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Avant-propos

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Les travaux effectués aux cours de cette thèse ont mené à la rédaction de quatre articles (***PI*** à ***PIV***) publiés, soumis ou en préparation pour des revues à comité de lecture. Des collaborations menées avec des collègues du laboratoire Evolution et Diversité Biologique de Toulouse (France) et du laboratoire d'hydrobiologie de Wuhan (Chine) ont donné lieu à la publication de deux autres articles (***AI*** et ***AII***) qui sont présentés en annexes.

PI. Chevalier M, Laffaille P, Ferdy J-B et Grenouillet G (2014). Measurements of spatial population synchrony: influence of time series transformations. Soumis à ***Oecologia***.

PII. Chevalier M, Laffaille P et Grenouillet G (2014). Spatial synchrony in stream fish populations: influence of species traits. ***Ecography*** 37: 001–009.

PIII. Chevalier M, Cornuault J, Laffaille P et Grenouillet G. Disentangling the influence of climatic variables on spatial and temporal variations of freshwater fish population dynamics. (En preparation).

PIV. Chevalier M, Comte L, Laffaille P et Grenouillet G (2014). Relating species traits to population dynamics in stream fishes. Soumis à ***Ecology***.

AI. Lin M, Chevalier M, Lek S, Zhang L, Gozlan R.E, Liu J, Zhang T, Ye S, Li W et Li Z (2014). Eutrophication as a driver of *r*-selection traits in a freshwater fish. ***Journal of freshwater biology*** (sous presse)***.***

AII. Paz-Vinas I, Comte L, Chevalier M, Dubut V, Veyssière C, Grenouillet G, Loot G & Blanchet S (2013). Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species. ***Ecology and Evolution*** 3: 2696–2710.

Introduction générale

Esox Lucius

1. Le réchauffement climatique

A l'échelle du globe, la température moyenne de l'air a augmenté de 0,85°C au cours des 30 dernières années et devrait continuer à augmenter dans le futur quelles que soient les politiques de gestion mises en place (Stocker *et al.*, 2013). Par ailleurs, bien que ces modifications de température puissent être considérées comme homogènes à une échelle plus ou moins locale, elles présentent une forte hétérogénéité à l'échelle mondiale (Walther *et al.*, 2002). Les régions continentales et de hautes latitudes présentent un plus fort réchauffement que les régions océaniques et de faibles latitudes (Figure 1). Ce réchauffement climatique, et plus particulièrement sa rapidité, a très largement mobilisé l'opinion publique, notamment pour des raisons socio-économiques. De larges ressources financières ont ainsi été allouées à la recherche sur le réchauffement climatique, afin de déterminer à quel point le climat se réchauffait, d'attribuer la part des activités humaines dans ce réchauffement, de prédire les changements attendus dans le futur et de déterminer comment ces changements allaient impacter les organismes vivants, la biodiversité, le fonctionnement des écosystèmes et les services que ces écosystèmes fournissent à l'homme (Stocker *et al.*, 2013).

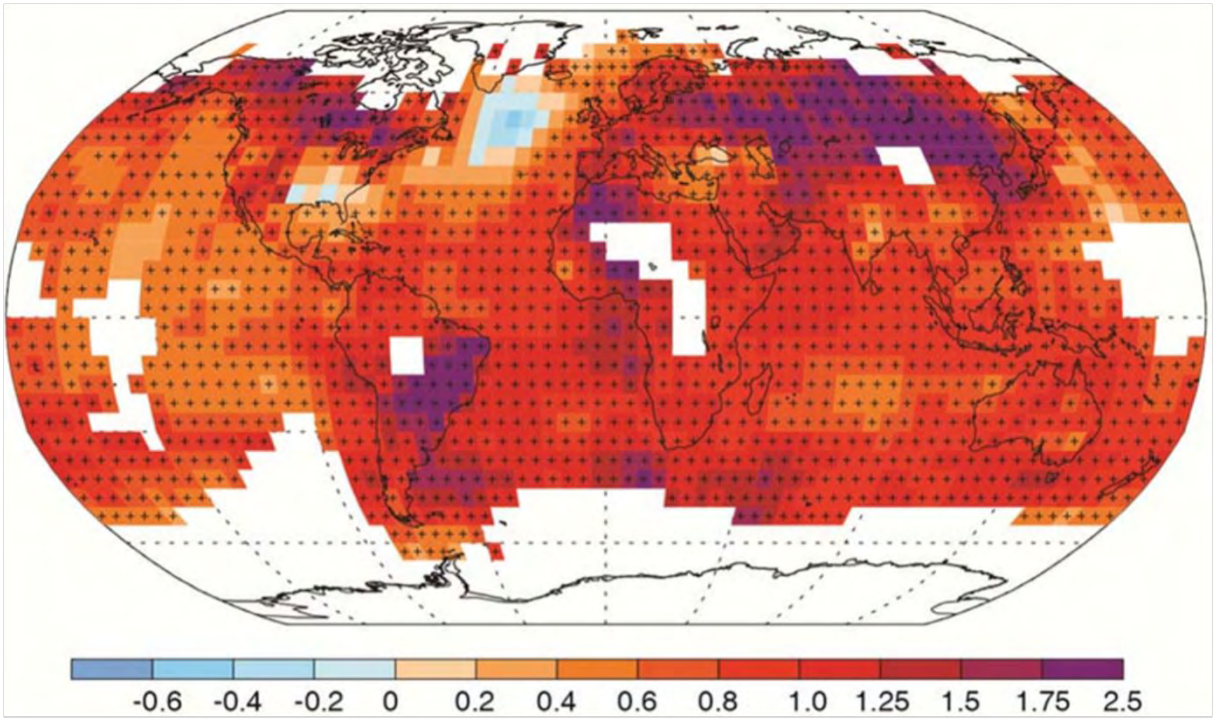


Figure 1. Carte représentant les changements de température observés pour la période 1901-2012 au niveau mondial (°C). Les zones blanches indiquent une absence d'information sur les données de température. (Source : Stocker *et al.*, 2013).

Depuis, plusieurs études ont montré que le réchauffement climatique avait une influence sur les espèces animales et végétales. Globalement, trois grands types de réponses écologiques (phénologique, distribution, physiologique) ont été mis en évidence (e.g. Parmesan, 1996; Hughes, 2000; Parmesan & Yohe, 2003; Root *et al.*, 2003). Le fait que ces réponses aient été décrites dans différents endroits du globe et sur des espèces très différentes fait qu'elles sont aujourd'hui considérées comme les empreintes du changement climatique sur les organismes vivants (Parmesan & Yohe, 2003; Root *et al.*, 2003). Par exemple, de nombreux événements du cycle de vie des organismes (e.g. la migration des oiseaux) sont déclenchés par des variations saisonnières ou interannuelles du climat (Jonsson & Jonsson, 2009). L'étude de ces événements, dits phénologiques, a montré des changements significatifs au cours des dernières décennies qui pouvaient s'expliquer par le réchauffement climatique. En effet, plusieurs études on mis en évidence une relation négative entre l'augmentation des températures et les dates de migrations des oiseaux (Végvári *et al.*, 2010), des poissons (Anderson *et al.*, 2013), les dates de floraison des plantes (Primack *et al.*, 2009) ou encore les dates de pontes des amphibiens (Gibbs & Breisch, 2001). Ainsi, ces événements phénologiques sont de plus en plus précoces. Les changements climatiques peuvent également conduire à des modifications du métabolisme et du développement de nombreux organismes ainsi qu'à des altérations de certains processus tels que la photosynthèse, la respiration ou encore la croissance chez les plantes (Hughes, 2000). Par exemple, une augmentation de température peut amener les organismes à excéder leur limite de tolérance thermique et ainsi causer la mort des individus (Cunningham & Moors, 1994). Outre les changements phénologiques et physiologiques, le réchauffement climatique peut conduire à des changements dans la distribution des espèces (Araújo & Rahbek, 2006). C'est par exemple le cas de nombreuses espèces de poissons d'eau douce en France qui remontent vers des altitudes ou des latitudes plus élevées pour suivre leur niche écologique, c'est à dire les conditions qui maximisent leur survie et leur reproduction (Comte & Grenouillet, 2013). Des changements similaires ont été observés chez plusieurs espèces de papillons (Parmesan, 1996; Parmesan *et al.*, 1999; Chen *et al.*, 2011), d'oiseaux (Thomas & Lennon, 1999; Devictor *et al.*, 2008), de mammifères (Moritz *et al.*, 2008) ou encore de plantes (Kelly & Goulden, 2008; Lenoir *et al.*, 2008). Ces changements de phénologies, de physiologies et de distributions peuvent conduire *in fine* à des réorganisations plus ou moins profondes des communautés qui peuvent alors se traduire par une altération du fonctionnement global des écosystèmes (Figure 2; Loreau *et al.*, 2001; Lavorel & Garnier, 2002). Par exemple, Sagarin & Barry (1999) ont observé une réorganisation des communautés de macroinvertébrés dans une zone intertidales qu'ils ont attribué à une augmentation des températures de plus de 0,7°C au cours des 60 dernières années.

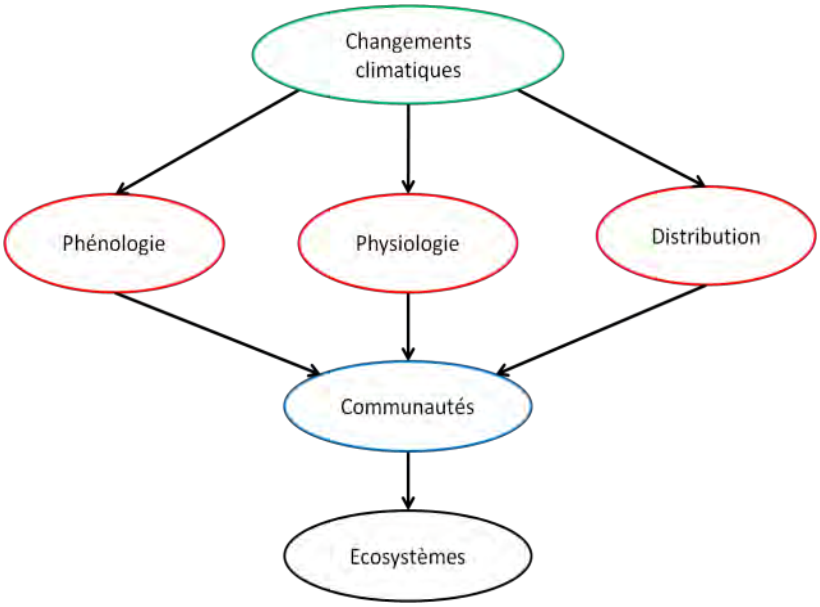


Figure 2. Réponses des espèces face aux changements climatiques et impact sur les communautés et le fonctionnement des écosystèmes (modifié d'après Hughes, 2000).

En dépit de l'important nombre d'études traitant de l'influence des changements climatiques sur les patrons de biodiversité, peu de ces études se sont intéressées à l'influence de ces changements sur les dynamiques de populations (i.e. sur les fluctuations spatio-temporelles des effectifs des populations). En effet, la grande majorité de ces études reposent sur des modèles prédictifs de distribution d'espèce qui consistent à comparer les distributions actuelles des espèces avec celles attendues sous l'influence du changement climatique (Guisan & Zimmermann, 2000). Une limite majeure de ces modèles est qu'ils ne prennent pas en compte les dynamiques des populations qui sont pourtant impliquées dans le déterminisme de la distribution des espèces, de la structure des populations ainsi que dans les risques d'extinction à une échelle locale (Bellard *et al.*, 2012). Les modèles de distribution d'espèces sont donc des modèles descriptifs qui ne permettent pas d'identifier les mécanismes par lesquels les espèces s'éteignent ou changent de distribution. Ainsi, bien que ces modèles permettent d'identifier de façon remarquable les effets des changements climatiques sur la distribution des espèces à de larges échelles, ils n'ont qu'une application limitée en ce qui concerne l'identification des mécanismes responsables de ces changements. En conséquence, de plus en plus d'études soulignent les limites des modèles de distribution et l'importance de prendre en compte la dynamique des populations pour décrire les patrons de biodiversité et l'influence des changements climatiques sur ces patrons (Guisan & Thuiller, 2005; Brook *et al.*, 2009; Bellard *et al.*, 2012).

2. La dynamique des populations

La dynamique des populations cherche à comprendre comment et pourquoi les tailles de populations changent dans le temps et l'espace (Figure 3; Turchin, 1999). Quatre composantes influencent le nombre d'individus dans les populations : les naissances (ou la natalité), les décès (ou la mortalité), l'émigration et l'immigration. Le "comment" concerne la quantification du changement de la taille des populations en fonction de ces composantes, qui dépendent elle-même de certains paramètres démographiques tels que la survie et la reproduction. Le "pourquoi" a pour but d'identifier les facteurs (biotiques et/ou abiotiques) qui ont mené à la modification de ces composantes. Ces facteurs sont généralement classés en deux catégories : intrinsèques (i.e. qui englobent toutes les interactions entre individus au sein de la population et qui sont densité-dépendants) et extrinsèques (e.g. le climat). Une population peut donc être définie (1) par un taux d'accroissement (facteur intrinsèque) qui quantifie le taux auquel la taille de la population augmente en l'absence de densité-dépendance, (2) par un processus de densité-dépendance (facteur intrinsèque) qui influence le taux d'accroissement de la population, (3) par une composante environnementale (facteur extrinsèque) qui influence le taux d'accroissement et (4) par une composante de migration (facteur extrinsèque ou intrinsèque s'il dépend de la densité d'individus dans la population). La contribution relative de l'influence des facteurs intrinsèques et extrinsèques à la dynamique des populations est à l'origine d'un très long débat (Cappuccino & Price, 1995).

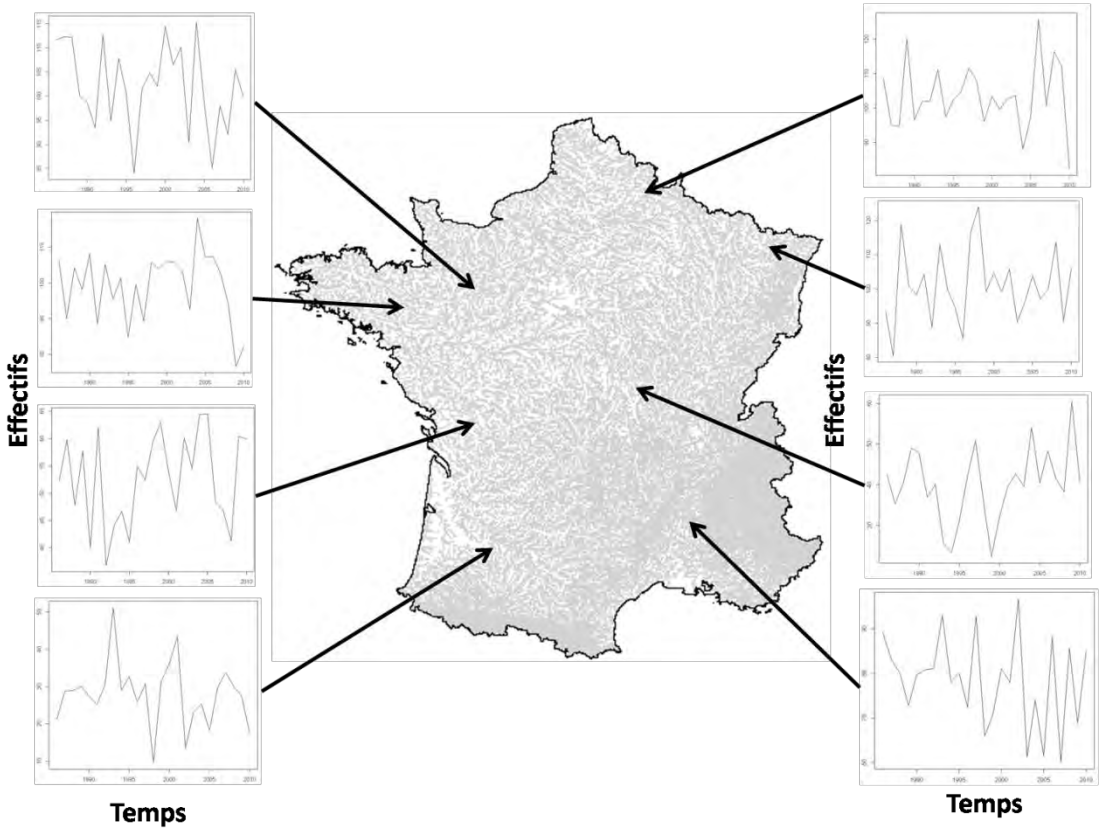


Figure 3. Dynamique temporelle de populations à différentes localité en France.

2.1. Un long débat

Depuis les travaux de Lotka (1925), Volterra (1927) et Elton (1924), s'en est suivi un long débat sur l'importance relative des facteurs intrinsèques et extrinsèques sur la détermination des variations de tailles des populations. Dans les années 1950, le débat a atteint plusieurs pics sous l'influence de deux principaux protagonistes. Nicholson (1933) considérait que les populations étaient principalement sous l'influence de processus densité-dépendants alors qu'Andrewartha & Birch (1954) soutenait que des processus environnementaux prédominaient. Après la publication des travaux de Nicholson en 1957, l'opinion scientifique s'est largement rangée à sa cause et de nombreuses études ont alors cherché à mettre en évidence des processus de densité-dépendances *via* l'étude de séries temporelles d'abondances (e.g. Morris, 1959; Varley & Gradwell, 1960). La découverte par May au cours des années 1970 (May, 1976) que de simples modèles de densité-dépendance pouvaient générer des dynamiques chaotiques suggéra que les fluctuations de populations apparemment anarchiques pouvaient s'expliquer en fait par de simples processus déterministes (e.g. densité-dépendance). Cette découverte renforça l'idée que les processus extrinsèques n'avaient pas ou peu d'influence sur les dynamiques de populations. Cependant, l'accumulation d'études ne parvenant pas à mettre en évidence de processus densité-dépendants dans les populations alimenta la controverse (e.g. Dempster, 1983; Gaston & Lawton, 1987; Stiling, 1987; Den Boer & Reddingius, 1989; Reddingius & Den Boer, 1989).

2.2. Difficulté de mettre en évidence de la densité-dépendance

2.2.1. Tester la densité-dépendance

Alors que le débat faisait rage, de nombreuses méthodes statistiques ont été développées pour détecter des processus de densité-dépendance dans les données empiriques (Bulmer, 1975; Pollard *et al.*, 1987; Reddingius & Den Boer, 1989; Turchin, 1990; Dennis & Taper, 1994; Wolda *et al.*, 1994). Quelles que soient les méthodes (paramétriques, non paramétriques, linéaires, non linéaires, ...), celles-ci consistaient à mettre en évidence une relation significative entre les effectifs d'une population au temps t et les effectifs de cette même population au pas de temps précédent (i.e. $N_t=f(N_{t-1})$, f étant une fonction quelconque). Une relation négative indiquait une influence négative de la densité qui peut s'expliquer, par exemple, par une augmentation de la compétition pour les ressources lorsque la densité d'individus est importante (Fowler, 1981). A l'inverse, une relation positive indiquait une influence positive de la densité comme par exemple un accès facilité à la reproduction lorsque les densités d'individus sont faibles (effet Allee, Courchamp et al. 1999, Morris 2002). Cependant, aucun de ces tests ne s'est avéré clairement supérieur aux autres (Brook & Bradshaw, 2006). Après plusieurs années de débats et de tests sur des séries temporelles d'abondances, un résultat s'est dégagé : plus les séries sont longues et plus la probabilité de détecter de la densité-dépendance est grande (Woiwod & Hanski, 1992; Wolda & Dennis,

1993). Par exemple, Woiwod et Hanski (1992) ont analysé près de 6000 séries temporelles d'abondances et ont trouvé qu'environ 50% d'entre elles présentaient de la densité-dépendance. Cependant, après avoir exclu les séries temporelles qui avaient moins de 20 années de données, ce pourcentage était de 70%. En conséquence, les absences de résultats significatifs dans les études antérieures ont été attribuées à l'utilisation de données inappropriées et non à l'absence de densité-dépendance dans les populations étudiées. Cependant, même en considérant des séries temporelles relativement longues, les résultats restent contradictoires. Par exemple, les résultats de Ziebarth et al. (2010) suggèrent que la plupart des populations ne présentent pas de densité-dépendance alors que les résultats de Brook & Bradshaw (2006) suggèrent l'inverse. Ces différences peuvent s'expliquer par la considération de différentes séries temporelles ainsi que par des différences dans les méthodes utilisées pour mettre en évidence les processus de densité-dépendance. Quelle que soit l'origine de ces différences, aucune de ces deux études n'a pris en compte les incertitudes associées aux estimations d'abondances ce qui rend leur interprétation difficile (Knape & De Valpine, 2012).

2.2.2. Les erreurs de mesures

Les estimations et les tests de densité-dépendance sont sensibles aux erreurs de mesures des effectifs de populations (Freckleton *et al.*, 2006). Ces erreurs augmentent le risque de première espèce (α) des tests de densité-dépendance et tendent à surestimer les effets de la densité-dépendance sur les dynamiques de populations (Shenk *et al.*, 1998). Or, les séries temporelles d'abondances ne contiennent que très rarement des comptages exacts des effectifs de populations (Freckleton *et al.*, 2006). Ces erreurs de mesures peuvent s'expliquer par des erreurs d'observations, par un protocole d'échantillonnage mal adapté à la population étudiée ou encore par le fait que les populations sont distribuées de façon hétérogène dans l'espace. De simples procédures ont été suggérées pour corriger les incertitudes de mesures des tailles de populations (e.g. Solow, 1998). Cependant, ces méthodes nécessitent de connaître la variance de l'incertitude concernant la taille de la population, une information qui n'est pas disponible pour la plupart des séries temporelles d'abondances. Une approche plus directe pour prendre en compte ces incertitudes réside dans l'utilisation de modèles états-espaces. Ces modèles comprennent deux équations, l'une qui modélise le processus de dynamique de populations (équation de transition ou de processus), l'autre qui prend en compte les erreurs de mesures (équation d'observation) (De Valpine & Hastings, 2002; Calder *et al.*, 2003; Clark & Bjørnstad, 2004; Dennis *et al.*, 2006). Les estimations de densité-dépendance issues des modèles états-espaces tendent à être moins biaisées que les estimations qui ignorent les incertitudes de mesures (Freckleton *et al.*, 2006) même si dans certains cas la variance des estimations peut être large (Knape, 2008). En utilisant ce modèle sur plus de 600 séries temporelles, Knape & De Valpine (2012) ont montré qu'environ 45% de ces séries présentaient de la densité-dépendance mais que son effet était faible et difficile à détecter pour une large fraction d'entre elles. Ils concluent que lorsque les incertitudes de mesures ne sont pas prises en compte, la magnitude et la

probabilité de détection de la densité-dépendance augmentent fortement et biaise les conclusions relatives à l'influence de ce processus dans les populations.

2.2.3. Un délai dans les processus de densité-dépendance

Les processus de densité-dépendance peuvent agir sur les populations avec un certain délai (Turchin, 1990; Forchhammer *et al.*, 1998; Fromentin *et al.*, 2001) qui est à l'origine des variations cycliques des effectifs de populations d'insectes (Turchin, 1990), de mammifères (Stenseth *et al.*, 1996; Huitu *et al.*, 2004) ou encore de poissons (Pedraza-Garcia & Cubillos, 2007). Les mécanismes sous-jacents sont variés et correspondent en général à des interactions trophiques. Par exemple, la compétition entre espèces pour les ressources et la prédation sont les facteurs principalement impliqués dans les processus de densité-dépendance différés chez les lemmings (Framstad *et al.*, 1997). La compétition entre individus appartenant à différentes classes d'âges (Briggs *et al.*, 2000) ou encore les maladies (Bjørnstad *et al.*, 2001) sont d'autres facteurs à l'origine d'une influence différée de la densité sur les populations. Ainsi, ne pas considérer l'influence de ces facteurs sur les dynamiques de populations peut mener à faussement conclure que les populations ne sont pas sous l'influence de processus densité-dépendants (Turchin, 1990). Au même titre que la densité-dépendance, ce phénomène tend cependant à être surestimé lorsque les erreurs de mesures ne sont pas prises en considération (Solow, 2001) ou lorsque les données présentent de l'autocorrélation temporelle (Williams & Liebhold, 1995).

Pour déterminer si les populations sont sous l'influence de processus densité-dépendants, il faut donc considérer des séries temporelles relativement longues, prendre en compte les erreurs de mesures avec des méthodes statistiques appropriées et prendre en compte le fait que la densité-dépendance puisse agir sur la dynamique des populations avec un certain retard.

2.3. Un consensus

Au cours de ces années de débats, un consensus est né au sein de la communauté scientifique; celui que les processus densité-dépendants et densité-indépendants peuvent agir simultanément sur les populations. Par exemple, la dynamique temporelle des populations de cerf élaphe (*Cervus elaphus*) et de mésanges charbonnières (*Parus major*) sont significativement influencées par des processus de densité-dépendance et par des perturbations climatiques (Forchhammer et al. 1998; Grøtan et al. 2009). Par ailleurs, Kölzsch et al. (2007) ont montré que la prise en compte de facteurs environnementaux dans les séries temporelles améliorait la détection et l'estimation des processus densité-dépendants. Enfin, il a été montré que les processus densité-dépendants et densité-indépendants pouvaient interagir l'un avec l'autre pour former des patrons complexes de dynamique de population en fonction de la structure d'âge de la population, de la présence ou non de prédateurs et/ou de parasites et de la disponibilité des ressources (Bjørnstad & Grenfell, 2001; Coulson *et al.*, 2001; Lima *et*

al., 2002; Stenseth *et al.*, 2002). Par exemple, les déclins récurrents de populations de moutons sur l'archipel S^t Kilda au cours de l'hiver s'expliquent par une modification des patrons de densité-dépendance en fonction du climat et de la disponibilité des ressources (Grenfell *et al.*, 1998).

Afin de prédire les effets du changement climatique sur les populations, il est donc primordial de quantifier l'influence relative des facteurs densité-dépendants et densité-indépendants et de déterminer comment ces facteurs interagissent pour générer les patrons observés de dynamique de populations. Aujourd'hui, la plupart des recherches se concentrent sur l'influence de chaque facteur séparément et les interactions sont rarement quantifiées.

3. Patrons spatiaux des dynamiques de populations

Une des questions essentielles qu'il faut se poser lorsqu'on étudie la dynamique des populations est de savoir à quel point l'étude d'une population peut être généralisable au niveau de l'espèce. De plus en plus d'études montrent que les dynamiques de populations peuvent présenter des patrons spatiaux plus ou moins complexes (Grenfell *et al.*, 1998; Saether *et al.*, 2003, 2008; Williams *et al.*, 2003; Grøtan *et al.*, 2009). Caractériser ces patrons et identifier leurs déterminants sont des objectifs centraux de la dynamique des populations puisque l'étude de ces patrons pourrait permettre de prédire les conséquences du réchauffement climatique sur les populations en fonction de leur répartition spatiale (i.e. géographique ou le long de gradients environnementaux).

3.1. Synchronisme spatial des dynamiques de populations

3.1.1. Un phénomène très répandu

Il a souvent été observé que les effectifs de différentes populations pouvaient fluctuer de façon plus ou moins synchrone (Figure 4A). Ce synchronisme spatial des dynamiques de populations a été décrit pour de très nombreux taxa comme par exemple les mammifères (Post & Forchhammer, 2002; Yoccoz & Ims, 2004), les oiseaux (Paradis *et al.*, 1999, 2000; Cattadori *et al.*, 2000, 2005), les plantes (Koenig, 1999; Liebhold *et al.*, 2004), les amphibiens (Trenham *et al.*, 2003; Petranka *et al.*, 2004; Aubry *et al.*, 2012), les insectes (Sutcliffe *et al.*, 1996; Peltonen *et al.*, 2002; Haynes *et al.*, 2009) ou encore les poissons (Tedesco & Hugueny, 2004; Cheal *et al.*, 2007; Alheit & Bakun, 2010; Aubry *et al.*, 2012). Généralement, le degré de synchronisme des populations décroît lorsque la distance entre les populations augmente (Ranta *et al.*, 1995; Bjørnstad *et al.*, 1999) même si dans certains cas les patrons peuvent êtres beaucoup plus complexes (Ranta *et al.*, 1997; Tenow *et al.*, 2007). Outre le synchronisme des effectifs de populations, certains paramètres démographiques tels que la reproduction (Chaloupka, 2001), la mortalité (Viboud *et al.*, 2006), le taux d'accroissement (Robinson *et*

al., 2013), ou encore la structure d'âge de la population (Trenham *et al.*, 2001) peuvent présenter du synchronisme spatial. Ce phénomène a également été observé entre populations de différentes espèces (Liebhold *et al.*, 2004; Raimondo & Liebhold, 2004; Robinson *et al.*, 2013) comme par exemple entre des proies et leurs prédateurs. Dans ce type d'interactions trophiques, on observe cependant un décalage des effectifs de proies et de prédateurs pouvant conduire à du synchronisme différé (Figure 4B). De la même manière, des espèces qui partagent un prédateur commun (Jones *et al.*, 2003) ou une ressource commune (Koenig, 2001; Jones *et al.*, 2003) peuvent présenter un certain degré de synchronisme spatial.

3.1.2. Mesurer et tester le synchronisme

Une des façons de mesurer le synchronisme entre deux populations est de calculer la corrélation entre les séries temporelles d'abondance de ces deux populations à l'aide de coefficients de corrélations de Pearson ou de Spearman (Liebhold *et al.*, 2004). Toutefois, Hanski & Woiwod (1993) suggèrent que le synchronisme soit mesuré non pas sur les fluctuations d'effectifs mais sur les fluctuations de changements d'effectifs entre années (i.e. sur le ratio des effectifs au temps t et des effectifs au temps t-1 ; N_t/N_{t-1}). Les différences entre les deux méthodes sont généralement faibles et la méthode la plus couramment utilisée est la première (Buonaccorsi *et al.*, 2001). Deux importants facteurs à prendre en considération dans les mesures de synchronisme concernent le degré d'autocorrélation temporelle et la tendance (croissante ou décroissante) à long terme (Bjørnstad *et al.*, 1999). En effet, ces deux facteurs tendent à augmenter le risque de première espèce et donc à détecter du synchronisme alors qu'il n'y en pas (Royama, 1992). La présence d'une tendance dans les séries temporelles tend également à masquer le synchronisme des fluctuations d'abondance à court terme (Buonaccorsi *et al.*, 2001). Plusieurs méthodes existent pour prendre en compte ces deux facteurs dans les mesures de synchronisme mais aucun consensus n'existe quant à la manière de les utiliser.

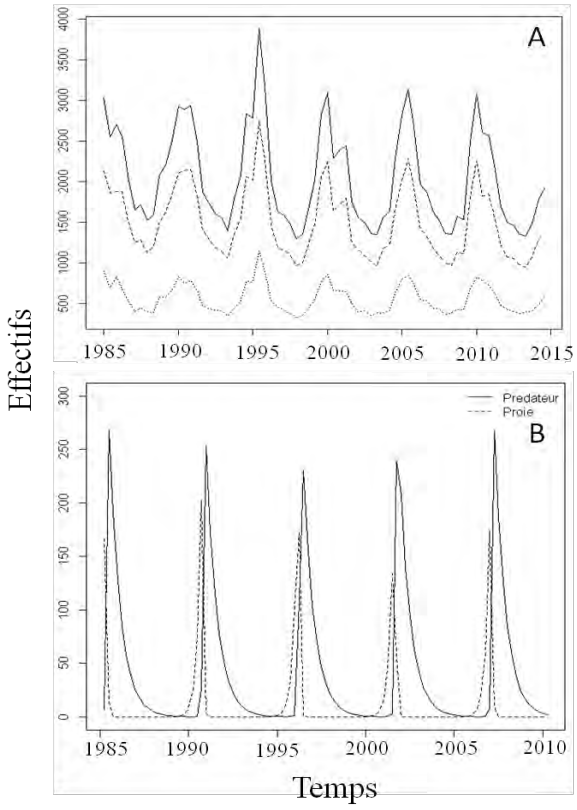


Figure 4. Exemple de synchronisme entre trois dynamiques de populations (A) et entre une dynamique de population de proies et de prédateurs (B).

Lorsque plusieurs séries temporelles sont disponibles, il est possible de tester si les populations sont significativement synchrones, si le synchronisme entre les populations diminue lorsque la distance qui les sépare augmente et d'estimer l'échelle du synchronisme (i.e. la distance à partir de laquelle les populations ne sont plus synchrones). Là encore, plusieurs méthodes existent (Bjørnstad *et al.*, 1999; Buonaccorsi *et al.*, 2001; Lillegård *et al.*, 2005). Ces méthodes sont pour la plupart des méthodes non paramétriques qui permettent de prendre en compte la non-indépendance des mesures de synchronisme entre les populations. En effet, parce qu'une même série temporelle (i.e. une population sur un site) est impliquée dans plusieurs mesures de corrélation (i.e. corrélations entre cette population et chacune des autres populations), les mesures de synchronisme entre populations ne sont pas indépendantes. Ainsi, pour tester si le synchronisme moyen des populations est significativement différent de zéro, il est recommandé d'utiliser une procédure de bootstrap (Lillegård *et al.*, 2005). Cette procédure consiste à rééchantillonner les années au sein de chaque série temporelle puis à recalculer les coefficients de corrélation entre chaque série. Pour déterminer si le degré de synchronisme diminue en fonction de la distance qui sépare les populations et estimer quelle est l'échelle de ce synchronisme il est possible d'utiliser le corrélogramme de Mantel (Mantel, 1967; Koenig, 1999) ou encore la fonction de covariance non paramétrique développée par Bjørnstad & Falck (2001). Cette dernière est basée sur des fonctions de lissages qui permettent de considérer des patrons complexes de corrélation spatiale.

Alors que l'influence des erreurs de mesures sur les paramètres de dynamiques de population tels que la densité-dépendance a reçu une attention grandissante au cours des dernières années, ce n'est que très récemment que l'influence de ces erreurs sur les mesures de synchronisme a été caractérisée (Santin-Janin *et al.*, 2014). A l'aide de modèles états-espaces, les auteurs montrent que l'incertitude autour des estimations de taille de population peut masquer le synchronisme entre populations.

3.1.3. Causes du synchronisme et risque d'extinction

Trois facteurs permettent de générer du synchronisme entre populations : la dispersion d'individus entre populations connectées, l'autocorrélation spatiale de facteurs environnementaux et les interactions trophiques ou de parasitismes (Bjørnstad *et al.*, 1999; Koenig, 1999; Liebhold *et al.*, 2004). Les populations qui sont liées entre elles par de la dispersion peuvent fluctuer de façon synchrones car l'augmentation des effectifs d'une population peut produire des émigrants qui vont alors conduire à une augmentation des effectifs dans les populations adjacentes (Ranta *et al.*, 1995, 1998). Les facteurs climatiques présentent en général de l'autocorrélation spatiale à plus ou moins large échelle spatiale (Koenig, 1999). Ainsi, dans des zones géographiques proches, le climat va avoir tendance à influencer les populations de la même manière. Moran (1953) a démontré que les populations qui avaient des coefficients de densité-dépendance égaux présentaient un degré de synchronisme identique à celui de facteurs environnementaux. Ce phénomène est appelé "effet Moran" (Royama, 1992). Enfin, des interactions impliquant des espèces qui dispersent

entre localités ou qui sont synchrones entre localités peuvent influencer le degré de synchronisme d'autres espèces (Liebhold *et al.*, 2004). Par exemple, les infections par des parasites permettent d'expliquer le synchronisme des populations de lagopède d'Ecosse (*Lagopus lagopus*) (Cattadori *et al.*, 2005).

En fonction du mécanisme impliqué dans le synchronisme des populations, la probabilité d'extinction peut varier (Hanski & Woiwod, 1993). En effet, si la cause du synchronisme des populations est la dispersion d'individus entre localités, alors une population qui subit un sévère déclin peut être "secourue" par une population d'une localité voisine, assurant ainsi la persistance de la métapopulation (Harrison & Quinn, 1989). A l'inverse, si le synchronisme des populations est causée par des facteurs environnementaux, alors l'ensemble des populations peut subir un fort déclin en même temps ce qui peut entraîner l'extinction de la métapopulation (Heino *et al.*, 1997). L'identification d'un effet Moran est d'un intérêt particulier dans un contexte de changement climatique puisque la mise évidence d'un tel mécanisme suggère que plusieurs populations peuvent répondre simultanément à certaines tendances climatiques ou à certains événements extrêmes. La mise en évidence de ce mécanisme pourrait donc permettre une meilleure identification des espèces présentant une plus grande probabilité d'extinction, et donc une meilleure évaluation de leur vulnérabilité aux changements environnementaux à venir.

Il est généralement considéré que la dispersion d'individus et les interactions entre espèces sont responsables du synchronisme à petite échelle spatiale (qui dépend la plupart du temps de la capacité de dispersion des individus) alors que les facteurs environnementaux sont responsables du synchronisme à large échelle (Ranta *et al.*, 1998). Cependant, il a été montré que la dispersion d'individus entre populations voisines pouvait interagir avec des paramètres démographiques locaux pour générer des patrons de synchronisme caractéristiques des facteurs environnementaux (Gouhier *et al.*, 2010). De plus, ces mécanismes ne sont pas mutuellement exclusifs et peuvent agir simultanément sur les populations, surtout à petites échelles spatiales (Ranta *et al.*, 1999). Tout l'enjeu est alors d'évaluer la contribution relative de chacun des facteurs au synchronisme spatial des populations. Cependant, très peu d'études ont réussi à identifier quel était le mécanisme responsable du synchronisme observé (e.g. Grenfell *et al.*, 1998; Tedesco & Hugueny, 2004). Une façon de mettre en évidence ce mécanisme est d'avoir recours à des méthodes statistiques qui permettent de retirer l'influence des autres mécanismes dans les séries temporelles (Bjørnstad *et al.*, 1999). Plusieurs méthodes existent mais leur capacité respective à mettre en évidence les mécanismes sous-jacents au synchronisme des populations reste mal appréhendée. Par ailleurs, des variations spatiales des dynamiques de populations peuvent fortement diminuer le degré de synchronisme des populations et ainsi compliquer l'identification des mécanismes à l'origine de ce synchronisme (Ranta *et al.*, 1997, 1999; Engen *et al.*, 2005a; Hugueny, 2006).

3.2. Variations géographiques

De nombreuses espèces présentent des variations intraspécifiques de la dynamique de leurs populations (e.g. Stenseth et al. 1996, Fromentin et al. 2001, Peltonen et al. 2002, Williams et al. 2003, Wang et al. 2008). Par exemple, des gradients de dynamiques de population on été mis en évidence en fonction de la latitude (Bjornstad *et al.*, 1995; Turchin & Hanski, 1997; Stenseth *et al.*, 1999; Saether *et al.*, 2003) ou de la position de la population par rapport à la limite de l'aire de répartition de l'espèce (Cattadori *et al.*, 1999; Williams *et al.*, 2003). Ces résultats suggèrent que les variations intraspécifiques des processus de dynamiques de populations peuvent être prédites à partir de connaissances sur la position géographique des populations.

L'étude des variations spatiales de dynamiques de populations requiert une estimation précise de la contribution relative des processus intrinsèques et extrinsèques qui influencent les variations interannuelles de taille de populations situées à différentes localités (Lande *et al.*, 2003). Selon Saether et al. (2008), deux mécanismes peuvent expliquer les variations intraspécifiques de dynamiques de populations. Premièrement, les conditions environnementales peuvent varier spatialement et causer des variations des patrons de densité-dépendance et/ou de taux d'accroissement, générant ainsi des variations spatiales de dynamiques de populations (Brown *et al.*, 1995; Gaston, 2003). Par exemple, Fukaya et al. (2013) ont montré que des variations spatiales de la taille des habitats avaient une influence sur les patrons de densité-dépendance. Deuxièmement, des variations spatiales de l'influence de facteurs environnementaux sur les populations peuvent générer des gradients spatiaux de dynamiques de populations (e.g. Curnutt et al. 1996, Stenseth et al. 1999, Williams et al. 2003, Saether et al. 2003). Par exemple, Williams et al. (2003) et Fukaya et al. (2014) ont montré que l'influence de l'environnement était plus forte sur les populations situées en marge des aires de répartition des espèces.

Malgré l'accumulation d'études montrant que les dynamiques de populations sont variables dans l'espace, peu (Williams *et al.*, 2003; Saether *et al.*, 2008) ont essayé d'identifier quels étaient les déterminants de ces variations. Pourtant, l'identification de ces déterminants pourrait permettre d'estimer les conséquences du réchauffement climatique sur les variations spatiales des dynamiques de populations et permettre de prédire les déplacements des espèces (Bellard *et al.*, 2012).

4. Variations interspécifiques

Des analyses comparatives de dynamiques de populations ont révélé de larges différences interspécifiques en ce qui concerne les patrons d'abondances (e.g. Fowler, 1981; Sæther & Bakke, 2000; Bjørkvoll *et al.*, 2012; Linnerud *et al.*, 2013). Ces différences suggèrent une certaine variabilité de réponse des espèces face aux changements climatiques

(Thomas *et al.*, 2004) qui pourraient s'expliquer par des différences de caractéristiques des espèces (McKinney, 1997). De fait, de nombreuses études ont cherché à identifier quelles étaient les caractéristiques des espèces qui les rendaient plus vulnérables face aux changements climatiques (e.g. Jiguet *et al.*, 2007, 2010a; Végvári *et al.*, 2010). L'approche la plus populaire à ce jour consiste à inférer le risque d'extinction des espèces à partir de changements de leur distribution (e.g. Thuiller *et al.*, 2005; Comte & Grenouillet, 2013). Cependant, cette approche ignore les dynamiques des populations qui sont pourtant directement impliquées dans le déterminisme du risque d'extinction des espèces à une échelle locale. Ainsi, identifier les caractéristiques des espèces à l'origine des variations interspécifiques de dynamiques de populations est d'un intérêt particulier dans le contexte actuel et pourrait contribuer à améliorer les prédictions relatives à l'influence des changements climatiques sur la vulnérabilité des espèces.

4.1. Les stratégies de reproduction

Depuis les travaux de MacArthur & Wilson (1967) les espèces sont répertoriées en deux grands types de stratégies de reproduction qui sont définies par des caractéristiques biologiques des espèces. Les espèces à stratégie "r" sont généralement caractérisées par une fécondité élevée, une taille réduite et une faible durée de vie alors que les espèces à stratégie "K" sont caractérisées par une fécondité réduite, une grande taille et une longue durée de vie. Les traits associées à ces stratégies de reproduction sont appelés "traits d'histoire vie" (Stearns, 1976). Les espèces à stratégie r sont supposées être plus performantes que les espèces à stratégie K dans les milieux fortement instables (i.e. stochastiques) alors que c'est l'inverse pour les milieux stables (i.e. espèces à stratégie K plus performantes). Certains taxa peuvent toutefois présenter des stratégies plus complexes. Par exemple, trois types de stratégies ont été identifiées chez les poissons (Figure 5; Winemiller 1992). Les espèces opportunistes, caractérisées par une faible durée de vie, une faible survie juvénile et une faible fécondité sont favorisées dans des environnements fortement stochastiques alors que les espèces périodiques (forte fécondité, longue durée de vie et faible survie juvénile) sont favorisées dans les environnements saisonniers. Enfin, les espèces équilibristes (forte survie juvénile, longue durée de vie et faible fécondité) sont favorisées dans des environnements stables.

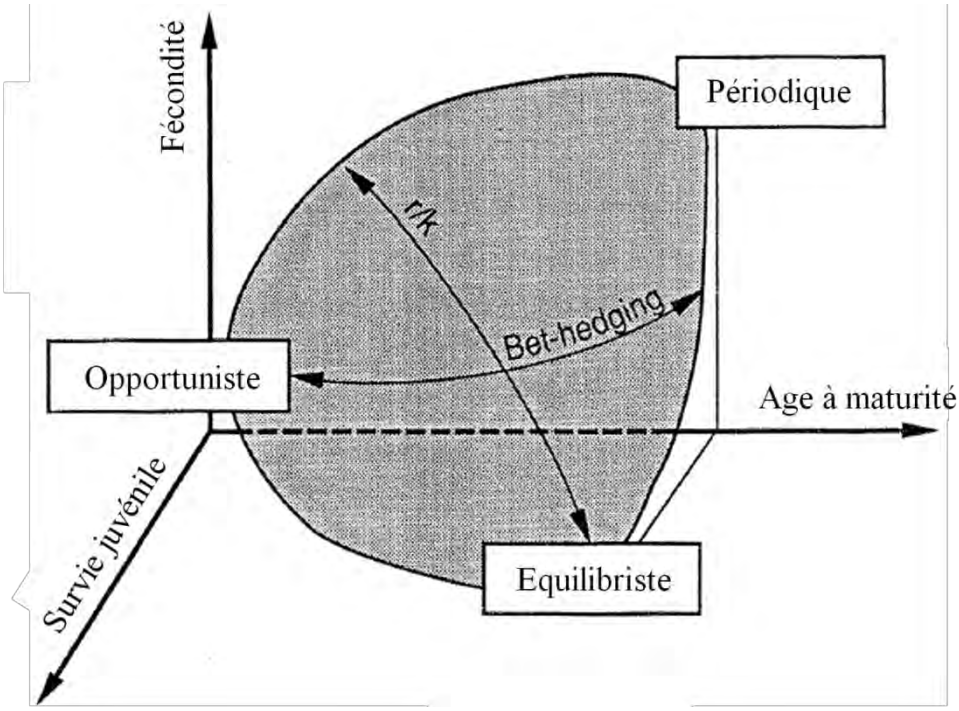


Figure 5. Modèle de surface adaptative des stratégies d'histoire de vie des poissons en fonction de trois traits démographiques (adapté de Winemiller, 1982). La stratégie opportuniste (faible survie juvénile, maturité précoce et faible fécondité) est favorisée en environnement stochastique alors que la stratégie périodique est favorisée dans les environnements saisonniers qui présentent des fluctuations cycliques. La stratégie équilibriste est favorisée dans les environnements stables. La surface grisée représente un gradient de stratégie r/K et de stratégie de bet-hedging (qui représente plus ou moins le degré d'investissement parental) dans le volume tridimensionnelle.

4.2. Influence des caractéristiques des espèces

A partir de modèles mathématiques simples, Gilpin & Ayala (1973) ont suggéré que les dynamiques de populations pouvaient présenter des patrons plus ou moins prévisibles en fonction des traits d'histoire de vie des espèces. Plus tard, Fowler (1981) a montré que les espèces à stratégies r présentaient un plus fort taux de densité-dépendance lorsque les tailles de population sont faibles alors que les espèces à stratégies K présentaient plus de densité-dépendance lorsque les densités sont élevées, c'est-à-dire proche de la capacité de charge du milieu. Depuis, plusieurs études ont montré que les dynamiques de populations (e.g. Fowler, 1981; Brown *et al.*, 1995; Saether & Engen, 2002; Saether *et al.*, 2003; Linnerud *et al.*, 2013; Sæther *et al.*, 2013) mais aussi les réponses des populations au réchauffement climatique (e.g. Jiguet *et al.*, 2007, 2010b; Végvári *et al.*, 2010) et le degré de synchronisme entre populations (e.g. Paradis *et al.*, 1999, 2000; Raimondo & Liebhold, 2004; Tedesco & Hugueny, 2006) dépendaient de certaines caractéristiques des espèces, dont les traits d'histoire de vie. Chez les poissons, Tedesco & Hugueny (2006) ont par exemple montré que les espèces périodiques étaient plus synchrones que les espèces équilibristes. En ce qui concerne les dynamiques de populations, les différences interspécifiques sont, pour le moment, largement attribuées à la position des espèces le long du gradient r-K (également appelé gradient rapide-lent, en

référence à la durée de vie moyenne des espèces appartenant à chacune des stratégies) (Myers *et al.*, 1999; Saether *et al.*, 2005; Bjørkvoll *et al.*, 2012; Linnerud *et al.*, 2013). Pour les réponses des populations au réchauffement climatique, les traits d'histoire de vie mais aussi les caractéristiques physiologiques des espèces semblent avoir un rôle déterminant. Par exemple, Jiguet et al. (2007) ont montré que les populations d'espèces qui avaient une faible gamme de tolérance thermique présentaient de plus forts déclins en réponse au réchauffement climatique que celles qui avaient une large gamme de tolérance thermique. Concernant les réponses phénologiques, les différences observées ont été attribuées à la position des espèces le long du gradient r-K (Végvári *et al.*, 2010)

Malgré l'abondante littérature traitant de l'influence des caractéristiques des espèces sur les patrons de dynamique de population, très peu (e.g. Raimondo & Liebhold, 2004; Sandvik & Erikstad, 2008; Reif *et al.*, 2011; Franzén *et al.*, 2013) ont considéré l'influence de caractéristiques écologiques et/ou physiologiques des espèces. De plus, ces études ne considèrent pas les interactions entre traits (par exemple entre les stratégies de reproduction et les capacités de dispersion des espèces) alors que celles-ci pourraient avoir une influence sur les différences observées. Enfin, ces études restent pour le moment focalisées sur les mammifères et les oiseaux. Ainsi, l'influence des caractéristiques des espèces sur les dynamiques de populations restent méconnue pour de très nombreux groupes taxonomiques.

4.3. L'importance de la phylogénie

Un facteur à ne pas négliger dans les études comparatives est l'influence de la phylogénie (Freckleton *et al.*, 2002). En effet, de part le partage d'un ancêtre commun, les espèces proches d'un point de vue phylogénétique ont plus de chance de partager des caractéristiques similaires relativement à des espèces plus éloignées dans la phylogénie (Figure 6). De ce point de vue, les espèces ne sont donc pas des entités statistiquement indépendantes (Felsenstein, 1985). Au même titre que l'autocorrélation spatiale ou temporelle, l'absence de prise en compte des liens de parentés entre espèces augmente le risque de détecter des relations significatives alors qu'il n'y en a pas. Il est donc primordial de prendre en compte ces liens de parenté dans les études comparatives. De nombreuses méthodes ont été développées pour prendre en compte cette non-indépendance (e.g. Felsenstein, 1985; Grafen, 1989; Harvey, 1996; Garland *et al.*, 1999; Pagel, 1999; Paradis & Claude, 2002; Blomberg *et al.*, 2003; Ives & Garland, 2010). Le choix de la méthode dépend du modèle d'évolution supposé du caractère étudié (e.g. Brownien). Ces méthodes nécessitent cependant d'avoir accès aux liens de parentés entre les espèces. Or les phylogénies de nombreuses espèces sont encore indisponibles ou mal résolues ce qui limite l'applicabilité de ces méthodes et explique en partie la grande proportion d'études comparatives qui ne prennent pas en compte les liens de parentés entre espèces (e.g. Forchhammer *et al.*, 1998; Rubolini *et al.*, 2005; Goodwin & Grant, 2006; Herrando-Pérez *et al.*, 2012; Franzén *et al.*, 2013).

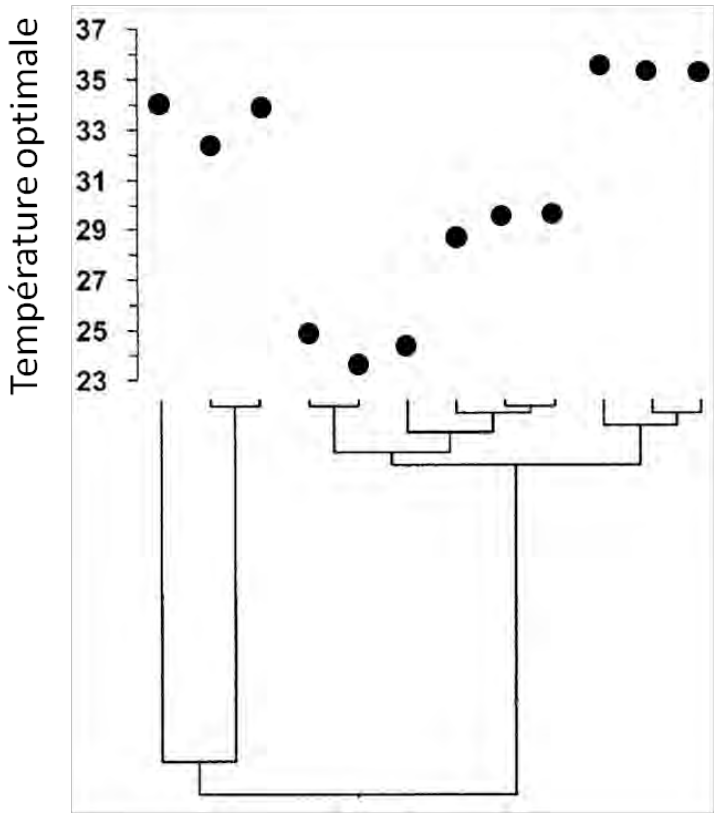


Figure 6. Température optimale de 12 espèces de lézards d'Australie (*Lampropholis guichenoti*) en fonction de leurs liens de parentés. (Modifié d'après Blomberg *et al.*, 2003).

Si les relations de parentés entre espèces peuvent introduire un biais dans les études comparatives à cause de la similarité des caractéristiques des espèces proches, pourquoi ces relations ne pourraient-elles pas expliquer les différences interspécifiques observées sur les patrons de dynamiques de population ? De façon assez surprenante, peu d'études (e.g. Willis *et al.*, 2008; Roy *et al.*, 2009; e.g. Végvári *et al.*, 2010) ont essayé de répondre à cette question. Or, mettre en évidence une influence de la phylogénie sur les différences observées pourrait permettre de regrouper les espèces en fonction de leur lien de parenté, d'inférer des caractéristiques sur les dynamiques de leurs populations, de déterminer quels sont les mécanismes à l'origine de ces dynamiques et de prédire les effets de changements environnementaux en fonction des liens de parenté entre espèces.

5. Quelles méthodes pour analyser les dynamiques de populations ?

Différentes approches ont été utilisées pour étudier les dynamiques de populations (Tuljapurkar, 1990; Royama, 1992; Caswell, 2001; Turchin, 2003). Ces méthodes peuvent grossièrement être classées en deux catégories.

Les modèles démographiques décomposent les statistiques qui décrivent les dynamiques de population en paramètres démographiques qui dépendent des classes de tailles ou d'âges de la population (Caswell, 2001). Sous leur forme la plus simple, ces modèles relient les paramètres démographiques au taux d'accroissement de la population. Ainsi, cette approche peut être utilisée pour estimer quelle est la contribution de la survie adulte au taux d'accroissement moyen de la population (Caswell, 2001) ou encore pour déterminer comment est-ce que ce taux varie lorsque les paramètres démographiques varient (analyse de sensibilité) (Tuljapurkar *et al.*, 2003; Engen *et al.*, 2005b, 2007; Haridas & Tuljapurkar, 2005). Les modèles basés sur cette approche ne décomposent généralement pas la dynamique des populations en processus intrinsèques et extrinsèques (cependant, voir Lande et al. 2006 pour une exception) mais permettent de prendre en compte la structure d'âge de la population et d'intégrer des paramètres associés aux processus de natalité et de mortalité (Coulson *et al.*, 2008). Bien que ces modèles soient très utiles pour identifier les paramètres démographiques qui ont le plus d'influence sur les populations, ils requièrent l'utilisation de données (e.g. survie et fécondité des différentes classes d'âge) qui sont très difficiles à acquérir à large échelle (Williams *et al.*, 2002). Par ailleurs, ils ne permettent pas d'évaluer la contribution relative des processus intrinsèques et extrinsèques aux dynamiques de populations.

La deuxième catégorie de modèles (appelés modèles phénoménologiques) est basée sur l'analyse de séries temporelles d'abondances où la structure démographique de la population n'est pas considérée mais où la dynamique de la population est décomposée en processus intrinsèques et extrinsèques (Royama, 1992; Saether & Engen, 2002; Stenseth *et al.*, 2004). Ce type de modèle permet par exemple de déterminer la forme de la fonction de densité-dépendance et de caractériser la dynamique attendue de la population en absence d'influence de l'environnement (May, 1976). Plusieurs modèles permettent d'analyser les séries temporelles d'abondances (e.g. Ricker, Gompertz, Beverton-Holt, logistique). Les différences principales entre ces modèles concernent la forme de la fonction de densité-dépendance. Par exemple, dans le modèle de Ricker, il y a une augmentation de la mortalité (surcompensation) lorsque la densité de la population atteint la capacité de charge du milieu alors que dans le modèle de Berveton-Holt, la population atteint un équilibre au niveau de la capacité de charge du milieu (Figure 7; Geritz & Kisdi 2004). Le modèle le plus couramment utilisé est le modèle logistique car la fonction de densité peut prendre des formes variables en fonction de la valeur d'un paramètre (Saether & Engen, 2002; Sibly *et al.*, 2005; Brook & Bradshaw, 2006). Cependant, la pertinence de ce modèle pour analyser les comptages de populations a récemment été remise en question (Clark *et al.*, 2010). Bien que les modèles basés sur les séries temporelles d'abondances ne permettent pas d'identifier quels sont les paramètres démographiques et les classes d'âges qui ont le plus d'influence sur la dynamique de la population, ils permettent de mener des études à larges échelles (car beaucoup de séries temporelles d'abondance sont disponibles) et d'étudier l'influence des processus intrinsèques et extrinsèques sur les dynamiques de populations.

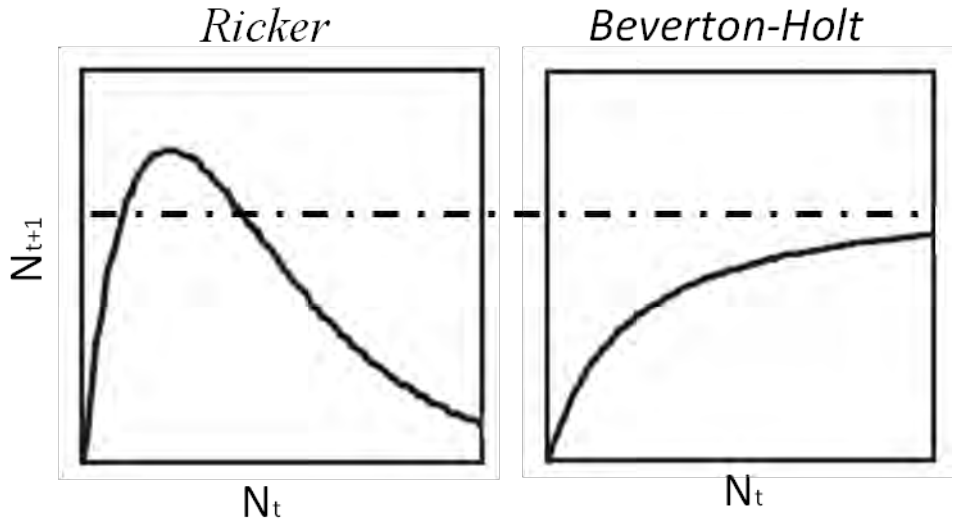


Figure 7. Représentation graphique des modèles de Ricker et de Beverton-Holt (adapté de Geritz & Kisdi, 2004). La ligne pointillée représente la capacité de charge du milieu. Le modèle de Ricker est caractérisé par une surcompensation (augmentation de la mortalité) lorsque les effectifs de la population atteignent la capacité de charge du milieu. Dans le modèle de Beverton-Holt les effectifs de la population tendent vers un équilibre.

6. Les poissons d'eau douce

Les poissons d'eau douce sont des organismes ectothermes, c'est-à-dire que la température de leurs corps dépend du milieu dans lequel ils vivent (Carpenter & Fisher, 1992; Drinkwater, 2005). Or, dans la mesure où les réactions biogéochimiques dépendent de la température corporelle, de nombreux aspects de la physiologie des organismes ectothermes dont la croissance, la survie et la reproduction sont directement influencés par des changements de températures du milieu extérieur. Ainsi, les conditions climatiques (et plus particulièrement la température du milieu) ont une influence déterminante sur les dynamiques de populations de poissons (Drinkwater, 2005).

6.1. Caractéristiques des rivières

Même si les écosystèmes aquatiques d'eau douce ne contiennent qu'une infime proportion de l'eau terrestre, ce sont des écosystèmes riches en terme de biodiversité (Dudgeon *et al.*, 2006). Ils fournissent par ailleurs un nombre de services considérables à l'homme comme par exemple l'eau potable, la production d'électricité, de la nourriture, des routes de navigation ou encore des possibilités d'irrigation pour les systèmes agricoles (Malmqvist & Rundle, 2002). Cependant, ces écosystèmes sont aujourd'hui fortement perturbés par les activités humaines et le réchauffement climatique avec des conséquences importantes sur les patrons de biodiversité (Dudgeon *et al.*, 2006; Heino *et al.*, 2009). En effet, les écosystèmes d'eau douce sont des milieux dendritiques, fragmentés qui limitent

fortement les mouvements d'individus aquatiques entre populations (Brown & Swan, 2010; Peterson *et al.*, 2013). Par ailleurs, les températures de l'eau ont augmenté au cours des dernières années avec des influences majeures sur les organismes (Kaushal *et al.*, 2010). Outre son influence sur les températures, le réchauffement climatique a également une influence sur le régime des débits des rivières (Döll & Zhang, 2010). Or, plusieurs études ont montré que le régime des débits avait un rôle majeur dans le déterminisme des communautés et que l'altération de ce régime avait une influence sur la biodiversité des écosystèmes d'eau douce (Poff & Ward, 1989; Poff & Allan, 1995; Matthews & Marsh-Matthews, 2003; Poff & Zimmerman, 2010). Par exemple, des événements extrêmes de crues ou d'étiages exercent une forte pression sélective sur les populations et déterminent le succès reproducteur des individus (Poff & Zimmerman, 2010). En plus des facteurs cités ci-dessus, l'acidification des sols, le changement d'utilisation des terres, les espèces invasives, l'eutrophisation, les pollutions diverses, la surexploitation des ressources ou encore la dégradation des habitats sont autant de facteurs qui influencent les patrons de biodiversité des organismes d'eau douce (Carpenter & Fisher, 1992; Sala, 2000; Malmqvist & Rundle, 2002; Ficke *et al.*, 2007; Heino *et al.*, 2009). Etant donné la multiplicité des facteurs qui influencent les écosystèmes aquatiques d'eau douce, et qui agissent souvent en synergie, mettre en évidence une influence du réchauffement climatique sur les organismes est une tâche difficile. Par exemple, même si l'effet du changement d'un facteur environnemental sur la physiologie d'un organisme est connu, un autre facteur peut avoir une influence opposée, ce qui ne permet pas de prévoir l'influence de ce changement au niveau de la population ou de la communauté (MacKenzie & Köster, 2004).

6.2. Réponse des poissons d'eaux douces aux changements climatiques

Comme pour les autres groupes taxonomiques, plusieurs types de réponses écologiques ont été mis en évidence chez les poissons d'eau douce. Les réponses les plus fréquemment observées sont des changements de distribution des espèces dues à des augmentations de la température de l'eau. Globalement, les résultats montrent que les espèces remontent vers des latitudes et des altitudes plus élevées, comme attendu sous l'hypothèse d'un réchauffement climatique (Carpenter & Fisher, 1992; Hickling *et al.*, 2006; Heino *et al.*, 2009; Comte & Grenouillet, 2013). Certaines études ont également mis en évidence des réponses phénologiques des poissons (Quinn & Adams, 1996; Dufour *et al.*, 2010). Ainsi, les dates de début de migration sont plus précoces qu'auparavant. Cependant, ces études sont très largement portées sur des espèces migratrices dont l'intérêt commercial est fort comme par exemple le saumon Atlantique (*Salmo salar*). L'influence du réchauffement climatique sur les événements phénologiques reste donc à déterminer pour de nombreuses espèces de poissons, notamment les espèces d'eau douce.

Une récente méta-analyse a révélé que le nombre d'études qui traitent de l'influence de l'environnement sur les dynamiques de populations étaient très largement biaisé autour des

mammifères et des oiseaux (Ockendon *et al.*, 2014) et que seulement 51 séries temporelles de poissons d'eau douce avaient été étudiées dans ce contexte. Alors que les populations d'espèces marines ont fait l'objet de nombreuses études dans une perspective de gestion des stocks de poissons à intérêt commerciaux (Myers *et al.*, 1997, 1999; Baum *et al.*, 2003; Baum & Myers, 2004; Bjørkvoll *et al.*, 2012), les poissons d'eau douce sont des espèces très peu prises en compte. Néanmoins, quelques études ont révélé un changement d'abondance de certaines espèces de poissons qui était corrélé avec des variables environnementales (Myers *et al.*, 1999; Grenouillet *et al.*, 2001; Cattanéo *et al.*, 2003). Par exemple, les variations interannuelles d'effectifs de juvéniles de l'année de gardon (*Rutilus rutilus*) s'expliquent par des variations de la température de l'eau (Grenouillet *et al.*, 2001). De même, plusieurs études ont révélé qu'une altération de la magnitude des débits avait une influence négative sur les poissons d'eau douce que ce soit en termes d'abondance, de paramètres démographiques ou de diversité des assemblages (revue dans Poff & Zimmerman, 2010). Une limite majeure de ces études est qu'elles ne considèrent généralement qu'une seule population et/ou une seule espèce ce qui ne permet pas d'inférer des résultats généraux sur l'influence du changement climatique sur les dynamiques de populations de poissons d'eau douce. Ainsi, l'influence du changement climatique sur les dynamiques de population de ces espèces reste encore à déterminer.

7. Objectifs de la thèse

Les objectifs de cette thèse ont été (1) de mettre en évidence une influence de l'environnement (plus particulièrement de la température) sur les dynamiques de populations de poissons, (2) de déterminer la contribution relative de facteurs environnementaux et densité-dépendants sur ces dynamiques et (3) de déterminer si les caractéristiques des espèces et leurs relations de parentés permettent d'expliquer les différences de réponses observées entre espèces. En étudiant plusieurs espèces, notre objectif a également été de mettre en évidence des patrons généraux et des réponses spécifiques. Après une présentation des données utilisées dans cette thèse, trois chapitres résument les principaux résultats obtenus. Le premier chapitre traite du synchronisme des dynamiques de populations de poissons et compare l'utilisation de différentes méthodes classiquement utilisées dans les études de synchronisme (***PI***). Notre objectif dans ce chapitre est de mettre en évidence l'influence d'un effet Moran et de comparer les résultats obtenus avec différentes méthodes. Dans le deuxième chapitre, nous évaluons la contribution relative des facteurs intrinsèques et extrinsèques aux dynamiques de populations de plusieurs espèces de poissons. Nous nous attachons également à déterminer au travers de quels paramètres impliqués dans le déterminisme des dynamiques de populations (taux de migration, taux d'accroissement et densité-dépendance) les facteurs extrinsèques ont le plus d'influence (***PIII***). L'objectif de ce chapitre est donc d'identifier les mécanismes responsables des variations interannuelles des effectifs des populations et d'identifier les déterminants des variations spatiales de dynamiques de populations. Dans un dernier chapitre, nous expliquons les variations de réponses observées entre espèces en

fonction de leurs caractéristiques ainsi que des liens de parentés qui existent entre ces espèces (***PII*** et ***PIV***). L'objectif est donc ici d'identifier si la phylogénie et/ou des caractéristiques intrinsèques des espèces permettent d'expliquer les différences observées.

Chapitre 1

Données piscicoles et environnementales

Gobio gobio

1. Introduction

Depuis plusieurs années, les écologues ont développé et maintenu des jeux de données à long-termes pour étudier l'évolution des populations animales et végétales. Ces jeux de données peuvent avoir été collectés par des citoyens (e.g. le comptage des oiseaux de noël aux Etats-Unis ; Dickinson et al. 2010), des biologistes ou par des organismes publics à l'aide de méthodes plus ou moins standardisées (e.g. la pêche électrique pour les poissons d'eau douce). La caractéristique commune et l'intérêt de ces jeux de données est qu'ils couvrent des échelles spatiales et temporelles importantes qui vont bien au-delà de la plupart des études scientifiques. Ces données ont donc une incroyable valeur dans la mesure où elles permettent d'étudier l'influence de processus qui agissent à de larges échelles spatiales et temporelles comme par exemple le climat. Les suivis de populations de poissons d'eau douce réalisés en France par l'Onema (l'Office National de l'Eau et des Milieux Aquatiques) font partie de ce type de données. L'Onema est un organisme public chargé de la surveillance des milieux aquatiques dans le cadre de la directive cadre européenne sur l'eau.

2. Les données de l'Onema

Les données qui ont servies au cours de cette thèse ont été extraites de la Banque de Données Milieux Aquatiques (BDMAP) et renseigne les effectifs de différentes populations pour plus de 90 espèces de poissons d'eau douce. Entre 1968 et 2011, plus de 26000 opérations de pêches ont été réalisées sur plus de 11000 stations réparties sur le territoire français (Figure 8). La longueur des séries temporelles varie de 1 à 27 années en fonction des stations étudiées (moyenne = 2.3 ans, écart-type = 3.6).

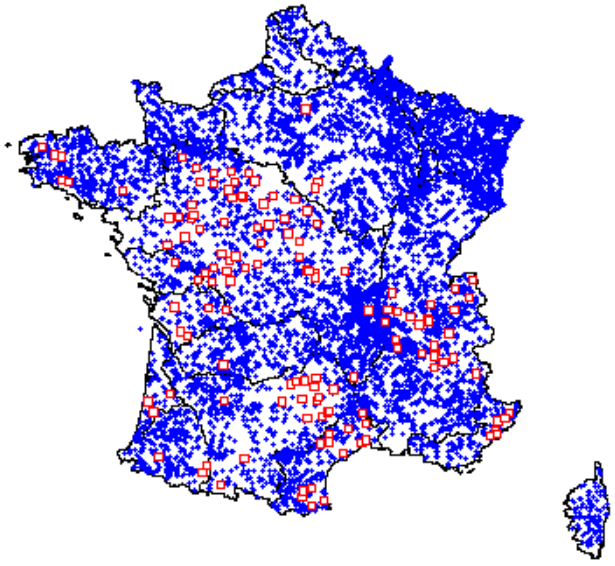


Figure 8. Représentation spatiale des stations d'échantillonnages de poissons (rond bleu) et des stations de mesures de la température de l'eau (carré rouge).

Les échantillonnages de poissons ont été réalisés à l'aide pêches électriques suivant un protocole standardisé, au cours des périodes de basses eaux (i.e. de Mai à Octobre)(voir

Oberdorff *et al.*, 2001; Poulet *et al.*, 2011). Malgré quelques biais, ce protocole est considéré comme le plus efficace pour décrire les assemblages et les effectifs de populations de poissons d'eau douce (Zalewski & Cowx, 1990). Plusieurs méthodes d'échantillonnages ont été utilisées en fonction de la largeur et de la profondeur des cours d'eau. Dans les rivières peu profondes, l'échantillonnage s'est fait à pied et est plutôt exhaustif tandis que dans les cours d'eau profonds, l'échantillonnage s'est fait en bateau avec des échantillonnages plus ponctuels. Quelles que soient les méthodes utilisées, l'échantillonnage consiste à prélever les individus présents sur une station, à les identifier, les compter, les mesurer puis à les relâcher vivant sur la station d'étude. Ce jeu de données a déjà fait l'objet de nombreuses études dont l'objectif consistait à mettre en évidence une influence du changement climatique sur les assemblages ou les dynamiques de populations de poissons (e.g. Grenouillet *et al.*, 2011; Poulet *et al.*, 2011; Comte & Grenouillet, 2013; Edeline *et al.*, 2013; Paz-Vinas *et al.*, 2013).

Tableau 1. Liste des espèces étudiées dans les 4 manuscrits

Nom scientifique	Nom vernaculaire	Code	***PI***	***PII***	***PIII***	***PIV***
Abramis brama	Brème commune	Abab	X	X		
Alburnoides bipunctatus	Spirlin	Albi	X	X		
Alburnus alburnus	Ablette	Alal	X	X	X	X
Ameiurus melas	Poisson chat	Amme	X	X		
Anguilla anguilla	Anguille	Anan	X		X	X
Barbatula barbatula	Loche France	Babb	X	X	X	X
Barbus barbus	Barbeau fluviatile	Babu	X	X	X	X
Blicca bjoerkna	Brème bordelière	Blbj	X	X	X	
Carassius carassius	Carassin	Caca	X	X		
Chondrostoma nasus	Hotu	Chna	X	X		
Cottus gobio	Chabot commun	Cogo	X	X	X	X
Cottus perifretum	Chabot fluviatile	Cope	X			
Cyprinus carpio	Carpe commune	Cyca	X	X		X
Esox lucius	Brochet	Eslu	X	X	X	
Gasterosteus gymnurus	Epinoche	Gagy	X	X	X	X
Gobio gobio	Goujon	Gogo	X	X	X	X
Gobio lozanoi	Goujon de l'Adour	Golo	X			
Gobio occitaniae	Goujon occitan	Gooc	X			
Gymnocephalus cernua	Grémille	Gyce	X	X	X	
Lampetra planeri	Lamproie de planaire	Lapl	X		X	
Lepomis gibbosus	Perche soleil	Legi	X	X	X	X
Leuciscus burdigalensis	Vandoise rostrée	Lebu	X			
Leuciscus leuciscus	Vandoise commune	Lele	X	X	X	X
Parachonstrostoma toxostoma	Toxostome	Pato				X
Perca fluviatilis	Perche	Pefl	X	X	X	X
Phoxinus phoxinus	Vairon	Phph	X	X	X	X
Pungitius pungitius	Epinochette	Pupu	X	X	X	X
Rhodeus amarus	Bouvière	Rham	X	X		
Rutilis rutilis	Gardon	Ruru	X	X	X	X
Salmo salar	Saumon Atlantique	Sasa	X		X	X
Salmo trutta	Truite	Satr	X	X	X	X
Sander lucioperca	Sandre	Salu				X
Scardinius erythrophthalmus	Rotengle	Scer	X	X	X	X
Silurus glanis	Silure	Sigl				X
Squalius cephalus	Chevaine	Sqce	X	X	X	X
Telestes souffia	Blageon	Teso	X	X		X
Thymallus thymallus	Ombre commun	Thth				X
Tinca tinca	Tanche	Titi	X	X	X	X

Pour répondre aux différents objectifs de la thèse, différentes espèces de poissons ont été étudiées (Tableau 1). Quelles que soient les analyses effectuées, nous n'avons considéré que les séries temporelles qui avaient au moins 8 années de données non nulles (i.e. où les effectifs de population étaient différents de zéro) et au cours desquelles la méthode d'échantillonnage était restée constante. Par ailleurs, nous avons supprimé les séries pour lesquelles plus de trois années consécutives manquaient afin de limiter l'influence des données manquantes sur nos résultats. Enfin, le choix définitif des espèces s'est fait, à la suite d'analyses exploratoires, en fonction du nombre de séries temporelles nécessaires pour limiter les biais associés aux différentes méthodes statistiques utilisées dans les différents chapitres.

3. Les données environnementales

Les températures journalières de l'eau mesurées entre les années 2009 et 2012 sur 135 stations réparties sur le territoire Français ont été fournies par l'Onema (Figure 8). L'altitude (m) de chaque site a été extraite à partir d'un modèle numérique de terrain à une résolution de 50m. Les températures journalières de l'air entre les années 1982 et 2010 ont été fournies par Météo France. Plus précisément, nous avons utilisé la base de donnés SAFRAN qui est une grille de 8 kms par 8 kms où la température journalière de chaque cellule est interpolée à partir de zones climatiques homogènes (Le Moigne, 2002).

4. Caractéristiques des espèces

Pour mettre en évidence une influence des relations de parentés entre espèces sur les patrons observés de dynamiques de populations, nous avons utilisé deux phylogénies. Dans le manuscrit ***PII***, nous avons utilisé une phylogénie reconstruite à partir de données moléculaires extraites de *GenBank* basée sur trois gènes mitochondriaux (décrite dans Grenouillet *et al.*, 2011). La publication d'une phylogénie plus récente et mieux résolue a été utilisée dans le manuscrit ***PIV*** (décrite dans Comte *et al.*, 2014)

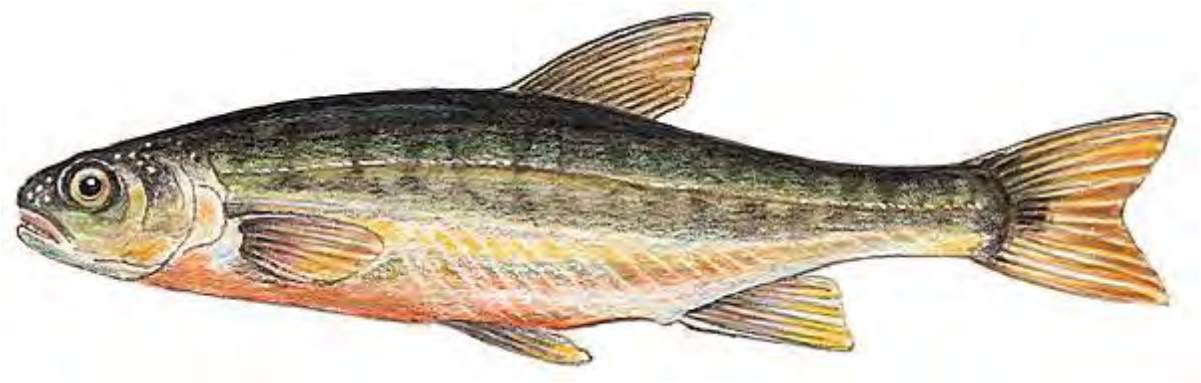
Pour déterminer l'influence des caractéristiques des espèces sur les patrons de dynamique de populations, nous avons utilisé plusieurs traits extraits de la littérature (Keith *et al.*, 2011; Souchon & Tissot, 2012), de Fishbase (Froese & Pauly, 2002) ou par avis d'expert. Nous avons choisi ces traits afin de représenter différentes composantes de l'écologie des poissons : la reproduction, l'écologie, la physiologie et la morphologie (Tableau 2). Parce que certains de ces traits étaient corrélés les uns aux autres, nous avons utilisé des méthodes d'ordination (analyse en composantes principales et analyse en coordonnées principales) pour synthétiser l'information contenues dans les différentes variables.

Tableau 2. Description des traits utilisés

Catégorie	Trait	Modalité	Description
Trait Physiologique	Tolérance thermique maximale	quantitative	Température optimale maximum (°C)
Traits Morphologiques	Taille du corps	quantitative	Taille du corps
	Longueur de la larve	1	≤ 4.2mm
		2	4.2-6.3mm
		3	> 6.3mm
	Facteur de forme	quantitative	Ratio de la taille du corps sur la hauteur maximale du corps
	Facteur d'aspect	quantitative	Ratio de la hauteur de la nageoire caudale au carré sur sa surface
	Facteur de nage	quantitative	Ratio de la hauteur minimale du pédoncule caudale sur la hauteur maximale de la nageoire caudale
Traits écologiques	Habitat de nourrissage	1	Benthivore
		2	Colonne d'eau
	Habitat de vie	1	Demersale
		2	Bentho-pelagique
		3	Pélagique
	Régime alimentaire	1	Omnivore
		2	Invertivore
		3	Invertivore-carnivore
		4	Piscivore
Traits d'histoire de vie	Fécondité absolue	quantitative	Nombre d'oeufs
	Nombre de reproduction	1	Une fois par an
		2	Plusieurs fois par an
	Diamètre des œufs	quantitative	Au moment de la ponte (mm)
	Durée de vie	1	< 8 ans
		2	8-15 ans
		3	> 15 ans
	Maturité de la femelle	1	≤ 2 ans
		2	2-3 ans
		3	3-4 ans
		4	4-5 ans
		5	≥ 5 ans
	Soins parentaux	1	Absence de protection
		2	Absence de protection mais présence d'un nid
		3	Présence d'un nid ou dissimulation des œufs
	Période d'incubation	1	≤ 7 jours
		2	7-14 jours
		3	> 14 jours

Chapitre 2

Déterminants du synchronisme spatial des dynamiques de populations



Phoxinus phoxinus

1. Introduction

Trois principaux mécanismes sont à l'origine du synchronisme spatial des dynamiques de populations : la dispersion d'individus entre les populations, l'effet Moran (i.e. l'autocorrélation spatial de facteurs environnementaux) et les interactions trophiques (Liebhold *et al.*, 2004). Ce dernier mécanisme ne représente cependant qu'un effet indirect de l'action des deux premiers mécanismes sur des niveaux trophiques supérieurs ou inférieurs (Forchhammer *et al.*, 2002; Cattadori *et al.*, 2005). Par ailleurs, son étude est rendue compliquée par la nécessitée de connaître les relations entre les proies et les prédateurs pour l'ensemble des populations étudiées. Pour ces raisons, les interactions trophiques ne sont pas considérées dans ce chapitre.

Identifier quel mécanisme (dispersion ou effet Moran) est responsable du synchronisme spatial des populations est primordial dans le contexte actuel de réchauffement climatique car la probabilité d'extinction des espèces peut varier en fonction du mécanisme impliqué dans le synchronisme des populations (Hanski & Woiwod, 1993). En effet, si des facteurs environnementaux sont responsables du synchronisme des populations, alors un événement climatique extrême peut causer le déclin simultanée de plusieurs populations et mener à l'extinction de la metapopulation (Heino *et al.*, 1997). A l'inverse, si la dispersion d'individus est responsable du synchronisme des populations alors une population qui subie un déclin peut être "secourue" par une population adjacente et ainsi assuré la pérennité de la metapopulation. Malgré l'abondance de littérature sur le synchronisme des populations, très peu d'études (e.g. Grenfell *et al.*, 1998; Benton *et al.*, 2001; Tedesco & Hugueny, 2006) ont réussies à clairement identifier le mécanisme sous-jacent au synchronisme des populations ce qui peut s'expliquer par la difficulté de séparer l'influence des deux mécanismes. L'approche la plus populaire pour identifier le mécanisme responsable du synchronisme des populations consiste à utiliser des transformations de séries temporelles (TSTs) c'est-à-dire des méthodes statistiques qui modifient les séries temporelles d'abondances pour supprimer la signature de l'un des deux mécanisme pour mettre en évidence la signature de l'autre (Bjørnstad *et al.*, 1999). Il a par exemple été suggéré que supprimer la tendance à long-terme dans les séries temporelles, à l'aide d'une procédure de "detrending" (voir encadré 1), permettait d'étudier l'influence de processus locaux comme la dispersion d'individus entre les populations (Koenig, 1999). L'hypothèse derrière cette approche est que la présence d'une tendance à long-terme dans les séries temporelles est due à l'influence de processus globaux comme le climat (Bjørnstad *et al.*, 1999). Cependant, la présence d'une telle tendance peut également s'expliquer par des facteurs qui agissent à une échelle beaucoup plus locale comme par exemple une pollution (Dauer & Alden, 1995). De la même manière, il a été suggéré que supprimer l'autocorrélation temporelle présente dans les données, à l'aide d'une procédure de "prewhitenning" (voir encadré 1), permettait de se focaliser sur des processus globaux (Koenig, 1999). L'hypothèse ici est que ce sont des processus locaux comme par exemple la densité-dépendance qui sont responsables de la présence d'autocorrélation temporelle dans les données. Cependant, la présence d'une tendance à long-terme dans les séries implique un certain degré d'autocorrélation temporelle (Pyper *et al.*, 1999). A notre connaissance, l'influence de différentes TSTs sur les mesures de synchronisme ainsi que leur capacité à

identifier les mécanismes sous-jacents au synchronisme spatial des dynamiques de populations n'a jamais été étudié.

Encadré 1. Méthodes statistiques utilisées pour transformer les séries temporelles

Supprimer la tendance ("detrending")

Pour supprimer la tendance à long-terme dans les séries temporelles, nous avons utilisé un modèle linéaire avec une distribution binomiale et une fonction de lien logarithmique :

$$\log(E(X_t)) = \alpha + \beta \log(\text{year}_t) + \log(S_t) + \varepsilon_t \quad \text{(eq. 1)}$$

où X_t est le nombre de poissons capturés à l'année t (E est son espérance mathématique), year_t est l'année d'échantillonnage, S_t est la surface échantillonnée à l'année t et ε_t est l'erreur du modèle. Le paramètre α est l'intercept du modèle et représente le nombre de poissons capturés par unité de surface à t=0. Le paramètre β est le coefficient de tendance à long-terme. Les résidus de ce modèle constituent les séries temporelles sans la tendance à long-terme.

Supprimer l'autocorrélation ("prewhitenning")

Pour supprimer l'autocorrélation temporelle présente dans les données, nous avons utilisé le modèle de Ricker avec une distribution binomiale négative et une fonction de lien logarithmique :

$$\log(E(X_{t+1})) = \log\left(S_{t+1}\frac{X_t}{S_t}\right) + \rho + \eta\frac{X_t}{S_t} + \varepsilon_t \quad \text{(eq. 2)}$$

où X_{t+1} est le nombre de poissons capturés à l'année t+1 et S_{t+1} est la surface échantillonnée à l'année t+1. Le paramètre ρ correspond au taux d'accroissement intrinsèque de la population tandis que le paramètre η est le coefficient de densité-dépendance. Parce que ce modèle ne prend en compte que du recrutement local de la population, il prédit que X_{t+1} est nul lorsque X_t=0. Or, certaines de nos données comprennent des transitions entre des valeurs nulles et des valeurs positives. De telles transitions peuvent s'expliquer par de la migration d'individus entre populations. Pour modéliser ces transitions, nous avons utilisé le modèle suivant :

$$\log(E(X_{t+1})) = \gamma + \log(S_{t+1}) \quad \text{(eq. 3)}$$

où γ est l'intercept du modèle et quantifie le nombre moyen de migrants par unité de surface au temps t+1.

Dans la pratique, le modèle défini par l'équation 2 a été appliqué à toutes les séries qui ne contenaient pas de transitions entre X_t=0 et X_{t+1}>0. Pour les séries qui contenaient de telles transitions, nous avons supprimé les valeurs nulles pour ajuster le modèle défini par l'équation 2 tandis que nous avons traité les transitions entre X_t=0 et X_{t+1}>0 avec le modèle défini par l'équation 3. Les résidus de ces modèles (qui ont été combinés dans le cas des séries qui avaient des zéros) constituent les séries temporelles sans autocorrélation.

Supprimer la tendance et l'autocorrélation

Pour supprimer la tendance à long-terme et l'autocorrélation temporelle dans les données, nous avons appliqué la même démarche que pour la procédure de "prewhitenning" mais en ajoutant la variable year_t dans les équations.

Le but de ce chapitre est de déterminer, au travers de différentes métriques, si un effet Moran influence les dynamiques de populations de poissons d'eau douce en France et de

comparer les résultats obtenus avec différentes TSTs classiquement utilisées dans les études de synchronisme ("detrending", "prewhitenning" et une combinaison des deux ; voir encadré 1). Notre objectif est également de déterminer comment les TSTs influencent les séries temporelles et les mesures de synchronisme en fonction de caractéristiques intrinsèques des séries temporelles (longueur de la série, densité-dépendance et tendance à long-terme). Finalement, dans la mesure où les caractéristiques des espèces peuvent influencer les dynamiques de populations (e.g. Gilpin, 1992), nous avons testé si la durée de vie des espèces (qui est un proxy de nombreux traits d'histoire de vie; Sæther *et al.* 2013) était lié aux caractéristiques des séries temporelles et donc à l'influence des TSTs sur les mesures de synchronisme.

2. Méthode d'identification des mécanismes

Afin d'identifier quel est le mécanisme à l'origine du synchronisme spatial des dynamiques de populations de poissons, nous avons utilisé différentes métriques, classiquement utilisées dans les études de synchronisme. Nous avons utilisé des coefficients de corrélation de Spearman pour évaluer le degré de synchronisme entre les populations de chaque espèce. Ensuite, le calcul de la moyenne des coefficients de corrélation mesurés entre chaque population nous a permis de déterminer le degré de synchronisme spécifique à chaque espèce (Buonaccorsi *et al.*, 2001). Nous avons alors testé si ce degré de synchronisme était significativement différent de zéro pour chaque espèce à l'aide d'une procédure de bootstrap (Lillegård *et al.*, 2005). Nous avons utilisé des tests de Mantel (Mantel, 1967) pour déterminer si le degré de synchronisme des populations de chaque espèce diminuait en fonction de la distance qui sépare les populations. Enfin, nous avons estimé l'échelle spatiale du synchronisme des populations de chaque espèce en utilisant un modèle additif généralisé. L'ensemble des mesures utilisées pour caractériser le degré de synchronisme de chaque espèce est résumé sur la Figure 9.

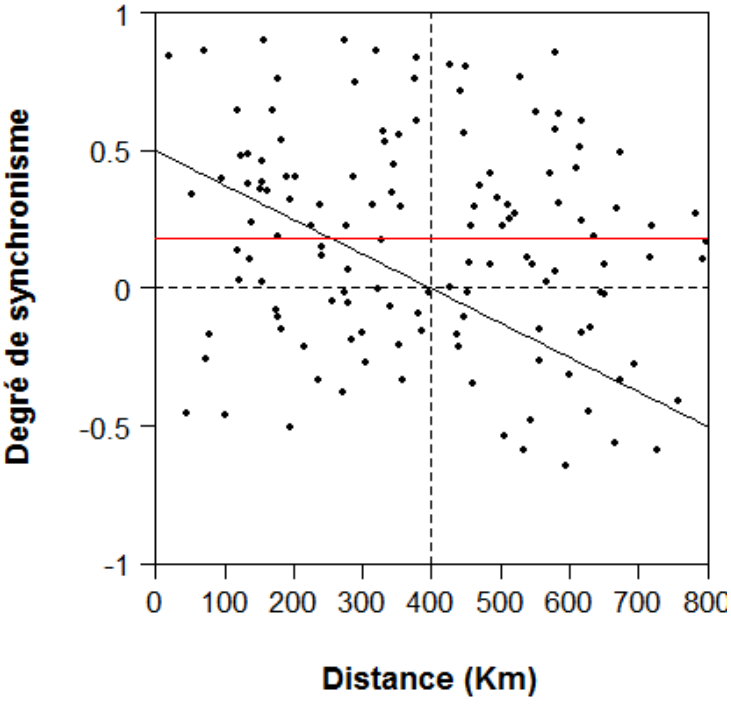


Figure 9. Représentation graphique des différentes mesures de synchronisme obtenues pour une espèce. Chaque point est une estimation du degré de synchronisme entre 2 populations séparées d'une certaine distance (km). La ligne rouge représente la moyenne de ces mesures. La ligne noire continue représente la relation entre le degré de synchronisme des populations et la distance qui les séparent. L'intersection des lignes noires pointillées définie l'échelle spatiale du synchronisme (i.e. la distance à partir de laquelle le synchronisme n'est plus différent de zéro).

La plupart des études de synchronisme ne considèrent en général qu'une seule des métriques présentées ci-dessus. Nous avons choisi d'en considérer plusieurs car ces métriques apportent différentes informations quant aux mécanismes sous-jacents au synchronisme des populations. Par exemple, une large échelle de synchronisme suggère que ce sont des facteurs environnementaux (e.g. climatiques) qui influencent le synchronisme des populations car ces facteurs peuvent présenter de l'autocorrélation spatiale sur de grandes distances (Koenig, 1999). De même, une diminution du degré de synchronisme en fonction de la distance qui sépare les populations peut s'expliquer par des processus de dispersion car la probabilité de dispersion des individus diminue en fonction de la distance (Ranta *et al.*, 1995). Cependant, les conclusions associées à ces patrons ne sont pas toujours vérifiées. En effet, la dispersion d'individus entre populations peut interagir avec des paramètres démographiques locaux et générer du synchronisme spatial à de larges échelles spatiales (Gouhier *et al.*, 2010). De même, une diminution du degré de synchronisme des populations avec la distance peut s'expliquer par une diminution du degré d'autocorrélation spatial des facteurs environnementaux en fonction de la distance (Ranta *et al.*, 1997).

De fait, nous avons choisi de considérer deux métriques supplémentaires. D'après la théorie, si un effet Moran agit sur les populations alors, le synchronisme spatial des populations doit pouvoir s'expliquer par le synchronisme spatial de facteurs environnementaux (Royama, 1992). Pour tester cette hypothèse, nous avons calculé, pour chaque espèce, le degré de synchronisme des températures entre chaque site de présence d'une population (i.e. d'une série temporelle) puis nous avons testé si ce synchronisme influençait celui des populations par des tests de Mantel. Nous avons utilisé les températures comme proxy de l'effet Moran car les poissons sont des organismes ectothermes qui sont particulièrement sensibles à des changements de températures du milieu extérieur (Drinkwater, 2005). Une autre façon de mettre en évidence un effet Moran est de considérer des populations entre lesquelles la dispersion d'individus est impossible (Grenfell *et al.*, 1998; Tedesco & Hugueny, 2004). Pour s'affranchir de l'effet de la dispersion, nous avons mesuré le degré de synchronisme de chaque espèce en ne considérant que les populations qui étaient situées dans des bassins versants différents (i.e. entre lesquels la dispersion d'individus est théoriquement impossible).

3. L'influence d'un effet Moran

Nos résultats montrent que plus de la moitié des espèces (61%) présentent un degré de synchronisme significativement différent de zéro mais que ce synchronisme est généralement faible (Tableau 3). Pour 32% des espèces, le degré de synchronisme diminue avec la distance qui sépare les populations. La plupart des espèces présentent des degrés de synchronisme sur de grandes distances (>300 km) qui s'approchent des échelles de synchronisme estimées pour le synchronisme des températures (i.e. >450 km, résultats non présentés). En ne considérant que les populations situées dans des bassins versants différents, nous avons trouvé que 47% des espèces présentaient toujours un degré de synchronisme significativement différent de

zéro. Enfin, pour 24% des espèces, nous avons mis en évidence une corrélation significative entre le degré de synchronisme des populations et le degré de synchronisme des températures.

Tableau 3. Valeurs des mesures de synchronisme obtenues pour chaque espèce. Npaire est le nombre de paire de populations. M_{synch} est la moyenne des mesures de synchronisme calculé en considérant toutes les paires de populations. MBV_{synch} est la moyenne du degré de synchronisme calculé en ne considérant que les paires de populations situées dans des bassins versants différents. E_{synch} est l'échelle spatial de synchronisme (les "-" indique que l'estimation de cette métrique n'était pas possible). $R_{distance}$ est le coefficient de corrélation calculé entre le degré de synchronisme des populations et la distance qui les sépare. R_{temp} est le coefficient de corrélation calculé entre le degré de synchronisme des populations et le degré de synchronisme des températures. Les valeurs en gras indiquent des résultats significatifs. (Modifié d'après ***PI***, Tableau S4 à S6).

Codes espèces	Npaire	M_{synch}	MBV_{synch}	E_{synch} (km)	$R_{Distance}$	R_{Temp}
Abab	233	-0.017	0.000	389	-0.023	0.037
Albi	745	**0.048**	**0.036**	200	-0.038	0.054
Alal	2830	0.003	-0.005	366	**-0.071**	0.022
Amme	64	0.023	0.081	-	0.022	-0.183
Anan	12680	**0.017**	**0.010**	292	-0.015	0
Babb	21312	**0.054**	**0.052**	276	**-0.035**	**0.029**
Babu	5162	**0.025**	**0.019**	369	**-0.096**	**0.043**
Blbj	94	0.001	0.000	282	-0.030	0.041
Caca	55	-0.039	-0.038	145	-0.012	-0.197
Chna	373	0.027	**0.032**	136	-0.003	0.09
Cogo	160	**0.146**	**0.186**	-	0.137	0.059
Cope	10724	**0.029**	**0.023**	311	**-0.087**	**0.081**
Cyca	55	0.024	0.007	-	0.063	-0.105
Eslu	1037	**0.03**	**0.034**	312	-0.019	0.006
Gagy	76	**0.172**	**0.154**	442	**-0.244**	0.224
Gogo	14354	**0.045**	**0.045**	320	**-0.040**	**0.036**
Golo	36	-0.025	-	11	0.062	-0.073
Gooc	1926	**0.02**	0.016	183	**-0.058**	**0.078**
Gyce	138	0.04	0.043	-	0.042	0.026
Lapl	1857	**0.069**	**0.068**	147	0.014	0.049
Legi	1595	**0.038**	**0.038**	227	-0.019	0.032
Lebu	522	**0.038**	**0.039**	-	0.050	-0.027
Lele	922	**0.071**	**0.068**	215	-0.066	0.065
Pefl	5404	**0.014**	**0.010**	208	-0.014	-0.04
Phph	22544	**0.043**	**0.041**	226	-0.008	0.003
Pupu	134	0.038	**0.075**	126	0.117	-0.114
Rhse	218	0.036	**0.047**	283	-0.016	-0.097
Ruru	16034	0.002	-0.001	287	**-0.032**	**0.017**
Sasa	110	**0.149**	**0.150**	319	-0.022	-0.044
Satr	29225	**0.038**	**0.031**	368	**-0.116**	**0.077**
Scer	134	-0.012	-0.020	390	**-0.165**	**0.187**
Sqce	28084	**0.031**	**0.028**	265	**-0.032**	0.012
Teso	179	**0.089**	**0.111**	-	0.053	0.013
Titi	490	**0.069**	**0.063**	485	-0.034	0.036

Ainsi, bien que les degrés de synchronisme mesurés pour chaque espèce soient faibles, nos résultats sont en accord avec de nombreuses études (Paradis *et al.*, 1999, 2000; Cheal *et al.*, 2007; Alheit & Bakun, 2010) et tendent à démontrer l'influence d'un effet Moran sur le synchronisme spatial des populations de poissons d'eau douce. En effet le fait que les populations de certaines espèces fluctuent de façon synchrone sur de larges distances et entre bassins-versants entre lesquels la dispersion d'individus est théoriquement impossible suggère l'influence de facteurs environnementaux et notamment climatiques (Tedesco & Hugueny, 2004). La température apparaît comme un candidat pertinent pour expliquer ce synchronisme dans la mesure où le synchronisme spatial des températures permet d'expliquer le synchronisme spatial des populations de certaines espèces. Cependant, il est fort probable que d'autres facteurs, comme par exemple le débit, aient une influence sur le synchronisme spatial des poissons d'eau douce (Cattanéo *et al.*, 2003) et d'autres études sont nécessaires pour déterminer si tel est le cas. Globalement, nos résultats suggèrent que les populations d'espèces de poissons d'eau douce pourraient fluctuer de façon synchrone en réponse aux augmentations prédites des températures (Stocker *et al.*, 2013). Dans la mesure où la probabilité d'extinction des espèces augmente en fonction du degré de synchronisme spatial des populations (Hanski & Woiwod, 1993), nos résultats donnent une vision plutôt pessimiste de l'influence du réchauffement climatique sur plus de la moitié des espèces de poissons d'eau douce. Cependant, les degrés de synchronisme que nous avons estimés sont faibles et de nouvelles études, intégrant d'autres mesures de la probabilité d'extinction des espèces sont nécessaires pour confirmer ces résultats.

4. Influence des TSTs

Les modèles statistiques que nous avons utilisés pour transformer les séries temporelles sont présentés dans l'encadré 1.

4.1. Capacité des TSTs à retirer le mécanisme d'intérêt

Parmi les 3119 séries temporelles considérées dans cette étude, 605 (19%) présentaient une tendance à long-terme alors que 250 (8%) présentaient de l'autocorrélation temporelle. Après avoir utilisé la procédure de "detrending", nous avons trouvé que 12 (0.3%) séries présentaient toujours une tendance à long-terme alors que 120 (3%) présentaient de l'autocorrélation temporelle. Après avoir utilisé la procédure de "prewhitenning", 18 (0.5%) séries présentaient toujours de l'autocorrélation temporelle alors que 155 (5%) présentaient une tendance à long-terme. Après avoir retiré ces deux facteurs, 30 (1%) séries présentaient toujours de l'autocorrélation temporelle et une (0.03%) série présentait toujours une tendance à long-terme. Ces résultats suggèrent donc que les TSTs ne permettent pas toujours de retirer le mécanisme d'intérêt et que retirer l'un des deux mécanismes sans affecter la signature de l'autre est une tâche particulièrement difficile.

4.2. Influence des TSTs sur les séries temporelles

Pour déterminer dans quelles proportions les séries temporelles étaient modifiées par l'utilisation des TSTs, nous avons calculé des coefficients de corrélation entre les séries temporelles brutes (i.e. non modifiées) et les séries temporelles modifiées par l'utilisation des TSTs. Globalement, nos résultats montrent que la procédure de "detrending " à moins d'influence sur les séries temporelles que la procédure de "prewhitenning" et que le retrait de ces deux processus a plus d'influence que le retrait de chaque processus pris séparément (Figure 10). Ces différences d'influence des TSTs pourraient s'expliquer par des différences de caractéristiques des séries temporelles. En effet, les séries qui présentent un fort coefficient de tendance à long-terme et/ou de densité-dépendance devraient être plus fortement affectées par les TSTs que les séries qui ne présentent pas de telles caractéristiques.

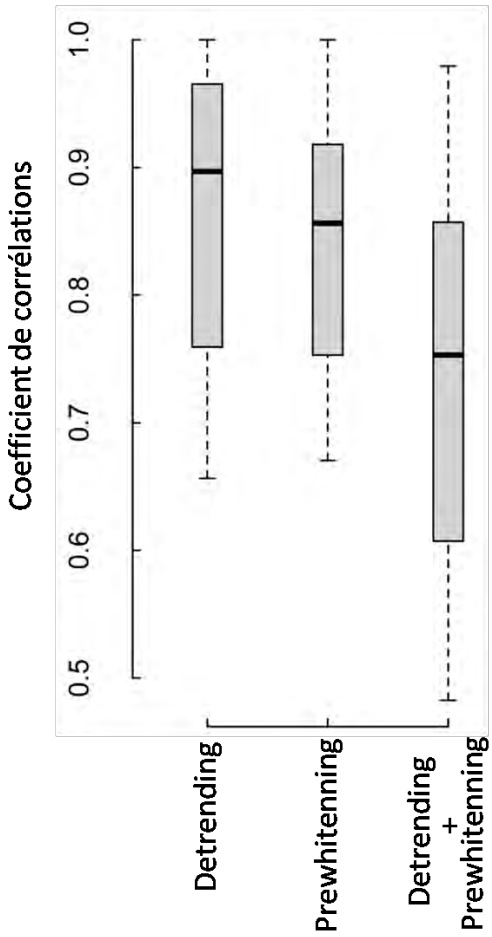


Figure 10. Comparaison des coefficients de corrélation calculés entre les données brutes et les données obtenues après l'utilisation de chaque TST. Une forte corrélation indique un fort degré de ressemblance entre les séries temporelles brutes et les séries temporelles modifiées et donc une fable influence de la transformation sur les données. Detrending = retrait de la tendance à long-terme ; Prewhitenning = retrait de l'autocorrélation temporelle. (Modifié d'après ***PI*** ; Figure 3).

Pour tester cette hypothèse nous avons utilisé des modèles linéaires avec comme variables dépendantes les coefficients de corrélations calculés entre les séries temporelles brutes et les séries temporelles obtenues après l'utilisation de chaque TST et comme variable indépendantes la longueur de la série temporelle et les valeurs des coefficients de densité-dépendance et de tendance à long-terme estimés pour chaque série temporelle. Une représentation visuelle de l'influence de chaque TST sur deux séries temporelles présentant des caractéristiques différentes est présentée en figure 11.

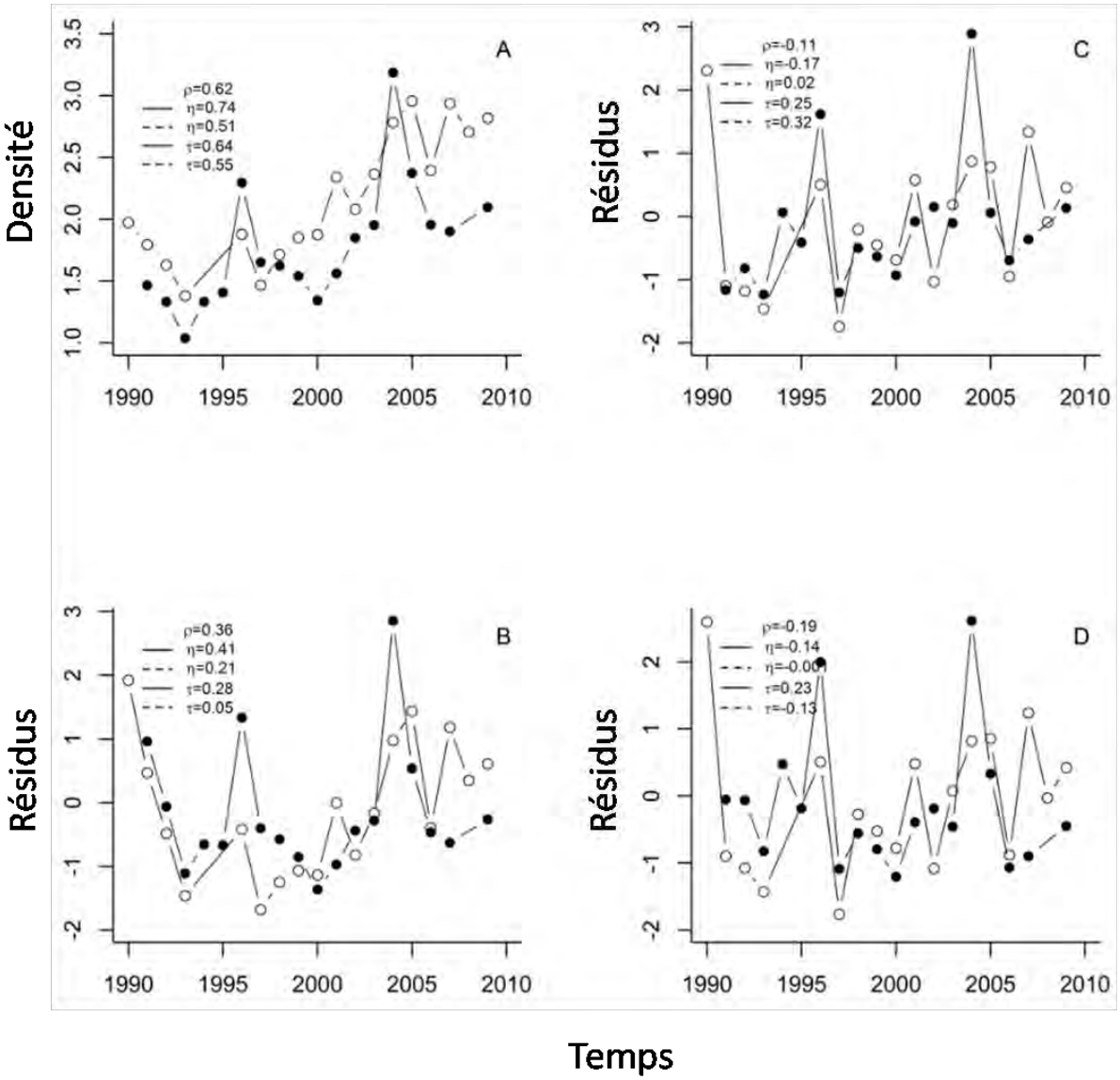


Figure 11. Représentation graphique de deux séries temporelles observées et de ces mêmes séries une fois qu'elles ont subies les procédures de "detrending" et/ou de "prewhitenning". Les coefficients d'autocorrélation temporelle (η1 and η2) et de tendance à long-terme (τ1 and τ2) de chaque série temporelle ainsi que le degré de synchronisme mesuré entre chaque série (ρ) sont également présentés. (A) données brutes, (B) séries temporelles issues de la procédure de "detrending", (C) séries temporelles issues de la procédure de "prewhitenning", (D) séries temporelles issues des procédures de "detrending" et de "prewhitenning". Les valeurs des séries présentées dans les graphiques B, C et D sont les résidus des modèles statistiques utilisés pour transformer les séries (encadré 1). (Modifié d'après ***PI*** ; Figure 2).

Les résultats montrent que les séries temporelles courtes qui présentent un faible coefficient de densité-dépendance mais un fort coefficient de tendance à long-terme sont plus modifiés par la procédure de "detrending" que les séries qui ont les caractéristiques opposées (Tableau 4), ce qui est en accord avec notre hypothèse. Nous avons obtenu les mêmes résultats lorsque les deux processus ont été retirés. En revanche, contrairement à notre hypothèse de départ, nous avons trouvé que les séries qui présentent de faibles coefficients de densité-dépendance sont plus modifiées par la procédure de "prewhitenning" que les séries qui ont un fort coefficient de densité-dépendance (Tableau 4). Ce résultat contradictoire peut

s'expliquer par une estimation biaisée des coefficients de densité-dépendances due à l'absence de prise en compte des erreurs de mesures dans les séries temporelles (Freckleton *et al.*, 2006). D'autres facteurs comme par exemple le nombre de valeurs manquantes dans les séries temporelles ou encore la variance autour de la moyenne des estimations dans les séries peuvent biaiser les estimations de densité-dépendance (Brook & Bradshaw, 2006) et peuvent expliquer pourquoi les séries qui présentent un faible coefficient de densité-dépendance sont plus modifiées que les séries qui présentent un fort coefficient de densité-dépendance.

Tableau 4. Coefficients issus de la relation entre l'influence des TSTs sur les séries temporelles (mesurés par la corrélation entre les séries temporelles brutes et les séries temporelles modifiée par chaque TST) et les coefficients de tendance à long-terme et de densité-dépendance. Sont également présenté les coefficients issus de la relation entre la durée de vie moyenne des espèces et les coefficients de tendance à long-terme et de densité-dépendance. Les résultats significatifs sont en gras. (Modifié d'après ***PI***, Tableau S2).

	Tendance	Densité-dépendance	Longueur
Detrending	**-11.8**	**25.2**	**0.34**
Prewithenning	-0.21	**2E-3**	**0.02**
Detrending+ prewhithenning	**-0.6**	**5E-4**	**0.01**
Durée de vie	**-0.02**	**0.13**	-

Nous avons mis en évidence une relation significative entre les caractéristiques des séries temporelles et la durée de vie des espèces (Tableau 4). Les séries temporelles des espèces qui ont une longue durée de vie présentent un plus fort coefficient de densité-dépendance et un plus faible coefficient de tendance à long-terme que les séries temporelles des espèces qui ont une durée de vie plus courte. Une telle relation avec le coefficient de densité-dépendance a déjà été mise en évidence chez d'autres espèces (Fowler, 1981; Saether *et al.*, 2005; Sæther *et al.*, 2013). Ces résultats suggèrent que l'influence des TSTs sur les séries temporelles varie en fonction de la durée de vie des espèces.

4.3. Influence des TSTs sur les mesures de synchronisme

Cette différence d'influence des TSTs en fonction des caractéristiques des séries temporelles se traduit par une influence variable des TSTs sur les mesures de synchronisme. D'un point de vue générale et quelles que soient les TSTs appliquées aux séries temporelles, nos résultats montrent que le degré de synchronisme mesuré entre deux populations est plus fortement modifié lorsque les deux séries temporelles impliquées dans la mesure de synchronisme sont courtes, ne présentent pas de densité-dépendance et présentent une tendance à long-terme (Tableau 5).

Tableau 5. Coefficients issus des modèles qui relient les différences de mesures de synchronisme calculées antre les mesure obtenues avec chaque TST et les mesures obtenues sur les données brutes aux caractéristiques des séries temporelles. Les résultats significatifs ($p<0.05$) sont en gras. "-" indique que le modèle n'a pas convergé. (Modifié d'après ***PI***, Tableau S3).

	Detrending			Prewhitenning			Detrending + Prewhitenning		
Codes espèces	Tendance	Densité-dépendance	Longueur	Tendance	Densité-dépendance	Longueur	Tendance	Densité-dépendance	Longueur
Abab	0,005	-0,007	**-0,012**	0,0033	0,0043	-0,0089	0,0047	-0,0059	**-0,0159**
Albi	**0,012**	-0,003	**0,01**	-0,0075	-0,0046	0,0033	0,0103	-0,0022	0,0001
Alal	**0,011**	-0,004	**-0,005**	0,0005	-0,0003	-0,0021	0,0115	-0,0029	**-0,0064**
Amme	0,006	-0,012	-0,01	-0,0207	0,0034	**-0,0272**	0,0076	-0,021	**-0,0437**
Anan	**0,015**	-0,002	**-0,003**	**0,004**	0,0019	**-0,0024**	**0,0095**	0,0013	**-0,0056**
Babb	**0,02**	**-0,007**	**-0,006**	**0,0041**	**-0,0071**	**-0,0055**	**0,014**	**-0,0056**	**-0,0068**
Babu	**0,018**	-0,003	**-0,01**	0,0025	**-0,0044**	**-0,006**	**0,015**	-0,0041	**-0,0092**
Blbj	0,006	**-0,024**	**-0,017**	0,009	0,002	**-0,0212**	0,0192	0,005	**-0,0271**
Caca	0,01	-0,013	-0,011	0,0025	0,0046	-0,0072	0,0024	0,0087	-0,0319
Chna	0,012	0,009	-0,001	0,0074	0,0042	-0,0079	**0,0251**	0,0089	-0,0001
Cogo	0,02	0,003	-0,011	0,0129	-0,0012	-0,0089	0,0166	0,005	-0,0149
Cope	**0,015**	**-0,012**	-0,001	**0,0047**	**-0,0153**	**-0,0041**	**0,0117**	**-0,0129**	-0,0028
Cyca	-0,003	-0,002	0,006	0,0027	-0,0144	-0,0042	-0,0005	-0,0211	-0,0294
Eslu	0,002	**-0,009**	**-0,006**	-0,0007	-0,0012	**-0,0076**	0,0029	-0,0053	**-0,011**
Gagy	0,022	-0,025	**-0,029**	0,0194	-0,0015	-0,0049	0,0376	-0,0076	-0,0006
Gogo	**0,017**	**-0,004**	**-0,008**	0,0001	-0,0025	**-0,0092**	**0,0142**	-0,0031	**-0,0106**
Golo	-	-	-	-	-	-	-	-	-
Gooc	**0,021**	**-0,01**	0,001	0,0024	**-0,0086**	-0,0001	**0,0086**	**-0,0096**	-0,0026
Gyce	0,004	-0,001	-0,008	-0,0017	-0,0077	-0,0111	0,0017	-0,0072	-0,0137
Lapl	**0,012**	0,001	0	**0,0062**	0,0033	**-0,0096**	**0,0141**	0,0039	**-0,0087**
Legi	**0,021**	-0,003	**-0,009**	0,0074	-0,0058	**-0,0088**	**0,018**	-0,0053	**-0,0138**
Lebu	**0,017**	0,003	**0,007**	-0,0005	0,0008	-0,0075	0,0064	0,0022	0,0014
Lele	0,008	-0,003	-0,006	0,0039	-0,0014	**-0,01**	**0,0093**	-0,003	**-0,0119**
Pefl	0,005	-0,001	**-0,006**	0,0009	0,0005	**-0,0078**	**0,013**	0,0021	**-0,0098**
Phph	**0,015**	**-0,01**	**-0,005**	0,0005	**-0,0073**	**-0,008**	**0,0105**	**-0,0076**	**-0,0084**
Pupu	0,009	-0,003	-0,006	-0,0058	0,0113	**-0,0169**	**0,0189**	-0,0007	-0,0111
Rhse	**0,023**	-0,016	0,002	0,0048	-0,0029	-0,0115	0,0124	-0,0048	-0,0095
Ruru	**0,016**	-0,002	**-0,002**	0,0014	-0,0006	**-0,0074**	**0,013**	-0,0009	**-0,0085**
Sasa	-	-	-	-	-	-	-	-	-
Satr	**0,012**	-0,001	**-0,003**	**0,0048**	**-0,0034**	**-0,0052**	**0,01**	**-0,0059**	**-0,0073**
Scer	0,004	-0,006	**-0,027**	0,0028	-0,0034	-0,0185	0,0046	-0,0104	**-0,0245**
Sqce	**0,015**	-0,001	**-0,004**	**0,0047**	-0,0021	**-0,0048**	**0,0113**	-0,001	**-0,0067**
Teso	0,013	-0,013	**-0,021**	0,0027	-0,0058	-0,0101	-0,0028	0,009	-0,0143
Titi	0,008	-0,007	**-0,008**	-0,0017	-0,001	**-0,0119**	**0,0133**	-0,0017	-0,0029

Globalement, la procédure de "detrending" a moins d'influence sur les mesures de synchronisme (i.e. sur les différentes métriques utilisées pour caractériser le synchronisme des espèces) que la procédure de "prewhitenning" ce qui peut s'expliquer par l'influence de ces deux procédures sur le degré de synchronisme mesuré entre les populations (i.e. plus faible influence de la procédure de "detrending" par rapport à la procédure de "prewhitenning"; Figure 12). En effet, quelles que soient les TSTs appliquées aux données, les mesures de synchronisme sont diminuées, que ce soit en termes de valeurs ou de proportion d'espèces qui présentent une relation significative (résultats non présentés). Par exemple, après avoir appliqué la procédure de "detrending" aux séries temporelles, le pourcentage d'espèce présentant un degré de synchronisme significativement différent de zéro est plus faible que lorsque le synchronisme est mesuré sur les données brutes, ce qui est en accord avec d'autres études (Pyper & Peterman, 1998; Pyper *et al.*, 1999; Cheal *et al.*, 2007; Batchelder *et al.*, 2012). Une telle diminution du niveau de synchronisme a classiquement été considéré comme une preuve de l'effet Moran (e.g. Paradis *et al.*, 1999) ce qui peut effectivement être le cas si l'ensemble des séries présentent une tendance à long-terme (Pyper & Peterman, 1998). Cependant, aucune des études ayant montré une telle diminution n'a au préalable testé si les séries temporelles présentaient une tendance à long-terme ce qui peut biaiser les mesures de synchronisme ainsi que les conclusions relatives à ces mesures.

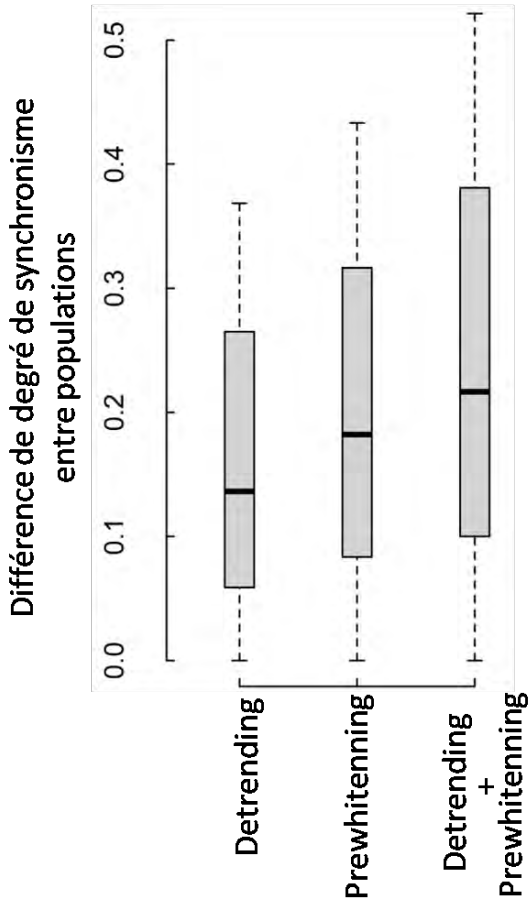


Figure 12. Comparaison des différences de niveau de synchronisme calculé entre chaque population pour les séries temporelles brutes et ceux calculés avec les séries temporelles transformées. Une forte différence indique un faible degré de ressemblance entre les mesures de synchronisme obtenues avec les séries temporelles brutes et les séries temporelles modifiées et donc une forte influence de la transformation sur les données. Detrending = retrait de la tendance à long-terme ; Prewhitenning = retrait de l'autocorrélation temporelle. (Modifié d'après ***PI*** ; Figure 4).

L'influence des TSTs sur les mesures de synchronisme varie fortement en fonction des espèces considérées et peuvent même mener à des conclusions opposées quant au mécanisme sous-jacent au synchronisme des populations (résultats non présentés). Par exemple, après avoir retiré l'influence de l'autocorrélation temporelle dans les séries, le synchronisme des populations de l'épinoche (*Gasterosteus gymnurus*) est significativement associé au synchronisme des températures (preuve de l'influence d'un effet Moran) alors que ce n'est pas le cas lorsque le synchronisme des populations est mesuré sur les données brutes. Ainsi, en fonction des espèces et des TSTs appliquées aux séries temporelles, les prédictions relatives à l'influence du réchauffement climatique sur les probabilités d'extinction des espèces peuvent être totalement différentes.

5. Quelles implications ?

Les TSTs influencent fortement les mesures de synchronisme et plusieurs de nos résultats posent question quant à leur capacité à mettre en évidence le mécanisme responsable du synchronisme des populations. En effet, les TSTs ce sont avérées peu efficaces pour supprimer l'influence de processus dans les séries temporelles ce qui peut biaiser les conclusions dans les études de synchronisme. Par exemple, si le retrait de l'autocorrélation temporelle retire une partie de la tendance à long-terme dans les séries temporelles alors le synchronisme peut faussement être attribué à de la dispersion d'individus entre localités. Ce phénomène est particulièrement problématique puisqu'il peut conduire à une sous-estimation de l'influence du réchauffement climatique sur les probabilités d'extinction des espèces. Dans certains cas bien particulier les TSTs peuvent permettre de mettre en évidence et de quantifier l'influence de différents processus sur le synchronisme des populations. Par exemple, éliminer une tendance à long-terme a du sens si toutes les populations présentent une tendance soit croissante soit décroissante car une telle ubiquité suggère l'influence d'un facteur commun à toutes les populations. Si tel est le cas, la comparaison des mesures de synchronisme obtenues sur les données brutes avec celles obtenues après l'utilisation d'une procédure de "detrending" devrait permettre de quantifier la part de synchronisme due au climat (Buonaccorsi *et al.*, 2001). En revanche, éliminer une tendance pour des raisons statistiques (e.g. augmentation du risque d'erreur de première espèce) pose question car son élimination peut mener à détecter du synchronisme alors qu'il n'y en a pas. Par ailleurs, un problème majeur avec les TSTs est qu'il est difficile de retirer un mécanisme sans affecter l'autre. Ce problème est d'autant plus compliqué que l'influence des TSTs sur les mesures de synchronisme dépend des caractéristiques des séries temporelles qui dépendent elle-même de certaines caractéristiques des espèces. Les TSTs doivent donc être utilisées avec parcimonie en respectant un certain nombre de consignes. Nous suggérons notamment de toujours vérifier si le mécanisme d'intérêt a bien été supprimé et de quantifier dans quelles proportions l'autre mécanisme a été modifié. Nous suggérons par ailleurs d'utiliser différentes TSTs et d'interpréter les résultats en fonction des caractéristiques des séries temporelles et des résultats obtenus avec chaque TST. Enfin, si les séries ne présentent pas (ou peu) d'autocorrélation temporelle nous suggérons de ne pas appliquer de procédure de "prewhitenning" car cette procédure modifie

fortement les mesures de synchronisme ainsi que les conclusions associées à ces mesures. Le respect de ces consignes devrait contribuer à améliorer notre compréhension des processus à l'origine du synchronisme spatial des populations ainsi que notre capacité à prédire les influences du réchauffement climatique sur les probabilités d'extinction des espèces.

Chapitre 3

Déterminants des variations spatio-temporelles des dynamiques de populations

Cottus gobio

1. Introduction

Identifier quels sont les facteurs qui influencent les fluctuations de tailles de populations est une question centrale de la dynamique des populations (De Valpine & Hastings, 2002). Au cours des dernières années, cette question a largement divisé la communauté scientifique entre ceux qui prônaient que les populations étaient principalement sous l'influence de processus déterministes et intrinsèques aux dynamiques de populations (e.g. la densité dépendance) (Andrewartha & Birch, 1954) et ceux qui soutenaient que les processus stochastiques (e.g. climat), extrinsèques aux dynamiques de populations, étaient la principale source de variation des tailles de populations (Nicholson, 1933, 1957). Aujourd'hui, bien que la plupart des chercheurs soient d'accord sur le fait que les deux processus sont pertinents et peuvent influencer simultanément les dynamiques de populations (Turchin, 1995; Berryman, 2002), leur contribution relative reste mal appréhendée pour de nombreuses espèces. Ceci peut notamment s'expliquer par le fait que les processus densité-dépendants peuvent interagir avec des facteurs environnementaux pour former des patrons complexes de dynamiques de populations (Fromentin *et al.*, 2001; Stenseth *et al.*, 2004) qui peuvent par ailleurs varier en fonction des espèces considérées (Davis *et al.*, 2014). Cette difficulté est également renforcée par la migration d'individus entre populations car ce processus peut modifier les patrons de densité dépendance (Ives *et al.*, 2004) et les réponses des populations aux variations environnementales (Ranta *et al.*, 2005).

La question relative à l'influence des facteurs intrinsèques et extrinsèques aux dynamiques de populations a récemment reçue un fort regain d'intérêt du fait du réchauffement climatique global (Knape & De Valpine, 2011). En effet, évaluer la contribution des facteurs extrinsèques aux variations de tailles de populations pourrait permettre d'évaluer et de prédire les conséquences du réchauffement climatique sur les dynamiques de populations. Les conséquences de ces changements sont d'autant plus visibles sur les populations situées en limite d'aire de répartition des espèces où des expansions (Sakai *et al.*, 2001) et des contractions (Hampe & Petit, 2005) des aires de distribution des espèces ont été mises en évidence. Par ailleurs, on peut s'attendre à des différences de dynamiques de populations aux extrêmes de gradients environnementaux avec par exemple des déclins de populations à un extrême et des augmentations à l'autre extrême (Matías & Jump, 2014). Ainsi, l'étude des variations spatiales des dynamiques de populations pourrait permettre de prédire les futures tendances des populations et la future distribution des espèces (Bellard *et al.*, 2012).

De manière intéressante, plusieurs études on mis en évidence des variations intraspécifiques des dynamiques de populations (Stenseth *et al.*, 1999; Fromentin *et al.*, 2001; Haydon *et al.*, 2002) fournissant ainsi une base de travail pour déterminer quels sont les facteurs impliqués dans les variations spatiales des dynamiques de populations. Il existe par exemple des gradients de dynamiques de populations en fonction de la latitude (Bjornstad *et al.*, 1995; Turchin & Hanski, 1997) et de la distance des populations par rapport à la limite de l'aire de répartition des espèces (Curnutt *et al.*, 1996; Williams *et al.*, 2003). De tels gradients suggèrent que les variations intraspécifiques de dynamiques de populations peuvent être

prédites à partir de connaissances sur la position géographique des populations (Saether *et al.*, 2008). Ces variations intraspécifiques peuvent refléter une certaine dépendance des facteurs intrinsèques des dynamiques de populations à des variations des conditions environnementales locales. Par exemple, des variations spatiales des ressources alimentaires peuvent générer des variations spatiales des patrons de densité dépendance (Wang *et al.*, 2008). Ces variations peuvent aussi s'expliquer par des variations spatiales de l'influence des facteurs environnementaux sur les dynamiques de populations. Il a par exemple été montré que l'environnement avait plus d'influence sur les populations situées en marges de l'aire de répartition des espèces (Fukaya *et al.*, 2014). La compréhension de ces patrons spatiaux requiert donc une estimation précise de la contribution des facteurs impliqués dans les fluctuations de tailles de populations situées à différentes localités.

Les rares études qui se sont intéressées aux variations intraspécifiques de dynamique de populations ont généralement été conduites sur une seule espèce. Cependant, la prise en compte de plusieurs espèces pourrait permettre de révéler des patrons spécifiques mais aussi des patrons beaucoup plus généraux comme par exemple des réponses communes des espèces aux variations des conditions environnementales. Saether *et al.* (2008) ont par exemple mis en évidence une influence globalement faible des processus densité-dépendants sur différentes espèces d'oiseaux mais une variabilité interspécifique du gradient latitudinal d'influence de la température sur les populations.

Dans ce chapitre, notre objectif est d'identifier quels sont les mécanismes à l'origine des variations spatio-temporelles des dynamiques de populations de 28 espèces de poissons d'eau douce. Pour cela, nous avons utilisé des modèles états-espaces pour étudier l'influence de quatre variables environnementales sur les fluctuations de tailles de populations en fonction de leurs effets sur trois paramètres qui décrivent les dynamiques locales de populations (i.e. taux de migration, taux d'accroissement et densité dépendance; voir encadré 2). La description et le calcul des variables environnementales sont présentés dans l'encadré 3.

2. Méthode d'identification des mécanismes et mise en évidence des effets

Les modèles états-espaces ont été ajusté pour chaque espèce en utilisant l'ensemble des séries temporelles qui avaient au moins 17 années de données. Les variations entre espèces des estimations de coefficients qui relient les variables environnementales aux paramètres de dynamiques de populations (encadré 2) reflètent des différences dans les déterminants de dynamiques de populations. Cependant, l'effet des variables environnementales sur les patrons d'abondances ne dépend pas seulement de la valeur de ces coefficients. En effet, les changements observés d'abondances dus à une variable environnementale avec une certaine valeur de coefficient dépendent également de la gamme de variation du prédicteur environnemental (e.g. pour un coefficient donné, l'effet de l'altitude sur les variations d'abondances n'est pas le même si la gamme d'altitude dans laquelle se trouve les populations est de 100 m ou de 1000 m) et de la taille de la population (e.g. pour un coefficient donné, l'effet de l'altitude sur les variations d'abondances est différent si la taille de la population est

de 100 ou de 1000 individus). Ainsi, les abondances d'une espèce à une localité i et a un temps t dépendent (1) de la valeur des variables environnementales, (2) du nombre d'individus au pas de temps précédent et (3) de la valeur du coefficient associé à la variable environnementale.

Encadré 2. Description des modèles état-espaces utilisés pour chaque espèce.

Les modèles états-espaces sont des modèles hiérarchiques qui décomposent les séries temporelles d'abondances en un processus de transition et un processus d'observation (De Valpine, 2002; De Valpine & Hastings, 2002). Ces modèles sont composés de deux équations. L'équation de processus (ou de transition) gouverne la dynamique et la variabilité du système (également appelé état et qui n'est pas directement observable) alors que l'équation d'observation détaille la relation entre le système et les observations faites de ce système. Ces modèles sont des modèles hiérarchiques car le processus d'observation est conditionné par le processus de transition.

Soit $N_{i,t}$ la vraie abondance et $X_{i,t}$ l'abondance observée à la localité i au temps t. Dans notre modèle, $X_{i,t}$ est considérée comme une variable aléatoire distribuée selon une loi binomiale avec $N_{i,t}$ le nombre d'essais et p_i la probabilité de capture à la localité i. Cette relation définie l'équation d'observation. $N_{i,t}$ est également considérée comme une variable aléatoire, distribuée selon une loi de poisson et dont l'espérance est calculée à partir d'une version modifiée du modèle de Ricker:

$$E(N_{i,t}) = \left[\gamma_{i,t} + N_{i,t-1} \exp\left(\rho_{i,t} - \eta_{i,t} N_{i,t-1}\right)\right] * \frac{S_{t-1}}{S_t} \qquad \text{(eq.1)}$$

où $\gamma_{i,t}$ est le taux de migration, $\rho_{i,t}$ est le taux d'accroissement de la population, $\eta_{i,t}$ est le coefficient de densité dépendance, et où S_t et S_{t-1} sont les surfaces échantillonnées au temps t et t-1, respectivement. Dans notre modèle, la dynamique de population est donc un processus Markovien dans la mesure où l'abondance au temps t ($N_{i,t}$) ne dépend que de l'abondance au pas de temps précédent ($N_{i,t-1}$).

Pour déterminer l'importance des facteurs environnementaux sur les dynamiques de populations, nous avons intégré dans notre modèle des modèles linéaires généralisés qui relient les paramètres de dynamiques de populations ($\gamma_{i,t}$, $\rho_{i,t}$ and $\eta_{i,t}$) aux variables écologiques:

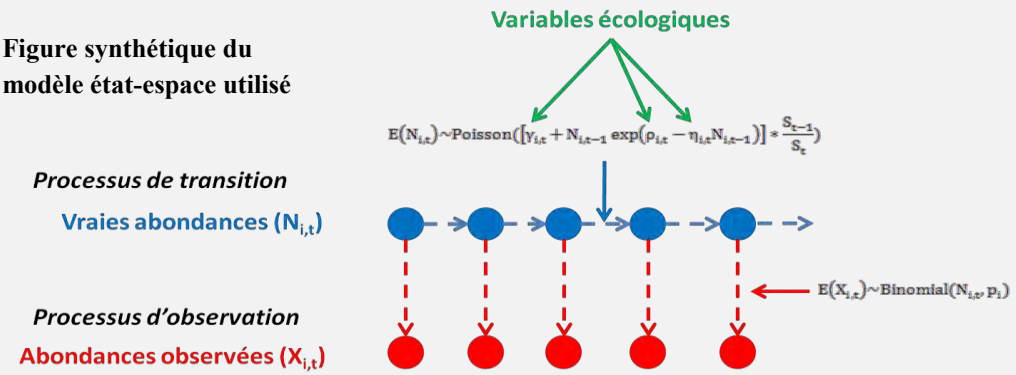
$$\gamma_{i,t} = \gamma_a + (\gamma_b * Alt_i) + (\gamma_c * CV_i) + (\gamma_d * meanT_{i,t}) + (\gamma_e * varT_{i,t}) \qquad \text{(eq. 2a)}$$

$$\rho_{i,t} = \rho_a + (\rho_b * Alt_i) + (\rho_c * CV_i) + (\rho_d * meanT_{i,t}) + (\rho_e * varT_{i,t}) \qquad \text{(eq. 2b)}$$

$$\eta_{i,t} = \eta_a + (\eta_b * Alt_i) + (\eta_c * CV_i) + (\eta_d * meanT_{i,t}) + (\eta_e * varT_{i,t}) \qquad \text{(eq. 2c)}$$

où Alt_i est l'altitude à la localité i, CV_i est le coefficient de variabilité des températures de l'eau mesurée sur toute la période d'étude à la localité i, $meanT_{i,t}$ est la moyenne annuelle des températures de l'eau et $varT_{i,t}$, sa variance. γ_a, ρ_a et η_a sont les intercepts des modèles tandis que les autres paramètres (γ_b, γ_c, γ_d, γ_e, ρ_b, ρ_c, ρ_d, ρ_e, η_b, η_c, η_d, η_e) sont les coefficients de pentes représentant l'effet des variables écologiques (Alt_i, CV_i, $meanT_{i,t}$ et $varT_{i,t}$) sur les paramètres de dynamiques de populations. Avant d'ajuster le modèle aux données, les prédicteurs ont été standardisés pour pouvoir comparer leur influence relative.

Figure synthétique du modèle état-espace utilisé



Encadré 3. Description et calcul des variables environnementales.

Prédictions des températures de l'eau

Les températures journalières de l'eau à chaque site ont été prédites à partir d'une procédure de random forest. Nous avons utilisé les sites pour lesquels nous avions les températures journalières de l'air et de l'eau pour calibrer un modèle prédictif avec comme variable dépendante la température journalière de l'eau et comme variables indépendantes le mois, l'altitude et la température journalière de l'air. Le modèle a été calibré sur 70% du jeu de donné et validé sur les 30% restants. La procédure a été répétée 100 fois pour s'assurer de la robustesse des résultats. Le modèle ayant révélé un bon pouvoir prédictif (R^2 moyen=0.86; SD=0.005), nous l'avons utilisé pour prédire les températures journalières de l'eau sur l'ensemble des sites échantillonnés.

Variables écologiques

Le changement climatique influence la moyenne mais aussi la variabilité des facteurs climatiques (Stocker *et al.*, 2013). Pour déterminer laquelle de ces composantes (moyenne ou variabilité) avait le plus d'influence sur les dynamiques de populations de poissons, nous avons calculé la moyenne et la variance annuelle des températures de l'eau à chaque localité. Nous avons également calculé le coefficient de variation des températures de l'eau sur l'ensemble de la période d'étude à chaque localité. Cette dernière mesure représente le degré de stochasticité environnemental à chaque site. La dernière variable écologique que nous avons choisi de considérer est l'altitude car cette variable peut être considérée comme une variable synthétique des variations spatiales de plusieurs paramètres physiques et climatiques.

Pour prendre en compte les variations spatio-temporelles des variables environnementales et des abondances, nous avons calculé des tailles d'effets pour chaque coefficient à chaque site et à chaque pas de temps. La taille d'effet de chaque coefficient (qui représente l'effet des variables environnementales sur les abondances aux travers de leurs influences sur les différents paramètres de dynamique de population) à la localité i et au temps t est exprimée par le pourcentage de changement d'abondances induit en fixant la valeur du coefficient considéré à zéro (e.g. en fixant γ_b à zéro pour étudier l'influence de l'altitude au travers du taux de migration), relativement à l'abondance calculée avec la valeur estimée de ce coefficient. Pour étudier l'influence de chaque variable environnementale sur les tailles de populations, indépendamment des paramètres de dynamiques de populations, nous avons calculé les tailles d'effets à chaque localité et à chaque pas de temps en fixant à zéro les valeurs des coefficient associées à la variable environnementale considérée (e.g. en fixant γ_b, ρ_b et η_b à zéro pour étudier l'influence de l'altitude). Finalement, pour étudier l'influence de l'ensemble des variables environnementales au travers des différents paramètres de dynamiques de populations, nous avons calculé les tailles d'effets à chaque localité et à chaque pas de temps en fixant à zéro les valeurs des coefficients associés au paramètre de dynamique de population considéré (e.g. en fixant γ_b, γ_c, γ_d et γ_e à zéro pour étudier l'influence des variables environnementales au travers du taux de migration). Les tailles d'effets associées aux coefficients, aux paramètres de dynamiques de populations et aux variables environnementales ont été considérées en valeurs brutes et en valeurs absolues pour mettre en évidence des différences d'influence et de magnitude des variables environnementales sur les patrons d'abondances, respectivement. Le calcul détaillé des tailles d'effets pour un coefficient donné est présenté dans l'encadré 4.

Encadré 4. Description et calcul des tailles d'effets

Nous détaillons ici le calcul des tailles d'effet pour un coefficient donné (e.g. γ_b). La même procédure a été utilisée pour calculé les tailles d'effets associées aux autres coefficients, aux paramètres de dynamiques de populations et aux variables environnementales. Les tailles d'effets ont été calculées pour chaque espèce en trois étapes.

Etape 1. Pour une espèce donnée, nous avons utilisé l'équation 2 (encadré 1) pour calculer à chaque site et à chaque pas de temps la valeur du taux de migration associée à l'estimation du coefficient γ_b et la valeur du taux de migration attendue en l'absence d'influence de l'altitude sur le taux de migration (i.e. en fixant la valeur du coefficient γ_b à zero):

$$\gamma_{i,t,0} = \gamma_a + (0 * \mathrm{Alt}_i) + (\gamma_c * \mathrm{CV}_i) + (\gamma_d * \mathrm{meanT}_{i,t}) + (\gamma_e * \mathrm{varT}_{i,t})$$

$$\gamma_{i,t,est} = \gamma_a + (\gamma_b * \mathrm{Alt}_i) + (\gamma_c * \mathrm{CV}_i) + (\gamma_d * \mathrm{meanT}_{i,t}) + (\gamma_e * \mathrm{varT}_{i,t})$$

Les deux autres paramètres de dynamiques de populations ont été calculés (en utilisant les équations 2b et 2c) en utilisant les valeurs de coefficients estimées par le modèle bayesien et les valeurs observées des variables écologiques à la localité i et au temps t.

Etape 2. Nous avons ensuite utilisé l'équation 1 (encadré 1) pour calculer les valeurs d'abondances associées aux coefficients estimés à l'étape 1 et les valeurs observées d'abondances à la localité i au temps t-1:

$$\mathrm{E}(\mathrm{N}_{i,t,0}) = \left[\gamma_{i,t,0} + \mathrm{N}_{i,t-1} \exp\left(\rho_{i,t} + \eta_{i,t}\mathrm{N}_{i,t-1}\right)\right] * \frac{\mathrm{S}_{t-1}}{\mathrm{S}_t}$$

$$\mathrm{E}(\mathrm{N}_{i,t,est}) = \left[\gamma_{i,t,est} + \mathrm{N}_{i,t-1} \exp\left(\rho_{i,t} + \eta_{i,t}\mathrm{N}_{i,t-1}\right)\right] * \frac{\mathrm{S}_{t-1}}{\mathrm{S}_t}$$

Etape 3. Nous avons finalement utilisé l'équation suivante pour calculer la taille d'effet du coefficient γ_b:

$$\mathrm{ES}_{\gamma b,i,t} = \frac{\mathrm{N}_{i,t,est} - \mathrm{N}_{i,t,0}}{\mathrm{N}_{i,t,0}} * 100$$

$\mathrm{ES}_{\gamma b,i,t}$ est la taille d'effet du coefficient γ_b à la localité i et au pas de temps. $\mathrm{N}_{i,t,0}$ et $\mathrm{N}_{i,t,est}$ ont été calculé à l'étape 2 avec les valeurs de $\gamma_{i,t,0}$ and $\gamma_{i,t,est}$ obtenues à l'étape 1. Ainsi, la taille d'effet du coefficient γ_b représente le pourcentage de changement d'abondance due à l'influence de l'altitude sur le taux de migration relativement à l'abondance attendue en l'absence d'influence de ce facteur sur le taux de migration.

3. Influence de l'environnement au travers des paramètres de dynamiques de populations

Nos résultats montrent que les variables environnementales ont globalement une influence négative sur les populations, indépendamment du paramètre de dynamique de population considéré (Figure 13A). Cependant, la gamme de variation interquartile des boîtes à moustache suggère de fortes variations de réponses des populations. Ainsi, quand bien même l'environnement a une influence globale négative sur les populations au travers des différents paramètres de dynamiques de populations, son influence peut varier en fonction de la localité et du pas de temps considéré. Ces variations traduisent en fait des variations spatio-

temporelles des paramètres de dynamiques de populations en fonction des conditions environnementales locales (Tableau 6). Globalement, l'environnement a plus d'influence sur les fluctuations de tailles des populations au travers du taux d'accroissement et, dans une moindre mesure, du taux de migration, qu'au travers de la densité dépendance (Figure 13B). Ce résultat suggère donc que les processus densité-dépendants n'ont qu'une influence limitée sur les populations de poissons ce qui est en accord avec les conclusions d'autres études sur des taxa différents (Saether *et al.*, 1996; Grøtan *et al.*, 2009; Ziebarth *et al.*, 2010; Knape & De Valpine, 2012). De fait, les changements climatiques devraient principalement influencer les populations de poissons d'eau douce au travers de modifications du taux d'accroissement et du taux de migration qu'au travers de modifications des processus densité-dépendants. Cependant, la contribution relative des variables environnementales au travers des différents paramètres de dynamiques de populations varie fortement en fonction des espèces considérées (Figure 13C) ce qui indique une certaine spécificité de réponse des espèces aux variations environnementales.

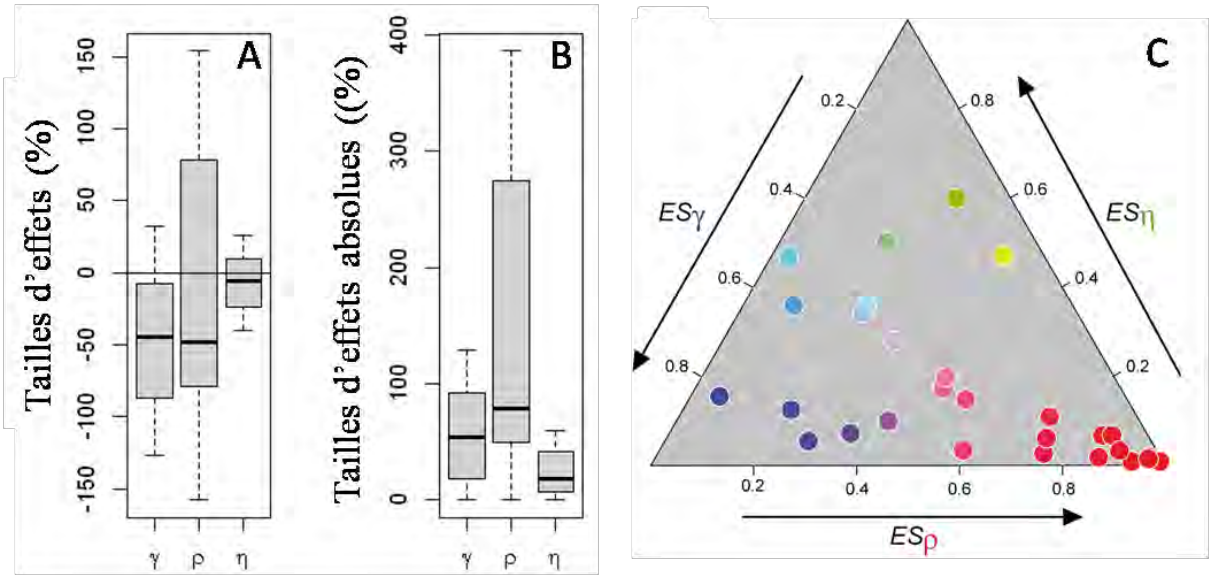


Figure 13. Tailles d'effets associées aux paramètres de dynamiques de populations (γ = taux de migration ; ρ = taux d'accroissement ; η = densité dépendance) en valeur brutes (A) et en valeur absolues (B). (C) Contribution des variables environnementales aux variations de tailles de populations au travers des paramètres de dynamique de populations pour chaque espèce. (Modifié d'après ***PIII***; Figure 1).

Tableau 6. Coefficients de pentes qui représentent l'influence de l'altitude à la localité i (Alt; indice b), du coefficient de variation environnemental à la localité i (CV; indice c), de la moyenne annuelle de température (meanT; indice d) et de sa variabilité (varT; indice e) sur le taux de migration (γ), le taux d'accroissement (ρ) et la densité dépendance (η). $P_{capture}$ est la probabilité moyenne de capture estimée pour chaque espèce. N_{series} est le nombre de séries temporelles pour chaque espèce. Les valeurs en gras représentent les coefficients pour lesquels les intervalles de crédibilité à 95% ne recoupent pas zéro. (Modifié d'après ***PIII***; Tableau 1).

Codes espèces	γ_b	γ_c	γ_d	γ_e	ρ_b	ρ_c	ρ_d	ρ_e	η_b	η_c	η_d	η_e	N_{series}	$P_{capture}$
Alal	**3.58**	**2.90**	**12.50**	-1.43	**-0.05**	**-0.26**	**-0.59**	**0.28**	**8.55E-04**	**-7.99E-04**	**-1.49E-03**	**9.57E-04**	72	0.35
Anan	-0.09	0.00	0.00	-0.02	0.00	**-0.04**	**-0.04**	**0.06**	**1.25E-03**	-3.38E-05	**1.86E-04**	1.59E-04	133	0.54
Baba	-0.15	**1.96**	0.75	0.32	0.00	**-0.10**	**-0.03**	0.00	**4.35E-05**	**-2.32E-04**	**8.04E-05**	**-1.54E-04**	154	0.39
Babr	**3.07**	**2.15**	0.33	**-4.56**	**-0.25**	**-0.10**	**0.18**	**0.11**	**-3.06E-03**	**-3.18E-04**	**3.35E-04**	**2.29E-04**	59	0.39
Blbj	**-16.13**	3.22	-3.46	**-6.04**	**0.73**	**-0.17**	0.00	**0.26**	**4.00E-03**	**2.09E-03**	**2.18E-03**	**-3.67E-03**	30	0.28
Cogo	-0.04	**0.38**	0.19	**-0.50**	**0.06**	**-0.21**	**-0.10**	**0.26**	**1.76E-04**	**-2.79E-04**	3.65E-05	**2.38E-04**	117	0.42
Cyca	**-3.29**	-1.40	-1.00	-0.44	0.82	0.72	-0.19	-1.10	-4.60E-02	6.15E-03	**-1.02E-01**	8.04E-04	11	0.29
Eslu	0.32	-0.21	-0.03	0.09	**-0.41**	**1.01**	0.46	-0.94	**-2.73E-02**	**4.74E-02**	6.28E-03	-5.89E-02	58	0.31
Gaac	**-1.92**	**3.95**	**2.66**	**-6.40**	**0.69**	**-2.13**	**-1.37**	**2.86**	**9.20E-03**	**-2.60E-02**	**-1.48E-02**	**3.59E-02**	21	0.22
Gogo	**-1.18**	**-0.41**	**-1.70**	**0.32**	**0.15**	0.01	**0.22**	0.01	**-2.79E-05**	2.59E-05	**2.50E-04**	**-1.48E-04**	152	0.42
Gyce	-0.94	**-2.55**	-1.43	**4.44**	0.17	**0.52**	**0.27**	**-0.94**	-6.09E-04	-3.61E-04	**-1.23E-03**	8.60E-05	20	0.29
Lapl	0.08	**-2.09**	0.40	0.38	**-0.16**	-0.04	**-0.36**	**0.29**	**-3.91E-03**	**1.16E-03**	**-3.43E-03**	**-4.90E-04**	78	0.28
Legi	-0.02	0.04	0.00	-0.07	**-0.21**	**0.22**	**-0.08**	**-0.28**	**-6.01E-03**	**2.99E-03**	**-5.01E-03**	**-4.54E-03**	53	0.35
Lele	0.09	-0.14	-0.29	0.47	**-0.10**	**0.48**	**0.54**	**-0.76**	**-1.62E-03**	**3.03E-03**	**2.01E-03**	**-4.59E-03**	74	0.39
Pato	**1.55**	**-5.03**	-2.64	**5.74**	**-0.40**	**0.76**	**0.47**	**-1.03**	**-1.28E-03**	-6.06E-04	**8.40E-04**	**-2.37E-03**	14	0.46
Pefl	**-0.64**	**-0.74**	**-2.51**	**1.58**	**0.10**	**0.22**	**0.63**	**-0.49**	**9.66E-04**	**6.68E-04**	**3.61E-03**	**-2.71E-03**	86	0.34
Phph	**-0.49**	-0.21	0.02	-0.04	**0.06**	**-0.07**	**-0.07**	**0.13**	**3.64E-05**	1.02E-06	7.35E-06	5.77E-06	148	0.41
Pupu	-0.68	**-1.84**	1.54	**2.20**	**0.20**	**0.37**	**-0.08**	**-0.42**	**3.05E-03**	**6.11E-03**	**-1.29E-03**	**-6.64E-03**	27	0.34
Ruru	**-1.01**	**8.36**	**8.74**	**-10.34**	**0.01**	**-0.18**	**-0.22**	**0.23**	**-4.64E-05**	**-1.91E-04**	**-3.23E-04**	**2.37E-04**	125	0.43
Salu	0.00	-0.50	-0.13	0.07	0.95	0.38	-0.21	**0.66**	1.03E-01	**-2.33E-02**	**-4.00E-02**	**9.26E-02**	16	0.20
Sasa	-0.53	0.18	-0.24	0.22	**0.48**	**0.20**	**0.55**	**-0.40**	**4.55E-03**	**1.14E-03**	**2.10E-03**	**-1.64E-03**	28	0.46
Satr	-0.58	-0.30	**-0.57**	0.00	0.01	**-0.02**	**-0.05**	**0.05**	-7.94E-06	**-2.00E-04**	**-3.70E-04**	**4.18E-04**	141	0.5
Scer	**-0.23**	**-0.92**	**-1.20**	**1.59**	0.08	0.01	-0.06	**-0.48**	**2.54E-02**	**-7.54E-03**	**-1.80E-02**	**7.20E-03**	31	0.38
Sigl	0.01	0.04	-0.02	-0.02	**-0.34**	**-0.53**	**0.44**	**0.64**	**-9.99E-03**	-7.15E-04	1.73E-04	**5.30E-03**	9	0.18
Sqce	**-10.43**	**-11.31**	**-20.65**	**15.89**	**0.28**	**0.13**	**0.37**	**-0.21**	**7.06E-04**	**1.86E-04**	**1.45E-04**	**-4.52E-04**	137	0.39
Teso	**-7.90**	-4.58	2.21	**25.13**	**0.60**	**0.27**	**0.48**	**-1.79**	**2.88E-03**	**-1.63E-03**	-6.24E-05	**-3.34E-03**	11	0.44
Thth	13.76	9.45	0.50	**6.97**	-0.65	-2.46	-0.66	1.50	2.61E-02	-4.54E-02	-1.22E-02	2.86E-02	6	0.67
Titi	0.16	-0.23	**-0.37**	0.32	0.06	**0.47**	**0.53**	**-0.65**	-1.70E-04	**1.17E-02**	**1.19E-02**	**-1.67E-02**	45	0.38

4. Influence des variables environnementales

Nos résultats indiquent une influence contrastée des variables environnementales sur les dynamiques de populations (Figure 14). Globalement, la variance intra-annuelle de la température de l'eau a une influence positive sur les variations d'abondances alors que les autres variables ont une influence négative (Figure 14A). Cependant, quelles que soient les variables environnementales, les réponses des populations sont contrastées ce qui témoigne d'une forte variabilité spatio-temporelle de l'influence de ces variables sur les dynamiques de populations. La moyenne annuelle de la température de l'eau et, dans une moindre mesure, la stochasticité environnementale ont plus d'influence sur les variations d'abondances que les deux autres variables (Figure 14B). En accord avec nos résultats, van de Pol *et al.* (2010) ont montré que la température moyenne avait plus d'influence que sa variabilité dans le déterminisme de la persistance des populations d'huîtrier pie (*Haematopus ostralegus*). Dans la mesure où les modèles climatiques prédisent de plus fort changements en termes de moyenne qu'en termes de variabilité des températures (Stocker *et al.*, 2013), nos résultats suggèrent que les populations de poissons d'eau douce devraient être particulièrement affectées par le réchauffement climatique puisque la moyenne annuelle de température a une influence globalement négative sur les populations. Cependant, l'influence de la moyenne et de la variabilité des facteurs environnementaux sur les patrons d'abondances peut varier en fonction des populations et des espèces considérées (Williams *et al.*, 2003; Saether *et al.*, 2008). Il a par exemple été suggéré que les populations situées en marges des aires de répartition des espèces sont plus sensibles à la variabilité des conditions climatiques alors que les populations situées au centre sont plutôt sensibles à des changements de conditions moyennes (Garcia-Carreras & Reuman, 2013). Ainsi, la compréhension de l'influence du climat sur les dynamiques de populations requiert de prendre en considération la moyenne mais aussi la variabilité des facteurs climatiques ainsi que la position géographique des populations par rapport à la limite d'aire de répartition de l'espèce.

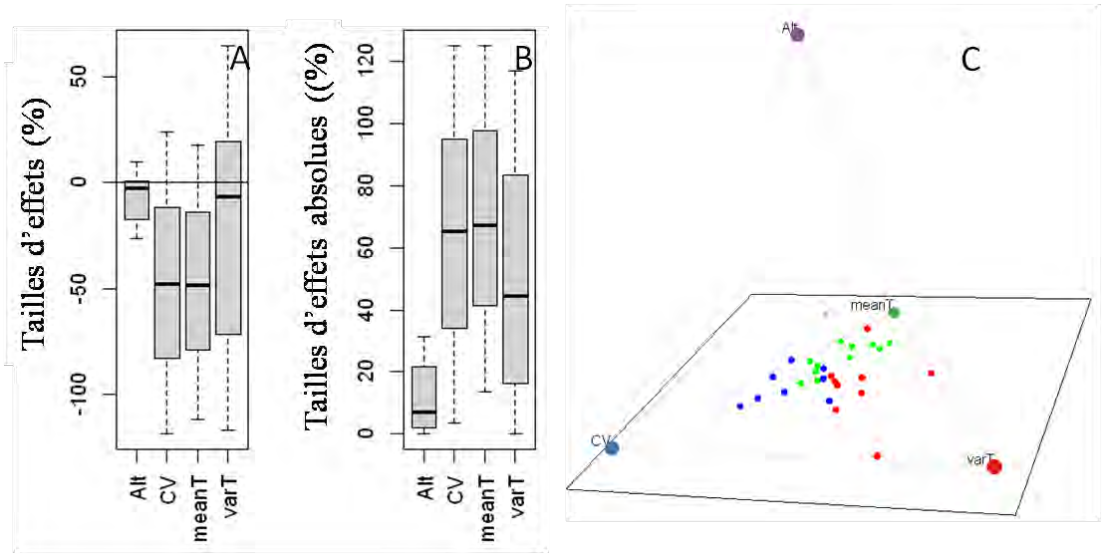


Figure 14. Tailles d'effets associées aux variables environnementales (Alt=altitude; CV=indice de stochasticité environnementale, meanT=moyenne annuelle des températures de l'eau et varT=variance annuelle des températures de l'eau) en valeur brutes (A) et en valeur absolues (B). (C) Contribution des variables environnementales aux variations de tailles de populations de chaque espèce, indépendamment des paramètres de dynamique de populations. (Modifié d'après ***PIII***; Figure 2).

5. Interaction entre variables environnementales et paramètres de dynamiques de populations

L'influence des variables environnementales sur les patrons d'abondances est globalement négative mais varie en fonction des paramètres de dynamiques de population (Tableau 6; Figure 15). Ainsi, la même variable environnementale peut avoir des effets opposés sur les différents paramètres de dynamiques de populations et les différentes variables environnementales peuvent influencer le même paramètre de dynamique de population dans des directions opposées (Figure 15A). Quelle que soit la variable environnementale considérée, son influence sur les patrons d'abondances est toujours plus importante au travers de son effet sur le taux d'accroissement (Figure 15B). Néanmoins, les patrons sont très variables en fonction des espèces (Tableau 6). Par exemple, les paramètres de dynamiques de populations de la truite (*Salmo trutta*) sont influencés équitablement par l'ensemble des variables environnementales alors que les populations de vairons (*Phoxinus phoxinus*) sont plutôt influencées par les variables environnementales au travers de leurs effets sur le taux d'accroissement (Figure 16). Ces résultats indiquent que les mécanismes sous-jacents aux variations interannuelles des effectifs de populations des différentes espèces sont complexes et peuvent être difficiles à détecter du fait de l'influence contrastées des variables environnementales sur les paramètres de dynamiques de populations. Une telle complexité a déjà été mise en évidence chez des populations de mésanges charbonnières (*Parus major*) où le recrutement local et le taux d'immigration sont influencés à la fois par l'abondance de nourriture et par des facteurs environnementaux (Grøtan *et al.*, 2009). De la même manière, Hart & Gotelli (2011) ont montré que les changements climatiques avaient une influence sur les abondances d'invertébrés aquatiques mais pas nécessairement au travers du même mécanisme. Les abondances de populations de *Culicidae* étaient influencées par le climat au travers du taux d'accroissement alors que les abondances de populations de *Chironomidae* étaient influencées par le climat au travers de processus densité-dépendants. Par ailleurs, il a déjà été montré que des variables climatiques pouvaient avoir des influences opposées sur des traits démographiques. Par exemple, l'étendue de glace influence la survie et la fécondité des populations de manchots empereurs dans des directions opposées (Barbraud & Weimerskirch, 2001).

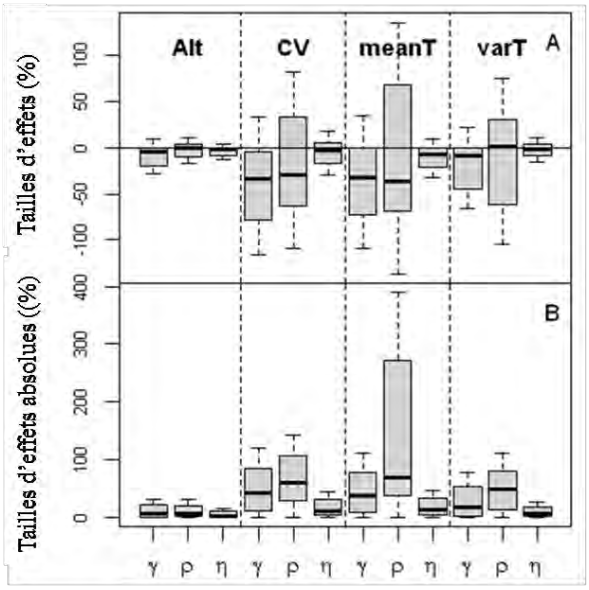


Figure 15. Tailles d'effets associées aux coefficients de pentes qui relient les variables environnementales aux paramètres de dynamiques de populations en valeur brutes (A) et en valeur absolues (B). (Modifié d'après ***PIII***; Figure 3).

Comprendre la complexité des mécanismes sous-jacents aux dynamiques de populations requiert donc de considérer l'influence de différentes variables environnementales et de déterminer au travers de quel paramètre de dynamique de populations ces variables ont le plus d'influence sur les patrons d'abondances. Modéliser les dynamiques de populations de cette façon devrait contribuer à améliorer notre connaissance des mécanismes à l'origine des variations de tailles de populations ainsi que notre capacité à prédire les effets du changement climatique sur les populations. Par exemple, nous avons trouvé une influence négative de la moyenne annuelle de température au travers du taux d'accroissement ce qui suggère que le taux d'accroissement des populations de poissons devrait diminuer en réponse au changement climatique. Ce paramètre étant dépendant de plusieurs traits démographiques (e.g. survie adulte, fécondité), il serait maintenant intéressant de déterminer la contribution de ces traits au taux d'accroissement et d'identifier les traits responsables de cette diminution. Une telle étude permettrait une meilleure évaluation de la vulnérabilité des espèces face au changement climatique.

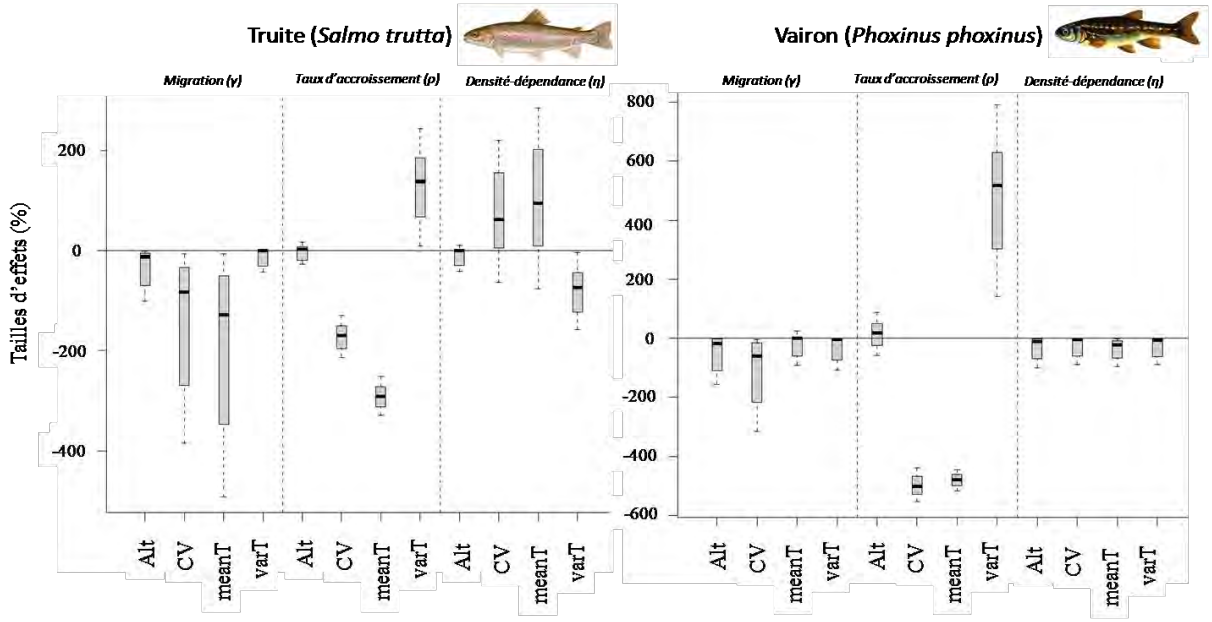


Figure 16. Exemple d'influence des variables environnementales sur les patrons d'abondances de deux espèces de poissons (la truite et le vairon) au travers des paramètres de dynamiques de populations. Pour l'abréviation des variables environnementales, voir la figure 14.

6. Patrons spatiaux

Pour étudier les patrons spatiaux des dynamiques de populations, nous avons calculé pour chaque espèce la déviation standard des tailles d'effets associée à chaque paramètre de dynamique de populations, chaque variable environnementale et à chaque coefficient de pente qui relie les variables environnementales aux paramètres de dynamiques de populations. D'une manière générale, nous avons mis en évidence de fortes variations spatiales des dynamiques de populations. L'influence de l'environnement sur les populations est plus spatialement hétérogène au travers de son effet sur le taux d'accroissement et sur la densité

dépendance qu'au travers de son effet sur le taux de migration (Figure 17A). Indépendamment des paramètres de dynamiques de populations, la moyenne de température annuelle est la variable dont l'influence sur les populations est la plus spatialement hétérogène (Figure 17B). En accord avec ces résultats, plusieurs études ont montré que l'hétérogénéité spatiale des dynamiques de populations pouvait s'expliquer par une variabilité spatiale de l'influence de l'environnement sur les populations (Saether *et al.*, 2003; Williams *et al.*, 2003; Fukaya *et al.*, 2014) ainsi que par des variations spatiales des conditions environnementales moyennes qui induisent des variations spatiales des paramètres de dynamiques de populations (Fukaya *et al.*, 2013). Néanmoins, la contribution des variables environnementales aux variations spatiales des dynamiques de populations dépendent fortement des espèces considérées et des paramètres de dynamiques de populations (Figure 17C et 17D). Par exemple, les variations spatiales des dynamiques de populations de la truite (*Salmo trutta*) dues à l'influence de la stochasticité environnementale sont complètement différentes selon que l'on considère l'influence de cette variable sur le taux d'accroissement, le taux de migration ou la densité dépendance (Figure 18).

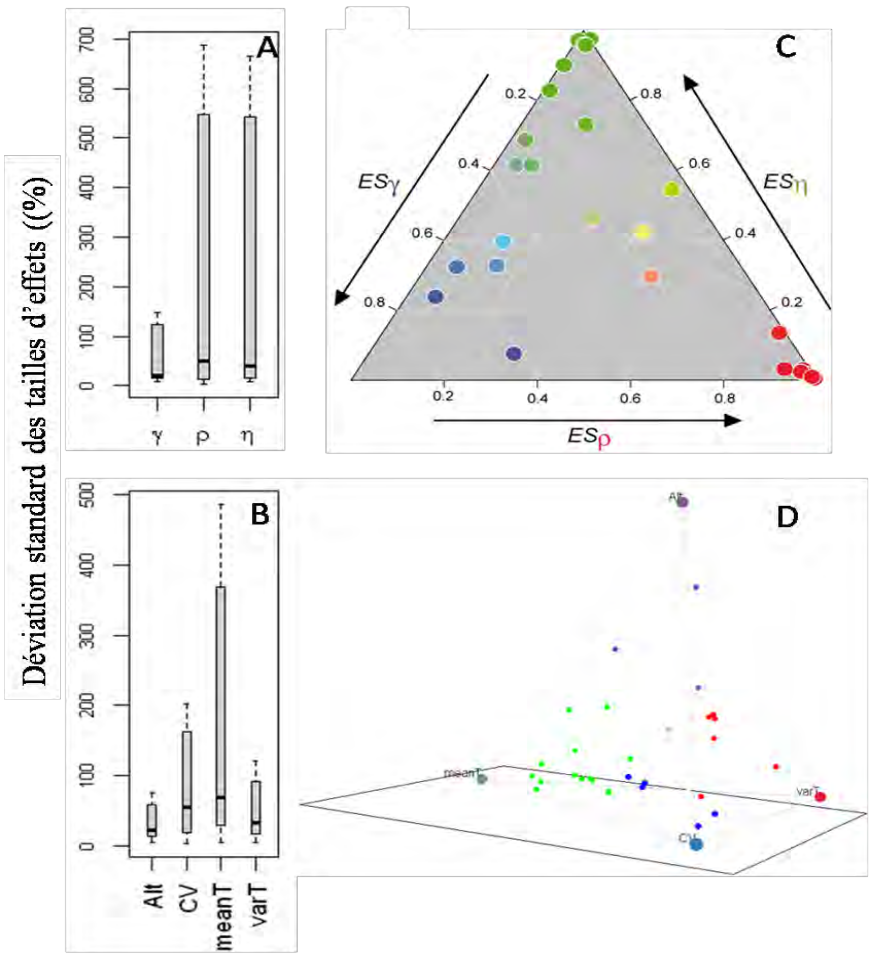


Figure 17. Déviation standard des tailles d'effets associées aux paramètres de dynamiques de populations (A) et aux variables environnementales (B). Contribution aux variations spatiales des dynamiques de populations de chaque espèce de l'ensemble des variables environnementales au travers des différents paramètres de dynamique de populations (C) et de chaque variable environnementale, indépendamment des paramètres de dynamiques de populations (D). (Modifié d'après ***PIII***; Figure 4).

Plusieurs études ont montré que les déterminants des dynamiques de populations pouvaient présenter des gradients géographiques (Saether *et al.*, 2008) et de l'autocorrélation spatiale (Liebhold *et al.*, 2004). Pour déterminer si les dynamiques de populations des différentes espèces de poissons d'eau douce présentaient des patrons géographiques, nous avons utilisé des modèles linéaires avec comme variable indépendante la latitude et comme variables dépendantes :

- les tailles d'effets associées aux paramètres de dynamiques de populations ;

- les tailles d'effets associées aux variables environnementales;

- les tailles d'effets associées aux coefficients de pentes qui relient les variables environnementales aux paramètres de dynamiques de populations.

Pour déterminer si ces variables dépendantes présentaient de l'autocorrélation spatiale nous avons utilisé la statistique I de Moran. En accord avec les études précédentes (e.g. Tkadlec & Stenseth, 2001; Saether *et al.*, 2008), nos résultats indiquent que les réponses des populations de certaines espèces aux variations environnementales présentent des gradients latitudinaux et de l'autocorrélation spatiale (Tableau 7). L'existence de tels gradients suggère que les réponses des populations aux changements climatiques peuvent être prédites à partir de connaissances sur la localisation des populations. L'autocorrélation spatiale des réponses des populations aux variations environnementales peut s'expliquer par un certain degré d'autocorrélation des conditions environnementales (i.e. the Moran effect; Royama 1992) ce qui est cohérent avec les résultats énoncés au chapitre 1.

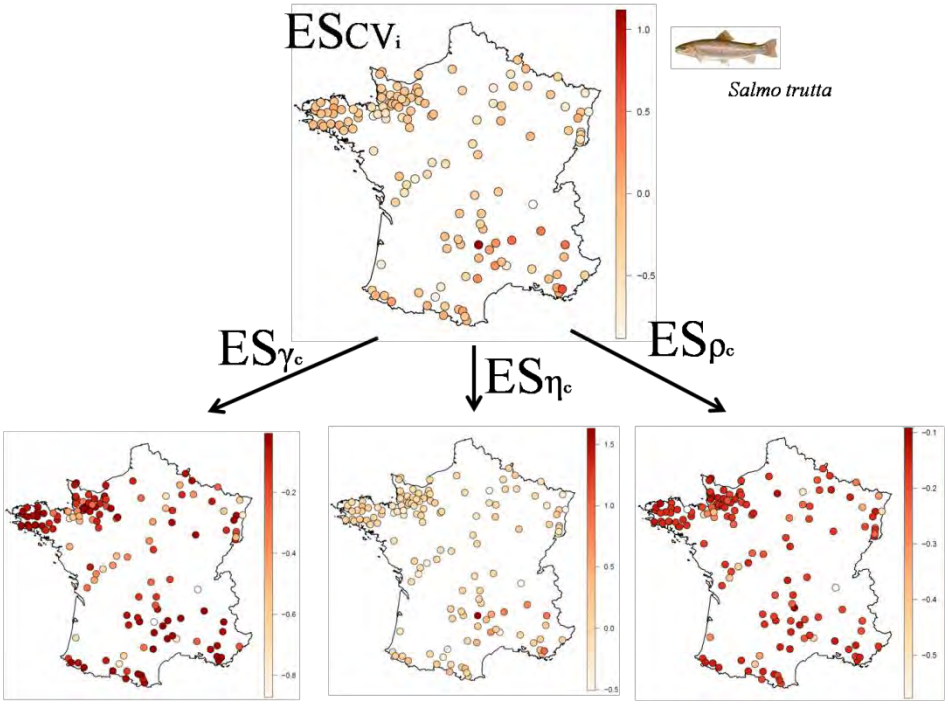


Figure 18. Patrons spatiaux des tailles d'effets associés à la stochasticité environnementales (ES_{CVi}) et patrons spatiaux de l'influence de cette variable sur les dynamiques de populations via son effet sur les différents paramètres de dynamiques de populations (ESγc, ESρc, ESηc) pour la truite (*Salmo trutta*). (Modifié d'après ***PIII***, Figure 5).

7. Conclusion

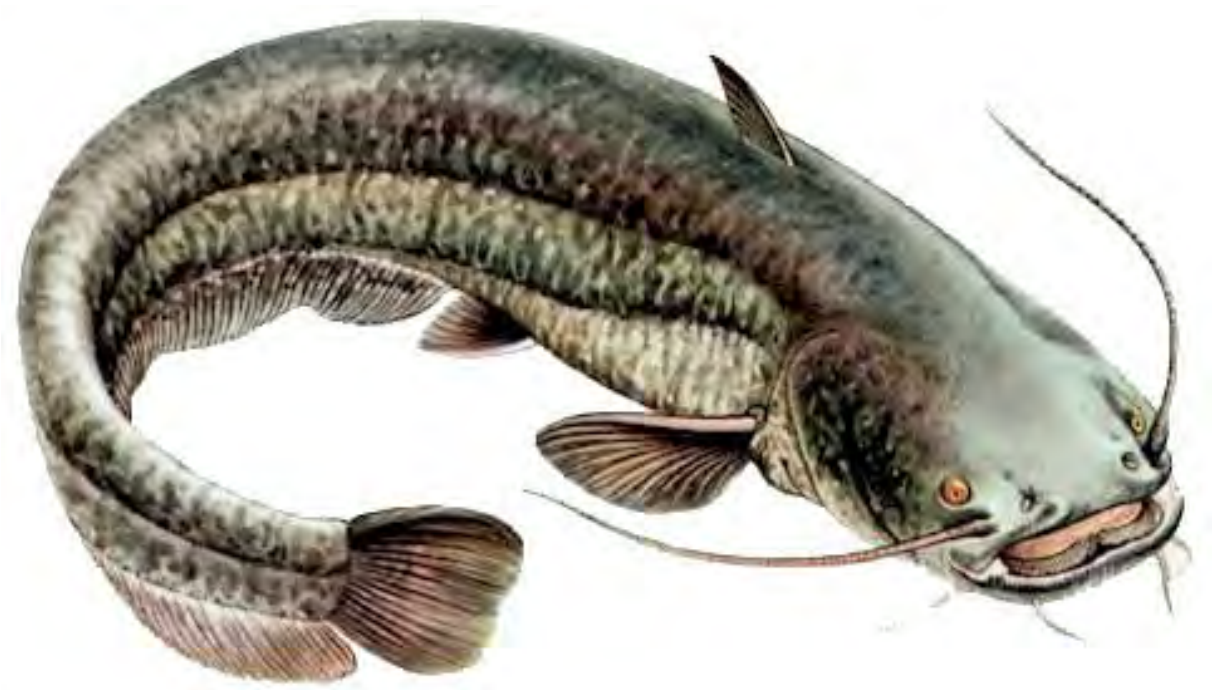
Globalement nos résultats indiquent que les processus densité-dépendants ont peu d'influence sur les dynamiques de populations de poissons d'eau douce alors que des facteurs environnementaux tels que la température de l'eau peuvent avoir une forte influence sur les populations, notamment *via* leurs effets sur le taux d'accroissement. Nous avons également montré que les mécanismes sous-jacents aux dynamiques spatio-temporelles des populations de poissons sont complexes et variables en fonction des espèces considérées. Cette complexité peut rendre difficile la mise en évidence de l'influence de facteurs environnementaux sur les patrons d'abondances dans la mesure où ceux-ci peuvent avoir une influence très contrastées sur les paramètres de dynamiques de populations. La prise en compte de cette complexité nous a permis d'identifier quels étaient les mécanismes sous-jacents aux variations interannuelles des effectifs de différentes espèces de poissons d'eau douce. Nos résultats fournissent ainsi une base de travail aux acteurs de la gestion de la biodiversité pour anticiper les conséquences des changements climatiques sur les populations de poissons d'eau douce. Bien que des mécanismes communs aux dynamiques de populations de chaque espèce aient été identifiés, il n'en demeure pas moins de fortes variations spatiales des dynamiques de populations. Pour certaines espèces, des patrons spatiaux de réponses des populations ont pu être mis en évidence. Ces patrons pourraient être utilisés pour inférer les déterminants et les conséquences potentielles des changements climatiques sur des dynamiques de populations en fonction de connaissances sur les conditions environnementales locales.

Tableau 7. Pourcentage d'espèces dont les variables dépendantes (tailles d'effets; voir texte) présentent un degré d'autocorrélation spatiale significatif et une relation significative avec la latitude. (Modifié d'après ***PIII***; Appendice S5).

		Latitude(%)	Moran (%)
Paramètres de dynamiques de populations	ρ	28.5	35.7
	γ	17.8	50.0
	η	28.5	28.5
Variables environnementales	Alt	14.2	35.7
	CV	14.2	35.7
	meanT	17.8	32.1
	varT	10.7	17.8
Coefficients de pentes	ρ_b	14.2	53.5
	ρ_c	14.2	21.4
	ρ_d	32.1	35.7
	ρ_e	14.2	32.1
	γ_b	21.4	50.0
	γ_c	14.2	46.4
	γ_d	14.2	46.4
	γ_e	10.7	25.0
	η_b	17.8	46.4
	η_c	10.7	25.0
	η_d	21.4	32.1
	η_e	7.1	25.0

Chapitre 4

Caractéristiques intrinsèques et histoire évolutive des espèces



Silurus glanis

1. Introduction

Les patrons de dynamiques de populations mis en évidence dans les chapitres 1 et 2 apparaissent comme complexes et variables en fonction des espèces considérées. De telles variations interspécifiques ont déjà été relevées dans de nombreux taxa (Paradis *et al.*, 1999; Tedesco & Hugueny, 2006; Végvári *et al.*, 2010; Linnerud *et al.*, 2013) et suggèrent que les caractéristiques des espèces ont une influence sur les différences observées. De fait, plusieurs études ont cherché à identifier quelles étaient les caractéristiques des espèces qui permettaient d'expliquer les variations interspécifiques de dynamiques de populations (Paradis *et al.*, 1999; Saether *et al.*, 2005, 2011; Sandvik & Erikstad, 2008; Linnerud *et al.*, 2013). En effet, étant donné que toutes les espèces ne présentent pas le même risque d'extinction face aux changements climatiques (Thomas *et al.*, 2004), il est important d'identifier quelles sont les caractéristiques (e.g. physiologiques, écologiques) qui les rendent plus vulnérables aux variations des conditions environnementales. Tedesco & Hugueny (2006) ont ainsi montré que les populations d'espèces de poissons qui ont une forte fécondité et des œufs de petites tailles (i.e. stratégie périodique) sont plus synchrones que les espèces qui ont des caractéristiques opposées (i.e. stratégie équilibriste), ce qui suggère que les espèces périodiques ont un plus fort risque d'extinction que les espèces équilibristes. Plus généralement, il semblerait que les dynamiques de populations peuvent être prédites en fonction de caractéristiques simples tel que la position des espèces le long du gradient r-K (Bjørkvoll *et al.*, 2012; Linnerud *et al.*, 2013). Ainsi, les espèces caractérisées par un temps de génération court, une maturité précoce, la production de beaucoup de descendants et une taille réduite ont des populations qui présentent généralement un fort taux d'accroissement, un faible coefficient de densité-dépendance et qui sont fortement influencées par la stochasticité (démographique et environnementale). A l'inverse, les espèces qui ont les caractéristiques opposées (temps de génération long, maturité tardive, production de peu de descendants et taille importante) ont des populations qui présentent un faible taux d'accroissement, un fort coefficient de densité-dépendance et qui sont faiblement influencées par la stochasticité.

Alors que ces patrons sont relativement bien documentés chez les oiseaux (Paradis *et al.*, 1999, 2000; Saether *et al.*, 2005), les mammifères (Fowler, 1981; Purvis & Harvey, 1995) et les poissons marins (Myers *et al.*, 1999; Bjørkvoll *et al.*, 2012), très peu d'études se sont consacrées aux poissons d'eau douce (e.g. Tedesco & Hugueny, 2006). Par ailleurs, la majorité des études antérieures se sont focalisées sur l'influence des traits d'histoire de vie et ont négligé l'influence d'autres traits potentiellement importants. Par exemple, l'influence de la gamme de tolérance thermique n'a été considérée que dans très peu d'études (e.g. Jiguet *et al.*, 2007, 2010) alors que ce trait a une influence majeure sur les organismes ectothermes tels que les poissons (Ficke *et al.*, 2007). Ainsi, la prise en compte d'autres traits pourrait permettre de révéler de nouveaux patrons et d'améliorer notre connaissance des mécanismes à l'origine des variations interspécifiques de dynamiques de populations.

Outre les caractéristiques intrinsèques des espèces, il a été suggéré que leur histoire évolutive pouvait expliquer les différences de dynamiques observées. En effet, dans la mesure où les espèces phylogénétiquement proches tendent à partager des caractéristiques communes

(McKinney, 1997), on peut s'attendre à ce que l'histoire évolutive des espèces conditionne leur réponse à des facteurs environnementaux et puisse expliquer les différences interspécifiques de dynamiques de populations. Conformément à ces attendus théoriques, certaines études ont montré que le risque d'extinction des espèces n'était pas distribué aléatoirement au sein de la phylogénie (Roy *et al.*, 2009; Thuiller *et al.*, 2011). Certains groupes taxonomiques ont donc plus de probabilités de contenir des espèces vulnérables que d'autres. De même, Willis *et al.* (2008) ont montré que les changements d'abondances et de phénologie de 429 espèces de plantes dépendaient de la position des espèces dans la phylogénie, ce qui suggère que l'histoire évolutive est importante pour comprendre les réponses des espèces face aux changements climatiques. Dans le contexte actuel, l'identification de patrons phylogénétiques dans ces réponses est donc particulièrement importante puisque la mise en évidence de ces patrons devrait permettre d'améliorer notre compréhension des processus à l'origine des déclins de populations et de prédire des futurs déclins en réponse au réchauffement climatique. Cependant, ce genre d'étude reste extrêmement limité et la capacité de la phylogénie à expliquer les différences interspécifiques de dynamiques de populations reste méconnue pour de très nombreux groupes taxonomiques.

Dans ce chapitre, notre objectif est de déterminer si les caractéristiques intrinsèques des espèces de poissons d'eau douce et leur histoire évolutive permettent d'expliquer les différences interspécifiques des patrons de dynamiques de populations mises en évidence dans les chapitres 1 et 2.

2. Méthodologie générale

2.1. Signal phylogénétique

Le conservatisme phylogénétique caractérise le fait que des espèces phylogénétiquement proches tendent à partager des caractéristiques similaires (Losos, 2008). Un signal phylogénétique fort indique que les espèces proches phylogénétiquement partagent des caractéristiques plus similaires que des espèces prises au hasard dans la phylogénie (Blomberg *et al.*, 2003). Pour tester la présence de signal phylogénétique, nous avons utilisé la statistique λ (Pagel, 1999) car il a été prouvé que cette mesure était plus performante que d'autres pour mesurer le signal phylogénétique (Freckleton *et al.*, 2002; Münkemüller *et al.*, 2012). Sa valeur varie de 0 à 1 et peut être intégrée dans des modèles statistiques pour prendre en compte la non-indépendance des données. Une valeur de 0 indique une absence de signal phylogénétique alors qu'une valeur de 1 indique un fort signal phylogénétique (sous l'hypothèse que les traits ont évolué selon un mouvement Brownien).

2.2. Relation avec les traits des espèces

Les relations avec les traits des espèces ont été testées à partir de modèles PGLS (Phylogenetic Generalized Least Square) qui prennent en compte la non-indépendance des données en ajustant une matrice de variance-covariance en fonction des relations de parentés entre espèces (Freckleton *et al.*, 2002). Idéalement, un seul modèle comprenant l'ensemble des variables indépendantes aurait dû être construit. Une procédure pas à pas descendante aurait alors permis de déterminer quelles sont les variables pertinentes pour expliquer les variations observées entre espèces. Cependant, étant donné le nombre de variables indépendantes par rapport au nombre d'observations, une telle procédure n'était pas statistiquement envisageable. A la place, nous avons utilisé une procédure d'inférence basée sur le critère d'information d'Akaike corrigé pour les faibles tailles d'échantillons (AICc) afin de sélectionner les modèles les plus vraisemblables (Burnham & Anderson, 2002) parmi l'ensemble des modèles possibles qui incluaient trois variables indépendantes ou moins (pour ne pas sur-paramétrer les modèles ; Knape & De Valpine, 2011). Nous avons également considéré les interactions entre variables indépendantes mais seulement dans les modèles qui incluaient deux variables. A partir des modèles sélectionnés, nous avons ensuite conduit une procédure de moyennage des coefficients de pentes associées aux variables indépendantes pour prendre en compte les incertitudes associées aux différents modèles (Johnson & Omland, 2004)

3. Degré de synchronisme

Parce que le degré de synchronisme moyen mesuré pour chaque espèce peut varier en fonction de l'aire de distribution des espèces (les espèces ayant des aires de distribution restreintes tendent à être plus synchrones du fait d'une plus faible distance entre les populations ; Sutcliffe et al. 1996), les analyses phylogénétiques (signal phylogénétique et modèles PGLS) ont été conduites sur les résidus d'un modèle de régression reliant le degré de synchronisme à l'aire de distribution de l'espèce (qui a été estimée par une enveloppe convexe; Barber *et al.*, 1996). Par ailleurs, pour prendre en compte le fait que le synchronisme des populations dépend du degré de synchronisme de l'environnement (les populations d'espèces situées dans des environnements très synchrones étant plus synchrones que les populations d'espèces situées dans des environnements moins synchrones ; effet Moran), nous avons calculé le synchronisme moyen des températures pour chaque espèce puis nous avons introduit ce facteur confondant dans les modèles PGLS.

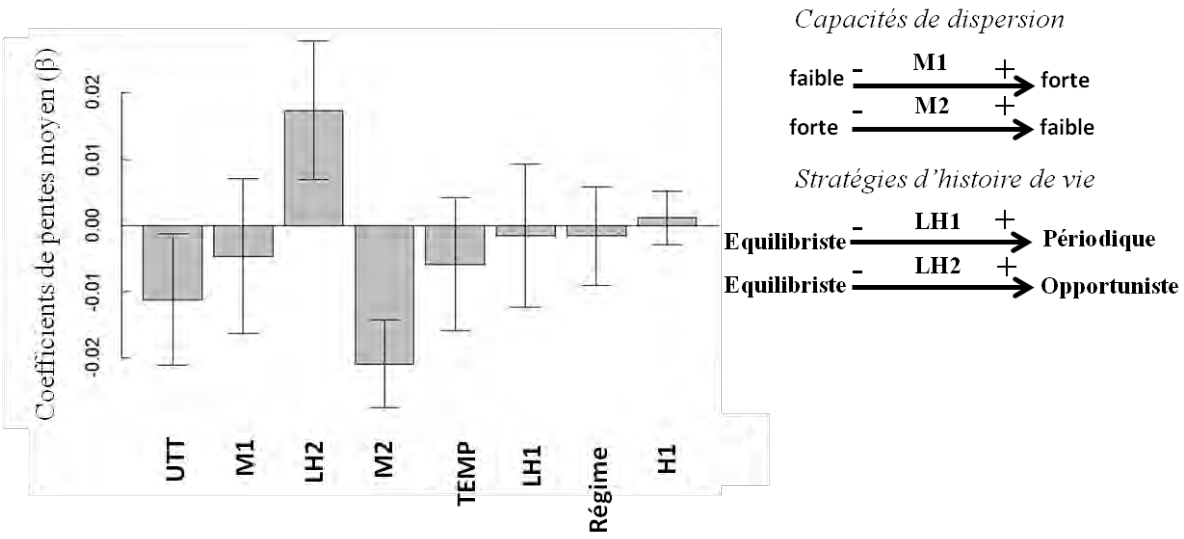


Figure 19. Coefficients de pentes standardisés moyens (β) calculé à partir des modèles PGLS sélectionnés pour le degré de synchronisme moyen des populations. UTT est la tolérance thermique supérieure; LH1 et LH2 représentent les stratégies d'histoire de vie; M1 et M2 représentent les capacités de dispersion; H1 représente l'habitat des espèces. (Modifié d'après ***PII***; Figure 3).

Alors que très peu d'études (e.g. Raimondo & Liebhold, 2004; Tedesco & Hugueny, 2006) ont réussi à mettre en évidence une influence des caractéristiques des espèces sur le degré de synchronisme des populations, nos résultats montrent que le synchronisme spatial des populations de poissons d'eau douce varie en fonction de caractéristiques clés des espèces. Plus particulièrement, nos résultats indiquent que la tolérance thermique supérieure des espèces, leurs traits d'histoire de vie et leurs capacités de dispersion ont une influence sur les patrons de synchronisme observés (Figure 19). Les espèces qui ont une tolérance thermique supérieure faible (e.g. *Gasterosteus gymnurus*, *Telestes souffia*) présentent de plus forts degrés de synchronisme que les espèces qui ont une tolérance thermique supérieure plus élevée (e.g. *Cyprinius carpio*, *Ameiurus melas*). Dans le contexte actuel, ce résultat peut s'expliquer par des déclins spatialement corrélés de populations qui seraient dus au fait que les populations d'espèces qui ont une tolérance thermique faible excèdent plus souvent leur limite de tolérance que les populations d'espèces qui ont une tolérance thermique plus élevée. Cette hypothèse est d'ailleurs étayée par les travaux de Jiguet et al. (2007) qui ont montré de plus forts déclins chez les populations d'espèces d'oiseaux qui avaient une faible gamme de tolérance thermique. Concernant les traits d'histoire de vie, nous montrons que les populations d'espèces qui présentent des caractéristiques reproductives associées à une stratégie opportuniste (i.e. maturité précoce, durée de vie courte et faible fécondité ; Figure 5) sont globalement plus synchrones que les espèces équilibristes et périodiques. Ce résultat peut s'expliquer par une plus forte influence de la stochasticité environnementale sur les espèces opportunistes (Sæther *et al.*, 2013) et suggère que ces espèces ont un risque d'extinction relativement plus élevé que les espèces associées à d'autres stratégies de reproduction. Enfin, conformément aux attentes théoriques (Ranta *et al.*, 1995; Peltonen *et al.*, 2002), nous montrons que les populations d'espèces qui présentent de plus fortes capacités de dispersion sont plus synchrones que celles qui présentent de faibles capacités de dispersion. Concernant

les relations de parentés entre espèces, nos résultats indiquent que la phylogénie n'a pas d'influence sur le degré de synchronisme des espèces, ce qui est en accord avec le fait que les traits impliqués dans le déterminisme de ce synchronisme ne présentent pas ou peu de signal phylogénétique (Tableau 8; Figure 20A). De même, le degré de synchronisme des températures ne permet pas d'expliquer les différences interspécifiques de synchronisme.

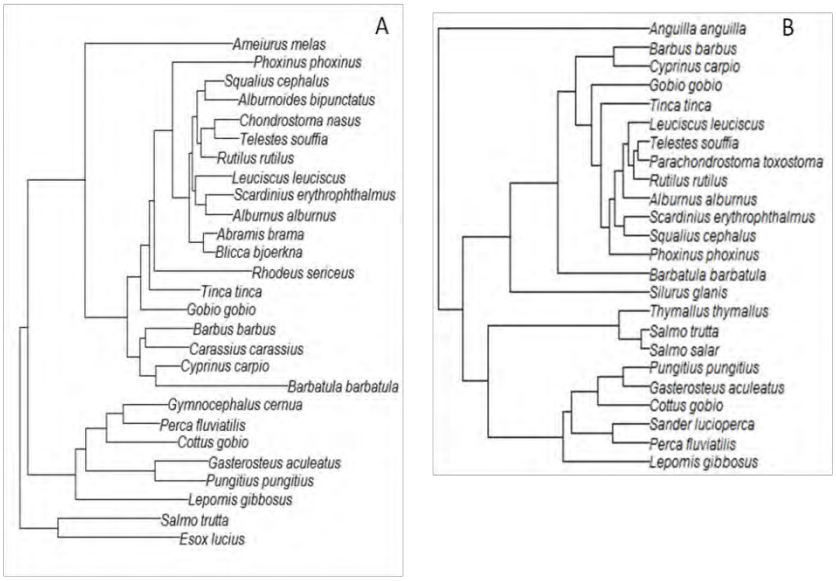


Figure 20. Phylogénie utilisée pour tester l'influence des traits des espèces sur (A) le degré de synchronisme moyen des populations (modifié d'après *PII*; Figure 2) et (B) les déterminants des variations spatio-temporelles d'abondances (modifié d'après ***PIV***; Figure S1).

Globalement, et dans la mesure où le synchronisme spatial des populations est lié au risque d'extinction des espèces (Hanski & Woiwod, 1993), nos résultats suggèrent que les relations de parentés entre espèces et le degré de synchronisme de l'environnement ne permettent pas d'identifier les espèces à risques (i.e. qui présentent les plus forts taux de synchronisme) alors que des caractéristiques simples, telles que la tolérance thermique supérieure, les capacités de dispersion et les stratégies de reproduction apparaissent comme des prédicteurs pertinents du risque d'extinction des espèces.

Tableau 8. Signal phylogénétique des traits des espèces et du degré de synchronisme moyen des espèces (SYNCH). Pour les abréviations des traits voir la figure 18. Pour leurs descriptions, voir le tableau 2. Les résultats significatifs ($p<0.05$) sont en gras. (Modifié d'après ***PII***; Tableau 3).

Variable	λ
LH1	0.65
LH2	0.37
M1	**0.99**
M2	0
Régime alimentaire	0.88
UTT	0.88
H1	0.67
SYNCH	0.18

4. Déterminants des variations spatio-temporelles d'abondances

Pour explorer plus en détail les questions relatives au déterminisme des variations interspécifiques de dynamiques de populations, nous avons testé si les caractéristiques des espèces et les relations de parentés entre espèces avaient une influence sur différents descripteurs des variations spatio-temporelles d'abondances. Plus spécifiquement, nous avons considéré, pour chaque espèce, 18 variables qui décrivent les variations spatio-temporelles des effectifs des populations :

- les paramètres de dynamiques de populations (taux de migration, taux d'accroissement et densité-dépendance) ;
- les déviations standards de ces paramètres (i.e. un indice de la variabilité intraspécifique des paramètres) ;
- les 12 coefficients qui relient les variables environnementales aux paramètres de dynamiques de populations.

En accord avec les résultats précédents, il apparaît que les variations interspécifiques de certains descripteurs des dynamiques de populations peuvent s'expliquer par des différences de caractéristiques des espèces (Figure 21). Cependant, la capacité des traits à expliquer ces variations dépend du descripteur considéré. Contrairement à ce qui était attendu (Saether & Engen, 2002), nous n'avons pas trouvé de relation significative entre les traits d'histoire de vie des espèces et le taux d'accroissement alors que nous avons trouvé une relation significative avec les capacités de dispersion des espèces (Figure 21A). Ce résultat peut s'expliquer par le fait que nous avons considéré la taille des espèces comme un proxy de leurs capacités de dispersion (Radinger & Wolter, 2014) et non comme un proxy de variations des traits d'histoire de vie, comme classiquement utilisé (Jeppsson & Forslund, 2014). Ainsi, les espèces qui présentent de fortes capacités de dispersion présentent un taux d'accroissement plus important que celles qui présentent de plus faibles capacités de dispersion.

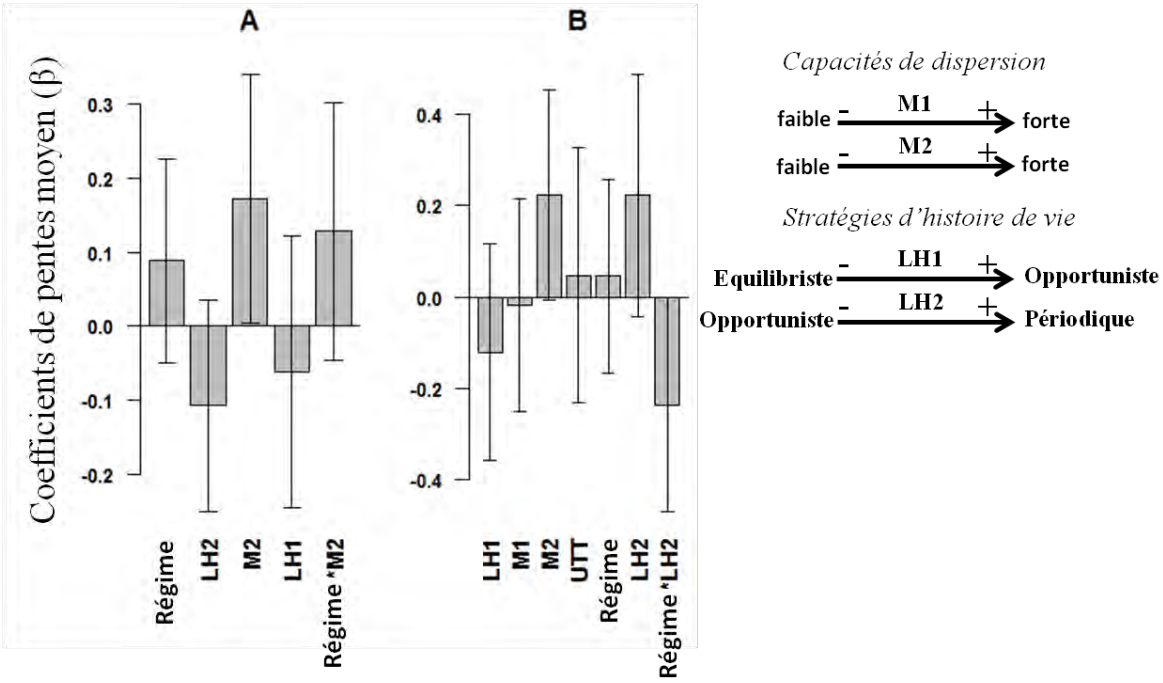


Figure 21. Coefficients de pentes standardisés moyens (β) calculés à partir des modèles PGLS sélectionnés pour (A) la moyenne des taux d'accroissement et (B) la moyenne des coefficients de densité-dépendance, estimée pour chaque espèce. Pour les autres abréviations de variables voir la Figure 14. (Modifié d'après ***PIV***; Figure 2)

Conformément aux attendus théoriques (Saether *et al.*, 2005; Bjørkvoll *et al.*, 2012), nous avons trouvé que les espèces périodiques (durée de vie longue, maturité tardive) ont un plus fort coefficient de densité-dépendance que les espèces opportunistes (durée de vie courte, maturité précoce) (Figure 21B). Nous avons également mis en évidence une interaction significative entre les traits d'histoire de vie des espèces et leur régime alimentaire, ce qui suggère que des traits écologiques peuvent interagir avec des traits d'histoire de vie pour générer des patrons complexes de densité-dépendance chez les poissons. En revanche, aucune des caractéristiques que nous avons considérées ne permettent d'expliquer les variations de taux de migration entre espèces, ce qui peut s'expliquer par une forte fragmentation du milieu qui masquerait les relations entre capacités de dispersion et taux de migration (Pringle, 2003). De même, aucune des caractéristiques des espèces ne permettent d'expliquer les variations intraspécifiques du taux d'accroissement et du taux de migration. A l'inverse, les variations intraspécifiques de densité-dépendance semblent dépendre d'une combinaison complexe de traits (Figure 22). Cependant, les relations avec les traits ne sont pas significatives, ce qui indique que bien que les caractéristiques des espèces semblent être impliquées dans les variations intraspécifiques de densité-dépendance, les mécanismes sous-jacents restent indéterminés.

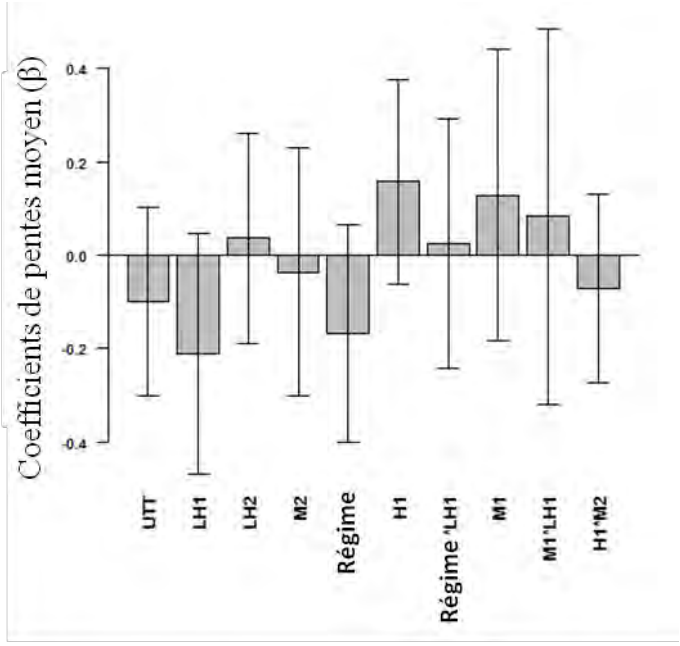


Figure 22. Coefficients de pentes standardisés moyens (β) calculés à partir des modèles PGLS sélectionnés pour la variation intraspécifique des coefficients de densité-dépendance. Pour les autres abréviations de variables voir la Figure 14. (Modifié d'après ***PIV***; Figure 3).

Le régime alimentaire et les capacités de dispersion des espèces apparaissent comme de bons prédicteurs de l'influence des variables environnementales sur les paramètres de dynamiques de populations (Tableau 9). De façon intéressante, un seul modèle a été sélectionné pour expliquer les variations interspécifiques de l'influence de la moyenne annuelle de température sur le taux d'accroissement. Ceci suggère que l'impact de l'augmentation de température sur le taux d'accroissement est fortement déterminé et peut être prédit à partir de caractéristiques simples comme le régime alimentaire et les capacités de dispersion des espèces. Cependant, nous montrons également des patrons beaucoup plus complexes (Tableau 9). Par exemple, la capacité des traits à expliquer les variations d'influence des facteurs environnementaux varie en fonction des paramètres de dynamiques de populations considérés. Ainsi, le régime alimentaire permet d'expliquer les différences interspécifiques de l'influence de la moyenne de température annuelle sur le taux d'accroissement mais pas sur le taux de migration ou sur le paramètre de densité dépendance.

Tableau 9. Coefficients de pentes standardisés moyens (β) calculés à partir des modèles PGLS sélectionnés pour expliquer les variations entre espèces des coefficients de pentes qui relient l'influence des variables écologiques aux paramètres de dynamiques de population. Pour les abréviations des traits, voir la Figure 14. Pour les abréviations des variables écologiques voir le Tableau 7. Les termes d'interactions ne sont pas présentés pour faciliter la lecture des résultats. Les résultats significatifs ($p<0.05$) sont en gras. (Modifié d'après ***PIV***; Tableau 2)

Traits des espèces	Paramètres de dynamiques de populations	Alt_i	CV_i	$meanT_{i.t}$	$varT_{i.t}$
Régime	ρ	**3E-01**	**-3E-01**	**2E-01**	2E-01
	η	1E-02	**-5E-05**	-5E-05	5E-02
	γ	-5E-01	-6E-01	-9E-01	2E-01
UTT	ρ	6E-03	2E-01	-	-
	η	**-5E-02**	**4E-05**	-	-
	γ	-2E-01	-3E-01	7E-01	-4E-01
LH1	ρ	-	-	-	-
	η	-1E-02	-	2E-05	2E-02
	γ	-5E-01	-6E-01	1E+00	4E-01
LH2	ρ	-	5E-01	-	-3E-01
	η	-1E-02	**2E-05**	3E-05	**-8E-02**
	γ	-3E-01	-1E+00	-6E-01	3E-01
M1	ρ	8E-02	5E-03	1E-01	**2E-01**
	η	4E-03	-2E-05	-6E-05	8E-02
	γ	-5E-02	3E-01	-2E-01	-2E-01
M2	ρ	-7E-02	-2E-01	-	-
	η	6E-03	-	-3E-05	-3E-03
	γ	7E-01	3E-01	-8E-01	-4E-02
H1	ρ	3E-02	-2E-01	-1E-01	-
	η	8E-03	-5E-05	-	7E-02
	γ	-7E-02	-1E-01	2E+00	5E-01

Quels que soient les descripteurs de dynamiques de populations considérés, les relations de parentés entre espèces ne permettent pas d'expliquer les différences observées (Tableau 10; Figure 20B). Pourtant, la majorité des traits impliqués dans le déterminisme des variations interspécifiques des descripteurs présentent de forts signaux phylogénétiques. A notre connaissance, aucune étude n'a testé l'influence de la phylogénie sur les différents descripteurs de dynamiques de populations que nous avons considérés. Néanmoins, l'influence de ce facteur a été testée sur d'autres descripteurs, tels que la tendance à long terme dans les abondances de populations (Willis *et al.*, 2008) ou la phénologie (Végvári *et al.*, 2010).

Cette faible capacité de la phylogénie à expliquer les différences interspécifiques que nous avons mises en évidence peut s'expliquer (1) par une faible puissance statistique due à l'utilisation d'un faible nombre d'espèces (Münkemüller *et al.*, 2012), (2) par des variations intraspécifiques des paramètres de dynamiques de populations (Williams et al. 2003, Saether et al. 2008) ou (3) par le fait que les traits impliqués dans le déterminisme des variations interspécifiques des différents descripteurs présentent des patrons phylogénétiques différents. Identifier laquelle de ces hypothèses est la plus probable requiert de nouvelles investigations.

Tableau 10. Signal phylogénétique des facteurs impliqués dans les variations de tailles de populations et des traits des espèces. Pour les abréviations des coefficients de pentes qui relient les variables environnementales aux paramètres de dynamiques de population voir le tableau 7. Les résultats significatifs ($p<0.05$) sont en gras. (Modifié d'après ***PIV***; Tableau S4).

Déterminants	Variables	λ
Paramètres de dynamiques de populations	ρ	0
	η	0
	γ	0
Variation intraspécifique	ρ	0
	η	0
	γ	0
Coefficients	γ_b	0
	γ_c	0
	γ_d	0
	γ_e	0
	ρ_b	0
	ρ_c	0
	ρ_d	0
	ρ_e	0.09
	η_b	0
	η_c	0.02
	η_d	0
	η_e	0.05
Traits	LH1	0.66
	LH2	**1**
	M1	**1**
	M2	**0.87**
	H1	0.76
	UTT	**0.62**
	Régime	**0.7**

Quels que soient les descripteurs de dynamiques de populations, nos résultats indiquent que la phylogénie n'est pas un prédicteur pertinent des différences observées entre espèces, contrairement à certaines caractéristiques des espèces associées à leur écologie, leur

physiologie, ou leur stratégie de reproduction. Nous avons également montré que les caractéristiques des espèces pouvaient interagir les unes avec les autres pour former des patrons complexes de dynamiques de populations. De plus, nos résultats montrent que la capacité des traits à expliquer les différences interspécifiques d'influence des variables environnementales sur les dynamiques de populations varie en fonction des paramètres considérés. Ces résultats mettent en avant la complexité des mécanismes sous-jacents aux variations interspécifiques des dynamiques de populations et suggèrent que certaines caractéristiques des espèces peuvent être utilisées pour expliquer ces différences.

5. Conclusion

Alors que l'influence des traits sur les variations interspécifiques de différents descripteurs des dynamiques de populations (e.g. synchronisme, changement de distribution, tendance à long-terme, réponse phénologique) a fait l'objet d'une attention particulière au cours des dernières années (Thuiller *et al.*, 2005; Tedesco & Hugueny, 2006; Williams *et al.*, 2008; Bjørkvoll *et al.*, 2012), celle de la phylogénie a été nettement moins considérée (Parmesan & Yohe, 2003; Root *et al.*, 2003) et les résultats sont contrastés. Par exemple, Davis et al. (2010) ont montré que l'influence du climat sur les réponses phénologiques des communautés de plantes dépendait de la position des espèces dans la phylogénie. A l'inverse, Végvári *et al.* (2010) n'ont pas trouvé d'influence de la phylogénie sur les réponses phénologiques d'oiseaux migrateurs en Europe. Bien que nos résultats accordent plus de support à ceux de Végvári *et al.* (2010), les différences qui existent entre les études soulignent le fait que notre compréhension des mécanismes à l'origine des différences de réponses des espèces face aux changements climatiques reste incomplète et témoignent de la nécessité de nouvelles études empiriques pour améliorer nos connaissances sur ce sujet. D'un point de vue général, nos résultats indiquent que les réponses des espèces aux changements climatiques futurs devraient varier en fonction de leurs caractéristiques intrinsèques. En identifiant quels étaient les traits des espèces associés aux variations interspécifiques du degré de synchronisme des populations et de différents descripteurs des dynamiques de populations, nos résultats fournissent une base aux acteurs de la conservation pour identifier les espèces potentiellement à risque et mettre en place des politiques de gestion adaptées aux différentes espèces.

Conclusions et perspectives

Perca fluviatilis

1. Conclusions générales

L'objectif général de cette thèse était de mettre en évidence l'influence de facteurs environnementaux sur les dynamiques de populations de poissons d'eau douce en France et plus particulièrement d'évaluer l'influence et la contribution relative des facteurs intrinsèques (e.g. densité-dépendance, taux d'accroissement) et extrinsèques (e.g. climatiques) aux variations de tailles des populations. Par ailleurs, en étudiant plusieurs espèces, notre objectif était de mettre en évidence des patrons généraux et des patrons spécifiques puis de déterminer si les caractéristiques intrinsèques des espèces et leur histoire évolutive permettaient d'expliquer les différences observées entre espèces.

Le degré de synchronisme spatial des populations mis en évidence dans le chapitre 1 est cohérent avec l'hypothèse de l'influence d'un facteur qui agit à large échelle sur les populations et suggère que le synchronisme spatial des populations est essentiellement dû à l'influence de facteurs environnementaux (Bjørnstad *et al.*, 1999; Buonaccorsi *et al.*, 2001; Liebhold *et al.*, 2004) tels que la température (Koenig, 1999; Fox *et al.*, 2000). Ainsi, les espèces qui présentent un fort degré de synchronisme en lien avec la température, devraient présenter un plus fort risque d'extinction en réponse aux changements de température (et plus largement climatiques) que celles qui ont un plus faible degré de synchronisme. En effet, une augmentation des températures à une large échelle spatiale peut augmenter la probabilité de déclins spatialement corrélés de populations et donc augmenter la probabilité d'extinction à l'échelle de l'espèce (Hanski & Woiwod, 1993; Heino *et al.*, 1997). Les transformations de séries temporelles (TSTs), classiquement utilisées dans les études de synchronisme, sont apparues comme problématiques et peu efficaces pour mettre en évidence les mécanismes responsables du synchronisme spatial des populations. L'étude de leur influence sur différentes mesures de synchronisme nous a amené à formuler quelques recommandations pour limiter les biais associés à leur utilisation. Ainsi, l'utilisation des TSTs pour des raisons statistiques (augmentation du risque de première espèce) est à proscrire dans la mesure où les conclusions peuvent être complètements différentes en fonction de la transformation utilisée. Néanmoins, la comparaison des résultats obtenus sur les données transformées avec ceux obtenus sur les données brutes peut donner des informations précieuses quant aux mécanismes sous-jacents au synchronisme des populations.

Dans le chapitre 2, nous avons étudié l'influence de différentes variables environnementales sur les dynamiques de populations de plusieurs espèces en fonction de leurs effets sur les paramètres qui déterminent les tailles de populations locales (i.e. taux de migration, taux d'accroissement et densité dépendance). Nos résultats montrent que les processus densité-dépendants n'ont qu'une influence limitée sur les populations. Au contraire, les facteurs environnementaux peuvent avoir une forte influence sur les variations spatio-temporelles de dynamiques de populations, notamment au travers de leurs influences sur le taux d'accroissement. Alors que la plupart des études (e.g. May, 1976; Coulson *et al.*, 2004; Saether *et al.*, 2008; Ohlberger *et al.*, 2014) ne considèrent que la composante stochastique des facteurs environnementaux (i.e. influences purement aléatoires et non déterminées sur les populations), nos résultats montrent l'importance de considérer la nature déterministe de ces

facteurs pour améliorer notre compréhension des mécanismes sous-jacents aux variations de tailles des populations et pour anticiper les conséquences des changements climatiques sur les variations spatio-temporelles d'abondances. Notre étude a permis de mettre en évidence une influence globalement négative de la température de l'eau sur les populations de poissons. Dans le contexte actuel, ce résultat confirme ceux obtenus dans le premier chapitre et atteste d'un certain pessimisme pour une partie des populations de poissons d'eau douce. Néanmoins, les patrons sont très variables en fonction des espèces, traduisant des différences interspécifique de sensibilité aux variations environnementales et une influence idiosyncratique des variables environnementales sur les paramètres de dynamiques de populations. Enfin, bien que des mécanismes communs aux populations de chaque espèce aient pu être identifiés, de fortes variations spatiales des dynamiques de populations ont été mises en évidence. En accord avec d'autres études (Williams *et al.*, 2003; Saether *et al.*, 2008; Fukaya *et al.*, 2013), nous avons mis en évidence des patrons spatiaux de réponses des populations aux variations environnementales pour certaines espèces. Ces patrons suggèrent une certaine prévisibilité de réponses des populations en fonction de leur position géographique.

Globalement, les mécanismes mis en évidence dans les chapitres 1 et 2 apparaissent comme complexes et variables en fonction des espèces. Dans le chapitre 3, nous avons identifié quelles étaient les principales caractéristiques des espèces à l'origine de ces variations. En effet, alors que l'histoire évolutive des espèces ne permet pas d'expliquer les différences observées, nos résultats montrent que ces différences peuvent s'expliquer par certaines caractéristiques des espèces associées à leur physiologie, leur écologie ou leur stratégie de reproduction. Ainsi, en fonction de leurs caractéristiques, les espèces de poissons ne répondent pas de la même façon aux variations environnementales, ce qui indique que les conséquences futures du réchauffement climatique sur les dynamiques de populations devraient varier en fonction des espèces.

Les patrons mis en évidence dans cette thèse pourraient avoir des implications importantes en termes de politiques de conservation. Par exemple, la mise en évidence d'un effet Moran sur les populations de poissons nous a permis d'identifier les espèces potentiellement menacées par le réchauffement climatique. Par ailleurs, en identifiant quelle était l'influence des variables environnementales sur les dynamiques de populations et au travers de quel paramètre de dynamique de populations ces variables avaient le plus d'effets, nos résultats renseignent sur les mécanismes sous-jacents aux dynamiques de populations des différentes espèces de poisson d'eau douce. Ces résultats pourraient permettre d'anticiper l'impact des changements climatiques sur les dynamiques de populations et de mettre en place des politiques de gestion adaptées. Les gradients spatiaux de réponses des populations que nous avons mis en évidence pourraient être utilisés pour prédire les réponses des populations à des variations environnementales en fonction de leur position géographique. De la même manière, les relations que nous avons mises en évidence entre les caractéristiques des espèces et les variations de réponses interspécifiques pourraient être utilisées pour inférer des patrons de dynamiques de populations et prédire l'influence des changements climatiques pour les populations d'espèces rares ou difficilement détectées mais pour lesquelles on dispose

d'informations sur des traits biologiques et/ou écologiques. Ces espèces sont justement celles qui requièrent une attention particulière dans le contexte actuel de réchauffement climatique (Hannah *et al.*, 2002).

2. Perspectives de recherches

Les résultats mis en évidence dans cette thèse soulèvent de nombreuses interrogations et la complexité des mécanismes mis en évidence pose la question de notre capacité à prédire correctement l'influence des changements climatiques sur les patrons de biodiversité. Nous discutons maintenant de quelques perspectives de recherches qui font suites aux travaux de cette thèse.

2.1. Synchronisme spatial des populations : mécanismes et méthodologies

Bien que notre étude ait permis de mettre en évidence une certaine influence de la température sur le degré de synchronisme spatial des populations de poissons, d'autres facteurs sont probablement à l'œuvre. Par exemple, Tedesco & Hugueny (2004) ont montré que la variabilité du régime des débits avait une influence sur le synchronisme spatial des populations de quatre espèces de poissons d'Afrique situées dans trois bassins-versants différents. Ainsi, bien que la température apparaisse comme un déterminant potentiel du synchronisme spatial des poissons d'eau douce en France, la prise en compte d'autres facteurs environnementaux pourrait révéler de nouveaux patrons. Les prochaines études devront prendre en compte ces facteurs, notamment la variabilité du régime hydraulique, pour améliorer notre compréhension des mécanismes à l'origine du synchronisme spatial des populations de poissons d'eau douce.

Dans notre étude, nous avons ignoré la structure d'âge des populations ce qui peut expliquer les faibles niveaux de synchronisme mis en évidence. En effet, si les dynamiques des différentes classes d'âge sont gouvernées par différents processus (e.g. densité-dépendants *vs* climatiques), les degrés de synchronisme mesurés au niveau de l'espèce peuvent être faibles (Grenouillet *et al.*, 2001). Par ailleurs, la décomposition du degré de synchronisme des espèces en fonction de la structure d'âge des populations pourrait permettre d'identifier les classes d'âge qui contribuent le plus au synchronisme spatial des populations et par la même occasion d'identifier les classes d'âge les plus vulnérables à des changements de conditions environnementales (voir aussi partie 2.2).

Etant donné que la dispersion d'individus entre populations est l'un des mécanismes sous-jacent au synchronisme spatial des populations, une des perspectives évidente de nos travaux est de prendre en compte les obstacles à la dispersion des poissons (Figure 23). En effet, les systèmes aquatiques continentaux sont des milieux très fragmentés (notamment par la présence de barrages) qui limitent la dispersion des individus au sein du réseau hydrographique (Malmqvist & Rundle, 2002) et qui pourrait conduire à sous-estimer

l'influence des facteurs climatiques sur le synchronisme des populations. En effet, bien que des populations soient proches d'un point de vue géographique, elles peuvent en réalité être totalement déconnectées, ce qui implique que le synchronisme de populations proches peut en fait s'expliquer par l'influence de facteurs climatiques. De plus, les relations entre degré de synchronisme et distance spatiale entre populations devraient être fortement affectées par la prise en compte des obstacles à la dispersion, ce qui pourrait amener à réévaluer les échelles de synchronisme que nous avons estimées. Par ailleurs, la mesure de distance que nous avons utilisé (i.e. euclidienne), ne rend pas compte des distances réelles entre populations (Peterson *et al.*, 2013). L'utilisation de la distance le long du réseau hydrographique pourrait permettre de révéler de nouveaux patrons.

Figure 23. Carte des barrages de classe A, B et C en France métropolitaine. (Modifié d'après MEDDTL, DGPR et ©IGN, GEOFLA®).

Dans notre étude, nous avons considéré l'influence de deux TSTs couramment utilisées dans les études de synchronisme pour retirer la tendance à long-terme et l'autocorrélation temporelle. Cependant, d'autres méthodes existent pour prendre en compte ces facteurs (e.g. modèle linéaire autorégressif d'ordre 1 pour prendre en compte l'autocorrélation temporelle) (Buonaccorsi *et al.*, 2001) et de nouvelles études sont nécessaires pour évaluer la capacité de ces méthodes à mettre en évidence le mécanisme d'intérêt. Nos résultats soulignent également la nécessité de développer de nouvelles approches, notamment méthodologiques, pour améliorer notre capacité à mettre en évidence les mécanismes à l'origine du synchronisme des populations. Cependant, étant donné l'inhérente complexité des séries temporelles (e.g. erreurs de mesures, structure et force de la densité-dépendance, tendance à long-terme, longueur), la capacité d'une seule méthode à traiter efficacement des séries temporelles dont les caractéristiques sont très différentes est peu probable.

2.2. Complexification des modèles de dynamiques de populations : tout est dans le détail

Les améliorations des performances de calculs combinées à l'accumulation des données empiriques ont conduit les scientifiques à élaborer des modèles de plus en plus complexes pour améliorer notre compréhension des mécanismes responsables des variations de tailles de populations (Sutherland & Norris, 2002). L'ensemble de ces travaux a mené certains chercheurs à conclure que la compréhension des dynamiques de populations requiert l'utilisation de données complexes et d'une connaissance approfondie du système étudié ("The devil is in the detail"; Benton *et al.*, 2006). Bien que le modèle utilisé dans le chapitre 2 apporte des informations clés sur les mécanismes à l'origine des variations spatio-temporelles d'abondances, celui-ci peut être amélioré de différentes façons. Sans être exhaustif, voici quelques pistes de réflexion.

Dans notre modèle, nous avons ignoré la structure d'âge (ou de taille) des populations. Outre le fait que l'absence de prise en compte de cette structure puisse introduire de l'autocorrélation dans les fluctuations de populations et amener à surestimer l'influence des processus densité-dépendants sur les populations (Lande *et al.*, 2002, 2006), sa prise en compte pourrait permettre de déterminer quelle classe d'âge contribue le plus au taux d'accroissement des populations et à terme d'identifier quels sont les paramètres démographiques (survie juvénile, survie adulte, fécondité,…) les plus importants sur les fluctuations d'abondances (voire aussi partie 2.1) (Caswell, 2001; Lande *et al.*, 2006). De plus, des études récentes soulignent l'importance de considérer toutes les classes d'âge pour prédire l'influence des changements climatiques sur les dynamiques de population (Radchuk *et al.*, 2013; Zeigler, 2013). La base de données de l'Onema que nous avons utilisé contient des informations sur les tailles des individus pêchés (Edeline *et al.*, 2013). En étudiant la distribution des tailles des individus dans chaque localité il est envisageable de délimiter les différentes classes de tailles de chaque population (Figure 24; Reyjol *et al.*, 2008). Intégrer l'abondance de chaque classe de taille dans les modèles de dynamiques de populations pourrait permettre (1) de déterminer quelle classe a le plus d'influence sur les dynamiques de populations, (2) d'évaluer l'influence des variables écologiques sur les différentes classes de tailles et (3) d'améliorer les prédictions relatives à l'influence des changements climatiques sur les populations.

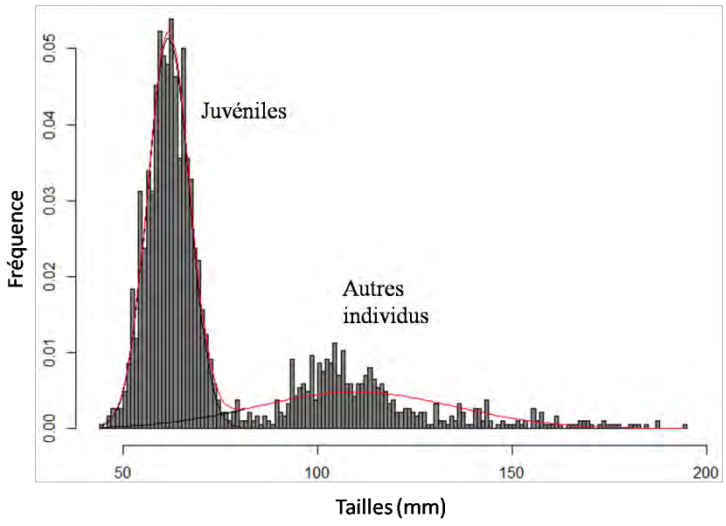


Figure 24. Exemple de distribution des tailles d'individus sur un site de pêche.

La stochasticité démographique est causée par des variations aléatoires de la contribution des individus de la même cohorte aux générations suivantes (Lande *et al.*, 2003). Ce phénomène est généralement attribué à des événements fortuits, indépendants des paramètres de survie et de reproduction individuelle, et qui provoquent des changements aléatoires dans le taux d'accroissement des populations (Lande *et al.*, 2006). Bien que les données individuelles soient extrêmement rares et disponibles seulement pour quelques espèces (Lande *et al.*, 2003), elles sont néanmoins essentielles pour améliorer notre compréhension des déterminants des dynamiques de populations (Benton *et al.*, 2006; Coulson, 2012; Merow *et al.*, 2014). En effet, il est reconnu que la stochasticité démographique a une forte influence sur les populations de petites tailles (Greenman & Benton, 2003; Engen *et al.*, 2005; Acker *et al.*, 2014) ce qui indique que ce facteur doit être pris en compte dans les modèles de dynamiques de populations. Nous voyons au moins deux approches pour prendre en compte ce processus. La première approche consiste à mesurer la variabilité de la contribution des femelles aux générations futures (e.g. par une approche expérimentale) et à intégrer cette variable dans les modèles de dynamiques de populations (Sæther *et al.*, 2004; Saether *et al.*, 2009). L'information sur le sexe des individus n'étant pas disponible dans les données de l'Onema, cette solution nécessite cependant de faire l'hypothèse d'un sex-ratio équilibré dans les populations. La deuxième approche consiste à considérer la stochasticité démographique comme un paramètre à estimer dans les modèles de dynamiques de populations (Kokko & Ebenhard, 1996; Grøtan *et al.*, 2009; Bjørkvoll *et al.*, 2012).

Les interactions trophiques (e.g. prédation, compétition interspécifique) peuvent avoir une influence sur les populations (Turchin, 1990, 2003; Stenseth *et al.*, 1998; Jiang & Shao, 2003; Kilpatrick & Ives, 2003) et plusieurs études ont montré que ces interactions pouvaient évoluer en réponse au réchauffement climatique (Harrington *et al.*, 1999; Edwards & Richardson, 2004; Winder & Schindler, 2004), avec des conséquences plus ou moins importantes sur les espèces et les populations (Cahill *et al.*, 2013). Ainsi, pour prédire les conséquences des changements climatiques sur les populations il est important de prendre en compte cette source de variation. La compétition entre espèces pour les ressources et la prédation sont considérées comme les interactions ayant le plus d'influence sur les dynamiques de populations (Huitu *et al.*, 2004). Pour prendre en compte la compétition interspécifique, il est envisageable d'intégrer l'abondance totale des individus des autres espèces dans les modèles de dynamiques de populations (Stenseth *et al.*, 1996, 1998; Pedraza-Garcia & Cubillos, 2007). En revanche, l'intégration de la prédation dans ces modèles requiert une connaissance plus détaillée du système étudié (Huitu *et al.*, 2004; Chesson & Kuang, 2008; Wang *et al.*, 2008), afin de décrire les interactions biotiques entre espèces et prendre en considération la structure des réseaux trophiques.

Le débit est un déterminant majeur de l'habitat physique dans les rivières et conditionne la distribution de nombreuses espèces aquatiques (Vannote *et al.*, 1980; Poff & Ward, 1989) ainsi que l'évolution de nombreuses caractéristiques intrinsèques des espèces (Bunn & Arthington, 2002). Par ailleurs, l'altération du régime de débit des rivières peut favoriser l'implantation d'espèces non-natives (Arthington *et al.*, 1990; Moyle & Light, 1996a,

1996b) avec des conséquences potentiellement importantes sur les dynamiques de populations (Huxel, 1999; Manchester & Bullock, 2000). Ainsi, une perspective importante de ce travail est d'intégrer l'influence du débit dans les modèles de dynamiques de populations de poissons.

Finalement, bien que nous ayons pris en compte l'influence de la migration dans notre modèle, plusieurs études à la fois théoriques et empiriques (e.g. Taylor & Norris, 2007; Grøtan *et al.*, 2009; Sutherland *et al.*, 2014) indiquent que ce paramètre peut dépendre de la densité d'individus dans les populations (i.e. migration densité-dépendante). Ce phénomène peut être causé par des mécanismes variés tel que la compétition ou les interactions sociales entre individus (Matthysen, 2005). Une perspective serait donc de prendre en compte ce phénomène dans les modèles de dynamiques de populations.

2.3. Identifier des patrons spatiaux de dynamiques de populations

Les variations intraspécifiques de dynamiques de populations mises en évidence dans le chapitre 2 soulèvent de nombreuses questions et témoignent de la nécessité de nouvelles investigations pour améliorer notre connaissance des processus à l'origine de ces variations et évaluer leurs conséquences sur la probabilité d'extinction des espèces. Il serait par exemple intéressant de tester si les espèces qui présentent une forte hétérogénéité spatiale de leurs dynamiques de populations présentent des degrés de synchronisme plus faibles, comme attendu en théorie (Engen & Saether, 2005; Hugueny, 2006). Si tel est le cas, ces espèces devraient présenter une plus faible probabilité d'extinction en réponse au réchauffement climatique (Hanski & Woiwod, 1993). En accord avec certaines études (Tkadlec & Stenseth, 2001; Williams *et al.*, 2003; Saether *et al.*, 2008), nous avons mis en évidence des patrons spatiaux de réponses des populations aux variations environnementales qui peuvent s'expliquer par des gradients latitudinaux de facteurs environnementaux ainsi que par un certain degré d'autocorrélation spatiale de ces facteurs. Bien que la mise en évidence de ces patrons fournisse des informations clés quant aux mécanismes responsables des variations spatiales des dynamiques de population de poissons, la prise en compte d'autres facteurs pourrait améliorer notre connaissance des processus sous-jacents à ces variations et améliorer les prédictions relatives aux conséquences des changements climatiques. Par exemple, il est aujourd'hui largement admis que les espèces tendent à remonter vers des altitudes et des latitudes plus élevées en réponse au réchauffement climatique (Hughes, 2000; Parmesan & Yohe, 2003; Root *et al.*, 2003). Ces changements peuvent mener à des différences de dynamiques de populations selon que celles-ci se situent aux limites inférieures ou supérieures des aires de distribution des espèces (Matías & Jump, 2014; Virkkala & Lehikoinen, 2014). L'étude des dynamiques de différentes populations, représentatives des dynamiques observées sur l'aire de distribution des espèces pourrait ainsi permettre d'identifier des fronts de colonisation et d'extinction, d'identifier les facteurs responsables des différences observés sur chaque front et de mieux prédire les changements de distribution des espèces.

2.4. Mesurer les variations intraspécifiques des traits des espèces

Dans le chapitre 3, nous avons considéré une valeur de trait moyenne par espèce. Cependant, les phénomènes de plasticité phénotypique et d'adaptation locale peuvent mener à de larges variations intraspécifiques des traits des espèces (Lavergne *et al.*, 2010; Kamilar & Cooper, 2013). Par exemple, dans l'annexe I (***AI***), nous avons montré que les stratégies de reproduction des populations peuvent fortement varier en fonction du degré d'eutrophisation du milieu. Comment ces variations influencent les patrons de dynamiques de populations reste pour le moment largement ignoré. Il serait donc très intéressant d'évaluer le degré de variation intraspécifique des traits des espèces pour améliorer notre compréhension des mécanismes à l'origine des variations spatiales de dynamiques de populations. Pour cela, il faudrait mesurer les traits des espèces dans différentes conditions, représentatives des environnements dans lesquels se trouvent les différentes populations de chaque espèce.

2.5. Conséquences sur les patrons de biodiversité et phénomènes de rétroactions

Dans ce travail, nous avons mis en avant une influence des caractéristiques des espèces sur différents descripteurs des dynamiques de populations. Ainsi, toutes les espèces ne répondent pas de la même façon aux variations environnementales et certaines espèces qui possèdent certains traits sont plus vulnérables que d'autres. Par ailleurs, nous avons montré de larges différences intraspécifiques en termes de dynamiques de populations qui témoignent d'une variabilité de réponse des populations à des variations des conditions environnementales locales. Ces différences, à la fois inter et intraspécifiques, devraient se traduire par des modifications plus ou moins profondes des communautés en fonction des espèces présentes et des conditions environnementales locales. Une perspective intéressante de ce travail serait donc de déterminer comment les communautés et les patrons de diversité associés à ces communautés (e.g. fonctionnelle, taxonomique, phylogénétique) ont évolué au cours de ces dernières années. Plusieurs études ont déjà mis en évidence des changements de composition de communautés (Parody, 2001; Waldrop & Firestone, 2006) et de richesse spécifique (Iverson & Prasad, 2001; Menéndez *et al.*, 2006). En revanche, les modifications des patrons de diversité fonctionnelle (Thuiller *et al.*, 2006) et de diversité phylogénétique (Thuiller *et al.*, 2011) ont été peu considérés et requièrent de plus amples investigations. Il serait par ailleurs très intéressant de déterminer comment les modifications des patrons de biodiversité influencent en retour les dynamiques de populations locales. Par exemple, une augmentation de la richesse spécifique dans une communauté devrait contribuer à déstabiliser les dynamiques de population (Tilman, 1996). Inversement, une diminution de la richesse spécifique pourrait diminuer les phénomènes de compétition interspécifique et favoriser les phénomènes de compétition intraspécifique (i.e. augmentation de la densité-dépendance intraspécifique). Par ailleurs, une érosion de la diversité génétique des populations pourrait augmenter les risques d'extinction des espèces en diminuant la résilience de la dynamique des populations en réponse à des événements extrêmes (Luck *et al.*, 2003). L'étude des patrons de diversité génétique est d'autant plus intéressante que de plus en plus d'études montrent que les espèces peuvent évoluer rapidement en réponse aux changements climatiques (Reznick &

Ghalambor, 2001; Gingerich, 2009; Pauls *et al.*, 2013) et que ces changements peuvent affecter en retour les dynamiques de populations (Hanski & Saccheri, 2006; Pelletier *et al.*, 2007; Razgour *et al.*, 2013). Enfin, il serait intéressant de tester si la variabilité des taux d'accroissement entre espèces et la variabilité de réponses des espèces aux variations environnementales favorise la stabilité des écosystèmes, comme attendu en théorie (Loreau & de Mazancourt, 2013).

La compréhension de l'influence des changements climatiques sur les populations, les espèces, les communautés et les écosystèmes requiert donc une approche intégrative qui évalue les conséquences de ces changements sur différentes composantes de la biodiversité (Devictor *et al.*, 2010). L'approche développée en annexe 2 (***AII***) qui combine des analyses génétiques à des analyses démographiques et de distribution d'espèces représente une perspective prometteuse dans ce contexte.

2.6. Prédictions futures : prise en compte des dynamiques de populations

L'approche la plus utilisée pour prédire les effets du changement climatique sur les espèces est la modélisation d'enveloppes climatiques (Araújo & Rahbek, 2006; Grenouillet *et al.*, 2011; Araújo & Peterson, 2012; Bellard *et al.*, 2012). Cette approche consiste à décrire les conditions climatiques favorables à l'espèce et à projeter la distribution de l'espèce dans le futur sous différents scénarios climatiques (Figure 25). Cependant, cette approche est surtout basée sur des données de présences-absences (ou de présences seules) et ne prend pas en compte les dynamiques de populations. Or, ce sont les tailles de populations et les tendances démographiques qui sont principalement utilisées pour déterminer le statut de conservation des espèces et définir les actions de gestion (Gregory *et al.*, 2005; Eaton *et al.*, 2009). En effet, les tailles de population et leurs tendances sont globalement corrélées au risque d'extinction des espèces (O'Grady *et al.*, 2004) et des déclins significatifs de populations peuvent survenir bien avant que l'aire de distribution de l'espèce soit modifiée (Chamberlain & Fuller, 2001). L'utilisation de modèles permettant d'estimer les futurs changements d'abondances des populations en réponse au réchauffement climatique pourrait fournir des informations précieuses quant aux futures probabilités d'extinction des espèces. Plusieurs méthodes ont été développées au cours des dernières années pour prédire les conséquences des changements climatiques sur les dynamiques de populations (Saether *et al.*, 2009; Hare *et al.*, 2010; Huntley *et al.*, 2012; Renwick *et al.*, 2012). Par exemple, les analyses de viabilité (Boyce, 1992) consistent à estimer la probabilité d'extinction des espèces en fonction de leurs caractéristiques démographiques et des variables climatiques (Keith *et al.*, 2008). Plus généralement, de plus en plus d'études soulignent l'importance des données d'abondance (Howard *et al.*, 2014) et suggèrent de coupler les modèles de distribution d'espèces avec les modèles de populations pour améliorer les prédictions relatives à l'influence des changements climatiques sur les patrons de biodiversité (Brook *et al.*, 2009; McMahon *et al.*, 2011; Pagel & Schurr, 2012; Schurr *et al.*, 2012). Ainsi, une perspective de ce travail de thèse serait d'utiliser le modèle de dynamique de populations défini au chapitre 2 et de le coupler avec des modèles de distribution d'espèces - déjà utilisés avec succès sur la base de donnée que nous

avons utilisée (Buisson & Grenouillet, 2009; Comte & Grenouillet, 2013) - afin d'améliorer les prédictions futures concernant les probabilités d'extinction des espèces de poissons et leurs changements de distributions.

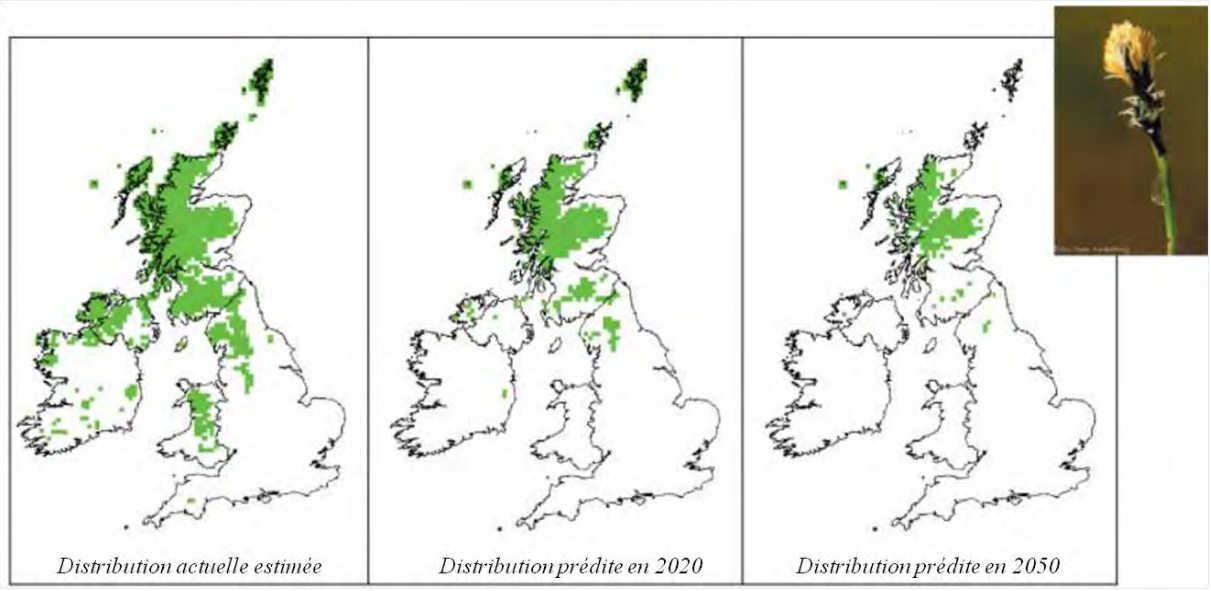


Figure 25. Exemple d'utilisation d'un modèle d'enveloppe pour prédire l'influence du changement climatique sur la distribution d'une espèce de Carex (Carex bigelowii) en Grande Bretagne. (Modifié d'après Pearson & Dawson, 2003).

2.7. Identification des mécanismes sous-jacents aux dynamiques de populations : vers une approche trans-espèces

Dans le chapitre 2, nous avons construit un modèle pour chaque espèce en considérant l'ensemble des populations. Ces modèles nous ont ainsi permis d'identifier des mécanismes communs aux dynamiques de populations de chaque espèce, malgré des variations spatiales importantes des patrons d'abondances. Etant donné la grande diversité des organismes vivants (Groombridge *et al.*, 2000) et les différences qui existent entre les grands groupes taxonomiques (Figure 26; Doolittle, 1999; Wolf *et al.*, 2002), pourquoi ne serait-il pas possible d'identifier des mécanismes communs aux dynamiques de populations de larges groupes taxonomiques ? En effet, on peut légitimement s'attendre à ce que les mécanismes qui régissent les dynamiques de populations de ces grands groupes taxonomiques soient différents. Pour tester cette hypothèse, il faudrait adapter le modèle défini dans le chapitre 2 en considérant l'ensemble des populations des différentes espèces. Etant donné le nombre très important de séries temporelles impliqués, ce modèle permettrait par ailleurs de prendre en compte d'autres facteurs tels que les débits, les obstacles à la dispersion des individus ou les interactions trophiques entre espèces. D'un point de vue général ce modèle permettrait d'identifier les déterminants des variations spatio-temporelles des dynamiques de populations de groupes d'espèces. D'un point de vue plus appliqué, les résultats de ce modèle pourraient permettre d'identifier les facteurs dont les modifications (e.g. changement de température, modifications des interactions trophiques) ont le plus d'influences sur les dynamiques de

populations de grands groupes taxonomiques et de mettre en place des politiques de gestion spécifique à chaque groupe.

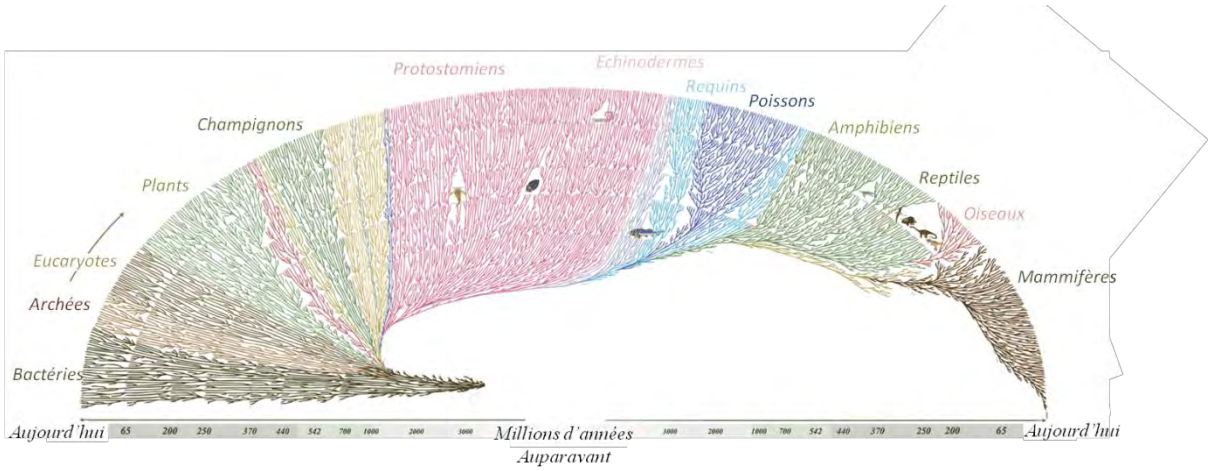


Figure 26. Arbre phylogénétique des grands groupes taxonomiques. (Modifié d'après Leonard Eisenberg 2008©).

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Article I (*PI*)

Chevalier M, Laffaille P, Ferdy J-B et Grenouillet G (2014). Measurements of spatial population synchrony: influence of time series transformations. Soumis à ***Oecologia****.*

Measurements of spatial population synchrony: influence of time series transformations

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Abstract

Two main mechanisms have been proposed to explain spatial population synchrony: dispersal among populations, and the spatial correlation of density-independent factors (the "Moran effect"). To identify which of these two mechanisms is driving spatial population synchrony, time series transformations (TSTs) have been used to remove the signature of one mechanism, in order to highlight the effect of the other. However, there are several issues with TSTs, and there is currently no consensus or guidelines about how population time series should be handled in synchrony studies.

Here, by using 3119 time series involving 34 fish species found in French rivers, we computed several metrics commonly used in synchrony studies to determine whether a large-scale climatic factor (temperature) influenced fish population dynamics at the French scale, and to test the effect of three commonly used TSTs (detrending, prewhitenning and a combination of both) on these metrics. We also tested whether the influence of TSTs on our measures of population synchrony was related to the features of the time series. For several species, and regardless of the TST used, we found evidence for a Moran effect on population dynamics. However, the results were globally biased downward by TSTs which reduced our ability to detect significant signals. Depending on the species and the features of the time series, we found that TSTs could lead to contrasting/contradictory results, regardless of the metric considered. We finished by suggesting guidelines on how population time series should be processed in synchrony studies.

Key words: population, prewhitenning, detrending, fish, synchrony.

Introduction

Population densities in different locations often fluctuate synchronously over time (Buonaccorsi et al. 2001). This phenomenon, known as spatial population synchrony, is common in animal populations ranging from parasites (Cattadori et al. 2005), insects (Powney et al. 2012), fish (Grenouillet et al. 2001), amphibians (Aubry et al. 2012), and birds (Koenig and Knops 1998) to mammals (Moran 1953). Two main mechanisms have been identified as the drivers of spatial synchrony (Liebhold et al. 2004): (1) dispersal among spatially-structured populations (Ranta et al. 1995), and (2) the spatially-correlated effects of density-independent factors that synchronize populations with the same linear density-dependent structure, a process known as the "Moran effect" (Moran 1953). Trophic interactions involving species that are themselves synchronized or mobile could also influence population synchrony (Forchhammer et al. 2002).

Depending on the main mechanism driving population synchrony, the fate of the metapopulations involved may vary (Hanski and Woiwod 1993). Indeed, if synchrony is caused by dispersal, then a population that suffers severe decline can be rescued by adjacent populations, ensuring persistence of the metapopulation. In contrast, if synchrony is caused by environmental factors, then all populations could suffer a severe decline simultaneously, which could lead to metapopulation extinction. It is generally thought that large-scale synchrony is caused by environmental factors, whereas local synchrony is mainly driven by dispersal or trophic interactions (Ranta et al. 1998). However it has been shown that dispersal between neighboring populations could interact with local demographic processes to generate patterns of spatial synchrony over very large distances (Gouhier et al. 2010). Moreover, it is likely that these mechanisms are not mutually exclusive, and in fact operate jointly in many systems, with varying relative importance (Ranta et al. 1999). Therefore, although identifying synchrony is important when studying population dynamics, the most difficult task is to identify which mechanisms are driving the observed synchrony.

Despite an abundant literature on population synchrony, very few studies (e.g. Grenfell et al. 1998; Tedesco and Hugueny 2004) have clearly identified which mechanism is involved in particular populations. This has been done experimentally (Benton et al. 2001) or by studying system where the influence of one of the mechanism could be discarded, as for instance with populations located in different islands between which dispersion is impossible (Grenfell et al. 1998). However, such systems are rare and experimental settings are not appropriate for studying large organisms (e.g. mammals) over long time periods. Consequently, the most common approach to identify which mechanism prevails in population synchrony has been to use time series transformations (TSTs) of abundance data. The idea in such procedure is to eliminate the signature of one mechanism to highlight the effect of the other (Bjørnstad et al. 1999). For instance, eliminating temporal autocorrelation (by a prewhitening procedure) in population time series makes it possible to focus on density-independent mechanisms, such as environmental noise (Hanski and Woiwod 1993). Likewise, eliminating long-term trends (by a detrending

procedure) makes it possible to focus on local processes (e.g. dispersal) rather than global ones, such as long-term climate change (Koenig 1999). However, removing trends in time series has been shown to reduce the power to detect real relationships (Pyper and Peterman 1998) and, in some cases, detrending can increase the autocorrelation in a dataset. For instance, if observations in time series are independent, detrending create a dependency among data points (Brown et al. 2011). Furthermore, the presence of temporal autocorrelation and/or long-term trends in a time series could indicate the presence of low-frequency (i.e. slowly changing) variability (Pyper et al. 1999). Yet, if low-frequency sources are also sources of real covariation between time series, then their removal (by a detrending or a prewhitenning procedure) can greatly reduce our ability to detect that covariation (increase of type II error rate). As far as we are aware, the effects of various TSTs on synchrony measurements remain to be compared.

Here we looked at time series of the abundance data for 34 fish species in a number of French rivers in four different ways: as raw data, as detrended data, as prewhitened data, and as a combination of both TSTs (prewhitening and detrending). We then computed various statistics, frequently used in synchrony analyses, to find out whether a large-scale climatic factor (temperature) had any influence on fish population dynamics in these four time series. Indeed, because of their biological characteristics, fish would be expected to be highly sensitive to environmental fluctuations, especially in temperature (Stenseth et al. 2002). We then compared the results obtained using each of the TSTs to those obtained using the raw data in order to identify the effect of each transformation on the different measures used. We also tested whether the influence of TSTs on the results depended on the features of the original time series (i.e. strength and evidence of density dependence and/or long-term trend). Finally, because the ecological characteristics of a species can influence its population dynamics (e.g. Gilpin 1992) and therefore the features of the time series, we tested whether the species life-span, which is considered to be a reliable metric to measure life-history variation among species (Sæther et al. 2013), was related to the features of the time series, and consequently to the influence of TSTs on the results.

Our expectations were as follows. First, by making it possible to eliminate the signature of one mechanism, TSTs should reduce our overall ability to detect significant synchrony, but could be used to identify drivers of population synchrony by comparing the results obtained using raw data, as previously suggested (Bjørnstad et al. 1999). However, we supposed that TSTs could lead to false outcomes by removing part of the signal of interest. Second, TSTs were expected to have different influences on the results depending on the features of the raw time series. For instance, for time series that do not display long-term trend (or density dependence), detrending (or prewhitening) should have little influence on the time series and therefore on the results. Finally, species with a long life-span were expected to display stronger density-dependence, but weaker long-term trends than species with a short life-span. This is because species with a short life-span undergo more reproduction events than species with a long life span in a given time. Thus, populations of these species should be more prone to respond to environmental fluctuations

and so to long-term climate change while species with a long life-span were expected to be rather regulated by density-dependent factors.

Material and Methods

FISH AND TEMPERATURE DATA SETS

Fish population abundances were provided by the French National Agency for Water and the Aquatic Environment (Onema). These annual data were obtained between 1982 and 2010 by electrofishing during periods of low flow (for further details see Poulet et al. 2011). Fish were identified to species level, counted, and then released back into the river. From this data set we conserved only the species for which at least ten population time series including at least eight years of non-null captures were available. This resulted in the selection of 34 fish species (Table 1). We chose to have at least ten population time series, because we wanted to have (1) populations that were representative of the different conditions experienced by the species in its geographic range and (2) enough populations to compute a reliable estimate of species synchrony levels. For the number of years within the time series, we chose the same number as that used in a study involving a previous version of our database (Poulet et al. 2011).We therefore used a data set consisting of 610 sites located throughout France (Fig. 1) with 8 to 25 years of sampling (mean: 12.5 years; sd: 3.6 years), corresponding to a total of 7634 sampling occasions. Method used neither required the same exact years to be covered for the different sites nor the years to be consecutive, but all times series that had more than three consecutive year missing were discarded to minimize the influence of missing information on our results. The number of zero counts ranged from zero to 14, depending on the time series (mean: 1.34; sd: 2.33).

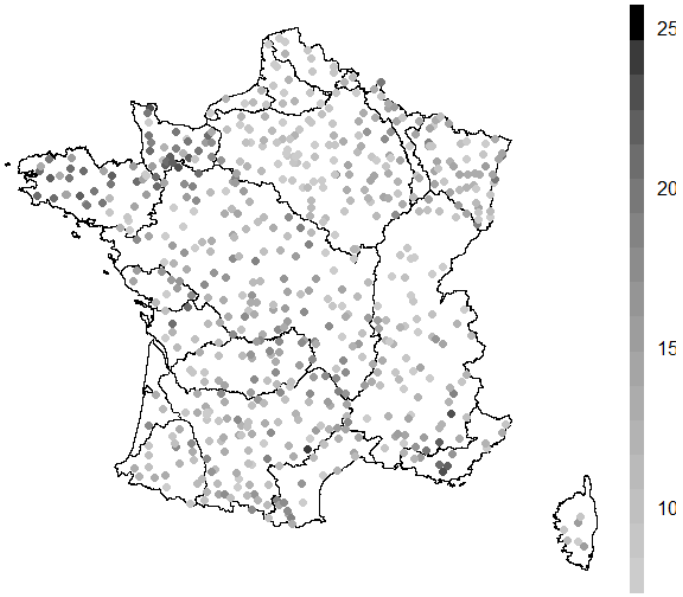

Figure 1. Study area showing the distribution of the sampling sites. The gray scale indicates the number of years available for each site. Sites shown in light gray are those for which we have the fewest years, while sites shown in dark gray are those for which we have the greatest number of years.

Table 1. Data for the 34 French fish species studied. Nseries is the number of time series. Npairs is the number of cross-correlation coefficients, GRS is the species geographic range size (km²) and LS is the species life-span (years). For some species the life-span is the mean of different values found in the literature.

Species name	Nseries	Npairs	GRS (km²)	LS (years)
Abramis brama	26	233	278589	14.5
Alburnoides bipunctatus	52	745	273135	6
Alburnus alburnus	110	2830	451797	6
Ameiurus melas	17	64	138562	9
Anguilla anguilla	208	12680	610044	17
Barbatula barbatula	245	21312	550434	7
Barbus barbus	131	5162	407407	14
Blicca bjoerkna	24	94	247209	10
Carassius carassius	13	55	195257	10
Chondrostoma nasus	30	373	185169	13.5
Cottus gobio	25	160	118620	5
Cottus perifretum	169	10724	358455	6
Cyprinus carpio	11	55	163528	15.5
Esox lucius	61	1037	399757	13
Gasterosteus gymnurus	16	76	233558	3
Gobio gobio	219	14354	411718	5
Gobio lozanoi	9	36	3732	5
Gobio occitaniae	75	1926	100833	5
Gymnocephalus cernua	21	138	219214	8.5
Lampetra planeri	64	1857	366203	7
Lepomis gibbosus	81	1595	382141	8
Leuciscus burdigalensis	39	522	235117	10
Leuciscus leuciscus	59	922	244492	10
Perca fluviatilis	154	5404	410109	14
Phoxinus phoxinus	249	22544	542819	6.5
Pungitius laevis	19	134	109912	4
Rhodeus amarus	33	218	170673	5
Rutilis rutilis	250	16034	523535	12
Salmo salar	19	110	229971	8
Salmo trutta	284	29225	634422	6.5
Scardinius erythrophtalmus	28	134	298309	8
Squalius cephalus	313	28084	534373	8
Telestes souffia	23	179	90144	10
Tinca tinca	42	490	415053	12

Daily air temperature data from 1980 to 2008 were provided by Météo France. This database (SAFRAN, Le Moigne 2002), is a regular eight kilometer grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically-homogeneous zones (for further details see Le Moigne 2002). Studies have shown that air temperature provides a reliable proxy for water temperature (e.g. Caissie 2006). Since warm temperatures during the summer have been shown to affect fish population synchrony (Grenouillet et al. 2001; Cattanéo et al. 2003), we calculated the mean air temperature during the warmest month of each year for each site. We then used this measure to estimate the degree of temperature synchrony (i.e. a proxy of the Moran effect) between the different sites to determine whether it influenced fish population synchrony.

TSTs: ESTIMATION OF TIME SERIES FEATURES AND RELATION WITH SPECIES LIFE-SPAN

Population time series were considered in four different ways: (1) as raw data, (2) as residuals obtained from a linear model with the year as a covariate to eliminate the long-term trend (detrended data), (3) as residuals obtained from a stock-recruitment Ricker model (Ricker 1958) to eliminate temporal autocorrelation due to intrinsic population dynamic (prewhitened data), and (4) as residuals obtained from a stock-recruitment Ricker model that included the year as a covariate to eliminate both the long-term trend and the temporal autocorrelation due to intrinsic population dynamic (prewhitened and detrended data). The precise specifications for the four types of time series are presented below. The models used for TSTs were fitted to the raw data using the iteratively reweighted, least square method (McCullagh and Nelder 1989). The coefficients of these models (i.e. trend and density dependence; see below) were then extracted, and used to characterize the raw time series. All calculations were performed in R (R Core Team 2013).

No transformation: raw data

Because the sampling area differed at the different sites, we expressed the abundance of fish as density of fish per $100m^2$ according to the following equation:

$$N_t = \frac{X_t}{S_t} * 100 \quad (1)$$

where N_t is the number of individuals per $100m^2$ at time t, X_t is the number of individuals sampled at time t, and S_t is the sampling area at time t.

TST I: detrending

To detrend the raw data we used a linear model with a negative binomial distribution and a log link function. We chose a negative binomial distribution, because it has been shown to perform well for small samples of over-dispersed count data (Welsh et al. 2000), especially

for freshwater fish (Vaudor et al. 2011). We thus fitted the following model independently to each time series:

$$\log(E(X_t)) = \alpha + \beta \log(\text{year}_t) + \log(S_t) + \varepsilon_t \quad (2)$$

where E denotes the expectation, year_t is the year of sampling at time t and ε_t is the remaining variance not accounted for by the covariates. The model therefore comprised one offset term ($\log(S_t)$), and three estimated parameters (the dispersion parameter, the intercept α and the slope β associated to the predictive variable year_t). The parameter α represents the number of fish caught per unit surface at t=0, while the parameter β is the long-term trend coefficient. For subsequent analyses, we used the residuals of this model.

TST II: prewhitening

Since the relationship between $\log(N_{t+1}-N_t)$ and N_t was linear for most of the time series, we used the stock-recruitment Ricker model with a log link function and a negative binomial distribution (i.e. accounting for overdispersion in the data) to eliminate temporal autocorrelation due to intrinsic population dynamic. We thus fitted the following model to each time series separately:

$$\log(E(X_{t+1})) = \log\left(S_{t+1}\frac{X_t}{S_t}\right) + \rho + \eta\frac{X_t}{S_t} + \varepsilon_t \quad (3)$$

where X_{t+1} is the number of fish caught at time t+1, and S_{t+1} is the sampling area at time t+1. The model therefore comprised one offset term ($\log\left(S_{t+1}\frac{Xt}{S_t}\right)$), and three estimated parameters (the dispersion parameter, the intercept ρ and the slope η associated to the predictive variable $\frac{X_t}{S_t}$). The parameter ρ corresponds to the intrinsic population growth rate, while the parameter η is the density-dependent coefficient. A significant negative slope indicated negative density-dependence, as caused for example by competition for resources. On the log-scale, this model is a linear, first order, autoregressive (AR(1)) model.

Because the model described by Eq. 3 incorporates only local recruitment, it predicts that X_{t+1} is necessarily null, when $X_t=0$. Yet, our data included some cases in which we observed transitions from $X_t=0$ to $X_{t+1}>0$. Such transitions can be explained in two different ways. First the true population size at time t could in fact have been greater than zero (i.e. false zero due to measurement error), and so $X_{t+1}>0$ could be explained by local recruitment. Second, the local population could really have been extinct (i.e. true zero), and so $X_{t+1}>0$ would be explained by recolonization from neighboring populations. Here, we have assumed that the first situation is unlikely, because of the previously documented efficiency of electrofishing (Zalewski and Cowx 1990, but see discussion). For series containing transitions from $X_t=0$ to $X_{t+1}>0$ we analyzed these transitions using the following model:

$$\log(E(X_{t+1})) = \gamma + \log(S_{t+1}) \quad (4)$$

where γ is the intercept of the model and quantifies the average number of migrant fish caught per unit surface at time t+1 while $\log(S_{t+1})$ is an offset.

In practice, any time series that did not contain at least eight non-null values of X_t or that contained multiple zeros were discarded (because multiple transitions from $X_t=0$ to $X_{t+1}=0$ cannot be handled by the recolonization model described above). The remaining series were used to fit the local recruitment model, after cases where $X_t=0$ had been removed (the value of X_{t+1} in Eq.3 is therefore conditional on $X_t>0$). For these series, transitions from $X_t=0$ to $X_{t+1}>0$ were modeled using the recolonization model described by Eq. 4 (the value of X_{t+1} in Eq.4 is therefore conditional on $X_t=0$). To ensure good parameter estimation, this model was adjusted only to time series containing at least three transitions from $X_t=0$ to $X_{t+1}>0$. Time series that contained one or two transitions like these (i.e. 111 time series) were discarded.

The combination of Eq. 3 and 4 to model time series that contained transitions from $X_t=0$ to $X_{t+1}>0$ is comparable to hurdle count models in which a truncated count component (e.g. truncated negative binomial distribution) is used to model positive values, and a binomial component (a negative binomial in our case) is used to model the transitions from zeros to positive values (Zeileis et al. 2008). For all series analyzed this way, residuals of both models were combined and used for subsequent analyses. Series that did not contain null values of X_t, were treated with the recruitment model (Eq. 3). We then extracted and used the residuals for subsequent analyses.

TST III: detrending and prewhitening

To take into account both long-term trends and population dynamics, we used the same approach as for TST II, above, but added the year as a covariate in Eq. 3 and 4.

Homogenization criteria

Because for TSTs II and III, we explained X_{t+1} in terms of X_t, and then used the residuals of the model, the resulting time series contained one fewer data point than the raw data or TST I. To have the same series length for all four types of time series, we therefore deleted the first year of all time series in the raw data. TST I was then computed from this raw data. To avoid any bias in comparing TSTs to raw data, any time series for which the algorithm used to estimate the parameters in the models did not converge were discarded. This selection process left us with 3119 time series for the 34 species (Table 1). Depending on the species concerned, the number of time series ranged from nine to 313 (mean: 91; sd: 106).

Species life-span and time series features

Species life-spans were determined from the literature (Keith et al. 2011) and FishBase (Froese and Pauly 2002) (Table 1). When multiple values were reported, we took the mean. We then used linear models to determine whether the coefficients of trend and density dependence, associated to each time series, varied depending on the species life-span. As the distribution of the coefficients of density dependence was highly skewed, this variable

was normalized by applying a Box-Cox power transformation (Box and Cox 1964). Because the results did not change qualitatively depending on whether the coefficients (i.e. long-term trend and density dependence) were estimated separately (using TST I and TST II) or simultaneously (using TST III), only the results from the latter are presented.

SYNCHRONY ANALYSES: MEASURES AND DETERMINANTS

Measuring synchrony: populations, species and scales of synchrony

For each species and the four types of time series, we measured population synchrony by computing Spearman cross-correlation coefficients (CCCs) between all pairs of time series with at least eight years in common (Buonaccorsi et al. 2001). From these CCCs, several statistics commonly used in synchrony analyses could be computed (Liebhold et al. 2004). We thus calculated species synchrony as the average of the CCCs weighted by the number of overlapping years of data between pairs of time series. To determine whether species synchrony was significantly different from zero, we used a bootstrap procedure with resampling of time-points within each time series, and then recalculated the mean between all the CCCs computed from the resampled time series (Lillegård et al. 2005). This procedure was repeated 1000 times to generate a distribution of mean species synchrony values under the hypothesis of no synchrony. Species synchrony was considered significantly different from zero if less than 5% of the simulated means (i.e. means calculated using the bootstrap algorithm) exceeded the observed mean. To rule out the effect of dispersion, the same analysis was conducted considering only the populations situated in different catchments.

As the variable distances over which the different populations were sampled could influence species synchrony levels (species with aggregated populations generally displaying higher synchrony levels; Sutcliffe et al. 1996), and so the subsequent analysis (see below), we tested whether the species geographic range size (GRS) had an influence on our measure of species synchrony using Spearman cross-correlation coefficients. For each species, GRS was measured as the area (km^2) of the smallest convex set of the subset of sites occupied by the species (i.e. the convex hull; Barber et al. 1996).The scale (i.e. the spatial extent) of synchrony is the distance beyond which population synchrony is overall no longer significantly different from zero (Bjørnstad & Falck 2001). To estimate the spatial extent of population synchrony for each species, we first calculated the Euclidean distance between each population. We chose the Euclidean distance because we considered this metric to be more representative of the similarity of the environmental conditions undergone by the different populations than a metric based on the distance along the river segments. Then, for each species and all four types of time series, we used generalized additive models to model the relationship between CCCs and distance, weighted for the length of the time series. We used the “x-intercept” (i.e. the intersection with the line y=0) of this relationship as a measure of the spatial scale of species synchrony (Bjørnstad & Falck 2001), whereas the "y-intercept" was used as a measure of species synchrony at small distances (i.e. for sites that were located

close together) (see Figure S1 of the "Electronic supplementary material" (ESM) for an example).

Identifying the determinants of population synchrony: distance between sites and temperature synchrony

For each species and for all four types of time series, we used Mantel tests (Mantel 1967) to determine whether population synchrony (i.e. CCC) was significantly influenced by the Euclidean distance between sites.

To find out whether population synchrony was related to temperature synchrony, we used population time series that covered the same time period as the temperature time series available (i.e. up to 2008). We measured temperature synchrony and population synchrony as above, using Spearman cross-correlation coefficients between all pairs of sites that had at least eight years in common. For each species and all four types of time series, we then used Mantel tests to find out whether there was any significant association between population synchrony and temperature synchrony. We also measured the scale of temperature synchrony over all the study sites using the same procedure as for the scale of population synchrony.

INFLUENCES OF TSTs

In this section, we performed multiple tests to compare the results obtained from each TST relative to raw data. We therefore adjusted the p-values according to the sequential Bonferroni procedure to conserve an initial error rate of 5%. To find out whether the influence of TSTs depended on the features of the time series, we computed mixed-effect models. To check for violations of model assumptions, we performed a visual inspection of the residuals for all reported models.

The ability to remove trend and temporal autocorrelation

For the four types of time series, we assessed the number of time series that showed a significant trend or temporal autocorrelation using a non-parametric Mann-Kendall trend test (Kendall 1955) and the autocorrelation function implemented in R (Venables and Ripley 2002), respectively. For the latter, we only considered the autocorrelation with a one-year lag. We then compared the number of time series that displayed significant trend or temporal autocorrelation for the four types of time series. In this way, we were able to assess whether the component of interest (e.g. trend) had in fact been eliminated by the corresponding TST (e.g. detrending), and whether the other (e.g. temporal autocorrelation) had not been affected.

Effects of TSTs on the time series

To determine the extent to which TSTs modified the raw time series, we first computed Spearman cross-correlation coefficients between the raw time series and the time series obtained with each TST. This led to the creation of three variables representing the

degree of similarity between the raw time series and the time series altered by each TST. A high correlation would indicate a high similarity (i.e. a low influence of the TST) whereas a low correlation would indicate a low similarity (i.e. a strong influence of TST). We used Wilcoxon-paired tests to find out whether the average correlation calculated between the raw time series and the modified ones depended on TSTs.

To determine whether the correlations calculated between the raw time series and the time series altered by each TST depended on the features of the raw time series, we computed three linear mixed-effect models with the length of the time series and the estimated coefficients of trend and density dependence as independent variables. The last two variables were entered into the model as absolute values so as to focus on the effect of their strength. To account for species variability, we added random effects on the intercepts and slope coefficients of each independent variable. Model equation and parameter descriptions are presented in the ESM.

Before running the models, the three dependent variables (i.e. correlations calculated between the raw time series and the time series altered by each TST) were normalized using a Box-Cox power transformation. As the results did not depend on whether the coefficients (i.e. trend and density dependence) were estimated separately (using TST I and TST II) or simultaneously (using TST III), only the results obtained using the latter are presented.

Effects of TSTs on population synchrony

To quantify the degree to which population synchrony was influenced by TSTs, we calculated the differences between the CCCs estimated using each of the TSTs and those estimated using the raw data. We thus obtained three variables representing the degree of dissimilarity between the CCCs obtained with each of the TSTs relative to those obtained with the raw data. To focus on the magnitude of these differences, we took the absolute values of these three variables. A high value would indicate a strong influence of TSTs whereas a low value would indicate a low influence. We then used Wilcoxon-paired tests to find out whether the average differences in the CCCs depended on the TST used.

To determine whether the features of the raw time series influenced the differences between the CCCs calculated using the raw time series and those calculated using each TST, we computed three linear, mixed-effect models. However, as each CCC involved two time series, it was not possible to use the specific features of each. Thus, for the length of the time series, we considered the common length used in calculating the CCCs while for density dependence and trend we focused on whether these features were significantly detected in the time series. If both time series showed significant trend/density dependence, the pair was assigned a value of two, whereas a value of zero was assigned to the pair if neither of the time series displayed significant values. If only one of the time series displayed significant trend/density dependence, we assigned a value of one to the pair. Thus, density dependence and trend were represented by ordinal variables. The models were constructed separately for each species to reduce the complexity of each model and ensure model convergence. To account for the variability associated to the sites involved in the calculation of the CCCs, we

added random effects on the slopes and intercepts of the trend and density-dependent variables. Model equation and parameter descriptions are presented in the ESM.

Before running the models, the three dependent variables (i.e. differences calculated between CCCs estimated with raw data and those estimated with each TST) were Box-Cox transformed. As the results did not depend on whether the coefficients were estimated separately or simultaneously, only the latter estimates are presented.

Effects of TSTs on species synchrony, spatial variation of synchrony and the determinants of population synchrony

We used Wilcoxon-paired tests (1) to find out whether TSTs had a significant influence on the different statistics calculated for the 34 fish species using the raw data (i.e. species synchrony, inter-catchment species synchrony, scale of synchrony, and synchrony at small distances) and (2) to determine whether TSTs modified our ability to identify the determinants of population synchrony for the 34 fish species (i.e. how TSTs modified the relationship between population synchrony and the Euclidean distance between populations as well as that between population synchrony and temperature synchrony).

Results

For the four types of time series considered, we did not found any significant ($p>0.05$) influence of GRS on our measure of species synchrony. Therefore, the results presented here should be weakly influenced by the variable distances over which the species were sampled.

FEATURES OF THE RAW TIME SERIES AND RELATION WITH THE SPECIES LIFE-SPAN

Separate estimation of trend and density dependence (TST I and TST II)

The percentage of time series showing a significant long-term trend ranged from 0% to 56% (mean: 32%; sd: 11.5%) depending on species (ESM, Table S1), with 0% to 44% of time series showing a positive trend (mean: 21.3%; sd: 10.9%), whereas the percentage of time series with a negative trend ranged from 0% to 28% (mean: 11.2%; sd: 6.7%). Time series showing a significant negative density-dependent coefficient ranged from 36% to 94% depending on species (mean: 73.9%; sd: 14.7%).

Simultaneous estimation of trend and density dependence (TST III)

When both components were estimated simultaneously, we found that the percentage of time series displaying significant coefficients differed from when they were estimated individually (ESM, Table S1), thus revealing that both coefficients were related to each other. Indeed, the percentage of time series found to display a significant long-term trend using

TST III was lower than that found using TST I (mean: 24%; sd: 9.3%), and ranged from 0% to 40%. The percentage of time series with a positive trend was lower (mean: 11.6%; sd: 8.5%), and ranged from 0% to 28%, whereas the percentage of time series with a negative trend was higher (mean: 12.3%; sd: 6.1%), and ranged from 0% to 30%. More time series showed significant negative density dependence relative to TST II (mean: 81%; sd: 13.2%). The percentage of time series displaying negative density dependence ranged from 36% to 100%.

Time series features depend on species life-span

We found a significant ($p<0.001$) negative relationship between the species life-span and the long-term trend coefficients, whereas a significant ($p<0.001$) positive relationship was found with the density-dependent coefficients (ESM, Table S2). Thus, time series of species with a long life-span tended to display higher density dependence and lower long-term trend than time series of species with a short life-span.

INFLUENCE OF TSTs

Figure 2 gives a visual example of the effect of each TST on two observed time series. For the four types of time series (raw data and TSTs), this figure also provides estimates of the level of synchrony between the two time series as well as an estimation of their coefficients of trend and temporal autocorrelation (R code used to transform the time series and to estimate these parameters is provided in the ESM).

The ability to remove trend and temporal autocorrelation

Among the 3119 time series, we found that 605 (19%) showed a significant long-term trend, whereas 250 (8%) displayed significant temporal autocorrelation. Once the long-term trend had been eliminated, 12 (0.3%) time series still displayed a significant long-term trend, while 120 (3%) showed significant temporal autocorrelation. When accounting for intrinsic population dynamic, 18 (0.5%) out of the 250 time series still showed significant temporal autocorrelation, whereas 155 (5%) displayed a significant long-term trend. When both components were removed simultaneously, 30 (1%) time series presented significant temporal autocorrelation, whereas one time series (<0.1%) still displayed a significant long-term trend.

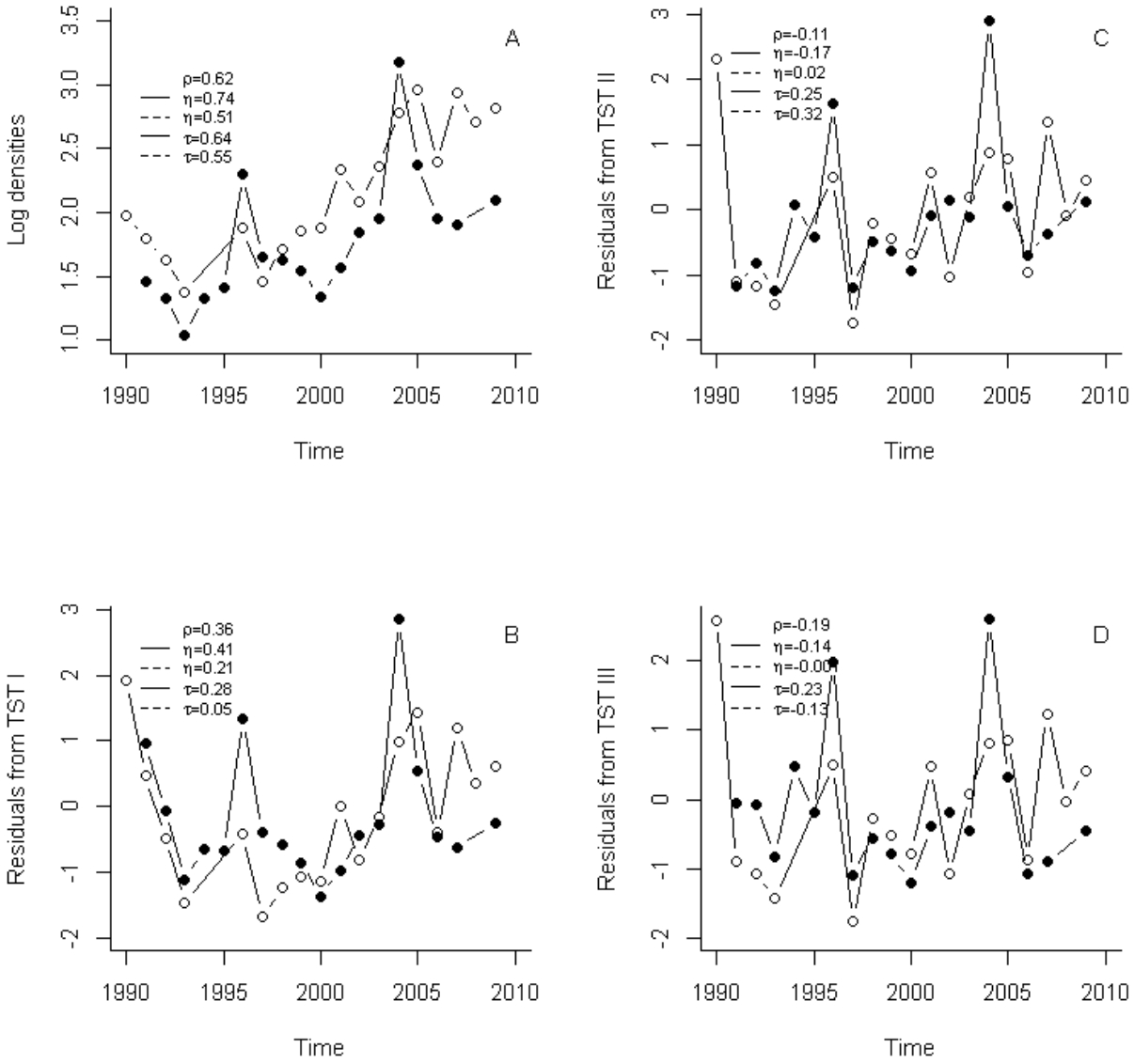

Figure 2. Two observed time series with their estimated trend (τ1 and τ2), their estimated lag-1 temporal autocorrelation (η1 and η2), and the degree of synchrony between them (ρ). Top left: raw data (the densities were log transformed to reduce the variance in both time series to facilitate graphical representation; the coefficients associated with each time series were calculated using the raw densities); Bottom left: Residual from TST I; Top right: Residual from TST II; Bottom right: Residual from TST III. For the definition of TSTs, see the text.

Effects of TSTs on the time series

The correlations calculated between the raw time series and the modified ones were on average greater when using the time series obtained from TST I (mean: 0.84; sd: 0.16), and smaller when using the time series obtained from TST III (mean: 0.71; sd: 0.18) (Figure 3). We found intermediate levels of similarity between raw data and time series obtained with TST II (mean: 0.81; sd: 0.13). Wilcoxon-paired tests revealed significant ($p<0.001$) differences between these correlations. Thus, TST I had less influence on the time series than either TST II or III.

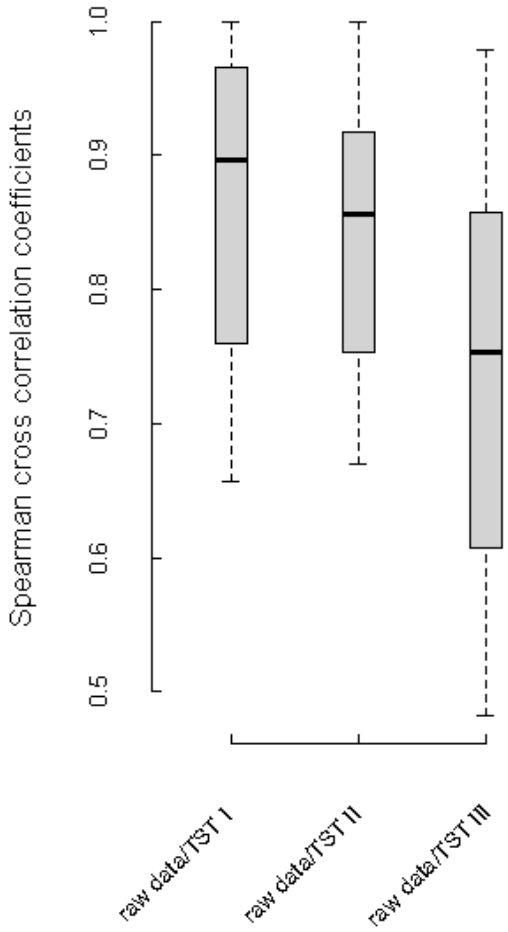

Figure 3. Correlations between the raw time series and the time series obtained with each of the TSTs. For the definition of TSTs, see the text.

With regard to the correlations calculated between the raw time series and the ones obtained with TST I, the mixed-effects model revealed a negative influence of the strength of the long-term trend ($p<0.001$), whereas positive influences were found for the strength of the density dependence and the length of the time series ($p<0.001$ and $p=0.04$, respectively; Table S2). Thus, time series that were short and that presented low density dependence, but a high long-term trend were modified by TST I to a greater extent than those with the opposite features. For the correlations calculated between the raw time series and the time series obtained from TST II, we found that the strength of density dependence had a positive influence ($p<0.001$), whereas the length of the time series had a negative influence ($p<0.001$), and the strength of the long-term trend had no influence (Table S2). Thus, TST II had more influence on long time series displaying weak density dependence. Finally, for the correlations calculated between the raw time series and the time series obtained from TST III, we found that the strength of the long-term trend had a negative influence ($p<0.001$), whereas both the strength of density dependence and the length of the time series had a positive influence ($p<0.001$ and $p=0.005$, respectively). Thus the influence of TST III on the time series was the same as that of TST I.

Effects of TSTs on population synchrony

Differences between the CCCs calculated using the raw time series and those calculated using the modified ones were on average higher for TST III (mean: 0.26; sd: 0.21), and lower for TST I (mean: 0.18; sd: 0.17) (Figure 4). We found intermediate differences between the CCCs calculated with the raw time series and those calculated with TST II (mean: 0.22; sd: 0.18). Wilcoxon-paired tests revealed that these differences were significantly influenced by TSTs ($p<0.001$). Thus, relative to the raw data, TST I had less influence on the CCCs than TSTs II or III.

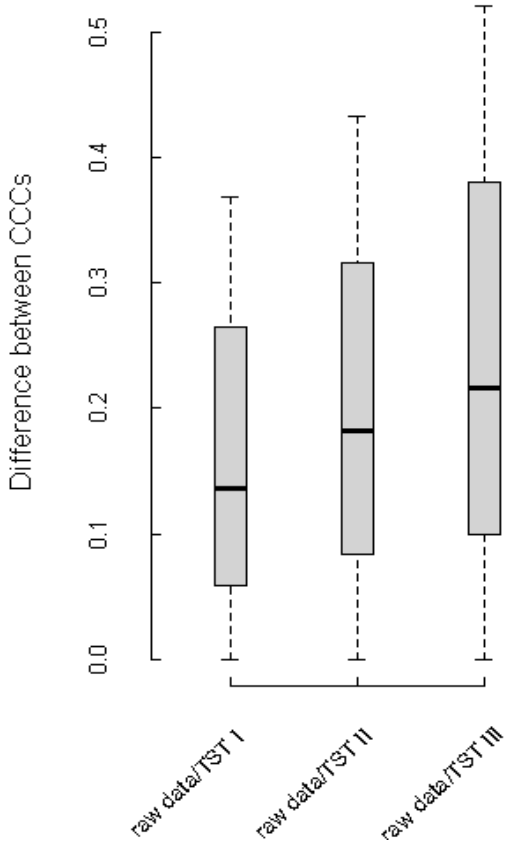

Figure 4. Differences between the CCCs calculated using the raw data and those calculated using the TSTs. For the definition of TSTs, see the text.

Mixed-effect models relating the differences in CCCs to the features of the time series converged for 17 out of the 34 species when the difference in CCCs obtained using raw data and those obtained using TST I were considered (ESM, Table S3). Among these, nine displayed differences in CCCs that were significantly ($p<0.05$) positively related to the long-term trend, whereas seven and 12 species displayed differences in CCCs that were significantly ($p<0.05$) negatively related to the density dependence and the length of the time series. Thus, the difference between the CCCs calculated using the raw data and those calculated using TST I was greater when neither time series displayed significant density dependence, both time series displayed a significant long-term trend, and the length shared by both time series was short. The same general pattern was found for the differences calculated

between the CCCs estimated from the raw data and those estimated from TSTs II and III (Table S3).

Effects of TSTs on species synchrony, spatial variation of synchrony and the determinants of population synchrony

Results describing (1) how the number of species displaying significant levels of synchrony (overall and inter-catchment species synchrony), (2) how the level of population synchrony vary spatially (scale of synchrony and synchrony at short distance) and (3) how the relationship between population synchrony and its determinants (temperature synchrony and the Euclidean distance between populations) changed depending on TSTs are presented in the ESM. For the raw data, we found that more than half (61%) of the species displayed significant levels of synchrony even though they were weak (Table S4). Most of the species were synchronous over large distances (>300 km, Table S5), which coincided with the scale of synchrony measured for temperature (i.e. >450 km, Figure S2). When considering only the populations that were located in different catchments (between which dispersion was impossible), we still found that 47% of the species displayed significant synchrony levels. For 24% of the species, the level of population synchrony was significantly related to the level of temperature synchrony (Table S6). Finally, for 32% of the species, we found a significant ($p<0.05$) negative relationship between the level of population synchrony and the Euclidean distance separating them (Table S6). Whatever the measure considered, the results were globally biased downward by TSTs. However, the influence of TSTs was highly variable depending on the species considered (see tables S4, S5 and S6).

On average, the transformed time series tended to display less overall species synchrony than the raw data, with the most striking difference being observed for TST III (Fig. 5A). We found significant differences between the overall species synchrony calculated from the raw data and that calculated using TSTs I ($p=0.01$) and III ($p=0.002$), but not with that calculated using TST II ($p=0.09$). The same was found when measuring species synchrony between catchments (Fig. 5B). For the measures of the scale of synchrony and the synchrony at short distances, we found no statistical differences between the results obtained with raw data and those obtained with TSTs ($p>0.05$; Fig. 6A and 6B).

For the relationship between population synchrony and the Euclidean distance between populations, we found no significant differences between the results obtained with raw data and those obtained with TSTs ($p>0.05$). Likewise, we found no influence of TSTs on the relationship between population synchrony and temperature synchrony ($p>0.05$).

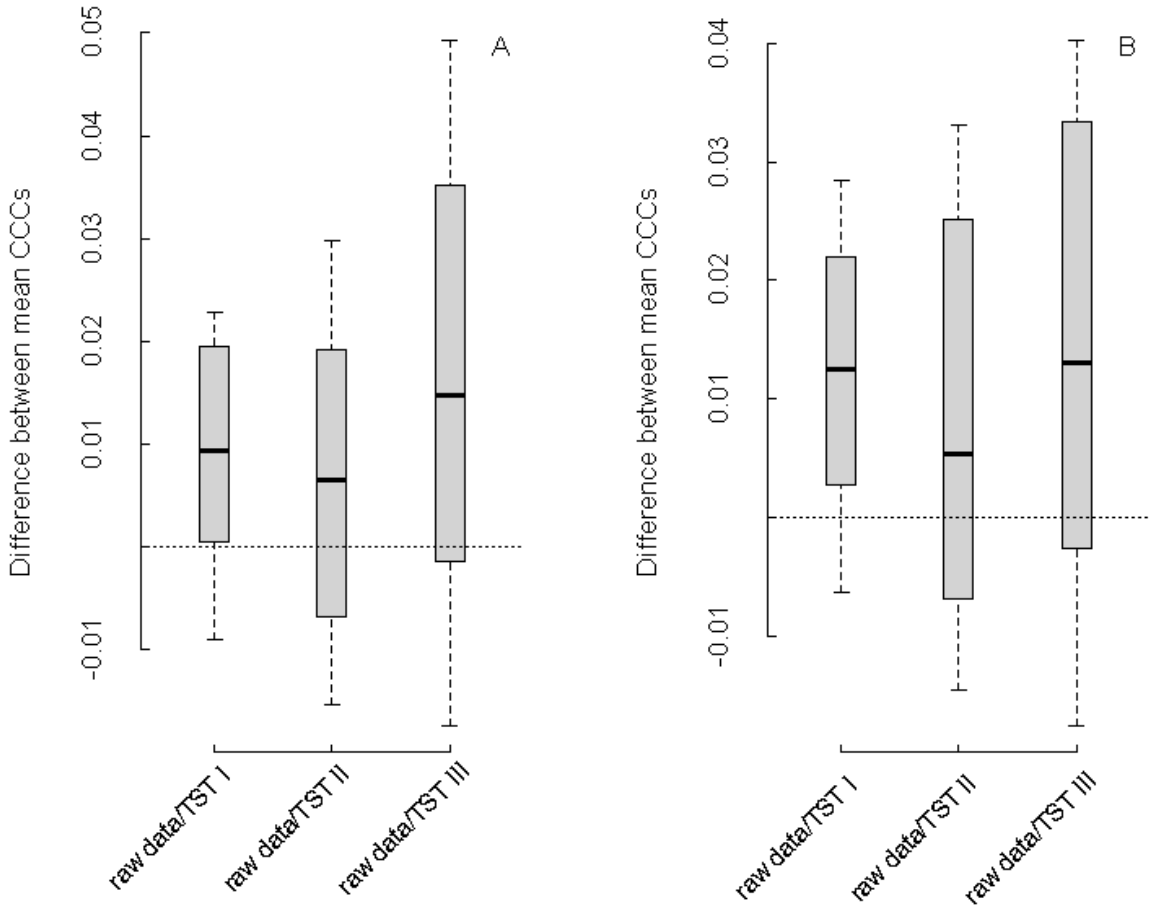

Figure 5. Difference between the mean CCCs (i.e. species synchrony) calculated for each species using the raw data and those calculated with TSTs. A all the populations, B only the populations located in different catchments. The horizontal dotted line indicates the absence of any difference between the results obtained using the raw data and those obtained with the TSTs. For the definition of TSTs, see the text.

Discussion

Our goals in this study were (1) to determine whether a Moran effect had any influence on fish population dynamics at the French scale and (2) to quantify the influence of three of the most commonly-used TSTs on synchrony measurements as well as on our ability to identify the determinants of population synchrony. To do this, we used time series of abundance data for 34 fish species, and computed several statistics commonly used in synchrony studies. We then compared the results obtained using the raw data to those obtained using the TSTs. We also tested whether the influence of the TSTs depended on the features of the time series, and whether they themselves depended on the species life-span.

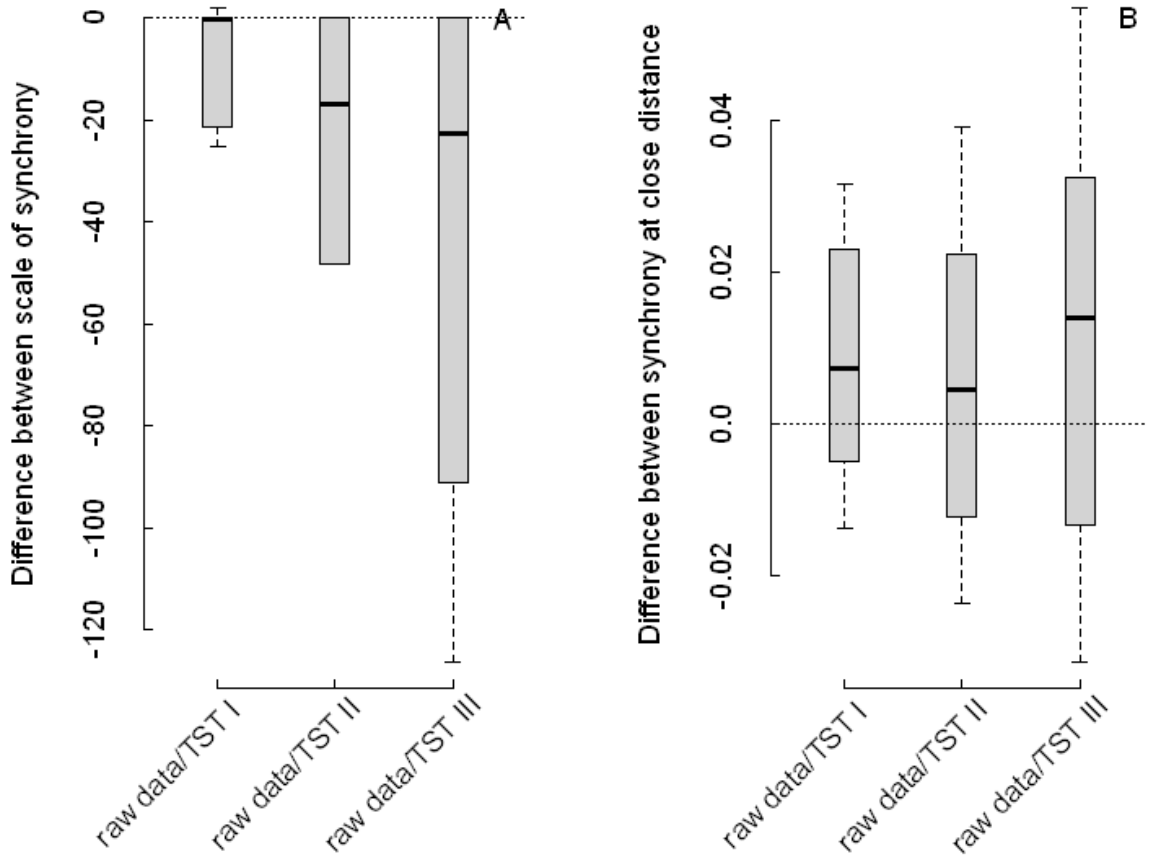

Figure 6. Difference between A the scale of synchrony estimated using the raw data and the scales estimated using TSTs, and B the synchrony at short distances estimated using raw data and the synchronies estimated using the TSTs. For the definition of TSTs, see the text.

EVIDENCE FOR A MORAN EFFECT

Using the raw data, we found that population synchrony, though generally significant, was weak for all 34 fish species found in French Rivers. Such weak pattern of population synchrony has already been shown in birds (Paradis et al. 2000), fish (Grenouillet et al. 2001) and amphibians (Trenham et al. 2003), and can be explained by several factors. For instance, most populations of the same species did not have the same dynamic, and such spatial variations in population dynamics (which violate Moran's assumption of identical density-dependent dynamics) can lead to very low levels of synchrony between populations (Hugueny 2006; Liebhold et al. 2006). Chaotic (Kendall et al. 2000) or non-linear (Benton et al. 2001) population dynamics can also reduce population synchrony, and we cannot exclude the possibility that some of the populations studied here may have had such dynamics. Moreover, Grenouillet et al. (2001) have shown that for age-structured species the different age classes can be governed by different processes (density-dependent *vs* density-independent), which reduces synchrony at the population level. Finally, the presence of measurement errors in population time series has been shown to biased downward synchrony levels (Santin-Janin et al. 2014). Thus, differences between the dynamics of populations or age classes as well as

measurement errors could explain the weak overall synchrony pattern observed for the 34 fish species.

For most of the species we found a negative relationship between population synchrony and the Euclidean distance between sites, which is consistent with the findings of previous studies. Such a relationship can be explained by dispersal (Ranta et al. 1995), as well as by the Moran effect (Koenig 2002). However, given that dispersal between catchments is limited for fish, and that some species were synchronous across catchments, fish population synchrony could partly be attributed to the Moran effect. Moreover, temperatures were synchronous over scales comparable to the scale of synchrony found for most of the species, thus reinforcing the Moran effect hypothesis. Further support for climate-driven population synchrony was provided by the significant relationship between population synchrony and temperature synchrony. Nevertheless, as this relationship did not hold for all the species displaying significant synchrony, other climatic factors are likely to be involved in population synchrony. For instance, rainfall could influence the frequency and intensity of river discharge, a factor that has already been suggested to influence both fish population dynamics (Lobon-Cervia 2008) and synchrony (Cattanéo et al. 2003).

INFLUENCES OF TSTS

We found that the method used to remove trend and/or temporal autocorrelation were not totally efficient as some time series still presented significant signals once TSTs had been applied to the raw time series. This could be explained by the method used to remove the component of interest. For instance, several competing methods exist to remove the long-term trend (Buonaccorsi et al. 2001) and we cannot exclude the possibility that another method would have done a better job. However, considering the number of time series analyzed in this study (i.e. 3119), a unique method is not expected to be efficient in all cases; as would also be the case for other studies involving such a high number of time series. We also found that removing one component in the time series without affecting the other is not straightforward . For instance, if removing temporal autocorrelation also remove some part of the long-term trend then, one could wrongly conclude that populations are not influenced by a large-scale climatic factors which could have dramatic consequences in a conservation perspective as population synchrony is to some extent, related to species extinction risk (Hanski and Woiwod 1993).

We expected that time series with a low long-term trend would be weakly affected by TST I, as would time series that displayed low density dependence and TST II. However, although we found the expected pattern for the long-term trend and TST I, we found that time series that displayed low density dependence were affected by TSTs to a greater extent than time series displaying high density dependence. However, estimating density dependence in population time series has always proved to be challenging (Dennis et al. 2006), notably because it depends on time series features (Clark and Bjørnstad 2004). For instance, even though the sampling procedure is considered efficient (as it is the case in this study),

population time series usually present census errors (Freckleton et al. 2006), which strongly influence the strength and evidence for density dependence (Knape and de Valpine 2012). To take these errors into account, state-space models have been used, and studies have shown that they usually provide less biased estimates of density dependence than models that do not account for census errors (e.g. Freckleton et al. 2006). However, state-space models could present identifiability issues when process and error variance are both unknown which could lead to large variances in parameter estimates (Knape 2008). This is particularly true when the time series are short, which is our case. Other features, such as the number of missing values in the time series or the variance around the mean of population censuses, could bias the estimation of density dependence (Brook and Bradshaw 2006), and could explain why time series with low density dependence were modified to a greater extent than others.

We have shown that the species life-span had an influence on the features of the time series; species with a long life-span displaying higher density dependence and lower long-term trend than time series of species with a short life-span. Thus, depending on the ecology of the species, populations could display different features (e.g. seasonal, chaotic) that could modify the influence of TSTs on the time series and so on the results. Further studies are needed to determine whether other traits, already known to affect population dynamics (e.g. life-history traits), modify the influence of TSTs.

On average, we found that detrending, prewhitening, or a combination of both, decreased the measures of synchrony, which was consistent with the findings of previous studies. For instance, it has been shown that overall synchrony tends to be higher when measured using raw data than when measured using detrended data (Batchelder et al. 2012). This decrease after detrending has classically been interpreted as an evidence for a Moran effect, and it can be explained if a long-term trend is an important and shared source of variation in the data (Pyper et al. 1999). Similarly, temporal autocorrelation in time series is known to inflate cross-correlation coefficients (Pyper & Peterman 1998; Pyper et al. 1999). Consequently, eliminating temporal autocorrelation can be expected to reduce the population synchrony and, therefore, the overall species synchrony. However, Cheal et al. (2007), using detrended time series of coral reef fish populations, found that eliminating temporal autocorrelation did not change their measures of synchrony. Likewise, even though we observed an overall decrease in fish population synchrony, no significant influence of prewhitening was observed. Nevertheless, we found that, depending on the species considered, TSTs can reverse conclusions on synchrony significance. For instance, once temporal autocorrelation had been eliminated, overall synchrony was no longer significant for *Barbus barbus,* while it had become significant for *Gymnocephalus cernua* (Tables S3).

In the same way, although we did not find any significant influence of TSTs on the estimation of the relationship between population synchrony and its determinants (i.e. distance between population and temperature synchrony) on average, we did find that using TSTs could lead to opposite conclusions depending on the species considered (Table S6). For instance, once temporal autocorrelation has been removed, we found that the main driver of population synchrony for *Gasterosteus gymnurus* was temperature synchrony, whereas the

distance between populations was the main driver when the raw data were used. Likewise, on a study involving 60 bird species, Paradis et al. (2000) found that detrending did not influence the relationship between synchrony and distance for 34 of them, whereas the relationship was strengthened for 12, and weakened for 14. Thus, depending on the species considered and the TSTs applied to the time series, the conclusions could be very different which could have major implications for defining specific management plans.

PROSPECTS FOR THE FUTURE AND GUIDELINES FOR FURTHER RESEARCH

For several species, we found some evidence of an effect of correlated environmental noise (i.e. a Moran effect) on population dynamics as (1) populations were synchronous on a large spatial scale and across catchments, (2) population synchrony was related to temperature synchrony, and (3) eliminating the long-term trend in time series reduced the overall synchrony of the species. However, although temperature appeared to be a plausible factor driving population synchrony for some species, other factors are also likely to be involved (e.g. the frequency and intensity of river discharges). Moreover, we only considered the influence of temperature during the warmest month of the year, which could have biased our conclusions. Indeed, other climatic descriptors (e.g. the temperatures during the coldest month) could have affected the observed relationship between population synchrony and temperature synchrony. Further studies are clearly needed to add to our knowledge about the factors that drive fish population synchrony in France.

In this study, we did not consider the log transformation (another widely-used transformation), because we calculated the population synchrony using Spearman cross-correlation coefficients, which is invariant to monotonic transformation (Buonaccorsi et al. 2001). However, several authors (e.g. Koenig 1998, Bellamy et al. 2003, Bunnell et al. 2010) have used Pearson cross-correlation coefficients for this purpose, and the influence of the log transformation in this context requires further investigation. More specifically, how the log transformation affects the strength of the long-term trend or the density dependence as well as their evidence, and how it modifies the estimation of population synchrony require further investigations.

In some cases, TSTs can be very helpful for quantifying the influence of various processes on population dynamics. For instance, eliminating a long-term trend that is due to common climatic influences makes sense if all the populations are either increasing or decreasing, because it makes it possible to focus on local rather than global processes (Buonaccorsi et al. 2001). However, it is questionable whether a trend that is not due to common global influences, but to local processes, or because its presence could give "spurious" correlations (inflation of CCCs) should be eliminated (Pyper and Peterman 1998). In the former case, removing the trend could make it more likely that we could detect an apparent correlation when in fact there was none, while in the latter it could eliminate important information that would reduce our ability to detect a real causal relationship (Brown et al. 2011). Another problem with TSTs is that the different components in the time

series are not independent of each other. For example, removing the temporal autocorrelation in the time series could affect the detection (as shown in this study) and the estimation of the magnitude (Hamed and Rao 1998) of the long-term trend and *vice versa*. Therefore, if two series do have a causal relationship that manifests itself, for example, as a trend in each series, this could be masked by the prewhitening procedure. Thus, a serious problem with using TSTs is that it is difficult to know exactly what has been eliminated, and so what has been measured. This problem is further complicated by the fact that the influence of TSTs depends on the features of the time series, which themselves depend on the ecology of the species. Thus, the use of TSTs should be subject to great care and should depend on the features of the time series. As a first step, we therefore recommend that the features of the time series should be estimated, and TSTs used in the light of these estimations. For this purpose, we suggest using population dynamic models (e.g. Ricker or Gompertz population models, depending on the data), as they make it possible to estimate both the density dependence and the long-term trend. Then, if one wants to focus on local processes, we recommend removing the long-term trend only if all the time series are either increasing or decreasing (Buonaccorsi et al. 2001). When studying global processes, the data should not be detrended. If the time series do not provide any evidence of density dependence (i.e. of lag-one temporal autocorrelation), we recommend to not remove temporal autocorrelation, as this transformation strongly modifies the time series and therefore any subsequent analyses (e.g. estimation of population synchrony). If the time series display density dependence, we propose using population dynamic models to remove temporal autocorrelation, because they can be used to account for more complex population dynamics than simple linear autoregressive models (e.g. by integrating non-linear density dependence). One interesting possibility for this purpose would be to use state-space models to account for observation errors in population censuses.

When using TSTs, we advocate always checking (i) whether the component of interest has really been eliminated, and (ii) whether the other component has not been affected. Finally, because TSTs can lead to differing (and sometimes even opposite) results depending on the species considered, we recommend using different TSTs, and interpreting the results in the light of the features of the time series, taking all the transformations into account.

We believe that analyzing time series in this way could improve our understanding of the processes that drive population synchrony by quantifying the relative importance of long-term trends and temporal autocorrelation.

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Electronic Supplementary Material

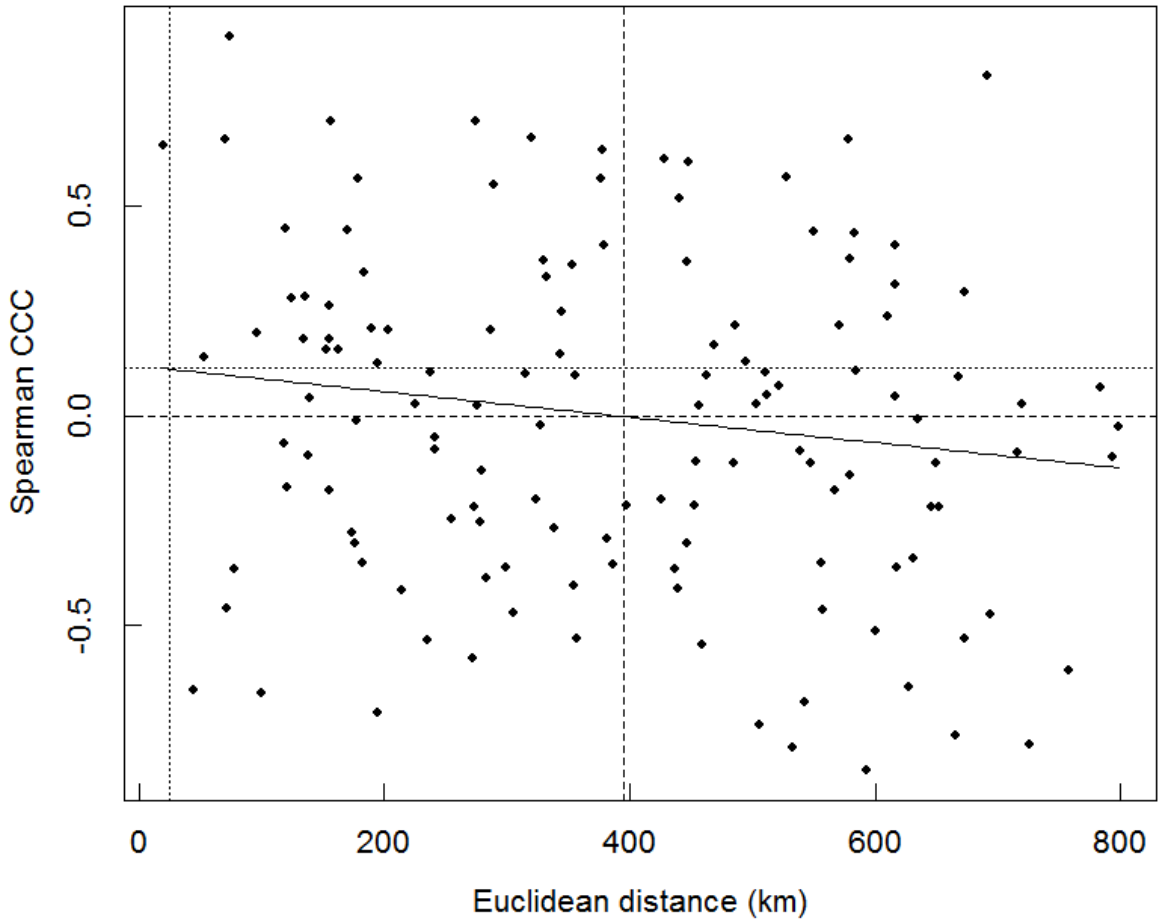

Figure S1. Example of an output from a generalized additive model modeling the relationship between population synchrony and the Euclidean distance (km) between populations for the species *Scardinius erythrophthalmus*. The intersection between the two dotted lines represents a measure of synchrony at close distance (i.e. the "y-intercept") whereas the intersection between the two dashed lines represents a measure of the spatial scale of population synchrony (i.e. the "x-intercept").

1. Model equation and parameter description

1.1. Effects of TSTs on the time series

$$Y_{ij} = \alpha + A_i + (\mu + M_i) * l_{ij} + (\beta + B_i) * d_{ij} + (\gamma + G_i) * t_{ij} + \varepsilon_{ij} \quad \text{(Eq. S1)}$$

Y_{ij} is one of the three dependent variables (i.e. the Spearman cross correlation coefficients calculated between the raw time series of species i at site j, and the time series altered by each TST for the same species and site); α is the intercept of the model and A_i its random coefficient; l_{ij} is the length of the time series for species i on site j, and μ and M_i are its associated fixed and random coefficients, respectively; d_{ij} is the absolute value of the estimated coefficient of density dependence of species i at site j, and β and B_i were its associated fixed and random effects, respectively; t_{ij} is the absolute value of the estimated coefficient of trend of species i at site j, and γ and G_i are its associated fixed and random effects, respectively; ε_{ij} is the random error term associated with species i at site j. A_i, M_i, B_i, G_i and ε_{ij} are all random normal variables with mean 0 and standard deviations σ_A, σ_M, σ_B, σ_G, and σ_ε respectively.

1.2. Effects of TSTs on population synchrony

$$Y_{ij} = \alpha + A_i + A_j + \mu * l_{ij} + (\beta + B_i + B_j) * d_{ij} + (\gamma + G_i + G_j) * t_{ij} + \varepsilon_{ij} \quad \text{(Eq. S2)}$$

Y_{ij} is one of the three dependent variables (i.e. the differences between the CCCs calculated using the raw data and those calculated using each of the TSTs); α is the intercept of the model, and A_i and A_j are the random intercepts associated with time series i and j, respectively; l_{ij} is the common length between the time series i and j; d_{ij} is the ordinal variable determining whether density dependence was detected in time series i and j, and β, B_i and B_j are its associated fixed and random coefficients on time series i and j, respectively; t_{ij} is the ordinal variable determining whether a long-term trend was detected in time series i and j, and γ, G_i, and G_j are the associated fixed and random coefficients for time series i and j, respectively; ε_{ij} is the random error term associated with time series i and j. A_i, A_j, B_i, B_j, G_i, G_j, and ε_{ij} are all random normal variables with mean 0 and standard deviations σ_{Ai}, σ_{Aj}, σ_{Bi}, σ_{Bj}, σ_{Gi}, σ_{Gj}, and $\sigma\varepsilon$, respectively.

Table S1. Percentage of time series with significant long-term trend (estimated with TSTs I and III) and density dependence (estimated with TSTs II and III). N is the number of time series. Positive (Negative) trend is the percentage of time series with significant positive (negative) long-term trends. Negative DD is the percentage of time series with significant negative density dependence. For the definition of TSTs, see the text.

		TST I		TST II	TST III		
Species name	N	Positive trend	Negative trend	Negative DD	Positive trend	Negative trend	Negative DD
Abramis brama	26	7.7	15.4	88.1	7.7	11.5	61.5
Alburnoides bipunctatus	52	42.3	3.8	73.5	28.8	3.8	88.5
Alburnus alburnus	110	16.4	12.7	83.9	11.8	13.6	91.8
Ameiurus melas	17	11.8	5.9	78.2	5.9	23.5	70.6
Anguilla anguilla	208	9.1	26.4	90.9	5.8	19.2	80.8
Barbatula barbatula	245	28.6	11.8	87.5	10.6	9.8	85.7
Barbus barbus	131	20.6	9.2	46.1	17.6	8.4	89.3
Blicca bjoerkna	24	16.7	8.3	62.2	8.3	12.5	95.8
Carassius carassius	13	7.7	7.7	46.1	0	7.7	61.5
Chondrostoma nasus	30	33.3	6.7	36.3	26.7	13.3	86.7
Cottus gobio	25	44	12	56.0	28	12	84
Cottus perifretum	169	29.6	12.4	82.8	12.4	12.4	84.6
Cyprinus carpio	11	0	0	79.5	0	9.1	36.4
Esox lucius	61	14.8	6.6	50.0	1.6	4.9	70.5
Gasterosteus gymnurus	16	25	25	68.4	18.8	18.8	56.3
Gobio gobio	219	23.3	11.4	83.2	13.2	15.1	86.3
Gobio lozanoi	9	22.2	0	77.7	0	0	88.9
Gobio occitaniae	75	17.3	18.7	73.3	9.3	12	82.7
Gymnocephalus cernua	21	19	4.8	81.2	9.5	4.8	90.5
Lampetra planeri	64	31.3	6.3	76.1	21.9	4.7	75
Lepomis gibbosus	81	32.1	4.9	76.6	21	11.1	77.8
Leuciscus burdigalensis	39	12.8	28.2	83.2	5.1	30.8	89.7
Leuciscus leuciscus	59	18.6	8.5	65.6	18.6	11.9	94.9
Perca fluviatilis	154	12.3	7.8	82.3	6.5	13	78.6
Phoxinus phoxinus	249	25.3	8.8	75.9	16.5	8	90.8
Pungitius laevis	19	21.1	10.5	69.1	15.8	15.8	73.7
Rhodeus amarus	33	39.4	6.1	67.8	15.2	6.1	93.9

Rutilis rutilis	250	14.4	16.4	94.7	10.8	14.8	84.4
Salmo salar	19	26.3	15.8	88.4	0	21.1	100
Salmo trutta	284	12.3	16.5	50.0	6	16.2	88.4
Scardinius erythrophtalmus	28	17.9	17.9	83.8	0	17.9	82.1
Squalius cephalus	313	18.5	13.1	87.1	12.1	11.8	89.1
Telestes souffia	23	43.5	8.7	89.8	26.1	8.7	82.6
Tinca tinca	42	9.5	14.3	76.9	4.8	16.7	61.9

Table S2. Coefficients of the linear mixed effects model performed on the relationship between the characteristics of the time series (independent variables) and the correlations calculated between the raw time series and the modified ones (dependent variables). Is also shown the results from the linear model performed between the characteristics of the time series and the species life-span. Significant results are in bold.

Dependent variables	Trend	DD	Length
raw data/TST I	**-11,8**	**25,2**	**0,34**
raw data/TST II	-0,21	**2E-3**	**0,02**
raw data/TST III	**-0,6**	**5E-4**	**0,01**
Life-span	**-0,02**	**0,13**	-

Table S3. Results from mixed-effects model. Dependent variables were the differences between the CCCs estimated with raw data and those estimated with TSTs. Each model included three independent variables: (i) the common length between the time series used to calculate the CCC (CL), and (ii) two ordinal variables determining whether density dependence (DD) and long-term trend (trend) were significantly detected in the two time series. "Convergence" indicates whether the model successfully converged (TRUE) or not (FALSE) to the parameters values. In bold are the significant results. For the definition of TSTs, see the text.

	Raw data/TST I				Raw data/TST II				Raw data/TST III			
Species name	Trend	DD	CL	converge	Trend	DD	CL	converge	Trend	DD	CL	Converge
Abramis brama	0.005	-0.007	**-0.012**	TRUE	0.0033	0.0043	-0.0089	FALSE	0.0047	-0.0059	**-0.0159**	FALSE
Alburnoides bipunctatus	**0.012**	-0.003	**0.01**	FALSE	-0.0075	-0.0046	0.0033	FALSE	0.0103	-0.0022	0.0001	TRUE
Alburnus alburnus	**0.011**	-0.004	**-0.005**	FALSE	0.0005	-0.0003	-0.0021	TRUE	0.0115	-0.0029	**-0.0064**	FALSE
Ameiurus melas	0.006	-0.012	-0.01	FALSE	-0.0207	0.0034	**-0.0272**	FALSE	0.0076	-0.021	**-0.0437**	FALSE
Anguilla anguilla	**0.015**	-0.002	**-0.003**	TRUE	**0.004**	0.0019	**-0.0024**	FALSE	**0.0095**	0.0013	**-0.0056**	FALSE
Barbatula barbatula	**0.02**	**-0.007**	**-0.006**	TRUE	**0.0041**	**-0.0071**	**-0.0055**	TRUE	**0.014**	**-0.0056**	**-0.0068**	TRUE
Barbus barbus	**0.018**	-0.003	**-0.01**	TRUE	0.0025	**-0.0044**	**-0.006**	TRUE	**0.015**	-0.0041	**-0.0092**	TRUE
Blicca bjoerkna	0.006	**-0.024**	**-0.017**	TRUE	0.009	0.002	**-0.0212**	FALSE	0.0192	0.005	**-0.0271**	FALSE
Carassius carassius	0.01	-0.013	-0.011	TRUE	0.0025	0.0046	-0.0072	FALSE	0.0024	0.0087	-0.0319	FALSE
Chondrostoma nasus	0.012	0.009	-0.001	TRUE	0.0074	0.0042	-0.0079	FALSE	**0.0251**	0.0089	-0.0001	TRUE
Cottus gobio	0.02	0.003	-0.011	FALSE	0.0129	-0.0012	-0.0089	FALSE	0.0166	0.005	-0.0149	FALSE
Cottus perifretum	**0.015**	**-0.012**	-0.001	TRUE	**0.0047**	**-0.0153**	**-0.0041**	TRUE	**0.0117**	**-0.0129**	-0.0028	TRUE
Cyprinus carpio	-0.003	-0.002	0.006	FALSE	0.0027	-0.0144	-0.0042	FALSE	-0.0005	-0.0211	-0.0294	FALSE
Esox lucius	0.002	**-0.009**	**-0.006**	TRUE	-0.0007	-0.0012	**-0.0076**	FALSE	0.0029	-0.0053	**-0.011**	FALSE
Gasterosteus gymnurus	0.022	-0.025	**-0.029**	FALSE	0.0194	-0.0015	-0.0049	FALSE	0.0376	-0.0076	-0.0006	FALSE
Gobio gobio	**0.017**	**-0.004**	**-0.008**	TRUE	0.0001	-0.0025	**-0.0092**	TRUE	**0.0142**	-0.0031	**-0.0106**	TRUE
Gobio lozanoi	NA	NA	NA	FALSE	NA	NA	NA	FALSE	NA	NA	NA	FALSE
Gobio occitaniae	**0.021**	**-0.01**	0.001	TRUE	0.0024	**-0.0086**	-0.0001	FALSE	**0.0086**	**-0.0096**	-0.0026	TRUE
Gymnocephalus cernua	0.004	-0.001	-0.008	FALSE	-0.0017	-0.0077	-0.0111	TRUE	0.0017	-0.0072	-0.0137	FALSE
Lampetra planeri	**0.012**	0.001	0	FALSE	**0.0062**	0.0033	**-0.0096**	TRUE	**0.0141**	0.0039	**-0.0087**	FALSE
Lepomis gibbosus	**0.021**	-0.003	**-0.009**	FALSE	0.0074	-0.0058	**-0.0088**	TRUE	**0.018**	-0.0053	**-0.0138**	FALSE
Leuciscus burdigalensis	**0.017**	0.003	**0.007**	FALSE	-0.0005	0.0008	-0.0075	FALSE	0.0064	0.0022	0.0014	TRUE
Leuciscus leuciscus	0.008	-0.003	-0.006	TRUE	0.0039	-0.0014	**-0.01**	FALSE	**0.0093**	-0.003	**-0.0119**	TRUE
Perca fluviatilis	0.005	-0.001	**-0.006**	FALSE	0.0009	0.0005	**-0.0078**	TRUE	**0.013**	0.0021	**-0.0098**	TRUE
Phoxinus phoxinus	**0.015**	**-0.01**	**-0.005**	TRUE	0.0005	**-0.0073**	**-0.008**	FALSE	**0.0105**	**-0.0076**	**-0.0084**	TRUE

Pungitius laevis	0.009	-0.003	-0.006	FALSE	-0.0058	0.0113	**-0.0169**	FALSE	**0.0189**	-0.0007	-0.0111	FALSE
Rhodeus amarus	**0.023**	-0.016	0.002	FALSE	0.0048	-0.0029	-0.0115	TRUE	0.0124	-0.0048	-0.0095	FALSE
Rutilis rutilis	**0.016**	-0.002	**-0.002**	TRUE	0.0014	-0.0006	**-0.0074**	FALSE	**0.013**	-0.0009	**-0.0085**	FALSE
Salmo salar	NA	NA	NA	FALSE	NA	NA	NA	FALSE	NA	NA	NA	FALSE

Table S4. Species synchrony (i.e. mean of the CCCs computed over all pairs of time series) and species inter-catchments synchrony (i.e. mean of CCCs computed over pairs of time series located in different catchments) estimated for the 34 fish species. Npairs is the number of cross-correlation coefficients. Significant results are in bold face. For the definition of TSTs, see the text.

		Overall species synchrony				Overall species inter-catchments synchrony			
Species name	Npairs	Raw data	TST I	TST II	TST III	Raw data	TST I	TST II	TST III
Abramis brama	233	-0.017	-0.008	0.012	0.013	0,000	0,006	0,034	0,029
Alburnoides bipunctatus	745	**0.048**	0.008	0.005	-0.013	**0,036**	-0,016	-0,009	**-0,035**
Alburnus alburnus	2830	0.003	0.002	0.01	**0.02**	-0,005	-0,005	0,009	**0,019**
Ameiurus melas	64	0.023	0.023	-0.053	-0.022	0,081	0,052	-0,002	0,050
Anguilla anguilla	12680	**0.017**	-0.002	**0.007**	0.001	**0,010**	-0,004	0,004	-0,003
Barbatula barbatula	21312	**0.054**	**0.035**	**0.027**	**0.025**	**0,052**	**0,032**	**0,024**	**0,023**
Barbus barbus	5162	**0.025**	**0.015**	0.006	0.003	**0,019**	**0,012**	0,002	-0,002
Blicca bjoerkna	94	0.001	0.019	0.029	0.026	0,000	0,006	0,027	0,018
Carassius carassius	55	-0.039	-0.047	0.01	0.017	-0,038	-0,044	0,004	-0,034
Chondrostoma nasus	373	0.027	-0.024	0.011	-0.001	**0,032**	-0,032	0,007	-0,008
Cottus gobio	160	**0.146**	0.041	**0.07**	0.021	**0,186**	**0,060**	**0,083**	0,028
Cottus perifretum	10724	**0.029**	**0.018**	**0.027**	**0.023**	**0,023**	**0,013**	**0,023**	**0,016**
Cyprinus carpio	55	0.024	-0.009	0.045	**0.064**	0,007	-0,007	0,046	**0,082**
Esox lucius	1037	**0.03**	**0.044**	**0.022**	**0.031**	**0,034**	**0,048**	**0,031**	**0,036**
Gasterosteus gymnurus	76	**0.172**	**0.125**	**0.108**	0.008	**0,154**	**0,094**	**0,074**	-0,019
Gobio gobio	14354	**0.045**	**0.032**	**0.031**	**0.027**	**0,045**	**0,030**	**0,028**	**0,026**
Gobio lozanoi	36	-0.025	-0.035	-0.002	-0.045	-	-	-	-
Gobio occitaniae	1926	**0.02**	**0.028**	**0.035**	**0.045**	0,016	**0,031**	**0,027**	**0,028**
Gymnocephalus cernua	138	0.04	0.036	**0.055**	0.032	0,043	0,028	**0,054**	0,044
Lampetra planeri	1857	**0.069**	**0.028**	**0.04**	**0.02**	**0,068**	**0,025**	**0,035**	**0,014**
Lepomis gibbosus	1595	**0.038**	**0.015**	**0.021**	0.003	**0,038**	0,012	**0,024**	0,004
Leuciscus burdigalensis	522	**0.038**	**0.034**	**0.025**	**0.052**	**0,039**	0,026	0,010	**0,042**
Leuciscus leuciscus	922	**0.071**	**0.062**	**0.041**	**0.067**	**0,068**	**0,063**	**0,035**	**0,064**
Perca fluviatilis	5404	**0.014**	**0.009**	**0.009**	0.006	**0,010**	0,007	0,007	0,006
Phoxinus phoxinus	22544	**0.043**	**0.029**	**0.031**	**0.029**	**0,041**	**0,027**	**0,028**	**0,028**
Pungitius laevis	134	0.038	0.028	0.035	-0.012	**0,075**	**0,058**	**0,074**	0,012
Rhodeus amarus	218	0.036	-0.02	0.014	-0.023	**0,047**	-0,014	0,022	-0,007
Rutilis rutilis	16034	0.002	0.002	**0.005**	0.004	-0,001	0,000	0,005	0,003
Salmo salar	110	**0.149**	**0.184**	**0.136**	**0.102**	**0,150**	**0,186**	**0,135**	**0,132**
Salmo trutta	29225	**0.038**	**0.035**	**0.036**	**0.031**	**0,031**	**0,028**	**0,030**	**0,025**

Scardinius erythrophtalmus	134	-0.012	-0.022	0.001	-0.025	-0,020	-0,031	-0,013	-0,040
Squalius cephalus	28084	**0.031**	**0.022**	**0.026**	**0.021**	**0,028**	**0,021**	**0,023**	**0,020**
Telestes souffia	179	**0.089**	**0.089**	**0.09**	**0.058**	**0,111**	**0,089**	**0,111**	0,055
Tinca tinca	490	**0.069**	**0.062**	**0.07**	**0.04**	**0,063**	**0,062**	**0,070**	**0,041**

Table S5. Scale of synchrony and synchrony at short distances estimated for the 34 fish species. Npairs is the number of cross-correlation coefficients; scale of synchrony (kms) is the estimated distance above which the level of synchrony is no longer different from 0 (for some species this value was not relevant as the level of synchrony was negative at short distances); synchrony at short distances is the overall level of synchrony for sites close to each others. For the definition of TSTs, see the text.

		Scale of synchrony (kms)				Synchrony at short distances			
Species name	Npairs	Raw data	TST I	TST II	TST III	Raw data	TST I	TST II	TST III
Abramis brama	233	389	389	-	408	0.013	0.024	-0.015	0.045
Alburnoides bipunctatus	745	200	303	200	303	0.050	0.019	0.011	0.002
Alburnus alburnus	2830	366	366	440	366	0.092	0.085	0.088	0.060
Ameiurus melas	64	-	-	-	-	-0.030	-0.053	-0.042	-0.046
Anguilla anguilla	12680	292	367	411	411	0.034	0.013	0.009	0.011
Barbatula barbatula	21312	276	283	302	306	0.066	0.058	0.057	0.046
Barbus barbus	5162	369	369	291	316	0.058	0.033	0.053	0.044
Blicca bjoerkna	94	282	193	282	340	0.011	0.022	0.065	0.052
Carassius carassius	55	145	126	163	174	0.042	0.054	0.146	0.289
Chondrostoma nasus	373	136	134	155	240	0.066	0.044	0.062	0.011
Cottus gobio	160	-	-	-	-	-0.082	-0.022	-0.020	-0.027
Cottus perifretum	10724	311	317	311	311	0.063	0.056	0.044	0.046
Cyprinus carpio	55	-	-	-	-	-0.016	-0.023	-0.018	-0.057
Esox lucius	1037	312	-	-	312	0.010	-0.015	-0.006	0.012
Gasterosteus gymnurus	76	442	469	384	348	0.042	0.018	0.084	0.054
Gobio gobio	14354	320	338	338	358	0.034	0.028	0.045	0.031
Gobio lozanoi	36	11	30	59	59	0.005	0.084	0.047	0.013
Gobio occitaniae	1926	183	183	183	183	0.036	0.037	0.031	0.060
Gymnocephalus cernua	138	-	386	-	-	-0.029	0.014	-0.017	-0.043
Lampetra planeri	1857	147	113	248	331	0.014	0.005	0.026	0.014
Lepomis gibbosus	1595	227	296	-	344	0.057	0.029	-0.006	0.007
Leuciscus burdigalensis	522	-	289	-	-	-0.027	0.005	-0.020	-0.011
Leuciscus leuciscus	922	215	215	221	215	0.032	0.012	0.043	0.035
Perca fluviatilis	5404	208	242	314	314	0.040	0.020	0.002	0.001
Phoxinus phoxinus	22544	226	243	242	245	0.055	0.043	0.047	0.034
Pungitius laevis	134	126	151	136	252	0.101	0.106	0.062	0.019
Rhodeus amarus	218	283	-	283	162	0.004	-0.015	0.028	0.078
Rutilis rutilis	16034	287	339	366	366	0.038	0.013	0.010	0.005

Salmo salar	110	319	319	57	35	0.000	0.014	0.019	0.013
Salmo trutta	29225	368	369	387	372	0.115	0.120	0.093	0.096
Scardinius erythrophtalmus	134	390	390	390	390	0.113	0.065	0.057	0.060
Squalius cephalus	28084	265	286	284	291	0.057	0.025	0.046	0.024
Telestes souffia	179	-	-	186	158	-0.030	-0.034	0.016	0.057
Tinca tinca	490	485	390	494	390	0.005	0.000	0.004	0.012

Table S6. Influence of the Euclidean distance between populations as well as the temperature synchrony on the level of synchrony between populations for the 34 fish species. Npairs is the number of cross-correlation coefficients. Results represents correlation coefficient computed between two dissimilarity matrices (Mantel tests). Significant correlations are in bold face. For the definition of TSTs, see the text.

		Euclidean distance				Temperature synchrony			
Species name	Npairs	Raw data	TST I	TST II	TST III	Raw data	TST I	TST II	TST III
Abramis brama	233	-0.023	-0.046	-0.077	**-0.114**	0.037	0.107	0.094	0.028
Alburnoides bipunctatus	745	-0.038	**-0.127**	-0.037	**-0.087**	0.054	0.048	0.019	**0.063**
Alburnus alburnus	2830	**-0.071**	-0.026	-0.027	0.002	0.022	0.012	0.015	-0.003
Ameiurus melas	64	0.022	0.060	0.056	0.068	-0.183	-0.101	-0.17	0.081
Anguilla anguilla	12680	-0.015	**-0.019**	-0.013	**-0.021**	0	0.01	0.003	0.001
Barbatula barbatula	21312	**-0.035**	**-0.036**	**-0.048**	**-0.038**	**0.029**	0.014	**0.029**	0.014
Barbus barbus	5162	**-0.096**	**-0.061**	**-0.061**	**-0.058**	**0.043**	**0.069**	**0.042**	**0.062**
Blicca bjoerkna	94	-0.030	-0.045	-0.184	-0.176	0.041	0.074	0.127	0.057
Carassius carassius	55	-0.012	0.047	-0.094	-0.250	-0.197	0.012	0.147	0.17
Chondrostoma nasus	373	-0.003	-0.001	-0.031	-0.025	0.09	0.024	-0.019	**-0.118**
Cottus gobio	160	0.137	0.043	0.046	0.045	0.059	-0.007	-0.06	-0.117
Cottus perifretum	10724	**-0.087**	**-0.085**	**-0.068**	**-0.069**	**0.081**	**0.048**	**0.055**	**0.049**
Cyprinus carpio	55	0.063	0.094	0.065	0.144	-0.105	-0.032	-0.01	-0.115
Esox lucius	1037	-0.019	-0.002	0.009	-0.016	0.006	0.048	-0.007	0.01
Gasterosteus gymnurus	76	**-0.244**	-0.146	-0.208	-0.089	0.224	-0.075	**0.294**	0.049
Gobio gobio	14354	**-0.040**	**-0.041**	**-0.069**	**-0.056**	**0.036**	**0.024**	**0.057**	**0.03**
Gobio lozanoi	36	0.062	0.019	-0.093	-0.026	-0.073	0.286	0.118	0.161
Gobio occitaniae	1926	**-0.058**	**-0.064**	**-0.057**	**-0.103**	**0.078**	**0.075**	**0.081**	**0.1**
Gymnocephalus cernua	138	0.042	-0.069	0.025	-0.027	0.026	0.056	0.108	0.041
Lampetra planeri	1857	0.014	0.014	-0.027	-0.024	0.049	-0.013	0	-0.015
Lepomis gibbosus	1595	-0.019	-0.014	-0.003	0.000	0.032	0.001	-0.004	-0.02
Leuciscus burdigalensis	522	0.050	-0.008	0.048	0.071	-0.027	0.027	0.006	-0.068
Leuciscus leuciscus	922	-0.066	-0.024	**-0.089**	-0.066	0.065	0.011	0.01	0.017
Perca fluviatilis	5404	-0.014	-0.024	0.015	-0.002	-0.04	0.02	0.002	-0.017
Phoxinus phoxinus	22544	-0.008	-0.011	-0.015	-0.010	0.003	0.004	0.012	0.009
Pungitius laevis	134	0.117	0.029	0.052	-0.025	-0.114	-0.071	0.016	-0.068
Rhodeus amarus	218	-0.016	0.033	-0.058	-0.006	-0.097	-0.036	0.097	-0.063
Rutilis rutilis	16034	**-0.032**	**-0.017**	**-0.016**	-0.009	**0.017**	-0.002	0.006	-0.01

Salmo salar	110	-0.022	-0.061	0.046	0.078	-0.044	-0.039	-0.164	-0.1
Salmo trutta	29225	**-0.116**	**-0.125**	**-0.109**	**-0.100**	**0.077**	**0.092**	**0.081**	**0.074**
Scardinius erythrophtalmus	134	**-0.165**	-0.103	-0.074	-0.084	**0.187**	0.021	-0.008	0.032
Squalius cephalus	28084	**-0.032**	**-0.019**	**-0.033**	**-0.024**	0.012	0.007	0.014	0.006
Telestes souffia	179	0.053	0.087	-0.044	-0.099	0.013	0.112	-0.074	0.093
Tinca tinca	490	-0.034	-0.013	-0.035	-0.023	0.036	0.069	0.043	0.088

```
# R code used to perform time series transformation, to estimate synchrony between time series
# and to determine whether long-term trend and density dependence are detected in the time series.

rm(list=ls())
#-------------------------------------------------------------------------------------------------
# Generation of a dummy  data set
# The data frame containing two time series and the  necessary information to perform TSTs
#-------------------------------------------------------------------------------------------------

df.TS1 <- NULL
df.TS2 <- NULL
df <- NULL

#--------- First time series
# this is the vector containing the observed population size
pop.size.TS1 <- c(50,31,26,17,26,28,90,32,31,30,35,33,53,53,187,88,50,51,54)
# this is the vector containing the sampling areas (m^2)
samp.area.TS1 <- c(887.84,930.8,930.8,930.8,930.8,906.3,1001.77,758.28,759.7,817.6,1235.1,875.16,989.05,876.12,807,904.4,825.11,895.5,756)
# this is the vector containing the sampling years.
samp.year.TS1 <- c(1990,1991,1992,1993,1994,1995,1996,1997,1998,1999,2000,2001,2002,2003,2004,2005,2006,2007,2009)

#--------- Second time series
# this is the vector containing the observed population size
pop.size.TS2 <- c(8,19,15,14,11,21,12,17,22,21,35,22,31,52,61,47,81,65,72)
# this is the vector containing the sampling areas (m^2)
samp.area.TS2 <-
c(525,307.05,298.2,340.8,369.2,378.48,360.24,372.4,408.88,380,373.16,313.12,320.72,342.76,334.4,471.45,453.49,465,457.66)
# this is the vector containing the sampling years.
samp.year.TS2 <- c(1987,1990,1991,1992,1993,1996,1997,1998,1999,2000,2001,2002,2003,2004,2005,2006,2007,2008,2009)


# filling the data frame
df <- list()
```

```
df[[1]] <- data.frame(pop.size.t=pop.size.TS1[-length(pop.size.TS1)],pop.size.t1=pop.size.TS1[-1],samp.area.t=samp.area.TS1[-
length(samp.area.TS1)],samp.area.t1=samp.area.TS1[-1],samp.year.t=samp.year.TS1[-length(samp.year.TS1)],samp.year.t1=samp.year.TS1[-1])
df[[2]] <- data.frame(pop.size.t=pop.size.TS2[-length(pop.size.TS2)],pop.size.t1=pop.size.TS2[-
1],samp.area.t=samp.area.TS2[length(samp.area.TS2)],samp.area.t1=samp.area.TS2[-1],samp.year.t=samp.year.TS2[-
length(samp.year.TS2)],samp.year.t1=samp.year.TS2[-1])

# compute densities at time t+1
# compute date, assuming there is no gap in the time series
for(i in 1:length(df)) {
  df[[i]]$densities.t1 = with(df[[i]],pop.size.t1/samp.area.t1*100)
  df[[i]]$date <- 1:nrow(df[[i]])
}

#------------------------------
# Transforming the  time series
#------------------------------

# Detrending
#~~~~~~~~~~~~

# To detrend the raw data we used a linear model with a negative binomial error and a log link function

require(MASS)

df.coef.detrend <- NULL
for(i in 1:length(df)) { # loop to apply the model to each time series
  model <- NULL
  model <- glm.nb(pop.size.t1 ~ log(date) + offset(log(samp.area.t1)), data = df[[i]]) # we perform the model
  df[[i]]$detrend <- residuals(model) # we extract the residuals form the model which corresponds to the detrended data
  df.coef.detrend <- rbind(df.coef.detrend,coef(model)) # stores the estimated coefficients
}

# Prewhitenning
```

```
#~~~~~~~~~~~~~~~

# To eliminate temporal autocorrelation due to intrinsic population dynamic we used the Ricker model with a log link function and a negative
#binomial distribution

df.coef.prewhit  <- NULL

for(i in 1:length(df)){

   df[[i]]$prewhitened <- NULL
   nb.0 <- df[[i]]$pop.size.t == 0 # this is the number of zero counts in the time series (there is no zero counts in our case)
   position.0 <- which(df[[i]]$pop.size.t == 0) # this is the position of the zero counts
   position.pos.counts <- which(df[[i]]$pop.size.t != 0) # this is the position of the positive counts

   #transitions from Nt=0 to Nt1>0
   if(sum(nb.0)>2) { # if there are at least 3 zero counts in the time series
   model.0 <- NULL
   model.0 <- glm.nb(pop.size.t1 ~ offset(log(samp.area.t1)),data=df[[i]][nb.0,])
   df[[i]][position.0,"prewhitened"] <- residuals(model.0)
   }

   #transitions Nt>0 to Nt1>0
   model.pos.counts <- NULL
   model.pos.counts <- glm.nb(pop.size.t1 ~ I(pop.size.t/samp.area.t)+offset(log(samp.area.t1)+log(pop.size.t/samp.area.t1)),data=df[[i]][!nb.0,])
   df[[i]][position.pos.counts,"prewhitened"] <- residuals(model.pos.counts)

   df.coef.prewhit <- rbind(df.coef.prewhit,coef(model.pos.counts))
}

# Prewhitenning and detrending
#~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

# To eliminate temporal autocorrelation due to intrinsic population dynamic and long term trend we used the
```

```
# Ricker model with a log link function and a negative binomial distribution with the year as a covariate

df.coef.prewhit.det  <- NULL

for(i in 1:length(df)){

   df[[i]]$prewhit.det <- NULL
   nb.0 <- df[[i]]$pop.size.t == 0
   position.0 <- which(df[[i]]$pop.size.t == 0)
   position.pos.counts <- which(df[[i]]$pop.size.t != 0)

   #transitions from Nt=0 to Nt1
   if(sum(nb.0)>2) {
   model.0 <- NULL
   model.0 <- glm.nb(pop.size.t1 ~ log(date) + offset(log(samp.area.t1)),data=df[[i]][nb.0,])
   df[[i]][position.0,"prewhit.det"] <- residuals(model.0)
   }

   #transitions Nt>0 to Nt1
   model.pos.counts <- NULL
   model.pos.counts <- glm.nb(pop.size.t1 ~ log(date) + I(pop.size.t/samp.area.t) + offset(log(samp.area.t1) +
log(pop.size.t/samp.area.t1)),data=df[[i]][!nb.0,])
   df[[i]][position.pos.counts,"prewhit.det"] <- residuals(model.pos.counts)

   df.coef.prewhit.det <- rbind(df.coef.prewhit.det,coef(model.pos.counts))
}

#-------------------------------------------------------------------------------
# Estimating synchrony between both time series for the raw data and the modified ones
#-------------------------------------------------------------------------------

cor.test(df[[1]][,"densities.t1"],df[[2]][,"densities.t1"],method="spearman")$estimate #0.63
cor.test(df[[1]][,"detrend"],df[[2]][,"detrend"],method="spearman")$estimate #0.36
```

```
cor.test(df[[1]][,"prewhitened"],df[[2]][,"prewhitened"],method="spearman")$estimate #-0.12
cor.test(df[[1]][,"prewhit.det"],df[[2]][,"prewhit.det"],method="spearman")$estimate #-0.07

#-------------------------------------------------------------------------------------
# detecting the presence of a long-term trend (Mann-Kendall trend test) in the time series
#-------------------------------------------------------------------------------------

require(Kendall)

# correlations for the first time series
with(df[[1]],{
print(Kendall(date,densities.t1)) #0.55
print(Kendall(date,detrend)) #0.05
print(Kendall(date,prewhitened)) #0.29
print(Kendall(date,prewhit.det)) #-0.15
})
# correlations for the second time series
with(df[[2]],{
print(Kendall(date,densities.t1)) #0.64
print(Kendall(date,detrend)) #0.28
print(Kendall(date,prewhitened)) #0.17
print(Kendall(date,prewhit.det)) #0.16
})

#-------------------------------------------------------------------------
# detecting the presnece of lag-1 temporal autocorrelation in the time series
#-------------------------------------------------------------------------

# temporal autocorrelation for the first time series
with(df[[1]],{
print(acf(densities.t1,lag.max=1,plot=F)$acf[2]) #0.29
print(acf(detrend,lag.max=1,plot=F)$acf[2]) #0.21
print(acf(prewhitened,lag.max=1,plot=F)$acf[2]) #-0.10
```

```
print(acf(prewhit.det,lag.max=1,plot=F)$acf[2]) #-0.16
})
# temporal autocorrelation for the second time series
with(df[[2]],{
print(acf(densities.t1,lag.max=1,plot=F)$acf[2]) #0.68
print(acf(detrend,lag.max=1,plot=F)$acf[2]) #0.41
print(acf(prewhitened,lag.max=1,plot=F)$acf[2]) #-0.31
print(acf(prewhit.det,lag.max=1,plot=F)$acf[2]) #-0.26
})
```

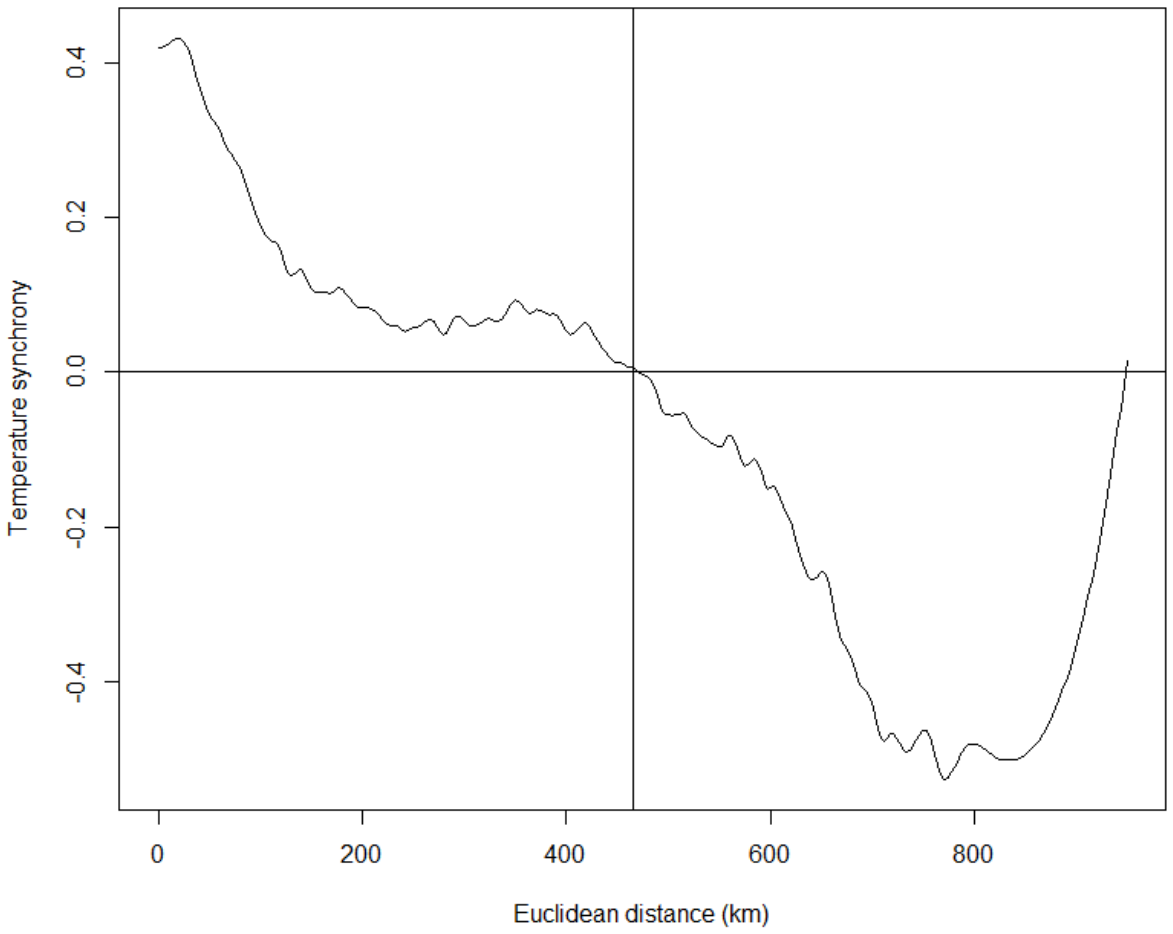

Figure S2. Relationship between temperature synchrony and the Euclidean distance between the different sites considered in this study. The intersection between the vertical and the horizontal lines represents a measure of the spatial scale of temperature synchrony.

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Spatial synchrony in stream fish populations: influence of species traits

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Spatial synchrony in population dynamics has been identified in most taxonomic groups. Numerous studies have reported varying levels of spatial synchrony among closely-related species, suggesting that species' characteristics may play a role in determining the level of synchrony. However, few studies have attempted to relate this synchrony to the ecological characteristics and/or life-history traits of species. Yet, as to some extent the extinction risk may be related to synchrony patterns, identifying a link between species' characteristics and spatial synchrony is crucial, and would help us to define effective conservation planning. Here, we investigated whether species attributes and temperature synchrony (i.e. a proxy of the Moran effect) account for the differences in spatial population synchrony observed in 27 stream fish species in France. After measuring and testing the level of synchrony for each species, we performed a comparative analysis to detect the phylogenetic signal of these levels, and to construct various multi-predictor models with species traits and temperature synchrony as covariates, while taking phylogenetic relatedness into account. We then performed model averaging on selected models to take model uncertainty into account in our parameter estimates. Fifteen of the 27 species displayed a significant level of synchrony. Synchrony was weak, but highly variable between species, and was not conserved across the phylogeny. We found that some species' characteristics significantly influenced synchrony levels. Indeed, the average model indicated that species associated with greater dispersal abilities, lower thermal tolerance, and opportunistic strategy displayed a higher degree of synchrony. These findings indicate that phylogeny and spatial temperature synchrony do not provide information pertinent for explaining the variations in species' synchrony levels, whereas the dispersal abilities, the life-history strategies and the upper thermal tolerance limits of species do appear to be quite reliable predictors of synchrony levels.

Spatial synchrony in population dynamics (i.e. the degree to which spatially distant populations rise and fall together through time) has been identified in most taxa, ranging from plants (Koenig 1999), parasites (Cattadori et al. 2005), insects (Sutcliffe et al. 1996), fish (Grenouillet et al. 2001), amphibians (Aubry et al. 2012), and birds (Paradis et al. 1999) to mammals (Moran 1953). Studies focusing on synchrony patterns are closely related to the debate about the relative importance of intrinsic versus extrinsic environmental factors in determining fluctuations in population size (Grenfell et al. 1998, Forchhammer et al. 2002). It is generally considered that population dispersal and synchronous stochastic effects of density-independent factors (known as the Moran effect) are the two main mechanisms involved in spatial synchrony (Liebhold et al. 2004). These are not mutually exclusive, and their relative importance has been shown to be scale-dependent (Paradis et al. 2000): while population dispersal prevails at the local scale, environmental stochasticity prevails at larger scales (Ranta et al. 1998). In addition, trophic interactions involving species that are themselves synchronized or mobile, could influence population synchrony (Liebhold et al. 2004).

In recent years, several studies have reported varying degrees of population synchrony among closely-related species (Sutcliffe et al. 1996, Koenig and Knops 1998, Paradis et al. 2000). These variations have generally been attributed to differences in parameters determining the dynamics of the populations, such as the strength and shape of density dependence (Kendall et al. 2000, Engen and Saether 2005) or differences in the spatial autocorrelation of environmental noise (Engen et al. 2005). Indeed, empirical analyses of population dynamics of many species have shown that the parameters describing population dynamics (e.g. density-dependent structure, carrying capacity) may show large spatial variations (Myers et al. 1997, Engen et al. 2005), thus reducing population synchrony (Engen and Saether 2005) and consequently species synchrony. Likewise, spatial variation in the effect of environmental covariates on population dynamics has been shown to influence species synchrony patterns (Engen and Saether 2005). Therefore, depending

on the spatial variability of 1) the parameters describing population dynamics and/or 2) the influence of environmental covariates on these dynamics, varying levels of species synchrony can emerge. However, such variations could also depend on species characteristics, because the influences of both density dependence (shape and strength) and environmental stochasticity have been shown to be dependent upon species characteristics (Lande et al. 2002, Sæther et al. 2013). For instance, several studies have shown that most density-dependent changes occur close to the carrying capacity for K-strategist species (long life-span, small clutches, large egg size), whereas the opposite is true for r-strategist species (Fowler 1981). Likewise, species with a short generation time have been found to be more sensitive to environmental stochasticity, and so also to the Moran effect (Sæther et al. 2013).

Despite these findings, very few studies have attempted to relate the level of spatial synchrony to ecological characteristics and/or the life-history traits of species, and most of the studies performed have failed to explain the observed differences in synchrony levels between species. However, it is crucial to identify a link between species characteristics and spatial synchrony, since this would help us to understand population dynamics and could also provide useful insights for management purposes; this is because to some extent the extinction risk may be related to synchrony patterns (Hanski and Woiwod 1993, Heino et al. 1997).

In this study, our goal was to identify the determinants of interspecies variations in synchrony levels for 27 stream fish species across France. To do this, we investigated whether 15 species characteristics (ecological and life-history traits) and/or the Moran effect explained the observed differences in the degree of spatial synchrony measured over the different species. Consequently, we first estimated the level of spatial synchrony for each species, and then carried out tests to find out whether these levels were ecologically relevant at the spatial scale considered. We then used a comparative analysis 1) to detect phylogenetic signals in the levels of synchrony in order to find out whether evolutionary relationships between species provide information pertinent to explaining interspecies differences in synchrony patterns, and 2) to compute various multi-predictor models in order to determine the extent to which species characteristics and/or the Moran effect play a role in determining species synchrony, while taking phylogenetic relatedness into account. Our first expectation was that species living in a highly synchronous environment would display higher levels of synchrony. For species characteristics, we hypothesized that dispersal abilities, thermal tolerance, life-history strategies, diet, and habitat requirements would explain interspecies differences in fish spatial synchrony. More specifically, we expected species with strong dispersal abilities to be synchronized to a greater extent than those with low dispersal abilities. For thermal tolerance, species with a low upper thermal limit were expected to display higher synchrony levels, because in a spatially-correlated global warming context, these species can be expected to exceed their upper limit more often than species with a high upper thermal limit, which could lead to spatially-correlated population decline. Furthermore, because short-lived species display more immediate responses to environmental stochasticity than long-lived species (Sæther et al. 2013), short-lived species can be expected to be more synchronous. Finally, the trophic position of the species along the food-web and the species habitat requirements were also expected to influence synchrony levels, as an influence of these characteristics on synchrony patterns has already been demonstrated for other species (Paradis et al. 2000, Liebhold et al. 2004).

Material and methods

Fish and temperature data sets

To calculate the level of spatial population synchrony for fish species, we used abundance time series data provided by the French National Agency for Water and Aquatic Environment (Onema; for more details see Poulet et al. 2011). These annual data were obtained between 1982 and 2010 by electrofishing during periods of low flow. Fish were identified to species level, counted, and then released back into the river. From this data set we conserved only the species for which at least ten population time series including at least eight years of non-null captures were available. This resulted in the selection of 27 fish species (Table 1). We chose to have at least ten population time series, because we wanted to have 1) populations that were representative of the different conditions experienced by the species in its geographic range and 2) enough populations to compute a reliable estimate of species synchrony levels. For the number of years within the

Table 1. Spatial synchrony for the 27 fish species. N is the number of time series (i.e. sites) for each species. Npairs is the number of zero-lag Spearman cross-correlation coefficients (CCCs), GRS (km²) is the estimated geographic range size. Mean CCCs is the mean of all zero-lag Spearman cross-correlation coefficients computed between all pairs of time series that had at least eight years in common. Statistically significant ($p < 0.05$) coefficients are shown in bold type.

Species name	Mean CCCs	N	Npairs	GRS (km²)
Abramis brama	–0.017	26	233	278589
Alburnoides bipunctatus	**0.048**	52	745	273135
Alburnus alburnus	0.003	110	2830	451797
Ameiurus melas	0.023	17	64	138562
Barbatula barbatula	**0.054**	245	21312	550434
Barbus barbus	**0.025**	131	5162	407407
Blicca bjoerkna	0.001	24	94	247209
Carassius carassius	–0.039	13	55	195257
Chondrostoma nasus	0.027	30	373	185169
Cottus gobio	**0.146**	25	160	118620
Cyprinus carpio	0.024	11	55	163528
Esox lucius	**0.030**	61	1037	399757
Gasterosteus aculeatus	**0.172**	16	76	233558
Gobio gobio	**0.045**	219	14354	411718
Gymnocephalus cernua	0.040	21	138	219214
Lepomis gibbosus	**0.014**	81	5404	382141
Leuciscus leuciscus	**0.071**	59	922	244492
Perca fluviatilis	**0.038**	154	1595	410109
Phoxinus phoxinus	**0.043**	249	22544	542819
Pungitius pungitius	0.038	19	134	109912
Rhodeus sericeus	0.036	33	218	170673
Rutilus rutilus	0.002	250	16034	523535
Salmo trutta fario	**0.038**	284	29225	634422
Scardinius erythrophthalmus	–0.012	28	134	298309
Squalius cephalus	**0.031**	313	28084	534373
Telestes souffia	**0.089**	23	179	90144
Tinca tinca	**0.069**	42	490	415053

time series, we chose the same number as that used in a study involving a previous version of our database (Poulet et al. 2011). All time series with more than three consecutive years missing were eliminated. In this way, little information was likely to be contained by the population change during the missing years (Engen et al. 2005). At the end of the selection process, the data set used was composed of 610 sites covering the whole of metropolitan France (Fig. 1), with 8–25 yr of sampling (mean: 12.5 yr; SD: 3.6 yr), corresponding to a total of 7634 sampling occasions. The number of time series (i.e. sites) varied from 11 to 313 depending on the species (Table 1).

Daily air temperature data from 1982 to 2010 were provided by Météo France. More precisely, we used the SAFRAN database (Le Moigne 2002), which is a regular eight kilometer grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically-homogeneous zones (for further details, see Le Moigne 2002). Although we do not have the corresponding water temperature data, studies have shown that air temperature provides a reliable proxy for water temperature (Caissie 2006). From this data set, we calculated the average annual temperature at each site, and used this measure to estimate the degree of environmental correlation between the different sites.

Species and temperature synchrony

For each species, we computed zero-lag Spearman cross-correlation coefficient (CCC) for all pairs of raw abundance time series (Buonaccorsi et al. 2001). Species synchrony was then calculated as the average of these CCCs weighted by the number of overlapping years between pairs of time series. The same procedure was used to estimate the level of temperature synchrony (TEMP) between the subset of sites occupied by each species. This measure was considered to provide a proxy of the Moran effect, and was used in the model selection procedure (see below) to determine whether it influenced species synchrony levels. To determine whether species synchrony was significantly different from zero, we used a bootstrap procedure with resampling of timepoints within each time series, and then recalculated the mean between all the CCCs computed from the resampled time series (Lillegård et al. 2005). This procedure was repeated 1000 times to generate a distribution of mean species synchrony values under the hypothesis of no synchrony (Buonaccorsi et al. 2001). Species synchrony was considered significant if less than 5% of the simulated means (i.e. means calculated using the bootstrap algorithm) exceeded the observed mean.

As the distribution of the estimated spatial synchrony for the 27 fish species was skewed (Shapiro–Wilk normality test; $p < 0.01$), which could lead to violation of the assumption of residual normality for most of the multi-predictor models computed, this variable was normalized using a Box–Cox power transformation (lambda = –7.05; Box and Cox 1964).

Species traits

To test our hypotheses regarding the different morphological, physiological, life-history, and behavioral characteristics

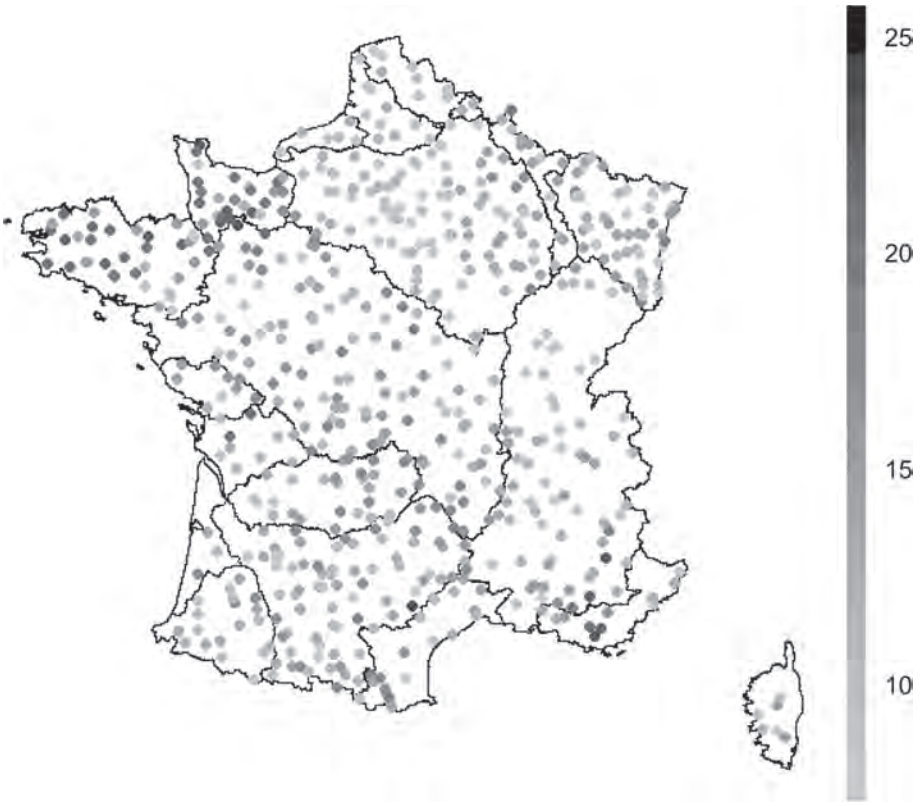

Figure 1. Study area showing the distribution of the sampling sites. The gray scale indicates the number of years available for each site. Sites shown in light gray are those for which we have the fewest years, while sites shown in dark gray are those for which we have greatest number of years.

of the 27 fish species studied, we used values for 15 different traits (Supplementary material Appendix 1, Table A1) taken from the literature (Buisson and Grenouillet 2009, Keith et al. 2011, Tissot and Souchon 2011), from FishBase (Froese and Pauly 2002), and from expert knowledge. We chose these traits for their diversity, the fact they could be expressed numerically or ordered hierarchically, and the likelihood that values would be obtained for most of the species. Among these, six were quantitative variables and the others were all ordinal variables (Supplementary material Appendix 1, Table A2). We chose to express the categorical variables as ordinal variables, because this allowed us to reduce the number of parameters that had to be estimated when computing the multi-predictor models.

To describe the dispersal abilities of the 27 fish species, we used morphological characteristics known to be representative of this parameter (Poff and Allan 1995). We therefore included two traits related to body size (body length and larval length), and two ratios describing the hydrodynamic profile of the fish (shape factor; i.e. the ratio of total body length to maximum body depth), and the fish's swimming ability (swimming factor; i.e. the ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin). Large species with a low swimming factor and a high shape factor were expected to display high dispersal abilities (Olden et al. 2008). To reflect the physiological characteristics of species, we used the upper thermal tolerance limit (UTT). We used seven traits to describe the different life-history strategies of the 27 fish species: life span, parental care, incubation period, sexual maturity, spawning time, absolute fecundity, and egg diameter. The diet was ordered to describe the trophic position along the food-web as follows: omnivorous, invertivorous, invertivorous-carnivorous, and piscivorous. Finally, for fish habitat requirements, we included two habitat variables that reflect the position of the fish in the water column during feeding (feeding habitat) and resting (resting habitat).

To describe species dispersal abilities, life-history strategies, and habitat requirements, we used various traits (four, seven and two, respectively) that could be correlated with one another. For each of these trait categories, colinearity was reduced by carrying out a principal coordinate analysis (PCoA, Gower 1966), and then using the axes of each analysis as synthetic variables of species' characteristics. Like principal component analysis, PCoA is a metric multidimensional scaling method based on projection, which uses spectral decomposition to approximate a matrix of distances from the distances between a set of points in a few dimensions. We chose this method instead of principal component analysis, because the matrix of distances can be computed from mixed type variables (i.e. both ordinal and quantitative) by using the dissimilarity coefficient proposed by Gower (1971). Once PCoA has been performed for each trait category, species dispersal abilities and species life-history strategies were described by two variables (MPC1, MPC2 and LPC1, LPC2, respectively), whereas species habitat requirements were described by one variable (HPC1) (Table 2).

Table 2. Pearson's correlations between the species traits and PCoA axes. Three PCoAs were performed, each summarizing different species characteristics. The percentage of variance explained by each axis is shown in parentheses.

	Correlation	
Trait	PC 1	PC 2
Dispersal ability	(26.8%)	(16.4%)
Body length	–0.41	0.31
Larval length	–0.94	–0.25
Shape factor	0.32	–0.81
Swimming factor	0.002	0.42
Life-history strategy	(24.3%)	(22.7%)
Fecundity	0.49	–0.46
Spawn time	0.91	0.32
Egg diameter	–0.6	–0.11
Life span	–0.09	–0.9
Female maturity	–0.01	–0.9
Incubation period	–0.66	0.32
Parental care	–0.35	0.62
Habitat preference	(31.4%)	
Resting habitat	–0.80	–
Feeding habitat	–0.82	–

Phylogeny and the phylogenetic comparative approach

One of the problems encountered in carrying out a comparative analysis is phylogenetic non-independence, i.e. the fact that closely-related species tend to be more similar than more distantly-related ones (Felsenstein 1985).

To take into account the phylogenetic relatedness between the species, we first built the phylogeny of the 27 species (Fig. 2A) using molecular data obtained from Genbank for three mitochondrial genes (Grenouillet et al. 2011). Sequence data consisted of 1124, 651, and 459 base pairs for cytochrome b, cytochrome oxidase I, and ribosomal 16S sub-unit, respectively. We used the Lamprey as an outgroup to root the tree, and we reconstructed phylogenetic relationships among species using the Bayesian method under the TVM + I + G substitution model. The phylogeny estimation was implemented with MrBayes and PAUP softwares.

We then used the phylogenetic generalized least squares (PGLS) comparative method described in Freckleton et al. (2002), first to detect phylogenetic signals in the levels of species synchrony and species traits, and second to construct multi-predictor models with species synchrony levels as the dependent variable and species traits and temperature synchrony as independent variables. This approach allows for the non-independence of data by adjusting a variance/covariance matrix based on the phylogenetic relatedness among species. Unlike phylogenetic independent contrasts (Felsenstein 1985), PGLS makes it possible to introduce some degree of trait liability, relative to a strict Brownian model of evolution, by multiplying the off-diagonal elements of the variance/covariance matrix (i.e. the covariances) by a measure of phylogenetic correlation. Here, we used Pagel's λ (Pagel 1999), which varies from 0 to 1, as a measure of phylogenetic correlation, because it has been shown to be a statistically-powerful index for measuring whether data exhibit phylogenetic dependence or not (Freckleton et al. 2002). $\lambda = 0$ means that all species are independent (star phylogeny), $\lambda = 1$ corresponds to a Brownian model of evolution, and $0 < \lambda < 1$ corresponds to some degree of trait lability.

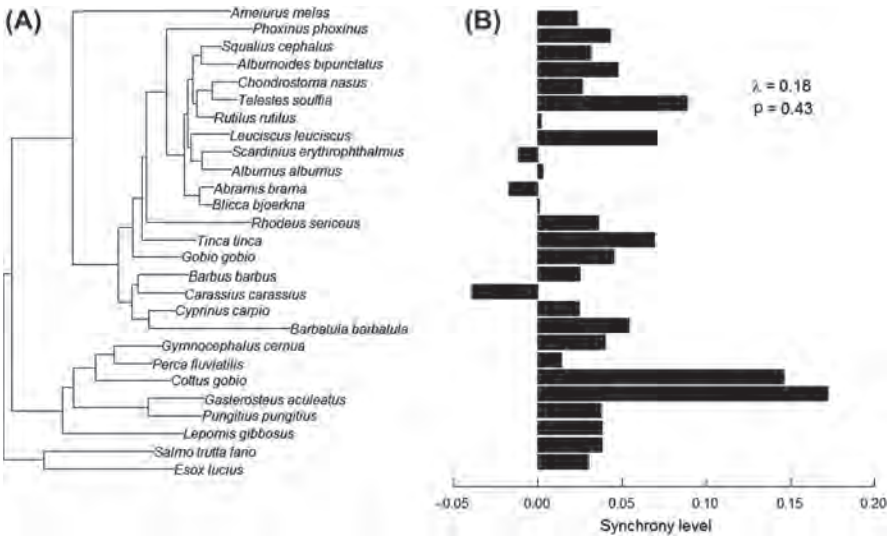

Figure 2. Phylogenetic tree (A) and synchrony level (B) of the 27 stream fish species. λ is the value of the phylogenetic signal in the synchrony level, and p its associated p-value.

Multi-predictor models and model averaging

Because the distance over which the species were sampled could influence the levels of population synchrony (Bjørnstad et al. 1999), and consequently the subsequent analyses (i.e. the estimations of the levels of species synchrony and so the inferences drawn from the multi-predictor models), we first performed a linear regression between the levels of synchrony estimated for each species and the geographic range size (GRS; Table 1) occupied by the species. For each species, GRS was measured as the area (km^2) of the smallest convex set of the subset of sites occupied by the species (i.e. the convex hull; Barber et al. 1996). The residuals of this model were then extracted and used as the dependent variable in the PGLS models we used to test the influence of species traits and the Moran effect on the level of spatial synchrony among species.

In order to compare the relative strength of the eight predictors on the level of spatial synchrony among species, the predictors were transformed to z-scores to standardize their slope coefficients (β). We then considered all possible multi-predictor models that included three terms or fewer. We chose to not include more than three terms in these models so as to limit the number of estimated parameters (i.e. four), regarding the number of data points at our disposal (i.e. 27). We also considered models that included interaction terms between independent variables. Interactions were tested only in models that included two variables. Once all the models had been computed, we used the Akaike information criterion adjusted for small sample size (AICc) to assess the information content of each model (Burnham and Anderson 2002). For each model, we calculated pseudo-R^2 following Nagelkerke (1991). To take model uncertainty into account, and obtain robust estimates of the slope coefficients associated with each predictor, we performed model averaging (Johnson and Omland 2004). Specifically, we summed the Akaike weights of each model (*wi*) from the largest to the smallest until the sum reached 0.95. The corresponding subset of models was then used to calculate a weighted average of the slope coefficients using the *wi* of each model (Burnham and Anderson 2002). For each weighted average coefficient, we calculated confidence intervals from the variance of the estimated coefficient among the selected models (Johnson and Omland 2004). As the predictors could be correlated with one another, we assessed the variance inflation factor; colinearity was considered to pose a problem if it had a value of more than five (Kutner 2005). For all models, we tested the residual normality using the Shapiro–Wilk normality test. All calculations were performed using R environment software ver. 2.15.3 (R Core Team).

Results

Fifteen of the 27 fish species displayed a significant ($p < 0.05$) level of synchrony (Table 1). The synchrony level was weak, but varied considerably in all species, ranging from –0.04 (*Carassius carassius*) to + 0.17 (*Gasterosteus aculeatus*). Furthermore, these levels were not conserved across the phylogeny ($\lambda = 0.08$; $p = 0.69$) (Fig. 2B) suggesting that variations occurred even amongst closely-related species. Similarly, among the seven traits considered, we found that only two of them, MPC1 and diet, displayed a significant ($p < 0.001$) phylogenetic signal ($\lambda = 0.98$ and $\lambda = 0.88$, respectively; Table 3).

Eight of the 120 multi-predictor models computed were sufficient to provide a sum of *wi* of more than 0.95 (Table 3). Consequently these models were used to perform model averaging. The amount of variance explained by the selected models varied from 0.70 to 0.76 (Table 3). Colinearity did not appear to be a problem for any of the models selected (the variance inflation factor was always less than two), and their residuals were normally distributed (Shapiro–Wilk normality test; $p > 0.05$). Taken together, these models encompassed all the predictors considered. Six out of the eight models included UTT as a significant predictor of synchrony levels. Likewise, MPC2 and LPC2 both appeared in four models, and were always significant. Diet appeared in three models, but was significant in only one model. Although included in the subset of models, none

Table 3. Phylogenetic conservatism of each traits and results from the models selected among the 120 multi-predictor PGLS models. LPC1 and LPC2: first and second axes extracted from the PCoA performed on the seven life-history traits; MPC1 and MPC2: first and second axes extracted from the PCoA performed on the four morphological variables; TEMP: temperature synchrony; UTT: upper thermal tolerance limit; HPC1: first axis extracted from the PCoA performed on the two habitat variables. The slope coefficients (β) of each predictor and their levels of significance are shown for each model. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. – indicate that the variables were not retained in the model. AICc, the weight of each model (*wi*), and R^2 are also shown.

	Phylogenetic conservatism	Selected models							
Trait	λ	M1	M2	M3	M4	M5	M6	M7	M8
LPC1	0.65	–	–	–	–0.004	–	–0.002	–	–
LPC2	0.37	0.018**	–	0.015**	0.016**	–	0.012**	–	–
MPC1	0.99***	–0.003	–	–	–	–	–	–0.01	–
MPC2	0	–	–0.021***	–	–	–0.018***	–	–0.022***	–0.019***
Diet	0.88	–	–	–	–	–0.001	0.001	–0.004*	–
UTT	0.88	–0.011*	–0.012*	–0.010*	–0.010*	–0.011*	–	–	–0.011*
HPC1	0.67	–	–	–	–	–	–	–	–0.001
TEMP	–	–	–	–0.005	–	–	–	–	–
AICc	–	–140.25	–137.73	–137.16	–136.22	–135.97	–134.67	–134.58	–134.36
wi	–	0.5	0.14	0.11	0.07	0.06	0.03	0.03	0.03
R^2	–	0.76	0.7	0.73	0.72	0.72	0.7	0.7	0.7

of the other predictors emerged as significant. MPC1 and LPC1 appeared in two models, while TEMP and HPC1 appeared in only one model. No interaction terms appeared in the models selected.

After averaging the slope coefficients for the eight models, we found a significant negative relationship between MPC2 and the level of spatial synchrony (Fig. 3), reflecting the fact that species associated with a low swimming factor, a high shape factor, a small body length, and a large larval length displayed higher levels of synchrony. We also found a significant positive relationship between LPC2 and the level of species synchrony (Fig. 3). Thus, species with a low age at maturity that produce small clutches several times per year were more synchronous than species with the opposite characteristics. Finally, we found a significant negative relationship between UTT and the level of species synchrony (Fig. 3) suggesting that species with a low UTT were more synchronized than species with a high UTT. Once the slope coefficients were averaged, we found no significant relationship between the level of species synchrony and diet, LPC1, HPC1, MPC1, or TEMP.

Discussion

Few studies have attempted to relate the levels of synchrony to species characteristics, and most of them have failed to identify any clear link between synchrony and any species characteristics other than dispersal (Koenig 1998, Paradis et al. 1999, Burrows et al. 2002). For instance, Paradis et al. (1999) studied 53 bird species and found no significant relationship between the degree of spatial synchrony and several life-history traits (clutch size, age at first breeding, juvenile and adult survival rates, migration status, and body size). Likewise, diet, clutch size and body size failed to explain the different levels of synchrony in 79 Californian land bird species (Koenig 1998). In a study involving 26 species of rocky shore communities, Burrows et al. (2002) found no influence

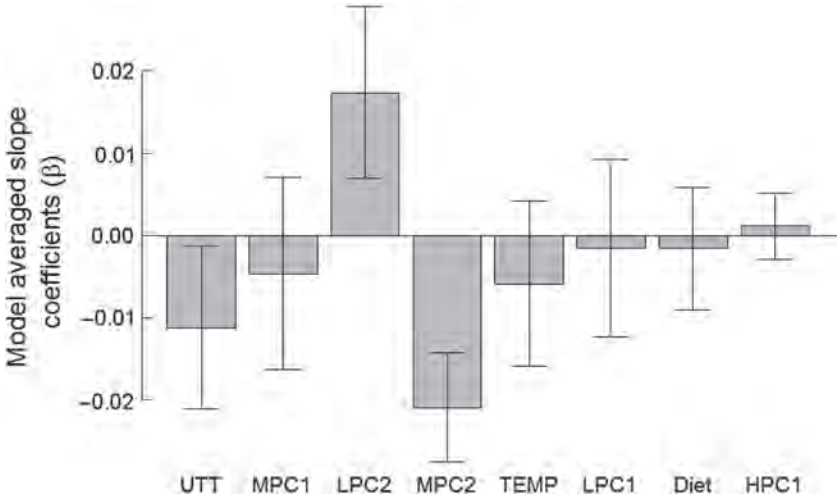

Figure 3. Weighted average slope coefficients (β) calculated for the eight selected models. LPC1 and LPC2: first and second axes extracted from the PCoA performed on the seven life-history traits; MPC1 and MPC2: first and second axes extracted from the PCoA performed on the four morphological variables; UTT: upper thermal tolerance limit; HPC1: first axis extracted from the PCoA performed on the two habitat variables; TEMP: temperature synchrony.

of reproductive biology or ecology on the levels of synchrony in the different species. Thus, although the dispersal abilities of species appear to be a reliable predictor of population synchrony in different taxa (Liebhold et al. 2004), this did not seem to be the case for other traits (but see Tedesco and Hugueny 2006, Franzén et al. 2013).

In this study, although the level of spatial synchrony was low for all species, it was highly variable and we found that some species characteristics could explain the observed differences in synchrony levels. Morphological attributes related to the dispersal abilities of species were significantly related to interspecies differences in the synchrony pattern, species with high dispersal abilities (i.e. species with a low swimming factor, a large larval length, and a high shape factor) being more synchronized than those with low dispersal abilities. This finding was consistent with previous studies. For instance, analyses of breeding bird population time series (Koenig 1998, Paradis et al. 1999) have indicated that species with greater dispersal capabilities were more highly synchronized, implying that dispersal was a major cause of the synchronous dynamics observed. However, dispersal is a scale-dependent phenomenon, and other studies have shown that this relationship vanishes at larger scales. This is borne out by Sutcliffe et al. (1996), who found that butterfly dispersal had a significant effect on the level of synchrony at the local scale, but not at the regional scale. Likewise, Peltonen et al. (2002) found that spatial synchrony was not directly associated with the dispersal capabilities of six forest insect species at the regional scale. Altogether, these findings have led to the general conclusion that dispersal can have the effect of synchronizing populations only at the local scale, whereas stochastic environmental correlation (i.e. the Moran effect) prevails at larger scales (Ranta et al. 1998). However, a study on mussels has demonstrated that dispersal between neighboring populations could interact with local demographic processes to generate patterns of spatial synchrony over quite large scales (Gouhier et al. 2010). In our study, although the spatial scale considered (i.e. France) was large, we found that environmental stochasticity (i.e. temperature synchrony) failed to explain differences in synchrony levels among species, whereas dispersal capabilities did, thus providing further confirmation of the findings of Gouhier et al. (2010). Therefore, although large-scale synchrony was usually attributable to the Moran effect, in some cases, it could also be the result of dispersion. It is noteworthy that we used the spatial correlation of the average annual temperature as a proxy for the Moran effect. However, other environmental factors, such as river discharge, could influence fish population synchrony (Cattanéo et al. 2003) and further studies are needed to determine the extent to which it influences our conclusions.

We found that species with a low thermal maximum were more synchronous than those with a high thermal maximum. However, as temperatures are increasing (Moisselin et al. 2002) and are spatially correlated (Koenig 2002), populations of species with a low thermal maximum can be expected to exceed their upper limit more often than those of species with a high thermal maximum, leading to population declines correlated over large distances. This hypothesis is supported by a study of 110 European bird species that revealed that species with the lowest thermal maximum showed the sharpest declines between 1980 and 2005 (Jiguet et al. 2007). Similar conclusions have been reached for ectothermic species in freshwater ecosystems. For instance, several studies have reported that warm-water species (which are characterized by a high thermal maximum) are globally increasing in abundance in response to increasing temperatures, whereas the abundances of cold-water species (which are characterized by a low thermal maximum) are decreasing (Daufresne and Boët 2007, Poulet et al. 2011).

To the best of our knowledge, only Tedesco and Hugueny (2006) have reported a significant relationship between species life-history traits and synchrony. Indeed, they showed that species associated with high fecundity, small egg size, and a high gonado-somatic index (what is known as the 'periodic' strategy, sensu Winemiller (1992)) were more synchronous than species associated with the opposite traits (what is known as the 'equilibrium' strategy). However, they excluded from their analyses any species that were characterized by early maturation, continuous reproduction, and low fecundity (known as the 'opportunistic strategy'), because of a low capture efficiency. Yet, these were exactly the species that we found displayed the highest levels of spatial synchrony. However, our results are difficult to compare to those of Tedesco and Hugueny (2006) as their study was based on tropical species that were sampled at only two sites between which dispersion of individuals was impossible as they were located in different catchments. Thus, any synchrony observed could only be due to the Moran effect, whereas in our study the synchrony observed could be attributable to dispersal and/or to the Moran effect.

We did not found any influence of the trophic position on synchrony levels which is in contradiction with some studies (Satake et al. 2004) but in accordance with others (Koenig 1998). One possible explanation would be that the effect of biotic interactions on synchrony levels is more likely to be detected on local spatial scale or simple trophic networks. In large scale studies such as ours and the one of Koenig (1998), we can expect large spatial variations in the complexity of trophic interactions, thus masking their effects on synchrony patterns. Likewise, we found that fish habitat requirements failed to explain interspecies differences in synchrony levels whereas Paradis et al. (2000) found an influence of habitat on spatial population synchrony for birds; populations located in farmland sites being more synchronized than those located in woodland sites. However, this result was not a test of the influence of species habitat requirements on the level of spatial synchrony but rather of whether the synchronizing factors were habitat dependent or not. That being said, our findings still suggest that habitat requirements have an influence on synchrony levels, and further studies are needed to find out whether this is true for other taxa or biogeographic regions.

In this study, we used a phylogenetic comparative framework that revealed that the level of synchrony was not conserved across the phylogeny. This suggests that the phylogenetic distance between species does not provide information that is pertinent for explaining spatial synchrony. Similarly, Raimondo et al. (2004) failed to detect any influence of the phylogeny on the levels of spatial synchrony measured on 10 Lepidopteran species. Even though their analysis was just a test of whether species within a family displayed higher synchrony relative to species between families, this result, coupled with ours, do not provide encouraging

support for an influence of the phylogeny. A possible explanation for our findings could be that the traits mainly involved in determining population synchrony (i.e. the dispersal ability, the upper thermal tolerance, and the life-history strategies) were themselves not conserved across the phylogeny. Such an interpretation has already been proposed, for instance in primates, to explain the low phylogenetic signal found for the 'total group size' variable (Kamilar and Cooper 2013). Another possible explanation is that closely-related species often experience different habitat-specific conditions that could lead to differing levels of population synchrony, and therefore to a low phylogenetic signal. It should also be noted that phylogenetic signals cannot account for within-species variations, even though many species do in fact have numerous traits (e.g. ecological, behavioral, morphological) that display considerable intra-species differences (Kamilar et al. 2012). This could also contribute to explain the low phylogenetic signal observed in the level of synchrony.

Spatial population synchrony may be related to the risk of species extinction, as it increases the likelihood of a correlated population decline across large areas (Hanski and Woiwod 1993, Heino et al. 1997). However, many studies have shown that the extinction risk is conserved across the phylogeny (Purvis et al. 2000, Cardillo et al. 2005), and it may be influenced by species traits linked to the common evolutionary history of species (Willis et al. 2008). Our data do not reveal any phylogenetic pattern in the level of synchrony among species, and suggest that species traits that promote spatial synchrony are not necessarily shared by close relatives. Thus, although the upper thermal tolerance limit, the life-history strategies, and the dispersal abilities can be useful for identifying the species most at risk (i.e. most synchronized), the phylogeny, and the spatial synchrony in average annual temperature do not seem to be pertinent. This highlights the fact that we still know little about the causes of population synchrony, and further studies are clearly needed to determine the extent to which species characteristics can provide insights into the causes of population synchrony. So far, any such studies have focused on just a few taxa even though synchrony has been demonstrated in nearly all taxa. It would be very interesting to find out whether ecological, behavioral, or physiological characteristics are related to the level of synchrony in other taxa. Moreover, although it has already been demonstrated that the dispersal abilities of a species are related to population synchrony (Sutcliffe et al. 1996, Paradis et al. 1999), we have shown that the upper thermal tolerance limit as well as the life-history strategies can also be reliable predictors of this pattern. In a context of global change, it is of the utmost importance to find out whether this is a general pattern found in the various different taxa. If it is, this pattern could be helpful for elucidating the mechanisms underlying spatial synchrony, and identifying the species that should be priority targets for conservation.

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Supplementary material (Appendix ECOG-00662 at <www.ecography.org/readers/appendix>). Appendix 1.

Ecography

ECOG-00662
Chevalier, M., Laffaille, P. and Grenouillet, G. 2014. Spatial synchrony in stream fish populations: influence of species traits. – Ecography doi: 10.1111/ecog.00662

Supplementary material

Supplementary material Appendix 1

Table A1. Trait values and levels of temperature synchrony (TEMP) for the 27 fish species. Trait descriptions are given in Table A2. Temperature synchrony was measured as for species synchrony i.e., as the mean of all the CCCs computed between pairs in the time series.

Species	TEMP	FH	FD	ST	LS	MA	LL	PC	HA	IP	UTT	FE	ED (mm)	SH	SW	BL (mm)
Abramis brama	0.81	1	3	1	3	4	2	1	2	2	24	50000	2.7	5.2	0.31	750
Alburnoides bipunctatus	0.70	2	2	2	1	2	3	1	2	2	19	1500	4.5	4.21	0.38	325
Alburnus alburnus	0.80	2	3	2	1	2	2	1	2	2	30	2000	1	2.41	0.42	150
Ameiurus melas	0.87	1	2	1	2	2	1	3	1	2	24	150	1.3	5.83	0.17	60
Barbatula barbatula	0.69	1	3	2	1	2	1	1	1	3	20	300	1.7	4.5	0.19	60
Barbus barbus	0.77	1	3	1	3	5	1	1	2	2	26	500	2.5	4.38	0.39	125
Blicca bjoerkna	0.79	1	2	2	2	3	2	1	1	1	27	20000	2.25	3.3	0.32	275
Carassius carassius	0.82	1	2	2	2	3	1	1	1	1	25	100000	1	4	0.28	125
Chondrostoma nasus	0.75	1	2	1	2	3	1	1	2	2	28	5000	1	6.5	0.58	100
Cottus gobio	0.79	1	3	1	1	2	3	3	1	3	32	800000	1.4	3.13	0.42	500
Cyprinus carpio	0.83	1	2	2	3	4	2	1	2	1	27	160000	1.5	2.71	0.42	325
Esox lucius	0.79	2	5	1	3	3	3	1	1	2	24	10000	2.2	5.23	0.3	500
Gasterosteus aculeatus	0.78	2	3	2	1	1	1	3	2	2	30	3000	1.7	5.72	0.28	125
Gobio gobio	0.78	1	3	2	1	2	2	1	2	3	26	300000	0.9	4	0.46	300
Gymnocephalus cernua	0.85	1	4	2	1	2	1	1	1	2	30	100	2.5	3.64	0.28	65
Lepomis gibbosus	0.85	2	3	2	2	2	1	3	2	1	25	109000	1.5	3.23	0.27	250
Leuciscus leuciscus	0.78	2	2	1	2	3	3	1	2	3	26	100000	1.75	2.81	0.33	400
Perca fluviatilis	0.80	2	4	1	3	3	2	1	1	3	30	5750	1.55	4.92	0.36	135
Phoxinus phoxinus	0.78	2	3	2	1	2	2	1	1	2	25	150000	1.4	2.95	0.36	225
Pungitius pungitius	0.86	2	3	1	1	1	1	3	2	2	25	10000	1.75	4.87	0.32	250
Rhodeus sericeus	0.78	2	2	2	1	1	3	2	2	2	25	50000	1.35	3.66	0.29	275
Rutilus rutilus	0.84	2	2	1	2	2	2	1	2	2	18	6000	2	4.95	0.29	150
Salmo trutta fario	0.87	2	4	1	2	3	3	2	1	3	24	100000	2.3	5.03	0.32	300
Scardinius erythrophthalmus	0.81	2	2	2	3	3	2	1	2	1	24	1500	2	3.58	0.31	110
Squalius cephalus	0.77	2	2	2	2	3	3	1	2	1	24	125000	1.5	3.97	0.36	400

Telestes souffia	0.76	2	3	1	2	3	2	1	2	1	25	1000	1.5	5.26	0.32	80
Tinca tinca	0.83	1	2	2	2	3	2	1	1	1	35	5000	1.45	4.43	0.37	250

Table A2. Description of the 15 traits used.

Trait	Code	Modality	Description
Diet	FD	1	Omnivorous
		2	Invertivorous
		3	Invertivorous-carnivorous
		4	Piscivorous
Body length	BL	quantitative	Total body length from the mouth to the fork of the tail (mm)
Larval length	LL	1	≤ 4.2mm
		2	4.2-6.3mm
		3	> 6.3mm
Shape factor	SH	quantitative	Ratio of total body length to maximum body depth
Swimming factor	SW	quantitative	Ratio of the minimum depth of the caudal peduncle to the maximum caudal fin depth
Feeding habitat	FH	1	Benthivorous
		2	Water column
Resting habitat	HA	1	Demersal
		2	Benthopelagic
		3	Pelagic
Absolute fecundity	FE	quantitative	Number of oocytes
Spawning times	ST	1	Once a year
		2	Several times a year
Egg diameter	ED	quantitative	At hatching (mm)
Life span	LS	1	< 8 years
		2	8-15 years
		3	> 15 years
Female maturity	MA	1	≤ 2 years
		2	2-3 years
		3	3-4 years

		4	4-5 years
		5	≥ 5 years
Parental care	PC	1	No protection
		2	No protection, but with nester or egg hiders
		3	Nester or egg hiders
Incubation period	IP	1	≤ 7 days
		2	7-14 days
		3	> 14 days
Upper thermal optimum	UTT	quantitative	Optimum maximum temperature (°C)

Article III (*PIII*)

Chevalier M, Cornuault J, Laffaille P et Grenouillet G. Disentangling the influence of climatic variables on spatial and temporal variations of freshwater fish population dynamics. (En preparation).

Disentangling the influence of climatic variables on spatial and temporal variations of freshwater fish populations.

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Abstract

Identifying the factors influencing population dynamics has long been debated, but whether intrinsic *vs* extrinsic processes are driving inter-annual variations in population size still remains unresolved for most organisms. In this study, we reveal general patterns in population dynamics for 28 freshwater fish species, which depend on a complex interplay between parameters determining local population size (i.e. population growth rate, migration rate and density-dependence) and environmental variables. We further demonstrate that spatial heterogeneity of population dynamics can be explained by spatial variation in the influence of environmental conditions. Overall, the contribution of environmental variables through density dependence to spatio-temporal variation in population size was weak, which contrast with the contribution of those variables through the population growth rate and the migration rate. Common mechanisms driving population dynamics were identified at the species level, but also revealed spatial patterns in their contribution to local population dynamics. While most of previous studies have considered the environment as a stochastic process influencing population dynamics, our study provide novel evidence that considering the deterministic nature of climatic factors can improve the identification of the determinants of population dynamics and could be used to predict future population declines.

Key words: population dynamics, climatic variables, freshwater fish, population dynamic parameters

Introduction

Identifying the factors contributing to fluctuations in population abundances is a central question in ecology (De Valpine & Hastings 2002). In particular, whether population dynamics of wild organisms are regulated by environmental factors (Andrewartha & Birch 1954) or by density-dependent processes (Nicholson 1933) has been much debated. Today, although most ecologists recognize that both intrinsic and extrinsic processes are relevant, their relative contribution to population dynamics in the wild remains unresolved (Knape & De Valpine 2011). This issue is made even more complex by the additional effect of migration on population dynamics (Grøtan *et al.* 2009a) as migration may strongly affect density-dependent processes (Ives et al. 2004) and population responses to environmental variations (Ranta *et al.* 2005). Complex patterns of population dynamics could also emerge from interaction between intrinsic and extrinsic processes (Fromentin *et al.* 2001; Stenseth *et al.* 2004) which further complicate the evaluation of the contribution of each process to population dynamics.

In recent years, evidence of climate warming (Stocker *et al.* 2013) made it ever more urgent to improve our capacity to predict species responses to environmental variation, calling for further research on the determinants of population dynamics. The consequences of climate change on populations are most evident at the edge of the geographical distribution of species, where range expansions (Sakai *et al.* 2001) or contractions (Hampe & Petit 2005) may occur. At both extreme of environmental gradients, population dynamics are therefore expected to vary with, for instance, population decline at one extreme and population increase at the other (Matías & Jump 2014). Studying spatial variations in population dynamics along environmental gradients may thus help predicting population trends and the future distribution of species. However, our present knowledge on the influence of climatic variables on population dynamics is largely biased toward few taxonomic groups (i.e. birds and mammals, Ockendon *et al.* 2014).

Interestingly, recent studies have reported large intraspecific variations in population abundance, providing the basis for disentangling which factors determine spatial variation in population dynamics. Spatial gradients in population dynamics have notably been related to factors such as latitude (e.g. Saether *et al.* 2008), distance from species range limits (Williams *et al.* 2003) or the abiotic environment (Saether *et al.* 2008), suggesting that intraspecific variation in population dynamics might be predicted from knowledge on geographical locations and environmental conditions. Such relationship between environmental factors and population dynamics may reflect a dependency of the deterministic components of population dynamics (e.g. strength of density dependence, population growth rate) on the environment (e.g. Post 2005). For instance, spatial variations in the strength of density dependence can reflect variations in the availability of critical resources (Wang *et al.* 2008). Similarly, spatial variations in the effects of environmental factors on population dynamics can exhibit a gradient from the core to the edge of species range (Fukaya *et al.* 2014), likely to generate spatial variations in population dynamic patterns (Saether *et al.* 2003; Williams *et al.* 2003). Thus, to further our understanding of the factors generating spatial variation in population

dynamics, accurate estimates of the relative contribution of both intrinsic and extrinsic processes to inter-annual changes in population size at different locations are clearly needed.

The few studies that have considered intraspecific variation in population dynamic processes have generally been conducted on a single species (Post *et al.* 2009). Consequently, these studies did not seek to pinpoint the common (cross-species) response of species to environmental factors, preventing the identification of general rules in the determinants of population dynamics. Indeed, cross-species comparisons could help distinguish species-specific processes from more general rules. For instance, Saether et al. (2008) revealed an overall weak influence of density dependent processes on bird species but species-specific latitudinal gradients in the effect of spring temperature on population size. Such comparative studies have however been restricted to few time series and taxa (i.e. mammals and birds) and cannot be generalized to other taxonomic groups, as the determinants of population dynamics are known to depend on species-specific life-history traits (Sæther *et al.* 2013).

In this study, we used an extensive database comprising 1856 time series of population abundance to examine spatio-temporal variation of freshwater fish populations using a hierarchical Bayesian approach. We used state-space models to assess the influence on population dynamics of four environmental variables recognized as important drivers of both, fish species distribution (Comte & Grenouillet 2013) and fish population dynamics (Chevalier *et al.* 2014). More specifically, we aimed at determining (1) the relative influence and contribution of environmental variables to population dynamics, (2) their interplay with parameters determining local population size (density dependence, growth rate and migration rate) and (3) their contribution to species-specific spatial variation of population dynamics. Overall, we demonstrated that environmental variables mostly influenced population dynamics through the growth rate. Among environmental variables, mean annual water temperature was the variable having the greatest influence on abundance patterns. Furthermore, although deterministic mechanisms were identified at the species level, we found that these mechanisms could translate into large spatial variation in abundance patterns because of contrasted influence of environmental variables on population dynamic parameters. These mechanisms greatly varied among species and suggest species-specific responses to environmental variations as well as species-specific sensitivity to future climate change.

Materials and methods

DATASETS

Population time series

Fish population abundances were provided by the French National Agency for Water and the Aquatic Environment (ONEMA). These annual data were obtained between 1982 and 2011 by electrofishing during periods of low flow (for further details see Poulet *et al.* 2011).

Fish were identified to species level, counted and released. Only time series comprising at least 17 years of data with a homogeneous sampling protocol and less than three consecutive years missing were retained. In total, 219 sites located throughout mainland France (Appendix S1; Figure S1) and representing 1856 time series (mean time series length = 19.02 ± 0.1) were retained.

Environmental variables

As temperature is recognized as an important determinant of both fish species distribution (Comte & Grenouillet 2013) and population dynamics (Chevalier *et al.* 2014), we calculated three variables related to water temperature that were subsequently used to characterize the environmental conditions prevailing at each fish sampling site: (1) an index of environmental stochasticity estimated by the coefficient of variation of daily water temperature over the whole study period at each site (CV_i), (2) annual mean water temperature ($meanT_{i,t}$) and (3) its associated variance ($varT_{i,t}$). Water temperature at each sampling site was predicted from air temperature data using a random forest procedure (Appendix S1). We also considered the influence of altitude (Alt_i) as a synthetic variable representing spatial variations in several parameters (e.g. physical, climatic).

MODELLING PROCEDURE

The number of fish of each species captured during each sampling event (hereafter observed abundances) is subject to sampling error and therefore represent only a fraction of the total number of individuals present on site (true abundances). To take sampling error into account, we fitted a state-space model to each species' abundance data. These models are described by two equations: an observation equation describing the sampling error and a state equation defining the evolution of the process through time (De Valpine & Hastings 2002).

Denote $N_{i,t}$ the true abundance and $X_{i,t}$ the observed abundance at site i and time t. In our models $X_{i,t}$ was considered a random variable binomially-distributed with parameters $N_{i,t}$ the number of trials and p_i the site-specific probability of capture. $N_{i,t}$ was also considered a random variable, Poisson-distributed with an expected value calculated as a modified version of the stock-recruitment Ricker model:

$$E(N_{i,t}) = \left[\gamma_{i,t} + N_{i,t-1}\exp\left(\rho_{i,t} - \eta_{i,t}N_{i,t-1}\right)\right] * \frac{S_{t-1}}{S_t}$$

where $\gamma_{i,t}$ is the migration rate, $\rho_{i,t}$ is the population growth rate, $\eta_{i,t}$ is the coefficient of density dependence, and $\frac{S_{t-1}}{S_t}$ is an offset term with S_t the sampling area at time t.

In our models, population dynamics are approximated by a Markovian process such that the abundance at time t ($N_{i,t}$) depends only on the abundance at time t-1($N_{i,t-1}$). It is therefore a memory-less process which does not account for delayed effects of density dependence, a possibly important driver of population dynamics (Turchin 1990). This choice

was made to avoid over-parameterization of the models. We nevertheless tested whether time series displayed significant delayed density dependence using a Box-Jenkins procedure (Turchin 1990). As only 5% of the time series presented evidence of delayed density dependence, this process should weakly influence our results.

To test for the importance of environmental factors in determining population dynamics, we included in our model a generalized linear model (GLM) relating the population dynamic parameters ($\gamma_{i,t}$, $\rho_{i,t}$ and $\eta_{i,t}$) to environmental variables. Specifically, we considered four environmental covariates according to the following equations:

$$\gamma_{i,t} = \gamma_a + (\gamma_b * Alt_i) + (\gamma_c * CV_i) + (\gamma_d * meanT_{i,t}) + (\gamma_e * varT_{i,t})$$

$$\rho_{i,t} = \rho_a + (\rho_b * Alt_i) + (\rho_c * CV_i) + (\rho_d * meanT_{i,t}) + (\rho_e * varT_{i,t})$$

$$\eta_{i,t} = \eta_a + (\eta_b * Alt_i) + (\eta_c * CV_i) + (\eta_d * meanT_{i,t}) + (\eta_e * varT_{i,t})$$

where γ_a, ρ_a and η_a are intercepts and the other parameters (γ_b, γ_c, γ_d, γ_e, ρ_b, ρ_c, ρ_d, ρ_e, η_b, η_c, η_d, η_e) are slope coefficients representing the effects of the environmental variables Alt_i, CV_i, $meanT_{i,t}$ and $varT_{i,t}$ on population dynamic parameters. For each species, all coefficients were constrained to be equal for all sites, as our goal was to identify general patterns for each species. All the predictors were transformed to z-scores, which standardizes the slope coefficients, allowing us to compare their relative strength.

ESTIMATION OF PARAMETERS

We adopted a Bayesian approach and used a Monte Carlo Markov Chain (MCMC) to sample posterior distributions of parameters (Clark & Bjørnstad 2004). We had no a priori belief about potential parameter values and consequently chose uninformative priors (i.e. large uniform distributions centered on zero) for all parameters. For the initial true abundance of each time series (N_1), we used as a prior a Poisson distribution with an expected value equal to the mean of observed abundances across the whole time series, increased by one (Kéry & Schaub 2012). For each species, between eight and 90 independent MCMC chains were run, depending on how well MCMC chains mixed. The length of chains varied between 2.10^5 and 9.10^6 iterations, depending on the number of iterations needed to pass burn-in. Different initial parameter values were used for each chain. After discarding burn-in iterations, the samples of all chains were combined for each species and convergence was visually assessed and confirmed by effective sample sizes greater than 195 for all parameters. Species for which convergence failed were discarded. Our study is therefore based on 28 species. The mode of the posterior distribution of each parameter was used as an estimate of the true value of this parameter. Highest Posterior Distribution (HPD) intervals were used as 95% credible intervals.

We used JAGS 3.3.0 for MCMC sampling (Plummer 2003). JAGS was run through the program R (R Core Team 2013) using the package R2jags (Su & Yajima 2013). Details

about the length of chains and burn-in, effective sample size and number of chains for each species are summarized in Appendix S2 (Table S1).

EFFECT SIZES

Among-species variation in the estimates of coefficients relating environmental variables to population dynamic parameters represents among-species variation in the underlying determinants of population dynamics. However, the actual effect of environmental variables on species abundance does not only depend on the value of these coefficients: the observed change in abundance entailed by a given environmental variable with a given coefficient value also depends on the range of spatio-temporal variation of the environmental predictor (e.g. the observed change in abundance entailed by altitude across the study region is different whether altitude range is 100m or 1000m) and on the population size (e.g. the observed change in abundance entailed by altitude across the study region may be different whether population size is 100 or 1000 individuals). Thus, the expected abundance of a given species at a given point in time and space depend on (1) the value of environmental variables, (2) abundance at this site on the previous year and (3) coefficient values. We therefore calculated effect sizes taking into account the natural variation of these environmental variables across the study region and period and relevant values of abundance.

We calculated for each coefficient, site and species, the effect size expected under our model with the values of coefficients estimated with the Bayesian analysis (i.e. γ_a, γ_b, γ_c, γ_d, γ_e, ρ_a, ρ_b, ρ_c, ρ_d, ρ_e, η_a, η_b, η_c, η_d, η_e). The effect size of each slope coefficient (representing the influence of each environmental variable through each parameter determining local population size) at site i and time t was expressed as the expected percentage of change in abundance induced by fixing the value of the coefficient considered to zero (i.e. no effect on the populations). To study the overall influence of each environmental variable on population size, through all population dynamic parameter simultaneously, effect sizes at site i and time t were calculated by fixing all the coefficients associated to the environmental variable considered at zero. Finally, to evaluate through which population dynamic parameter the overall environment (i.e. all environmental variables) influences population size, effect sizes at site i and time t were calculated by fixing all the coefficients associated to the parameter considered at zero. The detailed calculus of effect sizes is developed in Appendix S3.

POST-HOC ANALYSES OF PARAMETERS AND EFFECT SIZES

All parameters with a 95% HPD interval not overlapping zero were considered to represent a true effect (Table 1).

To determine whether effect sizes related to population dynamic parameters (ES_ρ, ES_γ and ES_η) and environmental variables (ES_{alt}, ES_{CV}, ES_{meanT} and ES_{varT}) were significantly different from zero and between each other's, we used Wilcoxon tests and Wilcoxon paired

tests, respectively. We also considered effect sizes in absolute values and used Wilcoxon paired tests to highlight differences in the magnitude of effect sizes related to population dynamic parameters and environmental variables. Wilcoxon tests were used to determine whether effects sizes associated to slope coefficients relating environmental variables to population dynamics parameters were significantly different from zero. To highlight species-specific patterns, the above effect sizes were considered separately for each species.

To study the within-species spatial heterogeneity of population dynamics we calculated for each species the standard deviation of effect sizes of each parameter studied. We then used Wilcoxon paired tests to determine whether the standard deviation of effect sizes related to population dynamic parameters, environmental variables and slope coefficients were significantly different between each other. For each species, we tested whether these effect sizes were spatially autocorrelated using the Moran's autocorrelation index and used linear mixed effect models to study their relationship with latitude, while taking into account catchment identity.

As multiple comparisons were performed, the p-values were adjusted according to the sequential Bonferroni procedure to conserve an initial type I error rate of 0.05.

RESULTS

Coefficients relating environmental variables to population dynamic parameters

The estimated parameters from the process and observation models for each species are given in Table 1. Whatever the species, at least one coefficient relating environmental variables to population dynamic parameters was significant. We found that 44% of the species had their migration rate that was significantly influenced by at least one of the four environmental variables whereas these percentages were 76% for both the growth rate and density dependence (Table 1). Considering environmental variables, 64% of the species had at least one of their population dynamic parameter that was significantly influenced by Alt_i whereas these percentages were 65%, 62% and 70% for CV_i, $meanT_{i,t}$ and $varT_{i,t}$, respectively. For most species, a concomitant influence of several environmental variables on population dynamic parameters was observed.

Table 1. Standardized slope coefficients representing the influence of altitude (subscript b), CV (subscript c), meanT (subscript d) and varT (subscript e) on the migration rate (γ), the growth rate (ρ) and density dependence (η). N_{series} is the number of time series for each species. $P_{capture}$ is the estimated mean probability of capture. Values in bold are values for which the 95% credible interval do not overlap zero.

Species name	Species code	γ_b	γ_c	γ_d	γ_e	ρ_b	ρ_c	ρ_d	ρ_e	η_b	η_c	η_d	η_e	N_{series}	$P_{capture}$
Common bleak	Alal	**3.58**	**2.90**	**12.50**	-1.43	**-0.05**	**-0.26**	**-0.59**	**0.28**	**8.55E-04**	**-7.99E-04**	**-1.49E-03**	**9.57E-04**	72	0.35
European eel	Anan	-0.09	0.00	0.00	-0.02	0.00	**-0.04**	**-0.04**	**0.06**	**1.25E-03**	-3.38E-05	**1.86E-04**	1.59E-04	133	0.54
Stone loach	Baba	-0.15	**1.96**	0.75	0.32	0.00	**-0.10**	**-0.03**	0.00	**4.35E-05**	**-2.32E-04**	**8.04E-05**	**-1.54E-04**	154	0.39
Barbel	Babr	**3.07**	**2.15**	0.33	**-4.56**	**-0.25**	**-0.10**	**0.18**	**0.11**	**-3.06E-03**	**-3.18E-04**	**3.35E-04**	**2.29E-04**	59	0.39
Silver bream	Blbj	**-16.13**	3.22	-3.46	**-6.04**	**0.73**	**-0.17**	0.00	**0.26**	**4.00E-03**	**2.09E-03**	**2.18E-03**	**-3.67E-03**	30	0.28
Common bullhead	Cogo	-0.04	**0.38**	0.19	**-0.50**	**0.06**	**-0.21**	**-0.10**	**0.26**	**1.76E-04**	**-2.79E-04**	3.65E-05	**2.38E-04**	117	0.42
common carp	Cyca	**-3.29**	-1.40	-1.00	-0.44	0.82	0.72	-0.19	-1.10	-4.60E-02	6.15E-03	**-1.02E-01**	8.04E-04	11	0.29
Pike	Eslu	0.32	-0.21	-0.03	0.09	**-0.41**	**1.01**	0.46	-0.94	**-2.73E-02**	**4.74E-02**	6.28E-03	-5.89E-02	58	0.31
Three-spined stickleback	Gaac	**-1.92**	**3.95**	**2.66**	**-6.40**	**0.69**	**-2.13**	**-1.37**	**2.86**	**9.20E-03**	**-2.60E-02**	**-1.48E-02**	**3.59E-02**	21	0.22
Gudgeon	Gogo	**-1.18**	**-0.41**	**-1.70**	**0.32**	**0.15**	0.01	**0.22**	0.01	**-2.79E-05**	2.59E-05	**2.50E-04**	**-1.48E-04**	152	0.42
Ruffe	Gyce	-0.94	**-2.55**	-1.43	**4.44**	0.17	**0.52**	**0.27**	**-0.94**	-6.09E-04	-3.61E-04	**-1.23E-03**	8.60E-05	20	0.29
Lamprey	Lapl	0.08	**-2.09**	0.40	0.38	**-0.16**	-0.04	**-0.36**	**0.29**	**-3.91E-03**	**1.16E-03**	**-3.43E-03**	**-4.90E-04**	78	0.28
Pumpkinseed	Legi	-0.02	0.04	0.00	-0.07	**-0.21**	**0.22**	**-0.08**	**-0.28**	**-6.01E-03**	**2.99E-03**	**-5.01E-03**	**-4.54E-03**	53	0.35
Common dace	Lele	0.09	-0.14	-0.29	0.47	**-0.10**	**0.48**	**0.54**	**-0.76**	**-1.62E-03**	**3.03E-03**	**2.01E-03**	**-4.59E-03**	74	0.39
European nase	Pato	**1.55**	**-5.03**	-2.64	**5.74**	**-0.40**	**0.76**	**0.47**	**-1.03**	**-1.28E-03**	-6.06E-04	**8.40E-04**	**-2.37E-03**	14	0.46
European perch	Pefl	**-0.64**	**-0.74**	**-2.51**	**1.58**	**0.10**	**0.22**	**0.63**	**-0.49**	**9.66E-04**	**6.68E-04**	**3.61E-03**	**-2.71E-03**	86	0.34
Eurasian minnow	Phph	**-0.49**	-0.21	0.02	-0.04	**0.06**	**-0.07**	**-0.07**	**0.13**	**3.64E-05**	1.02E-06	7.35E-06	5.77E-06	148	0.41
Nine-spined stickleback	Pupu	-0.68	**-1.84**	1.54	**2.20**	**0.20**	**0.37**	**-0.08**	**-0.42**	**3.05E-03**	**6.11E-03**	**-1.29E-03**	**-6.64E-03**	27	0.34
Roach	Ruru	**-1.01**	**8.36**	**8.74**	**-10.34**	**0.01**	**-0.18**	**-0.22**	**0.23**	**-4.64E-05**	**-1.91E-04**	**-3.23E-04**	**2.37E-04**	125	0.43
sander	Salu	0.00	-0.50	-0.13	0.07	0.95	0.38	-0.21	**0.66**	1.03E-01	**-2.33E-02**	**-4.00E-02**	**9.26E-02**	16	0.20
Atlantic salmon	Sasa	-0.53	0.18	-0.24	0.22	**0.48**	**0.20**	**0.55**	**-0.40**	**4.55E-03**	**1.14E-03**	**2.10E-03**	**-1.64E-03**	28	0.46
Brown trout	Satr	-0.58	-0.30	**-0.57**	0.00	0.01	**-0.02**	**-0.05**	**0.05**	-7.94E-06	**-2.00E-04**	**-3.70E-04**	**4.18E-04**	141	0.5
Rudd	Scer	**-0.23**	**-0.92**	**-1.20**	**1.59**	0.08	0.01	-0.06	**-0.48**	**2.54E-02**	**-7.54E-03**	**-1.80E-02**	**7.20E-03**	31	0.38
wels catfish	Sigl	0.01	0.04	-0.02	-0.02	**-0.34**	**-0.53**	**0.44**	**0.64**	**-9.99E-03**	-7.15E-04	1.73E-04	**5.30E-03**	9	0.18
European chub	Sqce	**-10.43**	**-11.31**	**-20.65**	**15.89**	**0.28**	**0.13**	**0.37**	**-0.21**	**7.06E-04**	**1.86E-04**	**1.45E-04**	**-4.52E-04**	137	0.39
western vairone	Teso	**-7.90**	-4.58	2.21	**25.13**	**0.60**	**0.27**	**0.48**	**-1.79**	**2.88E-03**	**-1.63E-03**	-6.24E-05	**-3.34E-03**	11	0.44
grayling	Thth	13.76	9.45	0.50	**6.97**	-0.65	-2.46	-0.66	1.50	2.61E-02	-4.54E-02	-1.22E-02	2.86E-02	6	0.67
Tench	Titi	0.16	-0.23	**-0.37**	0.32	0.06	**0.47**	**0.53**	**-0.65**	-1.70E-04	**1.17E-02**	**1.19E-02**	**-1.67E-02**	45	0.38

Effect sizes related to population dynamic parameters

Effect sizes associated to the three population dynamic parameters were all significantly different between each other (Wilcoxon paired tests; P<0.001). ES_ρ and ES_γ were significantly (Wilcoxon tests; P<0.001) different from zero whereas ES_η was not (Wilcoxon tests; P=0.09; Fig. 1A). Overall, the median values of ES_ρ, ES_γ and ES_η were negative, thus revealing a negative influence of environmental variables on abundance patterns through the three parameters determining local population size. However, considerable variations were found within ES which suggest species-specific responses to environmental variables (Table 2). All the comparisons between absolute effect sizes were significant (Wilcoxon paired tests; P<0.001). The greatest percentage of change in abundance was observed for ES_ρ followed by ES_γ and then ES_η (Fig. 1B). Nonetheless, the relative contribution of environmental variables to abundance patterns through the three population dynamic parameters strongly varied depending on the species considered (Fig. 1C).

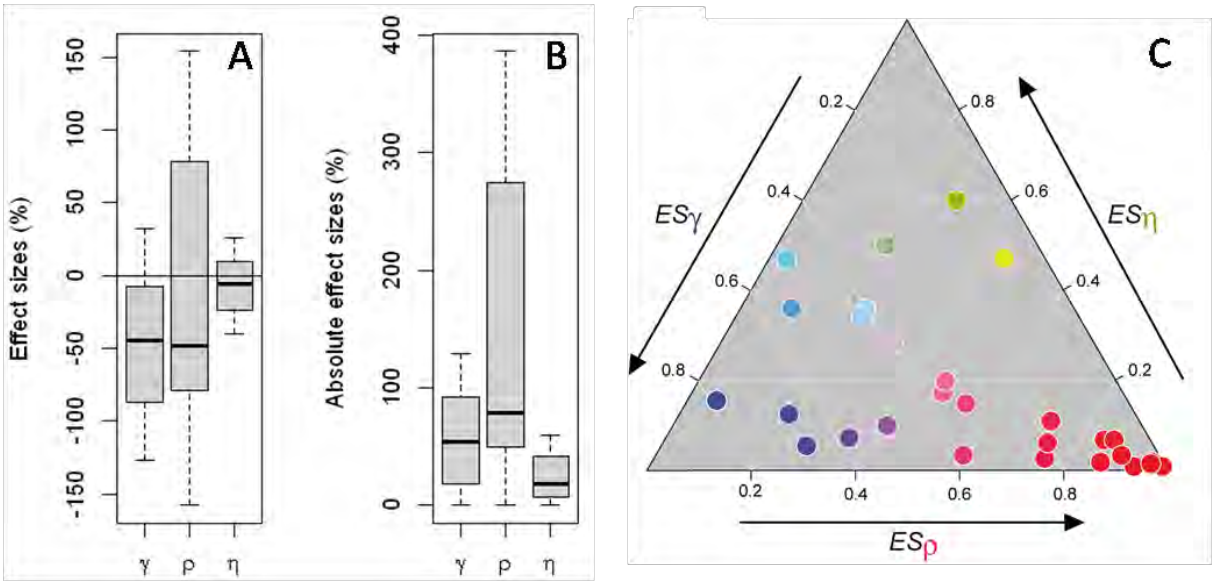

Figure 1. Overall effect sizes (A) and absolute effect sizes (B) related to population dynamic parameters (γ= migration rate; ρ=population growth rate; η=density-dependence). (C) Species-specific contribution of environmental variables to variation in abundance patterns through the three population dynamic parameters.

Effect sizes related to environmental variables

Effect sizes related to environmental variables were all significantly different between each other (Wilcoxon paired tests; P<0.05) and from zero (Wilcoxon tests; P<0.05). The median value of ES_{varT} was positive whereas it was the opposite for ES_{alt}, ES_{CV} and ES_{meanT} (Fig. 2A). However, considerable variations were found within ES due to species-specific responses to environmental variables (Table 2). Comparisons between absolute effect sizes were all significant (Wilcoxon paired tests; P<0.05) with ES_{meanT} displaying the greatest value and ES_{Alt} showing the lowest one (Fig. 2B). When considering absolute effect sizes at the species level, we found strong variations in the relative contribution of environmental variables to population dynamics (Fig. 2C).

Table 2. Species-specific effect sizes related to population dynamic parameters (ES_{γ}, ES_{ρ}, ES_{η}) and environmental variables (ES_{alt}, ES_{CV}, ES_{meanT}, ES_{varT}). Effect sizes significantly different from zero are in bold. Species code as in table 1.

Species code	ES_{γ}	ES_{ρ}	ES_{η}	ES_{alt}	ES_{CV}	ES_{meanT}	ES_{varT}
Alal	**-108.4**	**-93.7**	**82.1**	**-14.7**	**-89.3**	**-99.2**	**55.6**
Anan	**-4.6**	**-46.1**	**-8.9**	**-6.0**	**-31.8**	**-39.0**	**14.4**
Baba	**-49.4**	**30.7**	**4.1**	**-13.6**	**-68.7**	**64.3**	**-59.4**
Babr	-8.9	25.6	52.1	-5.6	-39.5	**-377.3**	**-98.2**
Blbj	**-45.2**	-3.2	**-9.6**	**-19.1**	-68.3	**-52.7**	-30.1
Cogo	**-30.4**	**698.4**	**-54.8**	**-36.1**	**223.5**	**639.8**	**-79.9**
Cyca	**-73.5**	**443.8**	**464.2**	**39.6**	28.0	51.2	**-69.7**
Eslu	5.4	**-87.8**	**5.1**	1.7	**-85.2**	**-67.2**	**98.7**
Gaac	**-92.0**	**-315.8**	**-11.2**	**-6.5**	**-76.9**	**-85.4**	**-49.3**
Gogo	**-103.1**	**-68.1**	**-83.6**	**-28.0**	**-99.9**	**-99.4**	**-85.2**
Gyce	**-141.2**	**51.1**	**-12.3**	**-2.8**	**-63.4**	**-96.5**	**-99.7**
Lapl	**-111.6**	**-94.7**	**22.8**	**-3.0**	**-83.7**	**-84.5**	**-35.4**
Legi	**-48.2**	**709.6**	**-12.1**	1.8	**-15.2**	**38.7**	**12.6**
Lele	**-95.0**	-90.6	-4.5	**-18.7**	**-89.2**	**-88.4**	**-96.9**
Pato	**-9.5**	**-68.8**	**9.9**	**-0.7**	**-46.2**	**-26.7**	**10.7**
Pefl	**-72.1**	**-84.4**	**-54.1**	0.6	**-192.4**	**-87.6**	**-35.9**
Phph	**-116.3**	**-83.2**	161.4	-52.3	**-97.5**	-77.4	-201.6
Pupu	**-75.6**	**254.7**	**-26.6**	**-6.7**	2.4	**-57.8**	**-72.7**
Ruru	**-26.0**	**-25.2**	**26.9**	**-35.4**	**127.6**	-39.3	**-68.2**
Salu	**-83.9**	**-54.5**	**74.9**	**-12.8**	**-72.5**	**-73.3**	**-82.0**
Sasa	**-70.6**	-120.8	7.5	-1.0	-14.5	**-79.0**	16.1
Satr	**-7.1**	**2739.0**	**-56.9**	-0.1	**155.2**	**564.8**	**-65.3**
Scer	**-47.5**	**-62.9**	-32.0	**-72.1**	**-94.8**	**323.5**	**240.9**
Sigl	**-61.4**	**402.4**	**-40.4**	0.7	**42.2**	2.3	**-103.3**
Sqce	**-100.5**	**-142.0**	**24.2**	**-27.0**	-82.3	-63.5	**-93.7**
Teso	**-19.3**	**-29.7**	**11.8**	**-0.5**	**-17.0**	**-27.9**	**5.9**
Thth	**-7.2**	**-55.6**	**-4.1**	1.0	**-51.7**	**-48.3**	**49.3**
Titi	**-34.0**	**1310.0**	**-32.5**	**-6.6**	**288.5**	**221.4**	**-105.5**

Effect sizes related to slope coefficients

Effect sizes associated to coefficients relating environmental variables to population dynamic parameters were all significantly (Wilcoxon tests; $P<0.001$) different from zero except for $ES_{\rho e}$ (Wilcoxon tests; $P=0.26$; Fig. 3A). The influences of environmental variables on abundance patterns were overall negative but varied among population dynamic parameters and could even exhibit opposite directions depending on the parameter considered (Fig. 3A). The greatest percentages of change in abundance were found for coefficients relating environmental variables to the growth rate (i.e. $ES_{\rho b}$, $ES_{\rho c}$, $ES_{\rho d}$, $ES_{\rho e}$) whereas the least percentages of change were found for coefficients relating environmental variables to density dependence (i.e. $ES_{\eta b}$, $ES_{\eta c}$, $ES_{\eta d}$, $ES_{\eta e}$; Fig. 3B). When considering species-specific effect sizes, strong variations among species revealed species-specific responses to

environmental variations and idiosyncratic influences of environmental variables through population dynamic parameters (Appendix S4, Table S2).

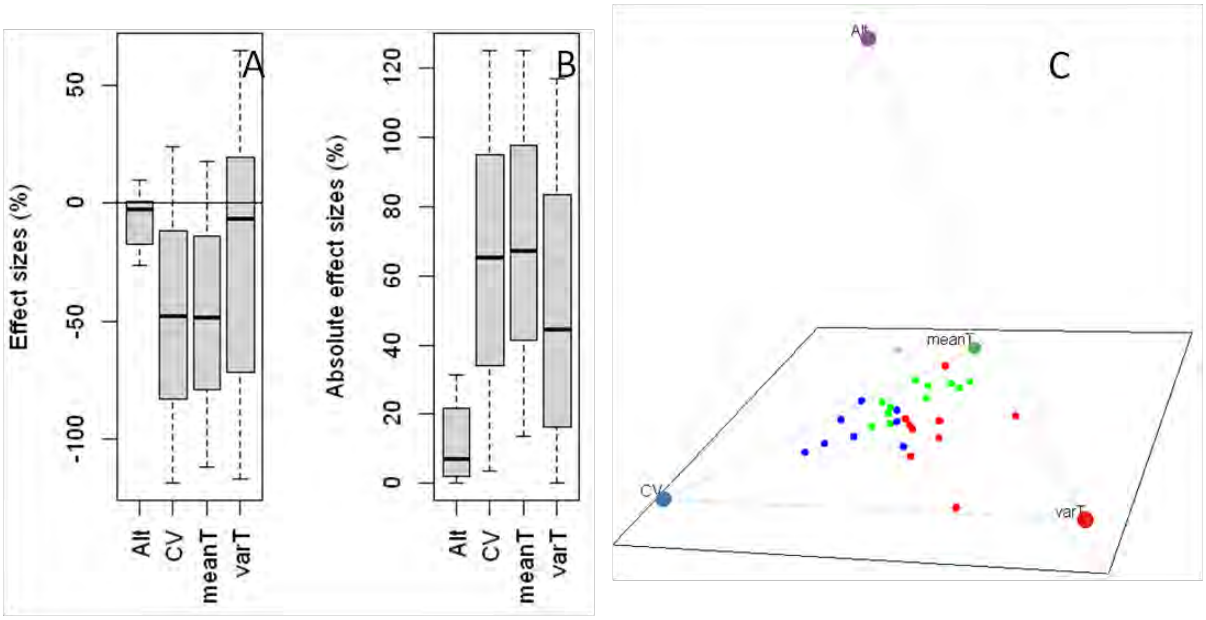

Figure 2. Overall effect sizes (A) and absolute effect sizes (B) related to environmental variables (Alt=altitude; CV=overall water temperature variability measured over the whole study period; meanT=mean annual water temperature; varT=variance of annual water temperature). (C) Species-specific contribution of environmental variables to variation in abundance patterns.

Spatial patterns of effect sizes

Overall, ES_{ρ} displayed significantly (Wilcoxon paired tests; $P<0.01$) more spatial variation than ES_{γ} (Fig. 4A). No significant (Wilcoxon paired tests; $P>0.05$) differences in spatial variations were found between ES_{ρ} and ES_{η} or between ES_{γ} and ES_{η}. The relative contribution of environmental variables to spatial variation in abundance patterns through population dynamic parameters strongly varied depending on the species considered (Fig. 4B). For effect sizes related to environmental variables, ES_{meanT} presented significantly (Wilcoxon paired tests; $P<0.05$) more spatial heterogeneity than ES_{CV} , ES_{varT} and ES_{alt} (Fig. 4C). All other comparisons between standard deviations of effect sizes related to environmental variables were not significant (Wilcoxon paired tests; $P>0.05$). We also found strong interspecific differences in the relative contribution of environmental variables to spatial variation in population dynamics (Fig. 4D). Nevertheless, spatial heterogeneity of effect sizes depended on the interplay between environmental variables and population dynamic parameters (Appendix S4, Table S3).

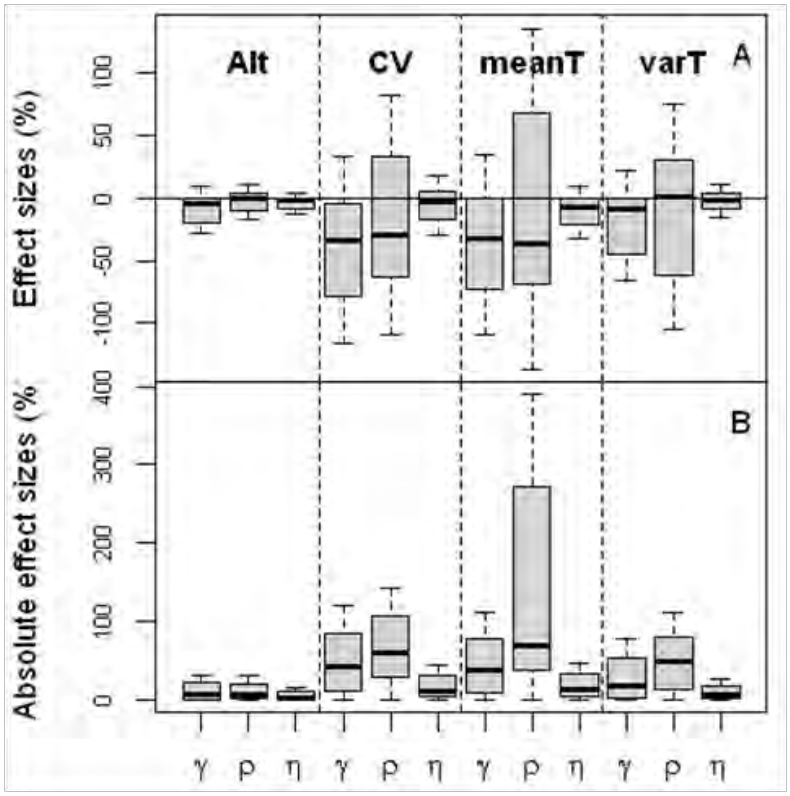

Figure 3. Overall effect sizes (A) and absolute effect sizes (B) associated to slope coefficients relating environmental variables to population dynamic parameters.

Strong within-species spatial variations and spatial patterns in effect sizes were detected for some species. Among the 28 species, 50%, 35% and 28% presented significant ($P<0.05$) spatial autocorrelation in ES_γ, ES_ρ and ES_η, respectively (Appendix S5, Table S4). For effect sizes related to environmental variables, 35%, 35%, 32% and 18% of the species displayed significant spatial autocorrelation for ES_{alt}, ES_{CV}, ES_{meanT}, ESv_{arT}, respectively (Appendix S5, Table S5). However, spatial autocorrelation of effect sizes depended on the population dynamic parameter through which environmental variables influenced abundance patterns (Appendix S5, Table S6). For instance, spatial variation of effect sizes related to CV_i for brown trout could be partitioned into spatial variation of effect sizes related to γ_e, ρ_e and η_e. This partition revealed contrasted spatial patterns depending on the population dynamic parameter considered (Fig. 6). Latitudinal gradients in effect sizes were also detected depending on the species and the effect sizes considered (Appendix S4, Table S7 to S9).

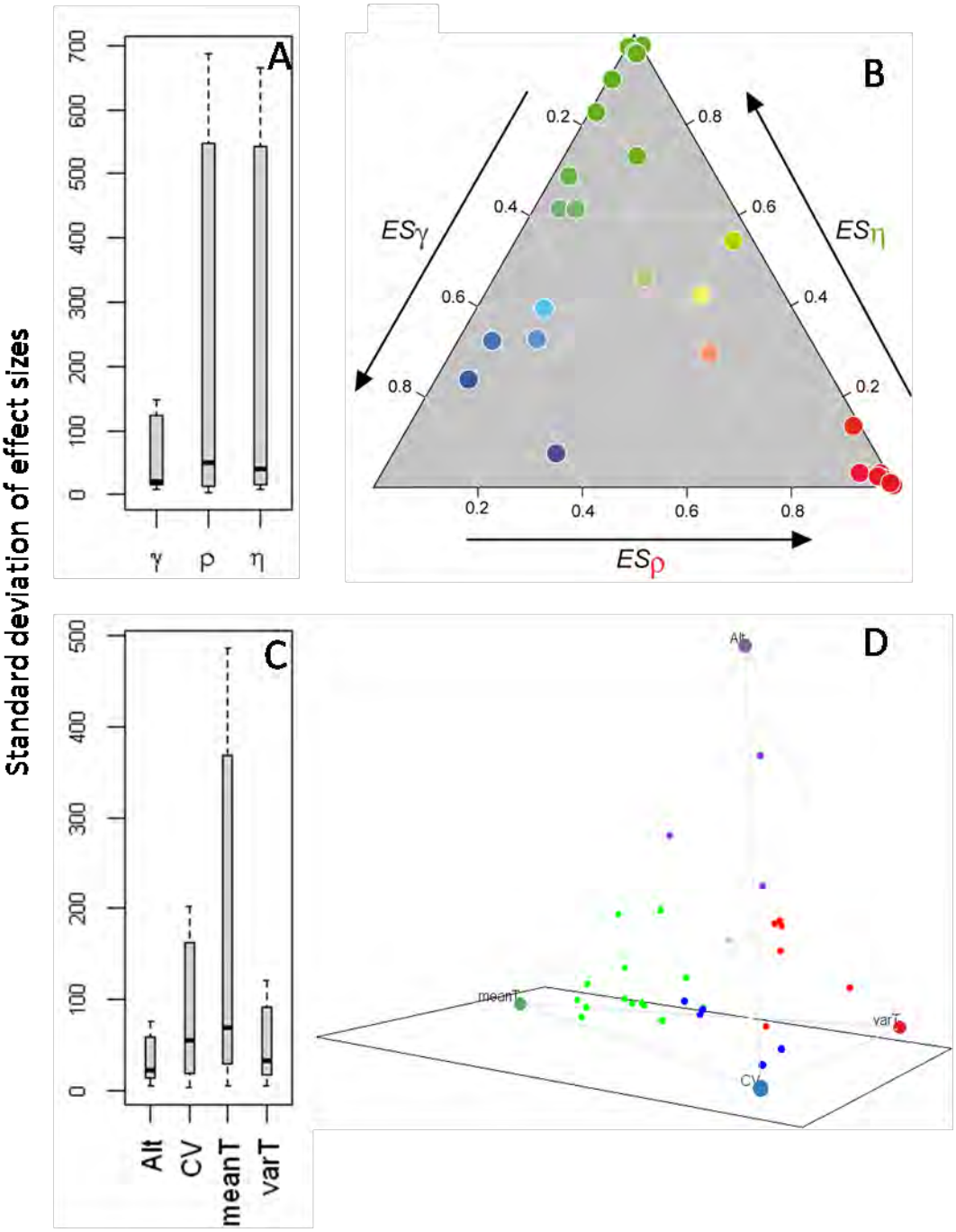

Figure 4. Overall standard deviation of effect sizes related to population dynamic parameters (A) and environmental variables (C). Species-specific contribution to spatial variation in abundance patterns of (B) all environmental variables through population dynamic parameters and (D) each environmental variable.

Discussion

For detecting the impact of climate on population dynamics it has been suggested to restrict analyses to a few number of covariates with well-founded hypotheses about their effects on population dynamics (Knape & De Valpine 2011). Here, by calculating effect sizes that quantify the percentage of change in abundance due to environmental variations, we

evaluated the influence and the relative contribution of four environmental variables to spatial and temporal variations in population size for 28 freshwater fish species. Four main results revealing global and species-specific patterns were raised. First, population sizes were not influenced in the same way and with the same magnitude by environmental variables. Second, the influence of environmental variables on inter-annual variations in population size varied depending on the population dynamic parameter through which environmental variables influenced abundance patterns. Third, the influence of environmental variables on abundance patterns was spatially heterogeneous but the degree of spatial heterogeneity in the influence of environmental variables varied depending on the population dynamic parameter considered. Fourth, the three aforementioned general patterns greatly varied depending on the species considered.

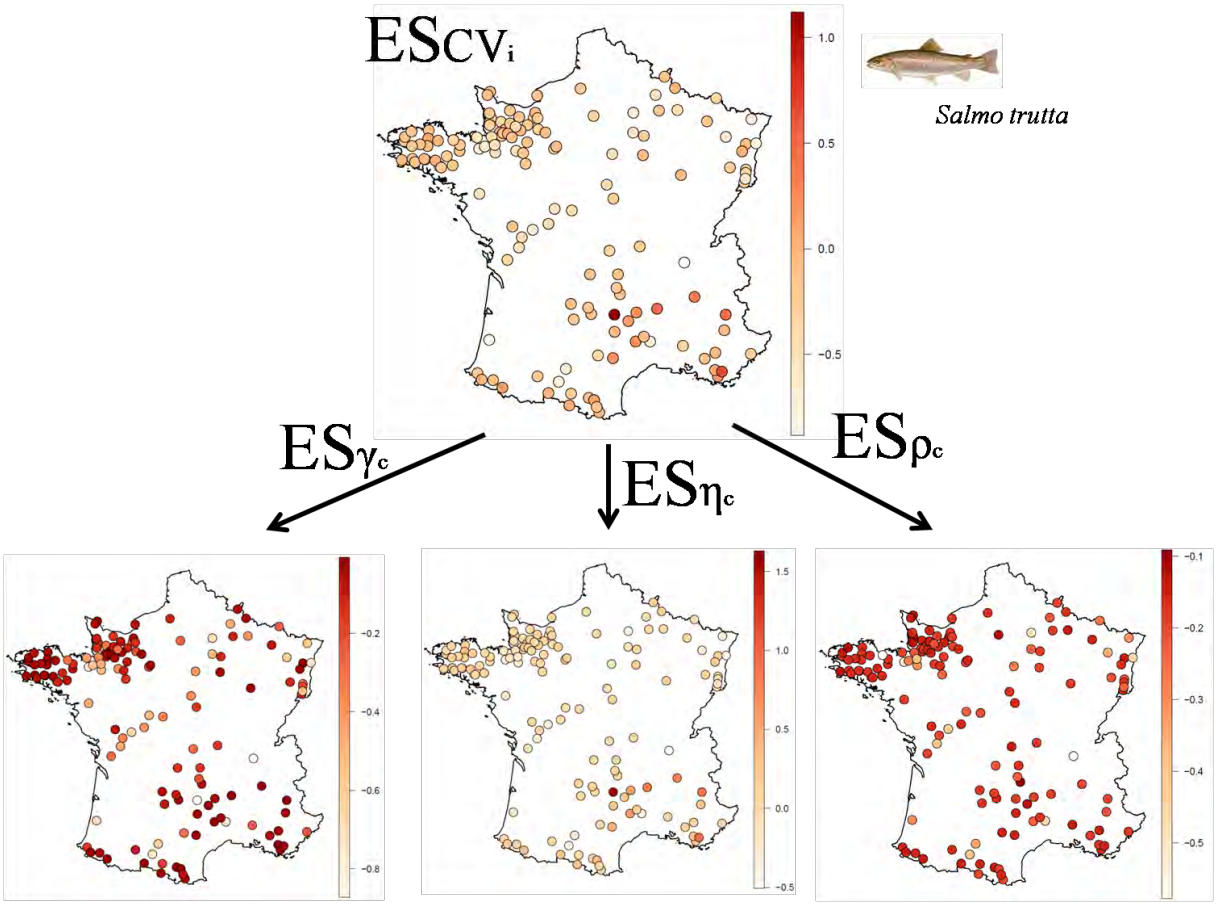

Figure 5. Spatial pattern of effect sizes related to overall environmental stochasticity (ES_{CVi}) and environmental stochasticity through the three parameters determining local population size (ESγc, ESρc, ESηc) for the brown trout.

Although several studies have examined the relative contribution of intrinsic and extrinsic processes to inter-annual variations in population size (Forchhammer *et al.* 1998; Saether *et al.* 2008; Grøtan *et al.* 2009b), few were able to quantify the degree to which these factors influenced populations (but see Saether *et al.* 2008). Although such studies could provide knowledge on which mechanism is influencing populations, they do not provide information on which process has the most influence on population dynamics. Furthermore,

the interplay between environmental variables and parameters determining the expected dynamics of population (i.e. the growth rate, the migration rate and the density dependence) has seldom been considered. One possible explanation for such a gap could be that the relative contribution of intrinsic and extrinsic processes is complicated by the existence of strong intraspecific variation in population dynamics (Saether *et al.* 2008; Grøtan *et al.* 2009b).

Influence of environmental variables through population dynamic parameters

Overall, we found contrasted influence of environmental variables through the three parameters involved in inter-annual variations in population size. Environmental variables had more influence on abundance patterns through the population growth rate and to a lesser extent, the migration rate, than through density dependence. The influence of environmental variables through density dependence was overall weak which suggest that variations in density-dependent processes due to climatic factors are unlikely to translate into large changes in population dynamics. Such weak influence of density dependence on population dynamics contrasts with the results of Coulson et al. (2008) who found that the influence of this parameter was approximately twice as important in determining the dynamics of Soay sheep populations as were the influences of age-structure variation or climate. Nonetheless, our results confirm other studies demonstrating that the influence of density-dependent processes on population dynamics is generally weak (e.g. Saether *et al.* 1996; Kölzsch *et al.* 2007; Grøtan *et al.* 2009b). Overall, our results suggest that future climate change is more likely to impact fish population dynamics through changes in population growth rate and migration rate than through changes in density-dependent processes.

Influence of environmental variables on abundance patterns

Mean annual water temperature and to a lesser extent the site-specific stochasticity were the variables that had the strongest influence on abundance patterns relative to water temperature variability and altitude. Surprisingly, we found that altitude had only a weak influence on population dynamics although this factor has already been demonstrated to be an important driver of both population dynamics (Pulliam & Danielson 1991) and species distribution (Comte & Grenouillet 2013). In accordance with our results, van de Pol *et al.* (2010) found that temperature average was more important than variability for population persistence of Oystercatchers. As climate models predict larger changes in the average than in the variability of local temperature (Stocker *et al.* 2013), the effects of future climate variability on population dynamics are expected to be overwhelmed by the effect of changes in climatic averages. Nonetheless, Garcia-Carreras & Reuman (2013) suggested that the patterns could be more complex. According to their simulations, changes in mean conditions are likely to have a greater impact than changes in variability for populations near species range boundaries than at the center of their range (i.e. close to their niche optimum). Furthermore, the relative influence of climate variability and climate means is expected to vary depending on species specific life-history traits (e.g. Morris *et al.* 2008). Consequently, to accurately estimate and predict the influence of climate change on population dynamics,

future studies should consider the influence of both mean conditions and variability of climatic variables on different populations and species.

Interplay between environmental variables and population dynamic parameters

Interestingly, we found that different environmental variables could have opposite effects on abundance patterns through the same population dynamic parameter and that the same environmental variable could influence populations in opposite directions through the three parameters determining local population size. These results suggest that the underlying mechanisms of population dynamics are complex and could be difficult to detect without considering the contrasting influence of environmental variables on population dynamic parameters. Such complex patterns have already been shown for instance in birds where local recruitment and immigration rate were influenced by food abundance, temperature and environmental stochasticity (Grøtan *et al.* 2009a). Furthermore, it has also been shown that climate variables can have opposite effects on some vital rates. For example, sea ice extent impacts survival and fecundity of emperor penguins in opposite ways (Barbraud & Weimerskirch 2001). Thus, to add to our knowledge of the mechanisms driving population dynamics, studies should consider the influence of different environmental variables simultaneously and should examine through which population dynamic parameters these variables influence abundance patterns. Modeling population dynamics in this way should improve our knowledge of the mechanisms influencing population dynamics and could provide insights about the potential consequences of global warming. For instance, our study revealed a negative influence of the mean annual water temperature on population dynamics through the growth rate which testify of some pessimism for freshwater fish populations in a global warming context.

Spatial patterns

Independently of the species considered, we found strong spatial variations in population dynamics. Overall, the influence of environmental variables on abundance patterns was more spatially heterogeneous through the population growth rate and the density dependence than through the migration rate. The environmental variables that contributed the most to spatial heterogeneity of population dynamics were the mean annual water temperature and the site-specific variability of water temperature whereas the one contributing the least was altitude. However, the relative contribution of environmental variables to spatial heterogeneity of population dynamics depended on the population dynamic parameter through which it influenced abundance patterns. This indicates that spatial variations in population dynamics are likely to depend on spatial variations in the influence of environmental factors on population dynamics as well as spatial variation of population dynamic parameters depending on local environmental conditions. Accordingly, several studies have showed that spatial heterogeneity in population dynamics could result from both spatial variations in population dynamic parameters (Saether *et al.* 2008; Fukaya *et al.* 2013) and fine-scale variability of the influence of environmental factors (Saether *et al.* 2003; Williams *et al.* 2003; Fukaya *et al.* 2014). However, such spatial heterogeneity of population dynamics could also reflect species-specific differences in the response of populations to environmental variations.

Species-specific patterns

We found large differences among species in slope coefficients relating environmental variables to population dynamic parameters indicating that different mechanisms are influencing population dynamics of the different species. Accordingly, Hart & Gotelli (2011) found that climate change can alter abundances of aquatic invertebrate taxa but not necessarily through the same mechanism. In the case of *Culicidae* the abundance was affected by changes in the growth rate whereas in *Chironomidae* the abundance was affected by changes in the strength of density dependence. For most species, several coefficients with contrasting influence on population dynamic parameters appeared as significant which translated into species-specific contribution of environmental variables to population dynamics that varied depending on the population dynamic parameter considered. This result clearly highlights that the mechanisms driving inter-annual variation in population size are highly complex. Consequently, complex species-specific responses are expected in the face of ongoing climate change.

Even though deterministic influences of environmental variables on population dynamic parameters were identified for the different species, we found that their influences could translate into large spatial variation in population dynamics. However, the relative contribution of environmental variables to spatial variation in population dynamics greatly varied depending on the population dynamic parameter and the species considered. Although such variations are expected to impede the identification of spatial patterns, for some species, we found that population responses to environmental variations might display significant latitudinal gradients as well as spatial autocorrelation. Accordingly, several studies have reported geographical gradients in the determinants of population dynamics (e.g. Saether *et al.* 2008; Grøtan *et al.* 2009b). For instance, in the common vole, Tkadlec & Stenseth (2001) reported latitudinal gradients in mean density, cycle amplitude, density variability, population growth rate and density dependence. The existence of such gradients suggest that population responses to climate change might be predicted from knowledge on geographical locations (Saether *et al.* 2008). Spatial autocorrelation in the response of population to environmental variation may reflect spatial autocorrelation in environmental conditions. Such spatial autocorrelation in the response of population to environmental variations may result in spatial synchrony of population dynamics (i.e. the Moran effect; Royama 1992), a process that has already been shown to correlate with species extinction risk (Hanski & Woiwod 1993) and has already been evidenced for stream fish species(Chevalier *et al.* 2014).

Implications

Our study reveals that the mechanisms influencing population dynamics are highly complex and could be difficult to detect without considering through which population dynamic parameters environmental variables influence abundance patterns. By identifying the mechanisms and the relative contribution of several environmental factors to spatio-temporal variations in population size, our results provide insights into the potential outcomes of future

climate change on stream fish populations. Nonetheless, although common mechanisms driving population dynamics at large spatial scales have been identified for the different species, we have shown that these mechanisms could translate into large spatial variation in population dynamics because of spatial heterogeneity in local conditions. This suggests that small-scale spatial variation could not be used to infer large-scale patterns of population dynamics (Jongejans *et al.* 2010). However, spatial patterns have been found for some species and could be used to infer population dynamics using knowledge on local conditions. Spatial variations in population dynamics has been shown to reduce the level of spatial population synchrony caused by environmental factors (Liebhold *et al.* 2006) which should ultimately reduce species extinction risk in the face of climate change (Hanski & Woiwod 1993).

Acknowledgements

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Electronic Supplementary Material

Appendix S1: Prediction of water temperature at sampling sites

Daily air temperature data from 1982 to 2011 were provided by Météo France. This database (SAFRAN, Le Moigne 2002) is a regular eight-kilometer grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically-homogeneous zones (for further details see Le Moigne 2002). Daily water temperature data measured from 2009 to 2012 at 135 sites located throughout France (Figure 1) were provided by the Onema.

We used air temperature to estimate water temperature at study sites for each sampling time, using a random forest procedure. Specifically, we performed a calibration-evaluation procedure using the 135 sites for which we had information on both air and water temperatures. Daily water temperature was modeled as a function of air temperature, month and altitude to take into account spatio-temporal variations in the relationship between air and water temperature (Caissie 1998). To calibrate the models, we randomly selected 70% of the data. Model performance was then estimated on the remaining 30% of sites by calculating Pearson cross-correlation coefficients between observed and predicted values, and daily water temperature was finally predicted for each fish sampling site. To ensure the robustness of the predictions, the whole procedure was repeated 100 times. The calibration-evaluation process revealed a good performance of the random forest procedure in predicting daily water temperature (mean R^2=0.86; SD=0.005).

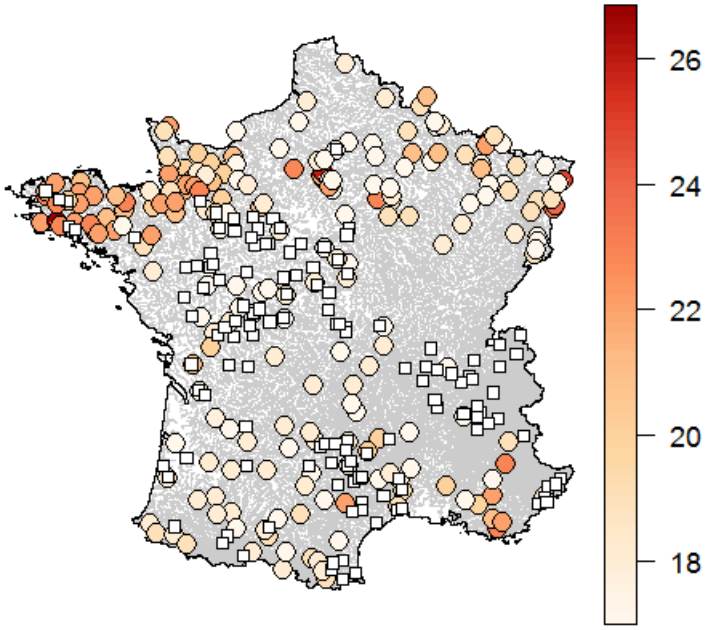

Figure S1. Study area showing the geographical distribution of sites for fish samplings (circles) and water temperature records (squared). The scale indicates the number of years available for each fish sampling site with dark colors indicating the longest time series.

Appendix S2. Summary of MCMC chains.

Table S1. Species-specific details about the deviance, the length of chains and burn-in, effective sample size and number of chains for each species. Species code as in Table 1. γ, ρ and η correspond to the migration rate, the intrinsic population growth rate and the density dependence, respectively. The subscripts "a" correspond to intercepts of GLM models whereas the subscript "b", "c", "d" and "e" correspond to slope coefficients associated to the influence of Alt_i, CV_i, $meanT_{i,t}$ and $varT_{i,t}$ on population dynamics parameters.

Species code	γ_a	γ_b	γ_c	γ_d	γ_e	ρ_a	ρ_b	ρ_c	ρ_d	ρ_e	η_a	η_b	η_c	η_d	η_e	Deviance	N.chains	N.iter	N.burn	Ierations saved
Alal	233,0	1994,9	388,1	323,9	601,5	35601,6	385,1	6387,1	679,0	661,8	938,7	209,8	7342,9	441,2	277,2	808,2	55	9E+05	8E+05	1000
Anan	933,2	12372,7	1541,6	1346,1	1652,3	152022,9	754,5	9020,1	959,9	1199,6	899,5	240,9	18052,2	675,7	351,5	856,2	25	5E+05	1E+05	10000
Baba	279,8	2187,3	636,3	505,8	1332,0	19957,7	358,5	3522,5	736,3	601,5	1101,9	227,2	7232,5	348,1	364,5	954,7	35	2E+05	1E+05	10000
Babr	273,3	2236,1	467,3	412,9	911,0	8616,1	332,0	1550,6	536,5	481,9	1014,9	218,4	930,0	210,2	991,6	2275,4	50	6E+05	5E+05	1000
Blbj	275,0	2530,6	274,6	374,7	929,0	16577,5	293,1	2896,4	498,5	384,2	1069,2	231,8	7941,2	214,1	236,7	587,8	50	2E+06	2E+06	4000
Cogo	275,3	2318,0	440,8	426,2	865,3	33247,5	289,6	2165,6	469,1	411,6	634,4	237,6	2645,4	316,3	335,4	1038,9	40	7E+05	6E+05	4000
Cyca	846,9	2724,0	1153,5	2671,7	2806,5	11920,5	458,5	2060,1	668,7	956,0	1116,7	258,9	2623,9	343,1	312,4	1308,9	50	3E+06	2E+06	10000
Eslu	251,1	2308,6	352,0	310,8	580,3	11703,3	262,7	2218,9	336,6	319,7	570,1	277,7	918,8	288,1	242,7	517,0	45	1E+06	1E+06	2000
Gaac	1582,7	12482,3	2627,2	2006,3	2849,1	126395,4	483,5	9033,2	1190,3	708,0	1193,2	201,9	1276,1	254,2	338,3	446,8	50	9E+06	8E+06	10000
Gogo	237,1	1597,0	295,9	300,4	595,5	16212,2	352,6	1364,4	518,1	478,6	591,3	205,2	924,7	237,4	303,5	486,5	35	6E+05	5E+05	4000
Gyce	310,5	4506,3	480,0	440,9	713,9	16125,3	314,6	3608,7	395,6	377,0	654,0	254,6	316,6	276,6	205,2	339,0	65	7E+05	6E+05	1000
Lapl	275,7	1106,0	315,0	319,0	819,7	13113,2	335,4	1757,5	527,5	442,4	818,6	255,3	550,8	225,2	223,4	744,7	60	2E+06	2E+06	1000
Legi	891,6	8122,5	2120,4	1244,3	3428,1	7183,7	361,3	2835,3	722,8	526,4	996,9	199,5	348,4	263,0	218,4	587,8	45	6E+05	5E+05	1000
Lele	663,7	18137,5	1173,0	945,3	1299,8	12991,6	614,0	5509,5	899,8	876,6	1116,1	233,0	2844,4	287,3	337,1	589,9	90	4E+05	3E+05	1000
Pato	278,6	1083,7	413,4	387,8	656,2	14804,4	319,7	2697,7	448,9	470,3	941,7	225,4	1516,4	199,2	248,3	312,7	55	1E+06	1E+06	4000
Pefl	220,3	1449,6	378,3	275,0	678,5	17475,2	341,1	2314,7	470,5	390,4	848,8	331,5	3368,5	390,6	579,0	919,0	40	4E+05	3E+05	1000
Phph	195,7	2420,7	309,5	480,8	960,5	32415,3	290,3	1507,2	543,6	376,3	609,1	224,2	1127,3	374,4	316,2	666,3	30	4E+05	3E+05	10000
Pupu	634,5	26467,8	2306,8	607,4	2849,8	9672,1	433,0	11900,1	804,1	447,7	1207,5	338,3	4435,9	453,8	297,8	766,1	30	2E+06	1E+06	10000
Ruru	304,7	7032,4	524,4	511,4	906,2	71508,4	415,4	6077,6	784,5	612,4	842,2	199,5	3823,2	418,6	307,9	1235,7	45	4E+05	3E+05	2000
Salu	951,8	11783,5	1269,3	2566,8	3600,5	10149,9	387,9	6322,0	600,2	734,4	785,5	240,5	1290,6	197,7	260,5	378,1	60	8E+05	7E+05	1000
Sasa	354,0	1719,6	716,0	455,7	812,3	25002,6	326,7	2832,0	628,1	434,1	1012,6	201,1	4563,2	380,2	280,2	580,6	40	3E+05	2E+05	2000
Satr	262,0	1495,4	629,7	381,2	725,7	54455,7	280,0	946,1	460,2	349,4	506,0	236,6	966,1	381,0	290,3	411,3	8	5E+05	1E+05	10000
Scer	302,0	18679,8	515,4	605,0	775,9	23988,3	308,4	5104,9	700,7	424,6	833,0	237,8	3297,5	290,1	224,7	822,7	60	2E+06	2E+06	1000
Sigl	532,8	2623,7	785,9	1214,0	1898,4	14654,8	291,6	1316,9	290,5	269,8	964,4	233,4	234,2	257,3	249,8	357,3	60	1E+06	1E+06	2500
Sqce	228,7	1756,2	649,9	338,5	829,1	38777,6	390,1	1429,8	683,1	460,7	549,5	195,1	1195,4	338,0	322,7	299,4	50	8E+05	7E+05	4000
Teso	635,5	4016,1	1045,9	1382,3	2753,9	17822,3	282,1	3366,2	549,1	545,8	906,0	216,7	2075,2	342,5	639,5	2641,1	45	1E+06	6E+05	4000
Thth	367,1	1268,1	442,4	966,6	2434,4	5904,7	226,0	690,6	513,0	298,8	1258,7	288,1	945,3	535,6	274,7	1112,0	20	2E+06	1E+06	10000
Titi	765,3	6343,6	1180,6	1211,3	1436,1	43897,9	427,6	1592,9	824,0	543,7	920,3	202,6	1431,4	324,7	266,2	925,4	60	8E+05	7E+05	1000

Appendix S3. Detail calculus of Effect sizes.

We detail the calculus of effect sizes for a given coefficient (e.g. γ_b). The same general procedure was used to calculate effect sizes related to other coefficients, population dynamic parameters and environmental variables. Effect sizes were calculated for each species in three steps.

Step 1. For a given species, we used equation 2 to calculate at each site and time the expected value of the migration rate from both the estimated value of γ_b and by fixing the value γ_b to zero.

$$\gamma_{i,t,0} = \gamma_a + (0 * \mathrm{Alt}_i) + (\gamma_c * \mathrm{CV}_i) + (\gamma_d * \mathrm{meanT}_{i,t}) + (\gamma_e * \mathrm{varT}_{i,t})$$

$$\gamma_{i,t,est} = \gamma_a + (\gamma_b * \mathrm{Alt}_i) + (\gamma_c * \mathrm{CV}_i) + (\gamma_d * \mathrm{meanT}_{i,t}) + (\gamma_e * \mathrm{varT}_{i,t})$$

The two other population dynamic parameters were calculated normally, using the estimated coefficients and the observed values of ecological variables at site i and time t.

Step 2. We then used equation 1 to calculate at each site and time the expected abundance values associated to population dynamic parameter values calculated in step 1.

$$E(N_{i,t,0}) = \left[\gamma_{i,t,0} + N_{i,t-1} \exp\left(\rho_{i,t} + \eta_{i,t} N_{i,t-1}\right)\right] * \frac{S_{t-1}}{S_t}$$

$$E(N_{i,t,est}) = \left[\gamma_{i,t,est} + N_{i,t-1} \exp\left(\rho_{i,t} + \eta_{i,t} N_{i,t-1}\right)\right] * \frac{S_{t-1}}{S_t}$$

Step 3. Finally, we used the following equation to calculate effect sizes of coefficient γ_b:

$$ES_{\gamma b,i,t} = \frac{N_{i,t,est} - N_{i,t,0}}{N_{i,t,0}} * 100$$

$ES_{\gamma b,i,t}$ is the effect size of the coefficient γ_b on site i at time t. $N_{i,t,0}$ and $N_{i,t,est}$ are calculated using equation 1 with values of $\gamma_{i,t,0}$ and $\gamma_{i,t,est}$ calculated using equation 2.

Appendix S4. Median and standard deviation of effect sizes related to slope coefficients

Table S2. Species-specific effect sizes associated to slope coefficients relating environmental variables to population dynamic parameters. Effect sizes significantly different from zero are in bold. Species code as in table 1.

Species code	$ES\gamma_b$	$ES\gamma_c$	$ES\gamma_d$	$ES\gamma_e$	$ES\rho_b$	$ES\rho_c$	$ES\rho_d$	$ES\rho_e$	$ES\eta_b$	$ES\eta_c$	$ES\eta_d$	$ES\eta_e$
Alal	**-3.1**	**-55.2**	**-107.1**	-11.1	**-5.0**	**-90.6**	**-93.6**	**104.2**	**-5.0**	**30.5**	46.0	**-14.1**
Satr	**-1.2**	**-8.3**	**-12.8**	**0.0**	0.3	**-16.9**	**-29.2**	**13.9**	0.0	**6.2**	**9.5**	**-7.4**
Sqce	**-21.6**	**-83.8**	**-89.9**	**-92.3**	**16.1**	**79.7**	**-270.9**	**-61.0**	**-4.6**	**-9.9**	**-8.6**	**6.6**
Gogo	**-6.7**	**-20.2**	**-43.8**	**1.7**	**7.8**	**7.9**	**566.7**	**3.4**	**0.0**	**-3.2**	**-13.1**	**1.4**
Phph	**-1.7**	**-6.0**	**0.1**	**-0.4**	1.8	**-50.2**	**-48.0**	**51.8**	**-1.1**	**-0.4**	**-2.2**	**-0.7**
Anan	**-3.0**	**-0.8**	**-0.2**	**-1.9**	**0.0**	**-32.1**	**-37.0**	**17.2**	**-4.2**	**0.2**	**-6.9**	**-2.9**
Baba	**-0.5**	**-8.2**	6.7	**2.6**	0.1	**-59.5**	**-23.5**	**0.9**	**-0.3**	**11.4**	**-5.4**	**2.6**
Babr	8.1	**-97.4**	7.5	**-66.9**	**-31.5**	**-64.3**	**87.3**	**31.7**	**7.3**	**4.2**	**-10.4**	**-5.0**
Blbj	**-26.6**	-54.0	**-45.2**	**-35.1**	**8.4**	**-36.1**	**-0.4**	**14.4**	**-1.2**	**-7.0**	**-6.9**	**4.7**
Eslu	**-12.6**	**-36.7**	**-14.2**	**-5.3**	**-44.6**	**698.4**	**736.9**	**-89.1**	0.1	**-66.3**	**-31.3**	**73.6**
Cogo	**-0.1**	5.3	3.0	**-7.7**	**3.2**	**-87.1**	**-67.1**	**164.2**	**-3.0**	**12.9**	**-5.6**	**-9.2**
Lapl	**-1.1**	**-198.3**	**-31.9**	**-11.5**	**-1.5**	-1.6	**-83.2**	**-26.9**	0.4	**-7.4**	**-51.6**	0.1
Pefl	**-12.6**	**-51.5**	**-74.4**	**-28.0**	**3.4**	**307.6**	**266.6**	**-71.7**	**-3.5**	**-11.3**	**-26.5**	**8.8**
Legi	**-25.0**	**-19.7**	**-24.8**	**-31.0**	**-45.1**	**311.5**	**-67.2**	**-73.1**	**-23.0**	**-45.9**	**38.4**	-9.1
Scer	**-10.6**	**-77.2**	**-79.1**	**-108.1**	-1.1	0.8	**-24.9**	**-51.2**	**-8.7**	**21.7**	**58.5**	**-9.4**
Titi	**-2.9**	**-44.6**	**-57.9**	**-19.2**	**-3.4**	**399.9**	**402.1**	**-71.1**	**-7.6**	**-31.8**	**-32.4**	**11.1**
Lele	0.4	**-25.2**	**-38.1**	-10.1	**-13.8**	**1113.0**	**1244.4**	**-81.0**	1.4	**-28.9**	**-25.7**	**34.0**
Teso	**-15.0**	**-51.3**	**40.7**	-146.3	**60.4**	26.3	10.4	**-98.6**	**-11.7**	43.6	**2.6**	**53.7**
Cyca	**-25.0**	**-62.0**	**-54.3**	**-16.8**	**78.4**	**483.6**	**-50.6**	**-53.2**	**13.7**	**-11.7**	**464.9**	**-0.4**
Gyce	**-27.5**	**-94.8**	**-94.6**	**-109.6**	-4.6	**-112.9**	-77.2	**-73.5**	**-12.8**	**-12.1**	-7.3	**-13.4**
Thth	-61.7	**-184.0**	26.4	-127.3	**-20.6**	**-83.2**	**-82.6**	111.7	**-14.5**	165.9	**282.8**	**-37.9**
Salu	**-33.5**	**-67.3**	**-63.2**	**-32.3**	7.6	180.0	**-74.3**	**134.9**	**-44.3**	**23.6**	**80.8**	**-56.2**
Sasa	**-4.3**	-1.2	**-19.7**	0.5	**11.9**	**351.9**	**3035.0**	**-71.9**	**-14.0**	**-35.2**	**-52.7**	**22.2**
Sigl	**-47.5**	**-43.2**	**-60.5**	**-49.9**	**-85.1**	**-94.8**	-102.6	**323.6**	-18.0	**-44.9**	**-49.0**	**-60.4**
Ruru	**-4.3**	**-110.8**	**-112.4**	**-52.8**	**0.6**	**-77.8**	**-87.0**	**86.3**	**0.1**	**8.4**	**16.7**	**-4.7**
Pato	**-15.7**	**-102.5**	**-114.1**	**-40.2**	**-29.1**	**-142.1**	**-143.4**	**-86.4**	**7.5**	**19.9**	**-19.6**	22.3
Gaac	**-41.0**	**-111.9**	**-93.9**	**-93.3**	-8.0	**-68.1**	**-68.1**	**-118.4**	**-17.7**	**-95.0**	**-110.1**	**-33.0**
Pupu	**-15.9**	**-70.2**	**-115.6**	**-86.2**	**19.4**	**156.9**	**-53.3**	**-59.3**	**-4.9**	**-29.3**	**15.4**	**18.5**

Table S3. Species-specific standard deviation of effect sizes associated to slope coefficients relating environmental variables to population dynamic parameters. Species code as in table 1.

Species code	$ES\gamma_b$	$ES\gamma_c$	$ES\gamma_d$	$ES\gamma_e$	$ES\rho_b$	$ES\rho_c$	$ES\rho_d$	$ES\rho_e$	$ES\eta_b$	$ES\eta_c$	$ES\eta_d$	$ES\eta_e$
Alal	43.7	139.6	199.8	48.2	7.1	19.6	17.2	141.4	5.4	1044.8	1322.1	13.5
Anan	10.9	9.1	9.0	9.3	8.9	4.1	3.1	15.4	8.3	9.4	9.3	8.5
Baba	5.3	99.5	62.2	15.0	4.5	11.3	6.3	4.6	4.5	55.2	6.3	8.5
Babr	105.9	143.4	41.3	25.3	14.8	19.6	509.7	72.2	821.1	72.8	10.6	6.0
Blbj	20.6	573.2	11.0	11.6	76.6	19.1	2.8	32.3	6.9	18.2	17.9	87.5
Cogo	11.4	46.0	31.0	27.9	14.6	5.4	3.6	86.1	10.8	112.4	10.3	10.5
Cyca	10.6	15.7	14.6	6.4	308.5	158729.5	20.6	20.7	127.1	13.2	182008.4	0.9
Eslu	22.7	15.0	13.3	19.1	13.0	687.0	610.3	10.2	67.0	14.5	11.0	388.9
Gaac	52.6	106.7	99.1	8.2	105.2	12.8	12.8	128.7	8.5	175.2	160.4	14.1
Gogo	17.3	22.0	24.9	18.2	19.7	9.4	329.4	8.6	8.1	7.6	14.8	12.0
Gyce	46.0	8.7	17.3	53.9	18.5	594.9	198.1	14.3	5.5	6.0	11.6	5.3
Lapl	2.6	67.1	28.1	8.4	23.1	34.0	17.8	133.3	6560.2	16.6	8047.7	372.3
Legi	18.5	22.0	18.4	18.7	17.5	255.9	7.0	7.4	104.7	13.5	971.9	174.9
Lele	8.8	13.4	17.0	37.3	7.7	1323.7	1953.2	13.4	20.3	19.9	18.2	976.1
Pato	20.7	21.4	32.9	84.5	34.6	197.4	213.5	17.2	16.9	118.8	16.5	384.9
Pefl	16.6	21.3	17.7	93.9	11.6	296.9	983.8	15.8	7.1	9.5	20.0	90.6
Phph	18.2	20.9	15.1	14.5	16.5	7.5	7.6	27.8	13.4	13.6	13.3	13.5
Pupu	17.4	13.3	108.3	122.2	22.0	296.3	12.9	13.5	10.3	20.0	132.6	150.8
Ruru	14.0	245.2	279.2	25.4	3.3	17.6	16.5	49.7	3.3	340.4	1785.9	7.5
Salu	13.8	9.5	19.4	16.2	232.6	489.5	8.9	131.0	17.0	57.5	85.0	10.8
Sasa	27.9	34.8	27.4	37.1	47.9	152.2	4636.7	13.8	13.8	19.1	24.5	77.8
Satr	12.4	20.7	23.1	10.3	10.6	8.2	7.7	13.6	10.3	25.7	30.5	10.0
Scer	7.9	10.2	9.2	77.4	7.5	5.5	5.1	10.0	7.3	224.8	401.2	6.0
Sigl	18.6	22.0	21.8	17.8	5.1	2.7	417.3	304.2	69.7	20.4	18.0	15.5
Sqce	62.6	19.0	12.7	193.7	76.6	289.1	992.0	31.5	5.3	7.2	6.6	27.6
Teso	49.7	17.6	94.5	226.8	210.6	611.0	941.9	16.0	22.9	1040.0	6.0	395.3
Thth	117.3	140.9	85.2	81.4	16.6	15.8	15.8	275.9	5.7	364.4	191.8	20.8
Titi	12.1	12.9	13.0	33.4	12.9	367.2	504.6	12.0	9.6	10.5	11.7	70.9

Appendix S5. Species-specific spatial autocorrelation of effect sizes and relationship with latitude.

Table S4. Moran's autocorrelation index calculated on effect sizes related to population dynamic parameters. Significant results are in bold. Species code as in table 1.

Species code	γ	ρ	η
Alal	-0,009	**-0,038**	-0,018
Anan	**-0,031**	-0,009	-0,005
Baba	-0,009	**-0,023**	**-0,014**
Babr	**-0,057**	-0,047	-0,013
Blbj	**-0,134**	**-0,097**	-0,035
Cogo	**-0,051**	**-0,042**	**-0,026**
Cyca	-0,036	-0,054	-0,070
Eslu	**-0,061**	-0,021	-0,021
Gaac	-0,039	-0,082	-0,046
Gogo	**-0,029**	**-0,064**	**-0,025**
Gyce	**-0,136**	-0,018	-0,067
Lapl	-0,012	-0,016	-0,012
Legi	-0,015	-0,018	-0,022
Lele	**-0,045**	-0,010	-0,019
Pato	-0,143	-0,085	-0,055
Pefl	**-0,047**	-0,009	-0,015
Phph	**-0,028**	-0,006	**-0,023**
Pupu	-0,046	**-0,115**	-0,068
Ruru	-0,010	**-0,027**	-0,009
Salu	**-0,152**	-0,055	-0,078
Sasa	**-0,114**	**-0,148**	-0,011
Satr	**-0,017**	-0,006	**-0,045**
Scer	-0,040	-0,039	-0,056
Sigl	**-0,286**	-0,111	**-0,309**
Sqce	-0,015	**-0,018**	**-0,047**
Teso	-0,200	-0,123	-0,132
Thth	-0,176	-0,358	-0,378
Titi	-0,035	-0,020	**-0,067**

Table S5. Moran's autocorrelation index calculated on effect sizes related to environmental variables. Significant results are in bold. Species code as in table 1.

Species code	Alt_i	CV_i	$meanT_{i,t}$	$varT_{i,t}$
Alal	-0,020	-0,012	**-0,040**	-0,016
Anan	**-0,032**	**-0,057**	-0,008	-0,010
Baba	**-0,031**	**-0,023**	**-0,018**	-0,004
Babr	-0,007	-0,011	**-0,049**	**-0,094**
Blbj	**-0,117**	-0,028	-0,048	-0,054
Cogo	-0,017	-0,013	**-0,039**	**-0,042**
Cyca	-0,038	-0,068	-0,071	-0,128
Eslu	-0,008	-0,037	-0,031	-0,022
Gaac	-0,026	-0,033	-0,092	-0,042
Gogo	-0,013	**-0,019**	**-0,035**	-0,004
Gyce	-0,037	-0,051	-0,051	-0,060
Lapl	-0,012	**-0,031**	-0,012	-0,010
Legi	-0,021	-0,031	-0,020	-0,019
Lele	-0,019	-0,027	-0,023	-0,016
Pato	**-0,307**	-0,093	-0,119	-0,042
Pefl	**-0,045**	**-0,042**	**-0,037**	-0,013
Phph	**-0,017**	**-0,040**	-0,006	**-0,024**
Pupu	-0,069	-0,068	-0,020	-0,023
Ruru	**-0,025**	-0,014	**-0,029**	-0,012
Salu	**-0,159**	**-0,209**	-0,059	-0,103
Sasa	-0,063	**-0,202**	-0,059	-0,049
Satr	-0,013	**-0,031**	**-0,041**	**-0,046**
Scer	**-0,165**	-0,049	-0,049	**-0,072**
Sigl	-0,181	-0,169	-0,168	-0,202
Sqce	-0,007	**-0,019**	**-0,017**	-0,003
Teso	-0,067	-0,111	-0,136	-0,124
Thth	-0,297	-0,192	-0,140	-0,137
Titi	**-0,178**	-0,020	-0,023	-0,008

Table S6. Moran's autocorrelation index calculated on effect sizes related to slope coefficients relating environmental variables to population dynamic parameters Significant results are in bold. Species code as in table 1.

Species code	γ_b	γ_c	γ_d	γ_e	ρ_b	ρ_c	ρ_d	ρ_e	η_b	η_c	η_d	η_e
Alal	-0,022	-0,017	-0,015	-0,020	**-0,037**	-0,010	**-0,038**	-0,019	-0,016	-0,010	-0,012	**-0,043**
Satr	**-0,019**	-0,014	-0,014	-0,008	-0,006	-0,014	**-0,019**	**-0,019**	-0,008	**-0,039**	**-0,032**	**-0,020**
Sqce	-0,004	-0,015	-0,016	-0,005	**-0,052**	-0,005	**-0,016**	-0,013	**-0,077**	**-0,019**	-0,015	-0,010
Gogo	-0,013	**-0,019**	**-0,029**	-0,005	**-0,058**	-0,006	**-0,044**	-0,006	-0,006	-0,006	**-0,026**	-0,010
Phph	**-0,036**	**-0,027**	**-0,016**	**-0,019**	-0,009	**-0,027**	-0,007	**-0,024**	**-0,023**	**-0,019**	**-0,019**	**-0,019**
Anan	**-0,029**	**-0,021**	**-0,020**	**-0,022**	**-0,019**	**-0,047**	**-0,022**	-0,010	**-0,023**	**-0,023**	-0,005	-0,015
Baba	**-0,030**	**-0,038**	**-0,024**	-0,012	**-0,014**	-0,013	**-0,021**	**-0,019**	**-0,022**	-0,013	**-0,015**	**-0,020**
Babr	-0,023	**-0,083**	**-0,048**	**-0,075**	-0,024	-0,022	-0,006	-0,017	-0,013	-0,019	**-0,042**	-0,007
Blbj	**-0,171**	-0,030	**-0,078**	-0,062	**-0,071**	-0,041	-0,032	-0,053	-0,057	-0,039	-0,043	-0,060
Eslu	-0,022	-0,040	**-0,065**	**-0,053**	**-0,125**	-0,021	-0,027	-0,017	**-0,055**	-0,019	**-0,048**	-0,014
Cogo	**-0,058**	**-0,035**	**-0,045**	**-0,054**	-0,009	-0,018	**-0,051**	**-0,026**	**-0,072**	-0,010	**-0,056**	**-0,054**
Lapl	-0,005	-0,030	-0,011	-0,008	-0,007	-0,026	-0,016	-0,005	-0,012	-0,016	-0,012	-0,012
Pefl	**-0,053**	**-0,058**	**-0,050**	-0,011	**-0,105**	**-0,046**	-0,010	-0,019	**-0,068**	-0,011	-0,016	-0,020
Legi	-0,015	-0,014	-0,016	-0,016	**-0,044**	-0,028	-0,024	-0,024	-0,036	-0,008	-0,017	-0,019
Scer	**-0,168**	-0,029	-0,028	-0,021	**-0,078**	-0,036	-0,016	-0,039	**-0,099**	-0,055	-0,055	-0,055
Titi	**-0,157**	-0,031	-0,037	-0,023	**-0,145**	-0,018	-0,021	**-0,064**	**-0,113**	**-0,078**	**-0,096**	-0,011
Lele	**-0,059**	**-0,042**	**-0,045**	**-0,039**	**-0,048**	-0,017	-0,009	**-0,032**	**-0,072**	-0,020	-0,016	-0,009
Teso	-0,123	**-0,247**	-0,098	-0,028	-0,063	-0,181	**-0,254**	-0,180	-0,115	-0,180	-0,201	**-0,233**
Cyca	-0,159	-0,036	-0,033	-0,030	-0,120	-0,069	-0,117	-0,122	-0,062	-0,068	-0,071	-0,089
Gyce	-0,029	**-0,142**	**-0,166**	-0,039	-0,056	**-0,106**	-0,019	-0,108	-0,033	-0,033	-0,054	-0,025
Thth	-0,352	-0,094	-0,127	-0,258	-0,121	-0,358	-0,357	**-0,439**	-0,079	-0,374	-0,152	-0,331
Salu	-0,066	-0,142	-0,120	-0,053	**-0,221**	**-0,227**	-0,072	-0,088	**-0,172**	-0,032	-0,054	-0,074
Sasa	**-0,139**	-0,032	-0,030	-0,016	**-0,198**	-0,074	-0,034	**-0,090**	**-0,142**	-0,013	-0,011	-0,011
Sigl	**-0,288**	**-0,262**	**-0,282**	**-0,274**	-0,144	-0,196	-0,157	-0,152	**-0,255**	**-0,283**	**-0,288**	**-0,266**
Ruru	**-0,029**	-0,005	-0,005	-0,010	-0,008	**-0,028**	**-0,020**	-0,013	-0,006	-0,011	-0,010	-0,008
Pato	-0,080	-0,143	**-0,214**	-0,115	-0,042	-0,085	-0,083	-0,033	-0,059	-0,071	-0,129	-0,027
Gaac	**-0,165**	-0,034	-0,047	-0,049	-0,039	-0,082	-0,082	-0,047	-0,061	-0,031	-0,053	-0,015
Pupu	-0,052	-0,076	-0,013	-0,040	**-0,110**	-0,049	**-0,125**	**-0,114**	-0,049	**-0,086**	-0,051	-0,050

Table S7. Species-specific regression coefficients from mixed effects model relating effect sizes associated to population dynamic parameters to latitude. Significant results are in bold. Species code as in table 1.

Species code	γ	ρ	η
Alal	-1,8E-06	**2,2E-07**	5,8E-06
Anan	8,6E-08	5,2E-09	2,1E-10
Baba	5,9E-07	**-9,3E-08**	**3,8E-07**
Babr	-1,2E-06	**-1,5E-06**	-3,7E-07
Blbj	1,5E-07	-1,7E-07	2,8E-07
Cogo	**7,4E-07**	**-9,6E-08**	**3,3E-07**
Cyca	-8,8E-08	1,1E-05	1,6E-04
Eslu	1,6E-07	1,8E-06	-4,6E-08
Gaac	1,9E-06	**4,6E-07**	2,9E-06
Gogo	**-2,7E-07**	**-7,5E-06**	**1,5E-07**
Gyce	-1,1E-07	-1,8E-06	9,5E-08
Lapl	-1,4E-06	-3,1E-08	4,7E-05
Legi	-1,4E-07	1,6E-07	-4,4E-06
Lele	6,8E-08	-1,8E-06	-1,4E-07
Pato	**-2,6E-06**	**2,6E-05**	-9,3E-06
Pefl	**3,7E-07**	5,7E-06	-1,9E-07
Phph	1,5E-07	3,3E-09	1,0E-07
Pupu	1,0E-06	-2,4E-07	4,8E-08
Ruru	1,4E-06	7,4E-09	9,4E-07
Salu	4,4E-08	-3,8E-06	-6,4E-07
Sasa	3,4E-07	**1,8E-04**	6,7E-08
Satr	-1,4E-07	-2,8E-08	**-6,5E-07**
Scer	3,8E-08	-1,0E-07	4,2E-06
Sigl	-9,3E-07	-1,7E-07	**-2,4E-06**
Sqce	-6,4E-08	4,3E-06	8,0E-08
Teso	-1,7E-05	8,1E-07	8,0E-06
Thth	-3,5E-06	-5,1E-07	6,8E-06
Titi	-1,8E-07	-6,7E-06	8,1E-08

Table S8. Species-specific regression coefficients from mixed effects model relating effect sizes associated environmental variables to latitude. Significant results are in bold. Species code as in table 1.

Species code	Alt_i	CV_i	$meanT_{i,t}$	$varT_{i,t}$
Alal	2,0E-07	-1,2E-06	1,5E-07	-4,3E-07
Anan	7,1E-08	1,4E-08	1,8E-08	2,3E-08
Baba	1,4E-08	2,8E-07	2,6E-07	-6,1E-08
Babr	-3,2E-07	-1,7E-07	**-4,7E-06**	**-5,3E-07**
Blbj	-8,4E-08	2,2E-06	1,6E-07	-9,0E-07
Cogo	4,6E-08	8,7E-08	**-7,9E-08**	**1,1E-06**
Cyca	1,2E-06	1,1E-05	2,5E-05	4,1E-07
Eslu	1,4E-07	1,8E-06	2,7E-06	4,0E-07
Gaac	-1,5E-07	1,8E-08	-2,3E-08	-2,4E-07
Gogo	-1,7E-07	-1,8E-07	**-1,3E-06**	-3,8E-08
Gyce	7,4E-07	7,6E-09	-1,2E-07	5,6E-08
Lapl	4,2E-05	-2,7E-07	3,4E-05	-4,7E-06
Legi	-1,4E-07	**-2,3E-06**	-3,7E-06	-2,5E-07
Lele	-6,0E-08	1,0E-06	2,1E-06	-2,8E-06
Pato	2,0E-06	**-1,1E-05**	-1,8E-05	-2,8E-08
Pefl	**3,8E-07**	**1,7E-06**	**9,8E-07**	1,4E-07
Phph	1,0E-07	5,7E-08	3,5E-08	1,9E-07
Pupu	-4,5E-07	-3,7E-07	-1,2E-06	2,5E-06
Ruru	**1,5E-07**	1,2E-07	-8,3E-07	2,3E-07
Salu	5,9E-07	1,8E-07	-1,6E-07	-1,6E-06
Sasa	1,5E-08	1,8E-06	-7,2E-06	-4,9E-07
Satr	-1,4E-08	**-3,0E-07**	**-3,8E-07**	**1,5E-07**
Scer	**2,5E-07**	4,4E-07	3,5E-07	2,2E-07
Sigl	-4,0E-07	1,1E-07	-1,5E-05	-7,0E-06
Sqce	2,5E-08	-2,1E-07	-1,8E-07	-1,3E-07
Teso	2,3E-06	-5,4E-06	2,6E-05	-6,0E-07
Thth	7,6E-07	2,3E-07	-3,6E-07	2,2E-06
Titi	**-5,4E-07**	-6,2E-07	-4,8E-07	7,2E-08

Table S9. Species-specific regression coefficients from mixed effects model relating effect sizes associated to slope coefficients relating environmental variables to population dynamic parameters. Significant results are in bold. Species code as in table 1.

Species code	γ_b	γ_c	γ_d	γ_e	ρ_b	ρ_c	ρ_d	ρ_e	η_b	η_c	η_d	η_e
Alal	-1,2E-08	9,9E-07	1,1E-06	3,7E-08	5,3E-08	1,1E-07	**2,2E-07**	-7,6E-07	2,3E-08	-3,2E-06	-7,2E-06	7,0E-09
Anan	7,7E-08	3,9E-08	3,7E-08	4,4E-08	3,5E-08	8,3E-09	**3,0E-08**	2,1E-08	3,0E-08	4,0E-08	5,1E-09	3,0E-08
Baba	1,5E-08	**9,6E-07**	1,9E-07	**-1,3E-07**	4,7E-09	-6,2E-08	**-4,5E-08**	1,0E-08	8,9E-09	**4,5E-07**	**-5,1E-08**	**7,3E-08**
Babr	-5,1E-07	**-2,1E-06**	-3,9E-07	**-3,8E-07**	1,4E-07	-4,8E-08	-2,9E-07	-4,0E-07	-5,0E-07	-3,1E-07	**1,0E-07**	-4,3E-09
Blbj	**8,5E-07**	-6,0E-06	-3,3E-08	-2,7E-08	-3,8E-07	1,2E-07	1,7E-09	-5,2E-07	7,9E-08	2,6E-07	2,5E-07	-1,6E-06
Cogo	**1,5E-07**	**5,7E-07**	3,0E-07	**4,2E-07**	1,9E-08	**-9,2E-08**	**-6,3E-08**	**1,1E-06**	**1,5E-07**	1,1E-06	9,5E-08	5,0E-08
Cyca	1,3E-07	-1,1E-07	-1,1E-07	-3,6E-08	7,6E-07	1,5E-04	5,1E-07	5,1E-07	-1,1E-07	1,6E-07	1,6E-04	8,6E-09
Eslu	1,8E-07	1,7E-07	1,5E-07	2,3E-07	1,3E-07	1,8E-06	3,3E-06	-4,8E-09	6,8E-08	-4,0E-08	8,7E-08	-5,1E-07
Gaac	6,8E-07	1,8E-06	-6,4E-10	-1,1E-07	-1,3E-06	**4,6E-07**	**4,6E-07**	1,8E-06	7,2E-08	2,9E-06	2,1E-06	6,7E-08
Gogo	2,0E-08	-1,8E-07	**-2,8E-07**	2,3E-08	**-2,3E-07**	-1,7E-08	**-5,0E-06**	-1,1E-08	-1,0E-08	1,6E-08	**1,7E-07**	-5,5E-08
Gyce	6,9E-07	-1,1E-07	-3,2E-07	3,4E-07	-2,3E-07	-4,6E-06	-1,3E-06	-1,5E-07	3,6E-09	-1,7E-08	1,9E-08	1,6E-08
Lapl	6,7E-09	-3,8E-07	-9,4E-08	-4,0E-08	3,0E-08	-1,0E-09	-1,5E-08	-2,9E-07	3,8E-05	1,3E-07	4,7E-05	-2,2E-06
Legi	-1,1E-07	-1,1E-07	-1,1E-07	-1,2E-07	-1,2E-07	-2,9E-06	-4,5E-09	5,9E-08	-1,0E-07	4,0E-08	-5,1E-06	-1,7E-06
Lele	-9,5E-08	5,7E-08	9,4E-08	3,3E-07	-8,2E-09	6,1E-06	-2,1E-06	-1,1E-07	-1,2E-07	-1,4E-07	-1,0E-07	-7,6E-06
Pato	-1,5E-07	-2,6E-06	**-4,5E-06**	-1,7E-06	-3,6E-07	**2,6E-05**	**2,8E-05**	-5,6E-07	-2,0E-06	**-1,5E-05**	**2,3E-06**	1,8E-05
Pefl	**3,9E-07**	**5,2E-07**	**3,9E-07**	9,1E-07	1,2E-07	**6,0E-06**	5,5E-06	-8,8E-08	**2,0E-07**	5,8E-08	-2,0E-07	9,1E-07
Phph	1,7E-07	1,4E-07	9,1E-08	9,6E-08	8,6E-09	2,0E-08	3,5E-08	**1,9E-07**	1,0E-07	9,3E-08	9,4E-08	9,3E-08
Pupu	-5,3E-07	-4,3E-07	-1,4E-07	-3,4E-06	-1,8E-07	-1,4E-06	7,4E-08	1,5E-07	-7,4E-09	2,0E-07	-2,6E-06	-2,9E-06
Ruru	**1,8E-07**	-1,1E-06	9,6E-07	1,5E-07	1,1E-09	1,2E-08	-3,6E-08	9,4E-08	5,8E-09	2,8E-07	-2,4E-08	-4,1E-08
Salu	1,7E-07	3,8E-08	-6,9E-08	1,4E-07	1,5E-06	-2,3E-06	2,9E-07	-1,9E-06	4,4E-10	-8,2E-08	-9,7E-07	2,0E-07
Sasa	3,7E-07	-2,2E-07	-2,7E-07	-3,5E-07	**-9,1E-07**	7,9E-07	4,8E-05	-1,4E-07	2,4E-07	-1,3E-08	1,3E-08	-3,8E-08
Satr	9,6E-09	-8,7E-08	-1,2E-07	-2,0E-09	-2,7E-08	-9,0E-09	**-6,8E-08**	8,0E-08	-4,8E-09	**-3,0E-07**	**-3,4E-07**	6,4E-08
Scer	1,5E-07	4,9E-08	5,5E-08	-3,6E-07	7,4E-09	4,9E-08	-2,5E-08	-7,9E-08	**1,8E-07**	1,7E-06	3,4E-06	2,7E-08
Sigl	-9,3E-07	-9,9E-07	-9,5E-07	-8,0E-07	**-2,1E-07**	1,1E-07	-1,3E-05	-1,1E-05	**-4,5E-06**	-1,0E-06	-8,8E-07	-4,8E-07
Sqce	1,4E-07	-9,9E-08	-6,9E-08	-1,1E-07	-6,0E-07	7,2E-07	**7,8E-06**	2,1E-07	5,7E-08	3,3E-08	3,7E-08	-1,6E-07
Teso	1,4E-06	2,8E-07	**1,1E-05**	-4,2E-08	-8,0E-06	1,1E-05	1,8E-05	**2,4E-06**	3,0E-07	3,4E-06	-3,7E-08	2,2E-06
Thth	**7,5E-06**	-4,8E-07	1,3E-07	-3,0E-06	1,4E-07	-5,1E-07	-5,0E-07	1,0E-05	-7,9E-08	6,7E-06	**8,2E-06**	**-1,3E-06**
Titi	**-3,5E-07**	-1,5E-07	-1,7E-07	-2,7E-07	**-4,1E-07**	-2,9E-06	-6,4E-06	**2,1E-07**	**-2,4E-07**	6,8E-08	8,5E-08	-2,3E-07

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Article IV (*PIV*)

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Relating species traits to population dynamics in stream fishes

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Abstract

In many taxa, there exist large interspecific differences in the magnitude of inter-annual variations in population size. Although such differences might be explained by the position of the species along the slow-fast continuum of life-history variation, the influence of other ecological and physiological traits remains to be explored. Moreover, the extent to which phylogeny affects the interspecific variability of population changes is unclear. In this study, we used 1670 time series regrouping 24 stream fish species found in French rivers to examine whether species characteristics and phylogenetic relationships between species explained interspecific differences in (1) the parameters determining local population dynamics (i.e. growth rate, migration rate and strength of density-dependence), (2) their spatial variation and (3) the influence of four environmental variables on these parameters, while correcting for phylogenetic inertia. Phylogeny never appeared as a good predictor of interspecific differences in any of the population dynamic descriptors considered. Likewise, none of the traits considered were pertinent to explain interspecific differences in the migration rate, its spatial variation or the spatial variation of the growth rate. By contrast, species dispersal abilities and life-history traits explained, to a large extent, interspecific differences in the growth rate and the strength of density-dependence, respectively. The spatial variation of the strength of density-dependence was related to a complex combination of traits. Although diet and species dispersal abilities appeared to be quite good predictors of the influence of environmental variables on population dynamics, we found that the overall propensity of species characteristics to explain these differences depended on the population dynamic parameter considered. Overall, our results demonstrate that species characteristics could be used to infer patterns of population dynamics. While adding to our general understanding of the mechanisms underlying population dynamics, our results also suggest that species traits are a promising path in seeking knowledge about species vulnerability under climate change.

Key words: species traits, population dynamics, fish, climate change, phylogeny.

Introduction

Inter-annual variations in population size depend on intrinsic (e.g. density-dependent) and extrinsic (e.g. climatic) processes (Saether et al. 2008). Indentifying the relative contribution of these processes to population dynamics has been debated over the past century (Nicholson 1933, Andrewartha and Birch 1954) and has recently received renewed interest in the context of global climate change (Knape and De Valpine 2011). Most studies that examined inter-annual variations in population size have revealed interspecific differences in the factors (intrinsic or extrinsic) influencing population dynamics (e.g. Fowler 1981, Sæther et al. 2004). Thus, an important area of research in ecology has been to relate interspecific differences in population dynamics to species characteristics (Saether and Engen 2002, Bjørkvoll et al. 2012). As species are not equally at risk when facing climate change (Thomas et al. 2004), it is important to identify the characteristics of species that make them more vulnerable to changing climatic conditions. To date, the most popular approach to quantify the threat of climate change on species has been to infer extinction risk from changes in modeled species distributions (Thuiller et al. 2005). This approach generally ignores important aspects of species biology such as population dynamics which determine species distributions, population structure and extinction risk at a local scale (Bellard et al. 2012). Furthermore, as population size and population trends are the most frequently used measures to assess the conservation status of species and determine priority actions (Gregory et al. 2005, Eaton et al. 2009), identifying species characteristics related to interspecific differences in population dynamics should provide additional insights that could improve the effectiveness of conservation strategies.

Several studies have examined whether species traits were related to interspecific differences in population dynamics. For instance, Saether and Engen (2002) found higher specific growth rate, larger stochastic effects (both environmental and demographic) on the population dynamics and stronger density-dependence at small densities in bird species with large clutch sizes or high adult mortality rates. The influences of demographic and environmental stochasticity on population dynamics have also been shown to decrease with generation time (Sæther et al. 2013). What emerges from these studies is that species population dynamics are spread along a slow-fast continuum of life-history variations (Sæther and Bakke 2000, Saether et al. 2005, Goodwin and Grant 2006, Linnerud et al. 2013). Species characterized by short generation time, low age at maturity, large clutch and small body size (i.e. r-selected species) display higher growth rate, lower density-dependence and are strongly influenced by stochasticity, whereas species at the slow end of the continuum (i.e. K-selected species) have lower growth rate, stronger density-dependence and are weakly influenced by stochasticity. Nonetheless, other studies suggest that these relationships may be context-specific. Whereas in marine fishes, Myers et al. (1999) failed to identify any relationship between growth rate and species traits, Bjørkvoll et al. (2012) found that population growth, temporal variability in natural mortality rate and annual recruitment were negatively related to generation time in this taxonomic group. Although most studies to date have focused on life-history characteristics, other traits (e.g. ecological, physiological, behavioral) may also influence population dynamics. For instance, Jiguet et al. (2007) observed that populations of

species with a low thermal maximum were more declining than populations of species with a high thermal maximum. Likewise, there was some evidence that dietary requirements could explain some patterns of population dynamics (Reif et al. 2010, Sandvik et al. 2012). These studies demonstrate that considering other species characteristics may help to unravel the determinants of population dynamics and thus deserves attention, especially in the context of ongoing climate change.

Besides the influence of density-dependent and environmental factors on population dynamics, immigration among populations that are separated in space is also expected to influence local population dynamics (Grøtan et al. 2009). However, few studies have incorporated a migration component in population dynamic models. Not considering this source of variation could bias the estimation of the deterministic components of population dynamics and therefore the relationship between these components and species characteristics. Furthermore, most of the studies described above were based on the theta-logistic model for which severe fitting issues have been recently raised (Clark et al. 2010). Consequently, the previous relationships highlighted between species traits and population dynamics should be reconsidered.

As closely related species tend to share similar characteristics (McKinney 1997), one might expect interspecific differences in population dynamics to be related to phylogenetic relationships between species. For instance, several studies have revealed that the distribution of extinction risk among species is phylogenetically non-random with some taxonomic groups more likely to contain threatened species than others (Willis et al. 2008, Roy et al. 2009, Thuiller et al. 2011). Identifying such phylogenetic patterns in population dynamics is especially valuable as it should help to understand the processes contributing to current species declines, and to predict future species vulnerability in the face of climate change (Cardillo et al. 2008) . However, the role of phylogeny in explaining interspecific differences in other aspects of population dynamics has seldom been considered and clearly deserves further attention.

In this study we used 1670 abundance time series of 24 freshwater fish species to construct state-space models to explore spatial and temporal variations in population size of the different species, while taking into account observation errors. Specifically, we estimated, for each species, the parameters determining local population size (i.e. the growth rate, the strength of density-dependence and the migration rate) and explored how these parameters varied across time and space depending on four environmental variables (altitude and three metrics related to water temperatures) known to influence freshwater fish populations. We then used a phylogenetic comparative method (Freckleton et al. 2002) to determine whether phylogenetic relationships and species characteristics explained interspecific differences in (1) the parameters determining local population dynamics, (2) the spatial variation of these parameters among populations and (3) the influence of four environmental variables on the spatial and temporal variations of these parameters. To the best of our knowledge, no such study has been conducted on freshwater fish even though these organisms are ectothermic and are therefore expected to be highly sensitive to future climate change.

Material and methods

DATA SETS

Population time series

Fish population abundances were provided by the French National Agency for Water and the Aquatic Environment (Onema). These annual data were obtained between 1982 and 2011 by electrofishing during periods of low flow (for further details see Poulet et al. 2011). Fish were identified to species level, counted, and released. From this database we selected time series that were composed of at least 17 years during which the sampling protocol remained the same (mean time series length = 19.02; SD = 0.05). The sampling years were not necessarily consecutive within a time series but all times series that had more than three consecutive years missing were discarded to minimize the influence of missing information on our results.

Temperature time series and environmental variables

Daily air temperature data from 1982 to 2011 were provided by Météo France. This database (SAFRAN, Le Moigne 2002) is a regular eight kilometer grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically-homogeneous zones (for further details see Le Moigne 2002). Daily water temperature data measured from 2009 to 2012 at 135 sites located throughout France (Figure 1) were provided by Onema. Altitude at each sampling site was derived from a digital elevation model at 50 meters resolution.

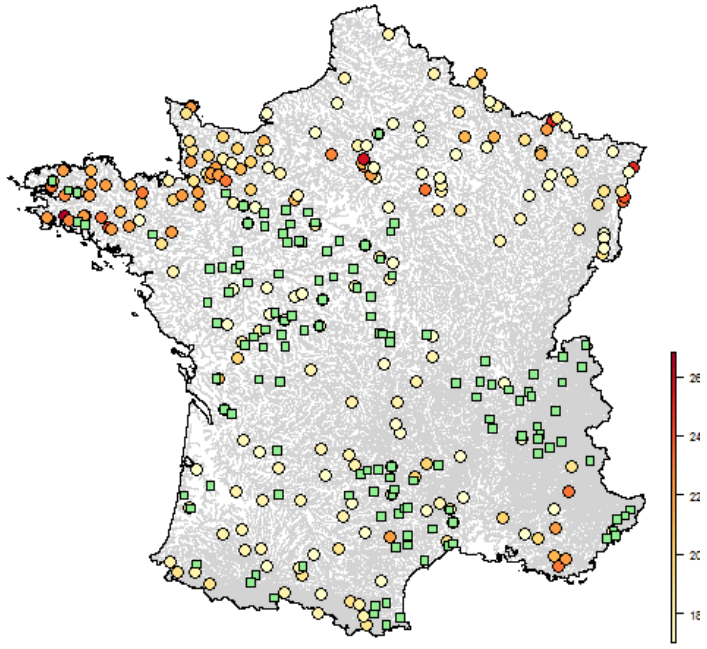

Figure 1. Study area showing the distribution of sites for fish sampling sites (circles) and water temperature records (green squares). The color scale indicates the number of years available for each fish sampling site with dark colors indicating the longest time series.

To predict daily water temperature at the sites where the populations were sampled, we used a random forest procedure. Specifically, we performed a calibration-evaluation procedure using the 135 sites for which we had information on both air and water

temperatures. Daily water temperature was then modeled as a function of air temperature, month and altitude to take into account spatio-temporal variations in the relationship between air and water temperature (Caissie 1998). To calibrate the models, we randomly selected 70% of the data. Model performances were then estimated on the remaining 30% of sites by calculating Pearson cross-correlation coefficients between observed and predicted values, and daily water temperature was finally predicted for each fish sampling site. To ensure the robustness of the predictions, the whole procedure was repeated 100 times. This calibration-evaluation process revealed a good performance of the random forest procedure in predicting water temperature (mean $R^2 = 0.86$, SD = 0.005).

As temperature has already been shown to be an important determinant of both fish species distribution (Comte and Grenouillet 2013) and population dynamics (Chevalier et al. 2014), we calculated three variables that were subsequently used to characterize the environmental conditions prevailing at each fish sampling site: (1) an index of environmental stochasticity estimated by the coefficient of variation of daily water temperature over the whole study period at each site (CV_i), (2) annual mean water temperature ($meanT_{i,t}$) and (3) its associated variance ($varT_{i,t}$).

Species traits

To illustrate the different ecological, physiological and life-history characteristics of the fish species studied, we used values for 15 different traits (Appendix 1; Table S1) taken from the literature (Buisson and Grenouillet 2009, Keith et al. 2011, Tissot and Souchon 2011) and from FishBase (Froese and Pauly 2002). We chose these traits for their diversity, the possibility of expressing them numerically or ordering them hierarchically, and the likelihood that values would be obtained for most of the species. Among these, four were quantitative variables and the others ordinal variables (Appendix 1; Table S2). We used seven traits to describe the different life-history strategies of fish species: life-span, parental care, incubation period, sexual maturity, spawning time, absolute fecundity, and egg diameter. Colinearity among these traits was reduced by carrying out a principal coordinates analysis (PCoA, Gower 1966). We chose this method because both ordinal and quantitative variables can be included. The first two PCoA axes (LH1 and LH2, respectively) were then used as synthetic variables summarizing the life-history characteristics of the different species (Appendix 1; Table S3). High values of LH2 and low values of LH1 are representative of K-selected species.

To describe the dispersal ability of the 24 fish species, we used four morphological variables (Poff and Allan 1995, Radinger and Wolter 2014): body length, and three ratios describing (1) the hydrodynamic profile of the fish (shape factor, i.e. the ratio of total body length to maximum body depth), (2) swimming ability (swimming factor, i.e. the ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin), and (3) swimming mode (aspect ratio, i.e. the ratio of the height of the caudal fin squared to the area of the caudal fin). Large species with a low swimming factor, a high shape factor and a high aspect ratio should display higher dispersal abilities than species with the opposite characteristics (Olden et al. 2008, Radinger and Wolter 2014). We performed a principal

component analysis (PCA) and the first two axes (M1 and M2) were then used as synthetic variables. High values of both M1 and M2 indicate greater dispersal abilities.

We included two habitat variables that reflect the position of the fish in the water column during feeding (feeding habitat) and resting (resting habitat). These two variables were summarized by the first axis (H1) of a PCoA (Appendix 1; Table S3).

Diet was ordered to reflect a gradient of trophic position: omnivorous, invertivorous, and piscivorous. To reflect the physiological characteristics of species, we used the upper thermal tolerance limit (UTT).

POPULATION DYNAMIC MODEL

The observed abundances in our database were affected by observation errors, as the individuals fished during a sampling event were just a fraction of the individuals present. To take these errors into account, we fitted state-space models to the different species. These models are described by two equations: an observation equation that describes how the latent process is observed and a state equation that defines the evolution of the process through time (De Valpine and Hastings 2002).

Let the vector $N_t = (N_{1,t}, N_{2,t}, \dots , N_{n,t})$ represent the true population abundance and let the vector $X_t = (X_{1,t}, X_{2,t}, \dots , X_{n,t})$ represent the observed population abundance at time t and site i = 1, 2, ... , n. To model population abundance at site i and time t, we used a modified version of the stock-recruitment Ricker model with a Poisson distribution with mean:

$$E(N_{i,t}) = \left[\gamma_{i,t} + N_{i,t-1} \exp\left(\rho_{i,t} - \eta_{i,t} N_{i,t-1}\right)\right] * \frac{S_{t-1}}{S_t}$$

where $\gamma_{i,t}$ is the migration rate, $\rho_{i,t}$ is the intrinsic growth rate, $\eta_{i,t}$ is the coefficient of density-dependence, and $\frac{S_{t-1}}{S_t}$ is an offset term with S being the sampling area at time t and t-1. Thus, local population abundance at time t was assumed to be a random variable such that $N_{i,t}$ is dependent only on $N_{i,t-1}$, according to a markovian process. Although delayed density-dependence (i.e. the influence of N_i at time t<-1) is considered as a potential important driver of population dynamics (Forchhammer et al. 1998), we found significant evidence of it for only 5% of the time series using a Box-Jenkins procedure (Turchin 1990). We therefore did not include this process in our model because of the already high number of parameters to estimate. In the models, the parameters $\gamma_{i,t}$, $\rho_{i,t}$ and $\eta_{i,t}$ varied depending on four environmental covariates according to the following equations:

$$\gamma_{i,t} = a_\gamma + (b_\gamma * Alt_i) + (c_\gamma * CV_i) + (d_\gamma * meanT_{i,t}) + (e_\gamma * varT_{i,t})$$

$$\rho_{i,t} = a_\rho + (b_\rho * Alt_i) + (c_\rho * CV_i) + (d_\rho * meanT_{i,t}) + (e_\rho * varT_{i,t})$$

$$\eta_{i,t} = a_\eta + (b_\eta * Alt_i) + (c_\eta * CV_i) + (d_\eta * meanT_{i,t}) + (e_\eta * varT_{i,t})$$

where Alt_i is the altitude at site i, a_γ, a_ρ and a_η are intercepts, whereas the other parameters (b_γ, c_γ, d_γ, e_γ, b_ρ, c_ρ, d_ρ, e_ρ, b_η, c_η, d_η, e_η) are coefficients associated to the variables Alt_i, CV_i, $meanT_{i,t}$ and $varT_{i,t}$. Before the models were run, the predictors were transformed to z-scores to compare the relative effect of each environmental variable on population dynamic parameters.

The relationship between the observed and the true abundances was modeled using a binomial distribution:

$$X_{i,t} \sim Bin(N_{i,t}, p_i)$$

where p_i is the site-specific probability of capture.

PARAMETER ESTIMATIONS

Maximum likelihood estimation for state-space model parameters often requires computation of high dimensional infinite sums that are analytically intractable. We adopted a Bayesian approach in combination with the Monte Carlo Markov Chain (MCMC) to obtain posterior distributions of parameters in the model (Clark and Bjørnstad 2004). As we had little prior information on the parameters (p_i, a_γ, b_γ, c_γ, d_γ, e_γ, a_ρ, b_ρ, c_ρ, d_ρ, e_ρ, a_η, b_η, c_η, d_η and e_η), we chose independent and uninformative priors (i.e. uniform distribution). The priors for the initial values N_1 of each time series were Poisson distributions with mean equal to the mean of the observed values, increased by one (Kéry and Schaub 2012). For each chain, we chose initial values in different regions of parameter space. Convergence was visually assessed and confirmed by effective sample sizes greater than 195 for all parameters. All species for which the convergence diagnostic failed were discarded. This left us with 24 species with the number of time series ranging from six to 154 (Table 1). Consequently, our study was based on 219 sites located throughout France (Figure 1) and represented 1670 time series. For each species, we monitored the following parameters b_γ, c_γ, d_γ, e_γ, b_ρ, c_ρ, d_ρ, e_ρ, b_η, c_η, d_η, e_η, γ_i, ρ_i, and η_i and took the mode of their posterior distribution as estimations. From the estimations of γ_i, ρ_i and η_i obtained at each site, we calculated, for each species, the mean ($M\rho$, $M\eta$, $M\gamma$) and the relative standard deviation ($RSD\rho$, $RSD\eta$, $RSD\gamma$) of these parameters. The mean was indicative of the overall dynamic of the populations of the different species, whereas the relative standard deviation was an index of the within-species spatial variation of the parameter. These six variables as well as the 12 coefficients associated with the influence of environmental variables on population dynamic parameters were subsequently used as dependent variables in the multi-predictor models. As the distributions of these 18 variables were skewed, they were box-cox transformed before analyses.

For all MCMC sampling, we used JAGS 3.3.0 (Plummer 2003) run through the program R (R Core Team 2013) and the package R2jags (Su and Yajima 2013).

Table 1. Species values for population dynamic parameters and their spatial variation. The species values for Mη, Mρ and Mγ correspond to the mean of the density-dependent coefficient (η), the intrinsic population growth rate (ρ) and the migration rate (γ) estimated for each population, respectively. RSDη, RSDρ and RSDγ are the relative standard deviation of η, ρ and γ, respectively.

Scientific name	Common name	Species code	Mη	Mρ	Mγ	RSDη	RSDρ	RSDγ	Number of time series
Alburnus alburnus	Common bleak	Alal	0.0014	-4.6152	0.3212	0.4919	0.2728	0.3083	72
Anguilla anguilla	European eel	Anan	0.0013	0.5845	-0.0128	0.7033	0.0832	0.2136	133
Barbatula barbatula	Stone loach	Babb	0.0003	0.9779	0.1271	0.5331	0.2268	0.5600	154
Barbus barbus	Barbel	Babu	0.0032	-2.5914	0.3904	0.3368	0.3820	0.3660	59
Cottus gobio	Common bullhead	Cogo	0.0002	0.3894	0.1492	0.4419	0.1852	0.2901	117
Cyprinus carpio	Common carp	Cyca	0.0388	3.2213	-0.3128	0.6064	0.5021	0.8421	11
Gasterosteus aculeatus	Three-spined stickleback	Gaac	-0.0064	0.5717	-0.0597	0.5794	0.5047	0.6195	21
Gobio gobio	Gudgeon	Gogo	0.0004	-0.0546	0.1719	0.2733	0.3552	0.2910	152
Lepomis gibbosus	Pumpkinseed	Legi	0.0065	0.1550	0.3530	0.3776	0.1263	0.3940	53
Leuciscus leuciscus	Common dace	Lele	0.0011	0.5456	0.1507	0.3608	0.3833	0.3674	74
Parachondrostoma toxostoma	Soiffe	Pato	0.0028	-0.7421	0.2961	0.7156	0.8076	0.3487	14
Perca fluviatilis	European perch	Pefl	0.0019	0.2484	0.1464	0.5289	0.3904	0.2255	86
Phoxinus phoxinus	Eurasian minnow	Phph	0.0002	0.1608	0.1665	0.1163	0.1867	0.2082	148
Pungitius pungitius	Nine-spined stickleback	Pupu	0.0005	0.8291	0.1014	0.3727	0.5615	0.3872	27
Rutilus rutilus	Roach	Ruru	0.0000	3.2784	-0.0316	0.3670	0.1412	0.5081	125
Salmo salar	Atlantic salmon	Sasa	0.0029	0.3222	0.3355	1.1210	0.2389	0.7781	28
Salmo trutta	Brown trout	Satr	0.0002	0.5218	0.0472	0.2365	0.2836	0.3128	141
Sander lucioperca	Zander	Salu	0.0719	0.7038	1.1577	0.6463	0.5068	0.4814	16
Scardinius erythrophthalmus	Rudd	Scer	0.0255	0.7815	0.1873	0.8809	0.1814	0.5010	31
Silurus glanis	Wels catfish	Sigl	0.0133	0.1897	0.8413	0.9672	0.1365	0.2685	9
Squalius cephalus	European chub	Sqce	0.0013	-8.9064	0.3638	0.5271	0.3873	0.3882	137
Telestes souffia	Vairone	Teso	-0.0017	18.8372	-0.6161	0.7306	0.4983	0.6850	11
Thymallus thymallus	Grayling	Thth	0.0404	-1.2429	0.7028	0.9484	0.5034	0.9383	6
Tinca tinca	Tench	Titi	-0.0022	0.6813	-0.0958	0.3239	0.2235	0.4337	45

ANALYSES

Phylogeny

A dated phylogeny (Appendix 2; Figure S1) reconstructed from complete mitochondrial genomes on 151 Teleostei fish species using Bayesian inference was used as our phylogenetic hypothesis (for further details see Comte et al. 2014). To test the robustness of our results due to uncertainties associated with phylogeny reconstruction, we ran our analyses on 100 trees selected at random from the posterior distribution of parameter space. However, as the detection of phylogenetic signal did not differ between the different trees (Appendix 2; Table S4), the PGLS models were built using the maximum clade credibility tree.

Phylogenetic signal

To evaluate whether species traits and the 18 dependent variables displayed significant phylogenetic signal, we used the λ statistic (Pagel 1999). This statistic measures how closely the variation in traits across species concurs with the prediction of a Brownian model of evolution (Pagel 1999). $\lambda=0$ means that all species are independent, $\lambda=1$ corresponds to a Brownian model of evolution, and $0<\lambda<1$ corresponds to some degree of trait lability (Blomberg et al. 2003). As within species variability may have important consequences when evaluating phylogenetic signal, we accounted for this source of variation in parameters for which we had multiple values per species (i.e. population dynamic parameters) following Ives et al. (2007).

Multi predictor models and model averaging

For each dependent variable, we considered all possible multi-predictor models (n = 84) that included three terms or fewer to avoid over-fitting (Knape and De Valpine 2011). We also considered models that included interaction terms between independent variables but only for models including two variables. To take into account phylogenetic relationships between species in the models, we used the phylogenetic generalized least square (PGLS) comparative method (Freckleton et al. 2002). This approach controls for the non-independence among species by adjusting a variance-covariance matrix based on the λ statistic. To provide unbiased estimates of fixed and random components in the models, we used a two step procedure. For each model, we first estimated the λ statistic by restricted maximum likelihood. Parameters of the models were then estimated by maximum likelihood while setting the value of λ to the previously estimated value. According to the variance inflation factor, colinearity never appeared to be a problem for any of the models considered (Kutner 2005).

For each dependent variable, we then investigated the relative importance of the predictors by information theoretic model-comparison (Burnham and Anderson 2002) in which inference was based on the entire set of plausible models. The predictors were transformed to z-scores to standardize their slope coefficients (β) prior to analyses. We

evaluated the candidate models using the Akaike information criterion adjusted for small sample size (AICc) and selected all the models that were contained within a ΔAICc of seven (Burnham and Anderson 2002). When several models were selected as best candidates, we calculated model-averaged slope coefficients using the Akaike weights of each model (w_i) (Burnham and Anderson 2002). For each weighted averaged coefficient, we then calculated confidence intervals from the variance of the estimated coefficient among the selected models (Johnson and Omland 2004). Finally, we also calculated for each model pseudo-R^2 following Nagelkerke (1991).

Results

GENERAL PATTERNS AND PHYLOGENETIC SIGNAL

Whatever the dependent variable, we found considerable variation among species (Table 1). The population growth rate varied from -0.61 to 1.15 (mean = 0.20; SD = 0.35), the migration rate from -8.90 to 18.80 (mean = 0.61; SD = 4.58) and the strength of density-dependence from -0.01 to 0.07 (mean = 0.01; SD = 0.02). For the relative standard deviation of population dynamic parameters, we found that density-dependence had the highest value (mean = 0.55; SD = 2.19; range = 0.11-1.21), whereas the population growth rate had the lowest value (mean = 0.33; SD = 3.01; range = 0.08-0.80). The migration rate had an intermediate value (mean = 0.44; SD = 2.02; range = 0.20-0.93), relative to the two other parameters (Table 1). We also found considerable interspecific variation in the 12 slope coefficients associated with the influence of environmental variables on the spatial and temporal variations of the population dynamic parameters (Appendix 3, Table S5).

Phylogenetic signal was weak and non-significant ($P>0.05$) for all of the 18 dependent variables (Appendix 2; Table S4). In contrast, five out of the seven predictors (i.e. UTT, Diet, M1, M2, and LH2) displayed a significant ($P<0.05$) phylogenetic signal ($\lambda = 0.62$, $\lambda = 0.7$, $\lambda = 1$, $\lambda = 0.87$ and $\lambda = 1$, respectively; Appendix 2; Table S4).

SELECTED MODELS AND AVERAGED COEFFICIENTS

Population dynamic parameters

For the population growth rate, three models that explained from 65% to 73% of the variance were selected (Appendix 3; Table S6). After averaging the slope coefficients, we found an overall significant positive influence of M2 on the growth rate (Figure 2A), indicating that species displaying the highest dispersal abilities (i.e. large body size and high aspect ratio) showed the highest growth rates.

For the strength of density-dependence, ten models were selected (Appendix 3; Table S7). The amount of variance explained ranged from 47% to 62%. We found a significant

negative interaction between Diet and LH2 indicating that the relationship between LH2 and density-dependence was weakened for piscivorous species. Density-dependence was also related, albeit weakly, to M2, LH1 and LH2 (Figure 2B).

For the migration rate, the null model was among the best selected models (Appendix 3; Table S8), thus providing evidence that none of the traits considered here had an influence on this parameter.

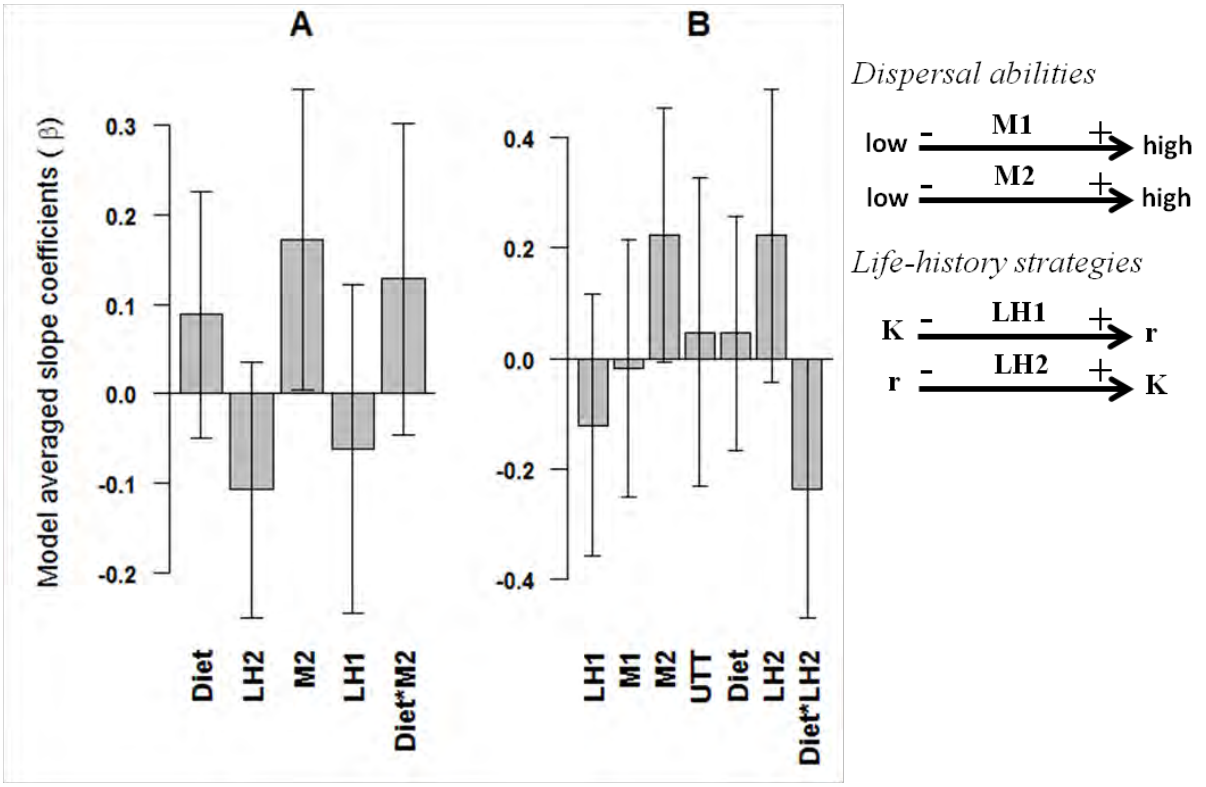

Figure 2. Weighted average slope coefficients (β) calculated from the selected PGLS models performed on (A) the mean population growth rate Mρ and (B) the mean strength of density -dependence Mη. LH1 and LH2, first and second axes extracted from the PCoA performed on the seven life-history traits; M1 and M2, first and second axes extracted from the PCA performed on four morphological traits; UTT, upper thermal tolerance limit; H1, first axis extracted from the PCoA performed on the two habitat variables.

Spatial variation in population dynamic parameters

The null model was among the selected models for both RSDρ and RSDγ (Appendix 3; Table S9 and S11). Thus, none of the traits considered here were pertinent enough to explain interspecific differences in these two variables.

On the contrary, ten models that explained from 29% to 49% of the variance were selected to explain interspecific differences in RSDη (Appendix 3; Table S10). Although none of the predictors appeared significant once the slope coefficients were averaged, RSDη

appeared to be influenced by a complex combination of traits, including LH1 and Diet (Figure 3).

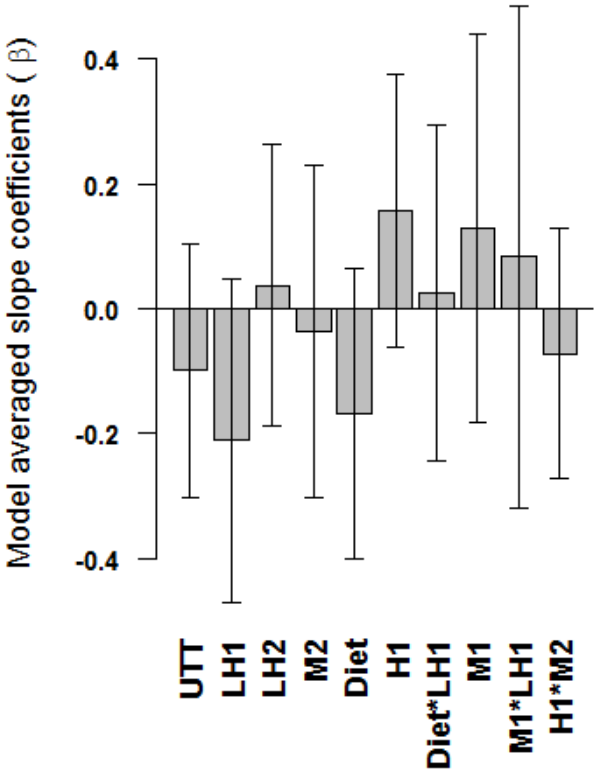

Figure 3. Weighted average slope coefficients (β) calculated from the PGLS selected models performed on the relative standard deviation of the strength of density -dependence RSD_{η}. For abbreviations, see Figure 2.

Influence of environmental variables

The PGLS model selection procedure performed on the 12 slope coefficients associated with the influence of environmental variables on the spatial and temporal variations of population dynamic parameters revealed some general patterns (Table 2). Whatever the parameter considered, Diet and M1 were always among the selected models. This suggests that these traits were important in explaining interspecific differences in the influence of environmental variables on these parameters. LH2 was always among the selected models explaining the varying influence of environmental variables on density-dependence whereas six traits were systematically selected (LH1, LH2, M1, M2, UTT and H1) concerning the migration rate. Among the 21 interactions tested, 16 were selected for at least one dependent variable. Only one model was selected to explain interspecific differences in the influence of $meanT_{i,t}$ on the growth rate. This model included Diet, M1 and H1.

The influence of Alt_i, CV_i and $meanT_{i,t}$ on the growth rate were significantly associated with Diet. LH2 and its interaction with M1 significantly explained interspecific differences in the influence of $varT_{i,t}$ on the growth rate. LH2 was also significantly related to the influence of CV_i on this parameter. UTT and its interaction with H1 were significantly related to interspecific differences in the influence of Alt_i on density-dependence whereas both UTT and Diet appeared to be good predictors of interspecific differences in the influence of CV_i on this parameter. The influence of $meanT_{i,t}$ and $varT_{i,t}$ on density-dependence were significantly associated with the interaction between H1 and LH1 and between M1 and LH1,

respectively. LH2 and the interaction between H1 and M1 were pertinent to explain interspecific differences in the influence of $varT_{i,t}$ on the migration rate.

Table 2. Weighted average slope coefficients extracted from the 84 PGLS models performed on the coefficients associated with the influence of ecological variables on population parameters. LH1 and LH2: first and second axes extracted from the PCoA performed on the seven life-history traits; M1 and M2: first and second axes extracted from the PCA performed on four morphological traits; UTT: upper thermal tolerance. Alt_i: altitude; CV_i: environmental stochasticity; $meanT_{i.t}$: annual mean of water temperature; $varT_{i.t}$: annual variance of water temperature; ρ: population growth rate; η: density regulation and γ: migration rate. Significant (P<0.05) results are in bold.

		Alt_i	CV_i	$meanT_{i.t}$	$varT_{i.t}$
	ρ	**0.30**	**-0.30**	**0.20**	0.20
Diet	η	0.01	**-0.0001**	-0.0001	0.05
	γ	-0.50	-0.60	-0.90	0.20
	ρ	0.01	0.20	-	-
UTT	η	**-0.05**	**0.00004**	-	-
	γ	-0.20	-0.30	0.70	-0.40
	ρ	-	-	-	-
LH1	η	-0.01	-	0.00002	0.02
	γ	-0.50	-0.60	1.00	0.40
	ρ	-	0.50	-	-0.30
LH2	η	-0.01	**0.00002**	0.00003	**-0.08**
	γ	-0.30	-1.00	-0.60	0.30
	ρ	0.08	0.01	0.10	**0.20**
M1	η	0.004	-0.00002	-0.0001	0.08
	γ	-0.05	0.30	-0.20	-0.20
	ρ	-0.07	-0.20	-	-
M2	η	0.01	-	-0.00003	-0.003
	γ	0.70	0.30	-0.80	-0.04
	ρ	0.03	-0.20	-0.10	-
H1	η	0.01	-0.0001	-	0.07
	γ	-0.07	-0.10	2.00	0.50
	ρ	-	-	-	-
H1*LH1	η	0.003	-	**-0.0001**	-
	γ	-	-	-	-
	ρ	-	-	-	-
H1*UTT	η	**0.03**	-	-	-
	γ	-	-	-	-
	ρ	-	-	-	-
H1*Diet	η	-	0.00002	-	-
	γ	-	0.20	-0.40	-
	ρ	-	-	-	-
Diet*LH2	η	-	-	-0.000003	-
	γ	0.20	-	2.00	-
	ρ	-	-	-	-
H1*LH2	η	-	-	-	-
	γ	-	-1.00	-	-
	ρ	-	-	-	-
Diet*M1	η	-	-	-	-
	γ	-	-	-0.30	-
	ρ	-	0.30	-	**-0.30**
M1*LH2	η	-	-	0.00	-
	γ	-	-	-	-
LH2*UTT	ρ	-	-0.20	-0.20	-

	η	-	-	-	-
	γ	0.50	0.80	-	-
	ρ	-	-	-	-
M1*LH1	η	-	-	-	**0.20**
	γ	-0.30	-	0.70	-
	ρ	-	-	-	-
LH1*LH2	η	-	-	-	-
	γ	-	-0.40	-1.00	-
	ρ	-	-	-	-
LH1*UTT	η	-	-	-	-
	γ	-	-	0.20	-
	ρ	-	-	-	-
Diet*UTT	η	-	-	-	-
	γ	-	-	0.10	-
	ρ	-0.01	-	-	-
H1*M1	η	0.01	-	-	-
	γ	-	-	-	**-2.00**
	ρ	-	-	-	-
Diet*M2	η	-	-	-	-
	γ	-0.30	0.50	1.00	-
	ρ	-	-	-	-
LH2*M2	η	-	-	-	-
	γ	-	-0.60	-	-
	ρ	-	-	-	-
UTT*M2	η	-	-	-	-
	γ	-	-	-0.20	-

Discussion

In this study, we combined trait-based and phylogenetic approaches to determine whether species traits and/or the evolutionary history of species could explain interspecific differences in population dynamic parameters, their spatial variations and the influence of four environmental variables on these parameters. We have provided four main results. First, phylogenetic signal was weak for all the population dynamic descriptors considered. Second, the population growth rate and the strength of density-dependence were significantly related to some species characteristics but not the migration rate. Third, spatial variation of density-dependence was related to species characteristics but not the growth rate nor the migration rate. Fourth, the influence of environmental variables on population dynamics parameters could be predicted from species characteristics.

Phylogenetic signal

Throughout our analyses, we did not find evidence for phylogenetic dependence in any of the population dynamic descriptors considered. This suggests that phylogeny did not provide pertinent information in explaining interspecific differences in these descriptors. To the best of our knowledge, although several studies have taken into account phylogenetic relationships between species when relating species characteristics to interspecific differences in population dynamics (e.g. Sæther et al. 2005, Saether et al. 2011), no study has explicitly

tested whether several population dynamic descriptors, such as those considered here, were underlined by the evolutionary history of species. Nonetheless, some contrasting results have already been observed when considering long-term trends in population abundance or phenology. For instance, Willis et al. (2008) found that changes in abundance and flowering time of 429 plant species were significantly phylogenetically conserved, indicating that species evolutionary history is important to understand species response to climate change. On the contrary, phylogeny failed to explain interspecific differences in the degree to which birds advanced their spring arrival dates in response to climate change (Végvári et al. 2010) or in the spatial synchrony of freshwater fish population dynamics (Chevalier et al. 2014). The lack of phylogenetic clustering in interspecific differences in population dynamic descriptors documented here might be explained to a certain extent by a low statistical power due to the use of a small phylogeny (Münkemüller et al. 2012). Alternatively, within-species variation in the deterministic components of population dynamics (Williams et al. 2003, Saether et al. 2008) could explain the low propensity of phylogenetic relationships to describe these interspecific differences. This may also be underlined by a weak phylogenetic signal in the traits involved or by the fact that different traits displaying different phylogenetic patterns are involved in interspecific differences in population dynamics, thus decreasing the strength of the phylogenetic clustering in species responses.

Population dynamic parameters

Species with a large body size have generally been associated with species with a low population growth rate (Denney et al. 2002). Although body size has generally been related to life-history characteristics to explain interspecific variations in population growth rate (Jeppsson and Forslund 2014), this trait has also been shown to correlate with species dispersal abilities (Radinger and Wolter 2014). Here, we found that species with a large body size and a high aspect ratio displayed higher growth rates than species with the opposite characteristics. This suggests that species dispersal abilities rather than life-history characteristics are relevant to explain interspecific variations in population growth rate. Although not significant once the slope coefficients were averaged, the diet was included in three of the four selected models explaining interspecific differences in growth rate, including an interaction with species dispersal ability. This indicates that diet might also be an important determinant of interspecific differences in population growth rate, although the underlying mechanisms remain unclear.

Several studies have found a significant association between the strength of density-dependence and the position of the species along the slow-fast continuum of life-history variation (Saether et al. 2005, Herrando-Pérez et al. 2012). Similarly, we found that the life-history characteristics of species were among the best predictors, albeit non-significant, to explain the strength of density-dependence. This result confirms those of previous studies that long-lived species maturing late, and having few reproductive events (i.e. K-selected species), generally display more density-dependence than r-selected species (Fowler 1981, Saether et al. 2005). We also found a significant negative interaction between life-history traits and diet, indicating that ecological traits could interact with life-history traits to generate complex

patterns of density-dependence in freshwater fish populations. In contrast, we found no influence of species characteristics on the migration rate. We see at least two but not mutually exclusive explanations for this result. First, fish are ectothermic organisms, so their body temperature and metabolic activity are directly dependent on the environment they are living in. Thus, a local increase in temperature may trigger or stop the migration of individuals (Sims and Wearmouth 2004), which may ultimately mask an influence of dispersal abilities on interspecific differences in the migration rate. Second, the nature of freshwater ecosystems may also be involved, since freshwater systems are highly fragmented by the presence of dams (Pringle 2003), which could prevent the migration of individuals between neighboring locations independently of their dispersal abilities.

Spatial variation of population dynamic parameters

We found no evidence for an influence of species traits on interspecific differences in the relative standard deviation of both the growth rate and the migration rate. This suggests that extrinsic factors (e.g. water temperature, local pollution) are more likely to influence the spatial variation of these parameters, as already shown (Saether et al. 2008). Nonetheless, although not significant, our analysis suggests that spatial variation of density-dependence depends on a complex combination of species characteristics, including ecological traits such as diet and habitat requirement. Consequently, although species traits appeared to be related to spatial patterns of density-dependence, the underlined mechanisms remain unclear. Unfortunately, this result is difficult to compare to others studies as we are not aware of similar studies to date. Further work is needed to add to our knowledge of the mechanisms underlying interspecific differences in the spatial variation of density-dependence.

Influence of environmental variables

Several studies have examined whether species characteristics could explain interspecific differences in the influence of environmental variables on population dynamics. For instance, Sandvik and Erikstad (2008) found evidence that both feeding ecology and life-history traits influenced how seabirds respond to climatic variability. In a recent study, Sæther et al. (2013) also showed that the influence of environmental stochasticity on population dynamics diminished with generation time, resulting in decreased stochasticity in population dynamics towards the slow end of the life-history continuum. Other studies further documented more complex patterns, thus suggesting that we still lack a complete understanding of the determinants involved in interspecific differences in the influence of environmental variables on population dynamics. For instance, Sandvik et al. (2012) demonstrated that bird species with slow life histories responded positively to climate at southern latitudes and negatively at northern latitudes. Here, we found that the diet and dispersal abilities of species were quite good predictors of interspecific differences in the influence of environmental variables on population dynamics parameters. Importantly, only one model was selected to explain interspecific differences in the influence of the annual mean water temperature on the growth rate. This suggests that the impact of increasing water temperatures on the growth rate is highly deterministic and could be predicted from simple specific traits such as diet and dispersal abilities. Nonetheless, our results also revealed more

complex patterns. We found that the propensity of most species characteristics to explain interspecific differences in the influence of environmental variables varied depending on the population dynamic parameter considered. More specifically, life-history characteristics were pertinent in explaining the influence of environmental stochasticity (CV_i) on the growth rate but not on the migration rate or on density-dependence. Taking the specific influence of environmental variables on population dynamic parameters into account revealed complex patterns that have not been demonstrated before. This suggests that future studies should consider this specificity to add to our knowledge of the mechanisms involved in interspecific differences in species responses to environmental variations.

Implications for conservation

This is the first study relating species characteristics to interspecific differences of several descriptors of population dynamics in freshwater fish. We showed that phylogenetic relationships between species did not provide pertinent information in explaining interspecific differences in various aspects of population dynamics, contrary to several species characteristics related to their ecology, physiology or life-history. We also showed that such relationships depended not only on a single combination of traits but also on their interactions, suggesting that unraveling the determinants of population dynamics may be more complex than previously thought. Furthermore, the propensity of species characteristics to explain interspecific differences in the influence of environmental variables on population dynamics appeared to vary depending on the parameter considered. Although our findings clearly highlight the complexity of the mechanisms driving interspecific differences in abundance patterns, they also demonstrate that ecological and life-history characteristics play a fundamental role in explaining interspecific differences in spatial and temporal variations in population size. By successfully identifying species characteristics related to various descriptors of population dynamics, we showed that population responses to global changes will be mediated by their intrinsic characteristics. Trait-based approaches therefore appear to be a promising avenue to identify species that will be the most at risk from climate change, while unraveling the underlying determinant of species responses. This is especially interesting for rare or difficult-to-sample species for which long-term data are not available, especially as these species are those that necessitate urgent efficient management strategies (Hannah et al. 2002).

Nonetheless, we found considerable uncertainty in the direction of the effects, which may impede the generalization of the relationships between species traits and population dynamics. In this study, we have considered the average of population dynamic parameters as general values governing abundance patterns of the species. However, the values of these parameters varied depending on the location of the different populations within the species' range. In particular, changes in population dynamic parameters have already been shown to correlate with geographic variables such as latitude (Saether et al. 2008) or the distance from species range limits (Williams et al. 2003). Furthermore, beyond the underlying determinants of species ranges, populations may not be equally at risk from environmental changes (Jiguet et al. 2010). In the context of ongoing climate change, populations within the species' range

are not experiencing similar exposure to environmental changes and are not similarly adapted to these modifications (Tingley et al. 2012). Whether populations are positively or negatively affected may thus depend both on their location within the species' range (Matías and Jump 2014) but also on intrinsic species characteristics (Comte et al., 2014). It would therefore be interesting to determine the extent to which interspecific differences in population dynamics located at different extremes of species range limits are predicted by different combinations of traits.

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Electronic supplementary material

Table S1. Species traits for the 24 freshwater fish species studied. Trait descriptions are given in table S2. PCoAs were performed on the life-history traits and the habitat traits to reduce colinearity between them whereas PCA was performed on morphological traits.

			Habitat		Life-history							Dispersal abilities					
Scientific name	Common name	Code	FH	HA	ST	LS	MA	PC	IP	FE	ED	BL	AR	SH	SW	UTT	FD
Alburnus alburnus	Common bleak	Alal	2	2	2	1	2	1	1	5750	1.55	135	1.59	4.92	0.36	30	2
Anguilla anguilla	European eel	Anan	1	1	1	3	5	1	1	2000000	1.15	650	0	17.80	1.00	20	3
Barbatula barbatula	Stone loach	Babb	1	1	2	1	2	1	1	5000	1	110	0.9	6.50	0.58	28	2
Barbus barbus	Barbel	Babu	1	2	1	3	5	1	1	10000	2.2	500	1.845	5.23	0.30	24	2
Cottus gobio	Common bullhead	Cogo	1	1	1	1	2	2	3	500	2.5	125	1.03	4.38	0.39	26	2
Cyprinus carpio	Common carp	Cyca	1	2	2	3	4	1	1	800000	1.4	500	1.885	3.13	0.42	32	1
Gasterosteus aculeatus	Three-spined stickleback	Gaac	2	2	2	1	1	2	3	300	1.7	60	2.04	4.50	0.19	20	2
Gobio gobio	Gudgeon	Gogo	1	2	2	1	2	1	1	3000	1.7	125	1.37	5.72	0.28	30	2
Lepomis gibbosus	Pumpkinseed	Legi	2	2	2	2	2	2	3	2000	1	150	0.72	2.41	0.42	30	2
Leuciscus leuciscus	Common dace	Lele	2	2	1	2	3	1	1	10000	1.75	250	2.01	4.87	0.32	25	1
Parachondrostoma toxostoma	Soiffe	Pato	1	2	1	2	4	1	1	8250	1.6	225	1.782	4.41	0.4	21.5	1
Perca fluviatilis	European perch	Pefl	2	1	1	3	3	1	1	20000	2.25	275	1.395	3.3	0.32	27	3
Phoxinus phoxinus	Eurasian minnow	Phph	2	1	2	1	2	1	1	1000	1.5	80	1.07	5.26	0.32	25	2
Pungitius pungitius	Nine-spined stickleback	Pupu	2	2	1	1	1	2	3	150	1.3	60	1.33	5.83	0.17	24	2
Rutilus rutilus	Roach	Ruru	2	2	1	2	2	1	1	50000	1.35	275	1.475	3.66	0.29	25	1
Sander lucioperca	Zander	Salu	2	1	1	2	4	2	3	300000	1.25	500	1.39	5.2	0.26	22	3
Salmo salar	Atlantic salmon	Sasa	2	2	1	2	5	3	2	10000	6	700	2.05	4.3	0.31	9	3
Salmo trutta	Brown trout	Satr	2	1	1	2	3	3	2	1500	4.5	325	1.615	4.21	0.38	19	3
Scardinius erythrophthalmus	Rudd	Scer	2	2	2	3	3	1	1	150000	1.4	225	1.77	2.95	0.36	25	1
Silurus glanis	Wels catfish	Sigl	1	1	1	3	5	2	3	100000	2.5	1500	0.63	5.06	0.64	28	3
Squalius cephalus	European chub	Sqce	2	2	2	2	3	1	1	125000	1.5	400	1.42	3.97	0.36	24	1
Telestes souffia	Vairone	Teso	2	2	1	2	3	1	1	6000	2	150	0.84	4.95	0.29	18	2
Thymallus thymallus	grayling	Thth	2	2	1	1	3	3	2	7500	2.6	300	1.96	4.9	0.3	14	2
Tinca tinca	Tench	Titi	1	1	2	2	3	1	1	300000	0.9	300	1.45	4	0.46	26	1

Table S2. Description of the 15 traits used.

Trait	Code	Modality	Description
Diet	FD	1	Omnivorous
		2	Invertivorous
		3	Piscivorous
Body length	BL	quantitative	Total body length from the mouth to the fork of the tail (mm)
Aspect ratio	AR	quantitative	Ratio of the squared height of the caudal fin to its surface area
Shape factor	SH	quantitative	Ratio of total body length to maximum body depth
Swimming factor	SW	quantitative	Ratio of the minimum depth of the caudal peduncle to the maximum caudal fin depth
Feeding habitat	FH	1	Benthivorous
		2	Water column
Resting habitat	HA	1	Demersal
		2	Benthopelagic
		3	Pelagic
Absolute fecundity	FE	quantitative	Number of oocytes
Spawn time	ST	1	Once a year
		2	Several times a year
Egg diameter	ED	quantitative	At hatching (mm)
Life span	LS	1	< 8 years
		2	8-15 years
		3	> 15 years
Female maturity	MA	1	≤ 2 years
		2	2-3 years
		3	3-4 years
		4	4-5 years
		5	≥ 5 years
Parental care	PC	1	No protection
		2	No protection with nest or egg hiders
		3	Nest or egg hiders
Incubation period	IP	1	≤ 7 days
		2	7-14 days
		3	> 14 days
Upper thermal optimum	UTT	quantitative	Optimum maximum temperature (°C)

Table S3. Pearson's correlations between species traits and principal components. PCoAs were performed on habitat and life-history traits whereas PCA was performed on morphological traits. The percentage of variance explained by each axis is shown in parentheses.

	Trait	PC1	PC2
Habitat traits		H1 (31.8%)	(18.7%)
	Resting habitat	0.8	-
	Feeding habitat	0.8	-
Life-history traits		LH1 (22.2%)	LH2 (21.3%)
	Fecundity	-0.02	0.61
	Spawn time	0.95	-0.02
	Egg diameter	-0.63	-0.18
	Life-span	-0.27	0.88
	Female maturity	-0.53	0.7
	Incubation period	-0.37	-0.7
	Parental care	-0.32	-0.44
Dispersal traits		M1 (63%)	M2 (22%)
	Body length	-0.52	0.84
	Aspect ratio	0.81	0.27
	Swimming factor	-0.93	0.03
	Shape factor	-0.83	-0.30

Figure S1. Maximum clade credibility tree of the 24 freshwater fish species.

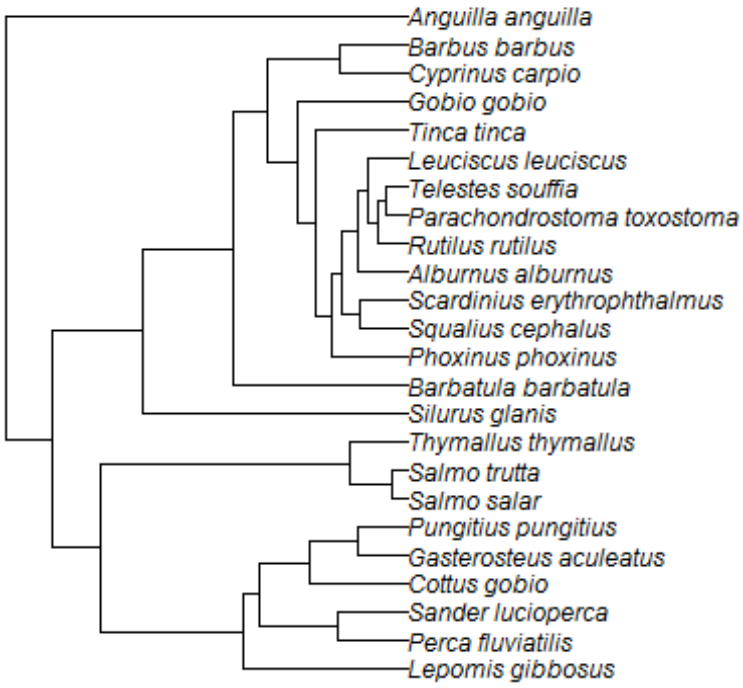

Table S4. Phylogenetic signal and its associated p-value for the 18 dependent variables and the seven predictor variables estimated using the maximum clade credibility tree. Are also shown the percentages of significant tests for phylogenetic signal using the 100 trees sampled from the posterior distribution.

	Variables	λ	p-value	Significant tests (%)
Dependent	Mη	0	1	0
	Mρ	0	1	0
	Mγ	0	1	5
	RSDη	0	1	0
	RSDρ	0	1	0
	RSDγ	0	1	0
	γ_b	0	1	0
	γ_c	0	1	0
	γ_d	0	1	0
	γ_e	0	1	0
	ρ_b	0	1	0
	ρ_c	0	1	0
	ρ_d	0	1	0
	ρ_e	0.09	0.57	0
	η_b	0	1	0
	η_c	0.02	0.89	0
	η_d	0	1	0
	η_e	0.05	0.76	0
Predictors	LH1	0.66	0.07	8
	LH2	1	0.002	100
	M1	1	<0.001	100
	M2	0.87	0.04	65
	H1	0.76	0.87	0
	UTT	0.62	0.02	100
	Diet	0.7	0.002	100

Table S5. Species specific-values of the standardized slope coefficients associated with the influence of Alt_i (subscript b), CV_i (subscript c), $meanT_{i,t}$ (subscript d) and $varT_{i,t}$ (subscript e) on migration rate (γ), growth rate (ρ) and density dependence (η). Mean values and standard deviations across species are also presented. Coefficient estimates for which 95% credible intervals do not overlap zero are shown in bold. Species code as in Table 1.

Species code	γ_b	γ_c	γ_d	γ_e	ρ_b	ρ_c	ρ_d	ρ_e	η_b	η_c	η_d	η_e
Alal	**3.58**	**2.90**	**12.50**	-1.43	**-0.05**	**-0.26**	**-0.59**	**0.28**	**8.55E-04**	**-7.99E-04**	**-1.49E-03**	**9.57E-04**
Anan	-0.09	0.00	0.00	-0.02	0.00	**-0.04**	**-0.04**	**0.06**	**1.25E-03**	-3.38E-05	**1.86E-04**	1.59E-04
Babb	-0.15	**1.96**	0.75	0.32	0.00	**-0.10**	**-0.03**	0.00	**4.35E-05**	**-2.32E-04**	**8.04E-05**	**-1.54E-04**
Babu	**3.07**	**2.15**	0.33	**-4.56**	**-0.25**	**-0.10**	**0.18**	**0.11**	**-3.06E-03**	**-3.18E-04**	**3.35E-04**	**2.29E-04**
Cogo	-0.04	**0.38**	0.19	**-0.50**	**0.06**	**-0.21**	**-0.10**	**0.26**	**1.76E-04**	**-2.79E-04**	3.65E-05	**2.38E-04**
Cyca	**-3.29**	-1.40	-1.00	-0.44	0.82	0.72	-0.19	-1.10	-4.60E-02	6.15E-03	**-1.02E-01**	8.04E-04
Gaac	**-1.92**	**3.95**	**2.66**	**-6.40**	**0.69**	**-2.13**	**-1.37**	**2.86**	**9.20E-03**	**-2.60E-02**	**-1.48E-02**	**3.59E-02**
Gogo	**-1.18**	**-0.41**	**-1.70**	**0.32**	**0.15**	0.01	**0.22**	0.01	**-2.79E-05**	2.59E-05	**2.50E-04**	**-1.48E-04**
Legi	-0.02	0.04	0.00	-0.07	**-0.21**	**0.22**	**-0.08**	**-0.28**	**-6.01E-03**	**2.99E-03**	**-5.01E-03**	**-4.54E-03**
Lele	0.09	-0.14	-0.29	0.47	**-0.10**	**0.48**	**0.54**	**-0.76**	**-1.62E-03**	**3.03E-03**	**2.01E-03**	**-4.59E-03**
Pato	**1.55**	**-5.03**	-2.64	**5.74**	**-0.40**	**0.76**	**0.47**	**-1.03**	**-1.28E-03**	-6.06E-04	**8.40E-04**	**-2.37E-03**
Pefl	**-0.64**	**-0.74**	**-2.51**	**1.58**	**0.10**	**0.22**	**0.63**	**-0.49**	**9.66E-04**	**6.68E-04**	**3.61E-03**	**-2.71E-03**
Phph	**-0.49**	-0.21	0.02	-0.04	**0.06**	**-0.07**	**-0.07**	**0.13**	**3.64E-05**	1.02E-06	7.35E-06	5.77E-06
Pupu	-0.68	**-1.84**	1.54	**2.20**	**0.20**	**0.37**	-0.08	**-0.42**	**3.05E-03**	**6.11E-03**	**-1.29E-03**	**-6.64E-03**
Ruru	**-1.01**	**8.36**	**8.74**	**-10.34**	**0.01**	**-0.18**	**-0.22**	**0.23**	**-4.64E-05**	**-1.91E-04**	**-3.23E-04**	**2.37E-04**
Salu	0.00	-0.50	-0.13	0.07	0.95	0.38	-0.21	**0.66**	1.03E-01	**-2.33E-02**	**-4.00E-02**	**9.26E-02**
Sasa	-0.53	0.18	-0.24	0.22	**0.48**	**0.20**	**0.55**	**-0.40**	**4.55E-03**	**1.14E-03**	**2.10E-03**	**-1.64E-03**
Satr	-0.58	-0.30	**-0.57**	0.00	0.01	**-0.02**	**-0.05**	**0.05**	-7.94E-06	**-2.00E-04**	**-3.70E-04**	**4.18E-04**
Scer	**-0.23**	**-0.92**	**-1.20**	**1.59**	0.08	0.01	-0.06	**-0.48**	**2.54E-02**	**-7.54E-03**	**-1.80E-02**	**7.20E-03**
Sigl	0.01	0.04	-0.02	-0.02	**-0.34**	**-0.53**	**0.44**	**0.64**	**-9.99E-03**	-7.15E-04	1.73E-04	**5.30E-03**
Sqce	**-10.43**	**-11.31**	**-20.65**	**15.89**	**0.28**	**0.13**	**0.37**	**-0.21**	**7.06E-04**	**1.86E-04**	**1.45E-04**	**-4.52E-04**
Teso	**-7.90**	-4.58	2.21	**25.13**	**0.60**	**0.27**	**0.48**	**-1.79**	**2.88E-03**	**-1.63E-03**	-6.24E-05	**-3.34E-03**
Thth	13.76	9.45	0.50	**6.97**	-0.65	-2.46	-0.66	1.50	2.61E-02	-4.54E-02	-1.22E-02	2.86E-02
Titi	0.16	-0.23	**-0.37**	0.32	0.06	**0.47**	**0.53**	**-0.65**	-1.70E-04	**1.17E-02**	**1.19E-02**	**-1.67E-02**
Mean	-0.289	0.074	-0.078	1.541	0.107	-0.078	0.028	-0.034	0.005	-0.003	-0.007	0.005
SD	4.180	4.028	5.490	6.884	0.382	0.750	0.464	0.905	0.025	0.012	0.022	0.021

Table S6. Multi-predictor PGLS models ranked by AIC_c for the mean population growth rate (Mρ).

Models	k	AIC_c	ΔAICc	ω_i
Diet+LH2+M2	**5**	**1.06**	**0.00**	**0.73**
Diet+LH1	**4**	**4.26**	**3.20**	**0.15**
Diet*M2	**5**	**6.64**	**5.58**	**0.05**
Diet	3	8.56	7.49	0.02
LH1	3	8.76	7.70	0.02
Diet+UTT	4	9.20	8.13	0.01
Diet+LH2	4	11.14	10.08	0.00
Diet*UTT	5	11.18	10.11	0.00
Diet+H1	4	12.26	11.20	0.00
UTT+LH1+LH2	5	12.44	11.38	0.00
Diet+UTT+LH2	5	12.63	11.57	0.00
LH1+H1	4	13.09	12.03	0.00
LH1+LH2	4	13.44	12.37	0.00
LH2+M1+M2	5	13.55	12.48	0.00
LH1+LH2+M1	5	14.58	13.52	0.00
Diet*H1	5	14.59	13.53	0.00
Diet+LH2+H1	5	15.51	14.45	0.00
Diet*LH1	5	15.54	14.48	0.00
LH1*LH2	5	15.58	14.52	0.00
Diet+UTT+H1	5	15.65	14.59	0.00
Diet+M2	4	15.72	14.66	0.00
UTT+LH1+H1	5	16.23	15.17	0.00
LH1+M1+H1	5	16.29	15.23	0.00
LH1*M1	5	17.79	16.73	0.00
Diet+M2+H1	5	18.57	17.50	0.00
Diet+M1+M2	5	18.61	17.55	0.00
Diet+LH1+M2	5	19.10	18.04	0.00
Diet+M1	4	19.77	18.70	0.00
Diet+UTT+M2	5	20.18	19.12	0.00
LH2+M2	4	20.41	19.35	0.00
M2	3	21.40	20.34	0.00
Diet+LH1+M1	5	21.79	20.72	0.00
Diet+UTT+M1	5	22.01	20.95	0.00
LH1*H1	5	22.15	21.09	0.00
LH1+LH2+M2	5	22.38	21.32	0.00
LH1+M1	4	22.52	21.46	0.00
Diet+UTT+LH1	5	22.61	21.55	0.00
UTT+LH1	4	22.67	21.61	0.00
LH2+M2+H1	5	22.84	21.78	0.00
LH2*M2	5	22.90	21.84	0.00
Diet+M1+H1	5	22.95	21.89	0.00
Diet+LH1+LH2	5	23.01	21.95	0.00
Diet+LH2+M1	5	23.05	21.99	0.00
Diet*M1	5	23.09	22.03	0.00

Diet+LH1+H1	5	23.16	22.10	0.00
Diet*LH2	5	23.26	22.20	0.00
LH1+LH2+H1	5	23.31	22.25	0.00
LH1+M2	4	23.70	22.64	0.00
NULL	2	24.03	22.97	0.00
UTT+LH2+M2	5	24.06	23.00	0.00
M2+H1	4	24.28	23.21	0.00
M1+M2	4	24.35	23.29	0.00
LH1*M2	5	24.37	23.31	0.00
UTT+M2	4	24.43	23.37	0.00
LH2	3	26.12	25.06	0.00
UTT*M2	5	26.18	25.12	0.00
UTT*LH1	5	26.53	25.47	0.00
H1	3	26.56	25.50	0.00
UTT	3	26.72	25.66	0.00
M1	3	26.74	25.68	0.00
UTT+LH1+M2	5	26.81	25.75	0.00
LH1+M2+H1	5	26.93	25.87	0.00
UTT+LH1+M1	5	27.03	25.97	0.00
LH1+M1+M2	5	27.11	26.05	0.00
M1*M2	5	27.33	26.27	0.00
M2*H1	5	27.52	26.45	0.00
UTT*M1	5	27.53	26.47	0.00
M1+M2+H1	5	27.56	26.50	0.00
UTT+M2+H1	5	27.63	26.57	0.00
UTT+M1+M2	5	27.75	26.69	0.00
LH2+M1	4	28.49	27.43	0.00
LH2+H1	4	28.68	27.62	0.00
UTT+LH2	4	29.17	28.11	0.00
UTT+H1	4	29.43	28.37	0.00
M1+H1	4	29.56	28.50	0.00
UTT+M1	4	29.79	28.73	0.00
LH2*H1	5	30.96	29.90	0.00
LH2*M1	5	31.63	30.57	0.00
LH2+M1+H1	5	31.68	30.62	0.00
UTT+LH2+H1	5	31.82	30.76	0.00
UTT*LH2	5	31.87	30.81	0.00
UTT+LH2+M1	5	31.99	30.93	0.00
UTT*H1	5	32.72	31.65	0.00
M1*H1	5	32.76	31.70	0.00
UTT+M1+H1	5	32.80	31.74	0.00

Table S7. Multi-predictor PGLS models ranked by AIC_c for the mean density dependent coefficient (Mη).

Models	k	AIC_c	ΔAICc	ω_i
LH1	**3**	**21.03**	**0.00**	**0.45**
M1+M2	**4**	**23.26**	**2.22**	**0.15**
UTT	**3**	**23.51**	**2.48**	**0.13**
UTT+LH1+M1	**5**	**25.41**	**4.37**	**0.05**
Diet*LH2	**5**	**25.74**	**4.71**	**0.04**
Diet+M1+M2	**5**	**26.15**	**5.12**	**0.03**
UTT+LH1	**4**	**26.16**	**5.13**	**0.03**
M1	**3**	**27.07**	**6.04**	**0.02**
UTT+LH2+M2	**5**	**27.12**	**6.09**	**0.02**
LH2+M2	**4**	**27.80**	**6.77**	**0.02**
Diet+LH1+H1	5	28.18	7.15	0.01
UTT+M1	4	28.41	7.38	0.01
Diet+LH2	4	29.37	8.34	0.01
UTT*LH1	5	29.91	8.88	0.01
LH2+M1+M2	5	30.04	9.00	0.00
UTT*H1	5	30.60	9.57	0.00
UTT+M1+H1	5	30.72	9.69	0.00
UTT*LH2	5	31.59	10.56	0.00
Diet+LH1+LH2	5	32.92	11.89	0.00
Diet+LH1+M2	5	32.95	11.92	0.00
Diet+M1+H1	5	33.44	12.41	0.00
M2*H1	5	33.56	12.53	0.00
UTT+LH1+M2	5	33.80	12.76	0.00
Diet*M1	5	34.07	13.04	0.00
Diet+M2+H1	5	34.08	13.05	0.00
Diet*M2	5	34.43	13.40	0.00
LH1+LH2+H1	5	34.71	13.68	0.00
LH1*LH2	5	35.57	14.53	0.00
M2	3	36.03	15.00	0.00
UTT+M2	4	37.44	16.41	0.00
Diet+H1	4	37.58	16.55	0.00
Diet+UTT	4	37.63	16.60	0.00
M1*M2	5	37.99	16.96	0.00
LH2*M2	5	39.13	18.10	0.00
M2+H1	4	39.24	18.21	0.00
Diet+M2	4	39.31	18.28	0.00
Diet+LH2+M2	5	39.69	18.66	0.00
LH1+M2	4	39.85	18.82	0.00
LH1*M2	5	39.90	18.86	0.00
NULL	2	39.95	18.92	0.00
LH1+LH2+M1	5	40.41	19.38	0.00
Diet	3	40.41	19.38	0.00
LH1+LH2+M2	5	40.44	19.41	0.00

Diet+UTT+M2	5	40.49	19.46	0.00
Diet*H1	5	40.55	19.52	0.00
LH1+LH2	4	40.68	19.65	0.00
Diet+UTT+H1	5	41.13	20.10	0.00
UTT+M1+M2	5	41.45	20.42	0.00
UTT+M2+H1	5	41.52	20.49	0.00
LH1+H1	4	41.55	20.52	0.00
LH1+M1	4	41.69	20.66	0.00
Diet+LH1	4	41.72	20.69	0.00
UTT+LH1+LH2	5	41.82	20.79	0.00
Diet+LH2+M1	5	41.87	20.84	0.00
LH2+M2+H1	5	42.30	21.27	0.00
H1	3	42.57	21.54	0.00
Diet+UTT+LH1	5	43.19	22.16	0.00
UTT+LH1+H1	5	43.21	22.18	0.00
M1+M2+H1	5	43.38	22.35	0.00
Diet+LH2+H1	5	43.47	22.44	0.00
UTT*M2	5	43.50	22.47	0.00
Diet+M1	4	43.51	22.48	0.00
LH1+M1+M2	5	43.52	22.49	0.00
LH1+M2+H1	5	43.59	22.56	0.00
LH1*M1	5	44.01	22.98	0.00
LH2	3	44.03	22.99	0.00
Diet*LH1	5	44.33	23.30	0.00
M1+H1	4	44.68	23.65	0.00
LH1*H1	5	44.71	23.68	0.00
LH1+M1+H1	5	44.89	23.86	0.00
UTT+H1	4	45.47	24.44	0.00
M1*H1	5	45.85	24.82	0.00
Diet+UTT+LH2	5	46.28	25.25	0.00
Diet+UTT+M1	5	46.60	25.57	0.00
Diet*UTT	5	46.68	25.65	0.00
LH2+H1	4	46.99	25.96	0.00
LH2+M1	4	47.29	26.26	0.00
UTT*M1	5	47.63	26.60	0.00
UTT+LH2	4	47.76	26.73	0.00
LH2*M1	5	48.97	27.94	0.00
LH2*H1	5	50.39	29.36	0.00
LH2+M1+H1	5	50.48	29.45	0.00
UTT+LH2+M1	5	51.26	30.23	0.00
UTT+LH2+H1	5	51.31	30.28	0.00
Diet+LH1+M1	5	58.69	37.66	0.00

Table S8. Multi-predictor PGLS models ranked by AIC_c for the mean migration rate (Mγ).

Models	k	AIC_c	ΔAICc	ω_i
LH1+H1	**4**	**93.69**	**0.00**	**0.22**
M1	**3**	**94.96**	**1.26**	**0.11**
LH1+M2	**4**	**95.20**	**1.50**	**0.10**
NULL	**2**	**95.65**	**1.95**	**0.08**
M2	**3**	**96.02**	**2.32**	**0.07**
LH2+M2+H1	**5**	**97.31**	**3.61**	**0.04**
Diet+M2	**4**	**97.50**	**3.81**	**0.03**
LH2+M2	**4**	**97.64**	**3.94**	**0.03**
UTT*H1	**5**	**97.66**	**3.96**	**0.03**
M1+M2+H1	**5**	**97.95**	**4.25**	**0.03**
LH2	**3**	**98.01**	**4.31**	**0.02**
UTT+M2	**4**	**98.07**	**4.37**	**0.02**
LH1*M2	**5**	**98.39**	**4.69**	**0.02**
M2*H1	**5**	**98.70**	**5.00**	**0.02**
M2+H1	**4**	**98.74**	**5.05**	**0.02**
UTT+LH2+M2	**5**	**98.86**	**5.16**	**0.02**
M1+M2	**4**	**99.05**	**5.35**	**0.01**
UTT*LH2	**5**	**99.52**	**5.83**	**0.01**
UTT+LH2	**4**	**99.85**	**6.15**	**0.01**
Diet+UTT+M2	**5**	**99.86**	**6.16**	**0.01**
LH1+LH2+M2	**5**	**99.87**	**6.17**	**0.01**
UTT+LH1+M2	**5**	**99.87**	**6.17**	**0.01**
UTT+LH1	**4**	**99.88**	**6.18**	**0.01**
Diet+M1+M2	**5**	**100.00**	**6.30**	**0.01**
LH2+H1	**4**	**100.37**	**6.67**	**0.01**
M1*H1	**5**	**100.37**	**6.67**	**0.01**
LH2+M1+M2	**5**	**100.64**	**6.94**	**0.01**
M1+H1	4	100.73	7.03	0.01
LH2*M2	5	100.97	7.27	0.01
UTT+M1+M2	5	101.43	7.74	0.00
Diet*UTT	5	102.31	8.61	0.00
Diet*M2	5	102.38	8.69	0.00
LH1*H1	5	102.73	9.04	0.00
Diet+UTT+M1	5	102.77	9.07	0.00
UTT+LH2+M1	5	102.99	9.30	0.00
UTT+LH1+M1	5	103.18	9.48	0.00
UTT+LH1+H1	5	103.20	9.51	0.00
LH1	3	103.53	9.83	0.00
Diet+UTT	4	104.53	10.84	0.00
Diet	3	105.17	11.47	0.00
H1	3	106.01	12.32	0.00
Diet+LH1+M1	5	106.53	12.84	0.00
Diet+LH1+H1	5	106.79	13.09	0.00
Diet+UTT+LH1	5	106.93	13.24	0.00

Diet*H1	5	107.74	14.04	0.00
Diet+H1	4	108.33	14.63	0.00
Diet+LH2	4	108.64	14.94	0.00
LH1+M1+M2	5	108.70	15.00	0.00
UTT	3	108.92	15.23	0.00
Diet*LH1	5	109.43	15.73	0.00
Diet+LH1	4	109.64	15.94	0.00
UTT+M1	4	109.75	16.05	0.00
Diet*LH2	5	110.11	16.42	0.00
Diet+M1+H1	5	110.19	16.50	0.00
Diet+M2+H1	5	110.44	16.75	0.00
Diet+LH2+M2	5	110.77	17.08	0.00
LH1+M1	4	110.92	17.22	0.00
LH1+LH2	4	110.95	17.26	0.00
Diet+M1	4	111.11	17.41	0.00
LH1+M2+H1	5	111.54	17.84	0.00
LH2+M1	4	111.55	17.86	0.00
UTT*M2	5	111.61	17.92	0.00
UTT+H1	4	111.64	17.95	0.00
Diet+LH2+M1	5	112.05	18.35	0.00
Diet+LH1+M2	5	112.36	18.66	0.00
Diet*M1	5	112.79	19.09	0.00
UTT+LH2+H1	5	112.96	19.26	0.00
Diet+LH2+H1	5	113.03	19.33	0.00
UTT+LH1+LH2	5	113.19	19.49	0.00
Diet+LH1+LH2	5	113.20	19.51	0.00
UTT+M2+H1	5	113.91	20.21	0.00
M1*M2	5	114.10	20.41	0.00
LH1*LH2	5	114.13	20.44	0.00
LH1+LH2+H1	5	114.17	20.47	0.00
LH1+M1+H1	5	114.17	20.48	0.00
UTT*M1	5	114.19	20.49	0.00
LH1+LH2+M1	5	114.22	20.53	0.00
Diet+UTT+H1	5	114.24	20.54	0.00
LH1*M1	5	114.29	20.60	0.00
Diet+UTT+LH2	5	114.53	20.84	0.00
UTT*LH1	5	114.57	20.87	0.00
LH2*M1	5	114.75	21.06	0.00
LH2+M1+H1	5	115.50	21.80	0.00
UTT+M1+H1	5	115.60	21.91	0.00
LH2*H1	5	115.71	22.02	0.00

Table S9. Multi-predictor PGLS models ranked by AIC_c for relative standard deviation of the population grwoth rate (RSDρ)

Models	k	AIC_c	ΔAICc	ω_i
UTT*H1	**5**	**47.73**	**0.00**	**0.28**
UTT+LH2	**4**	**49.35**	**1.61**	**0.13**
NULL	**2**	**49.44**	**1.71**	**0.12**
LH1+M1+M2	**5**	**49.53**	**1.80**	**0.11**
UTT*LH2	**5**	**50.13**	**2.40**	**0.08**
M2	**3**	**50.38**	**2.64**	**0.07**
UTT+LH2+M1	**5**	**50.85**	**3.12**	**0.06**
LH1	**3**	**50.92**	**3.19**	**0.06**
LH1+M2	**4**	**52.12**	**4.39**	**0.03**
UTT+M1+H1	**5**	**52.45**	**4.72**	**0.03**
UTT+M1	**4**	**53.23**	**5.50**	**0.02**
UTT+LH1+M1	5	56.06	8.33	0.00
UTT*M1	5	56.13	8.39	0.00
LH1*H1	5	59.36	11.63	0.00
M1	3	61.76	14.03	0.00
LH1+M1	4	62.39	14.66	0.00
M1+M2	4	62.62	14.89	0.00
M1+H1	4	64.26	16.53	0.00
LH2+M1	4	64.71	16.98	0.00
UTT+M1+M2	5	64.87	17.14	0.00
M1+M2+H1	5	65.08	17.34	0.00
M1*M2	5	65.14	17.40	0.00
LH1*M1	5	65.27	17.54	0.00
H1	3	65.85	18.12	0.00
LH2	3	65.96	18.23	0.00
LH1+H1	4	66.49	18.76	0.00
M1*H1	5	67.04	19.31	0.00
LH1+M1+H1	5	67.19	19.46	0.00
Diet+M1	4	67.27	19.54	0.00
LH2+H1	4	67.63	19.90	0.00
LH2+M1+H1	5	67.89	20.16	0.00
LH2+M1+M2	5	68.04	20.31	0.00
Diet+M1+M2	5	68.14	20.41	0.00
M2+H1	4	68.18	20.45	0.00
LH1+LH2+M1	5	68.73	21.00	0.00
Diet+H1	4	68.83	21.10	0.00
Diet+LH2+M1	5	68.94	21.20	0.00
LH1+LH2	4	68.98	21.25	0.00
LH2+M2	4	69.03	21.30	0.00
LH2*M1	5	69.20	21.47	0.00
Diet+LH1+M1	5	69.39	21.66	0.00
Diet+LH2	4	69.76	22.03	0.00
Diet*M1	5	70.17	22.44	0.00

Diet+M1+H1	5	70.46	22.73	0.00
Diet+UTT+M1	5	70.77	23.04	0.00
UTT+LH1+LH2	5	70.77	23.04	0.00
Diet*H1	5	71.01	23.27	0.00
LH2+M2+H1	5	71.10	23.36	0.00
LH1+LH2+H1	5	71.13	23.40	0.00
M2*H1	5	71.15	23.42	0.00
LH1+M2+H1	5	71.17	23.44	0.00
LH2*H1	5	71.41	23.68	0.00
Diet+LH1+H1	5	71.55	23.82	0.00
LH1*LH2	5	71.57	23.84	0.00
Diet+LH2+H1	5	71.66	23.93	0.00
UTT+LH2+H1	5	71.80	24.07	0.00
Diet+UTT+H1	5	71.94	24.20	0.00
LH1+LH2+M2	5	72.46	24.73	0.00
Diet*LH2	5	72.64	24.91	0.00
Diet+UTT+LH2	5	72.68	24.95	0.00
UTT*LH1	5	72.69	24.96	0.00
UTT	3	72.72	24.98	0.00
LH2*M2	5	72.82	25.09	0.00
Diet+LH1+LH2	5	72.85	25.12	0.00
UTT+LH2+M2	5	73.02	25.29	0.00
Diet+LH2+M2	5	73.30	25.57	0.00
Diet*LH1	5	74.55	26.82	0.00
Diet	3	74.92	27.19	0.00
UTT+M2	4	75.08	27.35	0.00
UTT+LH1	4	75.56	27.83	0.00
Diet+M2	4	75.65	27.92	0.00
UTT+H1	4	76.37	28.64	0.00
LH1*M2	5	76.60	28.87	0.00
Diet+UTT	4	76.65	28.92	0.00
Diet+M2+H1	5	76.82	29.09	0.00
Diet*UTT	5	77.10	29.37	0.00
UTT*M2	5	77.30	29.57	0.00
Diet+LH1	4	77.41	29.68	0.00
UTT+M2+H1	5	77.48	29.74	0.00
Diet+UTT+M2	5	77.58	29.85	0.00
UTT+LH1+M2	5	78.10	30.37	0.00
Diet+UTT+LH1	5	78.77	31.04	0.00
Diet*M2	5	78.81	31.08	0.00
Diet+LH1+M2	5	78.84	31.11	0.00
UTT+LH1+H1	5	79.19	31.46	0.00

Table S10. Multi-predictor PGLS models ranked by AIC_c for relative standard deviation of the density dependent coefficient (RSDη)

Models	k	AIC_c	ΔAICc	ω_i
UTT	**3**	**16.47**	**0.00**	**0.45**
LH1+LH2+M2	**5**	**18.91**	**2.45**	**0.13**
Diet+LH1	**4**	**19.50**	**3.04**	**0.10**
UTT+H1	**4**	**19.72**	**3.25**	**0.09**
LH2	**3**	**20.79**	**4.32**	**0.05**
Diet+LH1+H1	**5**	**21.87**	**5.40**	**0.03**
Diet*LH1	**5**	**22.31**	**5.84**	**0.02**
LH1*M1	**5**	**23.07**	**6.60**	**0.02**
M2*H1	**5**	**23.32**	**6.85**	**0.01**
UTT+LH2+H1	**5**	**23.40**	**6.93**	**0.01**
UTT*LH2	5	23.61	7.14	0.01
LH2+M1+H1	5	23.66	7.20	0.01
Diet*H1	5	24.09	7.62	0.01
Diet+UTT+H1	5	24.18	7.71	0.01
UTT*H1	5	24.33	7.86	0.01
UTT*M1	5	24.35	7.88	0.01
LH2+M2+H1	5	25.40	8.93	0.01
Diet*UTT	5	25.59	9.12	0.00
Diet+M1+H1	5	26.32	9.85	0.00
NULL	2	26.42	9.95	0.00
UTT+LH2+M1	5	26.75	10.28	0.00
LH2*M2	5	28.18	11.71	0.00
M1	3	28.73	12.26	0.00
Diet+H1	4	30.87	14.40	0.00
LH2+H1	4	30.89	14.42	0.00
M1+H1	4	31.08	14.61	0.00
Diet+UTT+LH1	5	32.50	16.03	0.00
M1*H1	5	32.67	16.20	0.00
M1+M2+H1	5	34.18	17.71	0.00
UTT+M2+H1	5	34.48	18.01	0.00
LH1	3	34.82	18.35	0.00
LH1+LH2+H1	5	34.86	18.39	0.00
H1	3	34.87	18.40	0.00
M1*M2	5	34.91	18.45	0.00
LH1+H1	4	35.04	18.57	0.00
M2+H1	4	36.04	19.58	0.00
LH1*H1	5	36.51	20.04	0.00
LH1+M2+H1	5	36.96	20.49	0.00
LH1+M1	4	37.02	20.55	0.00
M2	3	37.39	20.92	0.00
Diet	3	37.48	21.01	0.00
UTT+LH1	4	37.78	21.31	0.00
UTT+LH1+H1	5	37.89	21.42	0.00

LH1+M2	4	37.91	21.44	0.00
LH2*H1	5	38.06	21.59	0.00
UTT+M2	4	38.09	21.63	0.00
LH1+M1+H1	5	38.13	21.66	0.00
UTT+LH2	4	38.21	21.74	0.00
UTT+M1	4	38.21	21.74	0.00
LH1+LH2	4	38.80	22.33	0.00
Diet+M2+H1	5	39.00	22.53	0.00
Diet+LH1+LH2	5	39.10	22.63	0.00
Diet+LH1+M1	5	39.13	22.67	0.00
Diet+LH1+M2	5	39.15	22.68	0.00
LH1*M2	5	39.25	22.78	0.00
UTT*M2	5	39.30	22.84	0.00
LH1*LH2	5	39.50	23.03	0.00
UTT*LH1	5	39.53	23.06	0.00
Diet*M1	5	39.73	23.26	0.00
LH1+LH2+M1	5	39.81	23.34	0.00
M1+M2	4	40.09	23.62	0.00
UTT+LH1+M1	5	40.13	23.66	0.00
UTT+M1+H1	5	40.16	23.69	0.00
UTT+LH1+LH2	5	40.23	23.76	0.00
LH1+M1+M2	5	40.38	23.91	0.00
UTT+LH1+M2	5	40.42	23.95	0.00
LH2+M2	4	40.56	24.09	0.00
Diet+M1	4	40.75	24.28	0.00
Diet+UTT	4	40.83	24.36	0.00
LH2+M1	4	40.83	24.36	0.00
Diet+LH2+H1	5	42.26	25.79	0.00
LH2*M1	5	42.40	25.93	0.00
Diet+M2	4	42.40	25.93	0.00
Diet+LH2	4	42.46	25.99	0.00
UTT+M1+M2	5	42.67	26.20	0.00
UTT+LH2+M2	5	42.89	26.42	0.00
LH2+M1+M2	5	43.33	26.86	0.00
Diet+M1+M2	5	43.54	27.07	0.00
Diet+LH2+M1	5	44.59	28.12	0.00
Diet+UTT+M1	5	45.04	28.57	0.00
Diet+UTT+M2	5	45.64	29.17	0.00
Diet*M2	5	46.02	29.55	0.00
Diet+UTT+LH2	5	46.32	29.85	0.00
Diet+LH2+M2	5	46.87	30.40	0.00
Diet*LH2	5	46.99	30.52	0.00

Table S11. Multi-predictor PGLS models ranked by AIC_c for relative standard deviation of the migration rate (RSDγ)

Models	k	AIC_c	ΔAICc	ω_i
NULL	**2**	**12.22**	**0.00**	**0.25**
Diet*M1	**5**	**13.58**	**1.36**	**0.13**
LH1*H1	**5**	**13.83**	**1.61**	**0.11**
M2+H1	**4**	**14.05**	**1.83**	**0.10**
M1	**3**	**14.19**	**1.97**	**0.09**
UTT+M1	**4**	**14.64**	**2.41**	**0.08**
LH1	**3**	**15.88**	**3.66**	**0.04**
UTT+LH1	**4**	**16.58**	**4.35**	**0.03**
M1+M2	**4**	**16.97**	**4.75**	**0.02**
UTT*M1	**5**	**17.19**	**4.97**	**0.02**
UTT+M1+M2	**5**	**17.42**	**5.20**	**0.02**
LH1+LH2	**4**	**18.24**	**6.02**	**0.01**
LH1*M1	**5**	**18.27**	**6.05**	**0.01**
Diet+LH1+M1	**5**	**18.28**	**6.06**	**0.01**
LH1+M2+H1	**5**	**18.52**	**6.30**	**0.01**
H1	**3**	**18.57**	**6.35**	**0.01**
UTT+M2	**4**	**18.61**	**6.39**	**0.01**
UTT*M2	**5**	**19.18**	**6.96**	**0.01**
UTT+LH2+H1	5	19.63	7.40	0.01
UTT*LH1	5	19.87	7.65	0.01
M1+H1	4	20.70	8.47	0.00
M1*H1	5	20.82	8.59	0.00
LH2+M2+H1	5	20.93	8.71	0.00
M2	3	21.29	9.06	0.00
UTT	3	21.93	9.70	0.00
LH1+M2	4	23.18	10.96	0.00
UTT+LH2+M2	5	23.60	11.37	0.00
UTT+LH1+LH2	5	23.77	11.55	0.00
LH1+LH2+H1	5	24.47	12.25	0.00
LH1+LH2+M2	5	24.49	12.27	0.00
LH1+H1	4	27.61	15.39	0.00
LH1+M1	4	27.62	15.40	0.00
LH2*M1	5	27.81	15.59	0.00
UTT+H1	4	29.82	17.60	0.00
Diet+M1	4	30.23	18.01	0.00
Diet*H1	5	30.60	18.38	0.00
UTT+LH1+H1	5	30.76	18.54	0.00
LH1+M1+H1	5	30.80	18.58	0.00
LH2	3	30.84	18.62	0.00
UTT+M1+H1	5	32.09	19.87	0.00
LH1+M1+M2	5	32.28	20.06	0.00
LH2*H1	5	32.57	20.35	0.00
M1*M2	5	32.75	20.52	0.00

UTT+LH1+M2	5	33.41	21.19	0.00
Diet+H1	4	33.81	21.59	0.00
Diet+M1+M2	5	33.84	21.62	0.00
UTT+LH2	4	33.96	21.74	0.00
UTT*H1	5	34.23	22.01	0.00
M1+M2+H1	5	34.51	22.29	0.00
M2*H1	5	34.65	22.43	0.00
UTT+M2+H1	5	34.95	22.73	0.00
LH2+M1	4	34.96	22.74	0.00
LH1*M2	5	35.17	22.94	0.00
Diet	3	36.06	23.84	0.00
UTT+LH1+M1	5	36.26	24.03	0.00
LH2*M2	5	36.51	24.29	0.00
Diet+LH1+H1	5	36.86	24.63	0.00
Diet+M1+H1	5	36.96	24.74	0.00
LH2+M2	4	37.27	25.04	0.00
Diet+M2+H1	5	37.93	25.71	0.00
Diet+UTT	4	38.01	25.79	0.00
Diet+LH1	4	38.09	25.87	0.00
LH2+M1+M2	5	38.20	25.98	0.00
LH2+H1	4	38.46	26.24	0.00
LH1+LH2+M1	5	38.58	26.36	0.00
Diet+UTT+H1	5	39.17	26.95	0.00
DIET+M2	4	39.18	26.96	0.00
UTT+LH2+M1	5	39.23	27.00	0.00
LH1*LH2	5	39.91	27.69	0.00
Diet+LH2+M1	5	39.99	27.77	0.00
Diet+LH2	4	40.07	27.85	0.00
LH2+M1+H1	5	40.08	27.86	0.00
Diet+UTT+M1	5	40.14	27.92	0.00
Diet*M2	5	40.24	28.02	0.00
Diet+LH1+M2	5	40.49	28.27	0.00
Diet+LH2+H1	5	41.12	28.90	0.00
Diet+UTT+LH1	5	41.13	28.91	0.00
Diet*LH1	5	41.20	28.98	0.00
Diet*UTT	5	41.29	29.07	0.00
UTT*LH2	5	41.32	29.10	0.00
Diet+UTT+M2	5	41.47	29.25	0.00
Diet+UTT+LH2	5	41.87	29.65	0.00
Diet+LH1+LH2	5	42.54	30.32	0.00
Diet*LH2	5	42.85	30.63	0.00
Diet+LH2+M2	5	43.57	31.35	0.00

Annexe I (*AI*)

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Eutrophication as a driver of *r*-selection traits in a freshwater fish

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This study tested whether eutrophication could influence life-history traits of a cyprinid, *Chanodichthys erythropterus*, in 10 Chinese lakes. Using the von Bertalanffy growth model, the asymptotic length (L_∞) and the growth performance index (I_{GRO}) were significantly affected by eutrophication. The gonado-somatic index (I_G) and relative fecundity (F_R) were significantly lower in mesotrophic lakes than in eutrophic and hypertrophic lakes. These results indicate that increasing eutrophication affects the life-history tactics of a freshwater fish.

Key words: growth; overfishing; reproduction; trade-off; water quality.

INTRODUCTION

Freshwater ecosystems are increasingly under threat from increasing anthropogenic pressures on water and habitat quality (Vörösmarty *et al.*, 2010). Such environmental pressures are more noticeable in countries showing rapid economic growth in recent decades, *e.g.* in East Asia. It has now been clearly established that such environmental effects lead directly to changes in local biodiversity, with a decline of sensitive species, simplification of communities and extinctions of endemic species (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010). Even in communities where the diversity of species remains stable despite the abiotic changes, subtle changes in species life-history traits are likely to take place (Barausse *et al.*, 2011).

Based on community theory, during the process of ecological succession, it is to be expected that in the early stages, communities will include mostly pioneer species. Typically, these are *r*-strategy species that are quick to establish, have high dispersal capabilities, are short-lived, produce small gametes (low parental investment) and are limited competitors with limited specialization (Odum, 1969). It is less known,

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however, if the life-history traits of a single species are also affected in a similar way when the community is maintained at a sub-climax level, *e.g.* due to eutrophication. It has been shown that eutrophication (1) favours *r*-selected species (Barausse *et al.*, 2011), (2) affects the growth of aquatic organisms (Willemsen, 1980; Arter, 1989; Rijnsdorp & Leeuwen, 1996), (3) affects reproductive traits (Engstrom-Ost & Candolin, 2006; Han & Uye, 2010; Cothran *et al.*, 2012) and (4) affects mating and parental care activity (Edwards *et al.*, 2006; Candolin *et al.*, 2007, 2008; Järvenpää & Lindström, 2011), but still little is known about the effects of eutrophication on intraspecific life-history tactics.

In China, a rapid increase in human population size coupled with economic growth has led to over-discharge of agricultural and domestic sewage, which enhances phosphorus and nitrogen burdens in freshwater lakes (Jin *et al.*, 2005). Moreover, an increased dependence on aquaculture production to provide a cheap source of animal proteins also causes eutrophication pressure on freshwater ecosystems. This is particularly visible in the lakes along the Yangtze River floodplain, China where popular traditional farming techniques consist of the application of fertilizers to support the production of planktivorous fish species, thus directly increasing nutrient load and reducing water quality (Jin, 2005; Zhang, 2007).

This study investigated the effects of eutrophication on life-history traits of a small lentic fish, the predatory carp *Chanodichthys erythropterus* (Basilewsky 1855), in 10 large shallow lakes with different levels of eutrophication located in the Yangtze floodplain. Based on life-history theory (Stearns, 1976; Brown, 1983), it was anticipated that faster growth, smaller size at maturity along with an increase in fecundity should be favoured in eutrophic unstable and unpredictable environment (Stearns, 1976; Brown, 1983).

MATERIALS AND METHODS

STUDY LAKES AND ENVIRONMENTAL VARIABLES

A total of 10 shallow lakes located in the Yangtze River basin were selected along a gradient of eutrophication and included Lakes Zaohu, Tangxun, Wuhu, Biandantang, Luhu, Niushan, Dahu, Shanpo, Dianchi and Puhai (Table I). All lakes were historically connected to the Yangtze River, but were isolated by dyke construction.

To assess the current eutrophication level of each lake, five water quality variables were measured including transparency (measured by secchi disc; Trans), chemical oxygen demand (measured by the acid potassium permanganate method; COD), nitrogen concentration (measured by the alkaline potassium persulphate digestion-UV spectrophotometric method; TN), ammonium concentration (measured by Nessler reagent spectrophotometric method; AMM) and phosphorous concentration (measured by the ammonium molybdate spectrophotometric method; TP). Water environmental variables were measured in October 2010, except for Dianchi Lake where the variables were measured in September 2008. In order to minimize bias due to the possible spatial heterogeneity of the lakes, a minimum of four sampling locations (5 l of water for each location) were chosen for each lake with the exception of Dianchi Lake where 27 locations were sampled due to its extensive size. All measurement procedures strictly followed the protocol of the National Standards of China (Huang *et al.*, 1999).

FISH SAMPLING AND MEASUREMENTS

Chanodichthys erythropterus is a medium-sized cyprinid (maximum mass of *c*. 300 g), widely distributed in freshwater lakes and large rivers of East Asia. The diet of juveniles comprises

TABLE I. Physical characteristics and locations of 10 Chinese lakes located in the Yangtze River basin (data from Wang & Dou, 1998)

Lakes	Latitude (° N)	Longitude (° E)	Area (km^2)	Mean depth (m)	Average annual temperature (° C)	Vegetation (%)
Dianchi	24·40–25·02	102·36–102·47	298	2·9	14·4	1
Tangxun	30·22–30·27	114·18–114·25	10	1·9	16·3	0
Zaohu	24·40–25·04	102·36–102·49	5	2·8	17·0	0
Biandantang	24·40–25·05	102·36–102·50	3	2·9	16·7	0
Wuhu	30·47–30·50	114·28–114·33	21	2·6	16·3	30
Luhu	30·12–30·17	114·09–114·15	40	2·7	16·2	45
Dahu	24·40–25·08	102·36–102·53	17	4·2	16·8	80
Puhai	24·40–25·09	102·36–102·54	8	4·2	16·8	85
Shanpo	24·40–25·10	102·36–102·55	5	4·2	16·8	60
Niushan	30·16–30·22	114·27–114·38	38	3·5	16·8	70

zooplankton but gradually changes to fish following the transition to adulthood (Chen, 1989; Yu, 1991). It is a fish with a relatively short lifespan (*c*. 5 years) and early maturity (*c*. 2 years), and is iteroparous with annual spawning from April to July when the water temperature is above 22° C (Yu, 1991). The choice of *C. erythropterus* as a model species to show clear adaptation of life-history traits to environmental disturbance was motivated by (1) its lack of commercial value (almost no human selective pressure) and (2) by its medium longevity (neither too short > 2 years nor too long < 10 years).

Fish were sampled by trap (mesh size = 1–2 cm), set-net (mesh size = 0·5–3 cm) and gillnet (mesh size = 1–6 cm) in winter from 2008 to 2011 for growth comparison among the 10 lakes (Table II). A total of five to 10 scales for each fish in all the 10 lakes were sampled to determine individual age (Yu, 1991) following the methods reviewed by Murphy & Willis (1996). Reproductive variables were collected from three lakes (Niushan, Wuhu and Tangxun) along a gradient of eutrophication (mesotrophic, eutrophic and hypertrophic, respectively) during the reproductive season. In these three lakes, fish were measured (total length, L_T, ±0·5 mm) and as body mass could be influenced by the fact that individuals were sampled before or after they have been feeding, individuals were weighed without their viscera (M_E= ±0·5 g) to avoid any bias in the subsequent analyses. Sex of adults in these three lakes was determined by a visual inspection of the gonads, which were weighed (M_G = ±0·01 g) and preserved in 5% formalin. Later, the number of eggs (N_S) and estimated average egg diameter (E_G) for each fish were recorded. Gonad maturity stages were determined following Crim & Glebe (1990). Only mature fish (with gonads developed to stage IV or stage V) were analysed and used to test the influence of eutrophication on reproductive variables. The female gonado-somatic index (I_G) was calculated using the standard formula: $I_G = M_G M_E^{-1} 100$. Finally, the relative fecundity (F_R) was calculated using the following formula: $F_R = [(N_S M_S^{-1}) M_G] M_E^{-1}$, where N_S is the total number of eggs in a sub-sample and M_S is the mass of the sub-sample (g).

STATISTICAL ANALYSIS

For each lake, the parameterization of von Bertalanffy's growth model adopted by Beverton & Holt (1957) was used: $L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$, where L_t is the expected or average L_T at age t (mm), L_∞ the model asymptote for average L_T (mm), K a measure of the exponential rate of approach to L_∞ (*i.e.* the growth coefficient; $year^{-1}$) and t_0 is the theoretical age at which the average L_T would be zero. To estimate the parameters of the von Bertalanffy's growth model, the starting values for the 10 lakes were first calculated using the function vbStarts in R (R 2.14, R development Core Team; www.r-project.org), analyses

TABLE II. Somatic eviscerated body mass (M_E) and total length (L_T) of *Chanodichthys erythropterus* in 10 Chinese lakes (Table I). All samples were collected in winter from 2008 to 2011

		L_T (mm)		M_E (g)	
Lakes	Number of fish	Mean ± S.E.	Range	Mean ± S.E.	Range
Dianchi	97	158 ± 3	106–245	30 ± 2	14–93
Tangxun	85	205 ± 4	122–279	67 ± 4	10–180
Zaohu	42	215 ± 8	148–322	110 ± 16	21–339
Biandantang	154	168 ± 2	122–253	34 ± 2	8–121
Wuhu	308	195 ± 2	121–370	59 ± 2	10–455
Luhu	67	159 ± 4	105–333	31 ± 5	7–339
Dahu	96	164 ± 5	111–338	46 ± 7	8–388
Puhai	156	190 ± 4	101–336	84 ± 8	12–342
Shanpo	165	197 ± 3	103–315	67 ± 4	7–285
Niushan	256	167 ± 2	96–174	39 ± 2	5–174

were performed using libraries FSA (http://www.rforge.net/FSA/), quantreg (http://cran.r-project.org/web/packages/quantreg/quantreg.pdf) and NCStats (http://www.rforge.net/NCStats/). Then, the von Bertalannfy parameters were calculated using a non-linear model with quantile regression so as to minimize convergence problems (Grosjean *et al.*, 2003). Although quantile regression minimized convergence problems relative to least square regression, the model was not able to converge for four lakes (Dianchi, Tangxun, Wuhu and Zaohu). Therefore, following Grosjean *et al.* (2003) and because t_0 was not of biological interest (Beverton & Holt, 1957; Grosjean *et al.*, 2003; García-Berthou *et al.*, 2012), the parameter t_0 was fixed at a value of 0 in order to reduce the number of parameters in the model, the models then converged, and estimates of the parameters K and L_∞ for these four lakes were obtained.

TESTING FOR AN EFFECT OF EUTROPHICATION

Before each analysis, homogeneity of variance and normality of the data were tested using Bartlett and Kolmogorov–Smirnov tests, respectively. The assumption of homoscedasticity among the three lakes for which reproductive data were available was always satisfied. When the variables were not normally distributed, they were normalized using a Box–Cox power transformation (Box & Cox, 1964). Then, one-way analyses of variance (ANOVAs) followed by multiple comparison Tukey tests were performed to test for differences among the three lakes for I_G, E_G and F_R. As multiple comparisons were performed, the significance level for probabilities was adjusted according to the sequential Bonferroni procedure with an initial error rate of 0·05. Whether the three different lakes had any influence on age at maturity was tested using a χ^2 test. Furthermore, whether the length and mass relationship differed between these three lakes was tested using an analysis of covariance (ANCOVA).

Comparison of growth among different populations was very difficult due to the problem of correlation between K and L_∞. To overcome this problem, the phi prime index (I_{GRO}) was calculated (Pauly & Munro, 1984): $I'_{GRO} = \log10K + 2\ \log10(L_\infty)$. Then, in order to test for a relationship between I_{GRO}, L_∞ and eutrophication, an index of eutrophication was calculated by performing a principal component analysis (PCA) on the five environmental variables measured for the 10 lakes. The nutrient concentrations were ln transformed before analysis. The mean score of each lake was then recorded along the first PCA axis and a linear regression analysis between each parameter (I_{GRO} and L_∞) and PCA scores (S_{PCA}) was performed.

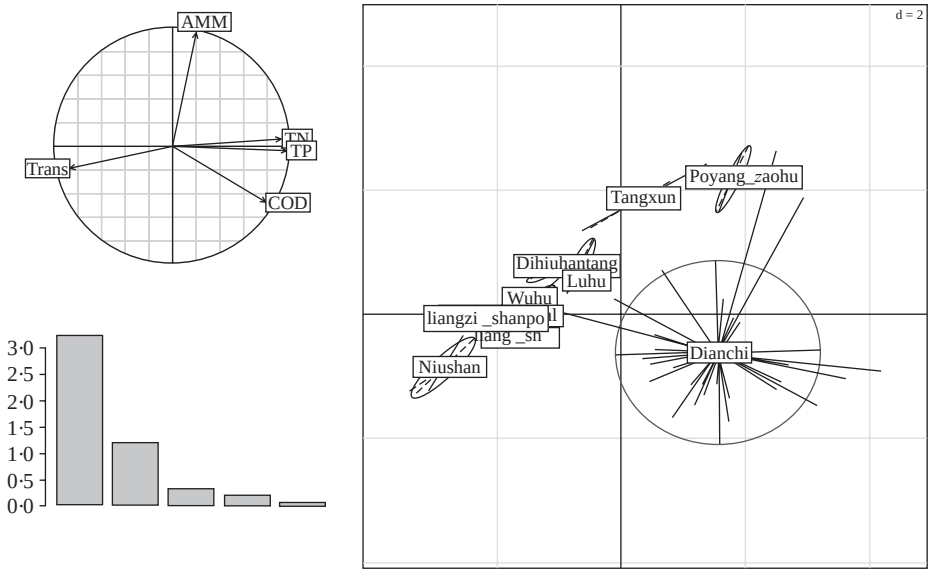

FIG. 1. Principal component analysis (PCA) performed on five water quality variables in 10 lakes in China (see Tables I and III). The first axis explained 64% of the total variance and represents an index of eutrophication level (S_{PCA}). The second axis explained 23% of the total variance and represents an index of ammonium concentration (AMM). Top insert shows the projection of the five variables on the first two axes of the PCA and the bottom one shows the eigenvalues. Before analysis, all variables were standardized and nutrient concentrations were ln transformed.

RESULTS

WATER VARIABLES AND EUTROPHICATION LEVEL

The first PCA axis explained 64% of the total variance (Fig. 1). It was positively related to COD, TN, TP and negatively related to water transparency (Trans; Fig. 1). The second axis explained 23% of the total variance and was positively related to AMM. According to Smith *et al.* (1999) and based on the values of the water quality variables (Table III), Niushan Lake could be classified as mesotrophic, Wuhu Lake as eutrophic and Tangxun Lake as hypertrophic. This classification is in line with the PCA results as Niushan Lake had the lowest score on the first axis, whereas Tangxun Lake is the third most eutrophic Lake (third highest score on the first PCA axis; Fig. 1).

INFLUENCE OF EUTROPHICATION ON LIFE-HISTORY TRAITS

Although a significant positive relationship between M_E and L_T (ANCOVA; $F_{1,203} = 8944{\cdot}5$; $P < 0{\cdot}001$; Fig. 2) was found, the slope coefficients were not significantly different between the three lakes (ANCOVA; $F_{2,203} = 1{\cdot}5902$; $P > 0{\cdot}05$; Fig. 2). Overall, the I_G was significantly different between sites [one-way ANOVA; $F_{2,102} = 4{\cdot}667$; $P < 0{\cdot}001$; Fig. 3(a)]. At both ends of the eutrophication spectrum, the population in Niushan Lake had the lowest I_G (mean $\pm$ S.E. $= 11{\cdot}54 \pm 1{\cdot}79$) and was significantly different from Wuhu Lake (Tukey test; $P < 0{\cdot}05$), which had the highest I_G (mean $\pm$ S.E. $= 15{\cdot}38 \pm 2{\cdot}65$). A significant difference (Tukey test;

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TABLE III. Mean ± S.E. for five water quality variables (Trans, transparency; COD, chemical oxygen demand; TN, nitrogen concentration; AMM, ammonium concentration; TP, phosphorous concentration) measured in 10 Chinese lakes. In order to minimize bias due to the possible spatial heterogeneity of the lakes, a minimum of four sampling locations were chosen in each lake except for Dianchi Lake where 27 locations were sampled

Lakes	Trans (cm)	TN ($mg\,l^{-1}$)	AMM ($mg\,l^{-1}$)	TP ($mg\,l^{-1}$)	COD ($mg\,l^{-1}$)	First PCA axis scores
Dianchi	44 ± 3	2·74 ± 0·31	0·33 ± 0·10	0·251 ± 0·043	11·68 ± 0·73	1·557
Tangxun	50 ± 10	1·99 ± 0·31	1·33 ± 0·22	0·054 ± 0·011	5·74 ± 0·26	0·386
Zaohu	10 ± 2	2·17 ± 0·22	1·71 ± 0·30	0·194 ± 0·011	7·11 ± 0·04	1·801
Biandantang	64 ± 2	0·94 ± 0·07	0·46 ± 0·05	0·030 ± 0·001	5·03 ± 0·17	−0·659
Wuhu	66 ± 5	0·37 ± 0·04	0·31 ± 0·02	0·025 ± 0·003	6·29 ± 0·22	−1·404
Luhu	83 ± 7	0·97 ± 0·02	0·48 ± 0·02	0·021 ± 0·005	5·69 ± 0·22	−1·076
Dahu	94 ± 1	0·70 ± 0·05	0·20 ± 0·01	0·019 ± 0·001	4·65 ± 0·19	−1·735
Puhai	77 ± 3	0·67 ± 0·05	0·23 ± 0·02	0·012 ± 0·001	5·34 ± 0·05	−1·635
Shanpo	83 ± 2	0·58 ± 0·04	0·20 ± 0·01	0·011 ± 0·001	4·55 ± 0·02	−1·928
Niushan	135 ± 8	0·46 ± 0·03	0·13 ± 0·02	0·012 ± 0·016	4·70 ± 0·14	−2·870

PCA, principal component analysis.

$P < 0{\cdot}05$) between Niushan Lake and Tangxun Lake (mean ± S.E. = 14·45 ± 2·48) was also found, whereas no significant difference was found between Tangxun Lake and Wuhu Lake (Tukey test; $P > 0{\cdot}05$). The F_R was also significantly different between the three lakes [one-way ANOVA; $F_{2,100} = 4{\cdot}722$; $P < 0{\cdot}05$; Fig. 3(b)]. Niushan Lake had the smallest F_R (mean ± S.E. = 209·6 ± 32·58) and was significantly different from both Wuhu Lake (mean ± S.E. = 270·53 ± 48·41; Tukey test; $P < 0{\cdot}05$) and Tangxun Lake (mean ± S.E. = 272·56 ± 44·89; Tukey test; $P < 0{\cdot}05$). The last had the highest F_R and was not significantly different from Wuhu Lake (Tukey test; $P > 0{\cdot}05$). There were no significant differences in average E_G [Fig. 3(c)] between the three lakes (Kruskal–Wallis; $P > 0{\cdot}05$).

All individuals older than 2 years were mature. Considering 1 year-old fish, 10 individuals (4%) were immature in Niushan Lake, whereas all were mature in Wuhu and Tangxun Lakes. Moreover, a significant influence of the lake on the proportion of mature individuals at age 1 year was detected ($\chi^2 = 6{\cdot}74$; $P < 0{\cdot}05$).

Finally, a significant positive correlation ($r^2 = 0{\cdot}52$; $P < 0{\cdot}05$) between the scores of the first PCA axis and I_{GRO} was found suggesting that *C. erythropterus* individuals grow faster in eutrophic lakes [Fig. 4(a)]. Likewise, the scores of the first PCA axis were significantly negatively related to L_∞ [$r^2 = 0{\cdot}49$; $P > 0{\cdot}05$; Fig. 4(b)] suggesting that adult size individuals in eutrophic areas tend to be smaller.

DISCUSSION

It is generally considered that early maturity, production of many small offspring, diminished body size, rapid development, reduced parental care, short lifespan and large reproductive efforts are the characteristics of species with *r*-selection tactics (MacArthur & Wilson, 1967; Stearns, 1976; Odum & Barrett, 2004). Here, even within the same species, environmental factors such as eutrophication drive life-history tactics

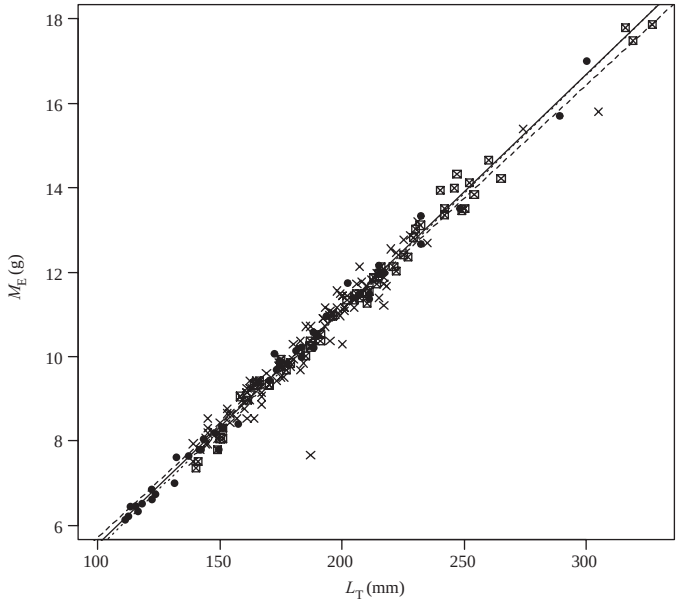

FIG. 2. Linear regression between eviscerated body mass (M_E) and total length (L_T) of *Chanodichthys erythropterus* for three Chinese lakes [Niushan (•) $y = -0{\cdot}03\ (\pm 0{\cdot}19) + 0{\cdot}05\ (\pm 0{\cdot}00)\ x$, Wuhu (⊠) $y = -0{\cdot}17\ (\pm 0{\cdot}28) + 0{\cdot}05\ (\pm 0{\cdot}00)\ x$ and Tangxun (×) $y = -0{\cdot}36\ (\pm 0{\cdot}28) + 0{\cdot}05\ (\pm 0{\cdot}00)\ x$] with different eutrophication levels.

of populations with individuals that grow faster, whilst having smaller adult sizes, along a gradient of increasing eutrophication. In addition, females in the most eutrophic lakes invested more in reproduction as they displayed a higher relative fecundity and a larger gonad mass (represented by I_G). Hence, it appears that eutrophication favours *r*-selection tactics in *C. erythropterus*.

It is generally considered that in a variable and unpredictable environment, *r*-strategist species have an advantage over *k*-strategists due to the high reproductive effort typical of pioneer species (Stearns, 1976). In a natural setting, the primary succession process includes a gradual change from communities consisting essentially of pioneer species (*r*-strategists) towards communities with species that invest more in somatic growth with a lower reproductive investment but with higher chance of survival [*k*-strategists; Odum (1969)]. The increasing eutrophication from fertilization of lakes is known to act as a source of disturbance, setting back the natural process of colonization and then ultimately changing the species composition from *k* to *r*-strategists (Caus *et al.*, 1997; Scheibner *et al.*, 2005). What is less known is the effect of eutrophication on the life-history tactics of a single species, leading to its displacement along the $k-r$ gradient. This, for example, would push an *r*-strategist such as *C. erythropterus* towards increased reproductive investment and decreased somatic growth.

Although the mechanisms by which eutrophication affects life-history traits is not considered in this study, three possible underpinning mechanisms exist. First, the increased level of nutrients in these lakes would induce an increase in algal bloom events, oxygen depletion and thus mortality risk for fish species during the

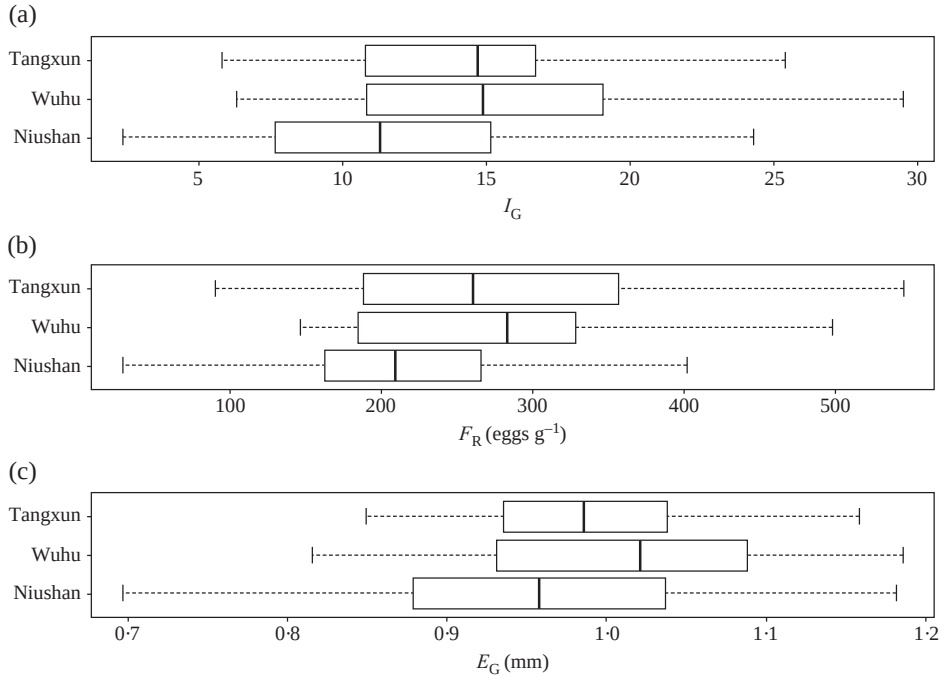

FIG. 3. Box plots representing the median (----) and 25th and 75th percentiles of three reproductive variables: (a) gonado-somatic index (I_G), (b) relative fecundity (F_R) and (c) egg diameter (E_G) for *Cultrichthys erythropterus* in three Chinese lakes with different levels of eutrophication (mesotrophic, eutrophic and hypertrophic).

summer months. These initially stable ecosystems will in effect become more and more variable and unpredictable, which would typically favour individuals that invest in their reproductive outputs to the detriment of those who invest in longevity and somatic growth instead. Second, an increase in nutrient level will also affect the turbidity of the lakes with a direct knock-on effect on macrophyte abundance and overall trophic structure (Smith & Schindler, 2009). In such eutrophic lakes, the first species to disappear are the top predators that often rely on ambush predation of high-energy prey such as mandarin perch *Siniperca chuatsi* (Basilewsky 1855) and that control the size of prey population. Thus, along with the decline in top predators, comes the proliferation of species that feed on the lower part of the food web, in turn, increasing trophic competition and forcing species to change from long-term investment in somatic growth to short-term reproductive outputs. Third, food resources are considered one of the most important drivers of body energetic allocation (Stearns, 1976; Noordwijk & Jong, 1986) and in some cases could mask the trade-off between reproduction and growth (Cothran *et al.*, 2012). For example, it has been shown that jellyfish produced more polyps when food resources are more abundant, and it has also been hypothesized that eutrophication could be the factor involved in their prominent blooms in East Asian coastal waters (Han & Uye, 2010).

This research raises several interesting questions and prompts further studies that could improve understanding of the relationship between eutrophication and

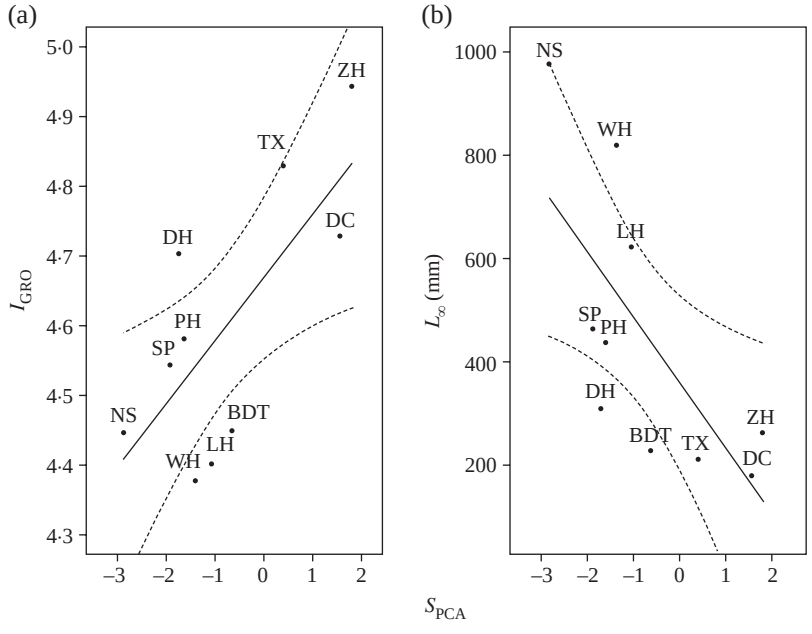

FIG. 4. Linear regression between eutrophication levels [*i.e.* principal component analysis (PCA) scores of the first axis; S_{PCA}] and (a) the growth performance index (I_{GRO}) and (b) the asymptotic length (L_∞) for *Channodichthys erythropterus* in several lakes in China (see Table I). I_{GRO} and L_∞ were calculated using the von Bertalanffy growth model and quartile regression. The fitted model for (a) I_{GRO} was $y = 4{\cdot}66\ (\pm 0{\cdot}05) + 0{\cdot}09\ (\pm 0{\cdot}03)\ x$ ($r^2 = 0{\cdot}52$), and the fitted model for (b) L_∞ was $y = 358{\cdot}42\ (\pm 73{\cdot}36) - 214{\cdot}84\ (\pm 44{\cdot}61)\ x$ ($r^2 = 0{\cdot}49$). -----, 95% C.I.

life-history tactics. The first question relates to the time frame underpinning these observed life-history trait changes in response to changes in eutrophication levels. This aspect is particularly relevant to the wider context of life-history trait modifications during biological invasion. Most freshwater fish species that are introduced into a novel ecosystem are introduced regardless of their specific life-history tactics and a key driver of establishment success could be their ability to modify their energetic allocation towards reproductive outputs (*e.g.* fecundity and early maturity) against their somatic growth (*e.g.* large adult size and longevity). This was clearly observed, for example, with the invasion of top mouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel 1846), a small cyprinid originating from China (Gozlan *et al.*, 2010; Britton & Gozlan, 2013). Another interesting aspect would be to test the role of eutrophication against other intrinsic factors such as food availability, functional diversity and overall fish density. This is of particular interest as the impact of eutrophication on life-history traits could be amplified by other biotic drivers such as the level of trophic competition. Such understanding would lead to better stock management of fisheries, where somatic growth of fish rather than their reproductive output is favoured. This would also provide an insight into the current miniaturization of fish species observed in Chinese Lakes (Zhao *et al.*, in press).

This study takes place in the wider Chinese context of an increasingly large lake aquaculture (*i.e.* 998 000 ha) that represents the main component of inland fisheries

in China (Fisheries Bureau of the Ministry of Agriculture, 2010) and traditional techniques that include application of fertilizers along with intensive stocking of carps [*e.g.* grass carp *Ctenopharyngodon idella* (Valenciennes 1844), planktivorous silver carp *Hypophthalmichthys molitrix* (Valenciennes 1844) and bighead carp *Aristichthys nobilis* (Richardson 1845)]. This fishery management has caused a significant decrease in macrophytes (Chen *et al.*, 1994; Sun *et al.*, 1999), increased nutrient load and reduced water quality (Stearns, 1976; Zhang, 2007) and, as seen here, has caused unexpectedly subtle, but deep changes in fish populations.

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Annexe II (*AII*)

Paz-Vinas I, Comte L, Chevalier M, Dubut V, Veyssière C, Grenouillet G, Loot G & Blanchet S (2013). Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species. ***Ecology and Evolution*** *3: 2696–2710.*

Ecology and Evolution

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Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species

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Keywords
Bottleneck, conservation genetics, demographic survey, *Parachondrostoma toxostoma*, rivers, species distribution models, temporal trends.

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Abstract

Prioritizing and making efficient conservation plans for threatened populations requires information at both evolutionary and ecological timescales. Nevertheless, few studies integrate multidisciplinary approaches, mainly because of the difficulty for conservationists to assess simultaneously the evolutionary and ecological status of populations. Here, we sought to demonstrate how combining genetic and demographic analyses allows prioritizing and initiating conservation plans. To do so, we combined snapshot microsatellite data and a 30-year-long demographic survey on a threatened freshwater fish species (*Parachondrostoma toxostoma*) at the river basin scale. Our results revealed low levels of genetic diversity and weak effective population sizes (<63 individuals) in all populations. We further detected severe bottlenecks dating back to the last centuries (200–800 years ago), which may explain the differentiation of certain populations. The demographic survey revealed a general decrease in the spatial distribution and abundance of *P. toxostoma* over the last three decades. We conclude that demo-genetic approaches are essential for (1) identifying populations for which both evolutionary and ecological extinction risks are high; and (2) proposing conservation plans targeted toward these at risk populations, and accounting for the evolutionary history of populations. We suggest that demo-genetic approaches should be the norm in conservation practices.

Introduction

Prioritizing and making appropriate plans to manage and conserve threatened species is a complex task. Global changes simultaneously affect multiple facets of individual species, making predictions difficult (Margules and Pressey 2000; McMahon et al. 2011). For instance, global changes such as habitat fragmentation or climate change can affect the genetic diversity (Olivieri et al. 2008; Blanchet et al. 2010), the demographic dynamics (Julliard et al. 2004; Dunham et al. 2008), the evolution of life-history traits (Conover et al. 2009; Blanchet and Dubut 2012), and/or the spatial distribution of species (Parmesan 2006; Buisson et al. 2008). Accordingly, the conservation biologists' toolbox includes several methods which emerged from multiple disciplines such as population genetics, population ecology, and biostatistics (Guisan and Zimmermann 2000; Green et al. 2005; Excoffier and Heckel 2006). Nevertheless, most conservation studies focus on a single facet of species health (e.g., the genetic diversity), and hence provide only partial information for biodiversity management and conservation (Frankham 2010; Geist 2011; Loss et al. 2011).

Integrative studies are, however, increasingly acknowledged as being valuable from a conservation standpoint (Purvis and Hector 2000; Geist 2011; Loss et al. 2011). For instance, at the community level, Devictor et al. (2010) showed that there was a strong spatial mismatch between phylogenetic, functional, and taxonomic measures of bird biodiversity. These measures provide different but complementary information, suggesting that reserve designs should be optimized accordingly (Devictor et al. 2010). Similarly, at the population level, diverse measures classically used to assess the health of a population (e.g., effective population size, abundance, and dispersal rate) provide complementary information that should be integrated into common analyses to set efficient conservation plans (e.g., Osborne et al. 2010, 2012). For instance, demographic monitoring programs (hereafter, DMPs) provide useful information regarding the ecological status of populations and enable predictions on future distributions under global change scenarios, whereas population genetics studies (hereafter, PGSs) obtain information regarding the evolutionary status of populations and their potential resistance to rapid environmental changes (Smith and Bernatchez 2008). Because evolutionary and ecological timescales and processes are sometimes confounded (Carroll et al. 2007), it is of prime importance to merge evolutionary and ecological information to (1) identify the populations that need to be prioritized for conservation actions; and (2) implement effective long-term management and conservation of endangered populations (Osborne et al. 2012).

The use of population genetics in biodiversity conservation has increased considerably in the last decades (Frankham 2010). Low genetic diversity in natural populations has been generally associated with pervasive effects such as inbreeding depression, loss of evolutionary potential, and the accumulation of deleterious mutations (Saccheri et al. 1998; Frankham 2010). These effects theoretically increase extinction risks, and are expected to be stronger in populations under anthropogenic or natural stresses (Spielman 2004). Accordingly, PGSs generally aim at (1) describing the genetic status of populations (i.e., genetic diversity and structure assessed during a snapshot survey, Schwartz et al. 2007); (2) identifying historical and contemporary factors affecting the genetic diversity of populations (Manel et al. 2003; Dubut et al. 2012); and (3) inferring past and contemporary demographic parameters such as effective population sizes (N_e) (Storz and Beaumont 2002). Although PGSs provide key information about demographic processes, linking genetics and population demography remains tricky (Osborne et al. 2012). For instance, the link between N_e and census population size (N_c) is notoriously difficult to assess (Luikart et al. 2010; Belmar-Lucero et al. 2012; Palstra and Fraser 2012), and genetic bottlenecks (i.e., strong decreases in N_e) can be detected even in the absence of demographic bottlenecks (Broquet et al. 2010; Chikhi et al. 2010). Furthermore, the effects of particular threats may be undetected through PGSs due to the lag time that often exists between an ecological cause and its evolutionary consequence (Landguth et al. 2010).

Analyses based on demographic data can overcome some of these gaps (Nichols and Williams 2006; Lindenmayer et al. 2010). DMPs provide information about the current status of populations by allowing the inference of key demographic parameters such as abundance and/or occurrence (Royle and Dorazio 2006). Combined with time series analyses, DMPs also permit the investigation of temporal trends and hence the identification of the causes and consequences of population declines or changes in spatial distribution (Daufresne et al. 2004). Additionally, these surveys are useful for the early detection of the effects of threats on populations as well as "ecological surprises" (Doak et al. 2008), which is notoriously difficult using only PGSs (Julliard et al. 2004; Lindenmayer et al. 2010). Finally, long-term and large spatial-scale surveys are of prime interest and may allow predictions about the future status of populations in a changing world through the use of species distribution models for instance (Guisan and Zimmermann 2000).

In this study, we attempt to demonstrate how combining PGSs and DMPs provides baseline information for prioritizing and initiating management and conservation plans. We focused on an endangered freshwater fish species (i.e., the South-west European nase *Parachondrostoma toxostoma*, Vallot 1837) which is considered vulnerable throughout its restricted native range (i.e., Southern France, Crivelli 2006). We used a microsatellite dataset gathered at the river basin scale (i.e., the Garonne river basin, South-Western France) to (1) describe the genetic diversity and structure of *P. toxostoma* populations, and (2) detect and quantify both contemporary and past N_e (i.e., contraction or reduction in N_e over time), as well as to date main changes in N_e following the last glacial maximum (i.e., approximately 10,000 years ago). In parallel, we used a demographic survey performed at the same spatial scale over the last three decades to (3) identify temporal trends in species abundance at the Garonne river basin scale; and (4) assess the current spatial distribution of the species and changes in the distribution over the last three decades.

Materials and Methods

Biological model

Parachondrostoma toxostoma is a threatened freshwater fish species of the Cyprinidae family endemic to France

and Switzerland, where its native range area is restricted to the Rhône, Adour and Garonne river basins. This species is listed as vulnerable in the IUCN red list, in the Annex II of the European Union Habitats Directive and in Appendix III of the Bern Convention (Crivelli 2006). The range of the species has been strongly reduced due to water pollution, habitat fragmentation by dams and weirs, artificial water releases and hybridization with a nonnative species, *Chondrostoma nasus* (Costedoat et al. 2007). Our study focuses on the Garonne river basin, which hosts the major stock of pure *P. toxostoma* (i.e., not introgressed by the *C. nasus* genome). This highlights the urge for conservation actions directed toward the Garonne drainage in order to preserve the *P. toxostoma* species.

Population genetics study

Sampling design

Ninety-two sampling sites belonging to 34 rivers of the Garonne river basin were investigated using electrofishing in 2010 and 2011 (Fig. S1). We did not catch *P. toxostoma* at 76 sites. Two hundred and 30 individuals of *P. toxostoma* were sampled at sixteen sites (Table 1, Fig. 1). Thus, we assume that these sixteen sites are representative of the current *P. toxostoma* populations. However, due to the low numbers of individuals captured at some sampling sites, individuals from sites belonging to the same river were pooled for subsequent analyses. All genetic analyses were therefore conducted at the river level ($n_{RIVER} = 9$). A small fragment of pelvic fin was collected and stored in 90% ethanol. Individuals were all released alive at their sampling site.

Genotyping

We used a salt-extraction protocol to extract genomic DNA from pelvic fins (Aljanabi and Martinez 1997). Fifteen microsatellite loci previously developed and/or evaluated for *P. toxostoma* (Dubut et al. 2010) were coamplified using two multiplexed polymerase chain reactions (PCRs; see Table S1 for details on loci and primers concentrations). PCR amplifications were performed with 5–20 ng of genomic DNA and using the QIAGEN® Multiplex PCR Kit (Qiagen, Valencia, CA). PCRs were carried out under conditions described by Dubut et al. (2010). Genotyping was performed on an ABI PRISM™ 3730 Automated Capillary Sequencer (Applied Biosystems, Foster City, CA) at the "Génopole Toulouse Midi-

Table 1. *Parachondrostoma toxostoma* sampling sites information.

River	Code	Location	Latitude	Longitude	PGS	$N_{(PGS)}$	DMP	$Y_{(DMP)}$
ARRATS	ARR	Aubiet	N 43°38′48″	E 0°46′45″	–	–	X	13
AUROUE	AUR	L'isle-Bouzon	N 43°54′32″	E 0°43′45″	–	–	X	13
AVEYRON	AVE	Feneyrols	N 44°07′52″	E 1°48′51″	X	5	–	–
		Monteils	N 44°17′09″	E 2°00′07″	X	4	–	–
ARIEGE	ARI	Vénerque	N 43°26′13″	E 1°26′15″	–	–	X	8
PETITE BARGUELONNE	BAR	Montbarla	N 44°12′34″	E 1°03′40″	X	9	X	17
CELE	CEL	Boussac	N 44°35′46″	E 1°55′02″	X	7	–	–
		Sainte Eulalie	N 44°35′36″	E 1°52′25″	X	8	–	–
		Sauliac-sur-Célé	N 44°31′09″	E 1°42′58″	X	25	X	11
COUZE	COU	Bayac	N 44°48′16″	E 0°43′45″	–	–	X	14
ELLE	ELL	Terrason-Lavilledieu	N 45°08′51″	E 1°15′37″	X	25	–	–
GARONNE	GAR	Muret	N 43°27′36″	E 1°19′52″	–	–	X	10
HERS	HER	Besset	N 43°05′03″	E 1°50′24″	X	4	X	10
		Calmont	N 43°17′10″	E 1°37′59″	X	25	–	–
LOUGE	LOU	Fousseret	N 43°16′27″	E 1°04′07″	X	8	X	13
SALAT	SAL	Touille	N 43°04′38″	E 0°58′05″	X	25	–	–
SAVE	SAV	Espaon	N 43°25′20″	E 0°51′21″	X	18	–	–
VENDINELLE	VEN	La Salvetat Lauragais	N 43°32′22″	E 1°48′15″	–	–	X	18
VERE	VER	Cahuzac-sur-Vère	N 43°59′12″	E 1°53′43″	–	–	X	17
VIAUR	VIA	La Calquière	N 44°09′12″	E 2°12′15″	X	13	–	–
		Saint Just	N 44°07′24″	E 2°21′57″	X	23	–	–
		Navech	N 44°09′25″	E 2°23′18″	X	25	–	–
		Serres	N 44°12′29″	E 2°31′25″	X	6	–	–
VOLP	VOL	Plan	N 43°10′16″	E 1°07′07″	–	–	X	8

PGS (for Point Genetic Study) indicates whether the site has (X) or not (–) been sampled for genetic analyses. $N_{(PGS)}$ indicates the number of individuals sampled per site for genetic analyses. DMP (for Demographic Monitoring Program) indicates whether the site has (X) or not (–) been selected for analyses of temporal trends in abundance. $Y_{(DMP)}$ indicates the number of years considered in the time series.

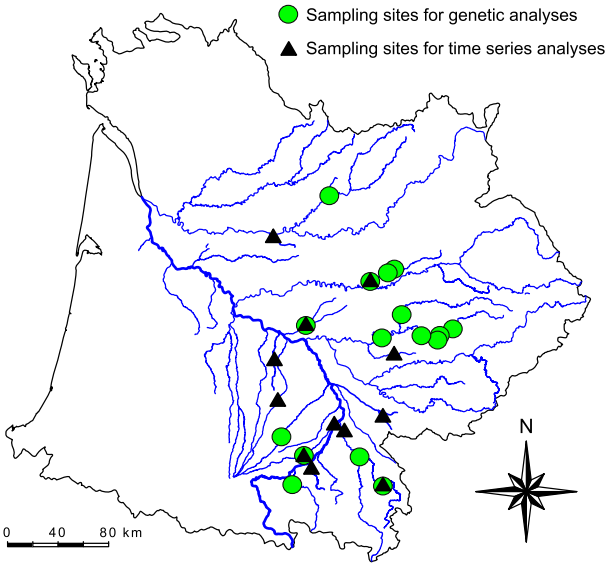

Figure 1. Map of the Garonne river basin (South–Western France) representing (1) sites where *Parachondrostoma toxostoma* was sampled for the genetic analyses (green circles) and (2) sites that have been selected for analyses of temporal trends in population abundances (black triangles).

Pyrénées" (France). Allele sizes were scored using the software GENEMAPPER® v.4.0 (Applied Biosystems).

Descriptive genetic analyses

The presence/absence of large allele dropouts and null alleles was determined using the software MICRO-CHECKER 2.3 (Van Oosterhout et al. 2004). Departures from Hardy–Weinberg (HW) equilibrium were estimated using the program GENEPOP v4.0 (Rousset 2008). Levels of significance for HW were adjusted using the false discovery rate (FDR) procedure (Benjamini and Hochberg 1995). Linkage disequilibrium among loci within sites was tested with the program FSTAT 2.9.3.2 (Goudet 1995).

The mean number of alleles per site, the average observed (H_o) and expected (H_e) heterozygosity over loci, as well as H_o and H_e per loci per site were estimated using ARLEQUIN 3.5 (Excoffier and Lischer 2010). We used a rarefaction procedure, as implemented in the software ADZE 1.0 (Szpiech et al. 2008), to estimate allelic richness (Petit et al. 1998) for each site, considering minimum sample sizes of $N = 8$ and $N = 18$ individuals.

Population structure

A Bayesian model-based clustering approach was used to search for the occurrence of independent genetic groups (i.e., clusters, K) in our dataset (as implemented in STRUCTURE 2.3.3; Pritchard et al. 2000; Falush et al. 2003, 2007; Hubisz et al. 2009). The burn-in length of the Markov Chain Monte Carlo (MCMC) was set to 50,000 followed by 200,000 iterations. The admixture model and the correlated allele frequencies model were used with priors on population sampling location (Hubisz et al. 2009). Ten runs were conducted for each K value, with K ranging from 1 to 10. We used CORRSIEVE 1.6.2 (Campana et al. 2011) to combine two approaches aiming at determining K: the ΔK test (Evanno et al. 2005) and the ΔF_{st} test (Campana et al. 2011).

To further assess the levels of genetic differentiation among *P. toxostoma* sites, two different indices were estimated: pairwise F_{st} (Weir and Hill 2002) and the unbiased pairwise D_{est} (Jost 2008), calculated using ARLEQUIN 3.5 and SMOGD (Crawford 2010), respectively.

Demographic history inference and current N_e estimation

We used two different approaches for inferring past changes in the effective population size (i.e., expansions or contractions) of *P. toxostoma*.

The first method, implemented in the BOTTLENECK v1.2.02 software (Cornuet and Luikart 1996; Piry 1999), uses summary statistics of the genetic diversity to assess significant deviations from mutation/drift equilibrium. Significant heterozygosity excesses are considered as evidence of recent bottlenecks, whereas significant heterozygosity deficiencies can be interpreted as signals of recent population expansion (Luikart and Cornuet 1998). We performed analyses considering two different microsatellite evolution models: the stepwise mutation model (SMM) and the two-phase model (TPM). For the latter, we set the percentage of multistep mutations at 30%. We tested the significance of mutation/drift equilibrium deviations for the two models using Wilcoxon's signed rank tests. To account for multiple comparisons, we applied the FDR procedure (Benjamini and Hochberg 1995). The second method is the full-likelihood Bayesian approach implemented in the program MSVAR 1.3 (Beaumont 1999; Storz and Beaumont 2002). This coalescent-based method relies on a hierarchical Bayesian model to detect, date, and quantify past demographic changes. The model assumes that a stable, closed population of ancestral size N_1 increased or decreased exponentially to its current size N_0 (i.e., its current N_e) over a time interval of T_a years. This method uses all the information contained in the data and lognormal priors to infer the parameters of the model $\Phi = \{N_0, N_1, T_a, \theta\}$, where $\theta = 4N_0\,\mu$ and μ is the mutation rate. The posterior probability density of Φ is assessed via MCMC algorithms. Microsatellite loci are assumed to be independent and to evolve under a strict SMM. For each river-scale analysis, we performed four

independent runs of 5×10^9 steps, considering different starting values and means for priors and hyperpriors for each run (Goossens et al. 2006). We set a generation time of 3 years for *P. toxostoma* (Keith et al. 2011). Parameters were thinned with an interval of 5×10^4 steps, resulting in output files with 1×10^5 values. We discarded the first 10% of the chains as burn-in to prevent bias induced by the starting values on parameter estimation. The convergence of the MCMC chains was checked with the Gelman and Rubin analysis implemented in the R package CODA (Gelman and Rubin 1992; Plummer et al. 2006). For each analysis, posterior parameter values obtained by the four independent runs were pooled together and subsequently used to calculate the median and the 5–95% quartiles for N_0, N_1, and T_a. We also calculated these statistics for the ratio $\log_{10}(N_0/N_1)$. Negative values of this ratio indicate that the population has experienced a decrease in effective population size, while positive values characterize demographic expansions. This approach was also used to estimate a current N_e at the Garonne river basin scale. To do so, we ran MSVAR by pooling all individuals from all rivers in a single analysis. At such a scale, estimates of current N_e were compared to those estimated using the linkage disequilibrium-based approach implemented in LDNe (Waples and Do 2008). LDNe was not used at the river scale due to its propensity to give negative N_e estimates (which are interpreted as infinity estimates, Waples and Do 2008) for most rivers. MSVAR 1.3 runs were performed on an ALTIX ICE 8200 EX and UV computer cluster (Silicon Graphics International, Fremont, CA) hosted by the CALMIP group at the University Paul Sabatier (Toulouse, France).

Demographic monitoring data

Database description

We used the surveillance monitoring database of the French National Agency for Water and Aquatic Environments (i.e., ONEMA) to carry out demographic trend and species distribution analyses. This database includes an extensive spatiotemporal set of monitoring surveys of French freshwater fish populations, representative of all fish assemblages and covering varying degrees of anthropogenic disturbances (Poulet et al. 2011). Surveys were conducted according to standard electrofishing procedures (Poulet et al. 2011). We used this database to (1) identify temporal trends in population abundance of *P. toxostoma* at 12 sampling locations; (2) assess the current spatial distribution of this species in the Garonne river basin; and (3) investigate whether the spatial distribution of this species in the Garonne river basin has declined or expanded over the last three decades.

Temporal trends in abundance

From this dataset, we selected all sites belonging to the Garonne river basin that have been sampled and investigated for *P. toxostoma* abundance for at least 8 years. This resulted in the selection of twelve sites (Table 1, Fig. 1) for which time series ranged between 8 and 18 years and occurred between 1991 and 2010. As sampling procedures were standardized over years, abundances (expressed as the number of individuals per m^2) were directly comparable across years. It is noteworthy that (1) this database and the genetic database have been gathered during independent research projects; and (2) *P. toxostoma* is relatively rare in this area (Fig. S1), which both explain why demographic and genetic data are not available for all sites (see Table 1). Some sites for which long-term demographic data were available have been unsuccessfully sampled for genetic, and inversely, some sites where genetic data were available had time series that were not long enough to be analyzed (i.e., <8 years).

First, we assessed the strength and significance of temporal trends at these sites, by using a modified Mann–Kendall trend test that we independently applied to each time series (Hamed and Rao 1998). In this test, the Mann–Kendall's *S* statistic (Kendall 1962) provide an estimate of the strength of the association between time and the response variable, while accounting for temporal autocorrelation present in a time series (Hamed and Rao 1998).

Second, we assessed whether or not these twelve time series showed an overall significant trend. For this purpose, we performed a meta-analysis (Gurevitch and Hedges 1993) on the twelve Mann–Kendall's trend statistics *S* calculated in the first step. We applied a mixed linear model approach using maximum likelihood, in which we assumed that the 12 time series included in the meta-analysis share a common effect size with a random variation among the twelve time series.

Current spatial distribution and recent distribution changes

We used the database described above to assess changes in the spatial distribution of *P. toxostoma* on the Garonne river basin over two distinct periods, separated by a time span of 10 years (i.e., "past period": 1980–1992, and "current period": 2003–2009). To account for potential sampling bias when comparing spatial distributions over time based on datasets not originally collected for this purpose (Shaffer et al. 1998; Shoo et al. 2006), we modeled the spatial distribution of the species across the French hydrographic network as a function of several climatic and environmental variables.

Accurately modeling species distribution requires performing analyses at the entire species range scale, so as to encompass all environmental conditions (Austin 2007). Therefore, for both time periods, initial models were calibrated at the French scale. We selected 3549 sites sampled over the 1980–1992 period and 3543 sites sampled over the 2003–2009 period scattered across France (see Fig. S2). The occurrence of the species was modeled independently for both time periods as a function of habitat and climatic data strongly related to fish spatial distributions (Buisson et al. 2008): elevation (m), slope (%), upstream–downstream position (G), mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), temperature variability, cumulated precipitations of the wettest quarter (mm), cumulated precipitations of the driest quarter (mm), and precipitation variability (Hijmans et al. 2005).

To account for uncertainty in estimating species range, we used a modeling approach allowing us to produce maps of species habitat suitability (e.g., Puschendorf et al. 2009; Grenouillet et al. 2011). Specifically, we used an ensemble modeling approach based on a consensus model averaging the probabilities of occurrence predicted by eight single-species distribution models (Marmion et al. 2009), as well as three threshold setting methods allowing the conversion of occurrence probabilities into binary data (i.e., presence or absence, Liu et al. 2005), and 30 iterations (see Appendix S1 for details on models' implementation).

The calibrated models set at the French scale were then used to predict the binary predictions of occurrence of the species for the two distinct periods in the hydrographic network of the Garonne river basin. The spatial distribution of the species for each time period was calculated as the length of the hydrographic network occupied by the species (e.g., Fagan 2002) in the Garonne river basin (expressed in % of the total network length). However, because the ability to detect changes in the spatial distribution of species may be confounded by the uncertainty arising from methodological strategies (e.g., threshold effect, Nenzén and Araújo 2011), temporal changes in the occupied stream length were evaluated using a linear model that controlled for the threshold effect. A linear model was thus fitted to the spatial distribution of *P. toxostoma* in both periods where the threshold-setting method and the period were used as explanatory variables. The change (i.e., extension or contraction) was then provided by the least-squares means intercepts of the contemporary period-group effect. Temporal trends analyses and spatial distribution models have been developed under the R statistical software 2.13.0 (R Development Core Team 2011).

Results

Population genetics study

Descriptive genetic analyses

After applying the FDR controlling procedure, no null alleles were detected in our dataset, there were no significant deviations from HW for any loci or any population (Tables S2 and S3), and we failed to detect significant linkage disequilibrium between pairs of loci (Table S4).

Overall, genetic diversity estimates were low (Fig. 2A and B, Table S3). Loci were weakly polymorphic at the basin scale (2–6 alleles per locus), with some loci being monomorphic at the river scale (na = 1; Table S2). Average H_e and H_o values across loci within rivers were moderately low (H_e = 0.320–0.450; H_o = 0.315–0.482), as well as mean number of alleles and allelic richness estimates (AR_8 = 1.868–2.536 alleles per river; AR_{18} = 2.147–3.037; Fig. 2A and B, Table S3). It is noteworthy that the Save River (SAV) displayed the lowest genetic diversity estimates (Fig. 2A and B, Table S3).

Population structure

The ten runs of the Bayesian clustering analysis were convergent. The ΔK and ΔF_{st} tests revealed three distinct clusters K = 3 (Fig. 3A–B). Most of the populations were hardly differentiable and were characterized by the occurrence of a main cluster, whose frequency range was from 62% (CEL) to 98% (VIA). Only SAV and HER were discriminated from the rest of the Garonne river basin, each site corresponding to a distinct cluster (Fig. 3C). Overall, genetic differentiation values between rivers were weak to moderate and ranged between 0.003 and 0.244 and 0.003 and 0.281 for F_{st} and $D_{est,}$ respectively (Table 2). All but five pairwise F_{st} values were significant (Table 2). The stronger differentiations were found between SAV/VIA (F_{st} = 0.244; D_{est} = 0.097) and SAV/BAR (F_{st} = 0.117; D_{est} = 0.281).

Demographic history inference and current N_e estimation

According to the BOTTLENECK software, and after corrections for multiple tests, there was no significant evidence for demographic changes in the Garonne river basin (Table S5). On the contrary, the MSVAR analyses revealed significant signals of bottleneck in all rivers (Fig. 2C, Table S6). The magnitude of these bottlenecks, as indicated by the median values of the $\log_{10}$ (N_0/N_1) ratio, ranged between −0.705 (ELL) and −1.345 (HER; Fig. 2C, Table S6). Overall, N_0 estimates (i.e., the current N_e of populations) were similar across rivers, with

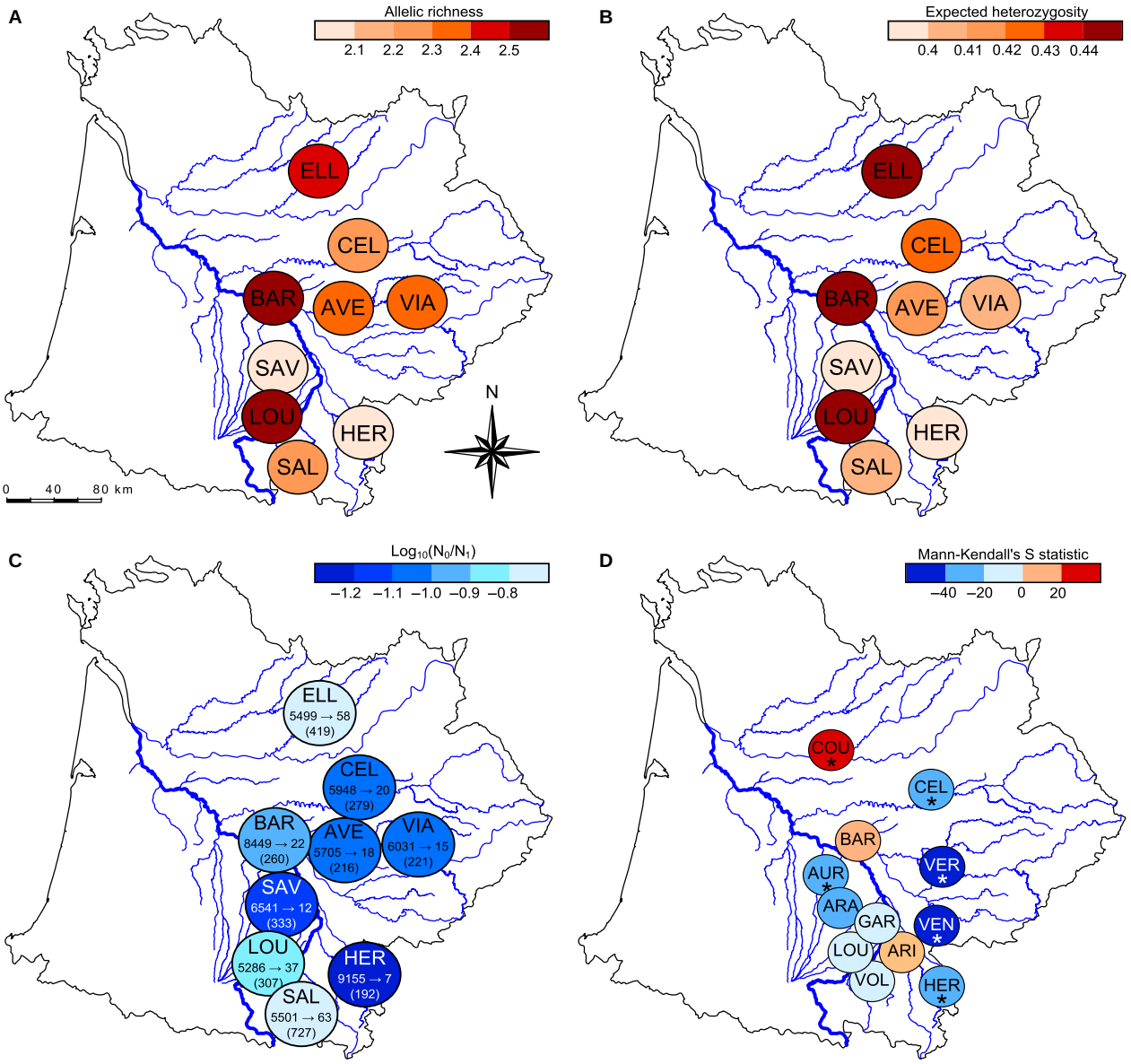

Figure 2. Maps representing (A) the allelic richness per population considering a minimum sample size of 8 (color scale), (B) the expected heterozygosity per population (color scale), (C) the past effective population size (N_1; left number in the bubbles, see also Table S6), the current effective population size (N_0; right number in the bubbles, see also Table S6), the time of the beginning of the bottlenecks (in years backward in time; numbers in brackets, see also Table S6), and the magnitude of bottlenecks (i.e., Log_{10} (N_0/N_1): color scale, see also Table S6), and (D) the value of the Mann–Kendall's S statistic (color scale) and the significance of Mann–Kendall trend tests for each time series: Asterisks (*) denote significant (i.e., $P < 0.05$) temporal trends. For all panels, the three-letter code in each bubble corresponds to the river codes (see Table 1).

medians ranging from 7 (HER) to 63 individuals (SAL). Concerning ancestral population sizes (N_1), median values ranged from 5286 (LOU) to 9155 individuals (HER; Fig. 2C, Table S6). These bottlenecks were estimated to have occurred between 192 (HER) and 727 years ago (SAL). The MSVAR method has often been considered as more powerful than the BOTTLENECK method (Williamson-Natesan 2005; Girod et al. 2011), which may explain the discrepancy observed between these two methods.

The analysis performed at the Garonne river scale confirmed the low estimates of current N_e found at the river scale. Indeed, at this scale, MSVAR provided an estimate of 147 individuals (5–95% quartiles: 35.6–534.4) in the whole drainage, whereas LDNe provided a global estimate of 74.6 individuals (95% CI: 54.4–104.6).

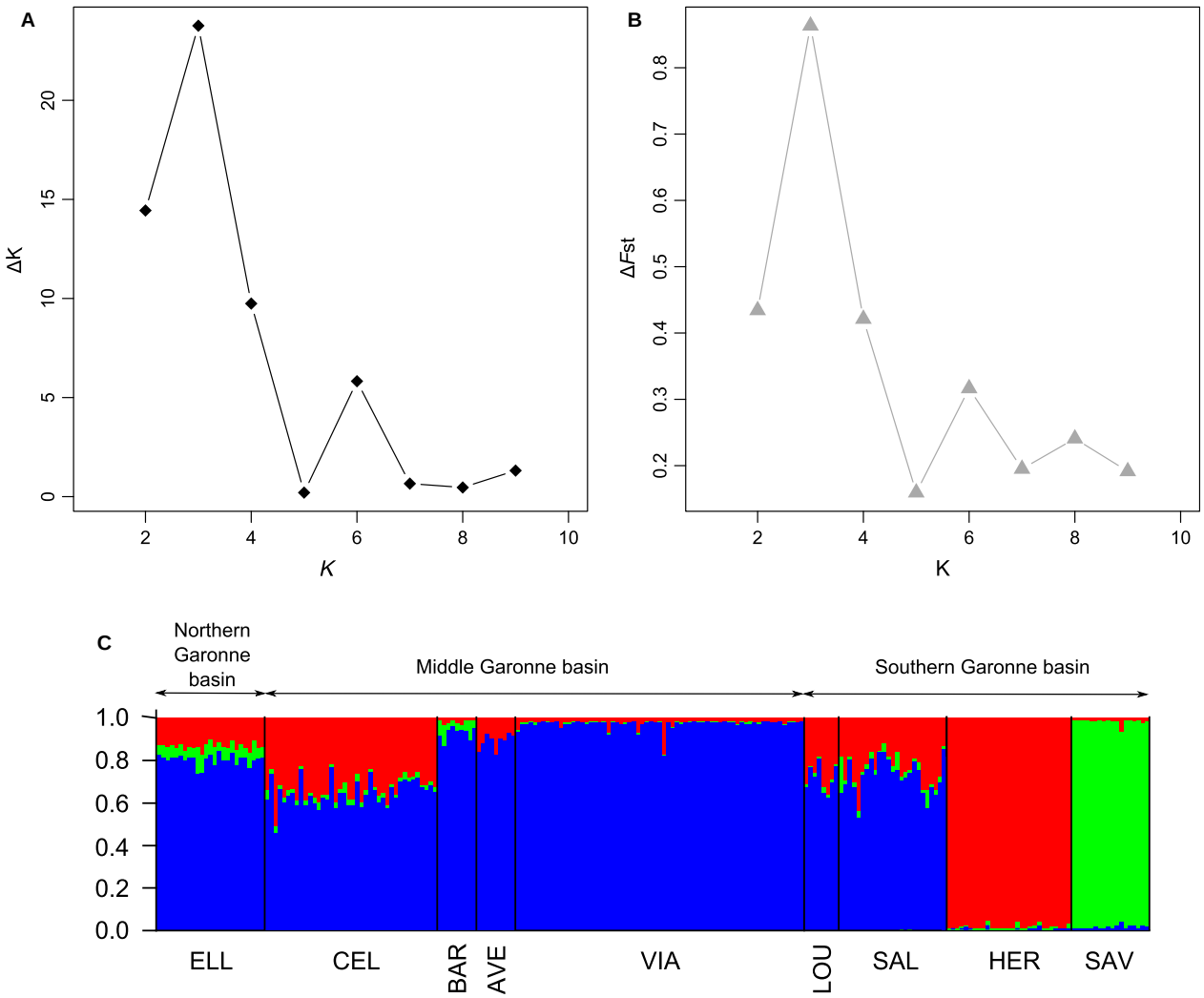

Figure 3. Analysis of the population structure of *Parachondrostoma toxostoma* in the Garonne river basin. (A) and (B) represent the results from ΔK and ΔF_{st} tests, respectively. (C) is a barplot representing the results of the Bayesian clustering analysis of microsatellites using STRUCTURE for $K = 3$.

Table 2. Population pairwise F_{st} (upper half-matrix) and pairwise D_{est} (lower half-matrix) values calculated between all rivers (denoted by their three-level code).

Code	AVE	BAR	CEL	ELL	HER	LOU	SAL	SAV	VIA
AVE	–	**0.117**	**0.067**	**0.070**	**0.042**	0.013^{ns}	**0.014**	**0.109**	0.005^{ns}
BAR	0.056	–	**0.102**	**0.052**	**0.054**	**0.025**	**0.026**	**0.130**	**0.017**
CEL	0.018	0.031	–	**0.023**	**0.023**	0.003^{ns}	**0.012**	**0.089**	**0.010**
ELL	0.035	0.008	0.003	–	**0.032**	0.008^{ns}	**0.014**	**0.115**	**0.008**
HER	0.132	0.165	0.077	0.096	–	**0.069**	**0.068**	**0.077**	**0.122**
LOU	0.054	0.057	0.029	0.029	0.019	–	0.004^{ns}	**0.114**	**0.050**
SAL	0.049	0.096	0.033	0.034	0.013	0.024	–	**0.090**	**0.037**
SAV	0.262	0.281	0.221	0.230	0.241	0.265	0.228	–	**0.244**
VIA	0.026	0.093	0.044	0.034	0.033	0.015	0.010	0.097	–

For pairwise F_{st}, significant values at level 0.05 after false discovery rate (FDR) correction are in bold. Nonsignificant pairwise F_{st} are denoted by ns.

Demographic monitoring data

Temporal trends in abundance

Five out of the twelve populations (i.e., HER, VEN, AUR, CEL, VER) showed a significant negative trend ($P < 0.05$; $S < 0$), one population (COU) showed a significant positive trend ($P < 0.01$; $S = 23$) whereas the remaining six populations (VOL, LOU, ARI, GAR, ARR, BAR) showed no significant trend in abundance (Fig. 2D, Table S7). Overall, the mixed model meta-analysis revealed a significant ($P < 0.001$) negative trend indicating a global decrease in the abundance of *P. toxostoma* populations in the Garonne river basin.

Modeling species distribution

The stream length occupied by the species was estimated at 24.0% (±2.5 SE) of the total river basin stream length in 1980–1992 (Fig. 4A) and 20.9% (±2.6 SE) in 2003–2009 (Fig. 4B). This represented an overall decrease of 3.2% ($P < 0.01$) with respect to the whole river basin, and of 13.1% of *P. toxostoma*'s 1980–1992 distribution (Figs. 4C, 5). The habitat suitability for the species decreased in the middle part of the river basin between 1980 and 1992 and 2003 and 2009 periods (Fig. 4).

Discussion

What did we learn from genetic data?

Using a full-likelihood Bayesian approach (as implemented in MSVAR, Storz and Beaumont 2002), we showed that all *P. toxostoma* populations have experienced significant decreases in effective population size (N_e), with reductions of more than 99% of their prebottleneck long-term N_e. We further showed that: (1) in all populations, bottlenecks started 192–727 years ago, and are hence relatively recent (i.e., within the last millennium); and (2) all populations show extremely low current N_e. Attempting to identify the causes of such bottlenecks would be highly speculative without further data and analyses. If natural causes (climatic or hydrological shifts) cannot be ruled out, anthropogenic causes are also likely (i.e., the first mill weirs date back from the 12th century, Blanchet et al. 2010). It is noteworthy that the bottlenecks highlighted here are "species-specific" rather than "basin-specific", given that for four other sympatric cyprinid fish species (i.e., *Squalius cephalus*, *Leuciscus burdigalensis*, *Gobio gobio*, and *Phoxinus phoxinus*), Paz-Vinas et al. (2013) demonstrated that bottlenecks were older (approximately 2000–6000 years ago) and of different magnitudes than those detected for *P. toxostoma*. We can hence reasonably conclude that the bottlenecks

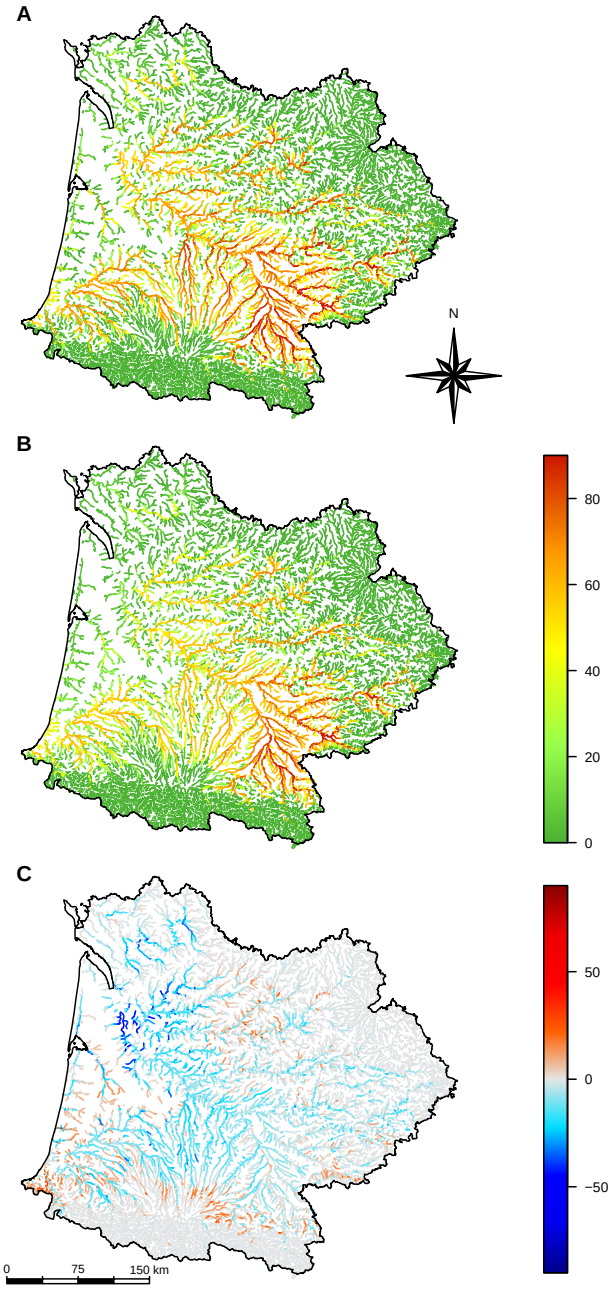

Figure 4. Spatial distributions of *Parachondrostoma toxostoma* modeled for (A) 1980–1992 and (B) 2003–2009 periods, and differences between these two distributions (C). The agreement between presence–absence predictions (i.e., habitat suitability) was measured by summing the 90 predictions (threshold × iteration) for each reach of the Garonne river basin for each period, with color scale varying from green (no predicted presence) to red (90 predicted presences). The differences in the spatial distribution of the species were expressed with a color scale varying from blue (90 presences predicted only for 1980–1992) to red (90 presences predicted only for 2003–2009).

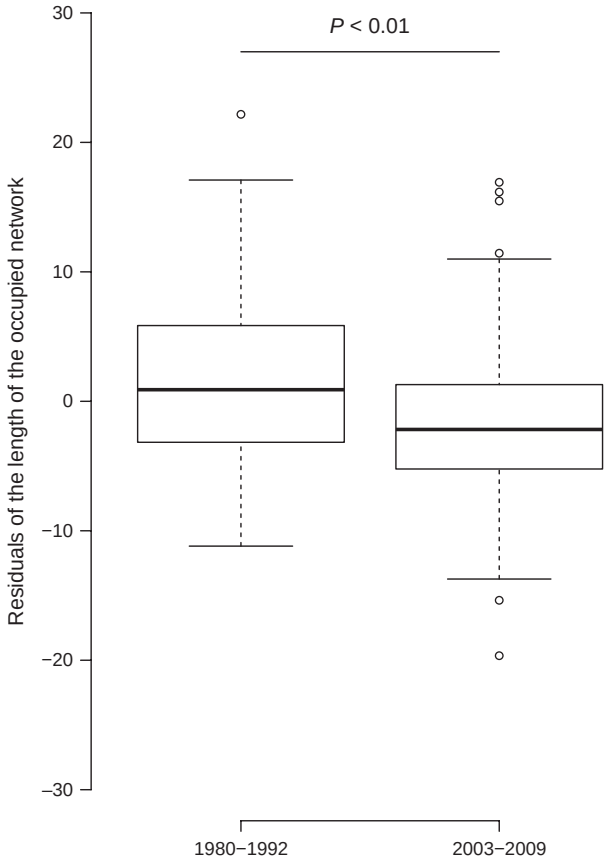

Figure 5. Boxplots of the length of the occupied network by *Parachondrostoma toxostoma* in the Garonne river basin modeled for the periods 1980–1992 and 2003–2009. The length of the occupied network was the residuals of a linear regression linking the length of occupied network in both periods with the threshold setting method effect.

inferred here occurred during the last millennium and affected specifically *P. toxostoma* populations.

Descriptive analyses revealed low levels of genetic diversity for all populations. Indeed, all diversity indices were up to approximately 3.3 times lower than those calculated for populations of other cyprinid fish species co-occurring with *P. toxostoma* in the Garonne river basin (Blanchet et al. 2010). They were all also remarkably lower than those calculated for *P. toxostoma* populations from the Rhône river basin (see Dubut et al. 2010). As an example, some microsatellite markers were monomorphic in certain populations, whereas these same markers were highly polymorphic in populations from the Rhône river basin (Dubut et al. 2010). Similarly, Costedoat et al. (2005) demonstrated that the diversity measured at mitochondrial genes for *P. toxostoma* was also significantly lower in the Garonne river basin than in the Rhône river basin, a result that may be a consequence of the recent colonization of the Garonne river basin from the Rhône river basin (i.e., approximately 57,000 years ago, Costedoat et al. 2005). Although the relatively poor genetic diversity found in the Garonne river basin probably has an important phylogeographical basis (Costedoat et al. 2005), it may reflect the more recent (200–700 years ago) and severe bottlenecks that we detected.

Finally, our PGS also highlighted that *P. toxostoma* populations in the Garonne river basin were relatively homogeneous from a genetic standpoint. Indeed, most populations formed a single cluster with relatively low genetic differentiation within this cluster. This result suggests that these populations constitute a single panmictic unit at the basin level. There were, however, two noticeable exceptions to this general pattern; HER and SAV were genetically differentiated from all other populations. These two populations also demonstrated the lowest contemporary N_e values, the lowest genetic diversities (i.e., H_e, H_o, and AR), and the strongest bottlenecks. Altogether, this indicates that these populations may be discriminated from others (1) because gene flow between these populations and others are weak; and/or (2) because genetic drift and inbreeding were particularly high in these populations, causing divergence from other populations in the Garonne river basin.

To summarize, PGS provided a precise description of the current genetic state of *P. toxostoma* populations from the Garonne river basin. Overall, these results clearly indicate that long-term management should integrate the fact that the evolutionary potential of the species in this geographic area may be weak.

What did we learn from demographic data?

Using time series abundance data at twelve locations, we found an overall demographic decrease of *P. toxostoma* populations that occurred in the last three decades. Evidence of a demographic decrease was further supported by comparing the *P. toxostoma* occurrence at the basin scale between two periods (1980–1992 and 2003–2009). This analysis revealed a significant decrease in the distribution range of *P. toxostoma,* representing 13.1% of the 1980–1992's distribution. These results confirm that over the range of the species, there is a decreasing trend in abundance (Crivelli 2006; Poulet et al. 2011). This decrease contrasts with the increase in occurrence, abundance, and density of several sympatric species at the French scale such as *Barbus barbus* or *Gobio gobio* (Daufresne and Boët 2007; Poulet et al. 2011). Despite this range-wide trend, we showed that not all local populations were subjected to a significant demographic decrease, as some of them display no particular trends, and one population even showed a significant demographic increase. There was no clear spatial pattern regarding these site-specific trends

(see Fig. 2D). However, such site-specific analysis provides a basis for further analyses exploring the regional and/or local causes of demographic trends in the Garonne river basin. Indeed, a comparison implying healthy versus non-healthy (from a demographic point of view) populations may highlight the leading environmental factors affecting the demography of this species.

To summarize, DMPs provided insights into the demographic dynamics and changes in the spatial distribution of *P. toxostoma* in the Garonne river basin, which indicates that this species is ecologically weakened in this area, and thus restoration plans should be engaged to ensure the persistence of populations.

Synthesis, implications, and conclusions: The conservation gain of combining genetic and demographic data

Synthesis

The history of *P. toxostoma* in the Garonne river basin is relatively recent and began approximately 57,000 years ago, when it colonized the Garonne from the Rhône river basin (Costedoat et al. 2005). Our results suggest that populations exhibited relatively large long-term N_e (approximately 5000–8000 individuals per population) until severe and recent (approximately 800 to 200 years ago) demographic collapses entailed N_e of less than a few hundred (sometimes less than a dozen) individuals. This means that very small numbers of effective breeders are currently sustaining populations in the Garonne river basin. This history led to genetically impoverished *P. toxostoma* populations in the Garonne river basin. Although most populations are genetically homogeneous, these demographic collapses also led to local differentiation in the Garonne river basin. In a more recent timeframe (i.e., the last two decades), we showed that this species experienced a global decrease in census size (N_c) over the entire Garonne river basin, although that some populations remained demographically stable or even increased locally. This recent decrease in N_c was accompanied by a significant reduction of its spatial distribution over the Garonne river basin. Because both N_e and N_c are reduced in these populations, *P. toxostoma* in the Garonne river basin is confronted with a combination of ecological and evolutionary extinction risks, which reinforces its status of vulnerable species in the IUCN red list, and supports the implementation of conservation plans.

Implications

Our results illustrate how combining genetic and demographic approaches is useful to target and to prioritize conservation and management plans for endangered populations. A main weakness of our study resides in the few number of sampling points common to both temporal trend and genetic analyses. However, this fact may well be the standard for most studies focusing on rare and threatened species. We therefore provide recommendations considering two cases. In the first case, both demographic and genetic are available at the sampling site level. In this case, combining genetic and demographic approaches allows identifying priority populations as those (1) having the lowest genetic diversity and N_e; and (2) being subjected to a significant and recent decrease in N_c. For instance, we identified the Hers River as a priority population as both genetic and demographic indices are weak. In this case, we propose conservation strategies involving a program of stocking from broodstock stemming from healthy populations, combined with the restoration of habitat and connectivity with other rivers. Healthy populations are those with stable N_c and higher N_e (such as the Petite Barguelonne and Louge rivers). In the second case, only one of the two metrics is available at the sampling site level. In this case, prioritizing conservation plans is less straightforward. For instance, some populations (e.g., the Vendinelle River) were subjected to a sharp decrease in N_c in recent years, however, no data are yet available regarding genetic diversity and N_e dynamics. In this case, managers can conduct a genetic monitoring of these populations to help clarify the populations' status. On the other hand, some populations (e.g., the SAV) have low N_e and low genetic diversity, but lack temporal data regarding N_c. In this case, it is impossible to get the temporal trend of the populations. Thus, invoking the precautionary principle, we propose considering these populations as conservation priority.

Conclusion

To conclude, we showed how combining analyses based on point genetic studies (PGSs) and DMPs (i.e., a "demo-genetic approach") reveal complementary information underlying different processes operating at different timescales. Demo-genetic approaches allow (1) identification of "at risk" populations; (2) prioritizing conservation and management actions; and (3) proposing plans that account for the evolutionary history and potential of populations. We hence argue that demo-genetic approaches should be the norm in conservation practices. Indeed, these surveys would allow not only prioritizing and initiation of conservation plans (this study), but would also allow the evaluation of dispersal and connectivity through the use of genetic-based inference methods (Broquet and Petit 2009), as well as evaluation of the effectiveness of conservation plans (Schwartz et al. 2007;

Osborne et al. 2012). We hope that this study will motivate conservation ecologists to invest in genetic monitoring, and conversely, conservation geneticists to initiate long-term demographic surveys.

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Current spatial distribution and recent distribution changes.

Figure S1. Map of the Garonne river basin (South–Western France) representing (1) sites where *P. toxostoma* was unsuccessfully sampled for genetic analyses (white circles); and (2) sites where *P. toxostoma* was successfully sampled for genetic analyses (green circles).

Figure S2. Maps representing sites where the occurrence of *P. toxostoma* was recorded (A) from 1 to 19 times during the 1980–1992 period and (B) from 1 to 14 times during the 2003–2009 period.

Table S1. Information on microsatellite loci and multiplexed PCR used in this study.

Table S2. Observed number of alleles (na), expected (H_e) and observed (H_o) heterozygosities and departures from Hardy–Weinberg equilibrium (F*is*) for all loci and populations of *P. toxostoma*. No significant departures from Hardy–Weinberg equilibrium were found after applying Benjamini and Hochberg (1995) false discovery rate corrections.

Table S3. Mean observed (H_o) and expected (H_e) heterozygosities, mean number of alleles over loci (NA), allelic richness (AR_8 for a minimum sample size of 8 individuals; AR_{18} for a minimum sample size of 18 individuals) and departures from Hardy–Weinberg equilibrium (F_{is}) for each *P. toxostoma* population.

Table S4. *P*-values for the linkage disequilibrium test for each pair of loci and population.

Table S5. Results for the Wilcoxon's sign rank test computed by BOTTLENECK for each river and for the TPM and SMM microsatellite mutation models.

Table S6. Median, 5 and 95% quartile values calculated for N_0 (the current effective population size), N_1 (the past effective population size), T_a (the time of the beginning of the demographic change, in years backwards from the present) and Log_{10} (N_0/N_1; the magnitude of the demographic change) for each river, through the posterior distributions obtained with MSVAR 1.3.

Table S7. Values for the Mann–Kendall's *S* statistic, variance in S (Var[S]), mean densities and *P*-values obtained for the twelve time series with the modified Mann–Kendall trend test.

Global change and freshwater fish: determinants and consequences on population dynamics

ABSTRACT

Climate change has been a subject of great interest across the past few years but its influence on population dynamics has seldom been considered. In this thesis, we demonstrate that climatic factors and in particular water temperatures have an influence on population dynamics of several freshwater fish species found in French rivers. Although common mechanisms acting at large spatial scales have been identified for the different species, considerable variations among populations have been revealed due to spatial heterogeneity of environmental conditions. Intrinsic characteristics of species appeared as important determinants of interspecific differences in population dynamics, contrary to their evolutionary history. Our results could be used to set up management conservation planning to limit the consequences of climate warming on freshwater fish species.

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TITRE : Changements globaux et poissons d'eau douce : déterminants et implications de variations démographiques

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RESUME

Les changements climatiques on fait l'objet d'une attention grandissante, mais leurs influences sur les dynamiques de populations restent mal appréhendées. Nos résultats montrent que la température influence les dynamiques de populations de plusieurs espèces de poissons d'eau douce en France. Bien que des mécanismes communs aient été mis en évidence, les dynamiques de populations varient fortement en fonction des conditions environnementales locales. Les caractéristiques intrinsèques des espèces, au contraire de leur histoire évolutive, apparaissent comme des déterminants importants des dynamiques observées. Ces résultats pourraient permettre de mettre en place des mesures de gestion adaptées pour ces espèces, visant à réduire l'impact des changements environnementaux à venir.

MOTS-CLES : Dynamiques de populations, poissons d'eau douce, changements climatiques, température, densité-dépendance, migration.

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