Brown Trout
Brown Trout: Biology, Ecology and Management

Edited by

Javier Lobón-Cerviá
National Museum of Natural Sciences, Spanish National Research Council, Madrid, Spain

Nuria Sanz
University of Girona, Girona, Spain
Contents

List of Contributors ix
Foreword xiii
Preface xv
Malcolm Elliott

1 Introduction 1
Javier Lobón-Cerviá

Section 1  Phylogeography and Genetic Structure 15

2 Phylogeographic History of Brown Trout: A Review 17
Nuria Sanz

3 Genetics of the Genus Salmo in Italy: Evolutionary History, Population Structure, Molecular Ecology and Conservation 65
Andreas Meraner and Andrea Gandolfi

4 Understanding the Brown Trout Population Genetic Structure in the Iberian Peninsula 103
J.L. García-Marín, R.M. Araguas, M. Vera, and Nuria Sanz

5 Understanding Brown Trout Population Genetic Structure: A Northern-European Perspective 127
L. Asbjørn Vøllestad

Section 2  Reproductive Traits and Early Ontogeny 145

6 The Velocity of Love. The Role of Female Choice in Salmonine Reproduction 147
Manu Esteve

7 Observations of Male Choice in Brown Trout (Salmo trutta) from Lar National Park, Iran 165
Manu Esteve, Asghar Abdoli, Iraj Hashemzadeh Segherloo, Kiavash Golzarianpour, and Amir Abbas Ahmadi
8 Energetic Trade-Offs Faced by Brown Trout During Ontogeny and Reproduction  179
   Ole Kristian Berg and Ian A. Fleming

9 Impact of Embeddedness on Salmo trutta at Different Periods of their Early Ontogenesis  201
   V. Bolliet and A. Bardonnet

Section 3 Life-History  227

10 Habitat as Template for Life-Histories  229
    Bror Jonsson and Nina Jonsson

11 Life-history Plasticity in Anadromous Brown Trout: A Norwegian Perspective  251
    Jan Henning L’Abée-Lund and L. Asbjørn Völlestad

12 Life-History of the Adfluvial Brown Trout (Salmo trutta L.) in Eastern Fennoscandia  267
    A. Huusko, A. Vainikka, J.T. Syrjänen, P. Orell, P. Louhi, and T. Vehanen

Section 4 Population Dynamics  297

13 Discharge-Dependent Recruitment in Stream-Spawning Brown Trout  299
    Javier Lobón-Cerviá, Gorm Heilskov Rasmussen, and Erik Mortensen

14 Population Dynamics of Juvenile Brown Trout (Salmo trutta L.), Recruitment, Mortality, Biological Production and Smolt Yield in Two Danish Baecks  319
    Gorm Heilskov Rasmussen

    John J. Piccolo and Johan Watz

16 Competition Within and Between Year Classes in Brown Trout; Implications of Habitat Complexity on Habitat Use and Fitness  383
    J. Höjesjö

17 Brown Trout on the Move – Migration Ecology and Methodology  401
    Kim Aarestrup, Niels Jepsen, and Eva B. Thorstad

18 Sea Trout (Salmo trutta) in Galicia (NW Spain)  445
    Pablo Caballero Javierre, Rufino Vieira-Lanero, and Fernando Cobo Gradín

19 Sea Trout (Salmo trutta L.) in Denmark  483
    Gorm Heilskov Rasmussen and Stig Pedersen
Section 5  Brown Trout as a Global Invader  523

20 Brown Trout as an Invader: A Synthesis of Problems and Perspectives in North America  525
Phaedra Budy and Jereme W. Gaeta

21 The Introduction of Brown Trout to New Zealand and their Impact on Native Fish Communities  545
Peter Jones and Gerard Closs

22 The Effects of Brown Trout on the Trophic Webs of New Zealand Streams  569
Phillip G. Jellyman, Peter A. McHugh, Kevin S. Simon, Ross M. Thompson, and Angus R. McIntosh

23 Brown Trout in Argentina: History, Interactions and Perspectives  599
Miguel A. Casalinuovo, Marcelo F. Alonso, Patricio J. Macchi, and Jorge A. Kuroda

24 Africa: Brown Trout Introductions, Establishment, Current Status, Impacts and Conflicts  623
Olaf L.F. Weyl, Bruce R. Ellender, Phillip Ivey, Michelle C. Jackson, Denis Tweddle, Ryan J. Wasserman, Darragh J. Woodford, and Tsungai A. Zengeya

Section 6  Conservation and Management  641

25 Why Conserve Native Brown Trout?  643
John J. Piccolo, Günther Unfer, and Javier Lobón-Cerviá

26 Fisheries Management of Stream-Resident Brown Trout Populations – Possibilities and Restrictions  649
Günther Unfer and Kurt Pinter

27 Ecology and Management of Stream-Resident Brown Trout in Michigan (USA)  667
Troy G. Zorn

28 History, Conservation and Management of Adfluvial Brown Trout Stocks in Finland  697
J.T. Syrjänen, A. Vainikka, P. Louhi, A. Huusko, P. Orell, and T. Vehanen

29 Brown Trout Management for the 21st Century  735
Kyle A. Young, P. Gaskell, T. Jacklin, and J.E. Williams

Index  771
List of Contributors

Kim Aarestrup
Technical University of Denmark, National Institute of Aquatic Resources, Silkeborg, Denmark

Asghar Abdoli
Department of Biodiversity and Ecosystem Management, Environmental Sciences Research Institute, Shahid Beheshti University (SBU), Tehran, Iran

Amir Abbas Ahmadi
Department of Environment (DOE), Tehran Provincial Directorate of Environment Protection, Tehran, Iran

Marcelo F. Alonso
Grupo de Evaluación y Manejo de Recursos Ícticos, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina

R.M. Araguas
Laboratory of Genetic Ichthyology, Department of Biology, University of Girona, LEAR, Campus Montilivi, Girona, Spain

A. Bardonnet
UPPA-UMR ECOBIOP, UFR Sciences et Techniques Côte Basque, Campus Montaury, Anglet, France and INRA-UMR ECOBIOP, Aquapôle INRA, Saint Pée sur Nivelle, France

Ole Kristian Berg
Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

V. Bolliet
UPPA-UMR ECOBIOP, UFR Sciences et Techniques Côte Basque, Campus Montaury, Anglet, France and INRA-UMR ECOBIOP, Aquapôle INRA, Saint Pée sur Nivelle, France

Phaedra Budy
U.S. Geological Survey, Utah Cooperative and Wildlife Research Unit and Utah State University, Department of Watershed Sciences and the Ecology Center, Logan, Utah, USA

Miguel A. Casalinuovo
Investigador Independiente, Ushuaia, Tierra del Fuego, Argentina

Gerard Closs
Department of Zoology, University of Otago, Dunedin, New Zealand

Bruce R. Ellender
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa and Center for Invasion Biology, SAIAB, Grahamstown, South Africa
List of Contributors

Manu Esteve
Avenida Puente Cultural, Madrid, Spain

Ian A. Fleming
Fish Evolutionary Ecology Research Group and Department of Ocean Sciences, Ocean Sciences Centre, Memorial University of Newfoundland, St. John’s, Canada

Andrea Gandolfi
Biodiversity and Molecular Ecology Department, Research and Innovation Centre – Fondazione Edmund Mach, San Michele a/Adige (TN), Italy

J.L. García-Marín
Laboratory of Genetic Ichthyology, Department of Biology, University of Girona, Edifici LEAR, Campus Montilivi, Girona, Spain

Jereme W. Gaeta
Utah State University, Department of Watershed Sciences and the Ecology Center, Logan, Utah, USA

P. Gaskell
The Wild Trout Trust, Waterlooville, UK

Kiavash Golzarianpour
Department of Biology, Faculty of Sciences, Gonbad Kavous University, Iran

Fernando Cobo Gradín
Estación de Hidrobiología ‘Encoro do Con’, Universidad de Santiago de Compostela, Pontevedra, Spain and Departamento de Zooloxía e Antropoloxía Física, Universidade de Santiago de Compostela, Santiago de Compostela, Spain

J. Höjesjö
Department of Biology and Environmental Sciences, University of Gothenburg, Göteborg, Sweden

A. Huusko
Natural Resources Institute Finland (Luke), Management and Production of Renewable Resources, Paltamo, Finland

Phillip Ivey
South African National Biodiversity Institute, SANBI, Claremont, South Africa

T. Jacklin
The Wild Trout Trust, Waterlooville, UK

Michelle C. Jackson
Imperial College London, Department of Life Sciences, Silwood Park Campus, Ascot, Berkshire, UK and Center for Invasion Biology, University of Pretoria, South Africa

Pablo Caballero Javierre
Servicio de Conservación de la Naturaleza de Pontevedra, Consellería de Medio Ambiente y Ordenación del Territorio, Xunta de Galicia, Pontevedra, Spain

Phillip G. Jellyman
National Institute of Water and Atmospheric Research, Christchurch, New Zealand

Niels Jepsen
Technical University of Denmark, National Institute of Aquatic Resources, Silkeborg, Denmark

Peter Jones
Department of Zoology, University of Otago, Dunedin, New Zealand

Bror Jonsson
Norwegian Institute for Nature Research, Gaustadalléen, Oslo, Norway
Nina Jonsson
Norwegian Institute for Nature Research,
Gaustadalléen, Oslo, Norway

Jorge A. Kuroda
Laboratorio de Ecología Acuática,
Dirección de Ecosistemas Acuáticos
Centro de Ecología Aplicada del Neuquén (CEAN), Junín de los Andes, Neuquén, Argentina

Jan Henning L’Abée-Lund
Norwegian Water and Energy
Directorate, Majorstuen, Oslo, Norway

Javier Lobón-Cerviá
National Museum of Natural Sciences (CSIC), Madrid, Spain

P. Louhi
Department of Ecology, University of Oulu, Finland
and
Metsähallitus Parks and Wildlife Finland, Oulu, Finland

Patricio J. Macchi
Grupo de Evaluación y Manejo de Recursos Ícticos, Centro Regional
Universitario Bariloche, Universidad Nacional del Comahue, Bariloche,
Río Negro, Argentina

Angus R. McIntosh
School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

Peter A. McHugh
Utah State University, Logan, Utah, USA

Andreas Meraner
Department of Forestry, Hunting and Fisheries Office of the Autonomous Province of Bolzano, Bolzano (BZ), Italy

Erik Mortensen†

P. Orell
Natural Resources Institute Finland (Luke), Management and Production of Renewable Resources, University of Oulu, Finland

Stig Pedersen
Technical University of Denmark, National Institute for Aquatic Resources, Silkeborg, Denmark

John J. Piccolo
River Ecology and Management Group, Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden

Kurt Pinter
Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria

Gorm Heilskov Rasmussen
Technical University of Denmark, National Institute for Aquatic Resources, Silkeborg, Denmark

Nuria Sanz
Laboratory of Genetic Ichthyology, Department of Biology, University of Girona, Edifici LEAR, Campus Montilivi, Girona, Spain

Iraj Hashemzadeh Segherloo
University of Shahre Kord, Shahre Kord, Iran

Kevin S. Simon
School of Environment, University of Auckland, New Zealand

J.T. Syrjänen
Department of Biological and Environmental Sciences, Jyväskylä University, Finland

† Deceased
Ross M. Thompson  
Institute for Applied Ecology, University of Canberra, Australia

Eva B. Thorstad  
Norwegian Institute for Nature Research, Trondheim, Norway

Denis Tweddle  
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

Günther Unfer  
Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Vienna, Austria

A. Vainikka  
University of Eastern Finland, Department of Environmental and Biological Sciences, Joensuu, Finland

T. Vehanen  
Natural Resources Institute Finland (Luke), Management and Production of Renewable Resources, Viikinkaari, Helsinki, Finland

M. Vera  
Laboratory of Genetic Ichthyology, Department of Biology, University of Girona, Edifici LEAR, Campus Montilivi, Girona, Spain

Rufino Vieira-Lanero  
Estación de Hidrobiología ‘Encoro do Con’, Universidad de Santiago de Compostela, Vilagarcía de Arousa, Pontevedra, Spain

L. Asbjørn Vøllestad  
Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, Blindern, Oslo, Norway

Ryan J. Wasserman  
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

and  
Center for Invasion Biology, SAIAB, Grahamstown, South Africa

Johan Watz  
River Ecology and Management Group, Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden

Olaf L.F. Weyl  
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

and  
Center for Invasion Biology, SAIAB, Grahamstown, South Africa

J.E. Williams  
Trout Unlimited, Arlington, USA

Darragh J. Woodford  
School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

and  
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

Kyle A. Young  
Institute of Evolutionary Biology and Environmental Studies, Universität Zürich, Zürich, Switzerland

Tsungai A. Zengeya  
South African National Biodiversity Institute, SANBI, Claremont, South Africa

Troy G. Zorn  
Michigan Department of Natural Resources Fisheries Division, Marquette Fisheries Station, Marquette, USA
Foreword

The brown trout is an extraordinary fish, endowed by its evolutionary history with the ability to changes its spots – literally and metaphorically – to adapt at lightning speed to new environments. Take the United States, where brown trout introduced in 1883 from a river in Germany, thrived so well and so fast that today they represent the most abundant and widely-distributed trout species in the entire USA, more numerous than the resident rainbow trout. Or Kerguelen, that isolated land mass in the southern Indian Ocean – known to the early English explorers as Desolation Island – where brown trout shipped in by French scientists in the 1950s quickly learned to go to sea, creating one of the most successful sea-trout populations in the world, many monster fish among them.

As any well-travelled angler or biologist will confirm, no two populations of brown trout are quite the same, from Russia to the Atlas Mountains and from the foothills of the Andes to the mountain lochs of Scotland. We even find different forms within the same lake, occupying different zones and breeding at different seasons in different places. Science tells us that the brown trout’s secret lies deep in its evolutionary past and has to do with the number of genes it has, which has enabled it to diversify and adapt with perhaps greater speed than any other fish. From the angler’s point of view (I have been both an angler and an amateur student of aquatic natural history since childhood), the result is a fascinating fish which offers an extraordinary variety of sport. Stalking small, darting wild trout in tiny streams; casting a dry fly for wise old chalk-stream monsters; trailing a fish bait for Salmo ferox in the deep northern lakes; hunting the mighty silver sea trout in summer night-time rivers – all these forms of trout fishing are as different from each other as football is from tennis. Indeed, it was not until the middle of the 20th century that the angling world realised that in pursuing these varied sports, they are hunting essentially for the same species. It has taken modern genetic analysis to give us a proper understanding of speciation in the trout, as is amply dealt with elsewhere in this book. In fact the one fish most anglers thought really was different – the sea trout – has turned out to be exactly the same species as Salmo trutta, but pursuing a very different lifestyle. It is the mystical sea trout, with its beauty, its great speed and strength and its habitual disdain of our flies and lures, which fascinates and tantalises me most of all fish.

A carp is a carp, a cod is a cod and a pike is a pike. Trout are different. They are the chameleons of the river, the jesters and jokers, tantalising, surprising and fooling us repeatedly with their ability to adapt almost as fast as the angler can change his tackle. Where food is rich, they can grow as big as salmon; where it is in short supply, they
mature when they are little more than fingerlings. There are races which have adapted to browsing the bottoms of lakes, while others spend their lives roaming the surface for wind-borne insects. River-dwelling trout may happily go to sea to feed if the cupboard is bare at home, even if their own parents had never been anywhere near salt water. You can almost imagine them swimming proudly back home to show off their smart new silver coats to the dull, stay-at-home relatives they left behind.

While the trout’s beauty, elusiveness and sweet taste have put a high price on its head throughout human history, sport fishing has rarely if ever been its true enemy; most fishermen value their quarry enough to avoid overfishing and do their best to protect the waters in which ‘their’ trout swim. Where the brown trout has struggled, the causes have been those far more insidious human-induced problems of pollution, acid rain, water abstraction, urban development, intensive agriculture and misguided stocking of hatchery-bred fish.

I like to think that in introducing the brown trout to new dominions around the world, we have helped to atone for the damage we have done to many of its home waters in the over-developed Western world. Having been distributed far beyond its original two native continents, Europe and Asia (plus a small part of northern Africa), the brown trout now swims rivers and lakes at suitable latitudes in every continent except Antarctica. With global warming now beyond dispute, I wonder if one day in the far distant future they will make their home there too.

Chris Newton
The Arches, Halmore, Berkeley,
Gloucestershire GL13 9HL, UK
Since Linnaeus first named brown trout as *Salmo trutta* in 1758, this species has been classified under many different common and Latin names. Linnaeus reserved the original name for river trout and recognized two other species; sea-trout *S. eriox* and stream trout *S. fario*. Thus the taxonomic problems started over 200 years ago! Arguments continue as to whether brown trout, including sea-trout, belong to a single species, *Salmo trutta* L., or many species. At the end of the last glacial period in Europe, some 10,000 years ago, different populations of brown trout were geographically isolated from each other. These populations slowly evolved into many varieties which caused the early taxonomic ‘splitters’ of the late 19th and early 20th centuries to elevate them to the species level with over 50 species being described. Their disparity of form, colour or habit may deserve such a distinction but, in my opinion, it is no more than a semantic argument. Unfortunately, a recent handbook of European freshwater fishes lists 27 different *Salmo* species, most being for *S. trutta* (Kottelat & Freyhof, 2007). Jonsson & Jonsson (2011) list over 60 so-called species that can be synonyms of *S. trutta*. These authors conclude that systematic splitting, such as that by Kottelat & Freyhof (2007), is erroneous because it is often based on sometimes accidental species descriptions and does not take into account the high variability of this polytypic species within and among localities, even within a limited geographical area. I strongly agree!

Originally, the brown trout was chiefly a European species, occurring as far north as Iceland, northern Scandinavia and Russia. Western limits were defined by the European coastline and southern limits by the northern coastline of the Mediterranean as well as the islands of Corsica, Sardinia and Sicily, and the Atlas mountains of North Africa. The eastern limits are more difficult to define, but they are probably the Ural mountains, Caspian Sea and as far south as the upper reaches of the Orontes (Asi) river in Lebanon. Anadromous sea-trout populations occur in Western Europe from latitude 42° northwards and in countries bordering the Black and Caspian Seas, but not, surprisingly, the Mediterranean. Some resident populations have undoubtedly arisen from deliberate introductions and this stocking has been practised in some countries for at least 200 years. Brown trout have also been introduced successfully in at least
24 countries outside Europe in the past 150 years. This species is probably one of the world’s 100 most invasive exotic species, and is often blamed for the reduction of native fish populations, due to predation, displacement and competition for food.

The early literature on brown trout is enormous, but is essentially descriptive with few quantitative data. Such material has provided copy for many books dealing with the natural history of brown trout and how to catch it! My 1994 book did not duplicate these texts, but emphasised the quantitative ecology of this successful species, especially the development, testing and use of realistic mathematical models for the population dynamics, growth and energetics of brown trout. This book illustrated the single author approach to a monograph on a particular species (Elliott, 1994), and a similar approach was followed in the more recent excellent text on the ecology of Atlantic salmon and brown trout by the husband and wife team of Jonsson & Jonsson (2011). The advantage of only one or two authors is that there is a coherent approach to the text that reflects the opinions of the author(s). The disadvantage is that the authors cannot be experts on all aspects of their subject. An alternative approach is the multi-author text, and this is well-illustrated by the recent excellent monograph on Atlantic salmon, edited by Aas, Einum, Klemetsen & Skurdal (2011). The obvious advantage of this approach is that it utilises the expertise of many authors and provides a wide, comprehensive coverage of the subject.

The latter approach was used in the present volume with 28 chapters divided into six sections. An introductory chapter covers in more detail some of the points mentioned in this Preface. Such an overlap is inevitable in a multi-author text and emphasises the same important points made by different authors. Section 1 covers phylogeography and genetic structure in four chapters, and reproductive traits in section 2 are also described in four chapters. This is followed by three chapters in section 3 on different aspects of the life-history. Section 4 is the largest in the book with seven chapters on different aspects of population dynamics, including those of the anadromous sea-trout. The impacts of brown trout as a global invader in North America, New Zealand, Argentina and Africa are discussed in the six chapters of section 5. Finally, important aspects of the conservation and management of brown trout are covered in four chapters in section 6. It can be seen from this brief summary that the coverage is comprehensive, and illustrates the evidence-based research that is essential for the successful management of brown trout populations. All the contributors, especially the editors, are to be congratulated on producing a book that will become one of the standard works in the future.

References

Brown trout *Salmo trutta* L. 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 & Maise 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 & Maise 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).
Introduction

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
species or sub-species from the sub-tropical Eurasia (Kottelat & Freyhof 2007). Finally, in Morroco, the so called ‘green trout’, *S. pallaryi* from Isli Lake (Vivier 1948, Mouslih 1987) and the ‘dwarf trout’, *S. akiros* (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

![Figure 1.3](image-url)  

**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. akiros*. 
'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 \textit{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 \textit{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 \textit{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.

**Acknowledgements**

Warm thanks are due to all individuals who contributed to this chapter. N. Sanz, G. Rasmussen, J. Epifanio, Ph. Budy, K. Young and J. Piccolo gave valuable comments of an early draft of this chapter. Meta Potz provided the *S. marmoratus* photograph (Figure 1.1). The advice of M. Esteves on the taxonomy of the southern populations was critical and gently allowed me to include his photographs of the Moroccan lakes (Figure 1.3) that were taken during the Esteve-Melero-Gener Expedition to the Atlas Mountains in 2012.

**References**


Fletcher, C. 1958. Brown trout around the world. The fisherman. US.


