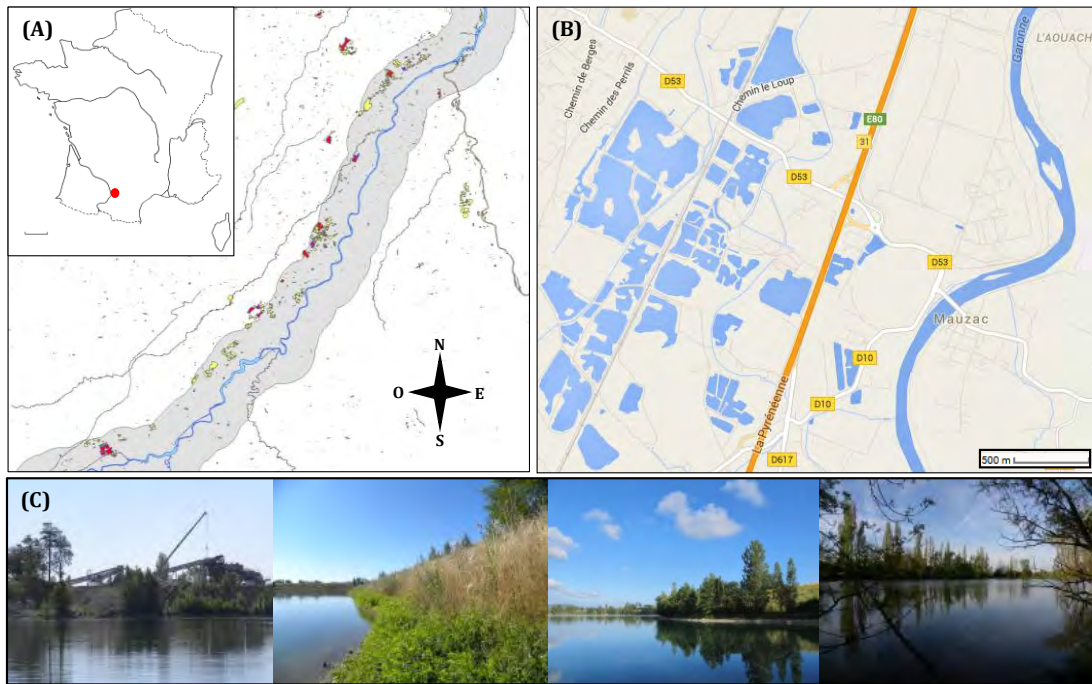


Figure II.1 (A) Les lacs de gravière étudiés sont localisés au sud-ouest de Toulouse dans la vallée de la Garonne. Les polygones jaune correspondent à l'ensemble des gravières répertoriées à partir de photographie aérienne, témoignant de l'étendu couverte par ces masses d'eau dans la région Toulousaine. Les polygones rouges représentent les 19 lacs de gravières étudiés dans cette thèse. (B) Illustration de la densité élevée de gravières rencontrées localement dans le secteur d'étude (source : Google Map, août 2016). (C) Activité d'extraction du granulat en bordure d'une gravière. Illustration de lacs de gravière d'âge de formation différents allant du plus jeune (à gauche) au plus âgé (à droite). © Charlotte Evangelista.

II.2 - Espèces modèles

L. gibbosus et *P. clarkii* (Fig. II.2A et II.2B) sont toutes deux originaires d'Amérique du Nord (du Nouveau-Brunswick à la Caroline du Sud pour *L. gibbosus*; Floride, Illinois, Louisiane et nord-est du Mexique pour *P. clarkii*) (Hobbs et al. 1989, Jordan et al. 2009). Contrairement à *L. gibbosus* qui fut introduite à Paris dès 1877 dans des bassins d'ornementation (Gensoul 1908), *P. clarkii* a été introduite plus tardivement en 1973 en Espagne pour l'aquaculture et sa progression rapide vers les autres pays européens demeure relativement mal connue (Gherardi 2006). Présente sur l'ensemble des continents exceptés l'Australie et l'Antarctique, *P. clarkii* est l'écrevisse la plus répandue à travers le monde (Hobbs et al. 1989). De part leur forte capacité d'adaptation à différents types de milieux (Hobbs et al. 1989, Vila-Gispert et al. 2002) et leur stratégie de type r (Copp & Fox 2007, Gherardi 2006; Tableau II.1), ces deux espèces se sont rapidement propagées à l'ensemble du territoire français et leur apparition en Haute-Garonne remonterait aux alentours de 1945 et 1995 pour *L. gibbosus* et *P. clarkii*,

respectivement. *P. clarkii* possède une tolérance environnementale très élevée pour des niveaux extrêmement bas d'oxygène dissous et une forte résistance à la dessiccation. Ces caractéristiques lui permettent de sortir du milieu aquatique pour se propager par la voie terrestre et coloniser de nouveaux écosystèmes (Banha & Anastacio 2014, Souty-Grosset et al. 2016). Omnivores opportunistes et décrites très voraces, ces deux espèces ont pour principaux effets écologiques de réduire considérablement l'abondance et la diversité des communautés d'invertébrés aquatiques et d'amphibiens dont elles se nourrissent dans les milieux qu'elles occupent (Gherardi & Acquistapace 2007, Renai & Gherardi 2004, van Kleef et al. 2008). Ces effets peuvent se répercuter par des cascades d'interactions sur le fonctionnement des écosystèmes (Jackson et al. 2014). De part leur comportement agressif, *L. gibbosus* et *P. clarkii* sont également des espèces très compétitrices pour l'accès à la ressource trophique et à l'habitat (Almeida et al. 2014, Souty-Grosset et al. 2016). De plus, *P. clarkii* utilise la matière végétale (litière de feuilles et macrophytes) comme source principale de nourriture, pouvant ainsi créer des changements dans les processus écosystémiques régulateurs du fonctionnement des écosystèmes. Par exemple, la consommation des macrophytes peut favoriser le passage de l'écosystème d'un état d'eau claire à eau turbide (Rodríguez et al. 2003) tandis que la décomposition annuelle de la litière peut être accélérée dans des plans d'eau fortement envahis par rapport à ceux peu envahis (Alp et al. 2016). Du fait de leurs impacts sur les écosystèmes aquatiques, *L. gibbosus* et *P. clarkii* sont réglementairement considérées en France comme des espèces susceptibles de provoquer des déséquilibres biologiques (Art. R. 323-3). Ainsi, tout individu capturé fait l'objet d'une réglementation stricte interdisant son transport vivant (Art. L. 432-11) et son introduction dans de nouveaux écosystèmes (Art. L. 432-10), obligeant ainsi la destruction des individus capturés. Tandis que le contrôle de *L. gibbosus* se fait principalement par le biais de la pêche récréative à la ligne, *P. clarkii* fait également l'objet de campagnes ponctuelles et intensives de piégeages à l'aide de nasses appâtées et d'approches basées sur la biomanipulation consistant à l'introduction de poissons prédateurs pour en diminuer les abondances (Paillisson et al. 2012).

Tableau II.1 Récapitulatif des traits d'histoire de vie de *Lepomis gibbosus* et *Procambarus clarkii* en France.

Traits d'histoire de vie	<i>Lepomis gibbosus</i>	<i>Procambarus clarkii</i>
Longévité	5 à 6 ans	2 à 3 ans
Age à maturité	1 an	1 an
Période de reproduction	de Mai à Août	du printemps à l'automne
Nb. de reproduction/an; Fécondité	plusieurs; 1500 - 3000 œufs	plusieurs; 50 - 600 œufs
Régime alimentaire	omnivore opportuniste à dominance animale	omnivore opportuniste à dominance végétale
Mode de dispersion naturelle	aquatique	aquatique et terrestre

II.3 - Collecte des données

Les individus de *L. gibbosus* et *P. clarkii* utilisés dans cette thèse lors des approches comparatives en milieux naturels (*Chap. III, IV, V, VI et VII*) ont été prélevés entre mi-Septembre à mi-October en 2012 et 2014, dans des conditions météorologiques similaires (Tableau II.2), à raison de l'échantillonnage d'un plan d'eau par jour. De plus, les différentes méthodes d'échantillonnage utilisées ont été mises en œuvre au même moment de la journée à chaque site. Plus précisément, les individus de *L. gibbosus* ont été prélevés par pêche électrique (Fig. II.2C) réalisée en début d'après-midi dans la zone littorale de chaque plan d'eau à l'aide d'un appareil DEKA 7000 (Deka, Marsberg, Allemagne) et en utilisant la méthode d'échantillonnage ponctuelle d'abondance (EPA, Copp & Garner 1995). Pour chaque point d'échantillonnage, l'anode était plongée dans l'eau, générant ainsi un champ électrique attirant les poissons et les faisant remonter à la surface. L'emplacement des EPA a été déterminé de façon pseudo-aléatoire et de manière à échantillonner la totalité du périmètre du lac considéré. Conformément à la procédure utilisée par Cucherousset et al. (2006a), les EPA étaient espacés de 25m les uns des autres. Le nombre d'EPA variait donc entre les lacs selon leur taille, allant d'un minimum de 20 à un maximum de 45. Les captures de *P. clarkii* ont été réalisées à l'aide de nasses préalablement appâtées (Fig. II.2D). Pour chaque site, des nasses ont été posées de nuit et pendant la journée à proximité des berges. Par conséquent, une relève des nasses a été effectuée le matin pour les poses de nuit et en fin de journée pour les

poses de jour. Dans certains sites, le nombre de *P. clarkii* capturées à l'aide des nasses était insuffisant pour effectuer les analyses prévues. Des individus supplémentaires ont donc été récoltés en effectuant des échantillonnages intensifs à l'aide d'un filet de type senne et d'épuisettes.

Concernant l'étude intercontinentale (*Chap. V*), des populations invasives de *L. gibbosus* et *P. clarkii* ont été échantillonnées dans des lacs naturels situés à proximité de Seattle (Etat de Washington, Etats-Unis; Tableau II.2). Du fait de la forte attractivité de ces lacs pour la baignade et les activités nautiques, l'utilisation de la pêche électrique était impossible et les individus de *L. gibbosus* ont été capturés à l'aide de filets de type senne et verveux (Fig. II.2E et II.2F). Les individus de *P. clarkii* ont été capturés suivant les méthodes précédemment décrites mais seules des poses de nasses de nuit ont été réalisées.

De façon à limiter le stress des individus utilisés lors des études expérimentales (*Chap. VI et VII*), les captures ont été réalisées au cours des automnes 2013 et 2015 (le 30 Octobre et du 29 au 30 Septembre, respectivement; Tableau II.2) lors de pêches à la senne et de piégeage par nasses pour *L. gibbosus* et *P. clarkii*, respectivement. Ces individus ont ensuite été maintenus vivants et acclimatés pendant plusieurs semaines dans des bacs de stockage dans les conditions expérimentales avant le début de chaque étude.

Pour finir, les paramètres environnementaux des sites d'études ont été mesurés lors des campagnes d'échantillonnages et lors de suivis annuels des conditions physico-chimiques. Le choix des paramètres environnementaux a été dicté à chaque fois par les objectifs et questions propres à chaque chapitre.

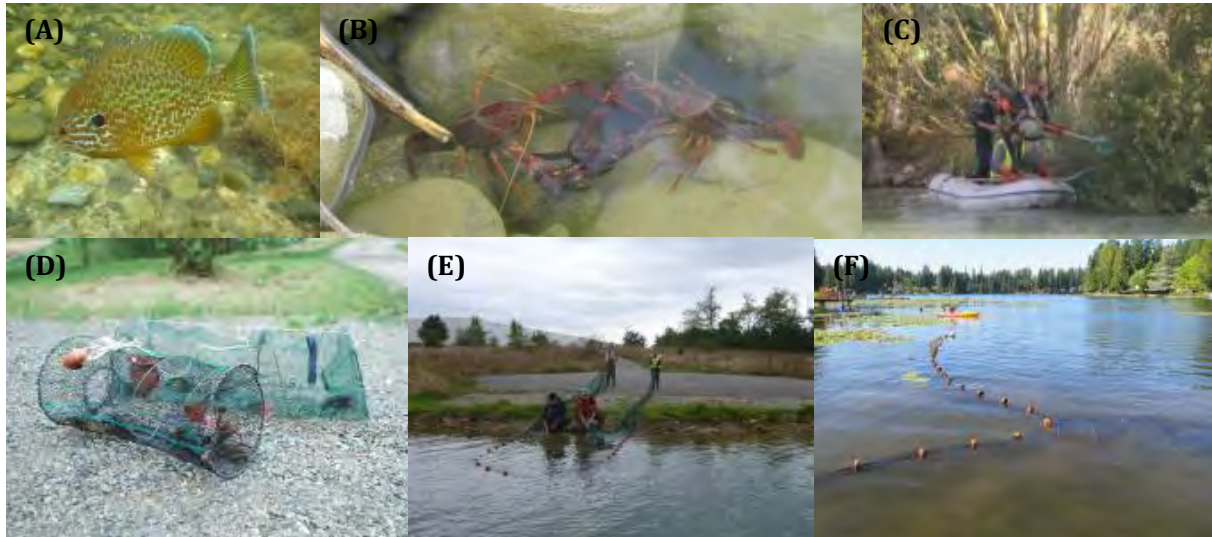


Figure II.2 (A) Perche soleil *Lepomis gibbosus*. (B) Ecrevisses de Louisiane *Procambarus clarkii*. (C), (D), (E) et (F) Illustrations des différentes méthodes d'échantillonnages utilisées pour capturer les individus de *L. gibbosus* et *P. clarkii*: pêche électrique, piégeage par nasses, pêche au filet de type senne et au filet verveux. © Nicolas Charpin (A, E), © Charlotte Evangelista (B, C, F), © Maria Alp (D).

Pour les approches comparatives, et après chaque capture, les individus de *L. gibbosus* et *P. clarkii* ont été euthanasiés à l'aide d'une overdose d'eugénol, transférés au laboratoire dans de la glace puis conservés à -20°C en vue des analyses biométriques ultérieures. Après décongélation, les individus des deux espèces ont été photographiés (voir détails ci-dessous), mesurés (longueur fourche et taille de carapace pour *L. gibbosus* et *P. clarkii*, respectivement; ± 0.1 mm) et pesés (± 0.1 g). Le sexe des écrevisses étant facilement identifiable extérieurement sur des critères macroscopiques, il a été déterminé pour chaque individu de *P. clarkii* avant les dissections. Des écailles ont été prélevées au dessus de la ligne latérale des individus de *L. gibbosus* dans le but de déterminer l'âge des individus, de recalculer leur longueur à âge en se basant sur la corrélation positive entre la taille du poisson et le rayon de l'écaille (Ombredane & Blaglinière 1992) et ainsi de rétro-calculer la croissance de chaque individu. Les estomacs de *L. gibbosus* ont également été prélevés et conservés dans de l'éthanol afin de réaliser des analyses de contenus stomacaux (voir détails ci-dessous et Chap. VII). Quand cela était possible, le sexe des individus de *L. gibbosus* a été déterminé pendant les dissections. Enfin, pour chaque individu, un échantillon de muscle a été prélevé sur la partie dorsale et l'abdomen de *L. gibbosus* et *P. clarkii*, respectivement, en vue des analyses des isotopes stables.

Tableau II.2 Récapitulatif du nombre d'individus de *Lepomis gibbosus* et *Procamburus clarkii* analysés entre 2012 à 2015 dans les différents lacs échantillonnés en France et aux Etats-Unis (*en gras*). Les principaux traits étudiés sont mentionnés ainsi que le Chapitre correspondant.

Année d'échantillonnage	Type d'étude	Nb. de lacs		Nb. d'individus		Traits mesurés	Chapitre de référence
		<i>L. gibbosus</i>	<i>P. clarkii</i>	<i>L. gibbosus</i>	<i>P. clarkii</i>		
2012	Approche comparative en milieu naturel	10	–	330	–	Trait d'histoire de vie	Chap. III
		–	15	–	218	Traits trophiques*	Chap. IV
		11	–	303	–	Traits trophiques*‡	Chap. VII
2013	Approche expérimentale	1	–	48	–	Taux d'excrétion des nutriments	Chap. VII
	(7 traitements; 6 répliques)					Croissance	
2014	Approche comparative en milieu naturel	6 - 6	6 - 5	120 - 107	120 - 89	Traits trophiques *	Chap. V
						Traits morphologiques	
		–	15	–	294	Traits morphologiques	Chap. VI
2015	Approche expérimentale	–	4	–	64	Traits morphologiques	Chap. VI
	(4 traitements; 1 contrôle; 4 répliques)					Taux de consommation	
						Croissance	

* analyses des isotopes stables du carbone et de l'azote. ‡ analyses des contenus stomacaux.

II.4 - Analyses de la niche trophique

Traditionnellement, l'étude du régime alimentaire des consommateurs est basée sur l'utilisation de méthodes directes et notamment sur les analyses des contenus stomacaux. Ces analyses nécessitent d'identifier des restes de proies présents dans l'estomac des consommateurs, permettant ainsi d'obtenir une composition détaillée (au niveau taxonomique) du régime alimentaire (García-Berthou & Moreno-Amich 2000b).

Sur la base des données issues des contenus stomacaux, un indice développé par Bolnick et al. (2002) permettant de calculer pour chaque individu son niveau de spécialisation trophique en se basant sur la distribution de fréquence de chaque taxon consommé a été utilisé. Cette distribution de fréquences est alors comparée à celle de l'ensemble des ressources consommées par la population qui définit alors la disponibilité en ressources, permettant ainsi de comparer chaque individu à l'ensemble de sa population plutôt qu'à la disponibilité des ressources dans son environnement (Bolnick et al. 2002; voir les détails au Chap. VII). Il faut toutefois noter que les analyses des contenus stomacaux présentent des difficultés méthodologiques (identification difficile des proies, contenus qui varient en fonction du moment de prélèvement, contenus vides) et n'informent pas sur les ressources énergétiques réellement assimilées par les consommateurs (Votier et al. 2003). Par conséquent, des analyses des isotopes stables ont également été utilisées pour caractériser la niche trophique à l'échelle individuelle et populationnelle (Chap. IV, V, VII).

L'utilisation des isotopes stables permet de quantifier de manière indirecte les interactions trophiques entre les consommateurs et leurs proies et d'estimer les ressources réellement assimilées, c'est-à-dire celles qui contribuent directement au métabolisme de l'individu (Fry 2007; Box II.A). De plus, les isotopes stables fournissent une vision temporellement intégrative des régimes alimentaires, allant de plusieurs jours à plusieurs mois en fonction des tissus analysés (Layman et al. 2012). Les isotopes du carbone et de l'azote sont les deux éléments les plus largement utilisés en écologie trophique. L'azote (ratio isotopique noté $\delta^{15}\text{N}$) est utilisé comme indicateur de la position trophique des organismes (Vander Zanden et al. 1997). Le carbone (ratio isotopique noté $\delta^{13}\text{C}$), quant à lui, renseigne sur l'origine de la ressource consommée (Post 2002). Par exemple, l'utilisation du $\delta^{13}\text{C}$ permet de discriminer des proies d'origine terrestre *versus* aquatique (Larson et al. 2011) ou encore d'origine littorale *versus* pélagique (Quevedo et al. 2009). L'utilisation conjointe du $\delta^{13}\text{C}$ et du $\delta^{15}\text{N}$ dans un espace à deux dimensions (valeurs de $\delta^{13}\text{C}$ en abscisse et valeurs de $\delta^{15}\text{N}$ en ordonnée; Box II.A) permet donc de positionner les entités écologiques considérées (consommateurs et ressources) les unes par rapport aux autres et ainsi représenter la niche isotopique. Cette représentation graphique permet de visualiser la structure générale du réseau trophique et d'inférer les interactions trophiques.

Les données issues des analyses isotopiques en écologie peuvent désormais être synthétisées de manière quantitative à l'aide d'indices. La définition de ces indices est ancrée dans le concept de niche écologique et notamment de l'idée que la dispersion des individus dans l'espace isotopique est révélateur de la niche trophique de la population (Bearhop et al. 2004, Newsome et al. 2007). La « *Standard Ellipse Area* » (SEA) développée par Jackson et al. (2011) est un indice représentatif de la variance du nuage de points formés par les individus d'une population dans l'espace isotopique. Cette métrique s'avère peu sensible à la présence de valeurs extrêmes et aux nombres d'individus échantillonnés (Jackson et al. 2011). En parallèle de cette mesure de la taille de la niche trophique, les modèles de mélange permettent d'estimer la contribution relative de chaque ressource trophique au régime alimentaire de chaque consommateur à partir des valeurs de $\delta^{13}\text{C}$ et de $\delta^{15}\text{N}$ des consommateurs et de leurs ressources potentielles (Philips & Gregg 2003; Box II.A). Dans cette thèse, les isotopes stables ont été utilisés pour l'étude des relations trophiques (Layman et al. 2012) et du rôle des consommateurs dans le fonctionnement des écosystèmes (Matthews et al. 2010, Kreps et al. 2016).

Dans le cadre des analyses isotopiques réalisées au cours de cette thèse, les échantillons de tissus prélevés sur les individus de *L. gibbosus* et *P. clarkii* ont été séchés à l'étuve (60°C pendant 48h) puis broyés jusqu'à l'obtention d'une poudre fine et homogène. Les ressources potentielles de chaque espèce ont également été collectées au cours des campagnes d'échantillonnage, nettoyées à l'aide d'eau distillée puis conservées dans de la glace et enfin ramenées au laboratoire. Exceptés pour le périphyton (*voir détails dans Chap. V*), les échantillons des ressources ont été séchés puis broyés suivant les mêmes procédures précédemment décrites pour les consommateurs. Enfin, tous les échantillons ont été analysés pour les valeurs isotopiques du carbone et de l'azote au Laboratoire d'Isotopie de Cornell (COIL, Ithaca, NY, Etats-Unis).

Box II.A Principe d'utilisation des isotopes stables en écologie trophique : "You are what you eat plus a few ‰" (DeNiro & Epstein 1976)

Les isotopes d'un même élément chimique possèdent le même numéro atomique (nombres identiques de protons) mais diffèrent de part leur masse atomique (nombres différents de neutrons), conduisant ainsi à la formation d'isotopes qualifiés de "légers" et "lourds". La stabilité énergétique d'un isotope est assurée par les neutrons contenus dans son noyau qui empêchent sa désintégration radioactive.

Le rapport entre isotopes stables d'une même espèce chimique s'exprime en unité δ (‰) qui compare le rapport isotope lourd / isotope léger à un rapport fixé par un standard international selon l'équation suivante:

$$\delta X = \left(\frac{R_{\text{échantillon}}}{R_{\text{standard}}} - 1 \right) \times 1000 \text{ (‰)}$$

où $X = {}^{13}\text{C}$ (carbone) ou ${}^{15}\text{N}$ (azote) et $R = {}^{13}\text{C}/{}^{12}\text{C}$ pour le carbone et ${}^{15}\text{N}/{}^{14}\text{N}$ pour l'azote. Pour le carbone ($\delta^{13}\text{C}$), la composition isotopique du standard est celle de la Pee Dee Belemnite (fossile calcaire, VPDB, $\delta^{13}\text{C} = 0$ ‰) et pour l'azote ($\delta^{15}\text{N}$), la référence est celle de l'azote atmosphérique ($\delta^{15}\text{N} = 0$ ‰).

Les propriétés chimiques des isotopes d'un même élément sont identiques car ils possèdent le même nombre d'électrons (et de protons). En revanche, la différence de masse entre les isotopes d'un même élément engendre des propriétés cinétiques et thermodynamiques différentes qui se traduisent par des vitesses de réaction et des concentrations différentes à l'équilibre. Ainsi, à chaque réaction chimique ou transformation biologique, l'isotope léger (${}^{12}\text{C}$ et ${}^{14}\text{N}$) est préférentiellement utilisé par le métabolisme et la matière organique s'enrichit en isotope lourd (${}^{13}\text{C}$ et ${}^{15}\text{N}$). Cet enrichissement crée une différence de composition isotopique entre une source et son consommateur appelé fractionnement isotopique. Par conséquent, la composition isotopique d'un consommateur dépend de la composition en isotopes stables de sa ressource alimentaire et du fractionnement isotopique pendant le processus d'assimilation et d'intégration dans le corps. Ce fractionnement isotopique dépend de plusieurs facteurs tels que le type de nourriture, les conditions environnementales ou encore le groupe taxonomique (Vander Zanden & Rasmussen 2001, Vanderklift & Ponsard 2003, Mc Cutchan et al. 2003) mais il est typiquement admis que les rapports en carbone et en azote stables sont enrichis de la ressource au consommateur de environ 1 ‰ et 3 ‰, respectivement (DeNiro & Epstein 1981, Minagawa & Wada 1984).

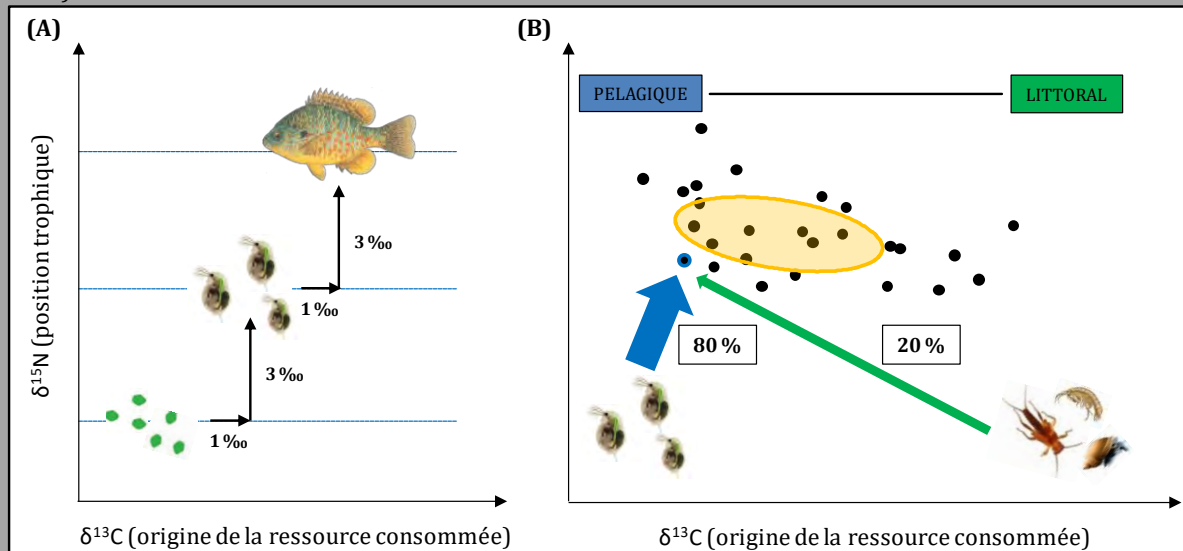


Figure II.A1 Bi-plot isotopique du carbone ($\delta^{13}\text{C}$) et de l'azote ($\delta^{15}\text{N}$) illustrant (A) un réseau trophique et l'enrichissement trophique d'environ 1 ‰ pour le carbone et 3 ‰ pour l'azote entre un consommateur et ses ressources et (B) la niche isotopique (« standard ellipse area », SEA; ellipse jaune) d'une population de consommateur. Chaque point représente un individu de la population et la surface de la SEA correspond à la taille de la niche isotopique. L'utilisation de modèles de mélanges permet d'estimer la contribution relative (%) de chacune des ressources dans le régime alimentaire d'un consommateur

II.5 - Analyses morphologiques

La morphométrie géométrique est une méthode de biologie comparative qui permet de quantifier les variations de forme entre organismes, et ce indépendamment de leurs tailles (i.e., conformation géométrique). Dans cette méthode d'analyse morphologique, la forme est spécifiée à partir de coordonnées de points-repères (ou « *landmarks* ») homologues positionnés sur le contour du corps ou d'organes externes de chaque organisme. Les profils géométriques ainsi obtenus servent de représentations graphiques des variations morphologiques et sont utilisés pour déterminer les facteurs environnementaux impliqués dans la mise en place de variations morphologiques inter- ou intraspécifique (Franssen et al. 2013, Kusche et al. 2014).

Afin de réaliser les analyses morphologiques, les individus de *L. gibbosus* et *P. clarkii* ont été photographiés sur le côté gauche et en vue dorsale, respectivement (Fig. II.3A). Des points-repères ont été sélectionnés de manière à intégrer la forme générale du corps des deux espèces modèles (Etchison et al. 2012, Parsons & Robinson 2007; Fig. II.3B et II.3C). Ces points-repères décrivent des coordonnées en deux dimensions et ont été digitalisés sur les photographies à l'aide du logiciel informatique TpsDig2 (v.2.17; Rohlf 2013). Ensuite, pour chaque individu, les coordonnées obtenues ont été importées dans le logiciel MophoJ (v.1v.06d) afin d'opérer un alignement des conformations. Cette étape d'uniformisation du référentiel est nécessaire pour comparer les conformations géométriques des différents individus en s'affranchissant de leur orientation, de leur taille et de leur position. La méthode traditionnelle d'alignement des conformations géométriques dite de superposition Procruste (« *Generalized Procrustes Analysis* », GPA) a été utilisée ici (Klingenberg 2011). La superposition Procruste se décompose en trois étapes (Fig. II.3D): une translation qui a pour objectif de centrer toutes les conformations sur leur centroïde (centre de gravité de la conformation), une normalisation qui vise à mettre à l'échelle l'ensemble des conformations en utilisant la taille centroïde (racine carré de la somme des distance entre les points-repères et le centroïde) comme unité de taille et, enfin, un ajustement généralisé selon la méthode des moindre carrés qui vise à aligner toutes les conformations par rotation (Mitteroecker & Gunz 2009). A la suite de cette étape de superposition Procruste, la forme de chaque individu est définie par de nouvelles coordonnées superposées et par sa taille centroïde. L'utilisation d'outils statistiques a ensuite été nécessaire afin de

synthétiser l'information morphologique contenue dans les coordonnées superposées. Plus précisément, des analyses en composante principale (ACP; *Chap. V*) ou des analyses canoniques (CVA; *Chap. VI*) ont été réalisées afin d'attribuer à chaque individu un score le long de plusieurs axes de variation morphologique. Finalement, le logiciel TpsRERGR (Rohlf 2011) a été utilisé afin de visualiser de manière synthétique et à travers des grilles de déformations en deux dimensions, les formes extrêmes le long de ces axes.

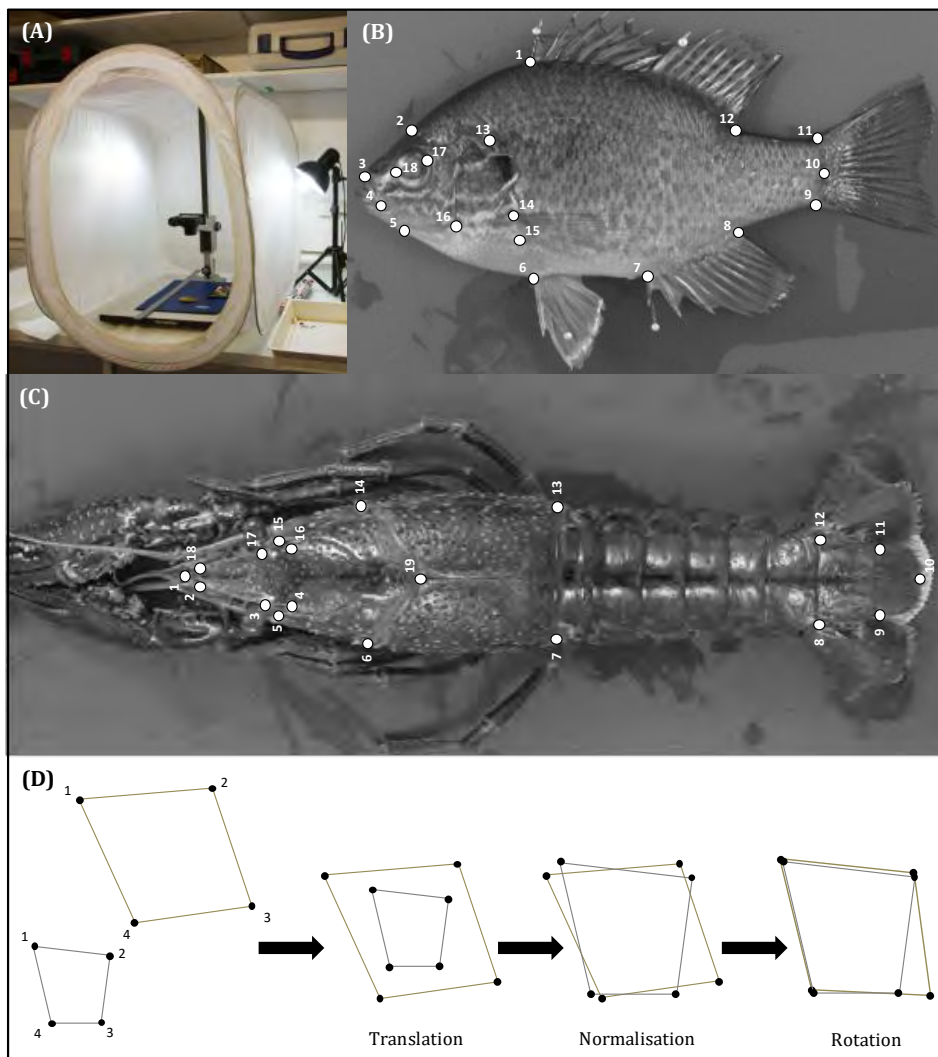


Figure II.3 (A) Dispositif utilisé pour photographier les individus de *Lepomis gibbosus* et *Procambarus clarkii*. Localisation des points repères homologues (« landmarks ») utilisés lors des analyses morphométriques sur (B) *L. gibbosus* (n = 18 points repères) et (C) *P. clarkii* (n = 19 points repères). (D) Illustration des trois étapes de la superposition Procruste (GPA): la translation permet de centrer les différentes conformations sur leur centroïde (centre de gravité), la normalisation permet de mettre à l'échelle les conformations en utilisant la taille centroïde comme unité de taille, la rotation permet d'aligner les conformations suivant un alignement généralisé. Adaptée de Mitteroecker & Gunz 2009. © Rémi Munier (a), Charlotte Evangelista (b, c).

Impacts of invasive fish removal through angling on population characteristics and juvenile growth rate

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*Adapted from an article published in Ecology and Evolution
(5(11): 2193 - 2202)*

Key-words biological invasions, non-random selection, *Lepomis gibbosus*, recreational angling, invasive species management

Résumé

L'exploitation halieutique, et notamment la pêche sélective, peut modifier les caractéristiques des populations naturelles de poissons et conduire à de rapides changements écologiques et évolutifs. En dépit des effets bien connus des poissons invasifs sur les écosystèmes aquatiques, les conséquences potentielles d'une méthode de contrôle communément utilisée et consistant à éradiquer les individus de manière sélective via la pêche récréationnelle demeurent peu connues. En utilisant la perche soleil (*Lepomis gibbosus*) originaire d'Amérique du nord comme espèce modèle, l'objectif de cette étude a été d'examiner, à travers le suivi de 10 populations établies dans des lac artificiels du Sud Ouest de la France, les conséquences de leur éradication sélective sur les caractéristiques des populations et la croissance des juvéniles. Nous avons observé que la masse maximale individuelle diminuait lorsque la pression d'éradication via la pêche récréationnelle augmentait. En revanche, nous n'avons pas observé de modification significative de la taille maximale individuelle avec l'augmentation de la pression d'éradication. L'abondance totale des populations n'augmentait pas avec la pression d'éradication, en revanche, il y avait une relation non-linéaire entre la pression d'éradication et l'abondance des individus de taille moyenne. De plus, la biomasse des populations indiquait également une réponse non-monotone (c.à.d. courbe en U) à la pression d'éradication, suggérant que les populations invasives pouvaient moduler leurs caractéristiques afin de compenser les effets négatifs induits par la pression d'éradication. Enfin, la taille des individus de 2 ans ainsi que le taux de croissance des juvéniles diminuaient avec l'augmentation de la pression de pêche récréationnelle, indiquant probablement une adaptation vers des individus ayant une taille à maturité plus petite et de manière générale, des phénotypes à croissance lente. Par conséquent, ces résultats remettent en question l'efficacité des méthodes sélectives de contrôle des populations invasives, suggérant l'utilisation de méthodes plus proactives dans le contrôle des populations invasives et le besoin d'approfondir nos connaissances à propos des potentielles répercussions écologiques et évolutives des éradications non-aléatoires.

Abstract

Exploitation can modify the characteristics of fish populations through the selective harvesting of individuals, with this potentially leading to rapid ecological and evolutionary changes. Despite the well-known effects of invasive fishes on aquatic ecosystems generally, the potential effects of their selective removal through angling, a strategy commonly used to manage invasive fish, is poorly understood. The aim of this field-based study was to use the North American pumpkinseed *Lepomis gibbosus* as the model species to investigate the consequences of selective removal on their population characteristics and juvenile growth rates across 10 populations in artificial lakes in Southern France. We found that the maximal individual mass in populations decreased as removal pressure through angling increased, whereas we did not observe any changes in the maximal individual length in populations as removal pressure increased. Total population abundance did not decrease as removal pressure increased; instead, here was a U-shaped relationship between removal pressure and the abundance of medium-bodied individuals. In addition, population biomass had a U-shaped curve response to removal pressure, implying that invasive fish populations can modulate their characteristics to compensate for the negative effects of selective removals. In addition, individual lengths at age 2 and juvenile growth rates decreased as removal pressure through angling increased, suggesting a shift toward an earlier size at maturity and an overall slower growing phenotype. Therefore, these outputs challenge the efficiency of selective management methods, suggesting the use of more pro-active strategies to control invasive populations, and the need to investigate the potential ecological and evolutionary repercussions of non-random removal.

III.1 - INTRODUCTION

Invasive species are recognized as a major driver of global change that can invoke major ecological, evolutionary and economic consequences (Pimentel et al. 2005). Freshwater ecosystems are particularly vulnerable to biological invasions, with non-native fish being introduced through a variety of pathways (e.g., aquaculture, fisheries, aquarium trade) and incurring ecological impacts across different levels of biological organization (Gozlan et al. 2010, Cucherousset & Olden 2011). Where introductions of non-native fish result in invasions, their management is inherently difficult and often limited to removals via targeted captures that are commonly performed through fishing, including angling (Britton et al. 2011). While the potential efficiency of methods used to decrease the stock of invasive populations has been reported (Cucherousset et al. 2006b, Britton et al. 2011), the removal of individuals is often selective (Coltman et al. 2003, Wilson et al. 2011) and might lead to counterproductive results, including an increased abundance of the targeted invasive species through releases from intraspecific competition or cannibalism (Lewin et al. 2006). Consequently, it can be hypothesized that the removal of a non-random subset of individuals from the invading population by recreational angling might modify their population characteristics.

The intensive exploitation of wild populations selectively removes the most profitable individuals, i.e., those that maximize the yield (Coltman et al. 2003, Belgrano & Fowler 2013), imposing '*unnatural*' selection for the less profitable individuals (Allendorf & Hard 2009). For instance, fishing typically involves the targeting of the larger individuals (Law 2000, Jørgensen et al. 2007), with the potential to affect subsequent reproductive success and recruitment (Biro & Post 2008). Changes in life-history traits can subsequently impact population structure and dynamics, and lead to a drastic decline in the exploited stock or even local extinction (Law 2000, Allendorf et al. 2008, Palkovacs et al. 2012). Freshwater recreational angling is a significant component of the worldwide fishery (Cooke & Cowx 2004), but extant knowledge on the effects of angling-induced selection on wild and/or invasive populations remains relatively scarce (e.g., Cooke & Cowx 2006, Lewin et al. 2006, Philipp et al. 2009, Wilson et al. 2011). Recreational angling is usually size-selective and orientated towards the capture of the largest individuals (Isermann et al. 2005, Cooke & Cowx 2006, Alós et al. 2008) and the higher catchability of larger individuals could be driven by their behavior (Biro & Post

2008, Uusi-Heikkilä et al. 2008) and/or by hook-size selectivity (Alós et al. 2008). A recent field-based study demonstrated recreational angling also selects individuals based on their morphological traits, leading to populations with smaller mouths and deeper bodies (Alós et al. 2014). In entirety, these findings indicate recreational angling can also act as an important human-induced source of selection (Philipp et al. 2009, Sutter et al. 2012).

In the present study, we tested whether fish removal by recreational angling impacts the population characteristics and juvenile growth rate (length at age and length increment) of an invasive freshwater fish species (*Lepomis gibbosus*) in 10 artificial lakes located in Southwest France. In this country, *L. gibbosus* is one of the only two freshwater fish species that has a legal status of being 'invasive' because of its potential for causing ecological disruption (Guevel 1997). This is important, as it means recreational anglers are legally required to remove any captured specimens and this is currently the only strategy in place for managing *L. gibbosus* in France. We therefore predicted that (1) populations with higher levels of removal pressure would comprise of smaller and lighter individuals through the largest individuals being more vulnerable to capture and so removal (Law 2000, Cooke & Cowx 2006, Jørgensen et al. 2007); (2) *L. gibbosus* populations in lakes with higher levels of removals would be of lower population abundance and biomass due to angling-induced mortality; (3) population abundance and biomass could increase under a certain minimal threshold of capture size, given that removal by angling is size selective; and (4) changes in growth rates of individuals will result from the increased risk of mortality that results from higher removal pressure and this would lead to either faster or slower growth rates (Enberg et al. 2011).

III.2 - MATERIAL & METHODS

III.2.1 - Model species

Pumpkinseed *L. gibbosus* (L.) is a North American centrarchid that was introduced into Europe in the late 19th century and is now one of the most widely-established introduced fishes in Europe (García-Berthou & Moreno-Amich 2000a, Copp & Fox 2007). In its introduced range, *L. gibbosus* has been reported in both natural and artificial lentic ecosystems, and also some lotic ecosystems. In southern Europe, *L. gibbosus* populations

display a high potential for invasiveness that is associated with high growth rate and fecundity (Copp & Fox 2007). Age and size at maturity varies between 1.0 and 3.9 years, and 61.4 to 96.2 mm respectively (Copp & Fox 2007). Introduced *L. gibbosus* can also spawn several times within the same year (Fox & Crivelli 1997). The most common impact of *L. gibbosus* in its introduced range is diet overlap with native species and the consumption of eggs and molluscs (García-Berthou & Moreno-Amich 2000a). Ontogenic diet shift is common in *L. gibbosus*, with individuals initially feeding on soft-bodied prey and then shifting towards hard-bodied prey (García-Berthou & Moreno-Amich 2000b).

III.2.2 - Study area

The study was completed during 2012 in 10 artificial lakes localized along the flood plain of the Garonne River in southern Toulouse (South-Western France). These artificial lakes are former gravel pits (hereafter referred as lakes) that were located within a small geographic range (maximum distance between the lakes: 32.4km) and with substrates dominated by a mix of sand, gravel and pebble that are recognized as adequate habitats for *L. gibbosus*, notably for spawning (Kleef et al. 2008). In the studied lakes, fish species richness ranged from 5 to 15 (mean = 9.3 ± 1.1 SE), and the proportion of non-native species in the community ranged from 37.5 to 80.0 % (mean = $54.6 \% \pm 4.5$ SE). Fish communities in the studied lakes were dominated by Cyprinidae (roach *Rutilus rutilus* and rudd *Scardinius erythrophthalmus*), centrarchidae (*L. gibbosus* and largemouth bass *Micropterus salmoides*) and Percidae (perch *Perca fluviatilis* and pike-perch Sander lucioperca). Four obligate piscivorous fish species were sampled in these lakes: northern pike *Esox lucius*, *M. salmoides*, *P. fluviatilis* and *S. lucioperca*.

III.2.3 - Fish sampling

L. gibbosus were sampled in the littoral habitat of each lake from mid-September to mid-October 2012 between 12:00 and 16:00 using point abundance sampling performed randomly by electrofishing (PASE, Nelva et al. 1979, Cucherousset et al. 2006a). This was completed from a boat along the shore to sample the shallow littoral habitat, i.e., where the recreational angling primarily occurs (Cooke & Cowx 2004). The total number of points sampled per lake ranged from 20 to 45 (mean = 33.4 ± 2.1), depending upon lake size (smaller lakes used less sampling points) and covered the entire lake perimeter. All captured individuals were identified to species and fork length (i.e., the

length measured from the tip of snout to the fork of the tail) was estimated for all specimens (FL_e , nearest 5 mm). Captured individuals of *L. gibbosus* were immediately euthanized using an overdose of eugenol, stored on ice and frozen in the laboratory (-20 °C) until subsequent processing. After defrosting, subsamples of *L. gibbosus* (mean = 33 ± 1.69 individuals per population depending upon the total number of individuals sampled) were selected to encompass the full range of fork length and to be representative of the population size structure, with fish in each 10 mm-size class selected according to their proportion in the population. Fish were individually measured for fork length ($FL_m \pm 1$ mm) and weighed ($W_m \pm 0.1$ mg). Scales were removed below the lateral line and behind the dorsal fin, analyzed on a micro-projector (magnification: 48×) and aged through the counting of annual marks, with 25% subsets of scales (including scales of the oldest specimens) aged by a second operator for validation.

III.2.4 - Removal pressure and environmental characteristics

Removal pressure was quantified in each lake by counting the number of 'coarse' anglers along the shoreline on 16 occasions during two consecutive years from April 2012 to March 2013 and from April 2013 to March 2014 so as to fully encompass the variability in angler numbers driven by weather conditions, seasons and time. In the studied lakes, coarse anglers preferentially target cyprinid species over certain size thresholds using gears and hook sizes that also enable the capture of *L. gibbosus*. While the number of pumpkinseed actually captured by anglers was not directly estimated, it was assumed that the number of anglers was a direct proxy of removal pressure for *L. gibbosus*. Therefore, an index of removal pressure was calculated for each lake as the mean number of coarse anglers per shoreline length (expressed in number of anglers.km⁻¹). A set of environmental characteristics of lakes was then selected that were known as having strong influences on the population and individual characteristics of fish. Lake surface areas were estimated using GIS (km²), lake productivity was quantified using the integrative trophic status index (TSI; < 40 Oligotrophic, 40-50 Mesotrophic, 50-70 Eutrophic, > 70 Hypereutrophic) calculated using chlorophyll a ($\mu\text{g.L}^{-1}$), total phosphorus ($\mu\text{g.L}^{-1}$) and Secchi (m) parameters (Carlson 1977). For each of these parameters, three replicate measurements were performed in each lake on 11th and 12th September 2012. Predation pressure was estimated as the catch per unit effort of

obligate piscivorous fish species captured during electrofishing (ind.PASE^{-1}) in the littoral habitat of each lake. As these piscivorous fishes are gape-size limited predators and *L. gibbosus* are deep-bodied prey, a threshold of 95 mm was used as their minimum FL_e at which they could predate on young-of-the-year *L. gibbosus* and thus only predators with $\text{FL}_e > 95$ mm were used to quantify predation pressure.

III.2.5 - Data analyses

For each *L. gibbosus*, individual weight ($W_e \pm 0.1$ mg) was estimated from the relationship between FL_m and W_m obtained in each lake and FL_e . At the population level, FL_e and W_e were used to calculate the 90% quantile population fork length and 90% quantile population mass, respectively, to provide a representative estimate of the upper distribution of maximal length and mass at the population level. The total abundance of *L. gibbosus* was calculated as the catch per unit effort (CPUE defined as the number of individuals per PASE, ind.PASE^{-1}). In addition, the abundance of three different size classes of *L. gibbosus* (i.e., small-bodied: $\text{FL}_e < 60$ mm, medium-bodied: $60 \text{ mm} \leq \text{FL}_e < 90$ mm and large-bodied: $\text{FL}_e \geq 90$ mm) was calculated (ind.PASE^{-1}). Finally, the biomass of *L. gibbosus* (g.PASE^{-1}) was estimated using W_e . At the individual level, the back-calculated length at age was calculated using scale measurements and the scale proportional method (Francis 1990). Due to the lack of older individuals in several populations, length was back-calculated at age 1 and age 2. Protracted spawning (i.e., a second spawning event occurred late in summer) was revealed in a minority of lakes. This resulted in some very small young-of-the-year at the end of their first growth year (< 20 mm). To remove the effect of such protracted spawning, juvenile growth rate was quantified here as the growth increment between the back-calculated lengths between ages 1 and 2 (Beardsley & Britton 2012).

III.2.6 - Statistical analyses

We first tested the temporal stability of removal pressure using a Spearman correlation between removal pressure obtained from April 2012 to March 2013 and from April 2013 to March 2014. Spearman correlations were then used to analyze the relationships between environmental characteristics (i.e., lake surface area, productivity and predation pressure) and removal pressure. Population responses (i.e., fork length (90% quantile), mass (90% quantile), total abundance, abundance of small, medium and large

individuals and biomass, $n = 10$) to removal pressure were tested using linear models. Since we predicted that the vulnerability to removal by angling was size-selective, removal pressure might act non-monotonically on population biomass and abundance below a certain capture size threshold. Therefore, linear models were performed to test the effect of removal pressure through angling on population biomass and abundance included both linear and quadratic terms to assess monotonic (linear and nonlinear) and non-monotonic (hump-shaped and U-shaped) relationships. The quadratic term was removed when it was not significant according to a marginal t-test (Crawley 2007). Departures from homoscedasticity and the normality of residuals were assessed graphically using Tukey Ascombe plots and Q-Q plots, respectively. Fisher and Shapiro-wilk tests were used to confirm the assumption of homoscedasticity and normality and appropriate transformations were performed when necessary. Specifically, the 90% quantile fork length, the 90% quantile mass, population biomass, total abundance and abundance of small-bodied individuals were log-transformed. Removal pressure was square-root transformed to ensure a more even dispersion of lakes.

To test the effects of removal pressure and environmental characteristics on individual length at age 1 and 2 and juvenile growth rate, linear mixed effects models were performed with lake as a random factor (Pinheiro et al. 2012). All models included removal pressure, lake productivity, predation pressure and *L. gibbosus* total abundance as fixed effects. These last three variables were selected to encompass the main drivers of individual variability within a population (namely resource availability, predation and competition, respectively; Araújo et al. 2011). Spearman correlation matrices were performed to detect potential collinearity between predictors and when collinearity was presented, the residuals from the relationship between the two predictors were used in the linear mixed effects models (Zuur et al. 2009), resulting in the residuals from the relationship between removal pressure and lake productivity being used in the final linear mixed effects models. Lengths at age 1 and age 2 were log-transformed to fit a normal distribution and individual age (categorical variable) was included in the models to account for a potential cohort effect. Length at age 1 was included in the model with the juvenile growth rate to account for the fact that fish growth was not isometric. All analyses that were run with a full model included one-way interactions between removal pressure and predation pressure, *L. gibbosus* total abundance and lake productivity. Interactions were subsequently removed when non-significant by using

backward selection based on marginal t-test (Crawley 2007). For each final linear mixed effects model, the assumption of homoscedasticity and normality of residuals were checked using graphical tools and the residuals were plotted against each explanatory variable to check for independence. All linear mixed effects models conformed to the assumptions. All statistical analyses were performed using R (R development Core Team 2013). Where error around the mean is expressed, it represents standard error.

III.3 - RESULTS

III.3.1 - *Removal pressure through angling and environmental characteristics of lakes*

Removal pressure through angling was highly variable across the 10 lakes, ranging from 0.06 to 1.94 anglers per km of shoreline (mean = 0.71 ± 0.20 anglers km^{-1} ; Table III.1). Removal pressure measured from April 2012 to March 2013 and from April 2013 to March 2014 were significantly and positively correlated ($r = 0.76$, $S = 40$, 8df, $P = 0.016$), indicating a strong temporal stability of removal pressure in each lake across years. Each year, the level of removal pressure peaked from April to September, overlapping with the spawning period of *L. gibbosus* when individuals are more vulnerable to removal through angling because of nest guarding behaviors. Lake surface area ranged from 0.018 to 0.208 km^2 (mean = 0.118 ± 0.023 km^2 ; Table III.1) and was not significantly correlated to removal pressure ($r = -0.28$, $S = 212$, 8df, $P = 0.427$). Lake productivity ranged from nearly mesotrophic to hypereutrophic, with TSI ranging from 52.97 to 72.16 (mean = 60.52 ± 2.15 ; Table III.1) and was significantly and positively correlated to removal pressure ($r = 0.67$, $S = 54$, 8df, $P = 0.039$). Predation pressure by piscivorous fish species ranged from 0.13 to 2.71 ind.PASE⁻¹ (mean = 0.79 ± 0.24 ind.PASE⁻¹; Table III.1) and was not significantly correlated to removal pressure ($r = 0.12$, $S = 145.94$, 8df, $P = 0.751$).

Table III.1 Environmental characteristics of the ten studied lakes monitored from April 2012 to March 2014.

Site code	BAA	BON	LAV	BAA	FDL	BIR	POU	LIN	BID	BVI
Removal pressure (anglers.km ⁻¹)	0.06	0.16	0.28	0.33	0.35	0.42	1.09	1.25	1.26	1.94
Surface area (km ²)	0.03	0.18	0.09	0.21	0.19	0.21	0.10	0.04	0.12	0.02
Productivity (TSI)	55.47	59.22	52.97	54.03	57.83	65.19	54.20	66.88	72.16	67.29
Fish species diversity	5	5	6	12	15	11	8	8	13	10
Predation (ind.PASE ⁻¹)	0.49	0.13	0.32	0.89	0.89	2.71	1.34	0.40	0.18	0.50
Abundance (ind.PASE ⁻¹)	0.84	2.81	0.53	4.24	1.50	0.74	1.79	7.52	1.25	5.93
Biomass (g.PASE ⁻¹)	30.46	14.27	9.01	8.21	20.57	5.52	4.60	24.03	11.48	42.11

III.3.2 - Population responses to removal pressure through angling

The 90% quantile population fork length was not significantly related to removal pressure ($R^2 = 0.37$, $F_{1,8} = 4.69$, $P = 0.062$; Table III.2, Fig. III.2A) while the 90% quantile population mass was significantly and negatively related to removal pressure ($R^2 = 0.44$, $F_{1,8} = 6.30$, $P = 0.036$; Table III.2, Fig. III.2B), revealing that maximal individual mass in the population decreased as removal pressure increased. The total abundance of *L. gibbosus* varied over a 14-fold range across lakes, but was not significantly related to removal pressure ($R^2 = 0.25$, $F_{1,8} = 2.63$, $P = 0.144$; Table III.2). *L. gibbosus* populations were mainly composed of medium-bodied individuals (mean proportion = 44.2 ± 8.6 %, Fig. III.2C), whereas the mean proportion of small- and large-bodied individual represented 35.0 % (± 10.1) and 20.8 % (± 8.0) of the total abundance, respectively. The abundance of small-bodied and large-bodied individuals did not vary significantly with removal pressure ($R^2 = 0.07$, $F_{1,8} = 0.60$, $P = 0.460$ and $R^2 = 0.18$, $F_{1,8} = 1.76$, $P = 0.222$, respectively; Table III.2, Fig. III.2C). However, the abundance of medium-bodied individuals was significantly related to removal pressure in a non-monotonic manner ($R^2 = 0.70$, linear term: $F_{1,7} = 9.34$, $P = 0.019$, quadratic term: $F_{1,7} = 7.11$, $P = 0.032$; Table III.2). Specifically, the abundance of medium-bodied individuals was higher at low and high levels of removal pressure (Fig. III.2C). The biomass of *L. gibbosus* also varied considerably among populations, ranging between 3.28 and 42.11 g.PASE⁻¹ (mean = 17.0 ± 3.9 g.PASE⁻¹). A significant U-shaped relationship between removal pressure and population biomass was detected ($R^2 = 0.60$, linear term: $F_{1,7} = 0.33$, $P = 0.583$, quadratic term: $F_{1,7} = 10.05$, $P = 0.016$, Table III.2), with population biomass being lower at intermediate levels of removal pressure (Fig. III.2D).

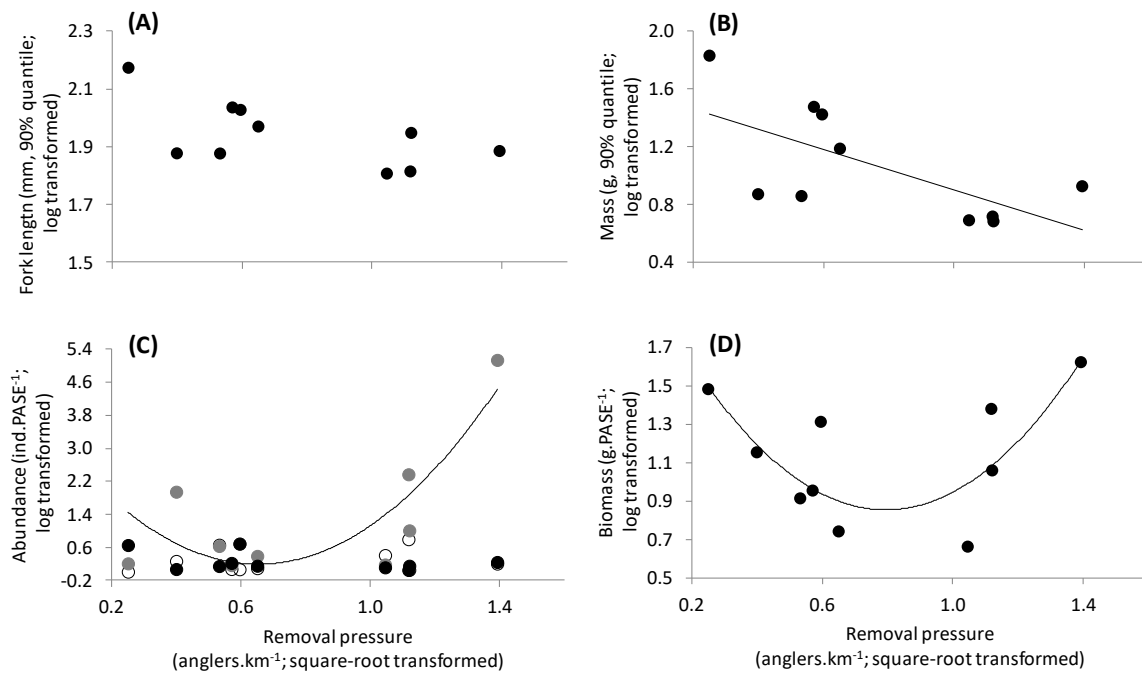


Figure III.2 Relationship between removal pressure through angling (anglers.km⁻¹, square-root transformed) and **(A)** fork length (mm, 90% quantile, log transformed), **(B)** mass (g, 90% quantile, log transformed), **(C)** abundance of small-bodied ($FL_e < 60\text{mm}$, open dots), medium-bodied ($60\text{mm} \geq FL_e < 90\text{mm}$, grey dots) and large-bodied ($FL_e \geq 90\text{mm}$, solid dots) individuals (ind.PASE⁻¹) and **(D)** biomass (g.PASE⁻¹, log transformed) across studied populations ($n = 10$). Significant relationships are depicted with solid lines. For panel **(C)**, the abundance of small-bodied individuals is log transformed and the significant relationship is between removal pressure and the abundance of medium-bodied individuals.

Table III.2 Results of the simplified regression models assessing linear and quadratic relationships between removal pressure through angling and population responses (90% quantile fork length, (mm), 90% quantile mass (g), total abundance (ind.PASE⁻¹), abundance of small-bodied (FL_e < 60mm), medium-bodied (60mm ≥ FL_e < 90mm) and large-bodied individuals (FL ≥ 90mm) (ind.PASE⁻¹) and biomass (g.PASE⁻¹); n = 10). Significant *P*-values are displayed in bold.

Response variables	Source of variation	df	Estimate (SE)	F	<i>P</i>		
Fork length (90% quantile)	Removal pressure	8	-0.18 (0.09)	4.69	0.062		
	Intercept	8	2.08 (0.07)				
Mass (90% quantile)	Removal pressure	8	-0.70 (0.28)	6.30	0.036		
	Intercept	8	1.60 (0.24)				
Total abundance	Removal pressure	8	0.52 (0.32)	2.63	0.143		
	Intercept	8	-0.12 (0.27)				
Small-bodied abundance	Removal pressure	8	0.19 (0.25)	0.60	0.460		
	Intercept	8	0.11 (0.21)				
Medium-bodied abundance	Removal pressure	7	-9.92 (4.78)	9.14	0.019		
	Removal pressure ²	7	7.63 (2.86)			7.11	0.032
	Intercept	7	3.42 (1.72)				
Large-bodied abundance	Removal pressure	8	-0.26 (0.20)	1.76	0.222		
	Intercept	8	0.44 (0.17)				
Biomass	Removal pressure	7	-3.42 (1.13)	0.33	0.583		
	Removal pressure ²	7	2.15 (0.68)			10.05	0.016
	Intercept	7	2.21 (0.41)				

III.3.3 - Individual responses to removal pressure through angling

At the individual level, none of the tested environmental parameters (i.e., productivity, predation pressure and abundance) had a significant effect on length at age 1 ($F_{1,196} = 1.19$, $P = 0.278$; $F_{1,6} = 2.14$, $P = 0.194$; $F_{1,6} = 1.18$, $P = 0.320$; Table III.3), length at age 2 ($F_{1,145} = 0.18$, $P = 0.675$; $F_{1,6} = 0.09$, $P = 0.774$; $F_{1,6} = 0.75$, $P = 0.419$; Table III.3) and juvenile growth rate ($F_{1,147} = 1.70$, $P = 0.194$; $F_{1,6} = 0.03$, $P = 0.877$; $F_{1,6} = 0.56$, $P = 0.482$; Table III.3). No significant relationship between removal pressure and the length at age 1 was found ($F_{1,6} = 0.58$, $P = 0.476$; Table III.3) whereas length at age 2 was significantly and negatively affected by removal pressure ($F_{1,6} = 8.62$, $P = 0.026$; Table III.3). We also found that length at age 1 had a significant and negative effect on juvenile growth rate

($F_{1,147} = 33.68$, $P < 0.001$; Table III.3), indicating that individuals with a larger body size at age 1 subsequently grew proportionally slower than individuals with smaller body size at age 1. Finally, juvenile growth rate was significantly and negatively affected by removal pressure ($F_{1,6} = 6.37$, $P = 0.045$; Table III.3).

Table III.3 Results of the linear mixed effects models used to test for the effects of removal pressure through angling and environmental characteristics (productivity, predation pressure and abundance) on length at age 1 (n = 211; R²m = 0.05 and R²c = 0.54), length at age 2 (n = 159; R²m = 0.10 and R²c = 0.58) and juvenile growth rate (n = 159; R²m = 0.17 and R²c = 0.63). Productivity refers to the residuals from the relationship between removal pressure and lake productivity. Significant P-values are displayed in bold.

	Length at age 1				Length at age 2				Juvenile growth rate			
	Df	Estimate (SE)	F	P	Df	Estimate (SE)	F	P	Df	Estimate (SE)	F	P
Fixed effects												
Age ^a or FL at age 1 ^b	4,196	*	3.25	0.013	3,145	*	2.07	0.107	1,147	- 23.11 (3.95)	33.68	< 0.001
Angling pressure	1,6	0.09 (0.07)	0.58	0.476	1,6	- 0.08 (0.04)	8.62	0.026	1,6	- 10.34 (6.05)	6.37	0.045
Productivity (residuals)	1,196	- 0.01 (0.01)	1.19	0.278	1,145	< 0.01 (< 0.01)	0.18	0.675	1,147	0.49 (0.42)	1.70	0.194
Predation	1,6	0.04 (0.03)	2.14	0.194	1,6	< 0.01 (0.02)	0.09	0.774	1,6	- 0.12 (2.62)	0.03	0.877
Abundance	1,6	- 0.09 (0.08)	1.18	0.320	1,6	- 0.04 (0.02)	0.75	0.419	1,6	- 4.67 (6.23)	0.56	0.482
Intercept	1,196	1.23 (0.07)	3157.9	< 0.001	1,145	1.92 (0.03)	22340.35	< 0.001	1,147	87.37 (7.22)	627.67	< 0.001
Random effect												
		Variance (SD)				Variance (SD)				Variance (SD)		
Intercept		< 0.01 (0.05)				< 0.01 (0.03)				26.65 (5.16)		
Residuals		0.05 (0.23)				0.01 (0.08)				112.29 (10.60)		

^a Age was included in the models with length at age, ^b FL at age 1 was included in the models with growth rate, * not available since Age was a categorical variable

III.4 - DISCUSSION

Human activities have been widely recognized as a driver of rapid trait change in wild animal populations (Hendry et al. 2008, Darimont et al. 2009b, Palkovacs et al. 2012), affecting individuals in a non-random manner (Coltman et al. 2003). However, the impacts of recreational angling on fish populations are usually underappreciated (Arlinghaus et al. 2010) and this is particularly true for the cases where angling is used as a removal method to extirpate or regulate invasive fish species. In the present study, we observed several modifications of population and individual characteristics of an invasive fish species driven by removal pressure through angling. We demonstrated that removal pressure might induce body mass truncation, with populations under high removal pressure mainly composed of lighter individuals, while the effects on individual maximal length were not significant. Contrary to our predictions, removal pressure in the present study did not affect the total abundance of invasive *L. gibbosus*. However, the abundance of medium-bodied individuals and population biomass were modified in a non-monotonic manner. Finally, we found that removal pressure decreased length at age 2 of individuals. Changes of individual length at age could be linked to difference in juvenile growth trajectories and we found a significant and negative effect of removal pressure on juvenile growth rate.

Exploitation of fish populations can induce selective mortality (Law 2000, Lewin et al. 2006, Belgrano & Fowler 2013). Here, selective harvesting was most likely occurring through the removal of larger individuals, as maximal individual mass in the populations decreased with increasing removal pressure. Such truncation in mass could potentially explain the observed increase in the abundance of medium-bodied individuals at high removal pressure through competitive release from the larger individuals (Lewin et al. 2006). Recreational angling gears are size-selective, with hook size being an important driver of captured individual size (Alós et al. 2008). Since anglers in the study area are not specifically targeting *L. gibbosus*, it is unlikely that they modify hook size (and therefore minimal capture size) as *L. gibbosus* length at age decreased. Consequently, the increase abundance of medium-bodied individuals could also be explained by the decrease in length at age because populations at high removal pressure were mostly composed of individuals included in smaller size classes that are less vulnerable to capture by angling and more adept at avoiding anglers' hooks. The U-

shaped relationship observed between removal pressure and population biomass was probably driven by the removal of larger individuals with increasing removal pressure that was compensated by the increase abundance of medium-bodied individuals at high removal pressure. Consequently, populations subjected to high selective removal through angling become dominated by smaller individuals and are potentially more sensitive to changes in environmental conditions and more subject to unstable dynamics (Anderson et al. 2008), revealing the need to temporally integrate the effects of selective removal pressure on invasive fish populations.

Decreases in length at age and in juvenile growth rate could reflect a shift toward a slower life-history phenotype as removal pressure increased and therefore be a potential mechanism to reduce their vulnerability of capture (Conover & Munch 2002, Biro & Post 2008). Nevertheless, juvenile growth rate in harvested fish populations often increases due to the release in intraspecific competition and the improvement of resource access (Fenberg & Roy 2008, Enberg et al. 2012). Here, the abundance of small-bodied individuals was not affected by removal pressure and we also observed a high abundance of medium-bodied individuals in sites with high level of removal pressure. This suggested that intraspecific competition probably persisted in the studied lakes, and might have potentially dampened the selection for faster juvenile growth rate. Such changes in life-history trajectories related to angling pressure can be driven by phenotypic plasticity or natural selection (Palkovacs et al. 2012, Van Wijk et al. 2013) and this remains to be tested to fully appreciate the evolutionary consequences of selective removal on invasive populations.

The existence of compensatory mechanisms is a common phenomenon in harvested wild populations and can notably lead to changes in reproductive investment (e.g., Lewin et al. 2006). Angling has been demonstrated to lead to an earlier age and size at maturity, with mature individuals potentially increasing their reproductive investment (Jørgensen et al. 2007, Fenberg & Roy 2008). In the present study, reduced length at age 2 is likely to decrease size at maturity. Indeed, the observed length at age 2 (mean = 70.1 mm \pm 1.2 SE) was included within the range of size at maturity reported in the literature for invasive populations of *L. gibbosus* in Europe (Copp & Fox 2007, Cucherousset et al. 2009). Reduced size at maturity could lead to a decline in fecundity and fitness (Walsh et al. 2006), with potential negative effects on fish population abundance. However, under stress conditions, multiple and protracted spawning

strategies could be adopted in *L. gibbosus* (Garvey et al. 2002) to counterbalance the negative effects of earlier size at maturity. Here, protracted spawning was observed in the two lakes that had the highest removal pressure, suggesting that recreational angling potentially modifies the reproductive strategy of *L. gibbosus*. Thus, further studies should aim at quantifying the impacts of selective removal on reproductive strategies and its ultimate consequences on population dynamics.

In the context of biological invasions, management methods used to control invasive populations are widely employed in lakes, where total eradication is either relatively inefficient or almost impossible to achieve (Britton et al. 2011). While the current removal strategy aims at reducing the abundance of invasive populations through angling, its real efficiency as a control method is questionable as the total abundance of populations did not decrease significantly as removal pressure increased. Instead, we found that the abundance of medium-bodied individuals was higher at high removal pressure. Removal selection against larger individuals leads to populations composed of smaller individuals with reduced mouth gape, which could strongly alter the prey-predators relationships and by extension reshape ecological interactions between organisms and food webs (Shackell et al. 2009, Palkovacs et al. 2012, Fraser 2013, Audzijonyte et al. 2013). Here, higher abundances of medium-bodied individuals could lead, for instance, to increased predation pressure on some specific invertebrate taxa (i.e., chironomids and heteroptera) and higher interspecific competition, with potential for cascading consequences. Overall, the current selective methods to control invasive species do not appear particularly successful, suggesting the development of more pro-active strategies and the use of less selective methods.

Human-induced environmental disturbances are a major agent of rapid evolution in wild populations (Hendry et al. 2008, Darimont et al. 2009b) that affect individuals in a non-random manner (Coltman et al. 2003). Variability of individuals within a population drives difference in vulnerability to angling (Uusi-Heikkilä et al. 2008). Therefore, in a context of biological invasions, further studies need to investigate the correlated traits (i.e., genetic, morphologic, trophic, physiologic and behavior) involved in the non-random removal of individuals to fully appreciate the potential ecological and evolutionary consequences of the management of invasive species.

III.5 - ACKNOWLEDGEMENTS

We are grateful to our numerous colleagues and the graviere team for their help during the fieldwork and lake owners for access to the field sites. Valuable comments on earlier drafts by Antoine Lecerf and two anonymous reviewers greatly improved the manuscript. This work was supported by The Fisheries Society of the British Isles (FSBI), an “ERG Marie Curie” grant (PERG08-GA-2010-276969) to JC, the ONEMA (Projet ISOLAC – Convention 13-V5-28) and by the French Laboratory of Excellence project "TULIP" (ANR-10-LABX-41; ANR-11-IDEX-0002-02).

Environment-dependent trophic niche shifts in an invasive omnivore

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Manuscript in preparation

Key-words stable isotope analyses, niche width, trophic ecology, size structure, invasive crayfish

Résumé

L'écologie trophique des espèces invasives joue un rôle dans les impacts qu'elles exercent sur les écosystèmes et les espèces invasives omnivores ont la possibilité d'affecter plusieurs niveaux trophiques. L'écologie trophique des espèces invasives est susceptible d'être affectée par leur taille et par les caractéristiques environnementale de l'écosystème. Dans cette étude basée sur l'analyses d'isotopes stables, nous avons examiné la niche trophique de 15 populations invasives d'écrevisse de Louisiane *Procambarus clarkii* établies dans le sud-ouest de la France le long d'un gradient de productivité, compétition (i.e., abondance d'écrevisse) et de prédation (i.e., biomasse de poissons prédateurs). Nous avons constaté que la position trophique des individus augmentait avec leur taille. De plus, le degré d'omnivorie des individus diminuait avec la compétition dans les lacs avec une faible prédation, mais augmentait avec la compétition dans les lacs avec forte prédation. De la même manière, la taille de la niche trophique des populations augmentait significativement avec la productivité dans les lacs à forte prédation, alors qu'elle diminuait avec l'augmentation de la productivité dans les lacs à faible prédation. Nos résultats indiquent donc l'existence d'une interaction complexe entre la productivité de l'écosystème, la compétition et la prédation dans le déterminisme de l'écologie trophique des écrevisses invasives. Par exemple, la largeur de la niche de la population et le degré d'omnivorie des individus augmentaient avec la productivité et la compétition, respectivement, mais uniquement quand le niveau de prédation était élevé. Ainsi, une forte biomasse de poissons prédateurs inversait les relations entre les métriques trophiques et les caractéristiques des lacs. Par conséquent, nous avons démontré que la niche trophique des individus invasifs pouvait fortement varier dans leur aire de distribution non-native et au sein d'une aire de répartition relativement restreinte. Les interactions entre les conditions environnementales biotiques (particulièrement la pression de prédation) influencent le régime alimentaire des populations invasives et par conséquent leur potentiels impacts écologiques.

Abstract

The trophic ecology of invasive species has important implications for their impacts on recipient ecosystems; with omnivorous invaders potentially affecting multiple trophic levels. The trophic ecology of invaders might be affected by both their body size and the environmental characteristics of ecosystems. Here, we investigated the trophic ecology of the invasive red swamp crayfish *Procambarus clarkii* in 15 populations in Southwest France over a gradient of productivity, competition (i.e., crayfish abundance) and predation (i.e., fish biomass) using stable isotope analyses. We found that the trophic position of individual crayfish in the food chain increased with body size. Additionally, the degree of omnivory among individuals decreased with competition in lakes with low fish predation, but increased with competition in lakes with high fish predation. Similarly, population trophic niche size increased with productivity in lakes with high predation, while it decreased with increasing productivity in lakes with low predation. Our results indicate that a complex interaction between productivity, competition and predation pressure determines crucial aspects of crayfish trophic ecology. Population niche width and individual omnivory increased with productivity and competition, respectively, but only when predation levels were high. In fact, high fish biomass caused the relationship between crayfish dietary metrics and lake variables to reverse entirely. Consequently, this study demonstrates that the trophic niche of invaders can vary across their invasive range and within a relatively narrow area. Biotic environmental variables (particular predation pressure) interact to influence the diet of invasive populations, and therefore their potential ecological impacts on native community and recipient ecosystems.

IV.1 - INTRODUCTION

The trophic ecology of invasive species has strong implications for their establishment success, their invasive distribution, and their impacts on native organisms and recipient ecosystems (Zhang et al. 2010, Griffen et al. 2012, Dick et al. 2013). The addition of invasive species to an established food web creates novel trophic links and thus modifies energy pathways, potentially resulting in modified food web structure (Vander Zanden et al. 1999, Woodward et al. 2008, Cucherousset et al. 2012a). This is important because food web structure is a fundamental ecological attribute that underlies species diversity, mediates community dynamics, and influences ecosystem processes (Thompson et al. 2012a, Thompson et al. 2012b). Understanding the trophic role of invaders in food webs is, therefore, essential in explaining the mechanisms driving their ecological impacts.

As trophic plasticity and omnivory are typical traits of successful invaders (Clavel et al. 2011), their trophic ecology may differ across their invasive range in a complex manner (Tillberg et al. 2007, Cucherousset et al. 2012b). Omnivorous species (i.e., species that forage on more than one trophic level) are important for food web structure through their bridging of multiple trophic levels (Parkyn et al. 2001, Moore et al. 2012). Omnivorous invaders can have disproportionate impacts on native communities via direct and indirect effects that cascade across trophic levels (e.g., Moore et al. 2012, Klose & Cooper 2013). Indeed, some omnivorous species have the potential to act as detritivores, herbivores, predators or scavengers in different habitats, implying that habitat characteristics has a strong influence on food choice. In addition, the diet of conspecific omnivores can vary according to their body size (García-Berthou & Moreno-Amich 2000b, Bondar et al. 2005) but this is usually explored through ontogenetic diet shift, neglecting that individuals of the same developmental stage would potentially differ in their foraging strategy. This highlights the requirement of understanding the mechanisms that drive omnivory to better assess the impacts of omnivorous invaders on recipient ecosystems (Stenroth et al. 2008, Griffen et al. 2012).

Environmental factors directly affect food production and population dynamics and, are therefore key drivers of the trophic attributes of animal populations, and the trophic ecology of omnivores is expected to vary with these environmental variables (Araújo et al.

2011). Indeed, environmental factors that limit resource availability (e.g., high levels of competition or low productivity) are expected to affect the level of diet variability within populations by decreasing the range of resources available to consumers (e.g., Jackson et al. 2012). Alternatively, evidence also suggests that intraspecific competition may increase population diet variability through the consumption of alternative prey items (e.g., Svanbäck & Bolnick 2007). Moreover, predation pressure, by modifying the density and the foraging strategy of consumers, is also a potential driver of individual trophic ecology (e.g., Eklöv & Svanbäck 2006). Together, this suggests that numerous and potentially interacting factors play a role in contributing to consumer trophic ecology variation. Therefore quantifying the effects of both biotic and abiotic environmental variables on the trophic ecology of omnivorous invaders will help us understand their impacts.

Freshwater crayfish are successful invaders with some species widely distributed across a number of continents (Capinha et al. 2011). Invasive crayfish often achieve the dominance of invertebrate biomass in freshwater systems, leading to dramatic impacts on native organisms and ecosystem functioning (Lodge et al. 2012, Twardochleb et al. 2013, Alp et al. 2016). Crayfish are opportunistic omnivores relying on terrestrial plant litter, aquatic primary producers, and animal prey (invertebrates and fish) from multiple trophic levels (Jackson et al. 2014). Whilst their diet in their invasive range has been assessed in several ecosystems (e.g., Rudnick & Resh 2005, Olsson et al. 2009, Jackson et al. 2012, Jackson et al. 2014), it has rarely been assessed in relation to environmental determinants and the exceptions found contradicting results (Stenroth et al. 2008, Larson et al. 2011). Often overlooked in omnivorous crayfish (*but see* Stenroth et al. 2008), body-size can also be an important driver of diet variation among sexually mature individuals. Thus, there remains considerable uncertainty as to how their trophic size and level of omnivory will vary over gradients of interacting environmental conditions and body size.

The aim of the present study was to investigate the influence of habitat characteristics and body size on the trophic ecology of an omnivorous invader. The red swamp crayfish *Procambarus clarkii* was used as the model invasive crayfish over 15 invaded water bodies located in Southwest France. The trophic niche of each population and the trophic position and level of omnivory of each individual were determined using stable isotope analyses. We predicted that population niche width would increase with lake

productivity, reflecting the wider diversity of available resources. However, this effect would be moderated by competition and predation that affect population foraging strategy. We also predicted that environmental factors (i.e., productivity, predation and competition) would interact to affect both the trophic position and omnivory of individuals. Finally, we predicted that individual diet would change with carapace length, given that mature crayfish display diet differences according to their body size (Stenroth et al. 2008).

IV.2 - MATERIAL & METHODS

IV.2.1 - Study area and model species

The study was completed in 15 artificial lakes with gradients of abiotic (lake productivity) and biotic (predation pressure and competition) environmental conditions (Table IV.1). All lakes were located south of Toulouse (southwest France) in the Garonne floodplain and were created from gravel extraction. The model crayfish, *P. clarkii* is one of the most invasive crayfish species worldwide (Capinha et al. 2011, Grey & Jackson 2012). Native to southern North America and parts of Central America, they are a large-bodied benthic omnivore invertebrate that is highly flexible in diet choice (Gherardi 2006, Grey & Jackson 2012). The species was introduced in France in 1976 (Laurent 1997) and has since spread throughout the country (Gherardi 2006).

IV.2.2 - Data collection

All lakes were sampled from mid-September to early October 2012 so that the isotope analysis reflects summer feeding when crayfish reach maximal activity prior to becoming less effective in winter. In six lakes, *P. clarkii* coexisted with another invasive crayfish species *Orconectes limosus* which represented only a small proportion of the crayfish population (number of individual per trap per hour ranged from 0.005 to 0.049) and thus was not included in the subsequent analyses. Sexually mature individuals of *P. clarkii* (hereafter crayfish) were sampled in the littoral area during night and day captures using traps baited with fish pellets (size = 62cm × 34cm × 34cm; 12.19 (± 1.64 SD) traps during the day and 4.25 (± 0.58 SD) traps overnight, on average). This was used to account for differences in catches between night and day, with most of the lakes having the highest

efficiency during the day (Cucherousset, *personnal observations*). Competition was estimated based on catch per unit effort (CPUE) determined from numbers of crayfish caught in these traps over a 24-hour period ($\text{ind.trap}^{-1}.\text{h}^{-1}$). Where required, additional individuals were collected for stable isotope analyses using seine and pond nets in the littoral habitat. Following their removal from traps and counting, crayfish were measured for carapace length using a calliper to the nearest 0.1 mm and euthanatized. Then a subsample of muscle was collected from the abdomen for subsequent stable isotope analyses. In addition, putative food resources including aquatic invertebrates, macrophytes and terrestrial leaves were collected using a pond net and by hand, whereas periphyton was collected from previously gently brushed stones (*see details below*). For each studied lake, these resources items were collected in three different locations along the shoreline to account for potential spatial variability within the lake.

The fish assemblages of the lakes were sampled using the same protocol in each lake and a combination of gillnetting and electrofishing by point abundance sampling (PASE). These complementary approaches were used to catch fish in the different types of substrates and habitats and encompass different species and life stages in the fish community (*see details in Zhao et al. 2016*). Gillnets were deployed in the pelagic ($n = 2$ gillnets; mesh size: 20 and 50 mm) and in the littoral zone ($n = 4-6$ depending upon lake size; mesh size: 12, 20, 30 and 60 mm) and electrofishing (Deka 7000; Deka, Marsberg, Germany) was performed by a point abundance sampling (PASE; mean = 30.50 ± 6.10 SD) using a boat working along the shoreline. All fish sampled were identified to species level, measured for fork length to the nearest mm and categorized into one life-stages (i.e., young-of-the-year, juveniles and adults) based on size distribution and literature about size at maturity (*see details in Zhao et al. 2016*). The body mass of each fish was then calculated using length-weight relationships calculated for each species (*Zhao et al. unpublished data*). Predation pressure was calculated as the total biomass (g) of fish predators including juveniles and adults of piscivorous species (*Anguilla anguilla*, *Esox lucius*, *Micropterus salmoides*, *Perca fluviatilis*, *Sander lucioperca* and *Silurus glanis*) and all specimen of *Cyprinus carpio* species. Finally, in September 2012, all lakes were visited (three sampling locations per lake) to measure Secchi disc depth, chlorophyll-a concentration (fluorescence photometer, BBE-Moldaenke, Kiel, Germany) and total phosphorus concentration. Lake

productivity was then calculated using these measurements based on the trophic status index (TSI; < 40: oligotrophic, 40-50: mesotrophic, 50-70: eutrophic, > 70: hypertrophic) following Carlson (1977).

Table IV.1 Environmental characteristics of the fifteen studied lakes.

Lake ID	Latitude (N)	Longitude (E)	Predation (e.g., fish predators; g)	Competition (CPUE crayfish; ind.trap ⁻¹ .h ⁻¹)	Productivity (TSI)
BAA	1.202	43.322	12259	3.2	51.1
BAU	1.203	43.317	28205	3.2	53.3
BIR	1.290	43.530	15564	1.5	62.5
BON	1.274	43.454	2398	0.0	57.8
BVI	1.355	43.519	16120	0.2	65.4
LAM	1.337	43.506	36658	0.8	61.3
LAV	1.266	43.386	26794	5.7	50.8
LIN	1.227	43.343	3099	0.0	64.6
PEY	1.194	43.320	0	2.4	54.6
POU	1.258	43.372	13980	3.1	53.7
SAB	1.251	43.365	1677	1.2	50.1
SOA	1.040	43.206	18565	0.2	54.5
SOB	1.047	43.208	16294	0.2	52.8
SOC	1.039	43.209	13323	0.8	53.0
TAA	1.262	43.552	1802	0.3	63.2

IV.2.3 - Stable isotope analysis

The carbon and nitrogen stable isotope ratios (¹³C:¹²C and ¹⁵N:¹⁴N) of crayfish (n = 11 to 15 individuals per lake; mean = 14.5 ± 1.06 SD) and their putative food resources were used to infer crayfish diet and calculate associated trophic metrics. Carbon ratios reflect the consumer diet with typical enrichment of 0-1‰ whereas nitrogen ratios indicate trophic position and show greater enrichment of 2-4‰ from resource to consumer (Post 2002, McCutchan Jr et al. 2003). At each site, the putative food resources sampled consisted of

mixed terrestrial leaves ($n = 3$), common aquatic macrophytes ($n = 3$), periphyton ($n = 3$), molluscs (Corbiculidae and Lymnaeidae; $n = 2-3$ where present), arthropods (Chironomidae, Ephemeroptera, Assellidae and Sialidae; $n = 5-10$) and young-of-the-year or juveniles of common fish species previously captured (*Rutilus rutilus* at all sites except lake 10, which had no fish; *Lepomis gibbosus* at lakes 1, 7, 8 and 12; and *Micropterus salmoides* at lake 15; $n = 3$ in all cases). Although it is unlikely that the crayfish are actively catching fish, they will readily consume fish carrion and there is also evidence that they prey upon juveniles and eggs (Reynolds 2011). Isotope analyses for molluscs and fish were performed on the soft muscle tissue and fin sample, respectively.

Once in the laboratory, periphyton samples were frozen using lyophilizer while others were oven dried (60 °C for 48 h). Then all samples were ground to a fine powder and analyzed for stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at the Cornell Isotope Laboratory (COIL, Ithaca, NY). Carbon and nitrogen stable isotope ratios are expressed relative to standards as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. As the C:N ratio of molluscs and arthropods were high (4.00 ± 0.05 SD and 4.79 ± 0.09 SD, respectively), their stable isotope values were lipid corrected before subsequent analyses (following Post et al. 2007, Fig. IV.1).

IV.2.4 - Data analyses

Resource sampled were categorized into four coherent isotopic and taxonomic groups (Fig. IV.1): leaf litter, primary producers (mixture composed of macrophyte and periphyton), invertebrates (mixture composed of molluscs and arthropods) and fish. These groups are not confounded by baseline variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and, therefore can confidently be used to compare crayfish diet between lakes. Moreover, to ensure comparison of diet variability between populations, stable isotope values were corrected using resource baseline values (Jackson & Britton 2014). $\delta^{13}\text{C}$ values were used to calculate the corrected carbon isotope ratio ($\delta^{13}\text{C}_{\text{cor}}$) adjusted for between-population variation using the following equation:

$$\delta^{13}\text{C}_{\text{cor}} = (\delta^{13}\text{C}_c - \delta^{13}\text{C}_{\text{litter}}) / (\delta^{13}\text{C}_{\text{primprod}} - \delta^{13}\text{C}_{\text{litter}})$$

where $\delta^{13}\text{C}_c$ is the carbon isotope values of crayfish, $\delta^{13}\text{C}_{\text{litter}}$ and $\delta^{13}\text{C}_{\text{primprod}}$ are the stable isotope values of leaf litter and primary producers. Likewise, the trophic position of each crayfish (TP_c) was calculated using the following equation:

$$TP_c = 2 + (\delta^{15}N_c - \delta^{15}N_{inv}) / 3.8$$

where $\delta^{15}N_c$ is the isotopic value of crayfish, $\delta^{15}N_{inv}$ is the isotopic value of primary consumers (average $\delta^{15}N$ of invertebrates), 3.8 is the fractionation between trophic levels (*see details further*) and 2 is the trophic position of the baseline organism (Post 2002, Olsson et al. 2009).

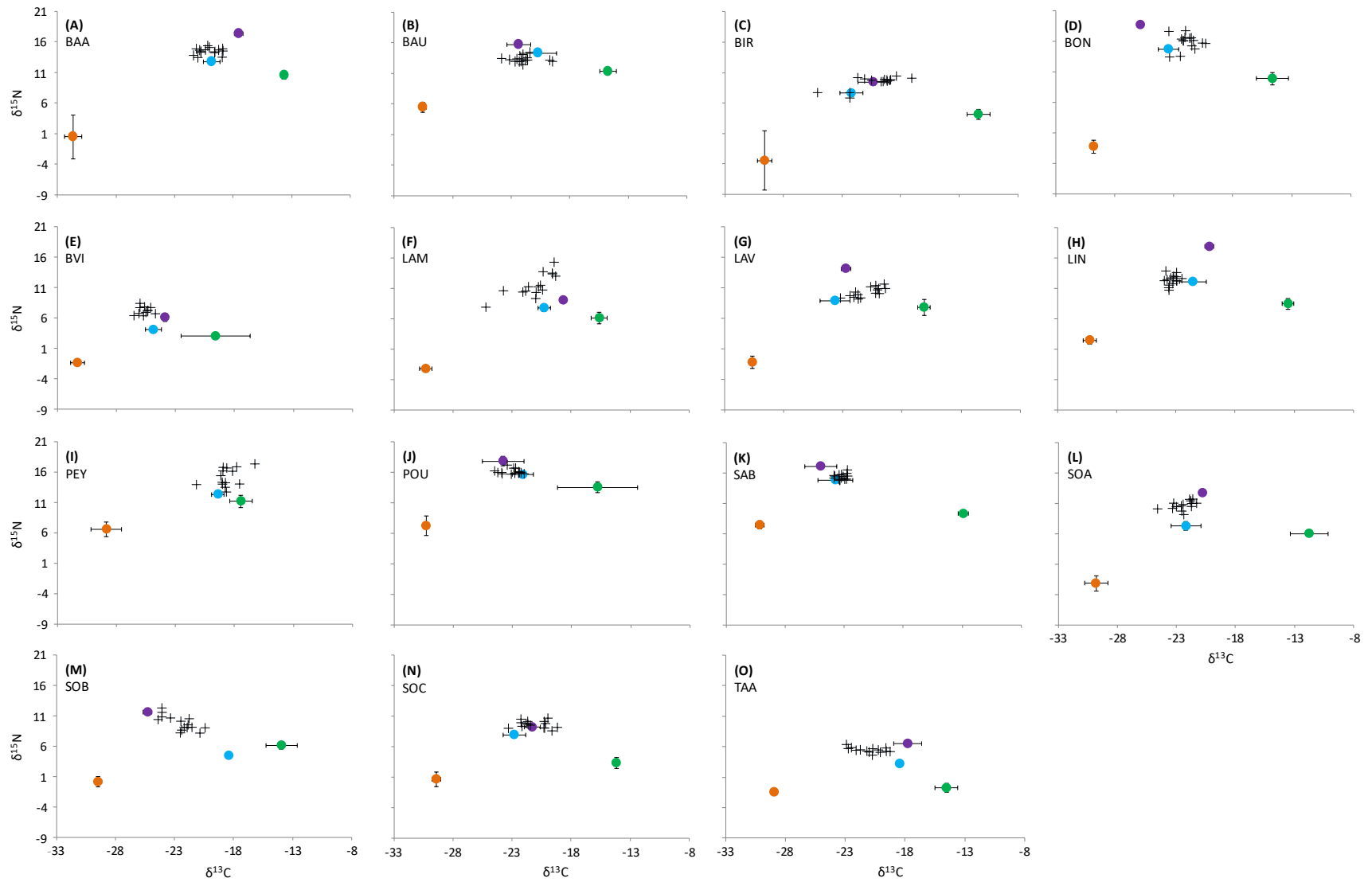
These corrected isotope values were then used to calculate the trophic niche of each population using SIBER in the SIAR package (R Core Team 2013, Jackson et al. 2011, Jackson et al. 2012). Bayesian standard ellipse areas (SEA_b , ‰²) were calculated as a measure of the isotopic niche width using 10 000 replicates. This measure of trophic niche width is based on the distribution of individuals in the isotopic space and is calculated from the variance and covariance of $\delta^{13}C$ and $\delta^{15}N$ values. Because it is based on a Bayesian framework, studies on simulated data have indicated that a sample size of 15 individuals per populations is sufficient for calculating trophic niche width using SEA (Jackson et al. 2011, Brind'Amour & Dubois 2013, Syvaranta et al. 2013).

We quantified the relative dietary contribution (%) of each resource to the diet of individuals crayfish using the Bayesian mixing model SIAR in R (R Core Team 2013, Parnell et al. 2010). Isotope mixing models were run with the raw $\delta^{13}C$ and $\delta^{15}N$ values of resource groups (mean and standard deviation values) and individual crayfish. Fractionation factors between consumers and resources were calculated using data from crustacean feeding experiments in the literature (Rudnick & Resh 2005, Yokoyama et al. 2005, Suring & Wing 2009, Carolan et al. 2012); 1.32 ± 1.53 ‰ and 2.04 ± 0.11 ‰ for $\delta^{13}C$, and 3.40 ± 2.23 ‰ and 4.24 ± 0.99 ‰ for $\delta^{15}N$ for animal and plant matter, respectively. The mean estimated proportional contribution of each resource to the diet of each individual was then used to calculate an index of individual omnivory (IO) using the following equation:

$$IO_c = \sum (\text{Proportion}_r) * (TP_r - (TP_c - 1))^2$$

where r is each resource group, c is an individual crayfish and TP is trophic position (Christensen & Walters 2004). The trophic position of resources was assigned as 1 for primary producers, 2 for invertebrates and 3 for fish. A high value of IO indicates that the consumer feeds on preys groups characterized by multiple trophic levels.

Figure IV.1 Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of individual *Procambarus clarkii* muscle tissue (cross) and putative prey lipid-corrected (circle; mean \pm SE) sampled in the 15 gravel pit lakes. Brown, green, blue and purple circles represent leaf litter, primary producers, invertebrates and fish, respectively.



IV.2.5 - Statistical analyses

Linear and linear mixed effects models (package lme4 v.1.1.10; Bates et al. 2015) were used to examine the effects of lake characteristics (productivity, competition and predation) on population trophic niche (SEA_b) and individual diet metrics (trophic position and index of omnivory), respectively. Spearman correlation matrices were performed between predictors and collinearity was detected between intraspecific competition and productivity. Consequently, the residuals from the relationship between productivity and intraspecific competition were used in the models as a estimate of competition (Zuur et al. 2009). Explanatory variables were measured on different scales and thus were standardized to have a mean of zero and a standard deviation of one. Linear mixed effects models included lake identity as a random factor and crayfish carapace length as a covariate. All full models were initially run with two-way interactions between environmental factors and the best models were selected using Akaike's information criterion. These best models were carried out using the dredge function in the MuMIn R package v.1.15.1 which performed automated model selection (Barton 2015). Then a model averaging approach was employed across all models with $\Delta AIC_c < 2$ to assess the relative importance of each predictor variable calculated based on AIC-weights (Burnham & Andersson 2002) using *importance* function in the MuMIn R package. Importance ranged from 0 (parameter not given explanatory weight) to 1 (parameter in all top models). Assumptions of linearity and homogeneity of variances on residuals from all models were checked visually and omnivory index was \log_{10} transformed. For each linear mixed effect model, both the marginal (R^2_M , effect of the fixed variables) and conditional (R^2_C , effect of the fixed and random variables) R^2 were calculated (Nakagawa & Schielzeth 2013). All statistical analyses were performed using R v.3.2.2 (R Development Core Team 2015).

IV.3 - RESULTS

Crayfish trophic niche width (SEA_b) varied among the 15 lakes from 0.44 to 0.72 %² (mean = 0.52 ± 0.08 SD). Trophic niche width was significantly affected by the interaction between predation pressure and lake productivity (interaction term: $z = 2.25$, $P = 0.025$; Table IV.2). Specifically, trophic niche width increased with productivity

in lakes with high predation while it decreased with increasing productivity in lakes with low predation (Fig. IV.2).

Table IV.2 Summary results after model averaging of the linear model used to test for the effects of lake characteristics (predation pressure [g. fish predators], competition [CPUE crayfish; ind.trap⁻¹.h⁻¹] and productivity [TSI]) on crayfish population niche width (SEA_b; n = 15). All explanatory variables are standardized. The relative importance value (RI) of each explanatory variable was presented. Significant *P*-values are highlighted in bold.

Source of variation	Estimate (SE)	z	<i>P</i>	RI
Intercept	0.52 (0.02)	23.97	< 0.001	NA
Productivity	0.04 (0.02)	1.82	0.070	0.65
Predation	0.02 (0.02)	0.77	0.440	0.31
Predation × Productivity	0.04 (0.02)	2.25	0.025	1

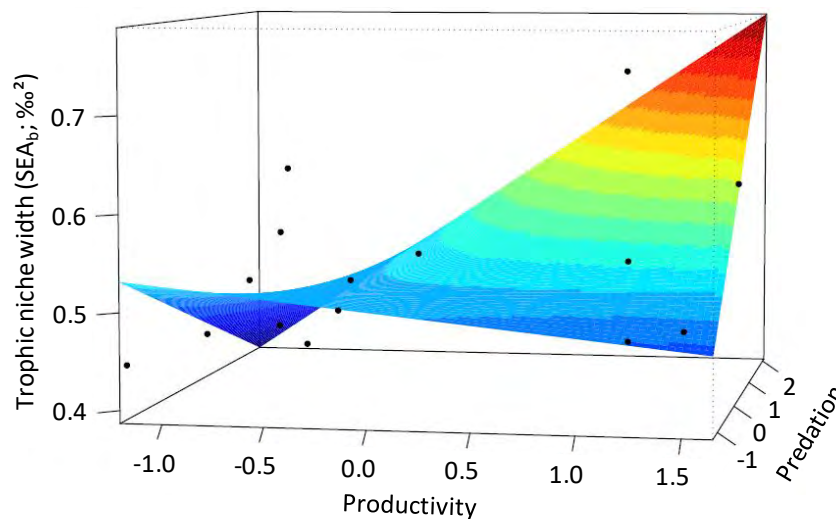


Figure IV.2 Three-dimensional plots of predation-dependent (g. fish predators) effect of productivity (TSI) on crayfish trophic niche width (SEA_b; %00²) (n = 15). The black circles and the coloured plane represent the observed and predicted values of trophic niche width, respectively. All explanatory variables are standardized.

The mean trophic position of individual crayfish was 2.49 (± 0.48 SD) and was significantly and positively affected by carapace length (z = 2.84, *P* = 0.005; Table IV.3, Fig. IV.3A) but did not significantly change with environmental factors (Table IV.3). Crayfish omnivory varied over a 10-fold range (mean = 0.95 ± 0.41 SD) and the interactions terms between predation and lake productivity significantly affected crayfish omnivory indices (interaction term: z = 3.65, *P* < 0.001; Table IV.3). Specifically,

omnivory decreased with competition in lakes with low predation but increased with increasing competition in lakes with high predation (Fig. IV.3B).

Table IV.3 Summary results after model averaging of the linear mixed effects models with environmental characteristics (predation [g. fish predators], competition [CPUE crayfish; ind.trap⁻¹.h⁻¹] and productivity [TSI]) and carapace length (mm) as factors affecting individual crayfish trophic niche (trophic position and index of omnivory [\log_{10} transformed]; n = 218). Lake identity was included as a random effect. Competition refers to the residuals from the relationship between productivity and competition. All explanatory variables are standardized. Significant *P*-values are highlighted in bold and the relative importance value (RI) of each explanatory variable was presented. Marginal (R^2_M , effect of the fixed effects) and conditional (R^2_C , effect of the fixed and random effects) R^2 are provided.

Response variables	Source of variation	Estimate (SE)	z	<i>P</i>	RI	$R^2_M - R^2_C$
Trophic position	Intercept	2.52 (0.10)	25.31	< 0.001	NA	0.29 - 0.73
	Carapace length	0.06 (0.02)	2.84	0.005	1	
	Predation	0.078 (0.10)	0.77	0.439	0.53	
	Competition	-0.15 (0.11)	1.29	0.197	0.84	
	Predation pressure × Competition (res.)	-0.05 (0.10)	0.47	0.639	0.25	
	Productivity	0.01 (0.05)	0.25	0.803	0.18	
Index of omnivory	Intercept	-0.11 (0.03)	3.94	< 0.001	NA	0.47 - 0.68
	Carapace length	0.01 (0.01)	0.83	0.409	0.56	
	Predation	0.01 (0.03)	0.20	0.843	1	
	Competition (res.)	-0.04 (0.05)	0.71	0.477	1	
	Productivity	-0.02 (0.03)	0.91	0.362	0.78	
	Predation × Competition (res.)	0.13 (0.04)	3.65	< 0.001	1	
	Competition × Productivity	0.10 (0.07)	1.44	0.149	0.78	
	Predation × Productivity	-0.02 (0.03)	0.59	0.554	0.38	

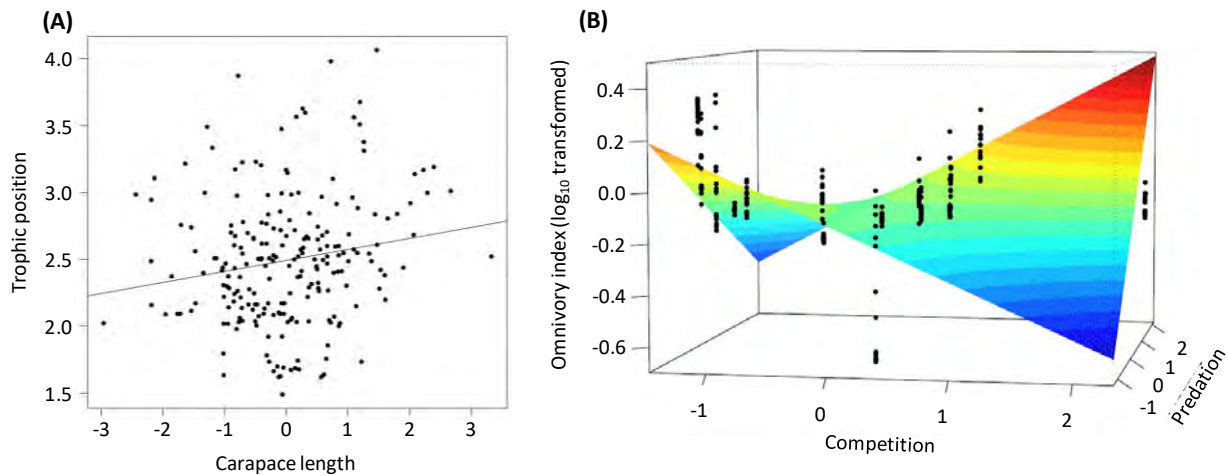


Figure IV.3 (A) Relationship between carapace length (mm) and trophic position ($n = 218$). The significant relationship is depicted using continuous line. **(B)** Three-dimensional plots of predation-dependent (g. fish predators) effect of competition (CPUE crayfish; $\text{ind.trap}^{-1}.\text{h}^{-1}$) on omnivory index (\log_{10} transformed) ($n = 218$). The black circles and the coloured plane represent the observed and predicted values of trophic niche width, respectively. All explanatory variables are standardized.

IV.4 - DISCUSSION

Understanding the drivers of the diet of invasive species can be an effective tool in predicting their impacts on recipient ecosystems (Alexander et al. 2014). Here, we have highlighted that the trophic ecology of a widespread omnivorous invader was influenced by multiple interacting environmental factors, with predation pressure even causing some trends to switch direction. Specifically, we found that the relationships between omnivory within population and competition and between crayfish population's isotopic niche width and lake productivity were directly opposed in lakes with low and high predation pressure. In addition, we found that the trophic position among sexually mature crayfish increased with their carapace length but was not related to any environmental parameters.

The presence of predators was found to influence the trophic ecology of individuals by regulating competition through changes in prey abundance or by affecting prey foraging behavior in response to risk predation (Eklöv & Svanbäck 2006). In this study, results showed that the isotopic niche width increased with productivity, but only in lakes with high fish predation. This suggests that the crayfish only make use of the wide range of available resources resulting from high productivity when the presence of predators forces them to change their behaviour and spend less time seeking out preferred prey (Stein & Magnusson 1976). Opposite relationship observed

in lakes with low predation pressure likely revealed that when preferred prey become more available with increasing productivity, crayfish will focus foraging on it as a result of little predation risk. This probably resulting in a uniform diet of low diversity, less individual specialisation, and hence a small isotopic niche (Jackson & Britton 2014), and can be linked to optimal foraging theory (Charnov 1976) which suggests that individuals will always consume the most valuable resource, ignoring lower-value resources when energy could be better spent searching for preferred prey. Therefore, our results suggest that, with an increase in predation risk from fish, access to preferred resources becomes too hazardous, and individuals will instead expand their niche to include previously unused resources. Niche expansion could be a result of an increase in between-individual variation, or individual specialisation (Bolnick et al. 2003) but our finding conflicts with niche theory which predicts that individual specialisation and niche width will increase in tandem when an organism is released from predation (Van Valen 1965, Bolnick et al. 2010). However, we found that omnivory increased with competition but only in lakes with high predation, revealing that crayfish consumed over more trophic levels when access to available resources was reduced. Although this required further investigations, it suggested that omnivory may favour niche segregation between individuals. Individual specialisation is a widespread occurrence in natural populations (Araújo et al. 2011), but few studies quantify its importance, particularly in invasive species where it may play a central role in the persistence of invasive populations by opening niche opportunities (Shea & Chesson 2002, Cucherousset et al. 2012b). Overall, these results highlighted that the access to resource availability was determinant in understanding the trophic ecology of omnivorous species, but was strongly mediated by a strong tradeoff between predation exposure and foraging strategy.

Ontogenetic dietary shifts have been described in many crayfish species, with it shown that juvenile crayfish preferentially feed on aquatic invertebrates whereas adults mainly feed on vegetal detritus (Guan & Wiles, 1998). This ontogenetic shift is particularly associated with differences in the nutrient requirements for growth and the inability of larger crayfish to forage on fast moving aquatic invertebrates (Momot 1995, Nyström et al. 1999). However, here we found that trophic position of sexually mature individuals crayfish increased with their carapace length, suggesting that the crayfish invaders incorporated more animal material in their diet as they get larger and probably more competitive for access to nutrient rich prey, even when size difference is small.

This trait may be specific to invasive crayfish, which tend to be both more flexible in diet choice and more predatory than their native counterparts (Grey & Jackson 2012, Olsson et al. 2009 *but see* Lagrue et al. 2014). Stenroth et al. (2008) found that the trophic level of invasive signal crayfish was higher in eutrophic lakes but we found no influence of lake productivity. This is contrary to the productivity hypothesis that suggests that food chain length and, therefore, the trophic level of consumers, increases with increasing productivity (Post et al. 2000, Post 2002, Takimoto & Post 2013). However, when lake productivity is high, there will be a high volume of detrital organic matter suggesting that crayfish may specialise in this low trophic level resource when it is available.

Variation in crayfish diet across gradients of lake characteristics is likely to influence the impact of crayfish on community structure and ecosystem functioning. For example, when crayfish occupy lower trophic levels and consume more plant material they may increase decomposition rates and decrease macrophyte cover (Twardochleb et al. 2013, Jackson et al. 2014, Alp et al. 2016). If crayfish become more important predators they may impact invertebrate community structure and perhaps instigate trophic cascades that subsequently reduce decomposition rates and increase macrophyte cover (Jackson et al. 2014, Lagrue et al. 2014). Invasive crayfish had thus the potential to modify trophic interactions (e.g., between decomposers and terrestrial detritus) and so future studies should investigate their subsequent impacts on ecosystem functioning. Importantly, these impacts were generally associated to trophic niche differentiation between species (Twardochleb et al. 2013, Jackson et al. 2014). Here, we can argue that strong differences in the trophic ecology can also be found between populations of a single species and this may drive context-dependent impacts on recipient ecosystems. Consequently, it would be of great interest to investigate the relative importance of intra *versus* interspecific variability in determining the ecological effects of invasive consumers on ecosystems (Palkovacs et al. 2015).

These results indicate that invasive omnivores can depict trophic plasticity across biotic environmental gradients, revealing an adaptation toward resource availability. Importantly, fish community structure can influence the invasion success of crayfish (e.g., Maceda-Veiga et al. 2013), with the study outputs indicating that this might be due to predator pressures on the trophic ecology of the invasive populations, particularly in systems where resources are limited. Increasingly, evidence indicates that individuals within species may differ in their functional role, notably through

variations in size (Miller & Rudolf 2011, Sato & Watanabe 2013). This intraspecific variability can exceed variability between species and result in changes in the functioning of ecosystem related to the size structure of the population (Rudolf & Rasmussen, 2013a, Rudolf & Rasmussen 2013b). Thus, determining the ecology of omnivorous invaders and their impacts on recipient ecosystems is reliant on understanding the interactions between environmental drivers and all potential drivers of intraspecific variability in resource use.

IV.5 - ACKNOWLEDGEMENTS

We are grateful to the gravière team and our numerous colleagues for their help during the fieldwork and lake owners for access to the gravel pit lakes. All sampling was performed under the authorization "Arrete Prefectoral - 31/07/2012". Financial support was provided by ONEMA (Projet ISOLAC – Convention 13-V5-28) and by an "ERG Marie Curie" grant (PERG08-GA-2010-276969) to JC in the lab EDB, part of the French Laboratory of Excellence project "TULIP" (ANR-10-LABX-41; ANR-11-IDEX-0002-02). MJ was supported by the 'RINSE' project which was partly funded through the Interreg IVA 2 Seas Programme, which promotes cross border cooperation between coastal regions, with the support of European Regional Development Fund (ERDF).

A transcontinental comparison of the phenotype-environment relationships among invasive populations

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Manuscript in preparation

Key-words biological invasions, *Lepomis gibbosus*, *Procambarus clarkii*, geometric morphometric, ecomorphology, stable isotopes

Résumé

L'histoire des populations et les conditions environnementales dans lesquelles elles se développent interagissent pour façonner les différences phénotypiques entre les populations. En raison de l'histoire contrastée de leur introduction dans de nombreuses localisations géographiques aux conditions environnementales contrastées, les espèces invasives distribuées à l'échelle mondiale devraient présenter des variations phénotypiques fortes dans leur aire de distribution non-native. Dans cette étude, nous avons exploré les patrons de relations phénotype-environnement entre différentes populations d'écrevisses de Louisiane *Procambarus clarkii* (n = 11) et de perche soleil *Lepomis gibbosus* (n = 12) dans des lacs Nord Américains (Etat de Washington) et Européens (Haute Garonne) aux histoires d'introduction très variables. Pour les deux espèces, nous nous sommes plus particulièrement intéressées aux différences morphologiques entre les populations le long d'un gradient de pression de prédation, de productivité et de complexité de l'habitat. En utilisant des analyses des isotopes stables, nous avons ensuite déterminé les patrons écomorphologiques liant la morphologie des individus à leur niche trophique. Les résultats indiquent que les populations de *P. clarkii* et *L. gibbosus* différaient fortement en terme de morphologie entre l'Amérique du Nord et l'Europe. Nous avons également démontré que les relations phénotype-environnement étaient très dépendantes du pays, pouvant même être totalement opposées d'un pays à l'autre. Les analyses des isotopes stables ont également permis de révéler l'existence d'une forte contexte-dépendance des patrons écomorphologiques chez *L. gibbosus*, tandis que la position trophique des *P. clarkii* différait entre les individus issus des populations Nord Américaines et Européennes. Ces résultats suggèrent donc que les patrons de variations phénotypiques entre les populations invasives peuvent être affectés par des histoires de colonisation différentes et induire probablement à des impacts écologiques distincts sur les écosystèmes d'accueil.

Abstract

Population history and environmental conditions interact in shaping phenotypic divergence between populations. Due to contrasting history of introduction, worldwide-distributed invasive species are thus expected to display strong phenotypic variations across their distribution range. In this study, we explored the patterns of phenotype-environment relationship among invasive populations of two widely introduced species, the red swamp crayfish *Procambarus clarkii* (n = 11) and the pumpkinseed *Lepomis gibbosus* (n = 12) established in North American (Washington state) and European (Southwest France) lakes with different introduction histories. For both species, we focused on morphological differences among populations over a gradient of predation pressure, ecosystem productivity and habitat complexity. Using stable isotope analyses, we then tested for the existence of ecomorphological patterns linking morphology and trophic niche. Our results showed that populations of both *P. clarkii* and *L. gibbosus* strongly differed in their morphological attributes between North America and Europe. We also found that phenotype-environment relationships were highly country-dependent, and may even be opposed between the two geographic areas. Stable isotope analyses released that trophic position of *P. clarkii* strongly differed between North American and European populations. In addition, we also observed a strong context-dependency of ecomorphological patterns for *L. gibbosus*. These findings strongly support the idea that patterns of phenotypic variations among invasive populations are affected by distinct introduction and colonization histories and would probably lead to different impacts on recipient ecosystems.

V.1 - INTRODUCTION

Organisms across their geographic range commonly exhibit considerable phenotypic variability in response to local environmental conditions, ultimately contributing to ecological speciation (Pfenning et al. 2010, Richardson et al. 2014). Geographic similarities in phenotype-environment associations provide strong evidence for convergent responses to the same environmental challenges encountered in nature (Langerhans et al. 2004, Ruehl et al. 2011). However, organisms can also exhibit divergent phenotypic trajectories under similar environmental conditions that relate to differences in their intrinsic history (Langerhans et al. 2006, Langerhans & Makowicz 2009), including those associated with several evolutionary factors (e.g., founder effect, genetic drift and mutation-order selection) (Langerhans & De Witt 2004, Blount et al. 2008, Rosenblum & Harmon 2011). Understanding the relative influences of intrinsic population history *versus* extrinsic environmental conditions in shaping spatial patterns in phenotypic variability remains a fundamental question in ecology (Langerhans & De Witt 2004, Franssen et al. 2013, Giery et al. 2015).

Evidence for morphological divergence among populations has been documented for all major vertebrates groups (Skúlason & Smith 1995). Body shape, for example, is often strongly dependent on local environmental conditions experienced by organisms (Smith & Skúlason 1996). The presence of predators can favour phenotypes associated with escape ability (Dayton et al. 2005, Domenici et al. 2008) and/or promote investment into morphological defenses against predators (Arnqvist & Johansson 1998, Laforsch & Tollrian 2004). Alternatively, organisms can also escape predators in habitat where they are more difficult to detect such as turbid water (DeRobertis et al. 2003) or structurally complex habitats in aquatic ecosystems (Eklöv 1997). This may indirectly influence their morphology by modifying the foraging strategies associated with acquiring resources in specific habitats. For instance, freshwater fish inhabiting complex habitats are often deeper-bodied to improve maneuverability and foraging efficiency on cryptic benthic invertebrates (Svanbäck & Eklöv 2002). Although it is common to reveal ecomorphological patterns arising from the relationships between morphological traits and ecological processes such as resource use (Wainwright 1996, Berchtold et al. 2015), knowledge of the interactions between environmental conditions, morphological variation and the resource use of individuals is still limited.

Biological invasions represent a unique opportunity to address this knowledge gap because the ability to display high phenotypic trait plasticity outside of the native range is a key factor predicting high invasion success (Sol & Lefebvre 2000, Davidson et al. 2011, Knop & Reusser 2012). The success of invasive populations is also influenced by invasion history describing propagule pressure and the origin of the initial colonists or founders (Lockwood et al. 2009). For instance, greater propagule size (number of individuals) and number (number of introduction events) are likely to promote phenotypic variability, especially if founders originate from different populations (Ahlroth et al. 2003). Time since initial introduction is also an important factor as phenotype-environment relationships may be weaker in younger populations. Widespread non-native species include populations with diverse introduction histories that are experiencing a broad spectrum of heterogeneous environments, consequently we expect to observe high variability in phenotype responses to environmental pressures across broad geographic scales.

In the present study we investigated trans-continental patterns and determinants of morphological and trophic variability across invasive populations of two co-existing global invaders to explore the context-dependency of phenotype-environment relationships. Pumpkinseed sunfish (*Lepomis gibbosus*) and red swamp crayfish (*Procambarus clarkii*) were used as model species (representing both a vertebrate and an invertebrate) and invasive populations were in lakes located in North America (northwestern USA) and Europe (southwestern France). We first hypothesized that the effects of environmental conditions (i.e., predation pressure, lake productivity, habitat complexity) on morphology would differ between North American and European populations due to contrasting history of introduction and potential origin of founders (Langerhans & De Witt 2004). We also hypothesized that predation pressure would modify individual morphology, reflecting selection toward fast-start escape ability (Langerhans et al. 2004). Because water turbidity influences consumer ability to detect their prey we hypothesized that lake productivity would affect consumer morphology (Bartels et al. 2012). We also hypothesized that individuals inhabiting structurally complex habitat would display morphological characteristics increasing maneuverability (Svanbäck & Eklöv 2002, Ruehl et al. 2011). Finally, to investigate the potential functional implication of morphological variations, we quantified the relationship between morphological traits and trophic niche.

V.2 - MATERIAL & METHODS

V.2.1 - Study system

Native to southern United States and north-eastern Mexico, *P. clarkii* has been widely introduced to western United States as well as throughout all continents except Australia and Antarctica (Hobbs et al. 1989). The species was introduced to the west coast of USA initially as forage for frog farms in the 1930s but more recently has expanded its nonnative distribution via introductions from the aquarium and biological supply trades (Larson & Olden 2011). *P. clarkii* is widespread in Europe, being first introduced for aquaculture purpose and continuing to spread across France and at least 8 other countries via both human-induced and natural dispersal (Souty-Grosset et al. 2016). In the two studied areas, *P. clarkii* might have very similar dates of introduction since it was first document around 1995 for both Washington State and south-western France (Mueller 2001, Changeux 2003). *P. clarkii* is an opportunistic omnivore with a vegetable-based diet preference (Gherardi 2006) and has been reported to induce important ecological impacts across entire aquatic ecosystems (Twardochleb et al. 2013, Alp et al. 2016).

Native to central and eastern North America, *L. gibbosus* was introduced into the Pacific Northwest as early as 1890, and to Washington State between 1930 and 1945 when approximately 160 lakes were stocked to establish a panfish sport fishery (Washington Department of Fish and Wildlife 2005). Pathways for European introduction were primarily motivated by ornamental reason over a century ago and its establishment in Haute-Garonne occurred around 1945 (Copp & Fox 2007). The species is an opportunistic omnivore with an animal-based diet and preferentially forage on both littoral and pelagic invertebrates (García-Berthou & Moreno-Amich 2000b). Consequently, the impacts of *L. gibbosus* mainly include reduction of native invertebrates species (van Kleef et al. 2008). In addition, *L. gibbosus* can also disrupt the behavior of native fauna through aggressive interactions (Almeida & Grossman 2012).

Our study examined lake ecosystems in the United States (*described in* Larson & Olden 2013) and in France (*described in* Zhao et al. 2016). A total of 15 lakes were included: 9 lakes in proximity to Seattle, Washington State (northwestern USA) and 6 lakes near Toulouse, Haute-Garonne (southwestern France) (Fig. V.1). Natural American lakes substrates are predominantly a mixture of silt and detritus with relevant

development of aquatic vegetation (e.g., macrophyte, water lily) and riparian forest dominated by native evergreen species. By contrast, gravel pit lakes depicted steep bank and their substrates are dominated by a mix of sand, gravel and pebble. Moreover, aquatic vegetation (e.g., macrophyte) in gravel pit lakes is very limited and vegetable matter mainly occurs through allochthonous inputs of leaf litter from deciduous trees (mainly *Populus sp.*). Lake size was estimated using GIS and lakes were selected to ensure comparable size (surface area ranging from 9 to 43 ha, mean France = 15 ha \pm 2.5 SE; mean USA = 23 ha \pm 3.7 SE).

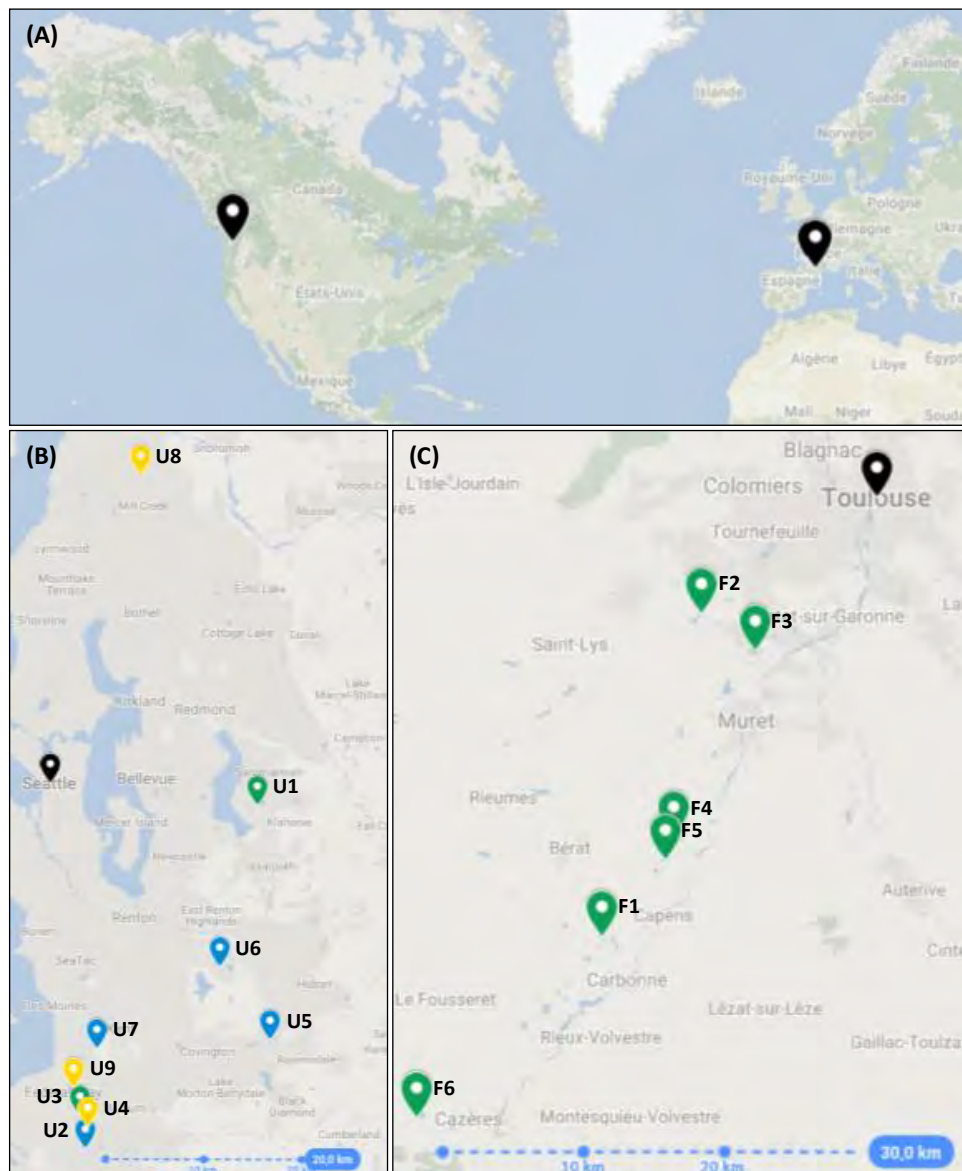


Figure V.1 (A) Location of the surveyed lakes in North America and Europe: (B) Seattle, Washington State, USA (U1-U9) and (C) Toulouse, Haute-Garonne, France (F1-F6). Green symbols represent lakes with coexisting *Procambarus clarkii* and *Lepomis gibbosus*, whereas yellow and blue symbols represent lakes with *P. clarkii* or *L. gibbosus*, respectively.

V.2.2 - Samples collection

P. clarkii and *L. gibbosus* were sampled in summer 2014 from August 4th to 11th (USA) and from September 16th to 24th (France), respectively. In each lake, *P. clarkii* were sampled in the littoral zone using baited trap set overnight and active searching with pond nets when needed. *L. gibbosus* from the littoral zone were collected using combination of baited fyke nets, seine netting and electrofishing. Following capture, individuals were immediately euthanized with an overdose of anesthetic, stored on ice and then preserved at -20°C in laboratory for subsequent analyses. After defrosting, individuals were measured for carapace length (CL \pm 0.1 mm) and fork length (FL \pm 1 mm) with an electronic caliper and an ichthyometer, respectively. To limit the potential effect of ontogeny on our analyses, a subsample of adults *P. clarkii* (CL from 30.0 - 71.0 mm) and *L. gibbosus* (FL from 65 - 170 mm) were selected to ensure consistent variability in morphological and trophic traits as well as body size overlap across the sampled lakes. These selected individuals (*P. clarkii*: 14 to 20 individuals per lake, mean = 19 ± 0.67 SE; *L. gibbosus*: 7 to 20 individuals per lake, mean = 18.92 ± 1.53 ; Table V.1) were weighted ($W \pm 0.1$ g), sexed and then used for subsequent analyses.

V.2.3 - Environmental characteristics of the lakes

For each lake, a set of environmental variables was selected based on their well-described role on individual morphology: predation pressure, lake productivity (used as a proxy of water turbidity) and habitat complexity. For each species, predation pressure was estimated as the number of predatory fish species present in each lake. In each American lake, predation was obtained from field surveys realized by Washington Department of Fish and Wildlife (from 1999 to 2016) based on electrofishing and gill netting and predation pressure in French lakes was quantified using the same approaches (Zhao et al. 2016). Predators common to both species in American lakes included *Ameiurus nebulosus*, *Micropterus salmoides*, *Perca flavescens*, *Oncorhynchus mykiss*, *Ambloplites rupestris*, *Micropterus dolomieu* and *Ictalurus punctatus*. In France, common predators included *Esox lucius*, *Perca fluviatilis*, *Micropterus salmoides*, *Sander lucioperca* and *Silurus glanis*. In addition, omnivorous *Cyprinus carpio* and *Ameiurus melas* were included as predators of *P. clarkii* as their consumption of crayfish has been observed during field sampling.

Lake productivity was quantified using the integrative trophic status (TSI) which is calculated based on measurements of chlorophyll a ($\mu\text{g L}^{-1}$), Secchi (m) and total phosphorus ($\mu\text{g L}^{-1}$) (Carlson 1997). Chlorophyll a and Secchi were calculated as average values measured on two occasions during early June and early September 2014. Total phosphorus was based on measurements performed in September 2014. In one lake (noted U7) however, TSI was calculated using data collected in 2004 since no recent information was available. Habitat complexity was calculated using the shoreline development ratio calculated following the formula:

$$\text{Pr} / (2\sqrt{\pi\text{SA}})$$

where Pr and SA were the perimeter and the area of the lakes, respectively (Hutchinson 1957).

Table V.1 Summary information of the biotic and abiotic characteristic of the studied lake localized in France (F1-F6) and in USA (U1-U9). Predation was quantified as the number of predatory fish in each ecosystem.

Lake code	Country	Lake area (ha)	Nb of individuals (<i>P. clarkii</i> - <i>L. gibbosus</i>)	Predation (<i>P. clarkii</i> - <i>L. gibbosus</i>)	Productivity (TSI)	Habitat complexity
F1	France	9	20 - 20	2 - 1	47.3	1.84
F2	France	21	20 - 20	6 - 4	54.9	1.66
F3	France	20	20 - 20	5 - 3	51.3	2.84
F4	France	21	20 - 20	7 - 5	55.8	2.05
F5	France	10	20 - 20	3 - 1	43.2	1.92
F6	France	9	20 - 20	1 - 1	45.1	1.18
U1	USA	35	20 - 20	5 - 5	34.8	1.84
U2	USA	15	0 - 6	0 - 4	52.1	1.34
U3	USA	23	15 - 20	4 - 4	40.5	1.62
U4	USA	11	20 - 0	4 - 0	45.2	1.37
U5	USA	28	0 - 20	0 - 3	41.2	1.53
U6	USA	29	0 - 20	0 - 3	53.4	1.40
U7	USA	10	0 - 20	0 - 4	47.5	1.78
U8	USA	43	14 - 0	7 - 0	38.6	1.25
U9	USA	19	20 - 0	4 - 0	47.2	1.41

V.2.4 - Morphological analyses

Morphological variation among populations was analyzed separately for each species using a geometric morphometric technique (Zelditch et al. 2004). This landmark-based thin-plate splin (TPS) analyses is a powerful approach for quantifying body shape variation and covariation between body shape and environmental factors (Bartels et al. 2012, Perry et al. 2013). *P. clarkii* were photographed dorsally whereas *L. gibbosus* were

photographed on the left side. To describe body shape morphology, homologous landmarks ($n = 19$ and $n = 18$ for *P. clarkii* and for *L. gibbosus*, respectively; see Fig. II.3 in Chap. II) were digitized by the same operator using the software TpsDig2 v.2.17 (Rohlf 2013). Landmarks were selected to approximate the overall body shape of individuals with emphasis on head and were similar to other landmark-based crayfish and sunfish morphology studies (Parsons & Robinson 2007, Etchison et al. 2012). For each species, the landmark data were then imported into the software MorphoJ v.1.06d where a Generalized Procrustes Analysis (GPA) was performed to obtain superimposed landmark coordinates (Klingenberg 2011). GPA allowed to remove from the original landmark coordinates differences in size, position and orientation among individuals, although allometric relationships remained. The GPA coordinates were projected into a weight matrix to characterize shape using non-affine (partial warps) and affine (uniform) components of thin plate spline. For each species, morphological variations between populations were explored by computing a principal component analyses of the weight matrix (relative warp analysis, RWA) in MorphoJ. Variation in body shape along the resulting principal component axes (RW) was visualized with extremes shapes along each axis created using thin-plate spline transformation grids in TpsRegr (Rohlf 2011). Only the first two RW axes which explained the maximum of variance (RW1= 26.80% and RW2 = 17.76% for *P. clarkii*; RW1 = 37.05% and RW2 = 13.07 for *L. gibbosus*) were used for further statistical analyses.

V.2.5 - Stable isotope analyses

Carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses of individuals and their putative resources were used to quantify the trophic niche of *P. clarkii* and *L. gibbosus*. Indeed, $\delta^{13}\text{C}$ is well used to determine the original source of carbon dietary (e.g., terrestrial *versus* aquatic, littoral *versus* pelagic) whereas $\delta^{15}\text{N}$ exhibits the trophic position of consumers (Layman et al. 2012). On each individual, a sample of white dorsal muscle was collected for subsequent stable isotope analyses. In addition, putative resources were collected in three different locations of each lake and during data collection sampling. Specifically, floating aquatic macrophyte and terrestrial leaf litter were collected by hand. In addition, periphyton samples were collected by gently brushing the surface of three randomly submerged cobbles and rinsing them rinsed with water. Finally, arthropods from the littoral zone (Chironomidae, Ephemeroptera,

Assellidae, Sialidae and Gastropoda; pooled samples with 1 to 23 specimens per sample) and zooplankton from the pelagic zone were collected with a pond net or a 100- μm mesh net, respectively. Stable isotope analyses for gastropod were performed on the soft muscle tissue. Once in the laboratory, periphyton samples were frozen using lyophilizer (-50°C for 5 days) while other samples were oven dried (60°C for 48h). All samples were then ground to a fine powder and analyzed for stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) at the Cornell Isotope Laboratory (COIL, Ithaca, NY). Carbon and nitrogen stable isotope ratios are expressed relative to standards as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Carbon isotope values of primary consumers were lipid-corrected for subsequent analyses because their average C:N were higher (invertebrates: mean = 4.57 ± 1.09 SD; zooplankton: 5.07 ± 1.09 SD) than the suggested limits (3.5 for aquatic organisms; Post et al. 2007).

The contribution of each resource (primary producers and consumers) to the diet of consumers was calculated for each individual using their $\delta^{13}\text{C}$ values and a two-end member mixing models in the SIAR package (Parnell et al. 2010). Isotope mixing models were run with the $\delta^{13}\text{C}$ values of consumers and the mean and standard deviation values $\delta^{13}\text{C}$ of resources. Those resources inputs were aquatic primary producers (mixture of macrophyte and periphyton) and terrestrial leaf litter for *P. clarkii*, and littoral arthropods and pelagic zooplankton for *L. gibbosus*. Trophic enrichment factors (TEF) between consumers and resources were calculated using data from crustacean feeding experiments (Rudnick & Resh 2005, Yokoyama et al. 2005, Suring & Wing 2009, Carolan et al. 2012) and using a conservative approach (Inger et al. 2010) for *P. clarkii* and *L. gibbosus*, respectively. Specifically, the TEF of *P. clarkii* and *L. gibbosus* were 2.04 ‰ (± 0.11 SD) and 1.00 ‰ (± 1.00 SD) for $\delta^{13}\text{C}$, respectively. Trophic positions of each *P. clarkii* and *L. gibbosus* were calculated using their $\delta^{15}\text{N}$ and the values of baselines measured in each ecosystem. Trophic position of each individual *i* was calculated following Vander Zanden et al. (1997) using the equation:

$$\text{TP}_i = ((\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{base}}) / \Delta\text{N}) + \lambda_{\text{base}}$$

where $\delta^{15}\text{N}_i$ is the isotopic value of an individual *i*, $\delta^{15}\text{N}_{\text{base}}$ is the mean stable isotope values of resources (aquatic primary producers and terrestrial leaf litter for *P. clarkii*; littoral arthropods and pelagic zooplankton for *L. gibbosus*), ΔN is the TEF obtained from previous studies (3.8 ‰ and 3.3 ‰ for *P. clarkii* and *L. gibbosus*, respectively; see details above) and λ_{base} is the trophic position of the resources used to estimate the baseline ($\lambda_{\text{base}} = 1$ for primary producers and $\lambda_{\text{base}} = 2$ for primary consumers). The $\delta^{15}\text{N}$ values of

putative resources in lake F3 were abnormal and samples from this lake were not used in subsequent trophic analyses.

V.2.6 - Statistical analyses

Linear models were used to assess the effects of environmental parameters, individual characteristics and geographic location on morphology (selected principal component axes, RW). Models were built independently for each species and for each RW axis. To investigate body shape variation independently of allometry, the centroid size of each individual was used as an surrogate of overall body size (mm), as typically done in geometric morphometrics (Bookstein 1991). Centroid size is the square root of the summed squared deviation of the coordinates from the centroid (i.e., the arithmetic mean of all landmarks). Full models included morphological axis RW as dependent variable, body size and sex (to account for potential sexual dimorphism) as covariates, whereas environmental parameters (i.e., predation, productivity and habitat complexity) and “Country” were included as fixed effects. Interactions between “Country” and other parameters were included in the models to test for continental-specific response of morphology.

For each species, the trophic position and contribution of resource consumed were used in linear models to assess the relationship between morphology and trophic niche. Specifically, trophic position of each individual, litter reliance (i.e., contribution of terrestrial leaf litter to *P. clarkii*) and littoral reliance (i.e., contribution of littoral arthropod to *L. gibbosus*) were used as dependent variables. Full models included morphology (i.e., RW1 and RW2 scores), “Country” and their interactions as predictor variables.

For all full models including all the variables and selected interactions, the best models were then selected using Akaike's information criterion. These best models were carried out using the *dredge* function in the R package MuMIn (v.1.15.1; Barton 2015). Then a model averaging approach was used based on all models with $\Delta AIC_c < 2$ to assess the relative importance of each predictor variable calculated based on AIC-weights using *importance* function in the MuMIn R package (Burnham & Andersson 2002). To standardize the dataset, all independent variables were scaled and centered to the mean (Murray & Connor 2009). Assumptions of linearity and homogeneity of variances on

residuals from all models were checked visually. All statistical analyses were performed using R v.3.1.2 (R Development Core Team 2013).

V.3 - RESULTS

V.3.1 - Morphological variation

Populations of both *P. clarkii* and *L. gibbosus* differed considerably between North America and Europe. There was a significant effect country on morphology of *P. clarkii* (RW1) ($P < 0.001$; Table V.2) and individuals from American lakes had lower RW1 scores than in France (mean = $-0.0067 (\pm 0.0071 \text{ SE})$ and $0.0050 (\pm 0.0065 \text{ SE})$, respectively). RW1 scores of *L. gibbosus* significantly differed between countries ($P < 0.001$; Table V.2), with individuals in USA having a higher score than in France (mean = $0.0178 (\pm 0.0011 \text{ SE})$ and $-0.0158 (\pm 0.0011 \text{ SE})$, respectively).

For *P. clarkii*, positive RW1 and RW2 scores were associated with a long and shallow rostrum (Fig. V.2A and V.2B). Increasing head and cephalothorax length and decreasing abdomen and telson width were positively correlated with RW1 (Fig. V.2A). Positive RW2 scores were associated with increased head length and width, shortened cephalothorax and increased abdomen and telson width (Fig. V.2B). For *L. gibbosus*, individuals with positive RW1 scores had a more rounded body with a wider anterior region compared to narrower anterior head region and a longer caudal peduncle for individuals with negative scores (Fig. V.2C). Differences in eye positions were also observed and positive RW1 scores were linked to smaller and more terminal eyes, whereas negative RW1 scores depicted large and downward-facing eyes (Fig. V.2C). Positive RW2 scores were associated with an elongated and narrow body, with large and terminal eyes (Fig. V.2D). By contrast, negative RW2 scores described reduced head length combined with a relatively rounded body and short caudal peduncle (Fig. V.2D). Negative RW2 scores were also associated with small and downward-facing eyes and downward-facing snout (Fig. V.2D).

Table V.2 Summary results of the model averaging of the linear models used to test the effects of sex, centroid size, environmental parameters (predation pressure, productivity and habitat complexity) and site location (country) on morphological traits (RW1 and RW2 scores; n = 209 and n = 226 for *P. clarkii* and *L. gibbosus*, respectively). RI: relative importance of the term. All quantitative independent variables were scaled and centered to the mean.

Species model	Morphological traits	Source of variation	Estimate	z value	95 % CI of estimate	RI
<i>Procambarus clarkii</i>	RW1	Intercept	0.005 ***	4.56	0.003, 0.007	NA
		Body size	0.003 ***	3.61	0.001, 0.004	1
		Country (USA)	-0.016 ***	9.24	-0.019,-0.013	1
		Sex (male)	0.003	1.81	-0.0002, 0.005	1
		Productivity	-0.001 *	2.53	-0.002, -0.0003	1
		Country (USA) × Sex (male)	0.003	1.86	-0.0002, 0.007	0.77
		Country (USA) × Body size	0.001	1.42	-0.003, 0.0005	0.57
	RW2	Intercept	-0.003	1.94	-0.006, 2.443 e-05	NA
		Country (USA)	0.024 ***	4.50	0.013, 3.416 e-02	1
		Predation	0.001	0.98	-0.001, 3.757 e-03	1
		Sex (male)	0.004 ***	4.30	0.002, 5.756 e-03	1
		Habitat complexity	0.001	1.26	-0.0005, 2.068 e-03	1
		Productivity	-0.002	1.35	-0.006, 1.100 e-03	1
		Country (USA) × Predation	0.019 ***	4.56	0.011, 2.769 e-02	1
		Country (USA) × Habitat complexity	0.022 ***	3.94	0.011, 3.280 e-02	1
Country (USA) × Productivity	0.020 ***	4.57	0.012, 2.885 e-02	1		
Body size	0.0003	0.60	-0.001, 1.284 e-03	0.28		
<i>Lepomis gibbosus</i>	RW1	Intercept	-0.016 ***	5.55	-0.022, -0.011	NA
		Body size	0.003 **	3.10	0.001, 0.006	1
		Country (USA)	0.036 ***	13.76	0.031, 0.041	1
		Habitat complexity	0.004 ***	4.81	0.002, 0.005	1
		Productivity	0.001	0.26	-0.007, 0.009	1
		Country (USA) × Body size	0.005 ***	3.37	0.002, 0.008	1
		Sex (male)	-0.002	1.11	-0.004, 0.001	0.22

	Country (USA) × Habitat complexity	0.015	1.03	-0.004, 0.013	0.30
	Predation	0.007 *	2.06	0.003, 0.013	0.15
	Country (USA) × Predation	-0.010 *	2.14	-0.019, -0.001	0.15
	Country (USA) × Productivity	0.006	0.98	-0.006, 0.019	0.28
RW2	Intercept	0.013 ***	4.52	0.007, 0.019	NA
	Body size	-0.009 ***	13.82	-0.010, -0.008	1
	Country (USA)	-0.008	1.93	-0.017, -0.0001	1
	Predation	0.013 ***	4.93	0.008, 0.018	1
	Habitat complexity	-0.004 ***	5.08	-0.005, -0.002	1
	Productivity	-0.020 ***	5.10	-0.028, -0.012	1
	Country (USA) × Predation	-0.014 **	3.28	-0.021, -0.005	1
	Country (USA) × Habitat complexity	0.007	1.87	-0.0004, 0.014	0.78
	Country (USA) × Productivity	0.022 ***	5.54	0.014, 0.030	1
	Sex (male)	-0.001	1.25	-0.004, 0.001	0.34

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

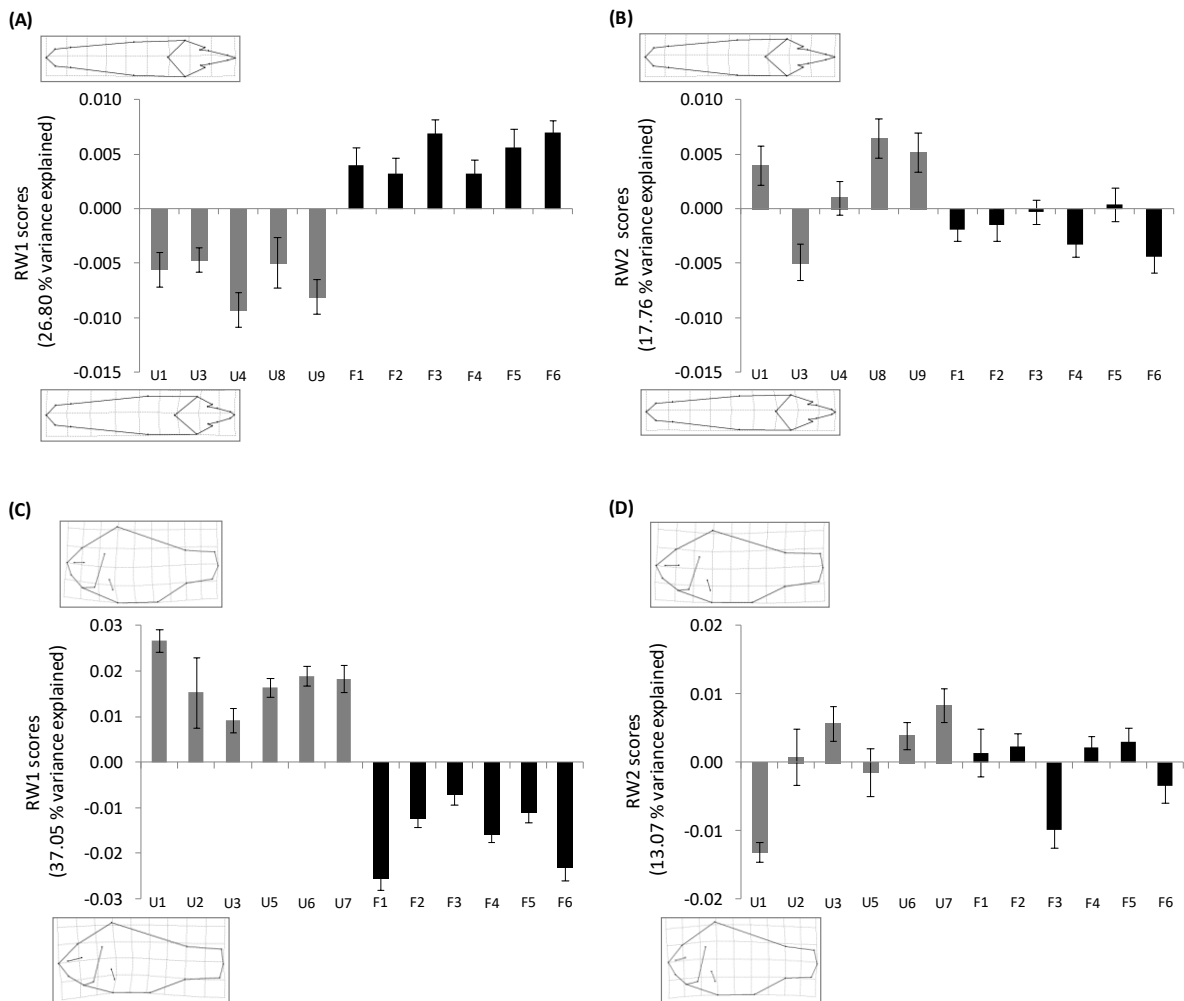


Figure V.2 Feature of body shape divergence between **(A)** **(B)** eleven populations of *Procamburus clarkii* (n = 209) and **(C)** **(D)** twelve populations of *Lepomis gibbosus* (n = 226). Landmark-based body shape is given for RW1 and RW2. American and French populations are depicted in grey and black, respectively. Thin-plate spline transformations represent the most extreme deviation from the consensus configuration and were generated using by regressing relative warp scores against landmark coordinates using tpsRegr software.

V.3.2 - Determinants of morphological variations

RW1 of *P. clarkii* scores significantly increased with body size ($P < 0.001$; Table V.2) and lake productivity ($P < 0.05$; Table V.2). Sex was a significant predictor of variation in RW2 scores ($P < 0.001$; Table V.2; females = $-0.0018 (\pm 0.0008 \text{ SE})$ and males = $0.0012 (\pm 0.0006 \text{ SE})$, respectively). RW2 scores were significantly affected by the three environmental factors but their effect was country-dependent (interaction terms: $P < 0.001$ for predation, habitat complexity and productivity; Table V.2). RW2 scores were not related to predation pressure in French lakes but they increased with increasing predation in American lakes (Fig. V.3A). In the USA, RW2 scores significantly decreased

with increasing habitat complexity while the opposite pattern was observed in France (Fig. V.3B). RW2 scores were not significantly affected by productivity in American lakes, whereas it significantly decreased with increasing productivity in French lakes (Fig. V.3C).

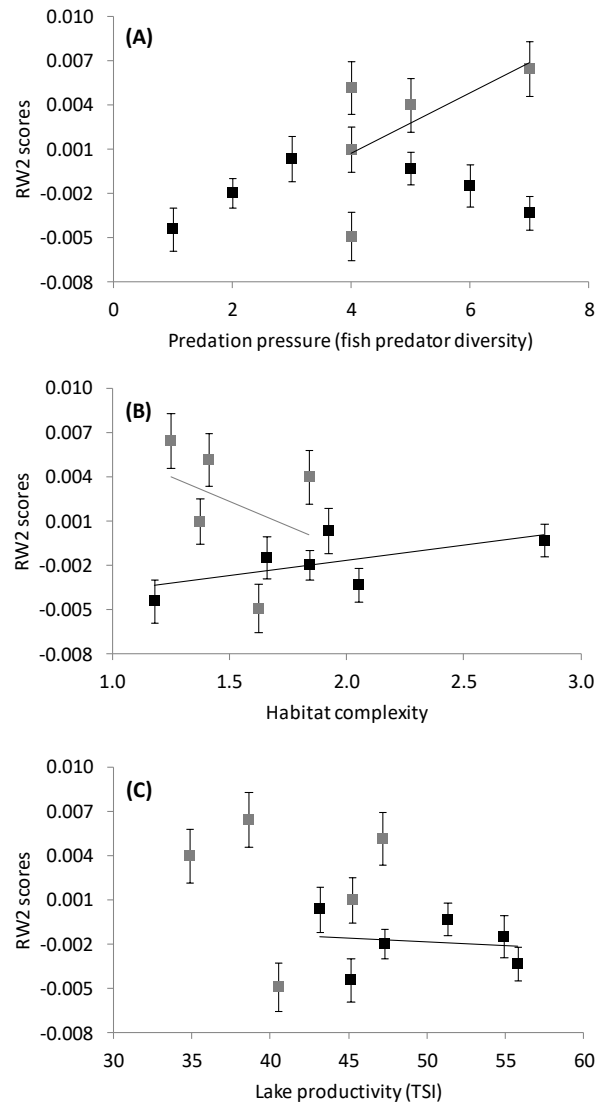


Figure V.3 Country-dependent relationships between *P. clarkii* body shape (RW2 scores; $n = 209$) and **(A)** predation pressure (fish predator diversity), **(B)** habitat complexity and **(C)** lake productivity (TSI). Grey and black symbols represent North American and European populations, respectively (mean \pm SE).

RW1 scores of *L. gibbosus* also significantly increased with increasing body size but this relationship was country-dependent ($P < 0.001$; Table V.2). RW1 significantly increased with body size in American lakes, whereas no relationships were observed in French populations (Fig. V.4A). Habitat complexity significantly affected RW1 ($P < 0.001$; Table V.2) and individuals had positive RW1 scores with increasing complexity. RW1

scores were also significantly affected by the interaction between country and predation ($P < 0.05$; Table V.2), although this interaction had a low relative importance (RI = 0.15; Table V.2). RW2 scores were negatively affected by habitat complexity ($P < 0.001$; Table V.2) and body size ($P < 0.001$; Table 2). Finally, the interaction terms between country and predation, and between country and productivity, significantly affected RW2 scores ($P < 0.01$ and $P < 0.001$, respectively; Table V.2). While no effect were observed in France, RW2 scores decreased and increased with predation pressure and productivity in American lakes, respectively (Fig. V.4B and V.4C).

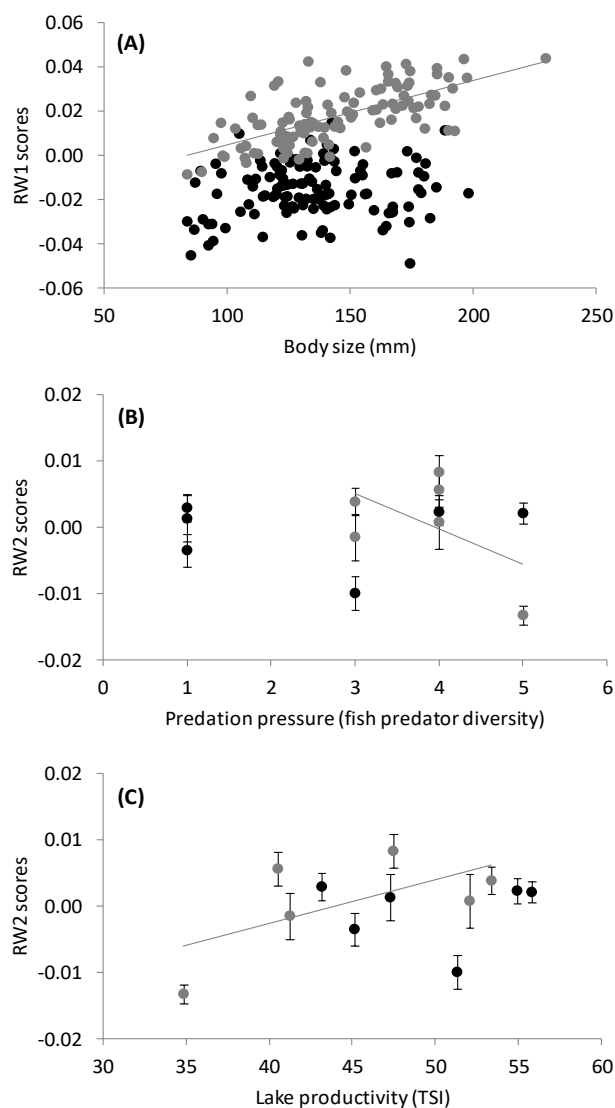


Figure V.4 Country-dependent relationships between *L. gibbosus* body shape (RW1 and RW2 scores; $n = 226$) and **(A)** body size (mm), **(B)** predation pressure (fish predator diversity) and **(C)** lake productivity (TSI). Grey and black symbols represent North American and European populations, respectively (mean \pm SE).

V.3.3 - Relationships between morphology and trophic niche

The average trophic position of *P. clarkii* populations varied between 1.90 (± 0.04 SE) and 3.30 (± 0.04 SE). Individuals in USA displayed a significantly lower trophic position than in France (mean = 2.37 (± 0.05 SE) and 2.75 (± 0.04 SE), respectively, $P < 0.001$; Table V.3) and there was no significant relationship between morphology and trophic position ($P > 0.05$; Table V.3). The proportion of litter consumed was not significantly affected by morphology or country ($P > 0.05$; Table V.3). The mean trophic position of *L. gibbosus* populations ranged from 2.60 ($0.02 \pm$ SE) to 3.46 ($0.05 \pm$ SE) and was significantly affected by the interaction term between country and RW1 ($P < 0.001$; Table V.3). Specifically, the trophic position increased and decreased with RW1 scores in American and French lakes, respectively (Fig. V.5). The contribution of littoral resources to the diet of *L. gibbosus* was not significantly influenced by morphology or country ($P > 0.05$; Table V.3).

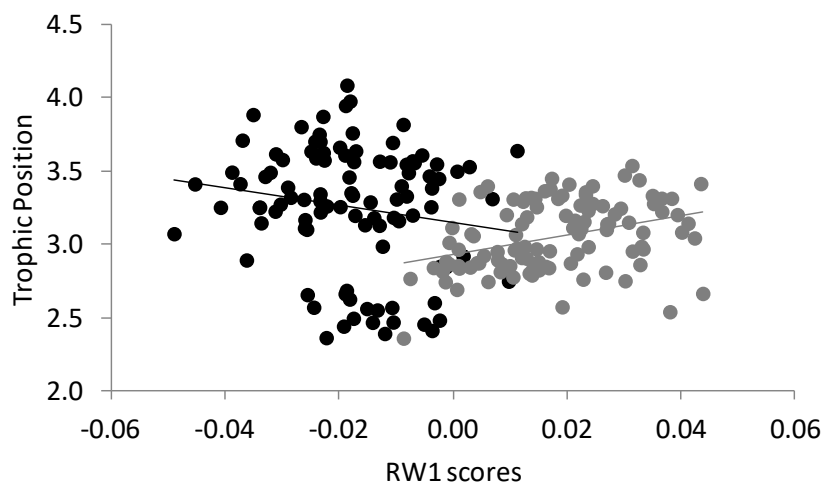


Figure V.5 Country-dependent relationship between body shape (RW1 scores) and trophic position of individuals *L. gibbosus* ($n = 226$). Grey and black symbols represent North American and European populations, respectively.

Table V.3 Summary results of the model averaging of the linear models used to test the effects of site location (country) and morphological scores (RW1 and RW2) on trophic niche (trophic position, litter reliance and littoral reliance; 189 and n = 206 for *P. clarkii* and *L. gibbosus*, respectively). RI: relative importance of the term. All quantitative independent variables were scaled and centered to the mean.

Species model	Trophic traits	Source of variation	Estimate	z value	95 % CI of estimate	RI
<i>Procambarus clarkii</i>	Trophic position	Intercept	2.744 ***	64.74	2.661, 2.883	NA
		Country (USA)	-0.371 ***	5.77	-0.496, -0.245	1
		RW2	-0.065	1.33	-0.160, 0.030	0.26
		Country (USA) × RW2	0.104	1.68	-0.017, 0.225	0.26
		RW1	0.028	0.75	-0.045, 0.101	0.24
	Litter reliance	Intercept	0.624 ***	30.39	0.584, 0.664	NA
		RW1	0.031	1.42	-0.012, 0.074	0.72
		RW2	-0.018	1.44	-0.043, 0.007	0.51
		Country (USA)	0.035	1.03	-0.032, 0.102	0.43
		Country (USA) × RW1	-0.045	1.49	-0.105, 0.014	0.22
<i>Lepomis gibbosus</i>	Trophic position	Intercept	3.186 ***	75.08	3.103, 3.269	NA
		Country (USA)	-0.289 ***	5.09	-0.400, -0.178	1
		RW1	-0.106 *	2.52	-0.189, -0.023	1
		Country (USA) × RW1	0.217 ***	3.73	0.103, 0.331	1
		RW2	0.009	0.54	-0.025, 0.043	0.29
	Littoral reliance	Intercept	0.544 ***	16.83	0.481, 0.607	NA
		RW1	0.038	1.58	-0.009, 0.086	0.54
		RW2	-0.023	1.08	-0.064, 0.019	0.61
		Country (USA)	-0.076	1.59	-0.017, 0.169	0.63
		Country (USA) × RW2	-0.036	0.99	-0.106, 0.035	0.11

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

V.4 - DISCUSSION

Aquatic ecosystems are particularly threatened by biological invasions and understanding the context-dependency of phenotypic variations among worldwide-distributed populations of invaders is crucial to assess their adaptive capacities across their distribution range. In the present study, we investigated the context-dependency of environment-phenotype relationships for two widely-distributed invasive species in North America and Europe. For both species, we observed strong continental differences in the patterns and environmental determinants of body morphology. Our findings provide strong evidence for the importance of invasion history in shaping morphological responses of organisms to common environmental conditions but in geographically disparate regions (Langerhans & Makowicz 2009). Finally, we found no ecomorphological patterns for *P. clarkii*, whereas the trophic position of *L. gibbosus* was associated with their morphology, and this relationship was country-dependent.

Phenotypic variability among conspecific organisms is usually caused by combined effects of environmental conditions (shared divergence), historical contingency (unique history) and unique response among groups to local environmental conditions (unique divergence) (Langehans & DeWitt 2004). Phenotypic plasticity is often associated with successful invasive species (Richards et al. 2006) which are therefore able to display rapid phenotypic changes to adapt to novel ecological conditions. In addition, distinct histories of colonization (e.g., time since introduction, propagule pressure, founders traits) might trigger phenotypic variability among populations through agents of evolutionary changes (i.e., founder effect, genetic drift and mutation-order selection) (Langerhans & De Witt 2004, Blount et al. 2008, Rosenblum & Harmon 2011). Here, country-dependent responses to environmental conditions accounted for a large proportion of the observed morphological variability for both invasive species. Consequently, further studies would investigate the relative effects of environmental conditions and historical processes (i.e., genetic predisposition) and their interplay on phenotypic variations by studying the genetic structure of invasive populations. This would provide new insights regarding how evolutionary history of populations influence patterns of phenotypic divergence (Weese et al. 2011).

Habitat complexity revealed the availability of heterogeneous habitats that are reported to induce morphological variation among populations. Particularly, contrasting patterns of littoral habitat availability induce predictable morphological divergence among populations (Svanbäck & Eklöv 2004, Riopel et al. 2008). Typically, populations in lakes with relatively more littoral habitat depicted deeper bodies whereas streamlined bodies are expected to occur in lakes with more pelagic habitat (Robinson & Parsons 2002). Shoreline development index used here indicated that lake with high values of complexity depicted more littoral habitat. Consequently, the prediction was supported for *L. gibbosus* while the gradient of habitat complexity induced unique morphological divergence for *P. clarkii*. Importantly, subtle changes in localized environmental conditions between geographic locations might produce different regime of selection and thus induce unique response (e.g., different resource type might favor different selection). In addition, *L. gibbosus* in North America, including our studied lake system, forage preferentially on benthic mollusks (Twardochleb & Olden 2016) that might require a higher maneuverability and thus produce deep-bodied individuals. Similarly, *P. clarkii* displayed an opposite response to habitat complexity between countries, also suggesting that phenotypic divergence might reflect both adaptation to local environment and contrasting history of invasion in each country that might ultimately produce spatially different pathways of phenotypic divergence.

Predation is predicted to generate phenotypes that facilitate fast-start escapes such as elongated body, larger caudal region and smaller anterior head/body region (Langerhans et al. 2004, Langerhans & Makowicz 2009). While this response is highly predictable because it has been described in multiple taxa across various geographical locations (Robinson & Parsons 2002, Faulks et al. 2015), this was not observed in the present study. However, we found that *L. gibbosus* experiencing high level of predation in American lakes displayed a rounded body, potentially to increase survival against gape-size limited piscivorous fish species (Nilsson et al. 1995). Different predators species might induce different selection on morphology through the use of various handling methods, entailing the need to use a more integrative assessment of predation pressure. For instance, it would be of great interest to integrate the role of human-induced morphological variations through harvest (Alós et al. 2014, Evangelista et al. 2015).

The relationship between morphology and ecological function is frequently related to food acquisition, potentially leading to resource polymorphism (Smith & Skúlason 1996). Phenotypic divergence between co-existing littoral and pelagic morphs have been observed in many fish species, including *L. gibbosus* with individuals foraging on benthic prey having deeper bodies, smaller eyes, shorter head and larger mouth (Jastrebki & Robinson 2004, Parsons & Robinson 2007). Consistent with previous study (Vander Zanden & Rasmussen 1999), we found that pelagic zooplankton was significantly ^{15}N -enriched relative to littoral arthropods within all lakes (paired t-test: $t_{11} = -3.76, P = 0.003$). Consequently, individuals fish specialized on littoral prey tend to have a lower trophic position than individuals specialized on pelagic prey (Matthews et al. 2010). This relationship was only suggested here by the decreasing trophic position of deep-bodied *L. gibbosus* in French populations, potentially highlighting the role of mobile predators to couple littoral and pelagic habitats (Vander Zanden & Vadeboncoeur 2002). *P. clarkii* is omnivorous and primarily consume primary producers (Gherardi 2006). However, resource availability and intraspecific competition could modify individual diet (Evangelista et al. 2014) and increase the trophic position through an increased consumption of aquatic invertebrates. The high density of macrophytes and the low level of intraspecific competition observed here in American lakes compared to French lakes might explain their lower trophic position. Therefore, these results might indicate that changes in the phenotypic characteristics of invasive individuals might modulate their impacts on recipient communities and ecosystems based on population history and local environmental conditions, although this would require further investigations.

In conclusion, the present study demonstrated the existence of species-specific and context-dependent phenotype-environment relationships and suggested the role of underpinning evolutionary processes related to the colonization histories of each species (Langerhans & De Witt 2004). In addition, the existence of ecomorphological patterns within invasive species strongly suggest that their impacts on recipient ecosystems might differ between populations, since intraspecific variability can modulate the effects of organisms on ecosystem functioning (Harmon et al. 2009, Bassar et al. 2010). Consequently, there is an urgent need to identify drivers that lead to phenotypic heterogeneity among invasive populations to better assess their effects on

the different habitats they inhabited. Ultimately, this should also help to provide appropriate management decisions.

V.5 - ACKNOWLEDGEMENTS

We are very grateful to our numerous colleagues for their help during sampling. Authorizations to perform this study were provided by the "Arrêtés Préfectoraux - 18/09/2014 and 30/10/2014". This work was supported by a CNRS-INEE "PICS" grant (Ind_Eco_Evo_Inva), the ONEMA (Projet ISOLAC - Convention 13-V5-28) and a PRES-Toulouse grant (Inva_Eco_Evo_Lac). CE and JC are part of EDB, part of the French Laboratory of Excellence project "TULIP" (ANR-10-LABX.41; ANR-11-IDEX-0002-02).

*Intraspecific trait variations among populations modulate the ecological effects of invasive *Procambarus clarkii**

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Manuscript in preparation

Key-words morphological variability, litter decomposition, community structure, ecosystem functioning

Résumé

Les espèces invasives sont considérées comme étant une des causes principales de l'altération écologique actuelle. A ce jour, néanmoins, le rôle de la variabilité intra spécifique sur les impacts écologiques des espèces invasives reste peu connu alors que de précédentes études ont révélé son influence dans la modulation des effets des espèces natives sur le fonctionnement de l'écosystème. Dans cette étude, nous avons d'abord utiliser une approche de terrain pour quantifier les variations morphologiques entre 15 populations invasives de *Procambarus clarkii* établies le long d'un gradient de conditions environnementales et en déterminer les déterminants écologiques. Ensuite, à l'aide d'une approche expérimentales en mésocosmes extérieurs, nous avons testé si la variabilité phénotypique observée au sein des populations naturelles pouvait modifier les effets des espèces invasives sur la structure des communautés de proies et les processus fonctionnels de l'écosystème receveur. Dans un premier temps, les résultats indiquaient que les variations morphologiques entre populations étaient fortes et que la productivité des lacs, fortement associée avec l'âge de formation des lacs et la date d'introduction de l'espèce, était le principal déterminant de la variabilité morphologique observée en milieu naturel. Ainsi, les individus aux corps les plus fins étaient caractéristiques des lacs les plus productifs. Dans un second temps, nous avons observé expérimentalement que les variations morphologiques entre populations modulaient les impacts de l'espèce invasive sur l'écosystème à travers des modifications du taux de consommations des ressources trophiques. Ainsi, la population issue du lac le plus jeune induisait le plus fort taux de décomposition des litières, la plus faible densité d'invertébrés et le plus faible recouvrement en macrophytes. Ensuite, nous avons comparé les effets écologiques induits par l'introduction de *Procambarus clarkii* à ceux causés par la variabilité intraspécifique à différents niveaux d'organisation biologique. Nous avons mis en évidence que les effets de la variabilité intraspécifique pouvaient excéder ceux induits par l'introduction de l'espèce et particulièrement au niveau des communautés. Ces résultats soutiennent fortement l'idée qu'intégrer la variabilité intraspécifique dans le contexte des invasions biologiques est essentiel pour mieux évaluer leurs impacts potentiels sur les écosystèmes receveurs.

Abstract

Invasive species are increasingly recognized as major drivers of ecological alterations. To date, however, the role of intraspecific variability in influencing the ecological impacts of invasive species has been poorly investigated despite the fact that previous studies have revealed its influence in modulating the effects of native species on ecosystem functioning. First, using a field based approach, we quantified morphological variations among 15 populations of invasive red swamp crayfish *Procambarus clarkii* established along a gradient of environmental conditions and investigated the ecological drivers this variability. Second, using an outdoor mesocosm experiment, we tested whether phenotypic variations observed in the wild can modify the effects of invasive populations on prey community structure and ecosystem functioning. Our results first demonstrated that morphological variation among lakes was high and that lake productivity, which was strongly associated to lake age and time since invasion, was the main driver of morphological variability among populations, with narrower bodies encountered in more productive lakes. Second, we found that morphological variations modulate the effects of invasion *P. clarkii* on ecosystem functioning through changes in consumption rates, with population inhabiting the youngest lake inducing the highest rate of litter decomposition, the lowest density of invertebrates and the lowest macrophytes cover. When comparing the ecological effects of *P. clarkii* introduction to those associated with intraspecific variability at different level of biological organizations, we found evidence that the effects of intraspecific variability could exceed the effects induced by species introduction, and this was particularly apparent at the community level. These novel findings strongly support the idea that integrating intraspecific variability in the context of biological invasion is essential to better appreciate their potential impacts on recipient ecosystems.

VI.1 - INTRODUCTION

Biological invasions are a major component of global changes, leading to biodiversity and ecosystem services loss through strong ecological impacts across all levels of biological organization (Vitousek et al. 1996, Clavero & García-Berthou 2005, Cucherousset & Olden 2011). This notably includes the disruption of the native communities and the alteration of ecosystem functioning (Matsuzaki et al. 2009, Jackson et al. 2014, Twardochled et al. 2013). Quantifying the ecological impacts of invasive species is of upmost important for anticipating appropriate management strategies (Britton et al. 2011). To date, most investigations have focused on quantifying the biological traits of successful invaders (Kolar & Lodge 2001, Marchetti et al. 2004) and on evaluating the species-specific impacts of invaders (Jackson et al. 2014). However, it has been increasingly recognized that invaders can rapidly phenotypically differ across their invasive range (Huey et al. 2000, Juetten et al. 2014), even at a local scale (*Chap. IV*), suggesting the potential contrasted effects of different populations on recipient ecosystems. To date, our understanding of the potential within-species variability in ecological traits and the associated ecological impacts of invasive species remains limited and this is primarily because invasive ecologists have considered invasive individuals as ecologically equivalent.

Within species, variability in phenotypic and life history traits can occur at different scales, both within and between populations (Bolnick et al. 2003, Violle et al. 2012), and can reflect adaptation to local environmental conditions. Recent experimental studies have demonstrated that intraspecific variability in morphological traits was important since it could modulate the effects of individuals on community structure and ecosystem functioning, mostly through changes in trophic niche and consumer-mediated nutrient recycling (Harmon et al. 2009, Bassar et al. 2010, Walsh & Post 2011, Rudolf & Rasmussen 2013a). Although intraspecific variability in invasive species has also been reported to be high (e.g., within population: Cucherousset et al. 2012b, Zhao et al. 2014; between populations: Novomeská et al. 2013), its ecological consequences on recipient ecosystems remains, to our best knowledge, poorly studied.

Intraspecific variability in invasive species could be driven by the nature of biological invasions; a multi-stage process with ecological filters acting at each stage (Lockwood et al. 2007). Indeed, individual invaders have first to be captured in their

native range and then transported into a new geographic area. After the successful establishment of self-sustained population(s), invasive species finally spread across their new distributional area. During this suite of stages of the invasion process, invaders have to overcome several environmental filters that will non-randomly select individuals with specific ecological traits (Jette et al. 2014). Depending in the vectors of introduction and spread and the environment in which they are introduced, invasive individuals are likely to phenotypically differ but this remains poorly quantified. For instance, the introduction of non-native fish species for recreational fishery is primarily based on body size (Blanchet et al. 2010) and larger-bodied individuals with fast growth may preferentially be introduced while the dispersal to new habitat patches can be behaviorally-biased with asocial individuals dispersing further (Cote et al. 2010b). The pace-of-life theory predicts the existence of a strong association between phenotypic traits such as behavioral, physiological and life history traits (Sih et al. 2004, Reale et al. 2010, Mittelbach et al. 2014). This is important because recent investigations have revealed that individuals also exhibited strong morphology-behavior associations (Kern et al. 2016, Raffard et al. *In prep*) and that phenotypic traits can covary with functional effects traits (e.g., litter decomposition and nutrient excretion rates; Raffard et al. *In prep*), i.e., those traits by which individuals can affect their ecosystems (Diaz et al. 2013). In entirety, these findings suggest that traits selected during invasion process are also strongly associated to those traits that modulate the ecological impacts of invasive species on recipient ecosystems. Consequently, since intraspecific variability in phenotypic traits among invasive populations occurs as an inherent consequence of the nature of biological invasions, the ecological impacts of invaders on native organisms and recipient ecosystems are predicted to differ among invasive population but this remains to be tested. This is particularly important to determine the relative importance of ecological impacts induced by the introduction of invasive species itself compared to the impacts caused by intraspecific variability in the invasive species.

The aim of the present study was to investigate if intraspecific variability in phenotypic traits among populations of invasive red swamp crayfish *Procambarus clarkii* modulate their impacts on native communities and ecosystem functioning. *P. clarkii* is a generalist omnivore that affects both primary producers and secondary consumers through consumption and it has been demonstrated to impact recipient ecosystem functioning through changes in litter decomposition rates and nutrient

cycling (Lodge et al. 2012, Alp et al. 2016). The species was first introduced in Europe for aquaculture purpose and then spread across the continent through human-induced introductions and natural dispersal facilitated by its ability for terrestrial dispersal (Cruz & Rebelo 2007, Banha & Anastacio 2014). It represents an interesting model species for the current study because multiple introduction pathways are likely to lead to important intraspecific variability in phenotypic traits, as already quantified (*Chap. V*). First, we used a field approach to investigate the patterns of morphological variation among 15 wild populations of *P. clarkii* and assessed the environmental determinants of this variability. Second, we selected morphologically divergent populations and used them in an outdoor mesocosm experiment to quantify the ecological impacts of phenotypically different populations on the structure of native communities and the functioning of recipient ecosystems. We predicted that the ecological impacts induced by the introduction of invasive crayfish on communities and ecosystems would differ between populations. Finally, we compared the intensity of the impacts induced by the introduction of the invasive species (*species effects*) to those induced by phenotypic variability within the invasive species (*intraspecific effects*). We predicted that species introduction would induce stronger effects on community level through direct consumption than intraspecific variability. Alternatively, the effects of species introduction at the ecosystem level would be dampened by interactions between top-down and bottom-up forces (Palkovacs et al. 2015).

VI.2 - MATERIAL & METHODS

VI.2.1 - Patterns and determinants of morphological variability

VI.2.1.a - Study area

Crayfish were sampled in 15 artificial lakes during late Summer 2014. These lakes are former gravel pits localized along the flood plain of the Garonne River in southern Toulouse (southwestern France). The end-year of dredging ranged between 1964 and 2007, providing a wide gradient of time since invasion and contrasted environment conditions between lakes. *P. clarkii* is very abundant in the littoral habitats of these lakes and density can vary by a 15-fold range across lakes, from 0.38 to 5.96 ind.trap⁻¹.h⁻¹.

VI.2.1.b - Crayfish sampling

P. clarkii were collected between mid-September and mid-October 2014 in the littoral habitat of each lake using baited trap set overnight (12 traps per lake) and active searching with pond nets when more individuals were needed. The abundance of *P. clarkii* was calculated as the catch per unit effort (CPUE) based on the number of *P. clarkii* captured in the traps during night (ind. trap⁻¹ h⁻¹). Individuals were then measured for carapace length using a caliper (CL; mm ± 0.1 mm), euthanized using an overdose of anesthetic, stored on ice and frozen in the laboratory (-20°C) until subsequent processing.

VI.2.1.c - Environmental monitoring

A set of relevant biotic and abiotic environmental parameters were quantified in each lake. Specifically, lake age was calculated as the difference between the last year of dredging and the sampling year. Lake surface area (SA; ha) and lake perimeter (Pr; m) were calculated using aerial pictures and GIS analyses. Lake morphology (MO) and shoreline development index (SLD) were calculated by as the SA/Pr ratio (Bolnick & Lau 2008) and using formula $SLD = Pr / 2\sqrt{(\pi SA)}$ (Hutchinson 1957), respectively. In early September 2014, Secchi depth (Secchi, m), total phosphorus concentration (TP, µg L⁻¹), chlorophyll-a concentration (Chla, µg L⁻¹) and turbidity (Tb, FTUs) were measured in three different locations in each lake using a Secchi-disk and a portable fluorescent photometer (BBE-Moldaenke, Kiel, Germany). The integrative trophic status index (TSI) was subsequently quantified using total phosphorus concentration, chlorophyll-a concentration and Secchi depth (Carlson 1977). Intraspecific competition was calculated as the number of *P. clarkii* captured in the littoral zone during night (ind. trap⁻¹ h⁻¹) when the species is more active (*see details below*). Predation pressure was assessed by quantifying the abundance of predatory fish species (juveniles and adults of *Micropterus salmoides*, *Esox lucius*, *Perca fluviatilis*, *Sander lucioperca*, *Silurus glanis* and *Cyprinus carpio*) using combination of electrofishing (point abundance sampling electrofishing PASE, Nelva et al. 1979) and gill-netting (Zhao et al. 2016). Captured fish were measured for fork length (mm) and then the body mass (g) of each specimen was estimated using length-weight relationships (Zhao et al. unpublished data). Three surrogates of predation pressure were then quantified: the total biomass of predators captured during electrofishing and net sampling (TBP, g), the biomass of predators captured by

electrofishing (BPE, g PASE⁻¹) and the biomass of predators captured by gill netting (BPN, g net⁻¹).

VI.2.1.d - Morphological analyses

For each lake, a maximum of 20 *P. clarkii* (adults, CL ranging from 35.4 to 64.2 mm; mean = 19.6 ± 1.55 individuals per lake) were randomly selected and photographed dorsally. Morphological analyses were performed using geometric morphometric technique (Zelditch et al. 2004) and 19 homologous landmarks (see Chap. II, Fig. II.3) were digitized using TpsDig2 v.2.17 (Rohlf 2013) to measure the overall body shape morphology of each individual. The file of digitized coordinates was then opened in MorphoJ v.1.06d and the data were brought into a common coordinate system through a Generalized Procrustes Analysis (GPA) that remove non-shape variation (e.g., variations due to positioning of fish ion pictures). Indeed, this procedure translates, rotates and scales all shapes to minimize their differences between their landmarks (Mitteroecker & Gunz 2009). The centroid size of each individual was also calculated as a measure of overall body size completely independent of shape (Bookstein 1991).

VI.2.2 - Ecological consequences of morphological variability

VI.2.2.a - Mesocosm experiment

An outdoor mesocosm experiment was conducted in Autumn 2015 (5 weeks) using twenty circular cattle tanks (550 L, 0.63 m deep, 1.28 m diameter). In early September, each mesocosm was prepared with 2 cm depth of clean gravel as a substrate, filled with approximately 350 L of dechlorinated water and inoculated with 2 L of unfiltered water from a gravel pit lake containing an inoculum of autotrophic and heterotrophic microorganisms. In each mesocosm, five sections of drainpipe (20 cm length, 5 cm diameter) and two halves of large alveolar construction brick (15 cm deep, 50 cm length, 15 cm width) were added to serve as shelters for crayfish. Mesocosms were supplied with freshwater snails (*Physa*; 16 individuals of the same size per mesocosm) collected from local ponds and benthic invertebrates collected using mesh bags containing 5 g of a leaf litter mixture and installed in a gravel pit lake during 20 days. Macrophyte (*Ceratophyllum sp.*) and mixture of air-dried alder (*Alnus glutinosa*) and oak (*Quercus robur*) leaf litter collected from local ponds and at abscission, respectively, were added in each mesocosm at similar biomass (mean = 20.50 ± 0.22 g fresh biomass; mean =

20.32 ± 0.16 g air-dried). Finally, each mesocosm was covered with a net (0.5 mm mesh size) and given 30 days to mature before *P. clarkii* were introduced.

VI.2.2.b - Experimental design

Based on results from field survey (*see details in Results section*), four populations from lakes with different ages (namely LAV, SAB, SOA and TAA) were selected to maximize the morphological differences along the PC1 axis (Fig. VI.2 and Fig. VI.3). A total of 110 *P. clarkii* (17, 30, 35, 28 individuals collected in TAA, SOA, LAV and SAB, respectively) was collected from September 29th to September 30th 2015 using baited traps set overnight. The experiment design comprised four replicates of five treatments (i.e., no crayfish, 4 individuals from LAV, 4 individuals from SAB, 4 individuals from SOA and 4 individuals from TAA). A total of 20 mesocosms were used and dispatched in 4 block of 5 mesocosms. A density of 3.10 ind. m⁻² was selected to fall within the range of *P. clarkii* density reported in the wild (Gherardi & Lazzara 2006). On October 2nd 2015, individuals were measured for initial carapace length (CL_i ± 0.1 mm) and a subsample was selected to minimize body size variation between treatments. However, CL_i was significantly different between two populations (i.e., TAA and SAB; ANOVA: Tukey's HSD $P = 0.004$). Selected individuals were then sexed, marked, dorsally photographed for subsequent morphological analyses and introduced into each mesocosm. Importantly, sex ratio (1 female and 3 males) could not be performed for SOA (3 females and 1 male). During the experiment, a total of 5 dead individuals were found and were immediately replaced with individual with similar CL from the same population. At the end of the experiment (November 5th 2015), all individuals were removed from the mesocosm, weighted ($W_f \pm 0.1$ g), measured for final carapace length (CL_f) and euthanized using an overdose of anesthetic. Three individuals were missing and probably died without detection during the experiment.

VI.2.2.c - Morphological variability

Geometric morphometric analyses were performed on experimental individuals following the methodology as previously described. The two first axes of the discriminant analysis (CVA) represented 83.0 % of the total variance (CV1 = 46.44, CV2 = 35.56 %; Fig. VI.1). The CVA also showed that SOA depicted significant differences in body shape with the other populations (permutation test for Procrustes distances: LAV-

SOA: $P = 0.002$; SAB-SOA: $P = 0.011$; SOA-TAA: $P = 0.041$). Although morphological analyses performed on 15 populations revealed strong divergence between the four selected populations (*see details in Results section*), analyses based on these populations showed that body shape was not significantly distinct between LAV, SAB and TAA (permutation test for Procrustes distances: $P > 0.403$).

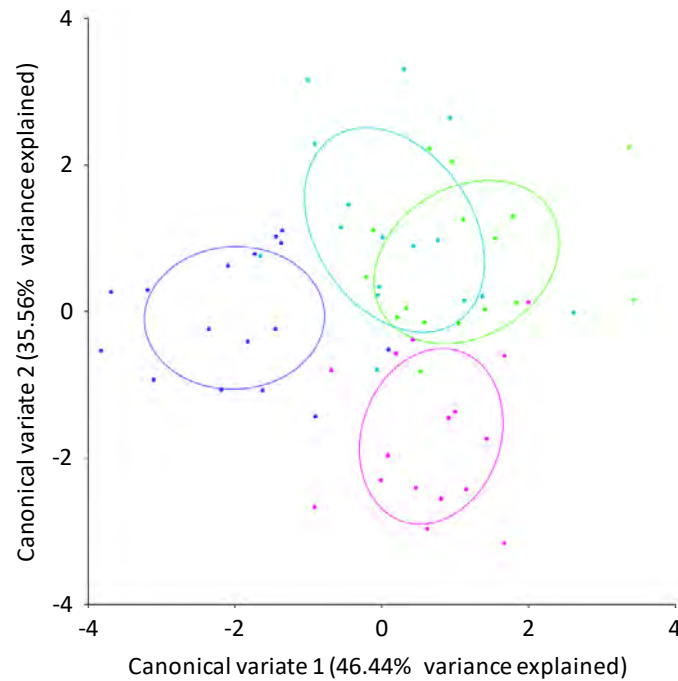


Figure VI.1 Ordination plots of canonical variates extracted by CVA computed on weight matrix. Points represent *Procambarus clarkii* individuals from experimental study ($n = 64$), colored by population (light blue = SAB, dark blue = SOA, green = LAV and purple = TAA) and confidence ellipses incorporate 50% of the population variance.

VI.2.2.d - Population and community responses

Crayfish growth rate was assessed by calculating the specific growth rate (SGR; % week⁻¹) and the increment in carapace length (ICL; mm week⁻¹) of each individual during the experiment using the following formulas:

$$\text{SGR} = 100 \times (\ln W_f - \ln W_i) / t$$

$$\text{ICL} = (CL_f - CL_i) / t$$

where W_i is the initial weight of *P. clarkii* estimated using length-weight relationships calculated from W_f and CL_f , t the duration of the experiment (5 weeks).

At the end of the experiment, a representative sample of invertebrates was taken from each mesocosm using a handnet pulled around the edge of the tank for two turns. Just prior to sampling, benthic invertebrates were dislodged by scrubbing the wall,

disturbing bottom sediments, and stirring round the water of the mesocosms. Samples were then preserved in ethanol and invertebrates were counted and identified to the lowest taxonomic level under microscope at the laboratory. A total of eight taxa of invertebrates (Chironomidae, Ostracoda, Caenidae, Odonate, Corixidae, Trichoptera, Baetidae and Physa) were identified and counted and data were used to calculate Shannon (H) and Simpson (Ds) diversity indices.

VI.2.2.e - Ecosystem responses

Prior to the collection of invertebrates, water samples (250 mL) were collected in the water column and total nitrogen and phosphorus concentration (mg L^{-1} and $\mu\text{g L}^{-1}$, respectively) were then quantified using the phenol-hypochlorite and molybdenum blue methods, respectively, performed by an automated continuous-flow colorimetric analyzer (ALPKEM Corporation, Clackamas, OR, U.S.A). Pelagic autotrophic biomass (chlorophyll-a concentration; $\mu\text{g L}^{-1}$) was measured in the water column with a portable fluorescent photometer (BBE-Moldaenke, Kiel, Germany). Coarse particulate organic matter were collected using handnet, sorted to either macrophyte fragments or leaf litter, oven dried (60°C for 48h) and weighed.

Then, change in macrophyte mass (% g dry mass change) was calculated as follows:

$$\text{Macrophyte mass change} = (\text{DM}_f - \text{DM}_i) \times 100 / \text{DM}_i$$

where DM_f was the final dry mass of macrophyte, DM_i was the initial dry mass of macrophyte estimated based on the relationship between air-dried and oven-dried macrophyte mass established using 4 extra batches of macrophytes.

Daily decomposition rate of leaf litter (day^{-1}) was calculated following Lecerf et al. (2005):

$$\text{Decomposition rate} = -\ln(R) / t$$

where R is the proportion of litter mass remaining calculated as the ratio of final (M_f) to initial (M_i) oven-dried mass of leaf litter, t the duration of experiment (35 days). M_i was determined based on a ratio of air-dried to oven-dried mass. Diel variation of oxygen concentration in mesocosms was monitored over a 24 hour period one week before the end of experiment (from October 28th to October 30th) to determine community-level metabolism. Oxygen concentration and water temperature were recorded every fifteen minutes and community respiration ($\text{molC m}^{-2} 24\text{h}^{-1}$) was calculated following Staehr et al. (2010).

VI.2.3 - Statistical analyses

VI.2.3.a - Patterns and determinants of morphological variability

Procruste coordinates were used as shape variable for the computation of Canonical Variate Analysis (CVA) in MorphoJ, which optimize inter-population differences relative to within-population variation (Zelditch et al. 2004). The degree of morphological differentiation between populations was estimated using pair-wise Procruste distances, whose significance was estimated using a bootstrap approach (10 000 replicates) implemented in MorphoJ. To further illustrate the morphological changes associated with variations in CV values, deformation wireframe graphs were created.

A synthetic multidimensional space was built to characterize the overall environmental conditions in the studied ecosystems using a principal component analysis (PCA) based on all environmental parameters. However, lakes TAB, LIN and SOC were not included in these analyses because environmental parameters were not quantified. The two first principal PCA axes (Eigen value > 1 and variance explained > 10 %) were then selected and used as synthetic environmental axes. The PCA axes were subsequently used in linear models to test their effects on mean values of morphological axes (2 CV axes). Models also included mean centroid size as a covariate to test for allometry. To standardize the dataset, all independent variables from the linear models were scaled and centered to the mean (Murray & Connor 2009).

VI.2.3.b - Ecological consequences of morphological variability

The effects of the treatment 'population' on responses variables measured at the end of the experiment at the individual (SGR and ICL), community (Shannon and Simpson indexes, density of *Chironomidae* and *Physa*, the two most abundant invertebrate taxa) and ecosystem (macrophyte mass loss, decomposition rate, gross primary productivity, pelagic primary production and total phosphorus and nitrogen concentrations) levels were tested using ANOVAs. A bloc effect was added in the model as covariate to control for potential variations in the experimental set-up. Tukey's post-hoc tests were then used to determine which pair of populations significantly differed. Difference between populations in the composition of invertebrate community (based on the density of each invertebrate taxa) were visualized by conducting a non-metric multidimensional scaling (NMDS, R package Vegan, Oksanen et al. 2013) based on Bray-Curtis dissimilarity distance. Variability in community structure (i.e. dispersion) among treatments was

investigated using a multivariate homogeneity of group dispersion test (Anderson 2006) with the *betadisper* function in the Vegan package, and ANOVA was used to test whether these differed significantly. A permutational multivariate analysis (PERMANOVA, permutations = 499) was then used to test whether the invertebrate community composition differed between populations (Anderson 2001) using the *adonis* function in the Vegan package.

An approach based on calculation of the size effects (Matthews et al. 2011a, Fryxell et al. 2015) was then used to compare the ecological impacts induced by crayfish introduction (comparison of responses in treatments with crayfish (*population treatments*) and without crayfish (*control treatment*)) to the ecological impacts induced by intraspecific variability (comparison of responses in population treatments between populations with the lowest and the highest effects). Effects size (Cohen's d) were calculated using the formula:

$$d = (M_1 - M_2) / S_{\text{pooled}}, S_{\text{pooled}} = \sqrt{[(s_1^2 + s_2^2) / 2]}$$

where M is the mean and s is the standard deviation of each response variable (Cohen 1992) for treatment 1 and 2. The effects of crayfish introduction and inter-population variability were tested using *a posteriori* contrast tests. Contrast 1 (introduction) tested the effects of the no crayfish treatment versus the population treatments on ecological responses. This introduction contrast compared the mean of the control treatment with the mean of the four crayfish treatments. Contrast 2 (inter-population) tested the effects of intraspecific variability on ecological responses by comparing the mean of the two populations showing the greatest effects. For all analyses, assumptions of linearity and homogeneity of variances on residuals from all parametric models were checked visually. All statistical analyses were performed using R v.3.1.2 (R Development Core Team 2013).

VI.3 - RESULTS

VI.3.1 - *Patterns and determinants of morphological variability*

The two first axes of the PCA on the environmental characteristics of the sampled lakes explained 48.6 and 29.1% of the total inertia, respectively. PC1 was mainly associated to ecosystem productivity (older, higher TSI, total phosphorus concentration and primary production and lower Secchi depth) while PC2 was principally associated with lake

morphology (larger perimeter and surface area, increased shoreline complexity) and predatory fish biomass (Fig. VI.2).

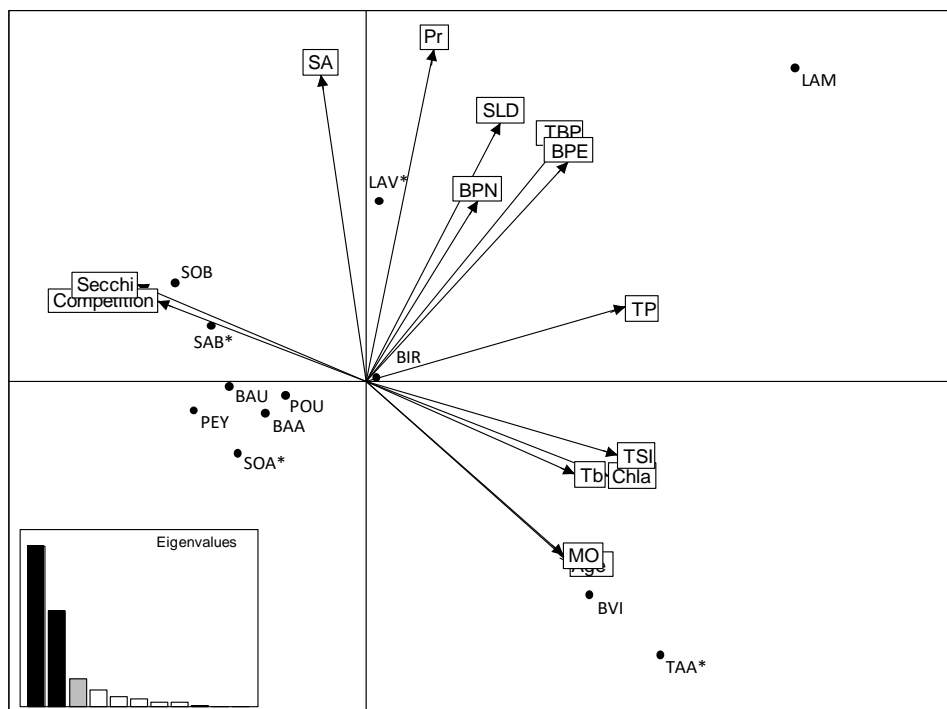


Figure VI.2 Results of the PCA analyses described the biotic (Competition, total biomass of predators [TBP], biomass of predators captured by electrofishing [BPE] and by gill netting [BPN]) and abiotic (lake surface area [SA], perimeter [Pr] and morphology [MO], shoreline development index [SLD], Secchi depth [Secchi], total phosphorus [TP] and chlorophyll-a [Chla] concentrations, turbidity [Tb] and trophic status index [TSI]) environmental conditions in each of the studied lakes sampled in 2014 ($n = 12$). Asterisks indicate populations sampled in 2015 for the mesocosm experiment.

The two first CV axes of the discriminant analyses between populations accounted for 32.05% and 14.79% of the total variance, respectively, and significant differences in body shape between populations were observed (permutation test for Procrustes distances; Table VI.1, Fig. VI.3). Specifically, individuals with high CV1 values displayed a narrow body while individuals with high CV2 were deep-bodied (Fig. VI.3). Individuals with narrower body (positive CV1) were smaller, as revealed by the significant negative relationship between CV1 and centroid size (linear model: $t_7 = -3.42$, $P = 0.011$; Table VI.2). A significant positive relationship was found between CV1 and PC1 (linear model: $t_7 = 5.09$, $P = 0.001$; Table VI.2), indicating that narrower individuals were encountered in the more productive lakes. No significant relationships were observed between CV2 and either centroid size nor environmental characteristics of the lakes (linear models: $P > 0.228$; Table VI.2).

Table VI.1 Results of the CVA permutation tests (n = 10 000) for Procrustes distances between *Procambarus clarkii* populations (n = 15) captured in 2014. Significant *P*-values are displayed in bold. Asterisks indicate populations sampled in 2015 for the mesocosm experiment.

	BAA	BAU	BIR	BVI	LAM	LAV*	LIN	PEY	POU	SAB*	SOA*	SOB	SOC	TAA*
BAU	0.008													
BIR	0.017	0.015												
BVI	< 0.001	< 0.001	0.001											
LAM	0.002	< 0.001	0.021	0.001										
LAV	0.010	0.003	0.030	< 0.001	< 0.001									
LIN	0.001	< 0.001	0.002	< 0.001	0.025	< 0.001								
PEY	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001							
POU	0.071	0.001	0.009	< 0.001	0.003	0.117	< 0.001	< 0.001						
SAB	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001				
SOA	0.012	0.002	0.028	0.003	0.051	< 0.001	< 0.001	< 0.001	0.004	< 0.001				
SOB	0.015	< 0.001	< 0.001	< 0.001	0.008	< 0.001	< 0.001	< 0.001	0.170	< 0.001	0.002			
SOC	< 0.001	0.001	0.010	0.003	0.018	< 0.001	0.004	< 0.001	< 0.001	< 0.001	0.099	< 0.001		
TAA	0.010	< 0.001	0.013	0.003	0.015	< 0.001	0.009	< 0.001	0.004	< 0.001	0.003	< 0.001	0.004	
TAB	0.005	< 0.001	0.159	0.001	0.024	< 0.001	0.001	< 0.001	0.002	< 0.001	0.017	< 0.001	0.011	0.130

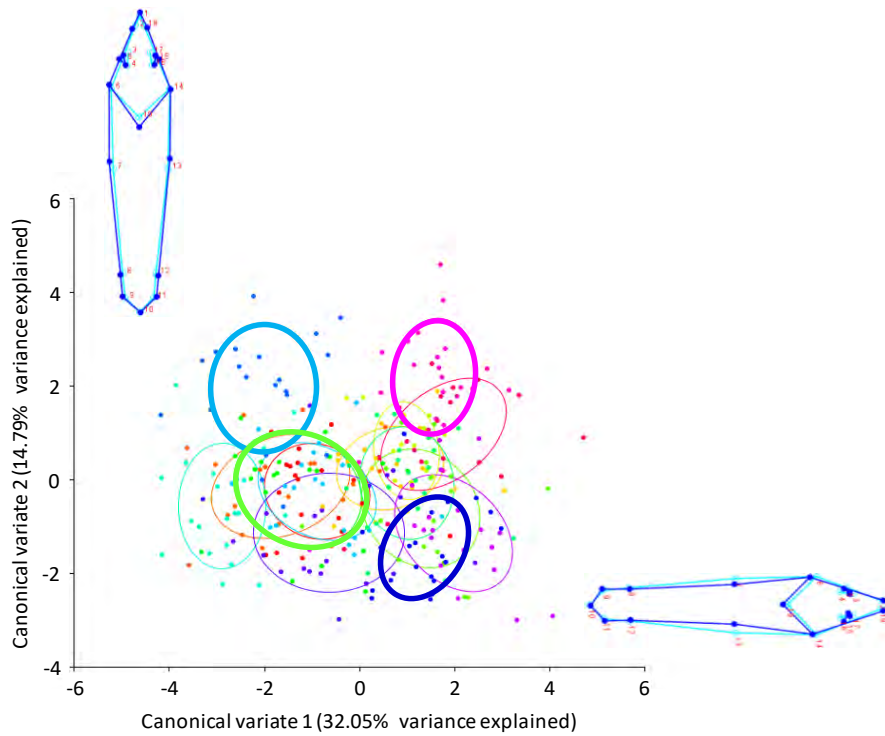


Figure VI.3 Ordination plots of canonical variates extracted by CVA computed on weight matrix. Points represent *Procambarus clarkii* individuals (n = 294), colored by population (n = 15) and confidence ellipses incorporate 50% of the population variance. Bold ellipses represent populations sampled in 2015 for the experimental study (light blue = SAB, dark blue = SOA, green = LAV and purple = TAA). Body shape variations between populations are displayed using wireframe representations and shape changes associated with CV1 and CV2 are displayed in dark blue.

Table VI.2 Results of linear models used to test the effects of centroid size and environmental characteristics (PC1 and PC2) on body shape (CVA axes) of red-swamp crayfish (*Procambarus clarkii*) (n = 12). All independents variables were scaled and centered to the mean. Significant *P*-values are depicted in bold.

CVA axes	Source of variations	df	Estimate ± SD	t value	<i>P</i>
CV1	Intercept	7	-0.35 ± 0.22	-1.60	0.154
	Centroid size	7	-0.97 ± 0.28	-3.42	0.011
	PC1 values	7	1.19 ± 0.23	5.09	0.001
	PC2 values	7	-0.30 ± 0.23	-1.27	0.245
CV2	Intercept	7	-0.07 ± 0.28	-0.25	0.812
	Centroid size	7	0.47 ± 0.35	1.32	0.228
	PC1 values	7	0.14 ± 0.29	0.45	0.668
	PC2 values	7	-0.33 ± 0.29	-1.12	0.299

VI.3.2 - Ecological consequences of morphological variability

VI.3.2.a - Crayfish and invertebrate prey responses

At the population level and despite the fact that some variability was observed, the specific growth rate (SGR) and the increment carapace length (ICL) of *P. clarkii* did not differ significantly between populations (ANOVAs: $P = 0.118$ and $P = 0.171$, respectively; Table VI.3, Fig. VI.4A and VI.4B). At the invertebrate community level, both Shannon and Simpson indices were not significantly different between crayfish populations (ANOVAs: $P = 0.360$ and $P = 0.454$, respectively; Table VI.3, Fig. VI.4C and VI.4D). The two most important taxa of invertebrates were *Chironomidae* larvae and *Physa* whose abundances were the lowest in presence of SAB-originating crayfish (Fig. VI.4E and VI.4F). However, across all treatments, differences in *Chironomidae* and *Physa* abundances were not significant (ANOVAs: $P = 0.212$ and $P = 0.128$, respectively; Table VI.3). Invertebrate community structure differed marginally significantly between populations (PERMANOVA: $R^2 = 0.32$, $pseudo-F = 1.85$, $P = 0.092$; Fig. VI.5) but with no effect on multivariate dispersion (betadisper: $F = 0.38$, $P = 0.767$; Fig. VI.5).

Table VI.3 Results from the ANOVAs used to test for difference in *Procambarus clarkii* growth rate (specific growth rate [% week⁻¹; square-root transformed], carapace length increment [mm week⁻¹]), invertebrate community (Shannon and Simpson index, *Chironomidae* and *Physa* densities) and ecosystem metrics (macrophyte mass change [% dry mass], decomposition rate [day⁻¹; log₁₀ transformed], community respiration [molC m⁻² 24h⁻¹] and chlorophyll-a [µg L⁻¹], total nitrogen [mg L⁻¹] and phosphorus [µg L⁻¹] concentrations) across four populations of crayfish. Significant *P-values* are depicted in bold.

Response variables	Source of variation	df	Mean square	F value	P
Specific growth rate	Block	3	0.101	0.46	0.715
	Population	3	0.563	2.58	0.118
	Residuals	9	0.218		
Total biomass of crayfish	Block	3	23.47	0.24	0.864
	Population	3	0.90	0.01	0.999
	Residuals	9	96.58		
Shannon index	Block	3	0.017	0.20	0.897
	Population	3	0.105	1.21	0.360
	Residuals	9	0.087		
Simpson index	Block	3	0.002	0.17	0.916
	Population	3	0.012	0.96	0.454
	Residuals	9	0.012		
<i>Chironomidae</i> density	Block	3	3197.7	1.87	0.205
	Population	3	3126.6	1.83	0.212
	Residuals	9	1706.7		
<i>Physa</i> density	Block	3	4049.7	0.76	0.544
	Population	3	13144.7	2.47	0.128
	Residuals	9	5318.6		
Macrophyte mass change	Block	3	267.67	2.22	0.156
	Population	3	382.04	3.17	0.078
	Residuals	9	120.72		
Decomposition rate	Block	3	0.090	2.63	0.114
	Population	3	0.298	8.69	0.005
	Residuals	9	0.034		
Community respiration	Block	3	0.001	5.16	0.024
	Population	3	< 0.001	1.88	0.203
	Residuals	9	< 0.001		
Pelagic autotrophic biomass	Block	3	45.555	0.80	0.525

	Population	3	131.162	2.30	0.146
	Residuals	9	57.038		
Total nitrogen	Block	3	0.178	4.52	0.034
	Population	3	0.040	1.01	0.431
	Residuals	9	0.040		
Total phosphorus	Block	3	59.094	1.57	0.260
	Population	3	48.892	1.31	0.330
	Residuals	9	37.262		

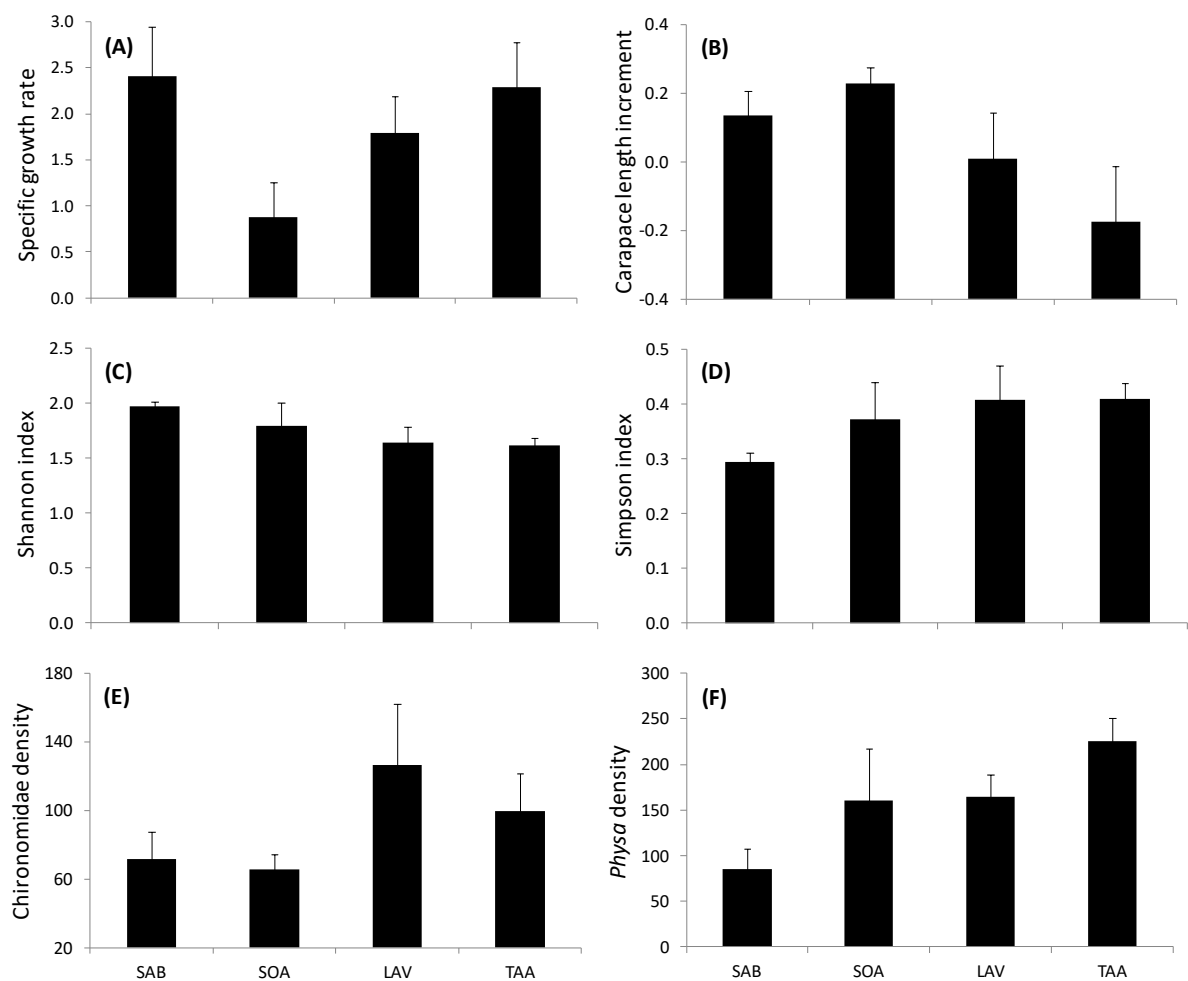


Figure VI.4 Population effects on *Procambarus clarkii* [(A) specific growth rate (% week⁻¹; squared-root transformed) and (B) carapace length increment (mm week⁻¹)] and on invertebrates [(C) Shannon and (D) Simpson diversity indices, (E) density of *Chironomidae* and (F) density of *Physa*]. Different letters indicate significant differences among treatments (Tukey's HSD, $P < 0.05$). Reported values are mean (\pm SE) for all mesocosms containing crayfish ($n = 16$).

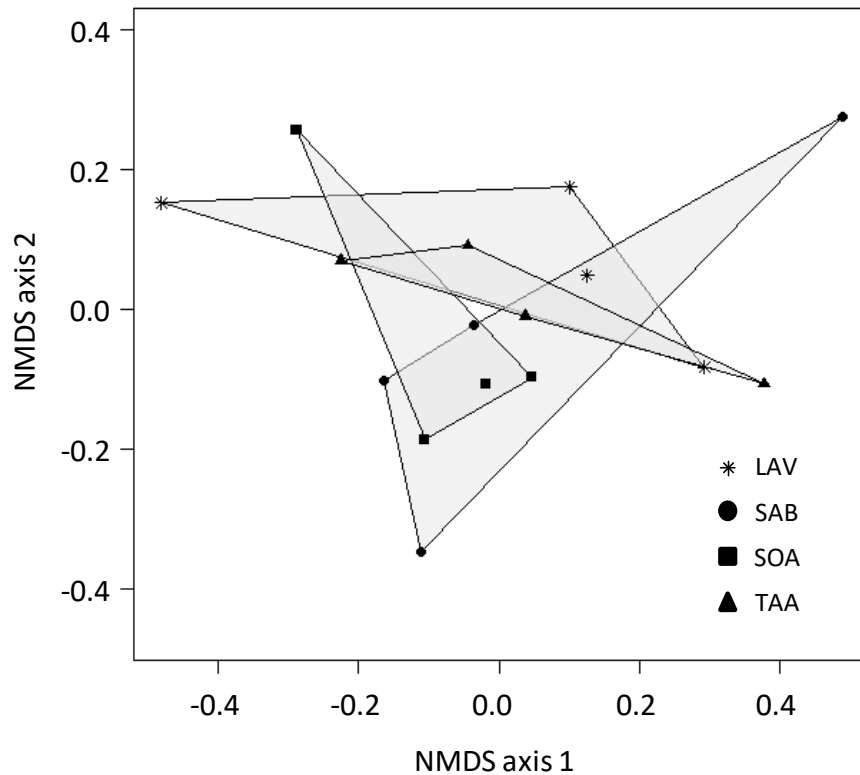


Figure VI.5 Non-metric multidimensional scaling (NMDS) plots of invertebrate community in mesocosms. Symbols represent individual replicates of a population and polygons surround all replicates for a given population. The NMDS stress is 0.11.

VI.3.2.b - *Ecosystem responses*

Macrophyte production, measured through the mass change of macrophytes in the experimental mesocosms, differed marginally between populations (ANOVA: $P = 0.078$; Table VI.3), with TAA population displaying a higher production of macrophytes compared to SAB (Tukey's HSD: $P = 0.092$; Fig. VI.6A). There was a strong and significant effect of populations on the rate of litter decomposition (ANOVA: $P = 0.005$; Table VI.3) with SAB population inducing a higher decomposition rate of organic matter than other populations (Fig. VI.6B). There was, however, no significant difference in term of gross primary productivity (ANOVA: $P = 0.466$; Table VI.3, Fig. VI.6C) and pelagic primary production (ANOVA: $P = 0.146$; Table VI.3, Fig. VI.6D) between populations. Regarding nutrients, there was no significant difference between populations in term of total nitrogen (ANOVA: $P = 0.431$, Table VI.3, Fig. VI.6E) and total phosphorus (ANOVA: $P = 0.330$, Table VI.3, Fig. VI.6F) concentrations.

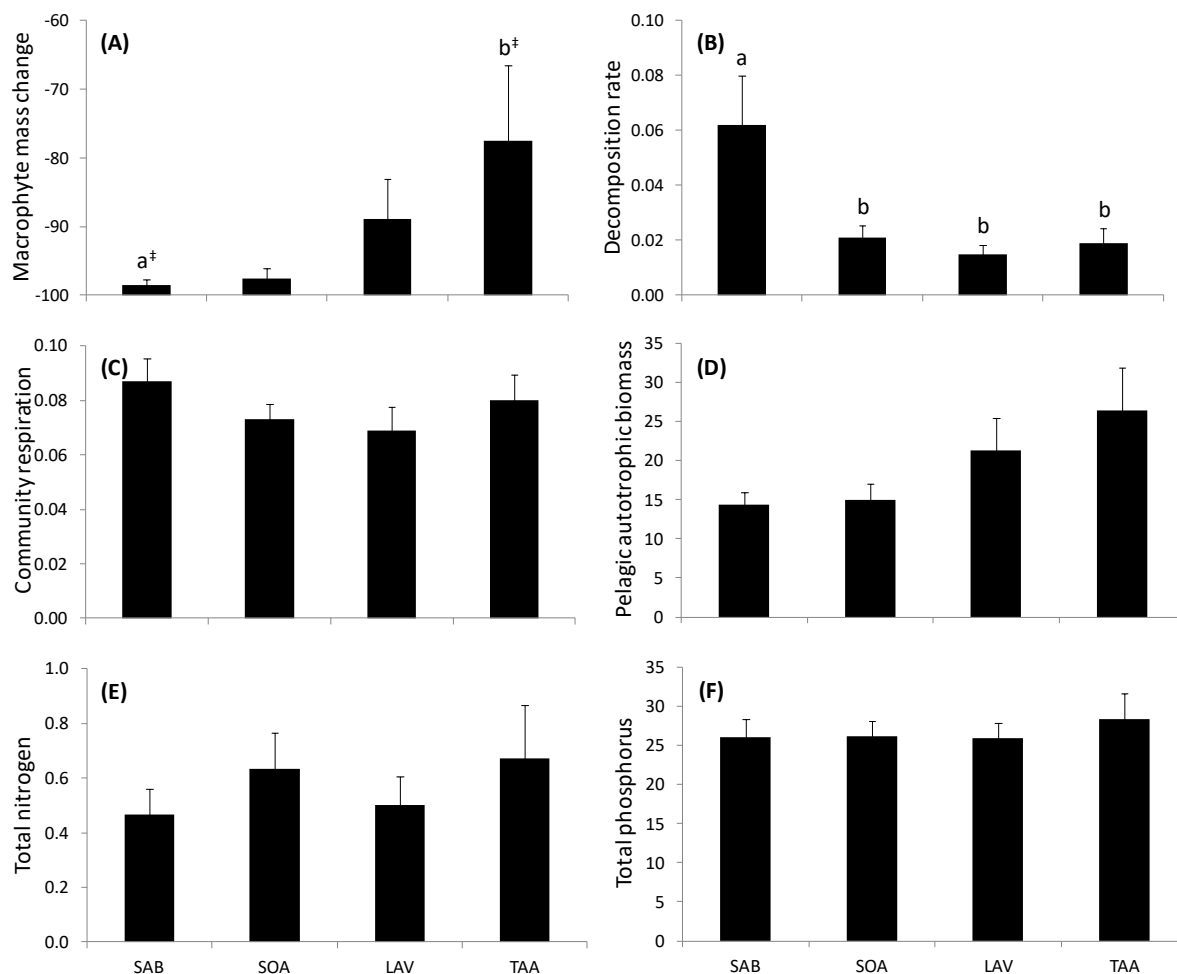


Figure VI.6 Ecological effects on (A) macrophyte mass loss (% dry mass), (B) decomposition rate (day⁻¹; log₁₀ transformed), (C) community respiration (molC m⁻² 24h⁻¹) (D) pelagic autotrophic biomass (chl-a, µg L⁻¹), (E) total nitrogen and (F) total phosphorus concentrations (mg L⁻¹ and µg L⁻¹, respectively)]. Different letters indicate significant differences among treatments (Tukey's HSD, $P < 0.05$). #Indicates marginally significant P values. Reported values are mean (\pm SE) for all mesocosms containing crayfish ($n = 16$).

VI.3.2.c - Impacts of species introduction and inter-population variability

Regarding invertebrates community, the introduction of crayfish significantly decreased the abundance of *Chironomidae* (Contrast test: $P = 0.024$; mean control = 147.75 ± 24.69 SE, mean crayfish = 90.94 ± 11.96 SE) and *Physa* (Contrast test: $P = 0.005$; mean control = 341.50 ± 102.31 SE, mean crayfish = 81.43 ± 20.36 SE). In addition, upper size effects calculated among extreme population responses revealed no significant global effects of inter-population variability on the Shannon and Simpson indexes of invertebrate community (Contrast test: $P = 0.093$ and $P = 0.135$, respectively) but marginally significant effects on the density of both *Chironomidae* and *Physa* (Contrast test: $P = 0.051$ and $P = 0.061$, respectively). Importantly, these effects induced by inter-

population variability were, overall, stronger than those induced by the introduction of crayfish (Fig. VI.7). Regarding ecosystem processes, the effects induced by inter-population variability were equivalent or smaller than those induced by the introduction of crayfish (Fig. VI.7). Specifically, upper size effects revealed overall significant effects of inter-population variability on litter decomposition (Contrast test: $P = 0.003$), community respiration (Contrast test: $P = 0.049$) and on pelagic autotrophic biomass (Contrast test: $P = 0.025$) whose intensities were similar to those induced by crayfish introduction (Fig. VI.7). The introduction of crayfish also induced significant decrease in community respiration (Contrast test: $P = 0.036$; mean control = 0.09 ± 0.003 SE, mean crayfish = 0.08 ± 0.004 SE) while macrophyte mass change (Contrast test: $P < 0.001$; mean control = 40.38 ± 31.23 SE, mean crayfish = -90.62 ± 3.56 SE), pelagic autotrophic biomass (Contrast test: $P = 0.031$; mean control = 5.30 ± 0.18 SE, mean crayfish = 5.67 ± 0.16 SE) and total phosphorus concentration (Contrast test: $P = 0.046$; mean control = 20.95 ± 0.56 SE, mean crayfish = 27.80 ± 1.66 SE) significantly increased. Total nitrogen concentration also marginally significantly increased with crayfish introduction (Contrast test: $P = 0.051$; mean control = 0.34 ± 0.09 SE, mean crayfish = 0.57 ± 0.06).

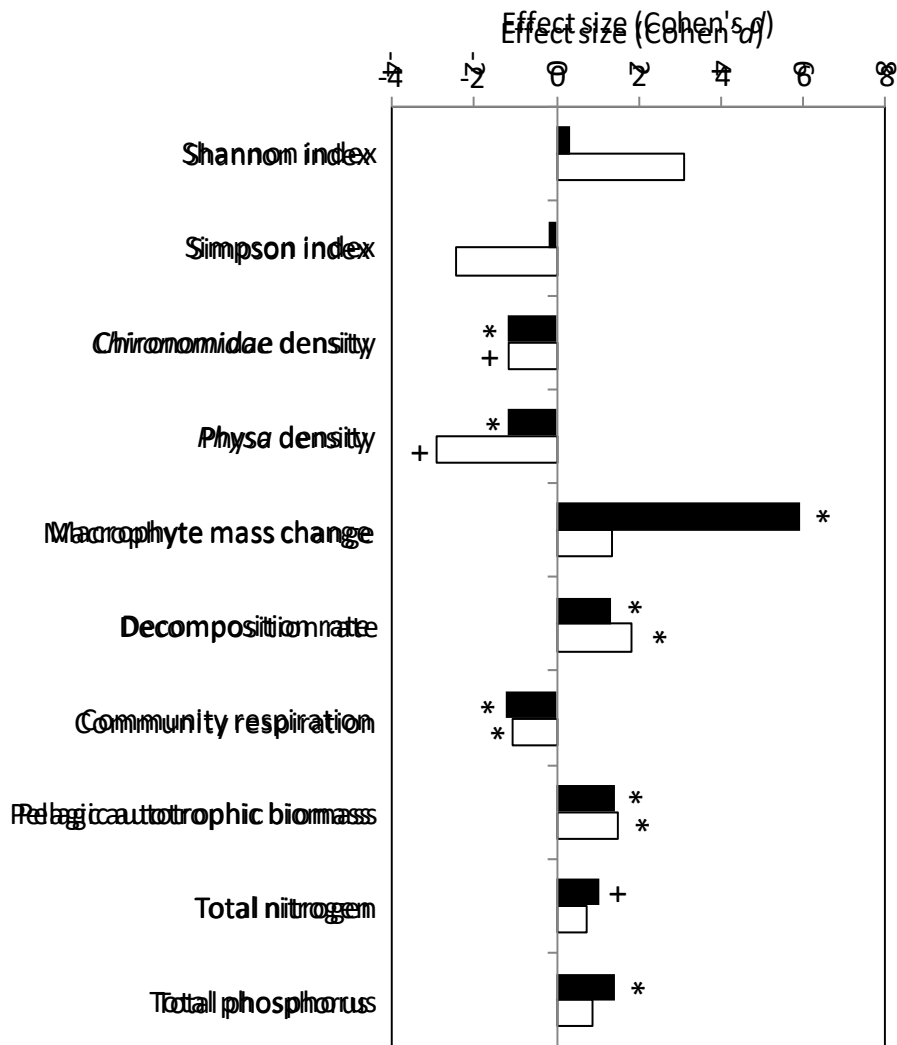


Figure VI.7 Effect sizes (Cohen's d) of the ecological changes induced by *Procamburus clarkii* crayfish introduction (black bars) compared with the upper effects induced by inter-population morphological variability (white bars). Symbols represent significant ($P < 0.05^*$) and marginally significant ($P < 0.06^+$) P -values.

VI.4 - DISCUSSION

Invasive species have been demonstrated to be phenotypically distinct across their invasive range (Huey et al. 2000, Juetten et al. 2014) and such intraspecific variability may produce variable impacts on resident communities and ecosystem properties. In the present study, we first observed that invasive populations of *P. clarkii* morphologically differed and this variability was best predicted by lake productivity. Specifically, individuals inhabiting lakes with high productivity displayed a smaller and narrower body than individuals from less productive lakes. Results from our mesocosm experiment further demonstrated that individuals from morphologically distinct populations can also substantially differ in their ecological impacts on key ecosystem

processes. Litter decomposition rate varied widely between the four crayfish populations tested, presumably as a result of variable rates of litter consumption by crayfish. Finally, our results demonstrated that the ecological effects induced by intraspecific variability in phenotypic traits were stronger at the community level and similar at the ecosystem level than the effects induced by species introduction. This highlighted that phenotypic variability in invasive populations could mediate the extent to which invasive species impact native organisms and recipient ecosystems (Fryxell et al. 2015).

Species typically exhibit phenotypic variations across their geographic range in response to changing environments. Although morphological variations among crayfish populations have previously been documented (Sint et al. 2005, Chybowski et al. 2014), their correlations with environmental conditions have been rarely studied (*but see* Chambers et al. 1979, Etchinson et al. 2012, Perry et al. 2013). In the present study, ecosystem productivity was mainly driven by natural- and human-induced eutrophication and was linked to lake age: older lakes were more productive (Zhao et al. 2016). Major decrease in water transparency (i.e., increased turbidity) in productive and old lakes can reduce visibility for consumers and thus alter foraging behavior (Bartels et al. 2012). Productive lakes in the present study exhibited higher biomass and abundance of predatory fish and increased productivity probably also enhanced the amount of resources such as mobile invertebrates. On this basis, active foragers such as crayfish might shift toward the use of sit-and-wait strategy from the burrow entrance to avoid predation and wait for passing resources, notably leaf litter falling into the water and invertebrates. The development of smaller and narrower body might aid in burrowing activity. However, these results suggested that both colonization history (i.e., time since arrival in the lakes) and environmental conditions could interact in shaping individual morphology. Consequently, the use of genetic tool would be useful to retrace the colonization history of populations and investigate the potential association between genetic and phenotypic variability in invasive populations.

Invasive *P. clarkii* has been widely documented to induce important negative impacts on both invertebrate communities and macrophytes (Twardochleb et al. 2013), and to accelerate detritus decomposition through direct consumption of leaf litter (Alp et al. 2016). Here, the rate of litter decomposition varied over a 4-fold range between populations, with SAB displaying the highest rate of litter decomposition, the lowest

density of invertebrates and the lowest macrophytes cover. However, this likely direct consumptive effect did not alter other ecosystem processes such as primary production and nutrient cycling). Interestingly, SAB was the youngest studied lake and thus was probably colonized later than the other lakes. Although this would require further investigations on a larger geographical scale, the effects of invasive populations may vary depending on population age, with the youngest populations inducing the strongest impacts. When new invaders successfully established in a novel habitat, population size rapidly increase in the first generations following invasions and this would require phenotypic traits that provide access to a large amount of resources (e.g., aggressiveness, foraging activity, metabolic rate) and selection toward r-strategy (e.g., short life, early reproduction, fast growth, high fecundity). Consequently, further studies should investigate the interplay between phenotypic traits (e.g., life-history, behavior, morphological, metabolic and physiological traits; Kern et al. 2016, Metcalfe et al. 2016) and functional effects traits (Raffard et al. *In prep*) that potentially drives intraspecific variability among invasive populations and its temporal dynamic along the different stages of the invasion process.

Ecologists, and particularly those interested in the relationship between biodiversity and ecosystem functioning, have long focused on the importance of biological diversity at the species level, neglecting intraspecific variability (Violle et al. 2012). This study provided novel evidence that the effects intraspecific variability can be stronger than species effects on prey communities and similar at the ecosystem level. In contrast, a recent study demonstrated that the introduction of species had stronger effects than intraspecific variability at both community and ecosystem level (Fryxell et al. 2015) whereas a meta-analysis found that the effects of species introduction and intraspecific variability on ecosystem level were of similar magnitude (Palkovacs et al. 2015). Although these contrasting results highlighted the importance of considering the effects of intraspecific variability, they revealed the complexity of ecological responses and the need to explicitly integrate intraspecific variability in a multiple trait approach across taxa.

Although the concept of intraspecific variability has been demonstrated to influence the effect of species on ecosystem (Harmon et al. 2009, Bassar et al. 2010), its importance in the context of biological invasions has been rarely quantified (*but see* Cucherousset et al. 2012b). Our study suggested that time since invasion and ecosystem

productivity can be a potential driver of phenotypic variability among invasive populations that can subsequently impact the functioning of ecosystem. As ecosystem engineers, *P. clarkii* play a relevant role in the niche construction process by which organisms modify their environment and alter selection pressure acting on future generations (Matthews et al. 2014). Consequently, quantifying the patterns and understanding the ecological consequences of phenotypic variability within invasive species is of particular importance to better appreciate the temporal dynamics of their ecological impacts.

VI.5 - ACKNOWLEDGEMENTS

We are very grateful to Serge Boutes for access to the experiment site, and to Maria Alp, Remy Lassus, Carine Rigolet and Libor Zavoroka for their help during the experiment. Authorizations to perform this study were provided by the “Arrêtés Préfectoraux - 18/09/2015 and 30/10/2015”. This work was supported by the ONEMA (Projet ISOLAC – Convention 13-V5-28) and a PRES-Toulouse grant (Inva_Eco_Evo_Lac). CE and JC are part of EDB, part of the French Laboratory of Excellence project "TULIP" (ANR-10-LABX.41; ANR-11-IDEX-0002-02).

Resource composition mediates the effects of intraspecific variability on ecosystem processes

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Adapted from an article under review in Oikos

Key-words nutrient excretion, trophic specialization, resource quality, ecosystem functioning, indirect effects

Résumé

Alors que l'existence de variabilité entre les niches trophiques des individus au sein des populations et ses conséquences directes sont de plus en plus couramment reconnues dans la littérature, ses effets indirects potentiels sur les processus écosystémiques demeurent mal connus. Dans cette étude, nous avons dans un premier temps quantifier le degré de variabilité trophique dans 11 populations de perche soleil *Lepomis gibbosus*, un poisson omnivore. Les résultats issus des analyses des contenus stomacaux et des analyses des isotopes stables ont révélé que le degré de spécialisation trophique ainsi que la position trophique étaient fortement variables au sein de ces populations. Plus particulièrement, la position trophique variait de plus de un niveau trophique au sein des populations, suggérant que les individus consommaient une large gamme de ressources végétales et animales. Nous avons ensuite évalué expérimentalement si la variabilité trophique intraspécifique modulait les effets du recyclage des nutriments par les consommateurs sur certains processus de l'écosystème. Ceci a été réalisé en manipulant la variabilité trophique intraspécifique à travers des changements du degré de spécialisation (spécialistes, intermédiaires et généralistes) et en utilisant trois types de ressources variant en terme de qualité (matière végétale, macroinvertébré et chair de poisson). Ces différents types de ressources ont été utilisées individuellement (individus spécialistes) ou en combinaison (individus intermédiaires et généralistes), conduisant ainsi à la mise en place de sept traitements expérimentaux. Les résultats indiquaient que les différences entre individus de taux de croissance et d'excrétion en azote étaient d'avantage liées à la composition du régime alimentaire plutôt qu'au degré de spécialisation trophique, et augmentait avec la position trophique de la ressource consommée. Nous avons ensuite utilisé des microcosmes dans lesquels ont été ajoutés les produits d'excrétion des individus. Nous avons montré que des fonctions primordiales de l'écosystème, telles que la production primaire et la respiration, étaient affectées par la variabilité des produits d'excrétions. Aussi, nos résultats ont démontré ces effets étaient dépendants de la masse des individus, elle-même affectée par les traitements alimentaires. Ces résultats mettent en évidence l'importance de l'interaction entre la niche trophique des individus et leur recyclage des nutriments dans la modulation via des effets indirects des processus écosystémiques.

Abstract

Despite the growing evidence for individual variation in trophic niche within populations, its potential indirect effects on ecosystem processes remains poorly understood. Here, we first quantified the level of intraspecific trophic variability in 11 wild populations of the omnivorous fish *Lepomis gibbosus*. Outputs from stomach and stable isotopes analyses revealed that the degree of trophic specialization and trophic positions were highly variable within these wild populations. There was intrapopulation variation in trophic position of more than one trophic level, suggesting that individuals consumed a range of plant and animal material. We then experimentally assessed how intraspecific trophic variability modulates consumer-mediated nutrient effects on relevant processes of ecosystem functioning. This was completed by manipulating intraspecific trophic variability through changes in the degree of specialization (i.e., specialist, intermediate and generalist) and using three food sources varying in nutrient quality (e.g., plant material, macro-invertebrate and fish meat). Food items were used individually (specialist individuals) or in combination (intermediate and generalist individuals) leading to the use of seven dietary experimental treatments. Results indicated that intraspecific variability in growth and nitrogen excretion rates were more related to the composition of the diet rather than the degree of specialization, and increased with the trophic position of the diet consumed. In contrast, phosphorous excretion rates did not change in accordance with these variables. We subsequently used microcosms in which excretory products were introduced and showed that critical ecosystem functions, such as primary production and community respiration, were affected by the variability in excretory products caused by the manipulation of intraspecific trophic variability, and this effect was biomass-dependent. These results highlight the importance of the interaction between individual trophic niche and consumer-mediated nutrient recycling in modulating ecosystem processes.

VII.1 - INTRODUCTION

Within populations, individual can vary in their trophic niche through specialization (e.g., Bolnick et al. 2003), which can have strong consequences for population dynamics and community structure (Araújo et al. 2011). Intraspecific trophic variability can also alter the extent to which and how species influence ecosystem functioning (Harmon et al. 2009), but the mechanisms underpinning these changes remain relatively unknown. Usually, consumers can exert top-down control through resource consumption, potentially causing cascading effects to lower trophic levels via density-mediated interactions (Pace et al. 1999). Concomitantly, they selectively sequester consumed nutrients into their body to meet their requirements for growth and reproduction (Sterner & Elser 2002). Excess nutrients and metabolic by-products are then released via excretion and egestion, potentially enhancing the "bottom-up" control of ecosystem processes (Glaholt & Vanni 2005, Knoll et al. 2009). As a consequence, consumer-mediated nutrient recycling is essential in the ecological dynamic of many ecosystems, and predicting patterns of variation in excretion rate appears relevant to better appreciate the effects of consumers on ecosystem functioning.

Early studies on consumer-mediated nutrient recycling have emphasized the role of interspecific variations and revealed disproportionate roles of nutrient recycling relative to species biomass within the system and nutrient imbalance between consumers and their resources (McIntyre et al. 2007, Small et al. 2011, Vanni et al. 2002). Recently, mounting evidence highlighted the existence of high variations in excretion rates among conspecific individuals (Villéger et al. 2012, El-Sabaawi et al. 2015a), with this potentially affecting ecosystem processes (Bassar et al. 2010, Taylor et al. 2012, El-Sabaawi et al. 2015b). However, the causes of such intraspecific variability in excretion rates remain difficult to predict, since some field-based studies found inconsistent results (Torres & Vanni 2007, McManamay et al. 2011, Vrede et al. 2011). This can probably due to the difficulty of characterizing the diet consumed in the wild, especially when individuals display trophic niche divergence (e.g., Bolnick et al. 2003). Intraspecific trophic variability may create variations in nutrient excretion rates of consumers by acting on both the degree of specialization and the quality of the resource consumed, which the two factors potentially interacting. Indeed, specialist individuals, by foraging on a single prey resource, should display strongest nutrient imbalance with

their resources compared to generalists (Frost et al. 2005). Therefore, they should excrete nutrient at higher or lower rates, depending on the quality of the resource consumed, with individual specialized on nutrient-rich resource expected to release nutrient at higher rate (Sterner & Elser 2002). In addition, individual specialists are also predicted to have superior fitness than generalists (Bolnick et al. 2003). Alternatively, generalists might maximize their fitness by foraging on a resource assemblage made of nutritionally complementary resources (DeMott 1998). Therefore, synergistic or antagonistic effects of diet mixing may affect consumer's traits, highlighting the need to quantify how intraspecific trophic variability affect consumer performance and nutrient excretion rates, in order to predict the magnitude of their potential effects on ecosystems processes.

Fishes are important regulators of the trophic dynamics of freshwater ecosystems, due to their excretion of potentially limiting nutrients which are essential to support primary producers and heterotrophic microbes (Small et al. 2011, Capps & Flecker 2013b). In addition, fishes are relevant examples of intraspecific trophic variability (Smith & Skulason 1996, Bolnick et al. 2003), with individuals within populations often exhibiting a diversity of dietary strategies, from generalist to specialist (Quevedo et al. 2009, Svanbäck et al. 2015). Fish diet composition also varies considerably across trophic levels, ranging from herbivores consuming plant and algal detritus to apex-predators consuming vertebrates, and including omnivores that consume both, potentially resulting in marked differences in nutrient excretion rates between these groups. For instance, intraspecific variability in nutrient excretion rates can occur during ontogeny, with ontogenetic dietary shift being potentially important in determining nutrient excretion rates (Pilati & Vanni 2007). In entirety, this highlights the requirement to account for intraspecific trophic variability to better appreciate how fish mediate nutrient recycling, ultimately affecting the functioning of aquatic ecosystems.

The aim of our study was to quantify the effects of intraspecific trophic variability on consumer-mediated nutrient recycling and determine its potential consequences for relevant ecosystem processes. Using field and experimental approaches, we selected the omnivorous fish *Lepomis gibbosus* (Linnaeus, 1758) as model species since it is an opportunistic omnivore that varies in its intensity of feeding on animals (e.g., macro-invertebrates and fish) (García-Berthou & Moreno-Amich 2000b, Rezsú & Specziar

2006) and plant materials (e.g., algae, macrophytes, wind-spread terrestrial seeds and detritus) and displays a high level of intraspecific trophic variability (McCairns & Fox 2004, Bhagat et al. 2011). We completed the present study in three parts. First, we conducted an initial comparative field approach to quantify the extent of intraspecific trophic variability within 11 wild *L. gibbosus* populations using stomach content and stable isotope analyses (SCA and SIA, respectively). We predicted that the degree of trophic specialization would vary within populations and individuals would display variable trophic positions, demonstrating that they forage on resources of different quality. We then conducted an aquaria based experiment to evaluate the prediction that intraspecific trophic variability would change the excretion rates of nutrients. We hypothesized that, independently of the diet quality, high level of specialization would lead to higher range of nutrient excretion rates within a population, given that diet diversity enables generalist individuals to cope better with nutrient imbalance than specialists (Frost et al. 2005). We also hypothesized that individuals feeding on nutrient-rich resource would excrete more nutrients (Sterner and Elser 2002, McIntyre & Flecker 2010). Finally, we used a microcosm experiment to quantify how increased nutrient availability through consumer recycling could subsequently affect important ecosystem processes, as *in-situ* measurements of these processes in wild are inherently difficult. Specifically, we hypothesized that the variation in the observed nutrient excretion rate would trigger changes in relevant processes such as litter decomposition and primary production. However, because decomposers are better competitors for nutrient resources than producers (Currie & Kalff 1984), we also hypothesized that the effects of nutrient availability would differ between heterotroph and autotroph organisms and the associated ecosystem processes.

VII.2 - MATERIAL & METHODS

VII.2.1 - *Field survey*

To assess intraspecific variability in the trophic niches of *L. gibbosus*, populations were sampled from 11 lakes that were former gravel pits in the flood plain of the Garonne River (Zhao et al. 2016). Sampling was completed between mid-September and mid-October 2012 by electrofishing along the littoral shoreline (Evangelista et al. 2015). To reduce biases between lakes in SCA related to the feeding period of consumers, one lake

was sampled per day and electrofishing was conducted during the same period of time in each lake (between 1:00 to 3:30 pm). Captured individuals were immediately euthanized using an overdose of anaesthetic, stored on ice and frozen in the laboratory (-20°C) until subsequent processing. After defrosting, a subsample of 28 adult individuals (mean fork length = 79.0 mm \pm 1.4 SE) was selected in each population when available (mean = 27.6 \pm 1.2 individuals per population; Table VII.1), measured for fork length (FL \pm 1 mm) and weighted (W \pm 0.1 g). Stomach contents were dissected under a microscope and prey items were counted and identified to the lowest taxonomic level (mostly family level). A total of 70 prey taxa were found, including numerous invertebrate families and eggs. To assist analysis, within orders, several families were grouped into similar morphotype groups (aquatic larvae, emergent invertebrates or terrestrial invertebrates) and ultimately provided 29 prey categories for SCA. Importantly, although present in stomach contents, plant debris (i.e., wind-spread seeds, algae, terrestrial detritus) could not be counted and were thus excluded from SCA. Stomach contents data provide information on prey taxonomy but have limitations mainly because they constitute only a snapshot of the diet (several hours) and can underestimate the consumption of highly digestible prey. Consequently, SIA were performed on the same individuals to assess trophic variability over a longer time period than SCA (Layman et al. 2012). Specifically, white dorsal muscle samples were collected for stable isotope analyses of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) which depict the origin of the resource consumed (e.g., littoral versus pelagic) and the trophic position of the consumers, respectively (Post 2002). Additionally, putative prey resources from the littoral and pelagic habitats of the lakes were collected at the same time as fish sampling. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of littoral prey consisted of mean values of the most common invertebrates sampled in the littoral habitat with a pond net (Chironomidae, Ephemeroptera, Gastropoda, Assellidae and Oligochaeta; n = 1 to 4 samples per lake; n = 1 to 6 individuals per sample). Isotope analyses for Gastropoda were performed on the soft muscle tissue. Stable isotope values of pelagic prey were obtained from zooplankton and Chironomidae samples (n = 3 - 4 samples per lake; n = 2 - 3 chironomids per sample) collected in the pelagic habitat with a 100- μm mesh net and an Ekman dredge, respectively. Prior to all analyses, stable isotope samples were oven dried (48h at 60°C), ground in a fine powder and then analyzed at the Cornell Isotope Laboratory (COIL, Ithaca, New York, USA). The analytical precision for all samples,

calculated as the standard deviation of an internal Mink standard, was 0.11 and 0.12 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Since the C:N ratio of prey (littoral prey : mean = 4.60 ± 0.10 SE; pelagic prey : mean = 4.15 ± 0.12 SE) were higher than the suggested limits (3.5 for aquatic organisms; Post et al. 2007), the stable isotope values of prey were lipid-corrected before subsequent analyses (*see details below*, Fig. VII.2).

VII.2.2 - Experimental approaches

VII.2.2.a - Collection and rearing conditions

Based on the field results, *L. gibbosus* were collected from a single lake (area = 20.8 ha, mean depth = 3.7 m) whose trophic outputs indicated an intermediate level of trophic specialization and a relatively large spectrum of prey consumed. On October 3rd 2013, 81 individuals (FL: 65 to 75 mm) were captured in the littoral habitat using a seine net (5-mm mesh size) and then acclimated to laboratory conditions in three tanks (200 L, photoperiod: 12/12 h; water temperature: 17 to 18.5 °C). During the 6-week acclimation period, individuals were fed *ad libitum* with commercial red maggots (*Diptera*) until the beginning of the experiment to minimize background variability in body elemental composition. At mid-acclimation period, *L. gibbosus* were anaesthetized with eugenol (0.1 mL.L^{-1}), measured for initial fork length ($\text{FL}_i \pm 1 \text{ mm}$), weighed ($W_i \pm 0.1 \text{ g}$), individually tagged with passive integrated transponder (FDX PIT-tags, Oregon RFID, Portland, Oregon), and released into the 200 L-tanks after recovery in well-aerated water. At the end of the acclimation period, 48 individuals belonging to the same cohort to limit the potential effect of ontogeny (FL_i ranging from 79 to 98 mm, mean = 89.0 ± 0.8 SE; age 1 and age 2 individuals) were selected and transferred individually to a total of 48 tanks filled with 50-L of dechlorinated tap water. Each tank was equipped with a filtration system, a plastic plant and a shelter. The 48 experimental units were dispatched in 6 vertical shelving units (blocks).

VII.2.2.b - Effects of intraspecific trophic variability on nutrient recycling rates

During the laboratory experiment (9 weeks), fish were provided with one of three diets comprising of one, two, or three food items in order to simulate three levels of decreasing trophic specialization. Indices were developed to calculate individual trophic specialization using the population's total diet to define resource availability, involving

that individuals are compared to their population niche rather than to the food availability (Bolnick et al. 2002). Trophic specialization was calculated here as the diet overlap between an individual i and all individuals used in the experiment (i.e., the population) using the proportional similarity index PS_i calculated following Bolnick et al. (2002):

$$PS_i = \sum \min (p_{ij}, q_j)$$

where p_{ij} is the frequency of the prey type j in the diet of individual i , and q_j is the frequency of the prey type in the overall diet distribution of the population. PS_i varied from 0 (when individual forages on resources that were scarcely used in the population, i.e., specialist individual) to 1 (when the individual consumes resources in the same proportion as the entire population, i.e., generalist individual). PS_i were calculated using the RInSp package (Zaccarelli et al. 2013). For each *L. gibbosus*, the counts of prey items was converted to proportions and averaged across all individuals for each resource (Bolnick et al. 2002). The significance of PS_i was evaluated using resampling methods based on Monte Carlo procedures (using 10 000 replicates). Here, PS_i ranged from 0.33 for specialist individuals and 0.99 for generalist individuals, and the PS_i of intermediate individuals was 0.66 (Fig. VII.1). The items represented vegetable matter (cooked white rice [R]), macro-invertebrates (chironomid larvae [C]) and fish (grounded rainbow trout dorsal muscle with skin [F]). These items were used as they represented the three different reported trophic levels of *L. gibbosus* prey (García-Berthou & Moreno-Amich 2000b) and cover a broad range of elemental composition (Fig. VII.1). White rice was selected as a plant-based source because it is readily available in a standardized size and quality and could mimic the quality of plant seeds and angling bait that are consumed by *L. gibbosus*. Rice was cooked to obtain a texture similar to the texture of plant seeds and angling bait after they have spent several days in water. Where mixtures of two and three items were used as the diet, their total wet mass partitioned equally among the items. The diets were hand-fed to *L. gibbosus* using a daily ration of 3% of individual initial body mass (Glaholt & Vanni 2005). Mixed diets (i.e., intermediate and generalist) were homogenized to reduce potential bias towards the consumption of potential preferred item(s).

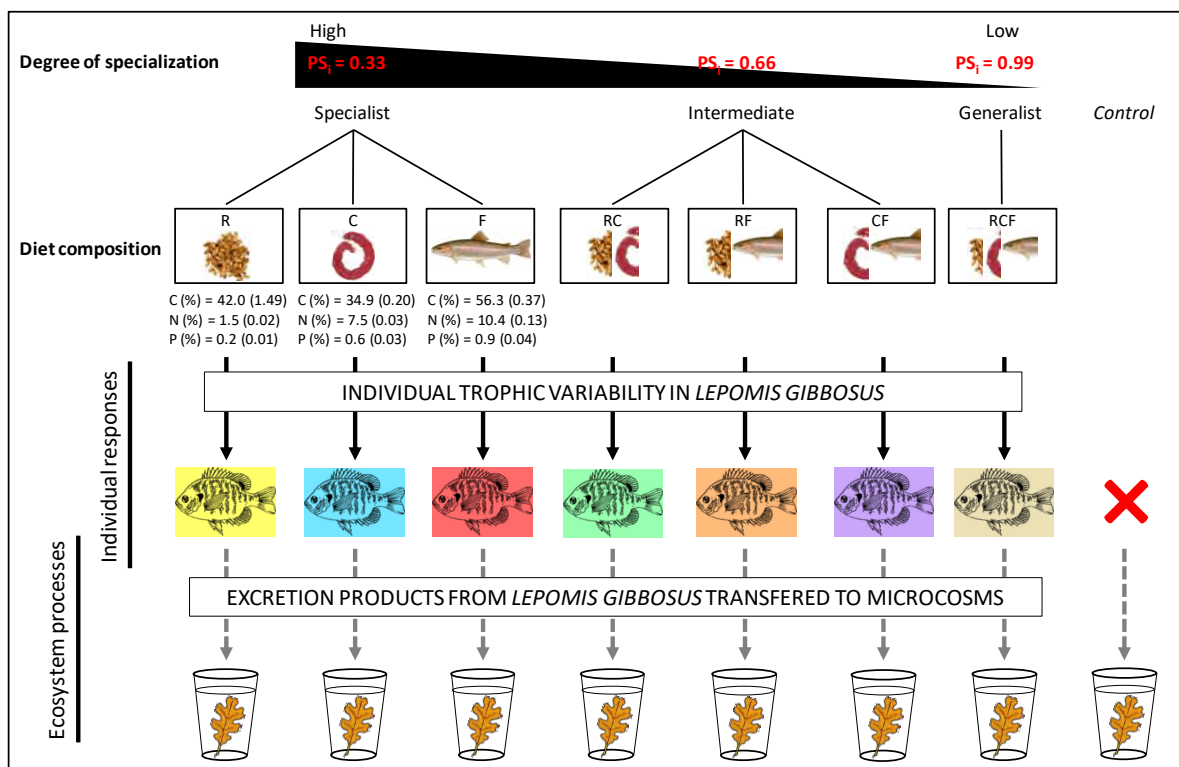


Figure VII.1 Schematic representation of the experimental design used to test the indirect effects (i.e., through nutrient recycling) of intraspecific trophic variability on individuals and ecosystem functioning. Trophic variability was manipulated with diet elemental composition nested within degree of specialization. Replicated treatments were dispatched in 6 vertical shelving units (blocks). The degree of individual trophic specialization (PS_i) was 0.33, 0.66 and 0.99 for specialist, intermediate and generalist treatments, respectively. Abbreviations: R: cooked rice; C: chironomid larvae; F: fish meat.

The experimental design composed of seven treatments (Fig. VII.1): three types of specialists feeding on a single diet item (cooked rice [R], chironomid larvae [C] or fish meat [F]), three types of intermediates feeding on a mixture of two diet items (cooked rice × chironomid larvae [RC], cooked rice × fish meat [RF] or chironomid larvae × fish meat [CF]), and one generalist type feeding on an even mixture of all the diet items (cooked rice × chironomid larvae × fish meat [RCF]). There were six replicates for each specialist and intermediate treatments, and twelve replicates for the generalist treatment to fully account for higher variability in the mixture. Individuals *L. gibbosus* placed in individual tank were randomly assigned to each treatment and there was no significant difference in both mean W_i and FL_i (ANOVAs, $P = 0.178$ and $P = 0.065$, respectively) between treatments at the start of the experiment.

Ammonium ($N-NH_4^+$, hereafter referred to as N) and soluble reactive phosphorus (SRP, hereafter referred to as P) excretion rates of *L. gibbosus* were quantified at the beginning of the experiment, just prior to the individuals being transferred in their experimental tanks (November 15th 2013) and at the end of the experiment (January

16th 2014). Specifically, *per capita* excretion rates (hereafter referred to as ‘excretion rate’; $\mu\text{mol ind.}^{-1} \text{ h}^{-1}$) were quantified, as per Vanni et al. (2002). Specifically, two hours after feeding (Glaholt & Vanni 2005), *L. gibbosus* were placed individually into a translucent plastic bag containing 0.8 L of spring water and stored in a covered bucket to minimize visual contact and reduce physiological stress during incubation (Whiles et al. 2009). The spring water was low in soluble N and P but had similar chemical characteristics, especially pH, to the water used in the experiments. An incubation time of 1h30 was used to ensure concentrations of ammonium and phosphorus in the water were above quantification levels (Glaholt & Vanni 2005). Filtered water samples (80 mL filtered using Whatman GF/C, pore size 1.2 μm) were analyzed for ammonium (N-NH_4^+ , hereafter referred to as N) and soluble reactive phosphorus (SRP, hereafter referred to as P) concentrations using the phenol-hypochlorite and molybdenum blue methods, respectively, run by an automated continuous-flow colorimetric analyzer (ALPKEM Corporation, Clackamas, OR, U.S.A.). *Per capita* excretion rates (ER; hereafter referred to as ‘excretion rate’) of N and P ($\mu\text{mol ind.}^{-1} \text{ h}^{-1}$) were calculated for each individual following Vanni et al. (2002):

$$\text{ER}_i = (([I]_{\text{ind}} - [I]_{\text{control}}) \times V) / t$$

where $[I]_{\text{ind}}$ and $[I]_{\text{control}}$ are the molar concentration ($\mu\text{mol L}^{-1}$) of the element I observed for fish and control, respectively, V is the volume (L) of spring bottled water in the plastic bag and t is the duration of the incubation (hours). At the start of the experiment, initial *per capita* excretion rates did not differ significantly between treatments (ANOVAs, $P = 0.154$ for N and $P = 0.341$ for P). Importantly, for each block, one control bag filled with bottled water but without fish was used to assess background levels of ammonium and phosphorus at the end of the excretion trials. At the end of the experiment, after the final excretion trial, *L. gibbosus* were euthanized using an overdose of anesthetic and weighted ($W_f \pm 0.1 \text{ g}$). Specific growth rate (SGR; $\% \text{ week}^{-1}$) during the experiment was calculated as follows:

$$\text{SGR} = 100 \times (\ln W_f - \ln W_i) / t$$

where t is the duration of the experiment (9 weeks).

VII.2.2.c - *Effects of consumer-mediated nutrient recycling on ecosystem processes*

Laboratory microcosms were then used to assess the indirect effects of intraspecific trophic variability on aquatic ecosystem processes through changes in fish-mediated nutrient recycling. Microcosms were used to mimic relevant processes occurring in the benthic littoral zone occupied by *L. gibbosus* in the wild, given that the ability to measure these processes *in-situ* is inherently challenging. Microcosms (n = 54, 48 for each experimental individual and 6 for each control) consisted of one-liter cylindrical containers initially filled with 0.25 L of dechlorinated water and initiated with 0.5 L unfiltered lake water containing an inoculum of autotrophic and heterotrophic microorganisms. They were supplied with oak (*Quercus robur* L.) leaf litter collected at abscission and cut into leaf discs of 15 mm diameter using a cork borer. Each microcosm received a set of 10 leaf discs that were previously weighed to the nearest 0.1 mg (mean = 0.1648 g ± 0.0004 SE). Microbial communities were allowed to develop from November 7th to 22th 2013 before the microcosms were gently emptied until 0.1 L left, avoiding losing particulate matter that remained on the bottom of the microcosm. Microcosms were then immediately supplied with 0.8 L of water containing fish excretory products (or clean spring water for controls) from fish excretion trials realized on November 22th 2013. Microcosm water was renewed on three more occasions, spaced two weeks apart, and followed the same procedure as described above until the end of the experiment (54 days; total of 4 additions). Microcosms were exposed to a 12 h light : 12 h dark photoperiod (mean instantaneous light intensity = 252.1 μmol m⁻² s⁻¹ ± 10.3 SE) at the laboratory temperature (17.0 - 18.5°C). They were assigned to the 48 experimental individuals and replicates were arranged in six blocks, corresponding to the level and the side (left or right) of a three-shelf unit.

Whole-microcosm metabolism, the standing biomass of algae and leaf-decaying fungi, litter mass loss rate and particulate nutrient concentration were assessed at the end of the experiment. The side of each microcosm was gently brushed to remove the biofilm, content was homogenized with blender and 0.06 L of water was filtered onto a Whatman GF/C filter. Filters were then oven-dried (60°C for 48h) and used to quantify the amounts of particulate nutrients (N and P; μmol) following the protocol previously described for fish excretion. Gross primary productivity (GPP) and community respiration (CR) were quantified using diurnal changes in oxygen levels (following

Harmon et al. 2009). Dissolved oxygen (DO) was measured right after the light was switched on (t_0 , sunrise), and after 12 h (t_1 , sunset) and 24 h (t_2 , following sunrise) to capture day-time and night-time variations. Daily CR and GPP (mg O_2) was calculated as follows:

$$\text{CR} = (\text{DO}_{t_1 - t_2}) \times 2 \times V \text{ and } \text{GPP} = (\text{CR} + \text{DO}_{t_1 - t_0}) \times V$$

where V was the volume of water in microcosms (0.9 L). Total algal standing biomass (μg) was assessed based on the chlorophyll-a concentration and a subsample of 0.1 L of homogenized water was filtered onto a Whatman GF/F filter (pore size $0.45 \mu\text{m}$) stored in the dark at -20°C until analysis. Chlorophyll-a was extracted in 90% acetone for 24h and its concentration was determined with a spectrophotometer (HITACHI U-1100) following Steinman et al. (2006). Before quantifying algal biomass, the leaf discs were gently removed from the microcosms, washed with deionized water, and freeze-dried to estimate the final litter mass. The remaining leaf material was coarsely crushed and an aliquot (mean = $0.0216 \text{ g} \pm 0.0001 \text{ SE}$) was used to determine the ergosterol content in the leaf litter as a surrogate of fungal biomass (mg g^{-1} of litter). Ergosterol was determined using high-performance lipid chromatography and was converted into dry mass using a factor of 182 (Gessner & Chauvet 1993). The rate of litter decomposition (k in day^{-1}) was calculated as follows:

$$k = -\ln (M_f / M_i) / t$$

where M_f and M_i are the final and initial freeze-dried mass of leaf litter remaining in the microcosm, respectively, and t is the duration of the microcosm experiment (54 days).

VII.2.3 - Statistical analyses

VII.2.3.a - Intraspecific trophic variability in wild populations

To ensure long-term comparisons of diet variability between and within populations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each *L. gibbosus* were used to calculate a measure of trophic position (TP) and the corrected carbon isotope ratio ($\delta^{13}\text{C}_{\text{cor}}$) adjusted for between-population variation in isotopic baseline following Post (2002):

$$\text{TP} = \lambda_{\text{base}} + (\delta^{15}\text{N}_{\text{ind}} - [\delta^{15}\text{N}_{\text{lit}} \times \delta^{13}\text{C}_{\text{cor}} + \delta^{15}\text{N}_{\text{pel}} \times (1 - \delta^{13}\text{C}_{\text{cor}})]) / \Delta_{\text{N}}$$

$$\delta^{13}\text{C}_{\text{cor}} = (\delta^{13}\text{C}_{\text{ind}} - \delta^{13}\text{C}_{\text{pel}}) / (\delta^{13}\text{C}_{\text{lit}} - \delta^{13}\text{C}_{\text{pel}})$$

where λ_{base} is the trophic position of the littoral and pelagic baseline ($\lambda_{\text{base}} = 2$), $\delta^{15}\text{N}_{\text{ind}}$ is the stable isotope value of the *L. gibbosus*, $\delta^{15}\text{X}_{\text{lit}}$ and $\delta^{15}\text{X}_{\text{pel}}$ are the stable isotope values of the littoral and pelagic baselines and Δ_{N} is the trophic enrichment factor obtained

from previous studies ($\Delta_N = 3.4$; Post 2002). Using these baseline-corrected isotope values, the size of the isotopic niche of each population was calculated using Bayesian standard ellipse area (SEA_b , ‰², 10 000 simulations) using Stable Isotope Bayesian Ellipse in R (SIBER; Jackson et al. 2011).

Based on SCA, PS_i was calculated as the diet overlap between an individual i and its population. The overall degree of individual specialization (IS) in each population was then determined as the average PS_i of all individuals (Bolnick et al. 2002). For the sake of clarity, the index $V = 1 - IS$ was used in the present study, with values closer to 1 indicating a high level of trophic specialization in the population. Significant differences in the level of specialization between wild populations were tested using Kruskal-Wallis test. Generalized linear mixed-effects model was used to test for the effect of body size on diet variation with PS_i and FL used as independent and dependent variables, respectively. Model specified a binomial family with a logistic link function and site as random factor.

VII.2.3.b - Effects of intraspecific trophic variability on nutrient recycling rates

Nested analysis of variance was used to assess independent effects of trophic specialization (i.e., the number of food items supplied to fish) and diet composition (i.e., the identity of each component food items) on growth and fish excretion rates. Because excretion rates are a function of size, allometry was integrated into the analyses of nutrient excretion rates by dividing *per capita* excretion rates by W_f raised to the $\frac{3}{4}$ power (mass-normalized *per capita* excretion rates; $\mu\text{mol g}^{-1} \text{h}^{-1}$; Torres & Vanni 2007). Diet composition was specified as a random factor and was thus the correct error term for testing the effect of trophic specialization (Quinn & Keough 2002). Tukey's post-hoc test was used to determine which pairs of treatments significantly differ. Non-additive effects of diet mixing on response variables were evaluated through a comparison of the observed versus expected values using one-sample paired t-test. Specifically, for each mixed-diet treatment (3 intermediates and 1 generalist), the expected value was calculated as the mean value of specialist fish fed with either one of the food items. Given the multiplicity of comparisons involved, the false discovery rate (FDR; Benjamini & Hochberg 1995) procedure was applied to correct for alpha inflation using the *p.adjust* function. The significant results after the FDR procedure are reported.

VII.2.3.c - Effects of consumer-mediated nutrient recycling on ecosystem processes

The general effects of the presence of excretory products on ecosystem processes were evaluated by comparing nutrient-less (i.e., control) with all treatments that contained fish excretory products using t-tests. Linear models were used to examine effects of amounts of excretory products (*per capita* N and P excretion rates) on ecosystem processes measured in the microcosms (i.e., particulate nutrient content, gross primary productivity, community respiration, algal standing biomass, fungal biomass on leaves and litter decomposition rates). To assess the mass dependence of nutrient excretion effects on ecosystem processes, linear models were also performed with mass-normalized *per capita* excretion rates and ecosystem processes as independent and dependent variables, respectively. Linear models were built with a block effect as covariate to control for potential variation in the experimental set-up. The assumption of homoscedasticity and the normality of the residuals were checked graphically using Tukey Ascombe and Q-Q plots, respectively. Prior to all statistical analyses, nutrient excretion rates and fungal biomass were \log_{10} transformed and growth rate was square-root transformed. Highly influential data points were identified by the Cook's distance (D_i) plot and values were considered as critical for $D_i > 4/N$, where N is the number of observations (Bollen & Jackman 1990). Critical values were removed from the dataset prior the model was refitted. All statistical analyses were performed using R v.3.1.2 (R Development Core Team 2013).

VII.3 - RESULTS

VII.3.1 - Intraspecific trophic variability in wild populations

Stable isotope niche size (SEA_b , mean = 0.33 ± 0.02 SE) varied over a 2-fold factor between populations, ranging from 0.25 up to 0.48 ‰^2 (Table VII.1, Fig. VII.2), indicating that variations in trophic niche across populations were consistent over time. Within-populations, SIA also indicated relatively high variability in trophic position, with the range of trophic position reaching more than one trophic level in several cases (mean TP = 3.37 ± 0.06 SE, mean within-population range = 1.32 ± 0.05 SE; Table VII.1, Fig. VII.3A). These results suggested that individuals of *L. gibbosus* could forage across a wide range of resources with different trophic positions (i.e., from primary producer to

secondary consumer) because organisms feeding exclusively on invertebrates would have a trophic position of 3.

Table VII.1 Mean value (\pm 95% CI or \pm SE) and range of trophic niche (SEA_b), trophic position (TP) and individual specialization (PS_i) in each studied wild population (n = 11).

Lake	SEA_b		TP			PS_i		
	Mean (\pm 95% CI)	n	Mean (\pm SE)	Range	n	Mean (\pm SE)	Range	n*
BAA	0.27 (0.18 - 0.37)	28	3.10 (0.02)	2.82 - 3.43	28	0.36 (0.05)	0.09 - 0.62	12
BID	0.38 (0.24 - 0.52)	28	3.13 (0.04)	2.85 - 3.72	28	0.83 (0.03)	0.27 - 0.97	26
BIR	0.32 (0.21 - 0.44)	28	3.41 (0.03)	3.13 - 3.64	28	0.77 (0.03)	0.22 - 0.92	26
BON	0.30 (0.20 - 0.42)	28	3.40 (0.04)	2.89 - 3.94	28	0.59 (0.04)	0.08 - 0.82	25
BVI	0.27 (0.18 - 0.37)	28	3.56 (0.03)	3.19 - 3.86	28	0.73 (0.04)	0.15 - 0.92	28
FDL	0.32 (0.21 - 0.44)	27	3.29 (0.04)	2.67 - 3.74	27	0.67 (0.04)	0.07 - 0.85	26
LAM	0.40 (0.26 - 0.55)	28	3.65 (0.06)	2.74 - 4.56	28	0.75 (0.05)	0.05 - 0.95	26
LAV	0.35 (0.23 - 0.48)	28	3.61 (0.06)	3.16 - 4.34	28	0.42 (0.03)	0.05 - 0.72	23
LIN	0.48 (0.31 - 0.67)	28	3.21 (0.07)	2.37 - 3.64	28	0.40 (0.03)	0.10 - 0.77	28
POU	0.32 (0.20 - 0.45)	24	3.35 (0.04)	3.01 - 3.63	24	0.81 (0.04)	0.08 - 0.94	22
RLA	0.25 (0.17 - 0.35)	28	3.36 (0.02)	3.13 - 3.52	28	0.50 (0.04)	0.08 - 0.78	26

* Differences between the number of individuals used for stomach content and for stable isotope analyses were caused by the presence of empty stomachs.

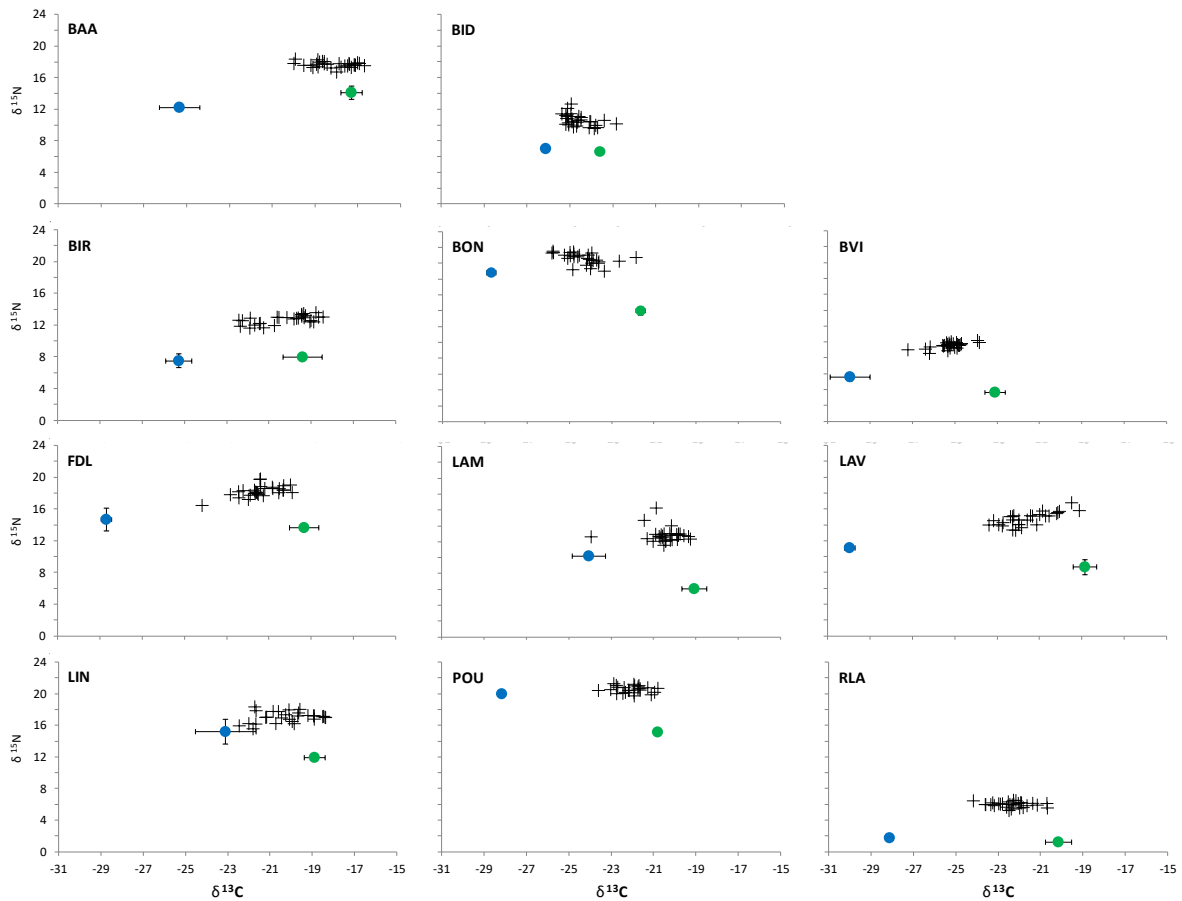


Figure VII.2 Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of individual *Lepomis gibbosus* muscle tissue (cross) and putative prey lipid-corrected (circle, mean \pm SE) sampled in the eleven studied lakes. Blue circles represent pelagic prey (Chironomidae and zooplankton $n = 3 - 4$ samples per lake; $n = 2 - 3$ chironomids per sample) and green circles represent littoral prey (Chironomidae, Ephemeroptera, Lymnaeidae, Assellidae and Oligochaeta; $n = 1 - 4$ samples per lake; $n = 1 - 6$ individuals per sample).

SCA revealed that the level of trophic specialization (V ranging from 0.17 to 0.64; mean = 0.38 ± 0.05 SE) was significantly different between populations (Kruskal-Wallis, $H = 144.62$, $P < 0.001$). Within populations, individual specialization (PS_i) was highly variable (Table VII.1, Fig. VII.3B) and could increased nine-fold on average among individuals (Table VII.1). The relationship between FL and PS_i was not significant (GLMM, $z = 0.55$, $P = 0.581$).

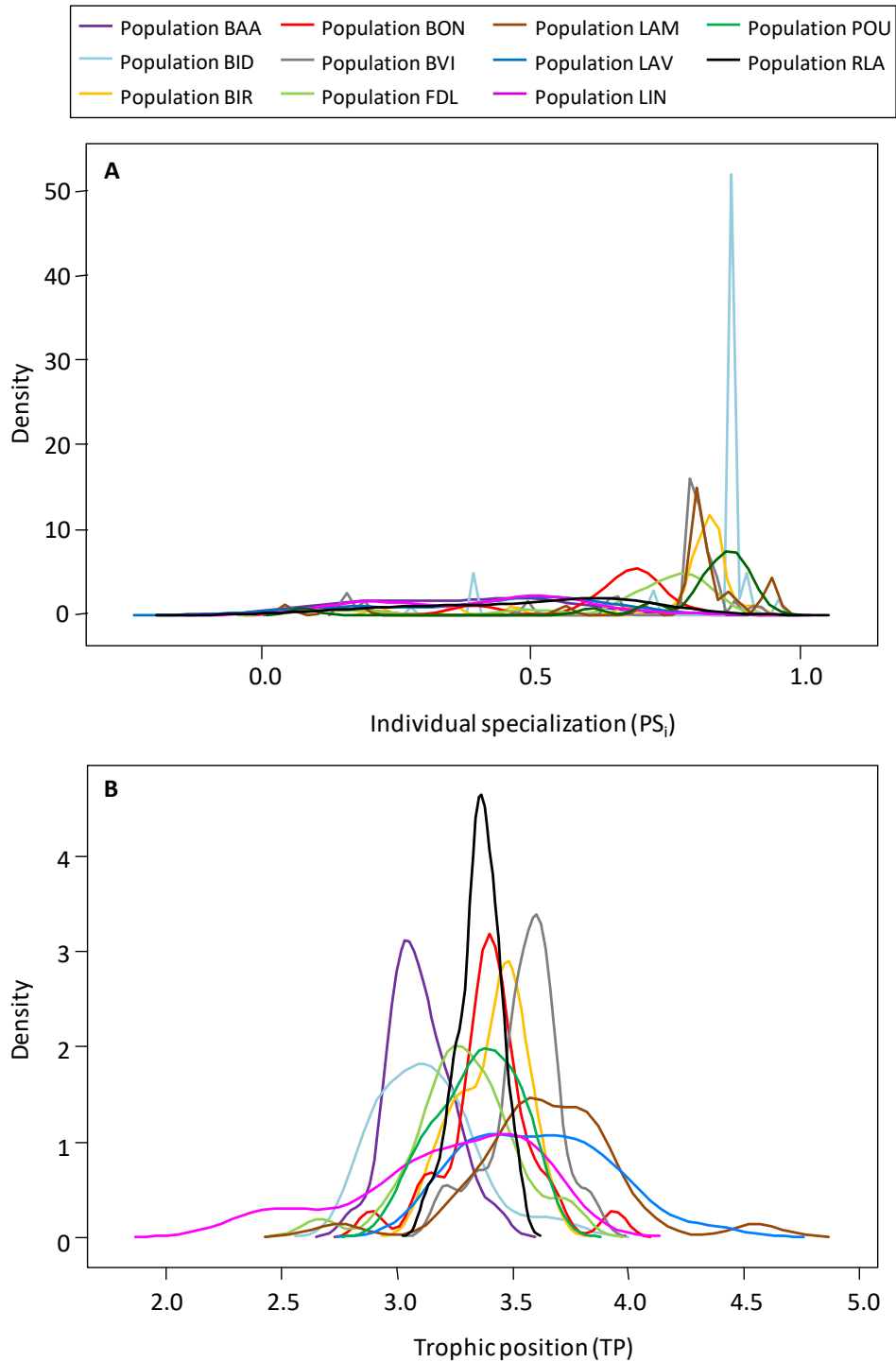


Figure VII.3 Kernel distribution of **(A)** the trophic position (TP) and **(B)** the individual specialization (PS_i) calculated for the 11 wild populations of *Lepomis gibbosus* and based on stomach content analyses and stable isotope analyses, respectively.

VII.3.2 - Effects of intraspecific trophic variability on nutrient recycling rates

Individual growth rate did not vary significantly with the degree of specialization but was significantly affected by diet composition (nested ANOVAs, $P = 0.627$ and $P < 0.001$, respectively; Table VII.2). Specialists feeding on rice grew significantly slower and the

presence of fish meat in the diet strongly increased individual growth rate (Fig. VII.3A). Mixing diet items lead to additive effect on individual growth rate ($P > 0.227$).

Table VII.2 Results of the nested ANOVAs used to assess the effects of diet composition nested under degree of specialization on growth (% week⁻¹; square-root transformed) and the mass-normalized N and P *per capita* excretion rates ($\mu\text{mol ind.}^{-1} \text{h}^{-1}$; log₁₀ transformed) of *Lepomis gibbosus*. Significant *P*-values are in bold.

Response variables	Source	df	Mean squares	F	<i>P</i>	Eta-squared
Growth rate	Degree of specialization	2	0.476	0.34	0.627	0.13
	Diet composition	4	1.415	87.72	< 0.001	0.78
	Error	38	0.016			
N excretion rate	Degree of specialization	2	0.011	0.07	0.897	0.03
	Diet composition	4	0.156	36.01	< 0.001	0.76
	Error	41	0.004			
P excretion rate	Degree of specialization	2	0.064	1.66	0.164	0.14
	Diet composition	4	0.039	2.34	0.072	0.17
	Error	39	0.016			

At the end of the experiment, the excretion rates of the individual *L. gibbosus* displayed a wide range of variation among individuals, ranging from 4.12 to 22.61 $\mu\text{mol N ind.}^{-1} \text{h}^{-1}$ and from 0.04 to 0.29 $\mu\text{mol P ind.}^{-1} \text{h}^{-1}$, but mass-normalized excretion rates did not significantly differ between the degrees of diet specialization (nested ANOVAs, $P = 0.897$ and $P = 0.164$, respectively; Table VII.2). Diet composition significantly affected mass-normalized N excretion rate (nested ANOVA, $P < 0.001$; Table VII.2, Fig. VII.3B) whereas it did not significantly affect mass-normalized P excretion rate (nested ANOVA, $P = 0.072$; Table VII.2, Fig. VII.3C). Mass-normalized N excretion rate was the highest and lowest for fish fed with fish meat (mean = 19.11 $\mu\text{mol N g.}^{-1} \text{h}^{-1} \pm 1.11 \text{ SE}$) and rice (mean = 5.94 $\mu\text{mol N g.}^{-1} \text{h}^{-1} \pm 0.47 \text{ SE}$), respectively. In general, results suggested that the presence of fish meat in the diet increased mass-normalized N excretion rate (Fig. VII.3B). For both N and P mass-normalized excretion rates, additivity was observed for all mixed-diet treatment ($P > 0.059$).

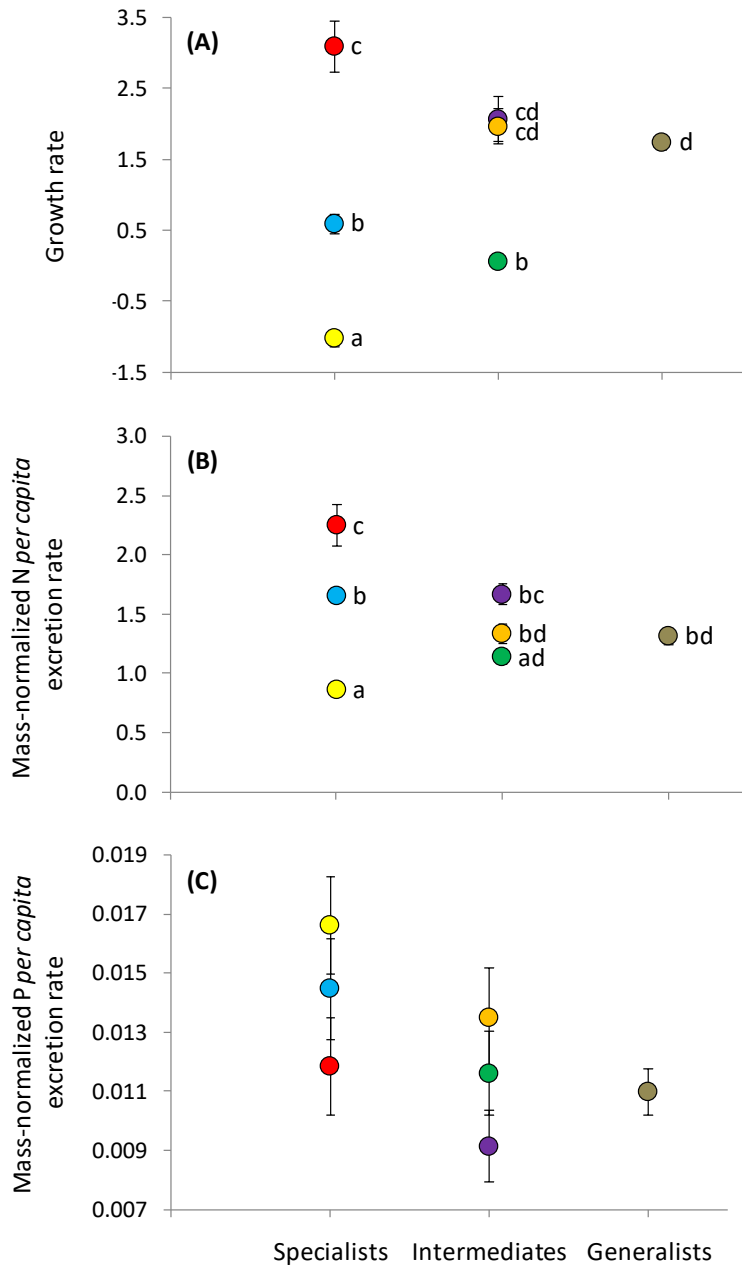


Figure VII.4 Effects of diet elemental composition treatment nested under degree of specialization treatment on mean (\pm SE) **(A)** growth rate ($\%$ month⁻¹) and **(B)** N and **(C)** P mass-normalized *per capita* excretion rates ($\mu\text{mol g}^{-1} \text{h}^{-1}$). Colored dots represent rice specialists (yellow), chironomids specialists (blue), fish specialists (red), intermediates rice \times chironomids (green), intermediates rice \times fish (orange), intermediates chironomid \times fish (purple) and generalists (greenish). Different letters indicate significant differences among these means (Tukey's HSD, $P < 0.05$).

VII.3.3 - Effects of consumer-mediated nutrient recycling on ecosystem functioning

Particulate N and P contents, gross primary production (GPP), community respiration (CR), and algal standing biomass (chlorophyll-a) were higher in microcosms supplied with fish excretory products than in control microcosms (t-tests, $P < 0.05$). Linear models showed that particulate N content, GPP and CR increased significantly with N excretion rate and that particulate P content and algal standing biomass increased significantly with P excretion rate (Table VII.3, Fig. VII.5). In contrast, whole-system metabolism did not change with P excretion rate (linear models, GPP: $F = 2.25$, $P = 0.142$ and CR: $F = 1.83$, $P = 0.184$; Table VII.3, Fig. VII.5B and VII.5D) and differences in algal standing biomass among microcosms were inconsistent with intraspecific variation in N excretion rate (linear model, $F = 0.12$, $P = 0.732$; Table VII.3, Fig. VII.5E). No difference was detected for the biomass of leaf-associated fungi and litter decomposition rate between treatment and control microcosms (t-tests, $P = 0.656$ and $P = 0.672$, respectively; Fig. VII.5K and VII.5L). Intraspecific variation in nutrient excretion rates did not explain differences in these ecosystem properties among microcosms that were supplied with fish excretory products (linear models, $P > 0.367$; Table VII.3, Fig. VII.5G to VII.5J). Except for algal standing biomass (linear model, $F = 6.08$, $P = 0.018$; Table VII.3), effects of N and P excretion rates on ecosystem properties were not statistically significant with mass-normalized excretion rates (linear models, $P > 0.071$; Table VII.3), indicating that consumer-mediated effects on ecosystem processes were primarily driven by the effects of diet treatment on individual body mass through differences in growth rate.

Table VII.3 Results of the linear models assessing the relationships between N and P *per capita* ($\mu\text{mol ind.}^{-1} \text{h}^{-1}$; \log_{10} transformed) and mass-normalized *per capita* excretion rates ($\mu\text{mol g.}^{-1} \text{h}^{-1}$; \log_{10} transformed) and ecosystem processes: nutrient particulate content (μmol), gross primary productivity (mg O_2), community respiration (mg O_2), algal standing biomass (μg), fungal biomass (mg ; \log_{10} transformed) and litter decomposition rate (day^{-1}). Significant *P*-values are in bold.

Response variables	Source	<i>Per capita</i> excretion rates				Mass-normalized <i>per capita</i> excretion rates		
		df	Mean squares	F	<i>P</i>	Mean squares	F	<i>P</i>
Particulate N concentration	Block	5	24490	4.84	0.002	24491	4.43	0.003
	N excretion rate	1	34660	6.85	0.013	19123	3.46	0.071
	P excretion rate	1	2070	0.41	0.526	219	0.04	0.843
	Residuals	37	5058			5528		
Particulate P concentration	Block	5	12.58	33.5	< 0.001	12.61	29.16	< 0.001
	N excretion rate	1	0.93	2.48	0.124	0.003	0.01	0.934
	P excretion rate	1	2.67	7.11	0.011	1.06	2.45	0.126
	Residuals	37	0.38			0.43		
Gross primary productivity	Block	5	6.63	2.34	0.061	6.32	2.16	0.080
	N excretion rate	1	15.07	5.32	0.027	3.22	1.10	0.302
	P excretion rate	1	6.39	2.25	0.142	5.20	1.77	0.191
	Residuals	37	2.84			108.51		
Community respiration	Block	5	4.20	2.36	0.058	4.05	2.10	0.087
	N excretion rate	1	8.20	4.62	0.038	4.64	2.41	0.129
	P excretion rate	1	3.26	1.83	0.184	1.76	0.91	0.345
	Residuals	38	1.77			1.93		
Algal standing biomass	Block	5	2115	0.27	0.927	3695	0.46	0.805
	N excretion rate	1	935	0.12	0.732	12327	1.53	0.224

	P excretion rate	1	88245	11.21	0.002	49079	6.08	0.018
	Residuals	38	7871			8072		
Fungal biomass	Block	5	0.17	3.72	0.008	0.17	3.72	0.008
	N excretion rate	1	0.01	0.19	0.664	0.02	0.39	0.538
	P excretion rate	1	0.02	0.46	0.500	0.01	0.26	0.610
	Residuals	37	0.05			0.05		
Litter decomposition rate	Block	5	1.33e-06	0.42	0.829	1.33e-06	0.42	0.829
	N excretion rate	1	2.91e-07	0.09	0.763	2.12 e-06	0.67	0.417
	P excretion rate	1	2.62e-06	0.83	0.367	6.94 e-07	0.22	0.642
	Residuals	37	3.15e-06			3.15 e-06		

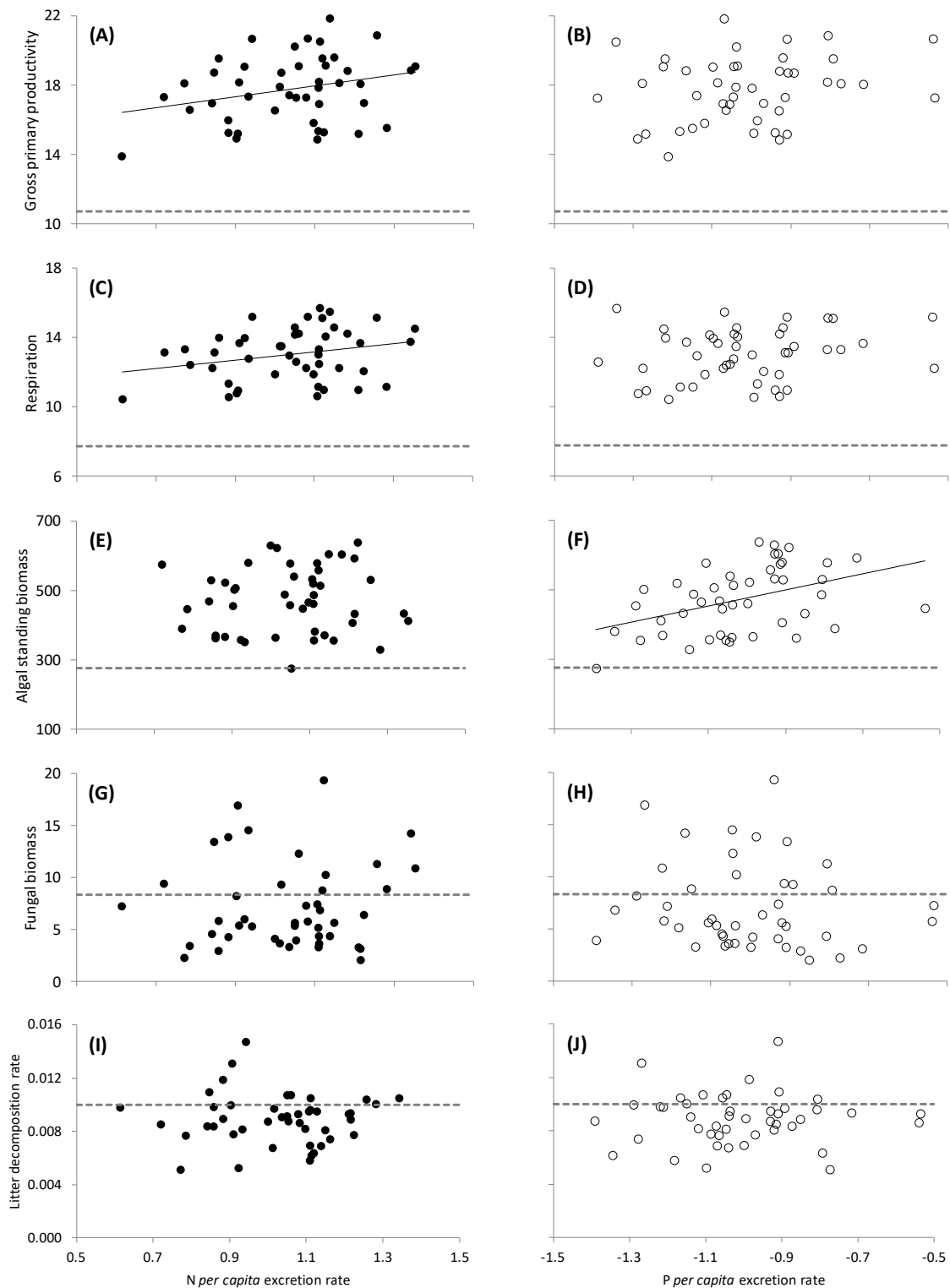


Figure VII.5 Relationship between N (left panels) and P (right panels) *per capita* excretion rates ($\mu\text{mol ind.}^{-1} \text{h}^{-1}$; \log_{10} transformed) and **(A-B)** gross primary productivity ($n = 45$), **(C-D)** respiration ($n = 46$), **(E-F)** algal standing biomass (μg ; $n = 46$), **(G-H)** fungal biomass (mg ; $n = 45$) and **(I-J)** litter decomposition rate (day^{-1} ; $n = 45$). Significant relationships are depicted using continuous black lines. The dotted lines represent the mean value of the control microcosms.

VII.4 - DISCUSSION

Generalist populations with wide trophic niches are composed of more heterogeneous individuals using only a subset of the available prey (Bolnick et al. 2003). Here, we found that trophic specialization differed widely among coexisting individuals of *L. gibbosus* and such individual trophic variability was consistently detected in the eleven wild populations surveyed. In addition, omnivorous *L. gibbosus* individuals did not occupy the same trophic position, as evidenced by stable isotope analyses that reflect dietary information over several weeks (Layman et al. 2012). Clearly, individuals within populations differed in respect of the relative contribution of plant- versus animal-derived resources to diet. While SCA suggested that *L. gibbosus* relied exclusively on invertebrate prey as animal food source, we cannot rule out that individuals displaying a high trophic position (> 3.5 as observed with stable isotope analyses; Vander Zanden et al. 1997) also consumed fish-derived food sources such as eggs and larvae (García-Berthou & Moreno-Amich 2000b). In the present study, fish were sampled in late summer, i.e., at a time when fish eggs and larvae had become scarce, which likely explained the absence of fish-derived prey in stomach contents.

The balanced diet hypothesis stipulates that generalist individuals consuming multiple prey have access to a more complete range of nutrients than specialist individuals, which could provide fitness benefits (DeMott 1998). Our laboratory experiment did not support this hypothesis, as diet mixing did not increase individual growth. By contrast, growth rate was higher for individuals feeding on the single best-quality food item (Lefcheck et al. 2013). These findings thus indicate that diet specialization toward high quality food may confer fitness advantages in generalist populations.

Nutrient cycling measured as *per capita* excretion rates was highly variable among individuals (ranging from 4.12 to 22.61 $\mu\text{mol N ind.}^{-1} \text{h}^{-1}$ and from 0.04 to 0.29 $\mu\text{mol P ind.}^{-1} \text{h}^{-1}$, respectively). These values fell within the range reported by Villéger et al. (2012) for wild populations of freshwater fish species (ranging from 0.20 to 518 $\mu\text{mol N ind.}^{-1} \text{h}^{-1}$ and from 0.03 to 29.34 $\mu\text{mol P ind.}^{-1} \text{h}^{-1}$). They were, however, slightly lower than the values observed for *L. gibbosus* (ranging from 13.46 to 26.12 $\mu\text{mol N ind.}^{-1} \text{h}^{-1}$ and from 0.13 to 1.74 $\mu\text{mol P ind.}^{-1} \text{h}^{-1}$; Villéger et al. 2012). Although the effects of diet composition on consumer excretion rates can be difficult to predict (but see Moody et al.

2016), our findings revealed that individuals feeding at higher trophic position (more animal-based diet) excreted N at higher rates (Bassar et al. 2010). This is probably because animal items used in this study were nutrient-rich compared to rice and thus consumers would release them at higher rates (Sterner & Elser 2002). Surprisingly, and contrary to findings reported in literature (Moody et al. 2016), we did not detect significant changes in P excretion rate in relation to intraspecific trophic variability. Fish require large amount of P that is allocated to the formation of bones and scales and to somatic growth (Pilati & Vanni 2007, McIntyre & Flecker 2010). The diet items used in the present study were relatively low in P (from 0.2 to 0.9 % dry mass; Fig. VII.1) and this could explain the high level of P retention by fish.

Some of the integrative ecosystem processes measured during the present study differed substantially among microcosms (i.e., gross primary productivity and community respiration) and a significant fraction of this variability was driven by intraspecific variation in the rate of nitrogen excreted by fish. Because we also demonstrated that diet composition determined nitrogen excretion rate, it indicates that intraspecific trophic variability can alter ecosystem functioning through consumer-mediated nutrient recycling (Bassar et al. 2010, Taylor et al. 2015). Based on our findings, specialization toward resources with higher trophic level should exacerbate the effects of individual fish excretion on ecosystem functioning. Within the same cohort, we also found that the biomass dependence of fish excretion mediated their effects on ecosystem functioning. This highlights the importance to integrate body size variation when assessing the effects of intraspecific variability on ecosystem functioning (Rudolf & Rasmussen 2013a).

The amount of N and P associated with fine particulate organic matter increased with the inputs of fish excretory products but also as a result of microbial immobilization of dissolved inorganic nutrients. Primary producers and decomposers rely on inorganic nutrients for growth and metabolism (Daufresne & Loreau 2001). In our experiment, neither decomposition rate of coarse particulate organic matter nor fungal biomass were modified by the addition of excretory products, suggesting that litter-associated decomposers did not use fish-derived nutrients. Therefore, and contrary to our prediction, producers may have contributed substantially to nutrient immobilization in microcosms as evidenced by the positive response of GPP and algal biomass to fish excretory products. Finally, the asymmetric responses between

autotroph and heterotroph organisms observed here highlighted the complexity of ecosystem processes responses to nutrient loading. Although these results are not trivial, we argue that future investigations are needed in less contrived experimental environment to fully encompass other additional effects that might modulate and interact with the relationship between nutrient recycling and ecosystem processes. For instance, the presence of top-predators can change the nutrient body composition of consumers (Hawlena et al. 2012), potentially altering nutrient recycling and subsequent effects on ecosystem functioning, but these effects, to our knowledge, have been poorly investigated in aquatic ecosystems.

In conclusion, this study demonstrated that intraspecific trophic variability can induce variations in consumer-mediated nutrient recycling, which can subsequently mediate relevant processes of ecosystem functioning through biomass-dependent effect. Specifically, structurally different populations (e.g., Evangelista et al. 2015) should probably affect ecosystem functioning with indirect effects of varying strength (Rudolf and Rasmussen 2013a). However animals affect ecosystems by combined effects of top-down (direct and consumptive) and bottom-up (indirect and nutrient-mediated) mechanisms (Knoll et al. 2009, Taylor et al. 2015) and future studies would benefit to quantify the relative importance of each force in driving the effect of intraspecific variability on ecosystem functioning.

VII.5 - ACKNOWLEDGEMENTS

We are very grateful to the graviere team for their help during fish sampling and to N. Charpin and T. Zhao for their help during experiment. D. Lambrigot and F. Julien are thanked for their laboratory assistance. We also thank S. Villéger for constructive comments on earlier version of the manuscript. Authorizations to perform this study were provided by the "Arrêtés Préfectoraux - 31/07/2012 and 10/07/2013". This work was supported by the ONEMA (Projet ISOLAC -Convention 13-V5-28), a Fisheries Society of the British Isles Research Grant, a PRES-Toulouse grant (Inva_Eco_Evo_Lac) and an "ERG Marie Curie" grant (PERG08-GA-2010-276969). CE and JC are part of EDB, part of the French Laboratory of Excellence project "TULIP" (ANR-10-LABX.41; ANR-11-IDEX-0002-02).

CHAPITRE VIII

Discussion générale et perspectives

Les chapitres présentés dans cette thèse ont d'abord permis de démontrer l'existence d'une forte variabilité phénotypique intraspécifique chez deux espèces invasives, à savoir *Lepomis gibbosus* et *Procambarus clarkii*. Cette variabilité concernait à la fois certains traits d'histoire de vie mais également certains traits trophiques et morphologiques, ces derniers ayant été quantifiés à l'aide d'analyses d'isotopes stables, de contenus stomacaux et de morphométrie géométrique, respectivement. Ces divergences intraspécifiques ont pu être observées entre les populations mais également entre les individus au sein des populations. Les déterminants écologiques de ces variations de traits ont été mis en évidence lors de suivis de populations établies dans des lacs artificiels relativement proches mais déconnectés les uns des autres et situés le long de gradients environnementaux. La présence d'espèces invasives est devenue une préoccupation majeure pour les différents gestionnaires de ces écosystèmes et le contrôle des populations invasives se fait notamment par le biais d'approches mécaniques telles que la pêche récréative. Cependant, il est apparu que la pêche récréative, en sélectionnant les individus les plus gros au sein des populations, favoriserait certains aspects de la stratégie r de développement (e.g., reproduction précoce, taille à maturité réduite) et conduirait à des effets potentiellement contre productifs (e.g., augmentation des biomasses) (*Chap. III*; Fig. VIII.1). Les résultats obtenus au cours de ce travail de thèse ont également permis de révéler la complexité des interactions environnementales dans le contrôle des niches trophiques des populations et des individus (*Chap. IV*; Fig. VIII.1). Ces résultats suggèrent que, d'une part, la mise en place des réponses des populations invasives aux conditions environnementales peut être rapide et que, d'autre part, l'effet des espèces invasives sur l'écosystème receveur peut varier localement. A plus large échelle, l'étude des variations phénotypiques entre populations invasives situées en Europe et en Amérique du Nord a permis de mettre en évidence la contexte-dépendance des réponses morphologiques des populations aux conditions environnementales, suggérant l'importance de l'histoire de la colonisation des espèces invasives (e.g., pression de propagule, effet fondateur) au

sein d'environnements géographiquement isolés dans le déterminisme des patrons de diversité phénotypique (*Chap. V*; Fig. VIII.1). Les chapitres présentés dans cette thèse ont ensuite permis de démontrer, par l'intermédiaire d'approches expérimentales, l'importance de la variabilité intraspécifique dans la modulation des impacts des espèces invasives sur le fonctionnement des écosystèmes. Cela a été révélé à travers l'étude des effets directs (i.e., consommation) et indirects des consommateurs (i.e., excrétion des nutriments). Les résultats ont permis de démontrer que des populations morphologiquement distinctes affectaient différemment la structure des communautés et le fonctionnement de l'écosystème via des variations dans les taux de consommation des ressources trophiques (*Chap. VI*; Fig. VIII.1). Bien que ces résultats demandent à être approfondis, ils suggèrent que les effets des espèces invasives peuvent être variables dans le temps au cours du processus d'invasion. Finalement, la variabilité trophique (i.e., position dans la chaîne alimentaire et niveau de spécialisation) qui persiste au sein même des populations invasives peut moduler les taux d'excrétion des nutriments (i.e., N et P) des consommateurs et ainsi conduire à des effets variables des individus sur le fonctionnement de l'écosystème (*Chap. VII*; Fig. VIII.1).

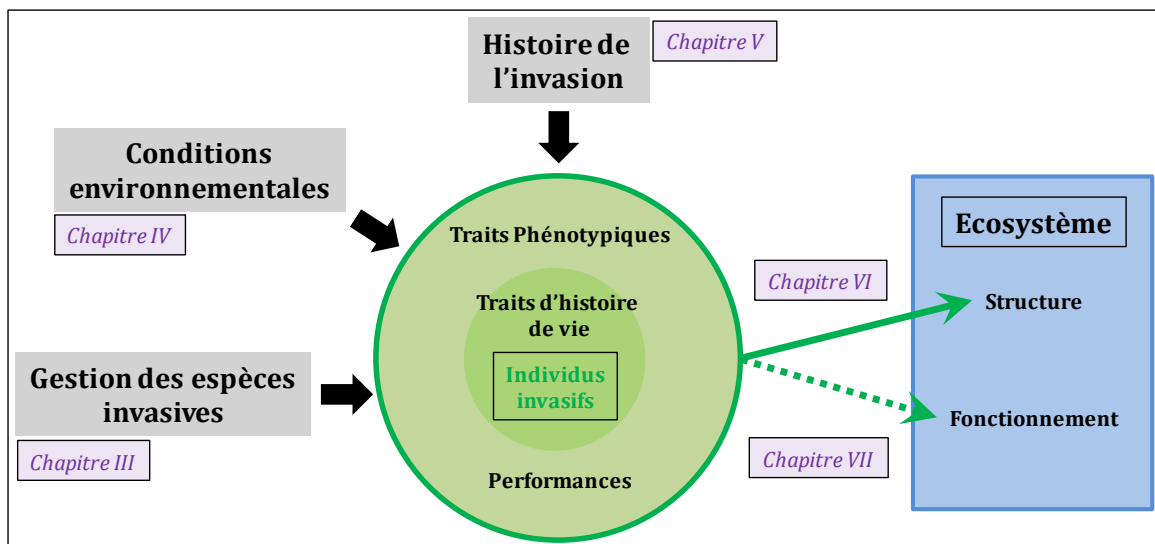


Figure VIII.1 Schéma synthétique des résultats obtenus au cours de ce travail de thèse consistant à étudier les déterminants écologiques de la variabilité phénotypique intraspécifique chez les espèces invasives et ses conséquences directes et indirectes sur l'écosystème.

VIII.1 - Déterminants écologiques de la variabilité intraspécifique chez les espèces invasives

Les lacs de gravières sont des écosystèmes artificiels de taille relativement limitée (en général de 2 à 20 ha) et dont les caractéristiques environnementales peuvent être modulées par différentes perturbations d'origine anthropique susceptibles d'intensifier les contrastes écologiques entre lacs. L'attractivité des milieux d'étude pour les activités humaines se traduisait principalement par le développement de la pêche récréative et l'intensité de cette activité peut modifier la composition piscicole (e.g., introduction d'espèce d'intérêt halieutique; Zhao et al. 2016) mais également accélérer l'eutrophisation via l'apport de ressources allochtones d'origine anthropique (i.e., appâts et amorces). Au cours de cette thèse, le rôle de ces trois facteurs dans la mise en place de la variabilité intraspécifique a été mis en évidence. En effet, il a été démontré que la pêche récréative (*Chap. III*), la présence de poissons prédateurs (*Chap. IV*) et la productivité (*Chap. IV, Chap. V, Chap. VI*) modulaient les variations trophiques et morphologiques des individus invasifs. Ces résultats suggèrent que les activités humaines peuvent avoir un rôle déterminant dans l'établissement de la variabilité intraspécifique soit en agissant directement sur les individus (Coltman et al. 2003) soit en modifiant les conditions environnementales dans l'écosystème (Layman et al. 2007, Giery et al. 2015). De plus, les lacs étudiés présentaient également l'intérêt d'être relativement jeunes (de 7 à 60 ans) et permettent donc de caractériser les réponses rapidement mises en place par les populations face aux changements environnementaux. Par conséquent il apparaît que ces milieux aquatiques périurbains représentent une opportunité unique pour tester les effets multiples des conditions locales sur les patrons de biodiversité et plus particulièrement d'intégrer la variabilité intraspécifique dans le contexte actuel des changements globaux (Moran et al. 2016).

Les espèces invasives sont généralement considérées comme étant une menace pour la biodiversité et les services rendus par les écosystèmes. Le parlement Européen a récemment établi une liste des espèces invasives indésirables qui incluait notamment *Procambarus clarkii*, et contre lesquelles les pays membres vont devoir prendre des mesures de gestion appropriées. La gestion mécanique des espèces invasives se base principalement sur l'utilisation de méthodes sélectives, telles que la pêche et la chasse, qui peuvent favoriser le maintien de certains traits d'histoire de vie des individus au sein

des populations invasives. Par conséquent, elles sont susceptibles de modifier l'ensemble des caractères phénotypiques des individus (Réale et al. 2010). La sélection induite par la pêche opère de manière unidirectionnelle et pourrait réduire la variabilité phénotypique. Ainsi, la pêche récréative tend à favoriser l'élimination des plus gros individus (*Chap. III*) et des modifications de la structure de taille des populations peuvent conduire à des modifications du fonctionnement de l'écosystème (Rudolf & Rasmussen 2013b). Ces conséquences écosystémiques peuvent résulter d'effets directs des consommateurs invasifs liés à des changements de niche trophique associés à la taille des individus (*Chap. IV*) ou bien d'effets indirects (i.e., cascade trophique, excrétion des nutriments). Ainsi, on peut supposer que les populations non pêchées constituées d'individus de tailles plus hétérogènes seraient caractérisées par une plus grande variabilité trophique. De plus, les changements de tailles des individus peuvent se répercuter à l'ensemble du réseau trophique notamment via des modifications des relations de compétition et de prédation. Par exemple, les individus de petites tailles ayant un corps allongé sont susceptibles d'être plus facilement prédatés par les espèces piscivores ayant une ouverture de bouche limitée, par rapport à leurs congénères plus grands ayant un corps plus arrondi (*Chap. V*). En parallèle, des divergences de niche trophique peuvent également conduire à des modifications des taux d'excrétion de nutriments par les consommateurs (Bassar et al. 2010, Moody et al. 2016) et donc potentiellement affecter le cycle des nutriments. De plus, à biomasse égale, les individus de petites tailles excrètent les nutriments à des taux plus élevés que leurs congénères de taille plus importante (Vanni 2002). Ainsi, l'élimination des individus de grande taille (*Chap. III*), caractérisés par une position trophique plus élevée (*Chap. IV, Chap. V*), pourrait réduire les apports de nutriments directement disponibles et altérer le développement de certains autotrophes (*Chap. VII*; Allgeier et al. 2016). De plus, il a récemment été mis en évidence que des méthodes de capture reposant sur l'utilisation de pièges qui ne sélectionnent pas les individus en fonction de leur taille, modifiait également la croissance des individus en sélectionnant certains comportements (Biro & Sampson 2015). Par conséquent, puisque les pratiques de gestion des espèces invasives utilisées actuellement modifient la structure des populations et le rôle fonctionnelle des individus, et ce parfois de manière contre productive (*Chap. III*), des études devraient être envisagées de façon à déterminer les conséquences écologiques des divergences

phénotypiques induite par la pêche récréative et, de manière plus générale, par les méthodes de gestion des espèces invasives.

Il est maintenant largement admis que les individus au sein d'une même espèce diffèrent selon de nombreux traits phénotypiques (Bolnick et al. 2011) et l'utilisation de ce principe a notamment permis de mieux répondre à certaines questions de l'écologie des communautés (Violle et al. 2012). Récemment, des études empiriques chez les plantes ont révélé que la variabilité intraspécifique chez certains traits pouvait représenter jusqu'à environ 30% de la variation totale (Albert et al. 2010, Jung et al. 2010, Auger & Shipley 2013), soulignant son importance dans la diversité globale des communautés. Cependant, une telle comparaison reste peu explorée chez les espèces animales. Ce travail de thèse a permis de quantifier les différences trophiques, morphologiques et physiologiques (i.e., taux de consommation et taux d'excrétions) au sein des deux espèces omnivores et d'évaluer leurs effets sur le fonctionnement de l'écosystème. Cependant, il serait maintenant nécessaire de quantifier l'importance relative de la variabilité intraspécifique par rapport à la variabilité interspécifique de façon à mieux révéler son rôle dans le fonctionnement des milieux naturels. Par exemple, des analyses supplémentaires ont été réalisées sur les valeurs isotopiques (i.e., $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$) des différentes espèces de quatre communautés piscicoles issues de lacs de gravières (i.e., BVI, LAM, POU et SOA) afin de déterminer l'ampleur des deux facettes de la biodiversité (*voir détails* Fig. VIII.2). Ces résultats préliminaires indiquent que la variabilité intraspécifique était plus faible que la variabilité interspécifique pour les valeurs de $\delta^{13}\text{C}$ mais le patron opposé a été observé pour les analyses sur les valeurs de $\delta^{15}\text{N}$ (Fig. VIII.2). Il semblerait donc que l'ampleur de la variabilité intraspécifique dépende fortement du trait considéré (Siefert et al. 2015). Néanmoins, puisque la variabilité intraspécifique est une composante déterminante de la mise en place des interactions biotiques entre les espèces, des réponses des communautés aux conditions environnementales et des processus écosystémiques (*voir* Siefert et al. 2015), les résultats obtenus ici suggèrent qu'il serait intéressant d'intégrer la variabilité intraspécifique afin de mieux prédire les patrons d'assemblages des communautés animales. De plus il serait également intéressant d'examiner si la contribution relative de la variabilité intra- et interspécifique à la diversité globale est modulée par les perturbations environnementales de façon à mieux prédire comment les processus qui structurent les communautés peuvent évoluer au cours du temps.

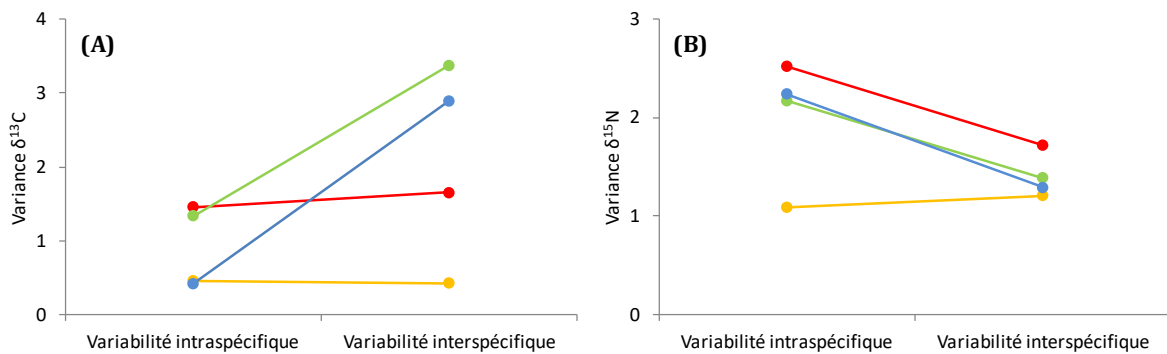


Figure VIII.2 Analyse de la variabilité intra- et interspécifiques des valeurs isotopiques **(A)** du carbone ($\delta^{13}\text{C}$) et **(B)** de l'azote ($\delta^{15}\text{N}$) au sein de quatre communautés piscicoles. Pour chaque site, les composantes de la variabilité ont été calculées à partir des résultats issus d'un modèle linéaire à effets mixtes incluant la signature isotopique de chaque individu et l'espèce comme effet aléatoire. Plus précisément, les variances intra- et interspécifique sont issus des déviations standards élevées à la puissance deux.

VIII.2 - Rôle de la variabilité intraspécifique dans la modulation des impacts des espèces invasives sur le fonctionnement de l'écosystème

Les prédateurs peuvent réguler le fonctionnement de l'écosystème via des effets directs (i.e., consommation) et des effets indirects (i.e., cascade trophique, excrétion de nutriment) agissant en interaction. En effet, ils peuvent favoriser la production primaire via la prédation des consommateurs primaires et l'excrétion de nutriment. De plus, en réduisant la biomasse et en modifiant la structure en taille des populations des consommateurs primaires, la prédation peut indirectement agir sur les apports en nutriments des proies (Vanni 2002). Par exemple, la présence de prédateurs, en sélectionnant les individus de petite taille, augmentait les taux d'excrétion des nutriments chez les guppys (*Poecilia reticulata*) (Palkovacs et al. 2009). Par conséquent, quantifier les effets relatifs des impacts directs et indirects des prédateurs sur le fonctionnement des écosystèmes se révèle souvent complexe du fait de leur action simultanée et des phénomènes de rétroaction impliqués (Knoll et al. 2007). Il serait pourtant envisageable de quantifier ces effets via la mise en place de plusieurs expériences permettant d'évaluer de manière indépendante chaque mécanisme. L'effet de la cascade trophique pourrait être testé en simulant un taux de prédation et donc en réduisant progressivement la biomasse de proie. L'effet indirect des prédateurs via leur excrétion pourrait être testé via le transfert des produits d'excrétion des prédateurs préalablement nourris dans des mésocosmes (*voir approche utilisée dans Chap. VII*).

L'effet des prédateurs sur les taux d'excrétion des proies pourrait être testé en plaçant des proies ayant un phénotype sélectionné par la prédation (e.g., individus de petites tailles) en contact visuel avec des prédateurs; on pourrait alors s'attendre à ce que la présence de prédateurs, par le biais d'un effet de peur, module la composition en nutriment des proies et affectent leur taux d'excrétion de nutriments (Hawlena & Scmitz 2010). De plus, comme la variabilité intraspécifique module les effets directs (*Chap. VI*) et indirects (*Chap. VII*) des prédateurs, il serait également intéressant de tenir compte de cette variabilité et d'estimer comment elle pourrait éventuellement modifier l'effet relatif de chaque mécanisme sur le fonctionnement de l'écosystème. Ceci pourrait être testé en utilisant plusieurs types de prédateurs spécialisés sur des consommateurs primaires avec des positions trophiques différentes.

Bien que les précédentes études se soient focalisées sur les différences des taux d'excrétion des nutriments entre espèces (Vanni et al. 2002, Torres & Vanni 2007), il a été démontré que ces différences pouvaient également être importantes au sein des espèces (Villéger et al. 2012) et avoir une incidence sur le fonctionnement des écosystèmes (Bassar et al. 2010). Cependant, les mécanismes responsables de cette variabilité demeurent peu étudiés à l'échelle intraspécifique à ce jour et leur étude nécessite des outils performants et intégrateurs. L'écologie stœchiométrique est l'étude des ratios des éléments chimiques (carbone, azote et phosphore ; C:N:P) et permet d'associer les traits des individus, leur composition chimique et leur excrétion (Elser et al. 2000). La composition chimique d'un organisme hétérotrophe est considérée comme homéostasique, c'est-à-dire qu'elle ne varie pas avec des changements en composition de son régime alimentaire (Person et al. 2010). Les déséquilibres entre la demande en nutriments de l'individu et son régime alimentaire sont donc tamponnés par l'élimination ou la séquestration sélective des éléments (Sturner & Elser 2002). De plus, la stœchiométrie prédit qu'il existe une relation négative entre la composition en nutriments de l'individu et les ratios stœchiométriques excrétés (Sturner & Elser 2002). Cependant, une étude récente menée sur des épinoches (*Gasterosteus aculeatus*) de morphes différents a révélé que les individus excrétant le plus de phosphore étaient ceux dont la composition corporelle était également la plus riche en phosphore (El-Sabaawi et al. 2016). Les auteurs suggéraient que ceci pouvait être expliqué par des différences de taux métaboliques tels que les taux de consommation et l'efficacité d'assimilation. Par conséquent, la physiologie des organismes semblent impliquée dans

la régulation des taux d'excrétion (Dalton & Flecker 2014) mais demeurent rarement explorée dans les populations naturelles. Au cours de ce travail de thèse, des différences morphologiques ont été mises en évidence entre les populations de *P. clarkii* le long d'un gradient de productivité (*Chap. VI*) fortement associé avec l'âge des lacs. Puisque la formation de la carapace requière du phosphore et du calcium, ces variations morphologiques pourraient être associées à des besoins en nutriments variables entre les individus et pourraient donc favoriser des différences de taux d'excrétion. De plus, la croissance des individus nécessite une quantité importante de phosphore, élément impliqué dans la formation d'ARN. Les individus à forte croissance ont une teneur en phosphore plus importante que les individus à croissance plus faible (Elser et al. 2003). En parallèle, des différences de taux de consommation des ressources trophiques entre les individus ont été observées, suggérant que les individus issus des populations les plus jeunes consommaient plus rapidement les ressources disponibles (*Chap. VI*). Par conséquent, il serait intéressant de quantifier les traits stœchiométriques (i.e., composition du corps et excrétion) des individus établis le long d'un gradient d'âge d'invasion afin de déterminer le rôle des différents mécanismes (e.g., métabolisme, composition en nutriment) influençant le recyclage des nutriments dans les systèmes naturels et ainsi estimer si les effets des populations invasives évoluent au cours du processus d'invasion.

Dans les milieux aquatiques, les consommateurs peuvent jouer un rôle important dans les cycles biogéochimiques en immobilisant des éléments présents dans l'environnement et en approvisionnant le milieu en nutriment limitant (Vanni 2002). Le rôle des espèces piscicoles dans le cycle des nutriments a particulièrement été étudié du fait de leur forte biomasse dans de nombreux écosystèmes (Vanni et al. 2002, McIntyre et al. 2008, Capps & Flecker 2013b), négligeant ainsi l'effet potentiel d'autres organismes (*mais voir exemples cités dans Vanni 2002, Fritschie & Olden 2015*). Les écrevisses font parties des plus gros invertébrés présents dans les écosystèmes aquatiques et leur biomasse peut être importante, particulièrement quand il s'agit des espèces invasives. Par exemple, dans les lacs de gravières étudiés ici, les biomasses de *P. clarkii* pouvaient atteindre 170.91 g d'écrevisse par nasse et par heure. Les observations de terrain indiquent également que *P. clarkii* est une espèce pionnière dans ces milieux et leurs densités peuvent être particulièrement importantes dans les lacs les plus jeunes (Alp et al. 2016). Par conséquent, ces décapodes pourraient éventuellement jouer un

rôle dans le développement des organismes en créant des « hot spot » biogéochimiques, même si cet effet potentiel est à tempérer du fait de la forte pression de prédation exercée par les écrevisses invasives (Twardochled et al. 2013). Les écrevisses apparaissent donc comme étant des organismes capables d'intervenir dans le recyclage des nutriments mais ceci a rarement été étudié en milieu naturel. Cette intervention pourrait se faire lors du relargage des produits d'excrétion mais également lors de la décomposition des mues riches en calcium et en phosphore et lors de la mort de l'individu (Boros et al. 2015). Des résultats préliminaires issus d'une expérience réalisée au laboratoire suggèrent que les taux d'excrétions en azote d'individus de *P. clarkii* ($\mu\text{mol N g}^{-1} \text{h}^{-1}$) étaient similaires à ceux d'individus de *L. gibbosus* soumis au même régime alimentaire (Fig. VIII.3). Ces résultats suggèrent que les écrevisses pourraient intervenir de manière significative dans le recyclage des nutriments et moduler les processus de l'écosystème (Chap. VII). Par conséquent, il semble indispensable de quantifier les taux d'excrétion des nutriments des écrevisses et de les comparer avec ceux des espèces piscicoles afin d'évaluer leur rôle indirect dans le fonctionnement des écosystèmes. Il serait également intéressant d'examiner comment l'élimination massive des écrevisses invasives pourrait altérer les cycles biogéochimiques dans les écosystèmes. Ceci permettrait de mieux évaluer les relations entre les méthodes de gestion par la pêche des espèces invasives et le fonctionnement des écosystèmes.

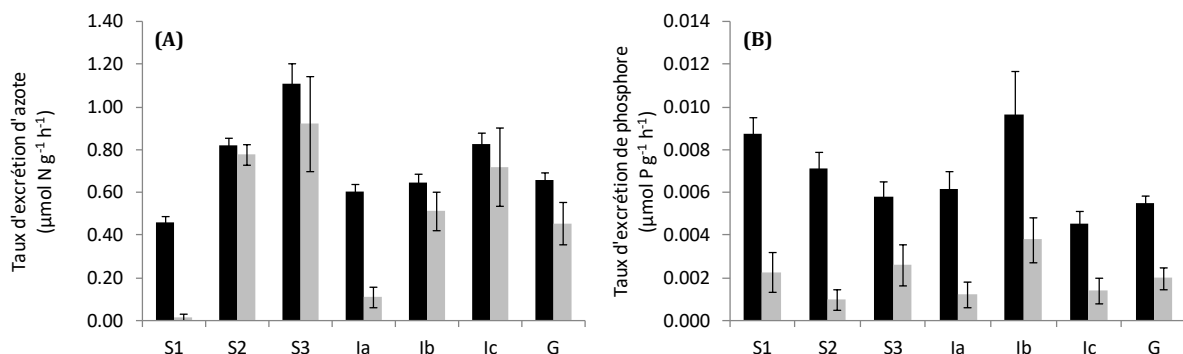


Figure VIII.3 Taux d'excrétion (A) de l'azote (B) du phosphore chez les individus de *Lepomis gibbosus* (noir) et *Procambarus clarkii* (gris) soumis à différents régimes alimentaires (voir détails Chap.; Fig. V.1). Réalisée à partir de données non publiées.

Les effets de la variabilité phénotypique intraspécifique sur le fonctionnement des écosystèmes ont principalement été étudiés en considérant la variabilité d'un seul trait (Harmon et al. 2009, Rudolf & Rasmussen 2013a, Fryxell et al. 2015). Pourtant, des corrélations entre différents traits ont été mises en évidence dans plusieurs études (Sih

et al. 2004, Mittelbach et al. 2014, Kern et al. 2016, Raffard et al. In prep). Ces corrélations peuvent être le résultat d'une évolution non indépendante des traits si la fitness de l'un dépend de la valeur des autres (Bell & Sih 2007) et la répétabilité des traits dans le temps permet le maintien des divergences intraspécifiques. Réale et al. (2010) ont également développé le concept de « Pace of Life Syndrome » qui permet de mieux décrire le phénotype général d'un individu par les liens qui s'établissent entre ses traits phénotypiques (i.e., morphologiques, comportementaux et physiologiques) et ses traits d'histoire de vie. Les résultats obtenus au cours de ce travail de thèse indiquent l'existence de liens entre la niche trophique et la morphologie des individus (*Chap. III, Chap. IV*) ainsi que des liens potentiels entre la morphologie et le taux de consommation des ressources (*Chap. VI*). La niche trophique et le taux de consommation des ressources sont susceptibles de modifier les effets indirects des individus sur les processus écosystémiques en modulant les taux d'excrétion des nutriments (*Chap. V*; Glaholt & Vanni 2005). Par conséquent ces résultats suggèrent que l'utilisation d'une approche multi-traits (Raffard et al. In prep), intégrant également des traits d'effets (e.g., traits stœchiométriques), pourrait permettre de mieux comprendre le rôle de la variabilité intraspécifique dans la modulation des effets des individus sur le fonctionnement des individus.

VIII.3 - Mécanismes évolutifs de la variabilité intraspécifique et boucle de rétroaction

Si ce travail de thèse a permis de déterminer le rôle de certains facteurs écologiques influençant la variabilité phénotypique au sein des espèces invasives, il n'a pas eu pour objectif d'expliquer les mécanismes évolutifs associés à cette variabilité intraspécifique (Fig. VIII.4). Les variations phénotypiques peuvent être dues à des différences génétiques (Losos 2000, Rundel & Price 2009) ou à une forte plasticité phénotypique (Agrawal 2001) des traits étudiés le long de gradients environnementaux. La plasticité phénotypique favorise les ajustements relativement immédiats des traits phénotypiques face aux changements rapides des conditions environnementales. Il est communément admis que la plasticité phénotypique est privilégiée dans des environnements où les pressions de sélection sont instables. Comprendre l'importance relative de ces deux mécanismes est d'un enjeu majeur pour prédire les réponses

phénotypiques des espèces aux contraintes environnementales. Cependant, la variabilité génétique et la plasticité phénotypique ne sont pas mutuellement exclusifs (Pfenning et al. 2010), notamment parce que la plasticité peut être sous contrôle génétique et donc peut également être modulée par la sélection naturelle (plasticité adaptative; Scheiner & Lyman 1991). Des études génétiques ont montré que des divergences de traits au sein des espèces étaient principalement induites par de la plasticité phénotypique mais incluaient également une composante génétique (Svanbäck & Eklöv 2006, Faulks et al. 2015). Ceci permettrait d'expliquer la forte variabilité généralement observée dans le degré de divergence entre plusieurs systèmes (Bartels et al. 2012, Faulks et al. 2015). L'adaptation locale est un cas particulier de l'adaptation génétique qui prédit que, dans un environnement donné, le génotype local possède une fitness relative plus élevée que les génotypes originaires d'un autre environnement (Williams 1966). C'est un processus qui nécessite des flux de gènes réduits entre les populations (i.e., faible dispersion), des traits fortement liés à la fitness et une interaction entre le génotype et l'environnement (Kawecki & Ebert 2004). L'adaptation locale a principalement été testée dans des aires de distribution natives des espèces (Waser & Price 1985, Grøndahl & Ehlers 2008, Brady et al. 2012), mais reste peu étudiée chez les espèces invasives (Wesley et al. 2012), malgré son rôle dans le maintien et l'évolution des espèces invasives. Les espèces invasives étudiées dans le cadre de ce travail de thèse semblent être propices au développement de l'adaptation locale du fait de l'isolement de chaque lac de gravière qui permet de limiter la dispersion des individus entre les populations. De plus, la pression de pêche imposait une forte sélection sur les populations invasives et affectait les performances des individus (*Chap. III*). Cette hypothèse d'adaptation locale peut être testée via une transplantation réciproque des individus du génotype 1 dans l'environnement 2 et des génotypes 2 dans l'environnement 1. L'hypothèse de l'adaptation locale est validée si la survie des génotypes locaux est meilleure que celle des génotypes non locaux dans chacun des environnements (Kawecki & Ebert 2004). La mise en évidence d'adaptation locale des espèces invasives dans des environnements récemment envahis témoignerait de l'adaptation rapide des espèces invasives et donc de leur capacité à coloniser de nouveaux habitats et continuer leur propagation (Facon et al. 2006).

Il est de plus en plus évident que les changements écologiques et évolutifs peuvent se produire sur des pas de temps similaires (Hairston et al. 2005, Pelletier et al.

2009). Le défi actuel en écologie est d'identifier les interactions réciproques entre l'évolution des traits des organismes et les dynamiques de l'écosystème, de façon à mieux prédire l'évolution des traits phénotypiques et de l'écosystème (Matthews et al. 2011b). Les boucles de rétroaction éco-évolutives (Fig. VIII.4) sont définies comme étant des interactions cycliques entre l'écologie et l'évolution, c'est-à-dire que les effets de l'écosystème sur les réponses évolutives des traits des individus influencent en retour le fonctionnement de l'écosystème (Post & Palkovacs 2009). Bien que le rôle de la variabilité intraspécifique sur le fonctionnement des écosystèmes a été démontré (Harmon et al. 2009, Bassar et al. 2010) et est indispensable dans la dynamique des boucles éco-évolutives, rares sont les études qui ont explicitement testé l'effet des divergences écosystémiques sur les générations futures (Matthews et al. 2016). L'étude des dynamiques éco-évolutives chez les espèces invasives semble être une piste prometteuse. Le développement des approches éco-évolutives en écologie des invasions biologiques permettrait en effet d'apporter une vision plus complète et intégrative des mécanismes responsables du succès des invasions biologiques et des impacts écologiques des espèces invasives sur les communautés natives et les écosystèmes receveurs (Saul et al. 2013).

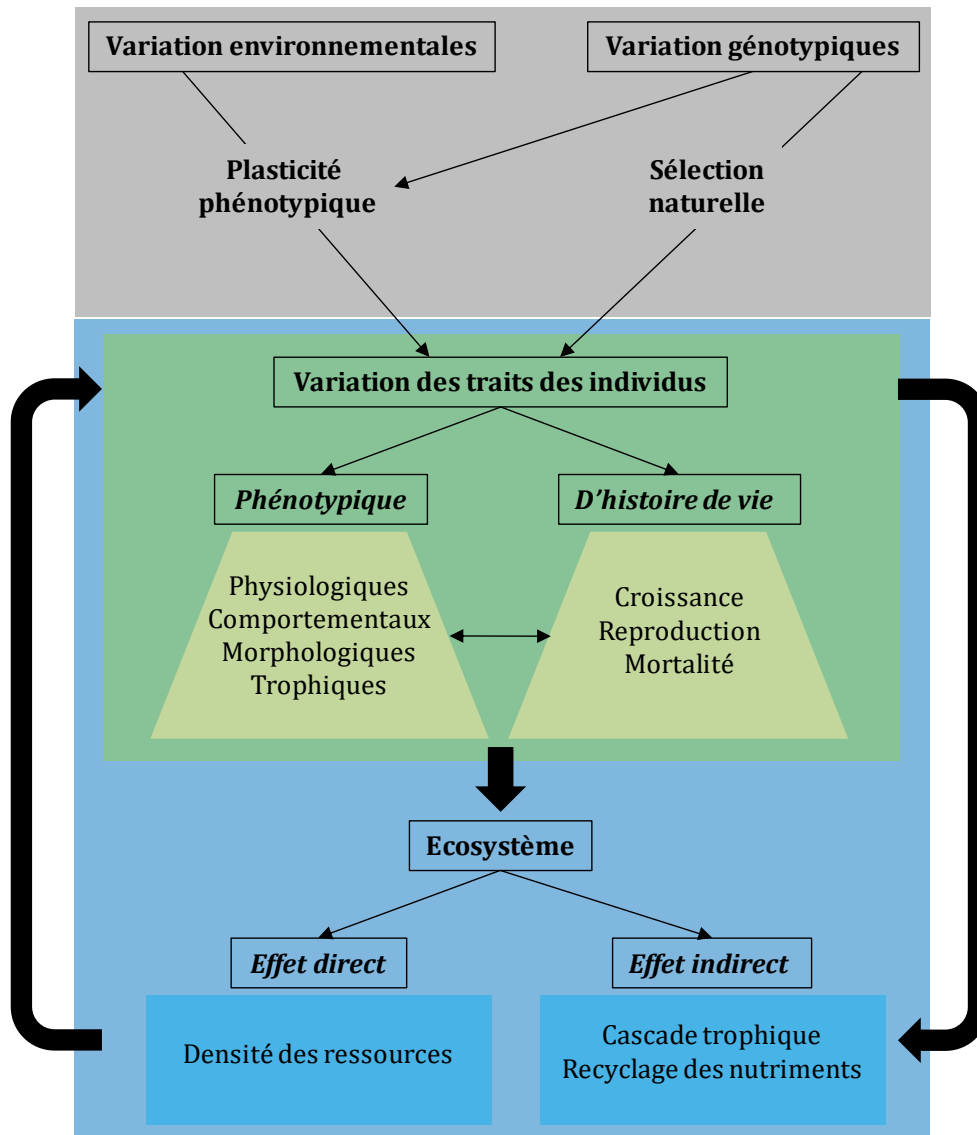


Figure VIII.4 Schéma synthétique des mécanismes évolutifs impliqués dans la mise en place de la variabilité phénotypique. Ces mécanismes en agissant sur l'évolution des individus affectent le fonctionnement des écosystèmes qui en retour modifient l'évolution des individus via des boucles de rétroaction éco-évolutives.

CHAPITRE IX

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INTRASPECIFIC VARIABILITY IN INVASIVE SPECIES AND ITS CONSEQUENCES ON AQUATIC ECOSYSTEM FUNCTIONING

ABSTRACT

While biological invasions are widely recognized as a major cause of ecosystem changes, the ecological impacts of invasive species could be modulated by intraspecific variability in ecological traits occurring between and within populations. The present work demonstrated, at different geographical scales, the existence of a strong phenotypic variability within two freshwater invaders, *Lepomis gibbosus* and *Procambarus clarkii*. In addition, phenotypic responses to environmental conditions was demonstrated to be complex, revealing notably that the methods used to control invasive populations can be counter-productive and that the colonisation history of invasive populations is an important driver of phenotype-environment relationships. Experimental approaches also demonstrated that intraspecific variability modulated the intensity of the ecological impacts of invasive species on community structure and ecosystem functioning. These findings strongly support the idea that integrating intraspecific variability in the context of biological invasions is essential to better appreciate their impacts on recipient ecosystem and ultimately improve the efficiency of management methods based on the characteristics of invasive populations.

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TITRE : VARIABILITE INTRASPECIFIQUE CHEZ LES ESPECES INVASIVES ET SES CONSEQUENCES SUR LE FONCTIONNEMENT DES ECOSYSTEMES AQUATIQUES

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LIEU ET DATE DE SOUTENANCE: Université Paul Sabatier, le 8 Décembre 2016

RESUME

Les invasions biologiques sont considérées comme étant une cause majeure de changement des écosystèmes. Les impacts écologiques des espèces invasives pourraient être modulés par la variabilité intraspécifique des traits biologiques et écologiques entre et au sein de leurs populations. Cette thèse a révélé, à différentes échelles spatiales, la présence de variabilités phénotypiques fortes chez deux espèces invasives, *Lepomis gibbosus* et *Procambarus clarkii*. Il est apparu que les réponses phénotypiques des individus aux conditions environnementales pourraient être complexes, révélant notamment la contre productivité des méthodes de gestion utilisées pour contrôler les populations invasives et l'importance de l'histoire de colonisation des populations dans les relations phénotype-environnement. Des expérimentations ont également démontré comment la variabilité intraspécifique pourrait moduler les effets des espèces invasives sur la structure des communautés et le fonctionnement des écosystèmes. Ces résultats soutiennent l'idée qu'intégrer la variabilité intraspécifique dans un contexte d'invasion biologique est indispensable afin de mieux évaluer les impacts et adapter les méthodes de gestion aux caractéristiques des populations invasifs.

MOT-CLES : Invasion biologique; Ecologie fonctionnelle; Relations trophiques; Ecosystème d'eau douce; Eco-morphologie; Variabilité intraspécifique

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