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Introduction

Princess of the Streams: The Brown Trout *Salmo trutta* L. as Aquatic Royalty

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Brown trout *Salmo trutta* is one of the most widely and collectively sought-after, studied, introduced, and actively managed salmonid species across the world, rivaled only, perhaps, by rainbow trout *Oncorhynchus mykiss* (see Crawford & Muir 2008, Newton 2013). Occurring historically on three continents, the range of the brown trout has been expanded to watersheds on all continents except Antarctica. Unlike rainbow trout, brown trout remains somewhat less 'synthetic' (*sensu* Halverson 2010) because of a lesser history of artificial propagation along with a broad range where the species has been less influenced by active fishery management.

Brown trout stands out as an iconic species whose values as recreational and food resources include a global interest in fishing by huge amounts of passionate, rod-and-line anglers who generate robust direct and derivative economies, leisure and other social interactions and subsequent management efforts. In addition to its value as a fishing interest, brown trout has amassed an extensive scientific value because of its complex taxonomic status, its evolutionary history, its trophic status as an apex aquatic predator, and its dizzying array of life-history expressions (Bernatchez 2001, Northcote & Lobón-Cerviá 2008). Ultimately, however, centuries of anthropogenic changes to their natural habitats at both localized and landscape scales has resulted in the extirpation of numerous populations across their historical range that has triggered substantial social and political concerns over the species and the aquatic ecosystems it occupies.

In part because of the previously described values, brown trout has been introduced widely on a global scale wherever habitat conditions have been deemed suitable. Consequently, brown trout has emerged as economically important in numerous places where it is now established (e.g., Australia, New Zealand, Argentina, Canada and the USA among others). While perhaps once heralded as a highly desirable addition to aquatic communities in decades past, brown trout are increasingly and simultaneously being viewed as one of the most destructive invaders in some watersheds where native

species are being displaced or otherwise harmed through competition or predation. For example, brown trout is emerging as a nuisance to native and imperiled fish fauna in the Colorado River and other drainages of southwestern US (See Budy & Gaeta, Chapter 20). Consequently, as a worldwide species, its image increasingly wanders into a maze of contradictory feelings including the opposite extremes of enthusiasm, love and passion *vs.* hate and confusion. To find the way out from such a maze (if there is one!) of competing complex socio-cultural and economical values likely requires reasoned and honest dialog along with some heroic and collaborative efforts from a diversity of experts and perspectives including aquatic ecologists and evolutionary scientists, fishery resource managers, developers, land-use planners and administrators, economists, elected politicians, and even land-ethicists – among others (see Young *et al.*, Chapter 29).

Iconic in so many ways, complexity and diversity are perhaps the most definitive key words that typify brown trout. Across the wide range of aboriginal habitats, brown trout populations display an overwhelming variability of morphological and life-history traits. Interestingly, such traits may differ and prove stable even at relatively fine geographic scales – such as in adjacent streams or even sympatric within a common stream. In other cases, locally adjacent populations may display a considerable plasticity of their morphological and ecological strategies in response to the environmental heterogeneity of the habitats where they complete their life-cycles including streams, rivers, lakes, estuaries and oceans, as well as systems with high levels of periodic ecological disturbances.

An area of considerable controversy is the brown trout's taxonomic status and associated nomenclature due to the overall complexity referenced previously. Complexity and diversity are expressed dramatically in the taxonomical position of numerous populations, a controversial issue since the earliest studies of the species. Lack of awareness of this complexity, along with more typological perspectives on naming and describing species was probably the keystone of the historical confusion. Specifically, Linnaeus (1758) in his 'Systema Naturae' described several species of the genus *Salmo* of which at least three *Salmo fario*, *S. trutta* and *S. eriox* can be assigned to what we synonymously name Brown Trout. A decade-long effort to disentangle that puzzle triggered a constellation of papers including the proposed descriptions of new species, sub-species and 'morphas'. Nevertheless, most recent investigations benefitting from inherited molecular markers such as mitochondrial DNA sequences (Bernatchez 2001) have offered a consensus in which all populations, independently of external designs, life-history strategies and other peculiarities, belong to a common species namely, *Salmo trutta* 'species complex'. Moreover, this super-species displays divergence into five or more phylogenetic lineages across their distributional area (see Sanz, Chapter 2) and supports a hypothesis that include all populations previously described that account for, at least, 83 species and sub-species (Jonsson & Jonsson 2011).

Elucidation of the boundaries of the brown trout complex's natural distributional range has been also controversial. Over the last decades, several authors have presented detailed maps covering the natural and exotic distributional areas including, in several instances, the dates and geographical origins of the introduced individuals (Fletcher 1958, MacCrimmon & Marshall 1968, MacCrimmon, Marshall & Gots

1970, Heacox 1974, Welcomme 1988, Baglinière & Maisse 1991). An updated description of the natural distribution covers a vast territory of millions of square kilometres that cut across climates, geologies and landscapes of three continents – implying that brown trout is among the most broadly distributed salmonids worldwide. This vast territory ranges from Iceland at one extreme across the east and south of Europe, continuing down through central Asia and terminating in the north of Africa, including Morocco and Algeria. The southern and eastern distribution include the Mediterranean Islands (except Balearic) and the Black, Caspian and Aral Seas, Turkey, Iraq, Iran (Mostafavi *et al.* 2014) as far east as Kazakhstan, Uzbekistan, Kyrgyzstan and Tajikistan at the ‘buttresses of the Himalayas’ (Baglinière & Maisse 1991, M. Esteve, pers. com.).

Within these vast territories, there is an exceptional amount of life-history diversity displayed by populations. For example, there are riverine populations that complete the entirety of their life-cycles as sedentary residents within a few hundred meters of a small stream (see Lobón-Cervia, Rasmussen & Mortensen, Chapter 13). Conversely, there are fluvial populations within larger rivers that migrate long distances upstream in search of suitable or natal spawning habitats. In some populations individuals grow at low rates and spawn at a later age whereas in other populations the growth rates are higher and spawn at an earlier age. There are semelparous populations that spawn only once in a lifetime and iteroparous that spawn several times (Cucherousset *et al.* 2005). Strictly riverine populations have been historically considered a sub-species or ‘morpha’ known as *S. t. fario*. In other populations, juveniles metamorphose into a silver-grey color and develop dark lateral marks under a process known as smoltification – which permits transition from freshwater to marine environments. Once completed, they migrate downstream towards the oceans where they spend varied time periods and is called anadromy (see Rasmussen, Chapter 14). In regions where lakes have no direct contact with the oceans, the fish migrate solely between rivers and the lakes. These migratory or, adfluvial individuals return to their original streams to spawn (see Husko *et al.*, Chapter 12) and transport back nutrients of major importance for the ecological processes of the streams (Stockner 2003). Sea-migratory and lake-migratory forms were also considered sub-species or ‘morphas’ known as *S. t. trutta* and *S. t. lacustris*, respectively. Yet another life-history type or set of populations known as ‘slob trout’ stay in estuaries under the influence of the tides where fresh- and marine waters mix. Finally, there are populations in which either ‘morpha’ may co-occur and may further hybridize with each other (Jonsson 1985) or with a phylogenetically-related sister species such as the Atlantic salmon, *S. salar* L. (Solomon & Child 1978; García de Leaniz & Verspoor 1989).

The anadromous marine ‘morpha’ or sea-trout, are distributed from Iceland and the British Islands to the Iberian Peninsula with a southern range limit at the Portuguese Mondego River (see Caballero, Vieira-Lanero & Cobos, Chapter 18) and an eastern limit at the Baltic and White Seas and the Kola Peninsula. In the Mediterranean region, sea-trout apparently also occur in the Black and Caspian Seas yet there is no evidence of their occurrence in France, Italy, Yugoslavia, Greece, Turkey, Morocco or Algeria. The lacustrine ‘morpha’ or lake-trout are abundant from Ireland to central and eastern Europe including sub-alpine lakes of northern Italy, Poland, the Scandinavian countries and Russian Karelia.

The morphological and genetic diversity of the southern, Mediterranean brown trout is remarkably greater than those from central and northern Europe. During the numerous inter-glacial periods over the last 2.5 million years (Darlington 1959, Brown & Lomolino 1998), the freshwater fish fauna of central and northern Europe became partially or totally extinct as glaciers covered the landmass and then retreated. Presently, most of the species that compose the fish assemblages of freshwater ecosystems and drainages of the northern versant of the Mediterranean mountains systems (Pyrenees, Alps, etc.) are recent colonizers associated with the glacial retreats during the last 500,000 years with a last retreat in the Holocene some 10,000–12,000 years ago. These processes may best explain the similarity of the fish fauna from the westernmost France to the remote extremes of Siberia. It also explains the dissimilarity between central and northern Europe and the southern versants where rivers flow south to the Mediterranean and are inhabited by an older and diverse fish fauna of endemic species, due to their resistance to glaciation effects (Crivelli & Maitland 1995).

Therefore, it is not surprising that markedly different assemblages of trout species flourish in the southern latitudes whose taxonomical positions remain somewhat controversial (Snoj *et al.* 2011). Several authors are reluctant to consider all these populations as genuine members of the *S. trutta* 'species complex' (see Meraner & Gandolfi, Chapter 3). This set of species include, at least, marble trout *S. marmoratus* (Cuvier 1829), a trout with a very different external design that attain uncommonly large sizes as 1.5 m length and >30 kg weight (Figure 1.1, Povz *et al.* 1996). Its distribution is limited

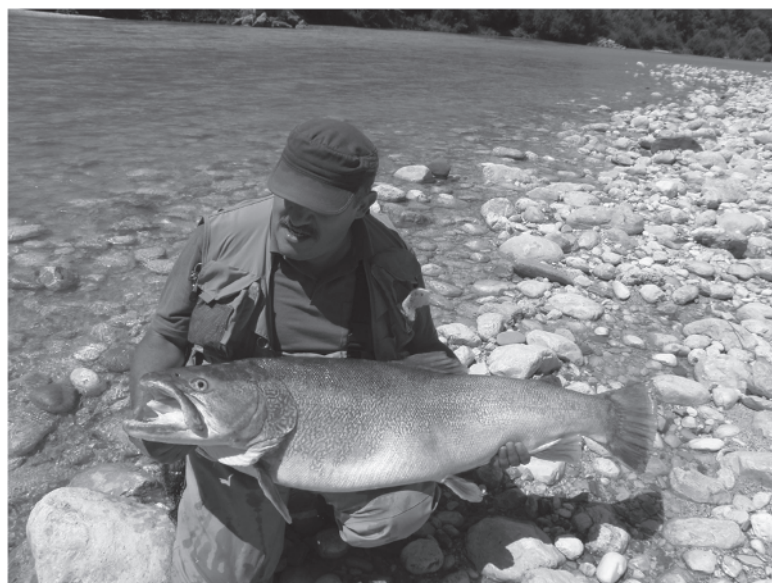


Figure 1.1 A 25 kg specimen of *S. marmoratus* caught by rod-and-line by a happy angler in Soča River (Eslovenia).

to the Po and Adige Rivers in northern Italy and a few rivers of Slovenia, Croatia, Bosnia-Herzegovina and Montenegro. Also *S. obtusirostris* (Heckel 1881) endemic to the Neretva, Zeta, Jadro and Vrijika Rivers. Moreover, *S. cettii* (Rafinesque 1810), probably a synonymous of *S. macrostigma* (Dumeril 1858). These brown trout relatives were considered endemic of Algeria, but recent investigations support their occurrence in the Tyrrhenian Sea and the Mediterranean Islands (Corsicans, Sardinia and Sicily), the Italian Magra River and according to Kottelat & Freyhof (2007), probably in the Easternmost Spanish and Southernmost French rivers.

Lake-dwelling species related to or synonymous with brown trout are common in central and southern Italy (Gandolfi *et al.* 1991), the Balkans (Pustovrh, Snoj & Susnik 2014) and minor Asia. These at least include *S. fibreni* (Zerunian – Gandolfi 1990) and *S. carpio* in the Italian Posta Fibreno and Garda Lakes (Melotto & Oppi 1987, Melotto & Alessio 2006). Also, *S. letnica* (Karaman 1924) and *S. Ohridanus* are found in Ohrid Lake at the border between Makedonia and Albania. *S. ischchan* (Kessler 1877) from Sevan Lake in Armenia (Berg 1962) and *S. ezenami* (Berg 1948) from Kezenoi-Am Lake in the Caucasus (Freyhof & Kottelat 2008). The populations of the Black and Azov Seas are also considered a nominal species, *S. labrax* (Pallas 1914). Another trout endemic of Turkey, *S. platycephalus* (Behnke 1968) and the unique Aral trout, *S. aralensis* (Berg 1908), are definitively extinct after one of the most important environmental cataclysm recorded in history, the dry up of 68,000 Km² of freshwaters (Figure 1.2). Moreover, *S. ciscaucasicus* (Dorofeeva 1967) originally described as a



Nick Hannes - "Desert Ships (Aral Sea)" - Courtesy © the artist. Nick Hannes' works are on view at BOZAR, Brussels in "Beyond the Document: Contemporary Belgian Photographers" from June 29th through September 26th.

Figure 1.2 The Aral Sea (Kazajistan-Uzbekistan), after the drying up of 68,000 km² of fresh water, following one of the most important human-induced environmental cataclysms in history. Camels relaxing in the shade of shipwrecks have replaced *S. aralensis* in their natural habitat.

species or sub-species from the sub-tropical Eurasia (Kottelat & Freyhof 2007). Finally, in Morocco, the so called 'green trout', *S. pallaryi* from Isli Lake (Vivier 1948, Mouslih 1987) and the 'dwarf trout', *S. akairos* (Dellinger & Doadrio 2005, Doadrio, Perea & Yahyaoui 2015) from Ifni Lake (Figure 1.3).

Brown trout and all other brown trout-like species are also iconic in terms of their Conservation status. The status of 'vulnerable' or 'near extinction' (IUCN 2010) covers practically all eastern and southern brown trout-like species with restricted distributional areas. The recent revision by Smith & Darwall (2006) accounts for 13 species of the Salmonidae family – including the genera *Acantholingua*, *Salmo* and *Salmothymus* (see Esteves *et al.* 2014) – whose status is 'vulnerable', 'endangered' or

(A)



(B)



Figure 1.3 Trout lakes in the Atlas Mountains (Morocco). (A) 'Isni' Lake inhabited by the 'green trout', *S. pallaryi* and (B) 'Ifni' Lake inhabited by the 'dwarf trout', *S. akairo*.

‘critically endangered’. In regards to the European native populations, the Red Data Books available assign no dramatic situation to any of these populations, however such status may be no more than a mirage. Since the darkness of the times, human interventions have induced dramatic changes in all salmonid habitats to the extent that just a few, scattered pristine trout habitats actually remain in the European continent. Canals, weirs, hydro-electrical stations, reservoirs and water diversions, intensive land use and the development of industries and mining operations are considered directly or indirectly related to numerous population extirpations at local and regional scales. Moreover, such changes have remarkably led to the extinction of land-locked and river-locked populations most common in the southerly latitudes.

Another human intervention became important in the wake of World War II. During the late 1940s and early 1950s, administrators and anglers began what can only be described as ‘industrial-scale’ stocking and transplantation as major tools to ‘improve’ sport fishing. Millions of captive-bred, reared and domesticated individuals from different aquaculture origins were stocked on an annual basis across the globe (Lobón-Cerviá, Elvira & De Sostoa 1989, De Sostoa & Lobón-Cerviá 1989, Vøllestad & Hesthagen 2001). Massive stocking resulted in direct and indirect risks to Salmonid biodiversity (Utter & Epifanio 2002). For example, propagation and stocking intensified the occurrence and facilitated the spread of undesirable pathogens (diseases) and parasites across broad geographical areas. Brood choice practices and the unnatural culture environment led to domestication effects and the narrowing the gene pool. The mixing of evolutionary divergent genetic lineages eroded gene pool architecture or eliminated original local adaptations (García-Marín, Sanz & Pla 1998). Inter- and intra-specific hybridization among divergent lineages actually obscures the real conservation status of many populations given the difficulty to identify natural *vs.* anthropogenic hybridization in some populations (Marzano *et al.* 2003, Sanz *et al.* 2006, Schenekar *et al.* 2014). Even where gene-level variation might remain high among populations with substantial hybridization, the reduction or extinction of evolutionarily integrated genomes may be lost albeit masked by large numbers of hybrids (Epifanio & Philipp 2001). Consequently, the conservation status of numerous European populations is still to be quantified.

In turn, brown trout is one of the most extensively introduced species globally with exceptional success to the extent to be known as the ‘fish that conquered an empire’ (see Newton 2013) and probably far beyond. After more than 170 years, intensive brown trout stocking is the subject of controversy and debate. Whilst it plays a similar and majestic role as the royal ‘Princess of the Streams’ in numerous exotic regions, as an invader it is highly problematic (see Chapters 20 to 24) to the extent to be considered one of the 30 most invasive freshwater species worldwide (McIntosh, McHugh & Budy 2012). And, despite substantive debates worldwide, developers and recreational fishery managers still consider brown trout a potential species to be further introduced in other regions where local fisheries are not possible or where under-developed economies clamor for new sources of recreational revenues.

On the other hand, the fascinating variability of the life-history modes exhibited by brown trout (Crisp, 2000; Antunes *et al.* 2006), together with the development of methods and techniques that permit manageable field sampling and population quantifications *vis-a-vis* the development of insightful genetic analysis has motivated the scientific community to focus on brown trout as an ‘umbrella species’. Studies on all aspects of their biology have been published during the last 150 years and several recent books summarize the advances and knowledge acquired (Lamond 1916, Menzies 1936, Frost & Brown 1967, McClane 1971, Heacox 1974, Bagliniere & Maisse 1991, Elliott 1994, Crisp 2000, Harris & Milner 2006, O’Grady, Kelly & O’Reilly 2008, Jonsson & Jonsson 2011, Polakof & Moon 2013). Yet, such abundant literature and insightful studies may be little more than a mirage. Practically all research efforts have been focused on European populations and a few exotic regions as New Zealand, USA and South-America. Unfortunately, our knowledge about all other populations and brown trout-like species from the southern and eastern regions is often limited to genetic approaches (Hashemzadeh *et al.* 2012, Kohout *et al.* 2013, Gratton *et al.* 2014, Jadan *et al.* 2015,) whereas our knowledge on their biology and ecology is comparatively scant (Crivelli 1996).

As aforementioned, the general status of brown trout as a worldwide species wanders in a maze of confusion. In many natural and exotic regions, brown trout generates substantial economic activity. These have yet to be quantified rigorously (see Baglinièri 1991), but are undoubtedly very important in terms of GDP as those underlying important exploited marine fishes. Interestingly, social demands for sport fishing *vis-a-vis* leisure purposes are increasing at the same rates as the national economies. Simultaneously, however, the brown trout populations and habitats are deteriorating at nearly identical rates. With no need to invoke the potential effects of global change and warming trends, this situation predicts that within a reasonably short period of time the ‘supply’ in terms of fishable populations will not be sufficient to meet the ‘demand’ for sport fishing, a disequilibrium that will necessary trigger profound social concerns. While there are no guarantees, we may be just in time to react and implement proactive solutions. Priorities of management include, at the minimum, to make compatible conservation *vs.* exploitation of natural populations. Priorities in exotic regions are the protection of the native biota and the underlying ecological processes threatened by the successful invasiveness of Brown trout (see Jellyman *et al.*, Chapter 22; Budy & Gaeta, Chapter 20). Such priorities require much more efficient management strategies driven by robust scientific analyses and intensive research efforts (see Young *et al.*, Chapter 29) supported by strict ethical principles consistent with a sustainable land ethic (see Piccolo, Unfer & Lobón-Cervia, Chapter 25). Thus, brown trout might be seen as an unprecedented new emblem for science and more specifically, for conservation biology and ecology.

This new book attempts to be a step in advance to offer updated studies of major interest for the best knowledge of brown trout, for the design of new management strategies and for the amelioration of undesirable human-induced effects on both natural and exotic populations. Authors from all over the world actively involved in the study and management of these populations offer chapters including reviews and case studies

that provide insight into theory and practice. If successful, this book will identify the exit from the complex maze of controversies and challenges associated with a most 'royal' fish – known to many as simply 'brown trout' and to many others as *S. trutta* 'species complex' and brown trout-like species.

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