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Using stable isotope analyses to determine the ecological effects of non-native fishes

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Abstract Freshwater fish ecology has greatly benefited from the use of innovative tools such as stable isotope analysis to determine the ecological effects of non-native fishes. Stable isotope analyses are based on the predictable relationship between the isotope composition of a consumer and its prey, and have become increasingly popular amongst aquatic ecologists. In parallel, they have been implemented as a sensitive, cost-effective and temporally integrative tool to analyse the trophic interactions between native and non-native species, and to detect some subtle ecological effects of human activities, such as the introduction of non-native freshwater fish species. This review aimed to understand how stable isotope analyses have been used and how they have provided new insights into the ecological impacts of non-native freshwater fishes. Specifically, the published literature (45 articles) was reviewed to establish the current state-of-the-art. The use of stable isotope analyses in the field is still an emerging approach. The majority of studies were conducted on lentic ecosystems in North America targeting three main families of non-native fish species. Measurements were most commonly made with carbon and nitrogen stable isotopes using muscle samples. The most recent theoretical and methodological advances were illustrated by selecting some case studies conducted with different non-native species and biotic interactions. Finally, several recommendations for an optimised use of stable isotope analyses for freshwater ecological studies related to trophic interactions of non-native freshwater fish species were established.

KEYWORDS: biological invasions, food web, trophic interactions, trophic subsidies.

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Introduction

Biological invasions occur worldwide and induce important ecological and economic consequences (Mack *et al.* 2000; Lockwood *et al.* 2007; Davies 2009; Gozlan *et al.* 2010). Fish are amongst the most frequently introduced species in freshwater ecosystems because of their strong association with human activities (Copp *et al.* 2005; García-Berthou *et al.* 2005). Although some introduced fish species failed to establish self-sustained populations and some established populations have no detected effects on the recipient ecosystems (Gozlan 2008), there is a large body of literature demonstrating that non-native freshwater fish can have strong ecological impacts at variable levels of biological organisation, ranging from genes to ecosystems (review in Cucherousset & Olden 2011). The effects of non-native freshwater fish include biodiversity loss and biotic homogenisation (e.g. Rahel 2000; Olden 2006), the introduction of pathogens (e.g. Gozlan *et al.* 2005) and hybridisation (e.g. Allendorf *et al.* 2001; Cucherousset *et al.* 2008). However, there are still many cases where potential ecological effects have not been investigated.

Although unintentional introductions can occur, freshwater fish are principally introduced in new ecosystems for four main reasons, i.e. aquaculture, angling/sport, fisheries and ornamental (Gozlan 2008). Introduced fish species are generally larger than native species as they represent a non-random subset of freshwater fish (Blanchet *et al.* 2010) and the most common example is the introduction of large-bodied predatory species (e.g. Eby *et al.* 2006; Syväranta *et al.* 2010). Although body size might not always be a biological trait that facilitates invasion success (Miller *et al.* 2002), body size plays an important role in determining trophic position (e.g. Woodward *et al.* 2005; Hildrew *et al.* 2007). Because of their functional role in ecosystems, introduced large-bodied species can induce new biological interactions with native species of prey, competitors and/or predators. These new interactions arise from direct (e.g. competition and predation) and indirect (e.g. trophic cascade) effects that can destabilise native communities and food webs (e.g. Baxter *et al.* 2004; Lockwood *et al.* 2007). As the mechanisms by which food webs can be destabilised by non-native fish species are extremely complex (Gozlan *et al.* 2010; Cucherousset & Olden 2011), new and integrative tools are needed to determine and quantify the potential ecological effects of non-native species on recipient food webs (e.g. Ehrenfeld 2010). In addition, differentiating between the effects of introduced fish and other environmental changes induced by human activities on aquatic ecosystems remains challenging (Cucherousset & Olden 2011).

Stable isotope analysis (SIA) has become popular amongst ecologists (reviews in Grey 2006; Fry 2006). Indeed, this method is based on the predictable relationship between the isotopic composition of consumers and their prey, allowing the investigation of diet composition and energy flow in food webs (Fry 2006). Compared with more conventional approaches used in freshwater ecology, such as the analyses of stomach contents that offer only a snapshot of diet composition, SIA is cost-effective and temporally integrative allowing the analyses of long-term diet patterns (e.g. Grey 2006; Rybczynski *et al.* 2008). The most common stable isotopes used by freshwater ecologists are nitrogen (δ^{15}N) and carbon (δ^{13}C) that allow the quantification of trophic position and energy sources of an organism, respectively (Peterson & Fry 1987; Fry 2006). Additionally, other stable isotopes such as sulphur (δ^{34}S) have been increasingly used (Grey 2006). In parallel, mixing models have been developed to determine the contributions of different prey items to the diet of the consumers (Phillips & Gregg 2003). Therefore, SIA appears as a sensitive and versatile tool to investigate competition and predation processes in food webs (Peterson & Fry 1987; Fry 2006) and is a promising approach to quantify the ecological effects of non-native freshwater fish.

This article aimed to understand how SIA has been used and how it has provided new insights into the ecological effects of non-native freshwater fishes. Specifically, (1) the literature published since the year 1999 was reviewed to establish the current state-of-the-art in the field; (2) the most recent theoretical and methodological advances were illustrated using case studies; and (3) these findings were discussed in the light of the new challenges facing fish ecologists to establish several recommendations for an optimised used of this tool.

State-of-the-art review

The literature published citing Vander Zanden *et al.* (1999), the first of its kind to quantify the ecological impacts of non-native freshwater fish on food web structure using SIA, was reviewed. To do so, the ISI Web of Knowledge was used to collect articles. Second, additional articles were collected by analysing the references in the articles from the initial search and by conducting additional searches. Based on these searches, articles that used SIA and that stated and/or discussed the status (i.e. non-native) of the fish species analysed for stable isotopes were selected. For each selected article, the publication year, geographic location, type of aquatic ecosystem, isotope(s) analysed, tissue used, and number, family and trophic position of the non-native fish species were collected. Trophic position was obtained from FishBase (http://www.fishbase.org). The use of mixing models and stomach contents analyses and the type of study (observationally or experimentally) were also determined.

Forty-five articles were collected (Supplementary Data 1). Between 1999 and 2008, the number of articles remained relatively low, i.e. ranging from 0 to 7 articles per year. The number of articles published thereafter has substantially increased, with 12 articles each year in 2009 and 2010 (Fig. 1a), showing the recent increased use of SIA in this field. As expected in any review on biological invasions (e.g. Pyšek *et al.* 2008), geographic and taxonomic biases in publication patterns were observed. Indeed, 62.2% of the studies were performed in North America and 26.7% in Europe. Only 4.4, 4.4 and 2.2% of the studies were conducted in Asia, Africa and South America, respectively. The greatest numbers of studies were performed on Cyprinidae (20.6%), Salmonidae (20.6%) and Centrarchidae (17.6%) as non-native species in the recipient ecosystem (Fig. 1b). These proportions differ from Cucherousset and Olden (2011) where the most studied families were Salmonidae (35.8%) and Centrarchidae (17.9%). This discrepancy might reflect the commonness of Cyprinidae in many fish assemblages.

The majority of studies (57.8%) were conducted in lentic ecosystems (lakes or ponds), whilst 42.2% were conducted in lotic ecosystems (rivers or streams). Virtually all these studies (95.6%) were conducted observationally (Table 1) and most (91.1%) used carbon and nitrogen stable isotopes in combination. Only one study used three stable isotopes, i.e. carbon, nitrogen and sulphur. In the majority of cases, stable

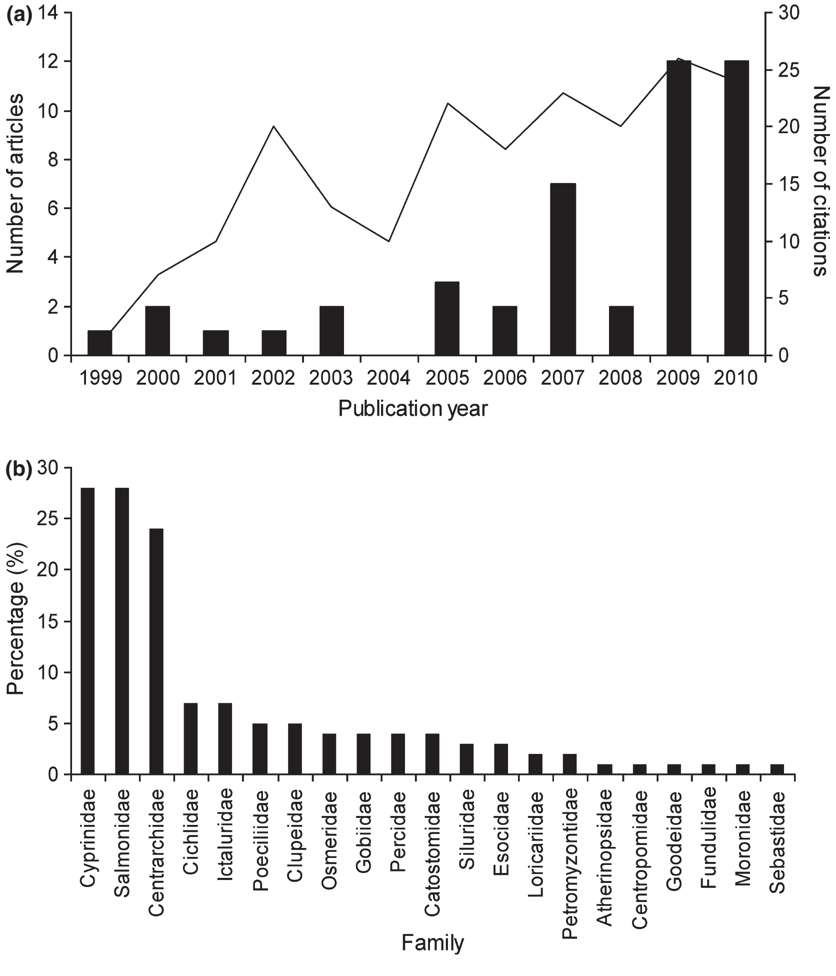

Figure 1. (a) Number of articles using stable isotope analyses in the context of non-native freshwater fish published per year since the year 1999 (bars) and number of citations per year of Vander Zanden *et al.* (1999) (line). (b) Families of the studied non-native freshwater fish.

Table 1. Distribution (number of articles and percentage) of 45 selected articles published since the year 1999 in terms of approach (experimental and observational), isotope analysis (C, carbon; N, nitrogen and S, sulphur), tissue (muscle, fin and scale), stomach contents and mixing models

Parameter	Variable	Number of articles	Percentage
Approach	Experimental	2	4.4
	Observational	43	95.6
Isotope	C	1	2.2
	N	2	4.4
	C & N	41	91.1
	C, N & S	1	2.2
Tissue	Muscle	36	80.0
	Fin	6	13.3
	Scale	2	4.4
	n.a.	1	2.2
Stomach contents	Yes	19	42.2
	No	26	57.8
Mixing models	Yes	16	35.6
	No	29	64.4

isotopes were measured in muscle samples (80.0%), whilst only 17.8% of the studies used non-lethal approaches measuring stable isotopes in fin (13.3%) or scale (4.4%) samples. Over 42% of studies used stomach contents analyses in combination with SIA and mixing models were performed in 35.6% of studies. Most studies focused their analyses on a low number of non-native species (one non-native species: 46.7%; two non-native species: 20.0%). On average, the trophic position of the non-native fish species studied was 3.3 (± 0.7 SD), ranging from 2.0 to 4.5. These trophic position values are likely to reflect the relative importance of Cyprinidae that are usually omnivorous.

Insights from selected case studies

Introduced bass in North American lakes

Vander Zanden *et al.* (1999) investigated the ecological effects of two non-native predatory species, smallmouth bass, *Micropterus dolomieu* (Lacepède), and rock bass, *Ambloplites rupestris* (Rafinesque). The study was conducted in Canadian lakes where lake trout, *Salvelinus namaycush* (Walbaum), is the native predatory species. They compared the abundance and diversity of prey fish and the trophic position of native *S. namaycush* in lakes with and without non-native species.

The authors found that the presence of the non-native species significantly decreased the diversity and abundance of littoral prey fish. Lakes without and with the non-native species had, on average, 5.3 and 0.6 species of prey fish, respectively; and 5.9 and 0.9 fish per trap per day, respectively. Stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) indicated a lower trophic position and lower $\delta^{13}C$ values of native *S. namaycush* in lakes with the non-native species compared with lakes without non-natives, whilst no changes in prey fish values were measured. Specifically, trophic position averaged 3.28 and 3.90 and $\delta^{13}C$ averaged −29.20 and −27.48‰ in invaded and un-invaded lakes, respectively. Using a two-source mixing model, a modification of *S. namaycush* diet composition was observed whereby the species had, on average, a higher proportion of zooplankton (84 vs 36%) and a lower proportion of littoral prey fish (16 vs 64%) in their diet in invaded lakes compared with lakes with no non-native fish species. A lower contribution of littoral prey and a higher contribution of pelagic prey in invaded lakes were also observed.

Competitive interactions between salmonids species

Salmonids are amongst the most widely introduced species because of their high values for angling and aquaculture, and ecological impacts of non-native salmonids have been reported across the globe (e.g. Townsend 2003; review in Cucherousset & Olden 2011). An insightful example is the reciprocal introductions of European brown trout, *Salmo trutta* L., into North America and North American brook trout, *Salvelinus fontinalis* (Walbaum), into Europe. When introduced in North America, non-native *S. trutta* negatively affected native *S. fontinalis*. Similarly, non-native *S. fontinalis* can affect native *S. trutta* in European rivers. In both cases, impacts included redd superimposition (e.g. Essington *et al.* 1998; Cucherousset *et al.* 2008), hybridisation (e.g. Sorensen *et al.* 1995; Cucherousset *et al.* 2008) or changes in habitat niche (e.g. Fausch & White 1981; Korsu *et al.* 2007; but see Blanchet *et al.* 2007). However, little was known about potential trophic interactions between the two species in Europe.

Using SIA, Cucherousset *et al.* (2007) studied the effects of the presence of non-native *S. fontinalis* on the trophic niche of native *S. trutta* in a Pyrenean stream of south-west France. The study area consisted of three stretches, i.e. one with the non-native species only, one with the native species only and one where both species coexist. Stable isotope analysis revealed that the trophic niche of the non-native *S. fontinalis* was not affected by the presence of native *S. trutta* as no significant differences in $\delta^{15}N$ and $\delta^{13}C$ values were observed between stretches. Conversely, significant changes in native *S. trutta* stable isotope values were measured between stretches. Specifically, $\delta^{13}C$ decreased by 1.6‰ and $\delta^{15}N$ increased by 0.6‰ when *S. trutta* coexisted with non-native *S. fontinalis*; the trophic niche of *S. trutta* becoming similar to that of *S. fontinalis* when the two species coexisted. Additionally, mixing models revealed an increased consumption of terrestrial invertebrates by *S. trutta* when coexisting with *S. fontinalis;* terrestrial invertebrates being the main prey items consumed by the non-native *S. fontinalis* in both stretches. This niche convergence was somewhat surprising as niche divergence or partitioning caused by competition was expected (e.g. Nakano *et al.* 1999). The authors hypothesised that it might be caused by behavioural interactions between the two species (Cucherousset *et al.* 2007).

Consumption of anadromous species by non-native catfish

Eggs and carcasses from anadromous fish are known to subsidise freshwater ecosystems with marine-derived nutrients (Schindler *et al.* 2003; MacAvoy *et al.* 2009). Many organisms use these nutrients directly and indirectly (Bilby *et al.* 1996), and SIA has been used to determine the importance of marine-derived nutrients for freshwater organisms because marine-derived nutrients have very distinct stable isotope values compared with freshwater-derived nutrients (e.g. Fry 2006). For instance, Gregory-Eaves *et al.* (2007) demonstrated that $\delta^{15}N$ and $\delta^{13}C$ values of periphyton, zooplankton and rainbow trout, *Oncorhynchus mykiss* (Walbaum), were positively correlated with the density of sockeye salmon, *Oncorhynchus nerka* (Walbaum), spawners in lakes of western North America. Stable isotope analysis has also allowed tracing of the fluxes of marine-derived nutrients transported from the ocean by anadromous fish to terrestrial organisms such as invertebrates (e.g. Hocking & Reimchen 2006), birds (e.g. Christie *et al.* 2008), wolves (Szepanski *et al.* 1999) or bears (e.g. Hilderbrand *et al.* 1999).

The presence of non-native fish species can modify the energy, nutrient and organism fluxes between ecosystems (e.g. Baxter *et al.* 2004) and two studies have used SIA to quantify predation of non-native catfish on anadromous fish. MacAvoy *et al.* (2000) quantified stable isotope values ($\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$) in native anadromous *Alosa*, native resident freshwater fish and non-native resident catfish, *Ictalurus furcatus* (Valenciennes), in the Rappahannock River (Virginia, USA). Irrespective of the stable isotope used, the stable isotope values for non-native *I. furcatus* differed significantly from those of resident freshwater fish and anadromous *Alosa*. Using mixing models, the contributions of anadromous *Alosa* to the diet of non-native *I. furcatus* were, on average, 42% (± 24 SD) and 43% (± 16 SD) using $\delta^{13}C$ and $\delta^{34}S$, respectively. Those values were highly variable amongst individuals, ranging from 0–86% to 10–69% using $\delta^{13}C$ and $\delta^{34}S$, respectively, but no significant correlations between catfish size and the contribution of anadromous prey to the diet were observed (MacAvoy *et al.* 2000).

Syväranta *et al.* (2009) examined the contribution of anadromous fish species such as allis shad, *Alosa alosa* (L.), to the diet of the non-native European catfish, *Silurus glanis* L., in the Garonne River (south-western France) using $\delta^{15}N$ and $\delta^{13}C$. *S. glanis* was introduced from eastern European waters to western Europe in the 1950s, and the species is considered as having an opportunistic diet, although few studies on its trophic ecology outside of its native range are available (review in Copp *et al.* 2009; but see Kopp *et al.* 2009; Syväranta *et al.* 2010 for studies using SIA). Syväranta *et al.* (2009) compared the stable isotope values of European catfish, *Silurus glanis* L., and their potential prey fish (*A. alosa* and cyprinids) below and above a dam that prevented the migration of anadromous fish. $\delta^{13}C$ values of freshwater prey fish differed only slightly below and above the dam (mean values = −26.3 and −24.6‰, respectively) and anadromous shad were highly ^{13}C-enriched compared with freshwater prey fish (mean value = −19.3‰). *S. glanis* sampled below the dam were ^{13}C-enriched compared with individuals sampled above the dam (mean values = −19.8‰ and −25.2‰, respectively). Using a two-source mixing model, the averaged contribution of anadromous fish to the diet of non-native *S. glanis* ranged between 53 and 65% below the dam. As observed by MacAvoy *et al.* (2000), the contribution of anadromous fish to the diet of non-native *S. glanis* was highly variable amongst individuals (ranging from 30 to 90%) and not significantly correlated with individual size (Syväranta *et al.* 2009).

Consequences of hybridisation between native common carp and non-native domesticated carp

Common carp, *Cyprinus carpio* L., is a worldwide invader (Vilizzi 2012) that has established self-sustained populations in many countries, except in some temperate areas (e.g. Britton *et al.* 2010). The species can potentially have strong ecological impacts on ecosystem functioning (e.g. Koehn 2004; Cucherousset & Olden 2011). A recent meta-analysis demonstrated that this engineer species affects nutrient dynamics and many organisms such as macrophytes, plankton and macro-invertebrates (Matsuzaki *et al.* 2009). Using SIA in Lake Navaisha (Kenya), Britton *et al.* (2007) found *C. carpio* can also display relatively high δ^{15}N values.

To understand further the ecological effects of *C. carpio*, Matsuzaki *et al.* (2010) performed a study that was based on the combination of SIA and molecular tools. The aim of the study was to quantify the functional consequences of hybridisation between native *C. carpio* and non-native domesticated *C. carpio* in Lake Kasumigaura (Japan). The authors used nuclear DNA markers (i.e. single nucleotide polymorphism) to establish the degree of hybridisation of each individual and SIA (δ^{15}N and δ^{13}C) with mixing models to determine functional differences amongst individuals with a variable degree of hybridisation. A significant correlation was measured between δ^{13}C and the degree of hybridisation, whilst no significant correlation was measured for δ^{15}N, indicating that *C. carpio* with higher levels of hybridisation displayed a more frequent use of littoral habitat compared with individuals with lower levels of hybridisation (Matsuzaki *et al.* 2010). When using a mixing model, these results translated into a higher proportion in the diet of limnetic primary consumers (as opposed to shrimps, periphyton and detritus) for individuals with lower levels of hybridisation compared with individuals with higher levels of hybridisation (Matsuzaki *et al.* 2010).

Conclusions

Stable isotope analysis appears as a powerful tool to determine the ecological effects (and their underlying mechanisms) of non-native fish species on recipient ecosystems. Stable isotope analysis has allowed ecologists to detect subtle and/or counter-intuitive ecological effects caused by non-native fish species at different spatial scales because of its ability to integrate ecological processes over a relatively long period of time. As costs of analyses are decreasing and SIA is becoming more popular amongst ecologists, its use should be generalised to many systems and new directions should be taken to strengthen its applicability. Although care should be taken to account for potential constraints associated with the methodology (e.g. Post *et al.* 2007; Perga & Grey 2010), the following research directions are suggested.

- Use of non-lethal approaches to collect samples for SIA. Indeed, recent methodological advances perform SIA based on the quantification of stable isotopes in fins (e.g. Jardine *et al.* 2005; Syväranta *et al.* 2010), scales (e.g. Grey *et al.* 2009) or mucus (e.g. Church *et al.* 2009).
- Use of archived tissues to study the long-effects of non-native species and reconstruct historical food webs (e.g. Grey *et al.* 2009). Preliminary work aiming to understand the potential effect of preservation methods of stable isotope values should be conducted in parallel.
- Development of approaches that will use SIA in conjunction with other new methodologies. For instance, Cunjak *et al.* (2005) demonstrated that SIA can be used in conjunction with individual fish tagging and tracking. Also the use of molecular tools (review in Blanchet 2012) in conjunction with SIA (e.g. Charles *et al.* 2006) should help to provide new insights simultaneously into both the ecological and evolutionary effects of non-native freshwater fish.
- Stable isotope data should be analysed using new analytical and statistical approaches developed to obtain a quantitative understanding of changes in stable isotope values and food web structure (e.g. Layman *et al.* 2007; Schmidt *et al.* 2007). Mixing models that take into account the variability in trophic fractionation and in stable isotope values of the prey and consumers when estimating diet composition should be preferentially used (e.g. Parnell *et al.* 2010).
- Stable isotope ecology should help future investigations into the ecological consequences of non-native fish species, notably on their effects on the fluxes of energy, nutrients and ecosystem across ecosystems. For instance, the stable isotope of hydrogen (δD) appeared useful to investigate the energy fluxes between freshwater and terrestrial ecosystems (e.g. Doucett *et al.* 2007).
- Further studies that include SIA should be developed to test whether the functional patterns observed in the field can be tested and validated experimentally. This would allow a generalisation of the findings, helping researchers to understand the applied and theoretical aspects associated with biological invasions.

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Supporting information

The following supplementary material is available:

Supporting Data 1: List of 45 selected articles published since 1999 and used in the analyses.

References

Allendorf F.W., Leary R.F., Spruell P. & Wenburg J.K. (2001) The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution* **16,** 613–622.

Baxter C.V., Fausch K.D., Murakami M. & Chapman P.L. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* **85,** 2656–2663.

Bilby R.E., Fransen B.R. & Bisson P.A. (1996) Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 164–173.

Blanchet S. (2012) The use of molecular tools in invasion biology: an emphasis on freshwater ecosystems. *Fisheries Management and Ecology* **19,** 120–132.

Blanchet S., Loot G., Grenouillet G. & Brosse S. (2007) Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. *Ecology of Freshwater Fish* **16,** 133–143.

Blanchet S., Grenouillet G., Beauchard O., Tedesco P., Leprieur F., Durr H. *et al.* (2010) Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule. *Ecology Letters* **13,** 421–431.

Britton J.R., Boar R.R., Grey J., Foster J., Lugonzo J. & Harper D.M. (2007) From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006. *Journal of Fish Biology* **71,** 239–257.

Britton J.R., Cucherousset J., Davies G.D., Godard M.J. & Copp G.H. (2010) Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology* **55,** 1130–1141.

Charles K., Roussel J.M., Lebel J.M., Bagliniere J.L. & Ombredane D. (2006) Genetic differentiation between anadromous and freshwater resident brown trout (*Salmo trutta* L.): insights obtained from stable isotope analysis. *Ecology of Freshwater Fish* **15,** 255–263.

Christie K.S., Hocking M.D. & Reimchen T.E. (2008) Tracking salmon nutrients in riparian food webs: isotopic evidence in a ground-foraging passerine. *Canadian Journal of Zoology* **86,** 1317–1323.

Church M.R., Ebersole J.L., Rensmeyer K.M., Couture R.B., Barrows F.T. & Noakes D.L.G. (2009) Mucus: a new tissue fraction for rapid determination of fish diet switching using stable isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **66,** 1–5.

Copp G.H., Bianco P.G., Bogutskaya N.G., Erős T., Falka I., Ferreira M.T. *et al.* (2005) To be, or not to be, a non-native freshwater fish? *Journal of Applied Ichthyology* **21,** 242–262.

Copp G.H., Britton J.R., Cucherousset J., García-Berthou E., Kirk R., Peeler E. *et al.* (2009) Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* **10,** 252–282.

Cucherousset J. & Olden J.D. (2011) The ecological impacts of nonnative freshwater fishes. *Fisheries* **36,** 215–230.

Cucherousset J., Aymes J.C., Santoul F. & Céréghino R. (2007) Stable isotope evidence of trophic interactions between introduced brook trout (*Salvelinus fontinalis*) and native brown trout (*Salmo trutta*) in a mountain stream of southwest France. *Journal of Fish Biology* **71**(Suppl. D), 210–223.

Cucherousset J., Aymes J.C., Poulet N., Santoul F. & Céréghino R. (2008) Do native brown trout and non-native brook trout interact reproductively? *Naturwissenschaften* **95,** 647–654.

Cunjak R.A., Roussel J.M., Gray M.A., Dietrich J.P., Cartwright D.F., Munkittrick K.R. *et al.* (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia* **144,** 636–646.

Davies M.A. (2009) *Invasion Biology*. Oxford, UK: Oxford University Press, 244 pp.

Doucett R.R., Marks J.C., Blinn D.W., Caron M. & Hungate B.A. (2007) Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. *Ecology* **88,** 1587–1592.

Eby L.A., Roach W.J., Crowder L.B. & Stanford J.A. (2006) Effects of stocking-up freshwater food webs. *Trends in Ecology and Evolution* **21,** 576–584.

Ehrenfeld J.G. (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **41,** 59–80.

Essington T.E., Sorensen P.W. & Paron D.G. (1998) High rate of redd surimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 2310–2316.

Fausch K.D. & White R.J. (1981) Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for position in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* **38,** 1220–1227.

Fry B. (2006) *Stable Isotope Ecology*. New York, USA: Springer, 308 pp.

García-Berthou E., Alcaraz C., Pou-Rovira Q., Zamora L., Coenders G. & Feo C. (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* **65,** 453–463.

Gozlan R.E. (2008) Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries* **9,** 106–115.

Gozlan R.E., St-Hilaire S., Feist S.W., Martin P. & Kent M.L. (2005) Biodiversity – disease threat to European fish. *Nature* **435,** 1046.

Gozlan R.E., Britton J.R., Cowx I.G. & Copp G.H. (2010) Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* **76,** 751–786.

Gregory-Eaves I., Demers M.J., Kimpe L., Krümmel E.M., Macdonald R.W., Finney B.P. *et al*. (2007) Tracing salmon-derived nutrients and contaminants in freshwater food webs across a pronounced spawner density gradient. *Environmental Toxicology and Chemistry* **26,** 1100–1108.

Grey J. (2006) Stable isotopes in freshwater ecology: current awareness. *Polish Journal of Ecology* **54,** 563–584.

Grey J., Britton J.R., Graham C. & Harrod C. (2009) Stable isotope analysis of archived roach (*Rutilus rutilus*) scales for retrospective study of shallow lake responses to nutrient reduction. *Freshwater Biology* **54,** 1663–1670.

Hilderbrand G.V., Schwartz C.C., Robbins C.T., Jacoby M.E., Hanley T.A., Arthur S.M. *et al*. (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* **77,** 132–138.

Hildrew A., Raffaelli D. & Edmonds-Brown R. (2007) *Body Size: The Structure and Function of Aquatic Ecosystems*. Cambridge: Cambridge University Press, 343 pp.

Hocking M.D. & Reimchen T.E. (2006) Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Canadian Journal of Fisheries and Aquatic Sciences* **63,** 2076–2086.

Jardine T.D., Gray M.A., McWilliam S.M. & Cunjak R.A. (2005) Stable isotope variability in tissues of stream fishes. *Transactions of the American Fisheries Society* **134,** 1103–1110.

Koehn J.D. (2004) Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwater Biology* **49,** 882–894.

Kopp D., Cucherousset J., Syväranta J., Martino A., Céréghino R. & Santoul F. (2009) Trophic ecology of the pikeperch (*Sander lucioperca*) in its introduced areas: a stable isotope approach in southwestern France. *Comptes Rendus Biologies* **332,** 741–746.

Korsu K., Huusko A. & Muotka T. (2007) Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. *Proceedings of the National Academy of Sciences of the United States of America* **104,** 9725–9729.

Layman C.A., Arrington D.A., Montaña C.G. & Post D.M. (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **88,** 42–48.

Lockwood J.L., Hoopes M.F. & Marchetti M.P. (2007) *Invasion Ecology*. Oxford, UK: Blackwell Publishing, 312 pp.

MacAvoy S.E., Macko S.A., McIninch S.P. & Garman G.C. (2000) Marine nutrient contributions to freshwater apex predators. *Oecologia* **122,** 568–573.

MacAvoy S.E., Garman G.C. & Macko S.A. (2009) Anadromous fish as marine nutrient vectors. *Fishery Bulletin* **107,** 165–174.

Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M. & Bazzaz F. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* **10,** 689–710.

Matsuzaki S.S., Usio N., Takamura N. & Washitani I. (2009) Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis. *Oecologia* **158,** 673–686.

Matsuzaki S.S., Mabuchi K., Takamura N., Hicks B.J., Nishida M. & Washitani I. (2010) Stable isotope and molecular analyses indicate that hybridization with non-native domesticated common carp influence habitat use of native carp. *Oikos* **119,** 964–971.

Miller A.W., Hewitt C.L. & Ruiz G.M. (2002) Invasion success: does size really matter? *Ecology Letters* **5,** 159–162.

Nakano S., Fausch K.D. & Kitano S. (1999) Flexible niche partitioning via foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology* **68,** 1079–1092.

Olden J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* **33,** 2027–2039.

Parnell A.C., Inger R., Bearhop S. & Jackson A.L. (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One* **5,** e9672.

Perga M.E. & Grey J. (2010) Laboratory measures of isotope discrimination factors: comments on Caut *et al*. (2008, 2009). *Journal of Applied Ecology* **47,** 942–947.

Peterson B.J. & Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology, Evolution, and Systematics* **18,** 293–320.

Phillips D.L. & Gregg J.W. (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* **136,** 261–269.

Post D.M., Arrington D.A., Layman C.A., Takimoto G., Quattrochi J. & Montaña C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152,** 179–189.

Pyšek P., Richardson D.M., Pergl J., Jarošík V., Sixtová Z. & Weber E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution* **23,** 237–244.

Rahel F.J. (2000) Homogenization of fish faunas across the United States. *Science* **288,** 854–856.

Rybczynski S.M., Walters D.M., Fritz K.M. & Johnson B.R. (2008) Comparing trophic position of stream fishes using stable isotope and gut contents analyses. *Ecology of Freshwater Fish* **17,** 199–206.

Schindler D.E., Scheuerell M.D., Moore J.W., Gende S.M., Francis T.B. & Palen W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment* **1,** 31–37.

Schmidt S.N., Olden J.D., Solomon C.T. & Vander Zanden M.J. (2007) Quantitative approaches to the analysis of stable isotope food web data. *Ecology* **88,** 2793–2802.

Sorensen P.W., Cardwell J.R., Essington T.E. & Weigel D.E. (1995) Reproductive interactions between sympatric brook and brown trout in a small Minnesota stream. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 1958–1965.

Syväranta J., Cucherousset J., Kopp D., Martino A., Céréghino R. & Santoul F. (2009) Contribution of anadromous fish to the diet of European catfish in a large river system. *Naturwissenschaften* **96,** 631–635.

Syväranta J., Cucherousset J., Kopp D., Crivelli A., Céréghino R. & Santoul F. (2010) Dietary breadth and trophic position of introduced European catfish *Silurus glanis* in the River Tarn (Garonne River basin), southwest France. *Aquatic Biology* **8,** 137–144.

Szepanski M.M., Ben-David M. & Van Ballenberghe V. (1999) Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* **120,** 327–335.

Townsend C.R. (2003) Individual, population, community and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology* **17,** 38–47.

Vander Zanden M.J., Casselman J.M. & Rasmussen J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401,** 464–467.

Vilizzi L. (2012) The common carp, *Cyprinus carpio*, in the Mediterranean region: origin, distribution, economic benefits, impacts and management. *Fisheries Management and Ecology* **19,** 93–110.

Woodward G., Ebenman B., Emmerson M., Montoya J.M., Olesen J.M., Valido A. *et al*. (2005) Body-size in ecological networks. *Trends in Ecology and Evolution* **20,** 402–409.