

Review

Impacts of non-native fishes on Iberian freshwater ichthyofauna: current knowledge and gaps

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Abstract

The Iberian Peninsula contains a highly endemic freshwater ichthyofauna that is being homogenized and threatened by an increasing number of non-native fishes. Here, in this paper, I reviewed the literature on the impacts of fish introductions and translocations on the native Iberian ichthyofauna. The aims of the present review were (1) to provide an overview of the already studied and proven impacts as well as of the suggested potential impacts that remain to be tested, (2) to synthesize the current knowledge in the Iberian Peninsula and (3) to suggest future research approaches. Despite some well-documented impacts, an increasing number of non-native fish species and a wide range of diverse ecological situations uncover knowledge gaps which hamper conservation and management efforts. Since the introduction of species is often pointed out as a major cause of extinctions, I encourage research groups and funding agencies to devote more resources to the study of interactions between non-native and native fishes in order to develop evidence-based species-specific impact assessments.

Key words: native fish, introduction, translocation, invasion, extinction threat, conservation, management

Introduction

The Iberian Peninsula is considered one of the freshwater fish biodiversity hotspots within Europe (Reyjol et al. 2007; Smith and Darwall 2006). The existence of historical biogeographic barriers to the movement of freshwater aquatic organisms (i.e. oceans, the Pyrenees, catchment divides, and climatic conditions) allowed the development of a highly endemic freshwater fish fauna in the Iberian Peninsula, composed mainly of small to medium sized Cyprinid, Cobitid and Cyprinodontid species (Crivelli 1995; Elvira 1995a; Encina et al. 2006; Filipe et al. 2009; Hernando and Soriguer 1992). Even though colonization and invasion of new aquatic habitats are common in nature as a result of climatic or geotectonic events, humans provide additional artificial pathways by which non-native fishes can overcome historical biogeographic barriers (Rahel 2007). As a result, there is a long history of fish species introductions and translocations that has greatly accelerated over time as methods

of transportation improved (Copp et al. 2005a). Among the most cited artificial fish introduction pathways are recreational fisheries activities (e.g., un- or authorized stocking, live-bait release), negligent or accidental aquaculture escapes, ornamental fish releases, water transfer systems, and ship ballast water (Welcomme 1992).

Specifically, during the 20th century and more acutely in recent decades, freshwater fish introductions into the Iberian Peninsula have significantly increased (Elvira and Almodóvar 2001; Ribeiro et al. 2009a). The spread of non-native fishes has often been pointed out as a leading cause of the decline of Iberian native fishes, both in their ranges and abundances (Almaça 1995b; Elvira 1998; Elvira and Almodóvar 2001). Moreover, the Iberian freshwater ichthyofauna is facing an increasing “faunal homogenization” (Clavero and García-Berthou 2006), defined as the domination of communities by few cosmopolitan introduced species at the expense of unique native species

(e.g. Moyle and Mount 2007; Rahel 2000; 2002; 2007). Although not universally accepted (Gozlan 2008; Gozlan 2009; Gozlan et al. 2010; Gozlan and Newton 2009), the ecological impacts of non-native freshwater fish species have been highlighted as a growing worldwide environmental and socio-economic problem (Copp et al. 2005a), especially due to their unpredictable ("The Frankenstein Effect" sensu Moyle et al. 1987) and, in most cases, irreversible nature. However, the real impacts of most fish introductions and translocations on Iberian freshwater fishes are unknown (Crivelli 1995; Elvira and Almodóvar 2001; Encina et al. 2006) but are often speculated. Here I reviewed the available scientific literature regarding the interactions between non-native and native fishes in the Iberian Peninsula with the aims (1) to provide an overview of the already studied and proven impacts as well as of the suggested potential impacts that remain to be tested, (2) to synthesize the current knowledge in the Iberian Peninsula and (3) to suggest future research approaches.

Fishes

First, an updated list of freshwater fish species introduced in Iberian waters was compiled. Even though we hereafter refer to species, we also review and discuss impacts at lower taxonomic levels (sub-species, races or varieties). The establishment status (Uncertain > Unsuccessful > Naturalized > Invasive) and introduction date into the Iberian Peninsula was also collected for each species. The date of introduction is important as different establishment rates have been recorded across introduced species and populations (Clavero and García-Berthou 2006; Copp et al. 2007; García-Berthou 2007; García-Berthou et al. 2005; Vila-Gispert et al. 2005) as well as being indicative of the time that has gone by before carrying out impact assessments. The list of non-native fishes was separated into two tables, in one grouping the fish species introduced into the Iberian Peninsula (Table 1) whilst the other records the Iberian freshwater fishes translocated across river basins (Table 2).

A total of 38 non-native freshwater fish species have been detected as introduced into the freshwater habitats of the Iberian Peninsula (Table 1). Among these, 26 fish species are considered successfully naturalized into Iberian freshwaters (i.e. they reproduce successfully and

sustain populations in the wild without human intervention). Species associated with records of temporary establishment in the wild were classified either as unsuccessful ($N = 3$) if they have no longer been detected or as uncertain ($N = 9$) if the success of establishment remains unknown due to scarce data. From those naturalized, 13 non-native fishes are considered invasive in Iberia, namely spread beyond the introduction site, with and/or without the aid of humans and become frequent and/or abundant producing significant ecological and/or socioeconomic impacts. Additionally, translocations of 15 Iberian native fish species have been reported (Table 2). Other failed introductions are unrecorded due to low survival of introduced specimens, especially those of ornamental aquarium fishes and angling baitfish, which continue to occur but at an unknown rate (Moyle and Marchetti 2006; Ribeiro et al. 2009a).

The timing of introductions of non-native fishes in the Iberian Peninsula is mostly similar to other European countries (Copp et al. 2005a; Crivelli 1995). Even though the introduction of the common carp *Cyprinus carpio* Linnaeus, 1758 dates back to the 17th century, most species were introduced during the 20th century, and mainly after the 1950's (Elvira 1995b; 1998; Elvira and Almodóvar 2001; Ribeiro et al. 2009a). The geographical origins of most introduced fishes are the rest of Europe and North America, and have been introduced largely through France into Spain, and then into Portugal (Clavero and García-Berthou 2006; Elvira 1995b; García-Berthou et al. 2005; Ribeiro et al. 2009a). For instance, the spatio-temporal reconstruction of the pikeperch *Sander lucioperca* (Linnaeus 1758) introduction has shown its first occurrence was in the northeastern part of the Iberian Peninsula with subsequent west- and southward dispersal (Ribeiro et al. 2009b). Main introduction pathways of non-native fishes into Iberian waters have been angling (stocking of target species and bait/"forage" species release), aquarium ornamental fish release and aquaculture escapes (Elvira and Almodóvar 2001; Ribeiro et al. 2009a). The number of ornamental fish species occurring in the wild is locally high although the certainty of several of these records remains to be determined. As regards translocations, angling and water transfer systems are the main pathways of fish species movements between Iberian river catchments.

Table 1. Review of the available literature about the ecological impacts of non-native freshwater fishes introductions on the native Iberian ichthyofauna. Potential impacts in italics are suggested by the author (P, Predation; TC, Competition for Trophic Resources; HC, Competition for Habitat; *C, unspecified Competition; BI, Behavioral Interference; Hy, Hybridization; DT, Disease Transmission; HEA, Habitat and Ecosystem Alteration). List of introduced freshwater fish species, establishment status, and introduction dates according to Spanish and Portuguese National Red Data Books [1-3], previous published literature listing introductions at regional [e.g., 4-8], national [9-18], Iberian [19-23] and European scales [19, 24-28] as well as specialized online databases [29-33] [Scientific and common names after 28, 30, 34].

| Introduced Species | Introduction Date | Establishment Status | Demonstrated Impact | Potential Impact |
|--|-------------------|----------------------|--------------------------|--|
| Acipenseridae | | | | |
| Siberian sturgeon <i>Acipinser baerii</i> Brandt, 1869 | 1990s | Uncertain | – | P[10], *C[10], DT[10], HEA[10], <i>TC, HC, Hy</i> |
| Adriatic sturgeon <i>Acipinser naccarii</i> Bonaparte, 1836 | 1990s | Uncertain | – | <i>P, TC, HC, Hy, DT, HEA</i> |
| Cyprinidae | | | | |
| Common bream <i>Abramis brama</i> (Linnaeus, 1758) | 2000s | Naturalized | – | <i>TC, HC, Hy, DT, HEA</i> |
| White bream <i>Blicca bjoerkna</i> (Linnaeus, 1758) | 1990s | Naturalized | – | *C[10], Hy[10], DT[10], HEA[10], <i>TC, HC</i> |
| Bleak <i>Alburnus alburnus</i> (Linnaeus, 1758) | 1990s | Invasive | – | P[10], TC[10,35], HC[35,36], Hy[10,35], DT[10], <i>HEA</i> |
| Spirlin <i>Alburnoides bipunctatus</i> (Bloch, 1782) | ? | Uncertain | – | <i>TC, HC, Hy, DT</i> |
| Goldfish (including varieties) <i>Carassius auratus</i> (Linnaeus, 1758) | 17 th | Invasive | DT[20, 37] | <i>P, TC, HC, HEA</i> |
| Common carp (including varieties) <i>Cyprinus carpio</i> Linnaeus, 1758 | 17 th | Invasive | HEA[38-40] DT[20, 37] | P[38], *C[10,38], HC[41,42], DT[10], HEA [10, 43], <i>TC</i> |
| Ide <i>Leuciscus idus</i> (Linnaeus, 1758) | 2000s | Uncertain | – | <i>P, TC, HC, Hy, DT, HEA</i> |
| Asian topmouth gudgeon <i>Pseudorasbora parva</i> (Temminck & Schlegel, 1846) | 2000s | Naturalized | – | P[10], TC[10], HC[10], DT[10,44] |
| Roach <i>Rutilus rutilus</i> (Linnaeus, 1758) | 1910s | Uncertain | – | HEA[2,10], *C[10], TC[2], Hy[10], DT[10] |
| Rudd <i>Scardinius erythrophthalmus</i> (Linnaeus, 1758) | 1910s | Naturalized | HEA[38, 45] | P[38], *C[10,38], Hy[10], DT[10], HEA[10] |
| Tinfoil barb <i>Barbonymus schwanenfeldii</i> (Bleeker, 1853) | 2000s | Uncertain | – | P[46], TC[46], HC[46], DT[46], <i>HEA, Hy</i> |
| Grass carp <i>Ctenopharyngodon idella</i> (Valenciennes, 1844) | 1990s | Unsuccessful | – | <i>DT, HEA</i> |
| Cobitidae | | | | |
| Italian spined loach <i>Cobitis bilineata</i> Canestrini, 1865 | 2000s | Uncertain | – | *C[10], Hy[10], DT[10], <i>TC, HC</i> |
| Oriental weatherfish <i>Misgurnus anguillicaudatus</i> (Cantor, 1842) | 2000s | Invasive | – | P[47], TC[47,48], HC[47,48], DT[47-49], HEA[47] |
| Ictaluridae | | | | |
| Black bullhead <i>Ameiurus melas</i> (Rafinesque, 1820) | 1910s | Invasive | P[50] | P[10,51-53], *C[10,52,53], TC[50], HEA[10,54], <i>BI, DT</i> |
| Channel catfish <i>Ictalurus punctatus</i> (Rafinesque, 1818) | 1990s | Invasive | – | P[2,10], DT[10], HEA[10], <i>TC</i> |
| Siluridae | | | | |
| European catfish <i>Silurus glanis</i> Linnaeus, 1758 | 1970s | Invasive | P[55] | P[2,10,14,51,56], DT[10,56], HEA[10] |
| Esocidae | | | | |
| Pike <i>Esox lucius</i> Linnaeus, 1758 | 1940s | Naturalized | P[57-60] | P[10,14-16,38,51,61-64], HC[41,42], DT[10] |

Table 1 (continued).

| Introduced Species | Introduction Date | Establishment Status | Demonstrated Impact | Potential Impact |
|--|-------------------|----------------------|---|---|
| Salmonidae | | | | |
| Huchen <i>Hucho hucho</i> (Linnaeus, 1758) | 1960s | Naturalized | – | P[2,10], *C[10], DT[10], TC, HC, BI |
| Coho salmon <i>Oncorhynchus kisutch</i> (Walbaum, 1792) | 1980s | Naturalized | – | P[10], *C[10], Hy[10], DT[10], TC, HC, BI |
| Rainbow trout <i>Oncorhynchus mykiss</i> (Walbaum, 1792) | 19 th | Naturalized | P[60,65] | P[2,10], *C[10,66], TC[62,65], HC[62], DT[10], BI, Hy |
| Brown trout (non-Iberian origin) <i>Salmo trutta</i> Linnaeus, 1758 | 19 th | Naturalized | Hy[67-96] | *C[10,66], TC[97], Hy[10,14], DT[10], P, HC, BI |
| Atlantic salmon (non-Iberian origin) <i>Salmo salar</i> Linnaeus, 1758 | 1970s | Naturalized | Hy[95, 96, 98-108] | DT, TC, BI, HC, P |
| Brook trout <i>Salvelinus fontinalis</i> (Mitchill, 1815) | 19 th | Naturalized | – | P[10], *C[10], DT[10], Hy, TC, HC, BI |
| Fundulidae | | | | |
| Mummichog <i>Fundulus heteroclitus</i> Linnaeus, 1766 | 1970s | Invasive | – | P[10], *C 10,12-16,66,109,110], HC[111], DT[10], HEA[111-113], TC, BI |
| Poeciliidae | | | | |
| Eastern mosquitofish <i>Gambusia holbrooki</i> (Agassiz, 1859) | 1920s | Invasive | P[114], TC[114-117], HC[114,117], BI[114,116,117], HEA[39,40,118] | P[119,120], *C[2,10,12-15,66,109], TC[119,121], HEA[122,123], DT |
| Guppy <i>Poecilia reticulata</i> Peters, 1859 | 2000s | Naturalized | – | *C[10,13], DT[10], P, TC, HC, BI |
| Cyprinodontidae | | | | |
| Mediterranean toothcarp <i>Aphanius fasciatus</i> (Valenciennes, 1821) | 1990s | Uncertain | – | *C[10,12], Hy[2,10], DT[10], P, TC, HC, BI |
| Percidae | | | | |
| European perch <i>Perca fluviatilis</i> Linnaeus, 1758 | 1970s | Naturalized | – | P[2,10,14], DT[10], TC, HEA |
| Pikeperch <i>Sander lucioperca</i> (Linnaeus, 1758) | 1970s | Invasive | – | P[2,10,14,36,124], DT [10] |
| Latidae | | | | |
| Barramundi <i>Lates calcarifer</i> (Bloch, 1790) | 2000s | Uncertain | – | P, TC, HC, BI, DT, HEA |
| Centrarchidae | | | | |
| Pumpkinseed <i>Lepomis gibbosus</i> (Linnaeus, 1758) | 1910s | Invasive | P[125-129], TC[115,129,130], HEA[39,40,129] | P[2,10,131-133], *C[2,134,135], TC[125,135-137], BI[133], DT[10], HEA[10] |
| Largemouth bass <i>Micropterus salmoides</i> (Lacépède, 1802) | 1950s | Invasive | P[115,137-143] | P[2,10,14,16,130,133], *C[2], DT[10], HC[144] |
| Characidae | | | | |
| Pirapitinga <i>Piaractus brachipomus</i> (Cuvier, 1818) | 1990s | Unsuccessful | – | P, TC, HC, BI, DT, HEA |
| Cichlidae | | | | |
| Chameleon cichlid <i>Australoheros facetus</i> (Jenyns, 1842) (syn. <i>Cichlasoma facetum</i>) | 1980s | Invasive | P[145] | P[2,10], TC[2,145], DT[10], HEA[10], HC, BI |
| Oscar <i>Astronotus ocellatus</i> (Agassiz, 1831) | 1990s | Unsuccessful | – | P, TC, HC, BI, DT, HEA |

[1] Doadrio (ed) (2002); [2] Doadrio (ed) (2001); [3] Rogado et al. (2005); [4] IHOBE (2009); [5] Hermoso et al. (2008); [6] Collares-Pereira et al. (2000); [7] Zaldivar (1994); [8] Zaldivar (2006); [9] Almaça (1995a); [10] Doadrio and Aldeguer (eds) (2007); [11] Elvira (1998); [12] Elvira (2001b); [13] Elvira and Almodóvar (2001); [14] Elvira (1997); [15] Elvira (1995a); [16] Elvira (1995c); [17] Almaça (1995b); [18] Ribeiro et al. (2009a); [19] Ribeiro et al. (2008); [20] García-Berthou et al. (2007); [21] Clavero and García-Berthou (2006); [22] Hernando and Soriguier (1992); [23] Capdevila et al. (2004); [24] Elvira (2001a); [25] Cowx (1997); [26] Welcomme (1991); [27] Welcomme (1992); [28] Kottelat and Freyhof (2007); [29] Ribeiro et al. (2007a); [30] Froese and Pauly (2009); [31] DAISIE (2008); [32] invasIBER (2004); [33] ISSG (2009); [34] Leunda et al. (2009); [35] Vinyoles et al. (2007); [36] Pérez-Bote et al. (2004); [37] Blanc (1997); [38] García-Berthou and Moreno-Amich (2000b); [39] Angeler et al. (2002a); [40] Angeler et al. (2002b); [41] Grossman and de Sostoa (1994); [42] Grossman et al. (1987a); [43] Blanco and Romo (2006); [44] Gozlan et al. (2005); [45] García-Berthou and Moreno-Amich (2000c); [46] Gante et al. (2008); [47] Franch et al. (2008); [48] Clavero et al. (2008); [49] Maceda-Veiga et al. (2009); [50] Leunda et al. (2008); [51] Elvira (1990); [52] Gante and Santos (2002); [53] Garcia-de-Lomas et al. (2009); [54] Ribeiro et al. (2006); [55] Carol et al. (2009); [56] Copp et al. (2009); [57] Pena et al. (1987);

Table 1 (continued).

[58] Domínguez and Pena (2000); [59] Elvira et al. (1996); [60] de Sostoa and Lobón-Cerviá (1989); [61] Elvira and Barrachina (1996); [62] Grossman et al. (1987b); [63] Rincón et al. (1990); [64] Almodóvar and Elvira (1994); [65] Oscoz et al. (2005); [66] Elvira (1996); [67] Vilas et al. 2010; [68] Sanz et al. (2009); [69] Araguas et al. (2009); [70] Araguas et al. (2008); [71] Santos et al. (2006); [72] Almodóvar et al. (2006); [73] Izquierdo et al. (2006); [74] Sanz et al. (2006); [75] Madeira et al. (2005); [76] Aparicio et al. (2005); [77] Araguas et al. (2004); [78] Sanz et al. (2002); [79] Almodóvar et al. (2002); [80] Antunes et al. (2001); [81] Almodóvar et al. (2001); [82] Sanz et al. (2000); [83] Machordom et al. (2000); [84] Machordom et al. (1999); [85] García-Marín et al. (1999); [86] Cagigas et al. (1999); [87] Blanco et al. (1998); [88] García-Marín et al. (1998); [89] García-Marín and Pla (1996); [90] Morán et al. (1996); [91] Arias et al. (1995); [92] Martínez et al. (1993); [93] Morán et al. (1991); [94] García-Marín et al. (1991); [95] Castillo et al. (2008); [96] Beall et al. (1997); [97] Teixeira and Cortes (2006); [98] Campos et al. (2008); [99] García de Leániz et al. (1989); [100] Vázquez et al. (1993); [101] Morán et al. (1994a); [102] Verspoor and García de Leaniz (1997); [103] Blanco et al. (2005); [104] Morán et al. (2005); [105] Consuegra et al. (2002); [106] Ayllon et al. (2006); [107] Morán et al. (1998); [108] Morán et al. (1994b); [109] Elvira (1995b); [110] Bernardi et al. (1995); [111] Gutiérrez-Estrada et al. (1998); [112] Arias and Drake (1987); [113] Arias and Drake (1989); [114] Rincón et al. (2002); [115] Rodríguez Jiménez (2001); [116] Alcaraz et al. (2008); [117] Caiola and de Sostoa (2005); [118] Cardona (2006); [119] Oscoz et al. (2008b); [120] Godinho and Ferreira (1998b); [121] Mieirol et al. (2001); [122] Blanco et al. (2004); [123] Cabral and Marques (1999); [124] Miñano et al. (2002); [125] Almeida et al. (2009); [126] Domínguez et al. (2002); [127] García-Berthou and Moreno-Amich (2000a); [128] Zapata and Granado-Lorencio (1993); [129] Tomeček et al. (2007); [130] Rodríguez Jiménez (1989); [131] Oliva-Paterna et al. (2005); [132] García de Jalón et al. (1993); [133] Blanco-Garrido et al. (2009); [134] Vila-Gispert et al. (2007); [135] Copp et al. (2004); [136] Godinho et al. (1997a); [137] Godinho et al. (1997b); [138] Nicola et al. (1996); [139] García-Berthou (2002); [140] Bravo et al. (2001); [141] Godinho and Ferreira (1994); [142] Godinho and Ferreira (2006a); [143] Godinho and Ferreira (1998a); [144] Prenda and Mellado (1993); [145] Ribeiro et al. (2007b).

Table 2. Review of the available literature about the ecological impacts arising from Iberian freshwater fishes translocation across river basins in the Iberian Peninsula. Potential impacts in italics are suggested by the author (P, Predation; TC, Competition for Trophic Resources; HC, Competition for Habitat; BI, Behavioral Interference; Hy, Hybridization; DT, Disease Transmission; HEA, Habitat and Ecosystem Alteration). (See Table 1 for the information sources on species records).

| Translocated Species | Status | Demonstrated Impact | Potential Impact |
|--|-------------|---------------------|--|
| Anguillidae | | | |
| European eel <i>Anguilla anguilla</i> (Linnaeus, 1758) | Naturalized | – | <i>P, TC, HC, BI, DT</i> |
| Cyprinidae | | | |
| Bermejuela <i>Achondrostoma arcasii</i> (Steindachner, 1866) | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Pyrenean gudgeon <i>Gobio lozanoi</i> Doadrio & Madeira, 2004 | Invasive | – | <i>P, TC, HC, BI, DT</i> |
| Iberian straight-mouth nase <i>Pseudochondrostoma polylepis</i> (Steindachner, 1865) | Invasive | Hy[1] | *C[2,3], BI[3], Hy[2,4], <i>P, DT, TC, HC</i> |
| Ebro nase <i>Parachondrostoma miegii</i> (Steindachner, 1866) | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Pyrenean minnow <i>Phoxinus phoxinus</i> Kottelat, 2007 | Invasive | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Ebro barbel <i>Barbus graellsii</i> Steindachner, 1866 | Naturalized | – | <i>TC, HC, Hy, DT</i> |
| Iberian barbel <i>Barbus bocagei</i> Steindachner, 1865 | Naturalized | – | <i>TC, HC, Hy, DT</i> |
| Calandino <i>Squalius alburnoides</i> (Steindachner, 1866) complex | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Southern Iberian chub <i>Squalius pyrenaicus</i> (Günther, 1868) | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Tench <i>Tinca tinca</i> (Linnaeus, 1758) | Cryptogenic | – | <i>P, TC, HC, BI, Hy, DT, HEA</i> |
| Salmonidae | | | |
| Brown trout <i>Salmo trutta</i> Linnaeus, 1758 | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Atlantic salmon <i>Salmo salar</i> Linnaeus, 1758 | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |
| Noemachelidae | | | |
| Pyrenean stone loach <i>Barbatula quignardi</i> (Băcescu-Mester, 1967) | Naturalized | – | <i>P, TC, HC, BI, DT</i> |
| Cobitidae | | | |
| Southern Iberian spined-loach <i>Cobitis paludica</i> (de Buen, 1930) | Naturalized | – | <i>P, TC, HC, BI, Hy, DT</i> |

[1] Elvira (1987); [2] Elvira (1997); [3] Doadrio and Aldeguer (eds) (2007); [4] Elvira (1995a).

Leprieur et al. (2008) demonstrated that the greater the number of non-native fishes' introductions in a region, the higher the probability of some of them becoming invasive and, consequently causing ecological and/or socioeconomic impacts. Actually, their results revealed that western and southern Europe – including the Iberian Peninsula – is one of the six global invasion hotspots where non-native fish species represent more than a quarter of the

total number of species per river basin (Leprieur et al. 2008). In fact, zoogeographic analyses (Clavero and García-Berthou 2006; Doadrio and Aldeguer 2007; Elvira 1995c; Ribeiro et al. 2009a) displayed exotic to total species ratios in the range 40–60% at drainage level in the Iberian Peninsula. Even though Ribeiro et al. (2008) recently concluded that the Iberian Peninsula does not have as many successful non-native fishes (N = 22) as other similar sized regions of

the globe such as California (N = 49, Marchetti et al. 2004) or Italy (N = 39, Bianco and Turin 2009), the number of high-impact fish invaders is positively correlated to the total number of established fish species (Ricciardi and Kipp 2008). Additionally, Ribeiro et al. (2008) report outdated numbers of non-native species compared to the present work (N = 26), reflecting the quick and continuous increase of introductions.

Impacts

Recent studies have shown that most native Iberian fish species (Hermoso et al. 2009) and communities (Ferreira et al. 2007a) somehow respond to non-native fish abundances. Introduced and translocated fish may on an individual-to-ecosystem scale, interact with, impact and force the decline of native ichthyofaunas throughout several mechanisms (Crivelli 1995; Moyle and Cech 2004; Taylor et al. 1984) which have been studied to variable degrees in the Iberian Peninsula. Hereafter I review the available scientific literature regarding the main interactions between non-native fish and native Iberian ichthyofauna. Every relevant reference demonstrating and/or suggesting potential impacts is presented for each introduced (Table 1) and translocated (Table 2) fish species. I completed both tables by suggesting probable impacts that are theoretically possible but have not been found in the reviewed literature. The literature sources for this review basically include databases such as the ISI Web of KnowledgeSM (© Thomson Reuters), ScopusTM (© Elsevier B.V.), Google ScholarTM beta (© Google), FishBase (Froese and Pauly 2009), Invasive Species Specialist Group (ISSG 2009) as well as grey literature in personal bibliographic databases.

Even though the review focused on fish-to-fish impacts it is expected that non-native fishes may also impact upon other aquatic biota and in fact, some well-documented cases exist for Iberian populations of, for example, amphibians (Bosch et al. 2006; Braña et al. 1996; Orizaola and Braña 2006), mammals (Blanco-Garrido et al. 2008) or birds (Carol et al. 2009). Moreover, since this review focused on fish-to-fish impacts, it was beyond the scope of this contribution to discuss any conceivable associated socio-economic and/or biodiversity benefits of non-native fish introductions, and thus, whether they could be socially acceptable (but see Gozlan

2008; Gozlan 2009; Leprieur et al. 2009; Simões Vitule et al. 2009).

Predation

Probably some of the best-documented cases of native fishes replacement by non-native species are via predation (Allan and Flecker 1993). Naturalized non-native fishes can rapidly and profoundly affect the population dynamic of native fishes via density reduction (Elvira 2001a; Elvira et al. 1996; Moyle et al. 2003). Many freshwater fish species introduced in the Iberian Peninsula have piscivorous feeding habits and may prey upon one or more life stages from eggs to adults. Predation pressure could also lead to native (prey) species displacement to suboptimal habitats due to predator avoidance behavioral responses. However, the natural absence of primary piscivorous fishes in Iberian freshwater communities suggests that Iberian fishes could have difficulties in terms of recognising and avoiding introduced predators, leading them to be more prone to predation.

At the beginning of the 20th century, piscivorous fishes of angling interest – e.g., pike *Esox lucius* Linnaeus, 1758, pikeperch, largemouth bass *Micropterus salmoides* (Lacépède, 1802) – began to be introduced especially at new reservoirs that were being built at that time (Godinho et al. 1998), which became popular and preferential angling locations (Copp et al. 2005a; Marta et al. 2001). As a result of the fast human-mediated dispersal, introduced piscivorous fishes – and accompanying “forage” species – are definitely suspected of profoundly altering some valuable ichthyofaunas at unique ecosystems such as Lake Banyoles (García-Berthou and Moreno-Amich 2000b; Moreno-Amich et al. 2006), the Ruidera Lakes (Almodóvar and Elvira 1994) or Las Tablas de Daimiel (Elvira and Barrachina 1996). At present, some native fishes are actually extinct – or facing extinction – in such ecosystems while non-native predatory fishes forage on non-native fish and crayfish (e.g., Elvira et al. 1996; Nicola et al. 1996).

Probably one of the famous cases of an introduced piscivorous predator fish into Iberian waters is that of the European catfish *Silurus glanis* Linnaeus, 1758, a popular sport fish amongst anglers. A study of the European catfish diet showed that the predominant prey item, in terms of biomass, were non-native red swamp crayfish (*Procambarus clarkii* Girard, 1852) and non-native fishes (common carp, roach *Rutilus*

rutilus (Linnaeus, 1758), bleak *Alburnus alburnus* (Linnaeus, 1758), pikeperch, pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758) and largemouth bass) whilst the Ebro barbel *Barbus graellsii* Steindachner, 1866 was the only endemic species, which co-occurred with the catfish and was consumed in high proportion in man-made reservoirs and canals in Catalonia (Carol et al. 2009). Non-native fishes are regularly reported to dominate Iberian reservoirs due to the artificially stable limnological conditions (Aparicio et al. 2000; Carol et al. 2006; Clavero et al. 2004; Corbacho and Sánchez 2001; Godinho et al. 1998; Prenda et al. 2006; Ruiz 1998), and thus the greatest potential impact of non-native piscivorous predators such as the European catfish would be restricted to natural or regulated river stretches (Copp et al. 2009).

Marked differences in fish community composition (total abundance and species richness) between locations with and without non-native pike were reported along seven tributaries of the River Esla (Rincón et al. 1990). Furthermore, interspecific differences between native fishes in terms of sensitivity to pike occurrence were detected, namely bermejuela *Achondrostoma arcasii* (Steindachner, 1866) and northern Iberian chub *Squalius carolitertii* (Doadrio, 1988), which were more reactive than Iberian straight-mouth nase *Pseudochondrostoma polylepis* (Steindachner, 1865) and Iberian barbel *Barbus bocagei* Steindachner, 1865 (Rincón et al. 1990). A preliminary dietary analysis showed that nearly 45% of the diet consisted of fish in pike larger than 20 cm, showing a preference for native cyprinids (Pena et al. 1987). Later a more comprehensive dietary study in the same River Esla basin demonstrated that pike preyed upon up to 13 fish species, including natives such as brown trout *Salmo trutta* Linnaeus, 1758, Iberian barbel, Iberian straight-mouth nase, northern Iberian chub, bermejuela, northern Iberian spined-loach *Cobitis calderoni* Băcescu, 1962 and tench *Tinca tinca* (Linnaeus, 1758); translocated Pyrenean gudgeon *Gobio lozanoi* Doadrio & Madeira, 2004; non-natives (eastern mosquitofish *Gambusia holbrooki* (Agassiz, 1859), common carp, largemouth bass and rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792); and conspecifics (Domínguez and Pena 2000). Likewise, native cyprinid species consisted nearly 90% of the pike' diet in the lower River Matarraña, however, the study concluded that no prey selection was displayed by the non-native

predator and no decline in native fish abundance related to its introduction could be demonstrated (de Sostoa and Lobón-Cerviá 1989).

Several studies have pointed out that endemic cyprinids (barbels, nases, chubs) and native freshwater blenny *Salaria fluviatilis* (Asso 1801) are common prey of the non-native largemouth bass in the Iberian Peninsula (García-Berthou 2002; Nicola et al. 1996). Nevertheless, in altered assemblages where native fish are scarce, largemouth bass prey upon other non-native species such as eastern mosquitofish, pumpkinseed, roach, common carp and conspecifics (García-Berthou 2002; Godinho and Ferreira 1994; 1996; 1998a; Godinho et al. 1997b; Nicola et al. 1996; Prenda and Mellado 1993; Rodríguez Jiménez 1989; 2001). There is empirical evidence that small-bodied Iberian cyprinids are more susceptible to be preyed upon by the largemouth bass than similar-sized non-native fishes (Godinho and Ferreira 2006; Godinho et al. 1997b). In fact, the largemouth bass presence was recognized as one of the main factors controlling the fish population dynamics in the Palancar stream, where the observed absence of 0+ individuals of the dominant native fish populations (southern Iberian chub *Squalius pyrenaicus* (Günther 1868) and southern Iberian barbel *Barbus sclateri* Günther 1868) was attributed to predation (Bravo et al. 2001). Similarly, the presence of large largemouth bass has been identified as the best biotic predictor of endemic fish assemblage composition in the Guadiana (Godinho and Ferreira 1998b; Godinho et al. 1997a; b) and Raia (Godinho and Ferreira 2000) rivers. Largemouth bass display a strong dietary shift through ontogeny, feeding mainly on invertebrates when young and preying upon fish and crayfish when adult (García-Berthou 2002; Godinho and Ferreira 1994; Nicola et al. 1996). The ontogenetic shift to piscivory is often reported at 50–70 mm (63 mm at Ruidera Lakes, Nicola et al. 1996) and, in general, largemouth bass are almost exclusively piscivorous at 80–100 mm. However, piscivory was delayed up to 106 mm in Lake Banyoles, probably associated with the observed low occurrence of fish predation (García-Berthou 2002). A literature review suggested that piscivory by largemouth bass might be generally lower in populations introduced outside North America, but warned that it does not imply a negligible impact on native fishes since piscivory was probably much stronger in the initial stages of introduction (García-Berthou 2002).

Several other studies have also reported predation on native Iberian species by non-native fishes not primarily piscivorous, e.g., black bullhead *Ameiurus melas* (Rafinesque, 1820) on Ebro nase *Parachondrostoma miegii* (Steindachner, 1866), Pyrenean gudgeon and Ebro barbel (Leunda et al. 2008); rainbow trout on Pyrenean minnow *Phoxinus phoxinus* Kottelat, 2007 (Oscoz et al. 2005) and other cyprinids (de Sostoa and Lobón-Cerviá 1989); or chameleon cichlid *Australoheros facetus* (Jenyns, 1842) on native Cyprinidae and Blenniidae (Ribeiro et al. 2007b). Surprisingly, I did not find any dietary studies of pikeperch in Iberia. Overall, it can be concluded that most of these studies have clearly indicated that predation on native Iberian fishes, particularly in the case of threatened Iberian endemic fishes with limited distribution range, may lead to local extinctions of special concern (e.g., Blanco-Garrido et al. 2009).

Traditionally, dietary studies are carried out by direct stomach content examination for the quantification of ingested food items, which may be digested from partial to totally (i.e. reduced to bony remains) (Miranda and Escala 2007). Even though, some non-native fishes are known or suspected to prey upon fish eggs and larvae of native species – e.g., pumpkinseed (Almeida et al. 2009; Blanco-Garrido et al. 2009; Domínguez et al. 2002; García de Jalón et al. 1993; García-Berthou and Moreno-Amich 2000a), common carp (Encina et al. 2004), eastern mosquitofish (Rincón et al. 2002) or goldfish *Carassius auratus* (Linnaeus, 1758) – identification of early life-stages is often difficult to detect due to rapid digestion (Schooley et al. 2008) and thus, its impact is probably underestimated (García-Berthou and Moreno-Amich 2000a). This problem could be solved, at least in part, using electrophoretic techniques to characterize specific proteins and biomolecular approaches that detect specific DNA sequences (see review by Teletchea 2009), however, to the author's best knowledge, such techniques have still not been used for dietary analysis of non-native fish in the Iberian Peninsula.

Usually, stomach samples are removed after dissection from sacrificed specimens from surveys, that in turn could be empty due to diel/seasonal feeding rhythms or sampling methods, therefore constraining the possibility of collecting large and representative samples sizes (Bowen 1996). As far as we know, non-lethal methods to collect stomach contents, such as stomach tubes or pulsed gastric lavage, have not

been used for non-native fishes' diet studies in Iberia. Moreover, although techniques in stable isotope analysis (SIA) have evolved during the last decade, providing a promising utility for trophic ecology studies including impacts of non-native fishes in freshwater ecosystems (Kopp et al. 2009), these have not been yet used in Iberia. By utilising fish tissue samples that can be obtained non-lethally, SIA analysis, based on the predictable isotopic composition ratios between consumers and preys, can be useful at discriminating trophic groups and in estimating the trophic position of organisms at a temporal level.

Competition for trophic resources

The trophic position and feeding habits of naturalized non-native fishes may overlap those of native species, thus resulting in trophic competition due to reduced amounts of available food resources. Ecological theory predicts that competition for trophic resources, forces species into further resource partitioning or to dietary shifts towards suboptimal food items, however, it is often difficult to empirically demonstrate in non-controlled environments. Some introduced species are successful due to their opportunistic or generalist feeding behavior, easily adapting to forage on the most abundant and available food item (Gido and Franssen 2007).

Despite several studies suggested trophic competition based on diet composition and preference similarities between co-occurring native and non-native fishes (Godinho et al. 1997b; Leunda et al. 2008; Mieirol et al. 2001; Oscoz et al. 2005; Ribeiro et al. 2007b), no studies have directly assessed food resources competition in the Iberian Peninsula. Some studies suggested that the voracity and aggressive behavior of some non-native species – eastern mosquitofish (Caiola and de Sostoa 2005; Rincón et al. 2002; Vargas 1993) and black bullhead (Leunda et al. 2008) – might lead to an unfavorable competition for the same food resources, subsequently displacing native fishes to suboptimal food resources. Actually, aquarium and mesocosm experiments have demonstrated that satiety and voracity of the eastern mosquitofish are higher compared to native cyprinodontiforms – samaruc *Valencia hispanica* (Valenciennes, 1846) and Iberian toothcarp *Aphanius iberus* (Valenciennes, 1846), producing a greater proportion of specimens with empty guts in the latter (Caiola and de Sostoa

2005; Rincón et al. 2002). Furthermore, this trophic exclusion occurs even when the individual ratios are disproportionately favorable to the native cyprinodontiforms and under conditions of non-limiting food resources (Caiola and de Sostoa 2005).

Nevertheless, most dietary studies of non-native fishes with suspected high potential for trophic competition did not address the possibility of this impact mechanism (e.g., Almeida et al. 2009; Blanco et al. 2004; Blanco et al. 2003; Cabral et al. 1998; Domínguez et al. 2002; García-Berthou 1999a; b; 2001; García-Berthou and Moreno-Amich 2000a; c; Godinho and Ferreira 1996; 1998a; Magalhães 1993; Rodríguez Jiménez 1987; Zapata and Granado-Lorencio 1993) whilst others suggested that it could be negligible due the high amount of available resources (e.g., Encina et al. 2004; Rodríguez Jiménez 1989; 2001). Definitely further analyses on the patterns of food resource availability, use and partitioning are needed to clarify how these non-native competitors might interact with Iberian freshwater fishes (Magalhães 1993; Mieiro et al. 2001; Oscoz et al. 2005; Ribeiro et al. 2007b).

Competition for trophic resources almost certainly may play an important role in the interaction between translocated or stocked species and the native ones. On one hand, translocated species may in most cases find a congener with similar habits in the recipient basin (e.g., *Chondrostoma* or *Barbus* groups), but to the author's best knowledge, studies on these interactions have not been carried out in Iberia (but see Oscoz et al. 2008a; Oscoz et al. 2006). On the other hand, diet of stocked and wild brown trout was analyzed in two headwater tributaries of the Douro River basin in order to address the question of trophic interaction (Teixeira and Cortes 2006). Stocked brown trout preferred to feed on terrestrial invertebrates captured near the water surface whilst wild trout displayed an ontogenetic diet shift from aquatic benthic invertebrates to terrestrial invertebrates, and thereby, significant diet overlap was only detected with larger wild brown trout size-classes. Nevertheless, stocked brown trout did not displaced wild trout from the energetically profitable areas even when stocking largely augmented trout density, and therefore, the study concluded that there was no evident trophic competition (Teixeira and Cortes 2006). To the author's best knowledge there is no published study analyzing the potential trophic interaction

between native brown trout and other non-native trout species (e.g. brook trout *Salvelinus fontinalis* (Mitchill, 1815) in the French Pyrenees, Cucherousset et al. 2007).

Competition for habitat

Even though non-native fish species more often dominate in altered aquatic environments (Aparicio et al. 2000; Bernardo et al. 2003; Carol et al. 2006; Clavero et al. 2004; Corbacho and Sánchez 2001; Ferreira et al. 2007b; Godinho and Ferreira 2000; Godinho et al. 1998; Prenda et al. 2006; Ribeiro and Collares-Pereira 2010; Ruiz 1998; Vila-Gispert et al. 2002a), their habitat preferences may overlap with those of native species. Resulting competition for available habitat could lead to habitat use changes, forcing native species to suboptimal habitats. In some cases, overcrowding after overly successful recruitment of the introduced species leaves no available habitat for the native fishes, being particularly critical during dry-season in Mediterranean areas when fish communities are confined to residual surface waters (pool and run refugia) (e.g. Magalhães et al. 2007).

Seasonal microhabitat use by fishes (common carp, pike, rainbow trout and native cyprinids) was quantified through underwater observation in the Matarraña River (Grossman and de Sostoa 1994; Grossman et al. 1987a; b). In the lower Matarraña River, changes in species microhabitat use were not correlated with changes in species abundances, and hence, interspecific competition did not appear to strongly influence microhabitat use (Grossman and de Sostoa 1994; Grossman et al. 1987a). In the upper Matarraña River, rainbow trout introduction did not produce microhabitat shifts in any of the native species and neither territoriality nor interspecific aggressions were observed. However, the study warned that the rainbow trout is more likely to exclude the nonaggressive native cyprinids from their preferred microhabitat than the opposite (Grossman et al. 1987b). The study finally remarks that the lack of apparent interspecific competition for habitat, however, does not exclude the possibility of existence of trophic competition (Grossman et al. 1987b). At the present moment there is no published study analyzing the potential competition for habitat between native brown trout and other non-native trout species (e.g. brook trout in the French Pyrenees, Blanchet et al. 2007).

Gutiérrez-Estrada et al. (1998) studied the distribution and mesohabitat preference of the non-native mummichog (*Fundulus heteroclitus* Linnaeus, 1766) along the Atlantic coast of southwestern Spain. The mummichog preferred both natural and man-modified marsh-related mesohabitats such as salt lagoons, salt marsh fishponds and marsh channels. Even though the mummichog was the most frequently captured fish species, it was found alone or with only another one sympatric fish in over 80% of the occurrences. Therefore, the study suggested that habitat competition could be the best explanation for the observed apparent segregation between the mummichog and native fishes (Gutiérrez-Estrada et al. 1998). The potential competitive interactions between largemouth bass and the native freshwater blenny were also studied at the Alcañiz Reservoir, and concluded there was no competition for the available habitat due to the strong differences found in species ecology (size-frequency, feeding and habitat use) (Prenda and Mellado 1993). There are several other studies on habitat use and spatial organization of mixed fish assemblages of native and non-native species in Iberian freshwaters (e.g., Godinho and Ferreira 1998b; 2000; Godinho et al. 1997a; Godinho et al. 1998; Zamora 2004), but few addressed the issue of competition. For example, the thorough ontogenetic and seasonal habitat use study of fishes in Lake Banyoles could not evaluate habitat competition since non-native fishes currently dominate the ichthyofauna of the lake over the scarce native species (Zamora 2004).

As pointed out above for trophic resources, competence for habitat may play an important role in the impacts of translocated or stocked species on native fishes because in most cases they may find a congener with similar habits in the recipient basin. For instance, interspecific competition with the extensively translocated Ebro barbel has been suggested to have caused the disappearance of the native Western Mediterranean barbel (*Barbus meridionalis* Risso, 1827) from lower reaches in many rivers in Catalonia, however, biotic interactions with other non-native fishes can not be excluded (Clavero et al. 2009; Pou i Rovira et al. 2007). Another possible case of competition that deserves further study is between the critically endangered Júcar nase *Parachondrostoma arrigonis* (Steindachner, 1866) and the translocated Iberian straight-mouth nase in the Júcar River. Unfortunately, to author's best

knowledge, specific studies on these interactions have not been carried out in the Iberian Peninsula.

Behavioral interference

In some cases, competition for trophic resources or habitat may be through direct interaction. Increased severity of such interactions can be through behavioral interference, such as direct aggression or disturbance during reproductive activities (e.g., courtship, spawning). The only studied case of behavioral interference concerning impacts of a non-native fish on Iberian species is between the eastern mosquitofish and the threatened endemic Iberian cyprinodontiforms. On one hand, aquarium and mesocosm experiments have shown and quantified that eastern mosquitofish displays aggressive behavior (orientations, chases and nips) towards Iberian cyprinodontiforms, especially towards the samaruc (Rincón et al. 2002). On the other hand, the eastern mosquitofish presence appears to lead Iberian cyprinodontiforms to discontinue the early phases of courtship, interfering with breeding activities and thus resulting in significantly lower reproductive success and offspring production (Rincón et al. 2002). The exact nature and intensity of these negative effects may vary with a number of biotic and abiotic factors, thereby, it is potentially possible that coexistence between eastern mosquitofish and native cyprinodontiforms can happen under certain, even if apparently uncommon in the wild, circumstances (Rincón et al. 2002). Iberian toothcarp populations are usually restricted to coastal lagoons with a wide range of salinities but are hypersaline during summer, constituting a competitive refuge against the eastern mosquitofish whose invasive success has been shown to be limited by water salinity (Alcaraz and García-Berthou 2007). In fact, salinity also mediates the competitive interactions between eastern mosquitofish and the Mediterranean toothcarp – *Aphanius fasciatus* (Valenciennes, 1821) – namely, increasing salinity reduced feeding activity and aggressiveness of eastern mosquitofish whilst Mediterranean toothcarp performed better (Alcaraz et al. 2008).

However, beyond the impacts of eastern mosquitofish on native cyprinodontiforms where these species co-occur – i.e. river mouths and coastal wetlands throughout the Mediterranean coast – little is known about the interactions with

other native fishes in the rest of Iberian freshwaters where the eastern mosquitofish is rapidly invading (e.g., Ebro River basin, Oscoz et al. 2008b). Behavioral interference has also been suggested as a potential cause of the spatial segregation and opposed population trends observed between the jarabugo – *Anaocypris hispanica* (Steindachner, 1866) – and the pumpkinseed sunfish in the middle Guadiana basin (Blanco-Garrido et al. 2009). Similar interactions may also occur with the introduced non-native mummichog or chameleon cichlid, but have not been studied yet in the Iberian Peninsula and, subsequently, there is no scientific evidence to support this supposition.

Hybridization

Hybridization is common among Iberian freshwater fish species, e.g., *Pseudochondrostoma polylepis* (Steindachner, 1865) × *Achondrostoma arcasii* (Steindachner, 1866) in the Douro River basin (Collares-Pereira and Coelho 1983); *Barbus meridionalis* Risso 1827 × *B. haasi* Mertens 1924 in northeastern Iberia (Machordom et al. 1990); or *B. bocagei* Steindachner, 1865 × *B. comizo* Steindachner, 1865 in the Tagus River basin (Almodóvar et al. 2008). Hybridization may be problematic when a non-native fish interbreeds with a related native species and the fertile hybrids backcross with the parental species producing a significant gene flow and mixing of the gene pools – or introgression – threatening the genetic integrity of the native population (Moyle and Cech 2004). Potential negative outcomes of hybridization include, among others, loss of local adaptations, reduced fitness, lower mating efficiency and reproductive output, altered behavior, alteration of migration patterns or life-cycle timing, and at the extreme the extinction of the pure forms due to homogenization of population structure patterns (Elvira 2001a).

An unintended consequence of fish stocking may be genetic introgression and homogenization from interbreeding between indigenous populations and genetically distinct hatchery strains. This fact has been extensively studied on native Iberian salmonids (Atlantic salmon *Salmo salar* Linnaeus, 1758 and brown trout), where both introductions of “races/varieties” imported from northern and central European populations as well as translocations of local strains have been carried out neglecting potential genetic impacts. Along the geographic distribution range

of the brown trout, six main phylogeographic lineages have been identified using nuclear and mitochondrial DNA (mtDNA) markers (Bernatchez 2001; Bouza et al. 2008; Machordom et al. 2000; Presa et al. 2002; Suárez et al. 2001), but further microgeographic differentiation exists. In the Iberian Peninsula, five Evolutionary Significant Units (ESUs) have been identified: North Atlantic, Duero and Tagus, along with two Mediterranean lineages with a mosaic distribution pattern in southern and Mediterranean rivers (Cortey et al. 2004; Machordom et al. 2000; Suárez et al. 2001). Different genetic markers – allozymes, mtDNA and microsatellites – have been used to analyze and evidence genetic introgression in many Iberian brown trout populations after decades of stocking with hatchery-reared non-native counterparts (Almodóvar et al. 2002; Almodóvar et al. 2001; Antunes et al. 2001; Aparicio et al. 2005; Araguas et al. 2009; Araguas et al. 2008; Araguas et al. 2004; Arias et al. 1995; Cagigas et al. 1999; Corujo et al. 2004; García-Marín et al. 1991; García-Marín and Pla 1996; García-Marín et al. 1998; 1999; Izquierdo et al. 2006; Machordom et al. 1999; Machordom et al. 2000; Madeira et al. 2005; Martínez et al. 1993; Morán et al. 1996; Morán et al. 1991; Santos et al. 2006; Sanz et al. 2009; Sanz et al. 2006; Sanz et al. 2000; Sanz et al. 2002; Vilas et al. 2010). A comprehensive analysis on genetic introgression variability revealed that nearly half of the 307 studied Iberian brown trout populations were introgressed with genes of hatchery origin (Almodóvar et al. 2006). However, introgression rates varied widely within and between ESUs, reaching alarmingly high rates in some Mediterranean rivers whereas North Atlantic and Duero ESUs showed little or no introgression, suggesting that this depended on several site-specific genetic and non-genetic factors (Almodóvar et al. 2006). Some authors assessed the consequences of stocking in brown trout populations and revealed a substantial reduction of the genetic differences between native populations (Machordom et al. 1999; Sanz et al. 2000; Sanz et al. 2002) with an estimated introgression rate of 1–5% per year (Araguas et al. 2004; García-Marín et al. 1999). To our best knowledge, there is no published genetic study that analyzed genetic hybridization with other introduced non-native trout species (e.g. brook trout in the French Pyrenees, Cucherousset et al. 2008). Almodóvar et al. (2006) concluded that the Iberian Peninsula is crucial for the

conservation of brown trout' genetic diversity, however, the genetic uniqueness of native wild stocks is currently threatened by introgression of foreign genes because of artificial stocking with hatchery-reared fish of central and northern European origin.

Genetic studies on Atlantic salmon support population differentiation at continental (North America and Europe), regional and even particular river scales (Verspoor et al. 2005) favored by the reproductive isolation of the homing behavior that has allowed the development of local adaptations. Native Atlantic salmon populations from the northern Iberian Peninsula were artificially supplemented with non-native stocks from northern Europe from the 1970s to 1990s. Genetic introgression could have been possible since stocked individuals had the potential to participate in reproduction both as precocious parr (Morán et al. 1994a) as well as returning adults (García de Leániz et al. 1989; Morán et al. 1998), even if returns of stocked salmon were significantly lower than that of native wild Atlantic salmon (Martínez et al. 2001; Verspoor and García de Leaniz 1997). Genetic studies based on allozymes commonly showed low introgression levels (Blanco et al. 2005; García de Leániz et al. 1989; Morán et al. 1994a; Morán et al. 1994b; Morán et al. 2005; Morán et al. 1998; Vázquez et al. 1993; Verspoor and García de Leaniz 1997) whilst mtDNA (Consuegra et al. 2002) and microsatellite (Ayllon et al. 2006; Martínez et al. 2001) detected some introgression of non-native genetic markers on native Atlantic salmon populations in Iberia (see review in Campos et al. 2008). This comprehensive study showed that introgression of northern European mitochondrial genomes in Atlantic salmon populations has been generally low in northwestern rivers but high in northeastern rivers of the Iberian Peninsula, being proportional to the stocking intensity (Campos et al. 2008). Nowadays, artificial supplementations of Atlantic salmon in Iberia are carried out with progeny from local parental stocks (e.g., Machado-Schiaffino et al. 2007; Saura et al. 2006).

Atlantic salmon and brown trout naturally co-occur and hybridize producing fertile hybrids in the wild (García-Vázquez et al. 2004), however, stocking pressure with hatchery-reared Atlantic salmon of north European origin was correlated with higher interspecific introgressive hybridization in sympatric salmonid Iberian populations (Castillo et al. 2008). During the period of

intensive non-native Atlantic salmon stocking, interspecific hybrid prevalence was among the highest throughout the sympatric distribution area (Beall et al. 1997; García-Vázquez et al. 2001) but significantly decreased after stocking cessation to frequencies similar to those naturally produced elsewhere (Castillo et al. 2008). Introgressive hybridization has also been demonstrated from crosses between non-native stocked brown trout males and Atlantic salmon females of wild origin (Castillo et al. 2008), emphasizing the hybridization risks associated with stocking programs to both conspecific and interspecific wild salmonid populations. Back-crossing experiments of interspecific hybrids with parental species suggest that the introgression of brown trout genes into Atlantic salmon gene pools is possible, but not the opposite (Castillo et al. 2007; García-Vázquez et al. 2003; García-Vázquez et al. 2004).

Several cyprinid species (e.g., bleak, bream, rudd, roach) introduced into Iberian freshwaters are known to hybridize with other cyprinids in their natural distribution areas (Kottelat and Freyhof 2007). Hence, it is possible and probable that interbreeding between non-native and native cyprinids may be occurring though hybrids have not been described yet in the Iberian Peninsula. The bleak is repeatedly mentioned as being of special concern and it has been suggested that it is very likely that its co-occurrence with several Iberian endemic species (e.g., genus *Squalius*, *Anaocypris*) could result in genetic introgression into the native populations (Vinyoles et al. 2007). Moreover, several closely related endemic species (e.g., *Chondrostoma*, *Barbus* or *Squalius* groups) have evolved and are maintained by biogeographic barriers within the Iberian Peninsula, which could easily hybridize, threatening their genetic integrity, due to human-mediated secondary contacts, specifically water transfers and translocations. For instance, the Júcar nase is threatened, amongst other reasons, by hybridization with the Iberian straight-mouth nase that was translocated by water transfer from the Tagus to the Júcar drainage (Elvira 1987; 1995a).

Disease transmission

The invasive success of non-native species can also be associated with the concomitant introduction of novel pathogens (virus, bacteria, fungi and macroparasites) to new areas and to native fishes. The introduction of generalist

pathogens are of special concern since they often can infect a wide range of host, have normally a simple life cycle (i.e. no intermediate host) and could be more infectious and virulent in naïve native hosts (Gozlan et al. 2006). Non-native fishes are usually accompanied by their pathogens because risk management measures such as quarantine controls are generally less stringent for fish than for other animal groups or plants (Copp et al. 2005b), but furthermore, because most introductions are illegal. There is little information available on the distribution and abundance of introduced pathogens because pathological studies of wild non-commercial species are scarce in the Iberian Peninsula – and elsewhere – and therefore it is suspected that the actual impact of pathogens introduced along with non-native freshwater fishes may be underestimated.

In fact, several invertebrate parasite species introduced from Asia with the common carp and goldfish (e.g., *Gyrodactylus katharineri* Malmberg, 1964; *G. cyprini* Diarova, 1964; *Bothriocephalus acheilognathi* Yamaguti, 1934; *Lernaea cyprinacea* Linnaeus, 1758; see reviews by Blanc 1997; García-Berthou et al. 2007) as well as with the oriental weatherfish *Misgurnus anguillicaudatus* Cantor, 1842 (*Ichthyophthirius multifiliis* Fouquet, 1876; Maceda-Veiga et al. 2009) are known to be infecting some Iberian fish species. The potential impact of the recently introduced Asian topmouth gudgeon, carrier of a eukaryotic intracellular parasite that may affect salmonids and cyprinids (Gozlan et al. 2005; Gozlan et al. 2009) in the Iberian Peninsula, has been suggested but many more already established and widely distributed non-native fishes and related pathogens – e.g., pumpkinseed (Sterud and Jørgensen 2006), pikeperch (Keith and Allardi 1997), eastern mosquitofish (Benejam et al. 2009), tinfoil barb *Barbonymus schwanefeldii* (Bleeker, 1853) (Gante et al. 2008) – should also increase our level of concern.

Disease transmission into wild native populations could happen even if the imported fish' destination is not for stocking. Such is the case of the Japanese eel (*Anguilla japonica* Temminck & Schlegel, 1846), which was imported into Europe for human consumption and whose parasites now infect Iberian populations of the European eel (e.g., *Dactylogyrus anchoratus* Dujardin, 1845; *Gyrodactylus salaris* Malmberg, 1957; *Pseudodactylogyrus anguillae* Yin & Sproston, 1948; *P. bini* Kikuchi, 1929;

Anguillicola crassus Kuwahara, Niimi and Itagaki, 1974; see reviews by Blanc 1997; García-Berthou et al. 2007; Gozlan et al. 2006). Similar disease transmission cases could also have happened with the introduction of non-native salmonids.

Habitat and ecosystem alteration

Determining unambiguously the impacts attributable to non-native fish species on the structure and function of aquatic ecosystems has proven difficult because (1) data prior to invasions are rarely available, (2) ecosystems have already been altered by a range of other anthropogenic stressors – including contamination, hydrological and hydromorphological alterations, land-use pressures – and/or (3) additive effect of multiple invasions of non-native species (Crivelli 1995; Moyle and Marchetti 2006; Rowe 2007). There is a clear research need to address the complex interactions between non-native fishes and other forms of anthropogenic stressors and their effect on ecosystem structural and functional attributes across different spatio-temporal scales. Nevertheless, preliminary evidence suggests that some non-native fishes are able to modify habitat features and ecosystem food web functioning through trophic cascades and bottom-up structuring forces in the recipient water-body, and thereby, may indirectly impact native ichthyofauna.

Non-native zooplanktivorous fish contribute to food web shifts essentially through top-down mediated effects by reducing the biomass and altering the community structure of zooplankton, which leads to relieving grazing pressure on phytoplankton (Angeler et al. 2003). The resulting high phytoplankton biomass often contributes to high water turbidity and increased trophic status, which in turn can constrain the development of submerged macrophytes. In contrast, the impact of non-native benthivorous fishes is manifested mainly through increased translocation of sediment-bound nutrients and particles to the water column during bottom foraging, which increases phytoplankton growth and water turbidity (Angeler et al. 2003). Benthivorous fishes also significantly impact submerged vegetation, either through direct consumption (herbivory) or uprooting during foraging activities, destroying the habitat they provided to native fishes for shelter, feeding and/or reproduction. Surely the best example of

an exotic fish with great potential to drive aquatic habitat and ecosystem changes is the common carp, a large-bodied benthivorous and herbivorous fish. In addition to feeding habits, reproductive behavior of the common carp also produces substantial resuspension of bottom sediments during nest digging and spawning activities. The decline of aquatic macrophytes in many aquatic ecosystems in the Iberian Peninsula during the first half of the 20th century (e.g., Albufera in Valencia, Blanco and Romo 2006; Lake Banyoles, García-Berthou and Moreno-Amich 2000b) has often been associated to the introduction of common carp. Non-native benthivorous, herbivorous and zooplanktivorous fishes often co-occur, and thereby, may be expected to synergistically accelerate the processes contributing to the eutrophication of lacustrine ecosystems leading to a turbidity-induced change from a macrophyte to algal dominated state (Rowe 2007).

Among the scarce empirical studies designed to assess the impacts of non-native fishes on an Iberian ecosystem are those carried out in the currently degraded floodplain wetland, Las Tablas de Daimiel National Park (Angeler et al. 2003). The impact of the three non-native fishes – common carp, pumpkinseed and eastern mosquitofish – that nowadays dominate the degraded ichthyofauna of the wetland, was assessed at enclosures simulating fish biomasses occurring during summer droughts. Relative to a fishless control, water quality diminished (increased chlorophyll a, total phosphorus, total nitrogen and turbidity) with the addition of common carp or pumpkinseed, but not eastern mosquitofish (Angeler et al. 2002a). The zooplankton community in all fish treatments shifted to dominance by ineffectively grazing rotifers and copepods mediated by the different foraging strategies of the fishes (i.e. benthivorous in common carp vs zooplanktivorous in pumpkinseed and eastern mosquitofish) (Angeler et al. 2002a). Regarding the microbial food web, densities of heterotrophic bacterioplankton were benefitted by the increased trophic state conditions in the carp and pumpkinseed treatments (Angeler et al. 2002b) whilst autotrophic picoplankton was regulated by physical disturbance rather than biota-mediated effects (Angeler et al. 2005).

However, food web impacts of non-native fishes may be highly context-dependent and interact in complex ways with natural disturbance regimes (Angeler et al. 2003). In

fact, as long as submerged macrophytes are available, the trophic cascade may be truncated as a result of plant-plankton competition for nutrients. For example, enclosure experiments in a Mediterranean oligohaline lagoon at the Delta del Llobregat Natural Reserve demonstrated considerable effects of eastern mosquitofish on zooplankton density and composition (Cardona 2006; see also Mieiro et al. 2001) but the reduced grazing pressure did not translate to an increased phytoplankton growth. Since zooplanktivorous specialist fishes are naturally lacking in the Iberian ichthyofauna, it is particularly important to characterize the ecological mechanisms associated with the impact of other introduced fishes such as bleak, bream or roach. Likewise, the impacts of many non-native benthivorous fishes – bream, goldfish, channel catfish and black bullhead – may be similar to those observed for the common carp (Braig and Johnson 2003; Rowe 2007), but specific studies have still not been carried out in Iberia.

Research needs

Invasive species are recognized as a leading cause of animal extinctions (Clavero and García-Berthou 2005) and subsequently increased attention is beginning to be paid to non-native freshwater fishes in the Iberian Peninsula. Research on the interactions between non-native and native fishes might be justified, taking into account that the highly endemic Iberian freshwater ichthyofauna is facing a growing homogenization (Clavero and García-Berthou 2006), impoverishment and even an extinction threat (Smith and Darwall 2006). Although there are some well-documented impacts thanks to the recent growing research effort, here I show that many gaps remain in our understanding of processes underpinning the ecological impacts of non-native fishes on native Iberian ichthyofauna. Certainly, naturalized non-native species attract much less research attention than invasive ones, and in addition, the more invasive a species is, the more likely it will become the subject of a scientific study (Pyšek et al. 2008). At this point, precaution warns against the misconception that “the published literature is a representative sample of ecological interactions” by which the “lack of data” would mean “no impact” (Pearsons 2008). The lack of evidence may reflect that studies have not been conducted or have not been published in international peer-

reviewed journals, and indeed part of the literature reviewed in this work was “grey literature”, i.e. published in local journals, unpublished thesis, reports or communications in congresses.

The current review demonstrates that our knowledge of the impact mechanisms of most non-native freshwater fish species in the Iberian Peninsula is scarce and incomplete. Such understanding of the impacts is necessary in order to:

(1) improve fishery management; when fishery management is not supported by the best available knowledge on the impacts of non-native fishes two opposite attitudes may be expected: the “permissive” manager who identifies introduced fishes as new members of potential value for recreational fishing without detrimental effects, or the “protectionist” manager who recognizes any non-native fish as an unacceptable threat. In the last two decades, a transition from the permissive-to-protectionist attitude has been developing but managers with intermediate pragmatic attitudes possibly are in the majority.

(2) improve conservation; biodiversity and wildlife managers require scientific knowledge about the mechanisms by which non-native fish may degrade ecosystems in order to support their management actions and optimize resources. Actually, the management of introduced species may surely be one of the biggest challenge and resource-consuming tasks that conservation biologists will face in the near future.

(3) gain public awareness; different stakeholders and generations assign different and potentially conflicting values to different fish species (Pearsons 2008) based on untested assumptions that could be overcome by means of convincing environmental education actions based on real measured impact data. These efforts could be especially effective in order to prevent or reduce future ornamental fish releases (Courtenay and Stauffer 1990) and illegal stockings of angling purpose (Johnson et al. 2009).

Despite the overall lack of demonstrated impacts, awareness about the potential threat of non-native fishes is sustained by the wide variety of ecological situations in which the unique Iberian freshwater ichthyofauna may interact with a large and increasing number of introduced fishes. Ecological interactions are context-specific (Pearsons 2008), thereby their outcomes can vary significantly across the Iberian

Peninsula depending upon the aquatic ecosystem type and its ecological conditions as well as upon the community characteristics of both non-native and native fishes. I encourage research groups and funding institutions to focus their efforts to broaden the knowledge on interactions between non-native and native fishes to measure the real impacts, their biological significance and discern if they really pose an extinction threat for native Iberian ichthyofauna. Likewise, research focused on life-history traits of introduced fishes in recipient Iberian novel environments is required (e.g., Alcaraz et al. 2005; Benejam et al. 2009; Cabral and Marques 1999; Carol et al. 2007; Fernández-Delgado 1989a; 1990; Fernández-Delgado and Rossomanno 1997; Gutiérrez-Estrada et al. 2000a; Gutiérrez-Estrada et al. 2000b; Lobón-Cerviá et al. 1991; Pérez-Bote and López 2005; Pérez-Bote et al. 2001; Ribeiro and Collares-Pereira 2010; Tedesco et al. 2008; Vargas and de Sostoa 1996; Vila-Gispert and Moreno-Amich 1998; 2002; 2003; Vila-Gispert et al. 2002b), but more interestingly if it is compared to their native areas (e.g., Copp et al. 2009; Copp et al. 2004; Domínguez and Pena 1996; Drake et al. 1987; Fernández-Delgado 1989b; Fox et al. 2007; Pou i Rovira 2004; Tomeček et al. 2007; Vila-Gispert et al. 2007; Vila-Gispert and Moreno-Amich 2000). Furthermore, the susceptibility of freshwater ecosystems and invasiveness potential of non-native fishes is expected to change with changing climatic conditions, so research aiming to forecast the evolution and impacts of introduced fishes throughout Iberia becomes of special relevance.

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