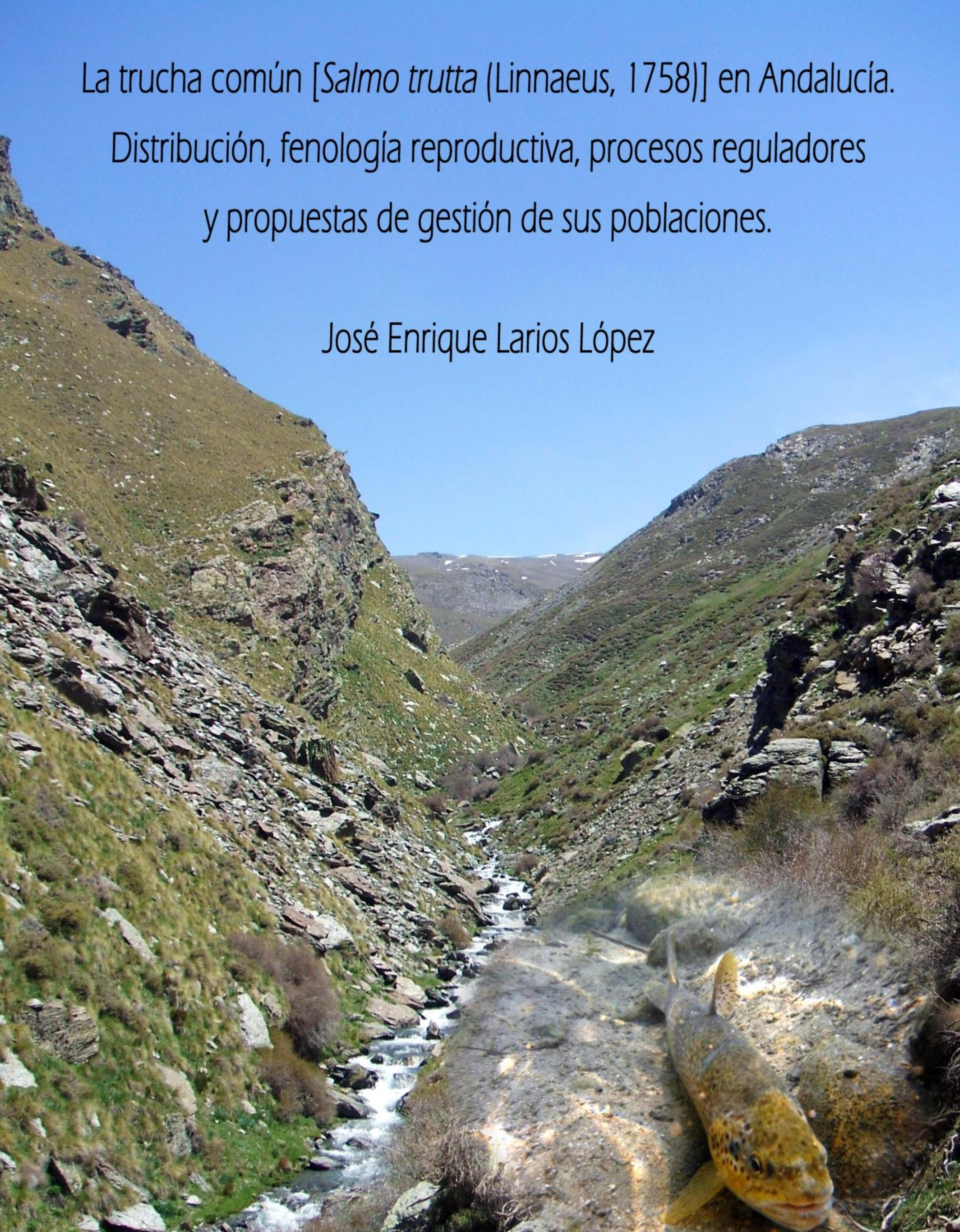
La trucha común [*Salmo trutta* (Linnaeus, 1758)] en Andalucía. Distribución, fenología reproductiva, procesos reguladores y propuestas de gestión de sus poblaciones.

José Enrique Larios López



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Memoria de tesis doctoral presentada por el Licenciado **José Enrique Larios López** para optar al grado de Doctor por la Universidad de Granada

Tesis realizada bajo la dirección de los **Drs. José Manuel Tierno de Figueroa** y **Carlos Alonso González**

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Fdo. José Manuel Tierno de Figueroa

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El doctorando **José Enrique Larios López** y los directores de la tesis **José Manuel Tierno de Figueroa** y **Carlos Alonso González**:

Garantizamos, al firmar esta tesis doctoral, que el trabajo ha sido realizado por el doctorando bajo la dirección de los directores de la tesis y hasta donde nuestro conocimiento alcanza, en la realización del trabajo, se han respetado los derechos de otros autores a ser citados, cuando se han utilizado sus resultados o publicaciones.

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A Aurora

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ÍNDICE

RESUMEN GENERAL

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Las poblaciones de trucha común (*Salmo trutta* Linnaeus, 1758) estudiadas en esta Tesis habitan la región más meridional de la península ibérica, y constituyen el límite geográfico suroccidental de la especie en Europa. Muestran una elevada diversidad genética y están sometidas a condiciones extremas de hábitat y alteraciones ambientales, estando catalogadas en peligro de extinción. Sin embargo, existe una carencia de trabajos científicos que hayan abordado su estudio. Describir su distribución espacial es un primer paso clave y necesario para preservarlas (Capítulo I). De este modo, la especie en la Comunidad Autónoma de Andalucía ha sido detectada exclusivamente en las cordilleras Béticas orientales, a lo largo de casi 710 kilómetros de aguas continentales. Existen 38 poblaciones que habitan ríos, arroyos y embalses en los cursos fluviales altos de tres cuencas vertientes (Guadalquivir, Segura y Cuencas Mediterráneas del Sur), en un rango altitudinal entre 200 y 2200 m. sobre el nivel del mar. Las poblaciones están constreñidas por causas naturales en sus límites superiores y por causas antropogénicas en los inferiores (relacionado principalmente con abusos en la gestión del agua). Se detecta un elevado grado de aislamiento que las mantiene fundamentalmente en el interior de áreas protegidas (62%) y en los primeros kilómetros de los ríos trucheros que abandonan el interior de estos espacios naturales protegidos (32%). Asimismo, al comparar la distribución actual de las poblaciones de trucha común en el área de estudio con la que mostraba la especie en el s. XIX, se observa una reducción de su área de distribución así como un aumento del rango altitudinal.

Por otro lado, entre 2008 y 2013, se ha llevado a cabo un estudio sobre el periodo reproductivo de 12 de estas poblaciones de trucha común en las tres cuencas de captación que habita la especie en este límite ecológico de distribución (Capítulo II). Se detecta cómo el periodo de freza muestra una marcada extensión temporal con respecto a los periodos reproductivos expresados por poblaciones situadas más al norte. La fecha media de freza sí coincide con la tendencia descrita para las poblaciones europeas en función de la latitud, pero se observan unas fechas de inicio y finalización previas y posteriores, respectivamente, a lo esperado. De ese modo, en la mayor parte de las poblaciones estudiadas hay hembras depositando sus huevos desde principios de Octubre hasta finales de Abril/principios de Mayo, lo cual da lugar a un periodo de freza de entre 150 y 170 días, el periodo reproductivo más largo y retrasado conocido para cualquier población de trucha común en toda su área de distribución. Es muy probable que este periodo de freza extendido sea generado en respuesta a la impredecibilidad del clima mediterráneo, si bien el estatus residente de las poblaciones aquí estudiadas haya favorecido este hecho. Asimismo, la temperatura del agua (resultado de latitud, altitud y régimen hidrológico) para una población determinada, podría ser otro de los factores que contribuyen al desarrollo del comportamiento reproductivo detectado. Estas hipótesis son discutidas en relación con los datos existentes para otras poblaciones europeas de *Salmo trutta*.

Otro de los aspectos estudiados en esta Tesis han sido los factores que regulan las dinámicas poblacionales de la trucha común en Andalucía (Capítulo III). Para ello, durante el periodo comprendido entre 2005 y 2014, se han analizado las tendencias poblacionales y ambientales en 18 estaciones de muestreo localizadas en dos cuencas de captación diferentes. Se ha comprobado cómo su reclutamiento es un parámetro poblacional totalmente densoindependiente, regulado de forma exclusiva por factores ambientales. Concretamente de forma negativa por las precipitaciones totales de invierno y positivamente por las de primavera. La baja capacidad de carga de las poblaciones periféricas podría ser un factor determinante en la inexistencia de procesos de retroalimentación negativa sobre la cohorte de alevines. Por contra, alevines y adultos no muestran regulación exógena, pero sí se aprecia reforzamiento de la cohorte en juveniles, así como un efecto positivo de la presencia de adultos del año anterior sobre la densidad de adultos al año siguiente. Sin embargo, no se detecta reforzamiento de la cohorte adulta por parte de los juveniles. Este hecho podría deberse a la escasez de mesohábitats diferenciados para cada clase de edad en esta región periférica, lo que podría estar promoviendo el desarrollo de fenómenos de competencia intraespecífica entre ambas cohortes y el consiguiente desplazamiento de los juveniles. Todos estos resultados son discutidos considerando el conocimiento científico previo existente sobre los mecanismos de regulación exógena en trucha común. Al mismo tiempo se observa un fenómeno muy significativo de sincronía en el reclutamiento debido a Efecto Moran. En este caso la precipitación de invierno principalmente, y las temperaturas de primavera y otoño con menos intensidad, parecen ser las responsables. Finalmente se comprueba cómo la sincronía se reduce cuanto mayor es la distancia geográfica de dos poblaciones dadas, así como sus diferencias en altitud, distancia hasta la cabecera del río y valor del índice de heterogeneidad fluvial (IHF). Debido a que los principales agentes reguladores de la sincronía son factores ambientales, perturbaciones ambientales síncronas tendrían la capacidad de poner el peligro las resiliencia de las poblaciones, aún más si se considera el carácter metapoblacional y de aislamiento que presenta la especie en esta región periférica de estudio, en donde los efectos del Cambio Global se prevé puedan ser devastadores.

Finalmente, considerando todos los resultados previos, se proponen actuaciones concretas y específicas sobre las poblaciones de trucha en Andalucía y los ecosistemas que las albergan (Capítulo IV). Se trata de medidas de gestión administrativa y adaptativa encaminadas a mejorar las políticas de pesca y luchar contra las causas que en la actualidad limitan a estas poblaciones (Capítulo I). Todas ellas están basadas en literatura científica que aborda la conservación de sistemas fluviales y peces de agua dulce, adaptándolas, en cada caso, a las particularidades regionales del área de estudio (política, gestión del agua y clima, principalmente). De este modo, se plantean intervenciones directas sobre el hábitat, modificaciones administrativas de la catalogación actual de algunos tramos trucheros en Andalucía (Ley Andaluza, *Orden 6 de mayo 2014*), restauraciones en fases para los tramos habitados por la trucha arcoíris, así como el mantenimiento de esta especie, y sin condición, en el Catálogo Español de Especies Exóticas Invasoras (*Real Decreto 630/2013*), al haber detectado poblaciones naturalizadas de este salmónido exótico con capacidad reproductiva. La recuperación de todos estos tramos, junto a la reintroducción y reforzamiento con ejemplares de trucha común de haplotipos endémicos de cada subcuenca, será otra de las medidas de gestión a realizar para la conservación de la especie en la región de estudio.

1. INTRODUCCIÓN Y OBJETIVOS GENERALES

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1.1. Origen de la ictiofauna en la península ibérica. Reseña biogeográfica

Las peculiaridades de la ictiofauna continental que habita hoy en día la península ibérica sólo pueden ser concebidas bajo la compleja historia geológica sucedida en esta región durante millones de años (Doadrio y Carmona, 2003). Su carácter casi insular, delimitado por el estrecho de Gibraltar al sur y por los Pirineos al norte (sin obviar otros sistemas montañosos internos menores), junto con la incapacidad de los peces continentales para atravesar estas barreras geográficas podrían hacer pensar, en un primer momento, en el aislamiento geográfico (a escala geológica relativamente reciente), como causa principal del elevado grado de endemicidad detectado para este grupo faunístico en esta región. Sin embargo, este fenómeno se inició mucho antes de la formación de estas barreras. Tres hipótesis (*rutas de colonización*) diferentes, y no excluyentes, se han planteado en relación al origen de los peces continentales en la península ibérica (Doadrio *et al.*, 2011).

I. La hipótesis clásica de Banarescu (1973, 1989, 1992) explica cómo hace 37 millones de años la ictiofauna del este de Asia pudo cruzar Siberia hacia centro Europa y alcanzar regiones mediterráneas, antes de que en el Estrecho de Turgai surgieran los Montes Urales (Figura 1.1). En el caso de la península ibérica la elevación de los Pirineos supondría el fin de este proceso. Si bien este modelo de colonización explica el origen de ciertas especies en las penínsulas mediterráneas (itálica e ibérica principalmente), no aclara en su totalidad la gran cantidad de endemismos ictiológicos surgidos en estas regiones.

II. Años después del desarrollo de la Teoría de Banarescu o "dispersión norteña", surgió la que se conoce como Teoría Lago Mare o "dispersión sureña" (Bianco, 1990), según la cual estos endemismos procederían de un fenómeno de colonización que tuvo lugar durante la *Crisis del Messiniense*, una etapa de la historia geológica en la que la cuenca mediterránea se secó casi por completo, hace unos 5,3 millones de años (Figura 1.1). Tras este periodo seco, el efecto del régimen monzónico existente en el norte de África (Griffin, 2002), junto con el agua dulce proveniente del Mar de Paratethys que rellenó la cuenca mediterránea (Hsü *et al*., 1977), originaron un sistema oligohalino que permitió la dispersión, colonización, diversificación y posterior especiación de peces continentales en las regiones más meridionales de Europa y norte de África.

III. Sin embargo, la Teoría Lago Mare no esclarecía por completo la existencia de todos los endemismos circunmediterráneos actuales. Finalmente, Perea *et al*. (2010) propusieron un fenómeno de dispersión previo, durante el Oligoceno Temprano, hace más de 25 millones de años (Figura 1.1). Según sus estudios, ciertos grupos de peces podrían haber colonizado Europa desde el suroeste de Asia, a través de un puente entre los Balcanes, Anatolia e Irán.

Figura 1.1. Distribución de tierras emergidas y sumergidas en la región de la actual cuenca mediterránea durante diferentes momentos de la escala geológica. De arriba abajo: hace 37 millones de años (Eoceno Tardío), hace 25 millones de años (Oligoceno Temprano) y hace 5,3 millones de años (Plioceno). Figura adaptada de Perea *et al.* (2010).

Sea cual fuera la ruta seguida por los taxones que alcanzaron la península ibérica, una vez en ella, y durante millones de años, la diversificación de los diferentes linajes hasta dar lugar a las especies que actualmente habitan la región ha seguido complejos procesos de aislamiento reproductivo, especiación y extinciones, todo ello asociado a drásticos eventos relacionados con la historia paleoclimática e hidrogeológica de esta región, sin obviar el histórico, intenso y generalizado impacto antropogénico asociado a los sistemas fluviales en las cuencas mediterráneas (Blondel *et al.*, 2010).

Comprender muchas de las adaptaciones de la ictiofauna mediterránea (y de la fauna en general de este área) que ha llegado hasta nuestros días requiere considerar un aspecto fundamental que ha moldeado todo el proceso evolutivo en esta región durante los últimos miles de años: el desarrollo paulatino del clima mediterráneo desde la finalización del último periodo glacial en el Pleistoceno. El retroceso progresivo del hielo dio lugar a un clima poco afable con los ecosistemas fluviales, caracterizado, en la actualidad, por presentar un régimen impredecible de precipitaciones anuales, limitado, a su vez, por la disponibilidad de agua durante el periodo de estiaje estival (Grantham *et al*., 2010). La presencia de estaciones frías seguidas por estaciones cálidas (generalmente húmedas y secas, respectivamente), provoca intensas variaciones en el nivel flujo de los cursos de agua (Gasith y Resh, 1999; Tierno de Figueroa *et al*., 2013), a lo cual han debido de adaptarse las especies residentes (Carmona *et al*., 1997; Giller y Malmqvist, 1998; Gortázar *et al*., 2007).

Hoy en día, a las exigencias ambientales del clima mediterráneo hay que sumar el notable efecto (directo e indirecto) que han tenido, y tienen, las civilizaciones humanas sobre las especies de peces continentales (Hamdy *et al*., 1995; Kondolf y Batalla, 2005). Su impacto puede resumirse en contaminación, extracciones de agua, desconexión fluvial e introducción de especies exóticas. Esto, *per se,* ya posee el potencial necesario para limitar la capacidad de dispersión de las especies, reducir sus áreas de distribución y, en algunos casos, extinguir poblaciones y especies completas.

Por todo ello, la realidad actual de los ríos circunmediterráneos es que el 36% de sus peces continentales están amenazados (catalogados en peligro crítico, amenazados o vulnerables), siete especies se han extinguido por completo y una de ellas lo está en la naturaleza (Tierno de Figueroa *et al*., 2013). Pero esta situación es aún más preocupante al considerar únicamente las especies endémicas de esta región. En ese caso el 56% de ellas se encuentra catalogada con algún grado de amenaza (Smith y Darwall, 2006). En el caso concreto de la fauna autóctona de la península ibérica, destaca el elevado número de endemismos ibéricos, gran parte de ellos tradicionalmente incluidos en el género *Barbus* (la mayoría actualmente transferidos al género *Luciobarbus*) en el género *Chondrostoma* (hoy día transferidos o descritos directamente en los géneros *Achondrostoma*, *Iberochondrostoma*, *Parachondrostoma* o *Pseudochondrostoma*) y en el género *Squalius* (algunos de ellos recientemente transferidos al género *Iberocypris*) (Doadrio, 2001; Tierno de Figueroa *et al*., 2007; Kottelat y Freyhof, 2007).

Si nos centramos en la Comunidad Autónoma de Andalucía, 19 de sus 22 especies nativas presentan algún grado de amenaza (siendo más de la mitad endemismos ibéricos).

1.2. Los salmónidos

Presencia de vejiga natatoria conectada al tubo digestivo (condición fisóstoma), aletas con radios blandos y aleta adiposa, son los principales rasgos taxonómicos que caracterizan al orden de los Salmoniformes. La relación entre sus diferentes familias es incierta (Greenwood *et al*., 1973), si bien la familia Samonidae posee un origen temprano dentro del orden (Carroll, 1988). Se trata de peces de tamaño medio/grande, con cuerpo fusiforme, línea lateral y escamas cicloideas (excepto en la cabeza).

Dominio: Eukaryota
Reino: Animalia
Filo: Chordata
Subfilo: Vertebrata
Clase: Actinopterygii
Subclase: Neopterygii
Infraclase: Teleostei
Orden: Salmoniformes
Familia: Salmonidae
Subfamilia: Salmoninae

Tabla 1.1. Encuadre taxonómico de la subfamilia Salmoninae

Poseen una distribución Holártica, por lo que habitan en Europa, norte de América y Asia y extremo norte de África (Snoj *et al*. 2011).

En el caso concreto de la subfamilia Salmoninae (Tabla 1.1), se diferencian, al menos, treinta especies repartidas en cinco géneros (Nelson, 2006): *Brachymystax*, *Hucho*, *Oncorhynchus*, *Salvelinus* y *Salmo* (a este último pertenece la especie estudiada en esta memoria de Tesis). Otros cuatro géneros extra han sido propuestos para esta subfamilia (King *et al*., 2007), pero todo parece indicar que pueden ser enmarcados en los cinco originales (Phillips *et al*., 2000; Crespi y Fulton, 2004; Kottelat y Freyhof, 2007; Jonsson y Jonsson, 2011).

1.3. El género Salmo

La enorme plasticidad fenotípica que caracteriza a este género (Elliot, 1994; Ayllón *et al*., 2010) en respuesta a su elevada capacidad de adaptación a distintos tipos de hábitats (velocidad de corriente, salinidad, temperatura, etc.), estrategias de vida (anadromía o residencia continental) y periodos de freza (Gortázar *et al*., 2007), hace que su taxonomía siga siendo a día de hoy una materia que suscita gran controversia. De hecho, más de 70 especies y subespecies han sido propuestas para señalar diferentes singularidades locales (Kottelat y Freyhof, 2007; Webb *et al*., 2007; McKeown *et al*., 2010).

La palabra *salmo* parece derivar de la palabra latina *salire* (saltar), haciendo referencia directa a la capacidad de salto que ponen en práctica los individuos de este género, fundamentalmente adultos durante su periodo reproductivo, para ascender hasta los tramos altos de los cursos de agua // La palabra *salar* podría hacer referencia a la palabra latina *salarius* (sal, salado), pudiendo hacer referencia a la fase marina que presenta el salmón // La palabra *trutta* podría derivar del latín *tructa*, que a su vez provendría del griego τρώκτης (trōktēs, "tragona") (Corominas and Pascual, 1992).

Actualmente, se asume que este género está compuesto por dos especies: el salmón atlántico (*S. salar* Linnaeus, 1758) y la trucha común (*S. trutta* Linnaeus, 1758). Así, mientras el salmón atlántico (a partir de ahora salmón) es una especie generalmente anádroma (aunque se han descrito excepcionalidades de poblaciones residentes en Europa [Kazakov, 1992] y norteamérica [Webb *et al.*, 2007]), la trucha común presenta ambas estrategias de vida (Marco-Rius, 2013; Cucherousset *et al.*, 2005) (a partir de ahora reos –estrategia anádroma – y trucha de río – residente –).

Esta capacidad anádroma del género *Salmo* presenta un gradiente latitudinal, cuyo punto de inflexión se sitúa frente a las costas de noroccidentales de la península ibérica (cuenca del río Lima, al norte de Portugal [SNPRCN, 1991]). De ese modo, el área de distribución del salmón y de los reos se sitúa exclusivamente por encima de esta región, mientras que la de la trucha de río se extiende a ambos lados (Figuras 1.2 y 1.3). Por tanto, los ríos situados en latitudes inferiores al *límite de anadromía* albergan exclusivamente truchas de río. Este último es el caso de las poblaciones estudiadas en la presente memoria de Tesis.

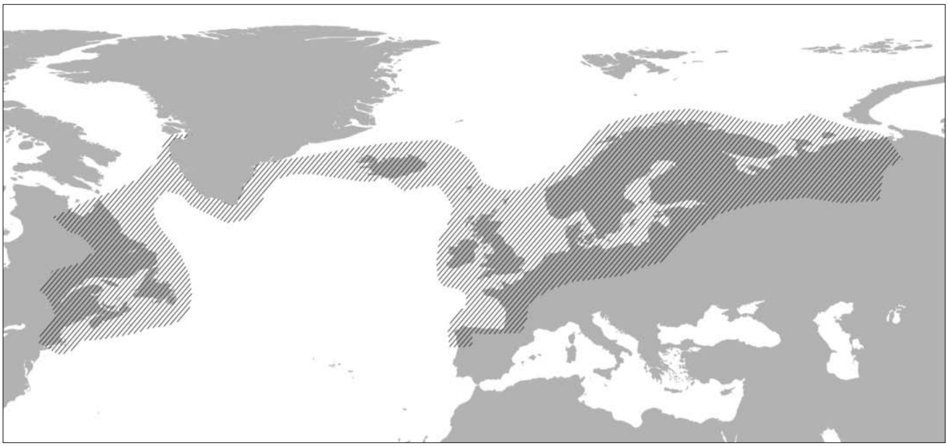

Figura 1.2. Distribución natural del salmón atlántico (*S. salar*) en sombreado. Figura adaptadas de Jonsson y Jonsson (2011).

La historia biogeográfica del género *Salmo* parece indicar que las dos especies (*S. salar y S. trutta*) sobrevivieron al último máximo glacial (UMG) al encontrar refugios no helados. Por un lado, refugios situados al sur (regiones no alcanzadas por el hielo) y por otro, refugios situados al norte de Europa y América (la cobertura helada durante el UMG no fue una masa de hielo continua) (Clark *et al*., 2004; MacKeown, 2005). Esta distribución en *parches aislados* favoreció la aparición de divergencias genéticas interpoblacionales durante el periodo glacial (Bernatchez, 2001; Mackeown *et al*., 2010).

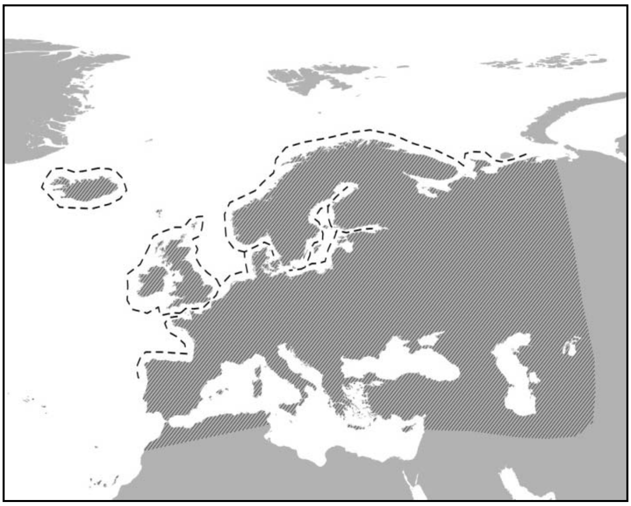

Figura 1.3. Distribución natural de *Salmo trutta*. En sombreado el de la trucha común residente y en línea discontínua se indican las costas donde habita el reo (estrategia anádroma). Figura adaptada de Jonsson y Jonsson (2011).

Posteriormente, hace entre 8.000 y 14.000 años, a la par que los hielos se fueron retrayendo, los refugios glaciales se comportaron como núcleos de expansión, y los diferentes linajes genéticos que albergaban se fueron expandiendo (Ferguson, 2006). En esta expansión postglacial, en ocasiones, linajes procedentes de diferentes refugios glaciales contactaron y tuvieron la oportunidad de entrecruzarse.

Este hecho ha sido corroborado por medio de estudios de ADN mitocondrial en trucha común (p. ej. García-Marín *et al.* 1999; Suárez *et al.*, 2001; Sanz *et al.* 2002; Antunes *et al.* 2006; Apostolides *et al.* 2007). Estos trabajos no obvian el hecho de que a partir del s. XIX el factor humano ha sido el mayor causante de cruces e introgresiones genéticas, principalmente por medio de traslocaciones y cría en cautividad. Todo esto ha dado lugar a la compleja distribución haplotípica que muestra la trucha común en nuestros días (Figura 1.4), una característica aún no resuelta y que muy probablemente sea campo de investigaciones futuras conforme nuevas técnicas moleculares sean desarrolladas (Jonsson y Jonsson, 2011).

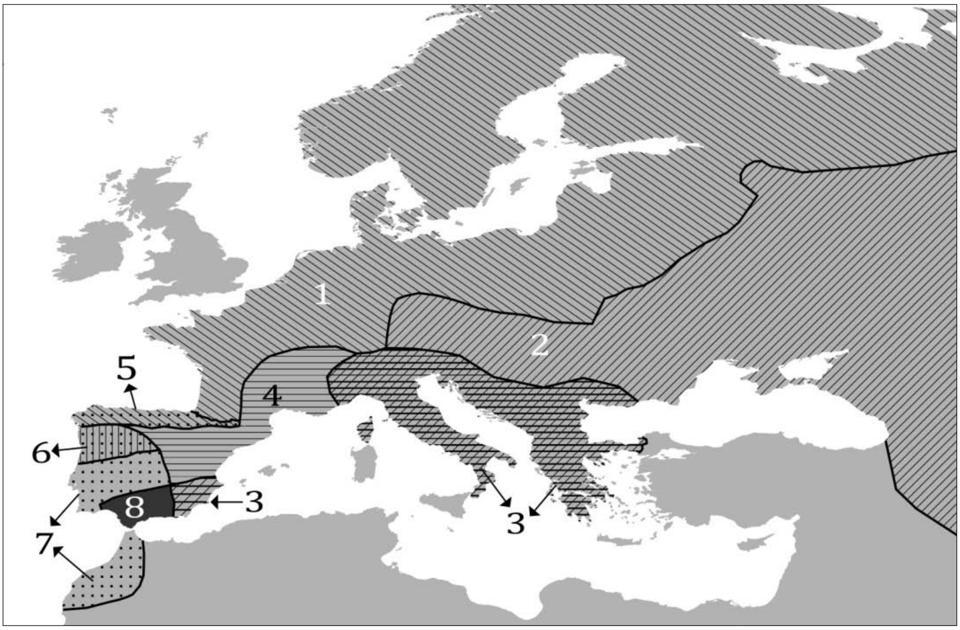

Figura 1.4. Modelo de las áreas biogeográficas de *Salmo trutta* según análisis de ADN mitocondrial. 1) Noratlántico; 2) Danubio; 3) Adriático andaluz más mediterráneo; 4) Mediterráneo; 5) Suratlántico y Noratlántico; 6) Duero más Suratlántico; 6) Duero; 7) Suratlántico; 8) Adriático andaluz. Figura adaptada de Suárez *et al.* (2001).

1.4. La trucha común

La plasticidad fenotípica característica del género *Salmo* presenta su máximo exponente en la trucha común, mostrando gran cantidad de singularidades locales a lo largo de toda su área de distribución (Kottelat y Freyhof, 2007). Su elevado potencial adaptativo, junto al carácter globalizador del ser humano, ha hecho de este pez una de las especies más invasoras de la Tierra (Valiente *et al*., 2010), provocando que su distribución natural (principalmente europea, aunque alcanza el norte de África; Figura 1.3) se haya expandido artificialmente a todos los continentes (Klemetsen *et al*., 2003).

En la península ibérica la trucha común alcanza las cabeceras de casi todos los ríos, excepto los de las cuencas del Guadiana y algunos cursos del agua del este y sur de España (Doadrio 2001).

En el caso de Andalucía, esta especie es el único salmónido endémico presente y las poblaciones se encuentran en uno de sus bordes de distribución meridional. Además, debido a su carácter residente y elevado grado de aislamiento poblacional, esta especie se encuentra en un grave estado de conservación. Así, la trucha común es catalogada en Europa como "preocupación menor" (Freyhof 2011), en España como "vulnerable" (Doadrio 2001) y en Andalucía "en peligro" (Franco Ruíz y Rodríguez de los Santos 2001). Esta tendencia a intensificar su grado de amenaza conforme las poblaciones se acercan a su borde de distribución es un hecho reconocido (Hampe y Petit, 2005). Por todo ello, desde el año 2005, la trucha común en Andalucía únicamente puede ser pescada en la modalidad deportiva de *captura y suelta*.

1.5. Justificación de la Tesis

Son muy numerosos los trabajos que han abordado diferentes aspectos biológicos y ecológicos de la trucha común en todo su área de distribución (Jonsson y Jonsson, 2011). En el caso de la península ibérica muchos investigadores podrían ser destacados por las aportaciones realizadas. Además, son frecuentes las colaboraciones científicas entre ellos con la intención de favorecer, de un modo multidisciplinar, el avance del conocimiento en diferentes ámbitos de estudio de la especie en la península. Por tanto, y de forma sucinta, se hace necesario mencionar a algunos de estos investigadores, ya sea por su relevancia en el estudio sobre la ictiofauna en general, o por sus aportaciones al conocimiento de la trucha común en particular.

- Destaca la intensa labor de los Dres. Javier Lobón-Cerviá, Diego García de Jalón, Graciela Nicola, Irene Parra, Daniel Ayllón o Carlos Alonso, por haber arrojado luz sobre los factores reguladores de la densidad y las dinámicas poblacionales de la trucha común (p. ej. Alonso *et al*., 2011; Parra *et al*., 2011; Lobón-Cerviá, 2014)
- Los trabajos de los Dres. Ignacio Doadrio y Benigno Elvira por sus aportaciones sobre conservación y genética de la ictiofauna continental (p. ej. Elvira *et al*., 2015), y las investigaciones de la Dras. Ana Almodóvar, Nuria Sanz y Annie Machordom sobre la genética de la trucha común de forma concreta (Machordom *et al*., 2000; Sanz *et al*., 2000). Gracias a todos ellos, entre otros, se ha podido comenzar a dilucidar la historia evolutiva de esta especie en la península.
- Los estudios del Dr. Javier Sánchez-Hernández sobre alimentación y crecimiento (p. ej. Sánchez-Hernández *et al*., 2011), los del Dr. Alfredo Ojanguren en relación al efecto de la temperatura sobre diferentes aspectos biológicos de la trucha común (p. ej. Ojanguren y Braña, 2003), o los del Dr. Javier Gortázar con respecto a la reproducción de la especie (p. ej. Gortázar, 2015), también han permitido sentar sólidas bases para futuras investigaciones.
- Los trabajos de los Dres. Carlos Fernández Delgado, Virgilio Hermoso o José Prenda, encaminados a la conservación de la ictiofauna en sistemas mediterráneos, y en la región andaluza en particular (p. ej. Fernández-Delgado *et al*., 2014; Hermoso *et al*., 2009).

Sin embargo, todos estos trabajos han centrado sus esfuerzos en poblaciones de trucha común situadas en el centro y norte de la península ibérica. De hecho, no es hasta el año 2007 cuando surge la primera publicación científica[1] que focaliza su investigación en una población andaluza (concretamente en el río Castril, Granada) (Gortázar *et al*. 2007). En este trabajo los autores observaron una fenología reproductiva excepcional, al parecer adaptada al clima mediterráneo.

De hecho, se sabe que las poblaciones de cualquier especie que habitan áreas situadas en su límite ecológico (bordes de distribución) se encuentran sometidas a fuertes procesos selectivos (clima mediterráneo, por ejemplo), por lo que puede verse favorecida la aparición de adaptaciones locales (Lesica y Allendorf, 1995; Antunes *et al*., 2006), aún más si la especie es especialmente plástica, tal y como es el caso de la trucha común (Pakkasmaa *et al*., 2001). Si además consideramos que las poblaciones de trucha que viven en las Cordilleras Béticas han estado aisladas desde hace miles de años (García-Marín *et al*., 1999), los procesos de diferenciación genética no se habrían visto interrumpidos.

Entonces, ¿cómo es posible que poblaciones de una especie con elevado interés social, habitando su borde de distribución natural más meridional de Europa, aisladas desde hace miles de años, bajo influencia del exigente clima mediterráneo y catalogadas en peligro de extinción, no hubieran sido investigadas científicamente hasta el año 2007?

Es probable que el interés de la especie desde el punto de vista de la pesca deportiva haya enmascarado la importancia científica que estas poblaciones pueden tener para el conjunto global de la especie. Aunque también es posible que la escasez de grupos de investigación en ictiología

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[1] Cabría destacar también un trabajo no publicado, pero presentado en congreso, sobre distribución histórica de la especie en el siglo XIX, para Castilla la Mancha y Andalucía (Menor y Prenda, 2006).

en esta región, lo que contrasta con la existencia de numerosos grupos centrados en el estudio de otros organismos, se encuentre tras la respuesta.

Debido a la carencia de información sobre la especie en Andalucía y a su catalogación en peligro de extinción, en el año 2005 la Consejería de Medio Ambiente de la Junta de Andalucía puso en marcha el "*Proyecto de restauración de las poblaciones de trucha común en Andalucía*", a través del cual surgieron varios trabajos científicos sobre: (1) distribución histórica (Sáez Gómez, 2010), (b) genética (Almodóvar *et al*., 2010), (c) capacidad de carga (Barquín *et al*., 2010), y (d) caudales ecológicos y preferencias tróficas (Barquín *et al*. 2015). Los resultados de estos trabajos (v .g. desaparición de gran cantidad de poblaciones desde el s. XIX, descubrimiento de cinco haplotipos genéticos nuevos a nivel mundial, necesidad de control de caudales, o la selección activa de presas en función de la clase de edad, respectivamente, entre otros resultados) volvieron a poner de manifiesto la necesidad de continuar la investigación de las poblaciones de trucha que habitan esta región.

Es por ello que, a finales de 2010 y tras haber llevado la dirección técnica del proyecto, se plantea por parte del doctorando la posibilidad de avanzar en el estudio científico de la trucha común en Andalucía utilizando parte de la información de campo obtenida y centrándose en aspectos de su distribución, reproducción, dinámicas poblacionales y gestión.

1.6. Objetivos de la Tesis

De forma específica, los objetivos de esta Tesis son:

1. Identificar factores históricos, geográficos y administrativos responsables de la distribución actual de la trucha en las cordilleras béticas meridionales.
2. Determinar el número de poblaciones de trucha común que habitan la región.

3. Establecer los límites exactos de distribución (superiores e inferiores) de cada población e identificar sus causas (naturales y/o antropogénicas).
4. Describir los patrones regionales y locales del periodo reproductivo de la trucha común en las Cordilleras Béticas meridionales.
5. Comparar las fechas de freza obtenidas con el resto de poblaciones europeas.
6. Discutir los resultados obtenidos dentro del marco del clima mediterráneo.
7. Determinar los factores que regulan la variabilidad temporal de la dinámica de poblaciones en la región de estudio por medio del análisis de las abundancias de grupos de edad.
8. Cuantificar la sincronía poblacional e identificar sus causas (posible efecto Moran).
9. Identificar las características del hábitat que favorecen la sincronía entre las poblaciones.
10. Proponer medidas de gestión administrativa a escala local, encaminadas a mejorar la conservación de la especie, una vez conocidos los aspectos de distribución, reproducción y dinámica poblacional característicos de estas poblaciones.
11. Discutir los efectos del Cambio Global sobre la distribución actual de la especie en la región de estudio y proponer medidas de gestión adaptativa encaminadas a paliar sus efectos.

1.7. Estructura de la memoria de Tesis

Tras el **resumen** inicial, se realiza una **introducción** en la que se enmarca a la ictiofauna europea y al género *Salmo* en un contexto biogeográfico y taxonómico, repasando aspectos generales sobre la trucha común en su área de distribución, así como en la península ibérica, justificando a continuación la necesidad de realizar trabajos de investigación sobre las poblaciones situadas más al sur. Unas poblaciones que se encuentran amenazadas de extinción (Franco Ruíz y Rodríguez de los Santos 2001) y que apenas han sido objeto de estudio, a pesar de haber mostrado un elevado grado de diversidad genética (Almodóvar *et al*. 2010) y encontrarse inmersas en un proceso activo de retracción poblacional (Sáez Gómez, 2010).

Considerando esos escasos trabajos previos, a continuación se presentan los **objetivos** de esta Tesis. Su consecución, presentada a lo largo del resto de capítulos de los que se compone la memoria de Tesis, aportará un valioso conocimiento y sentará unas bases sólidas para la realización de futuras investigaciones sobre estas poblaciones meridionales de trucha común y para la gestión de sus poblaciones.

En un capitulo posterior sobre "**Materiales y Métodos**", se presenta una descripción general del área de estudio, así como de la metodología empleada, la cual será ampliada notablemente en cada uno de los siguientes capítulos específicos.

Así, esta memoria de Tesis se compone de cuatro **capítulos principales**, citados a continuación, por medio de los cuales se pretende dar respuesta a los objetivos planteados anteriormente:

Capítulo I. *Distribución de la trucha común (*Salmo trutta *Linnaeus, 1758) (Teleostei: Salmonidae) en su límite europeo más suroccidental: posibles causas*.

- Se delimitarán de forma exhaustiva (coordenadas GPS) todas las poblaciones de trucha común situadas en la región andaluza. Se indicarán los límites superiores e inferiores de cada una de ellas, así como los factores (naturales o antropogénicos) que hacen que cada población comience (límite superior) o finalice (límite inferior) en los puntos indicados. Además, se comparará la distribución histórica que tuvo la trucha común en el área de estudio con la que presenta hoy en día, y se analizarán qué factores geográficos y administrativos han promovido su distribución actual.

Capítulo II. *Freza extendida en poblaciones de trucha común (*Salmo trutta*) del sur de la península ibérica: el papel de la variabilidad climática*.

- Se analizará el periodo reproductivo observado durante seis campañas anuales consecutivas de muestro en 12 poblaciones independientes de trucha común (diferentes cuencas y subcuencas), distribuidas a lo largo de todo el área de estudio. Se indicará la fecha más temprana y más tardía en la que se han detectado hembras con huevos, lo cual permitirá indicar periodos totales susceptibles de encontrar reproducción activa en cada uno de los ríos estudiados. Esto se llevará a cabo mediante la manipulación directa de los ejemplares capturados (masajes abdominales para sexar cada individuo e identificar su estado de maduración). La intención de este trabajo es comprobar si la reproducción extendida detectada en el río Castril (Gortázar *et al*., 2007) es un fenómeno aislado o bien un carácter expresado por la especie de forma generalizada en sus poblaciones meridionales. Los resultados obtenidos serán discutidos en el contexto de la tipología mediterránea de los ríos de estudio.

Capítulo III. *Factores reguladores de las dinámicas síncronas en poblaciones de trucha común en el borde trasero de su distribución nativa*

- Analizando series temporales (precipitaciones, temperatura y datos demográficos) de 13 puntos de muestreo repartidos por las cuencas del río Segura y río Genil (vertientes hidrográficas independientes) durante 7 campañas (años) de muestreo, se pretende determinar qué factores modulan las dinámicas poblacionales de la trucha común en la región de estudio. Además se comprobará si estos factores moduladores de las dinámicas pueden estar determinando la sincronía poblacional en la región de estudio a través de un Efecto Moran. En caso de ser así, se determinarán qué características de sitio (aspectos geográficos, fisiográficos, edafológicos, de mesohábitats, y variables relacionadas con los índices de calidad de riberas, QBR, de hábitat fluvial, IHF, y de refugio, IR) podrían estar favoreciendo dicho Efecto Moran.

Capítulo IV. *Cómo prevenir la extinción de poblaciones amenazadas viviendo en un borde de distribución: propuestas de gestión para las poblaciones más meridionales de trucha común (*Salmo trutta*) en Europa.*

- En este capítulo se pretende aportar un conjunto de herramientas útiles que permitan conservar todas y cada una de las poblaciones de trucha común que habitan el área de estudio, las cuales ya están catalogadas en peligro de extinción. Se tratará de un compendio de medidas de gestión administrativa y adaptativas, en ocasiones específicas para cada población (río). Para ello serán considerados todos los resultados obtenidos previamente: distribución de la especie en la región de estudio (Capítulo I), así como aspectos relacionados con su reproducción (Capítulo I) y con los factores reguladores de sus dinámicas poblacionales (Capítulo III).

Aunque cada capítulo posee sus propias discusiones, finalmente se presenta una breve **discusión global**, en la cual se relacionan todos los resultados obtenidos en cada uno de los capítulos. De este modo se obtendrá una visión integradora de los diferentes aspectos estudiados sobre la especie en la región de estudio. Además se propondrán una serie de **líneas de investigación futuras** complementarias a los resultados aquí obtenidos. Dichas investigaciones, en caso de ser llevadas a cabo, aumentarán el conocimiento general de la especie, y el de estas poblaciones meridionales en particular.

Por último se presentan, una a una, las **conclusiones** más relevantes obtenidas en esta memoria de Tesis.

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2. MATERIAL Y MÉTODOS GENERALES

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2.1. Área de estudio

La trucha común se encuentra de forma natural en las cabeceras de casi todos los cursos fluviales de la península ibérica, excepto en la cuenca del Guadiana y algunos ríos del sur y del este de España (Doadrio, 2001). Debido a que los datos recabados, analizados y discutidos en esta Tesis se centran en sus poblaciones residentes en las sierras Béticas más meridionales, los resultados aquí obtenidos hacen referencia a las poblaciones que habitan tres grandes vertientes hidrográficas: cuenca del Guadalquivir, cuencas Mediterráneas del Sur y cuenca del Segura (Figura 2.1). En concreto, son objeto de estudio todas las poblaciones de trucha común de los ríos y arroyos que discurren por el interior de la Comunidad Autónoma de Andalucía.

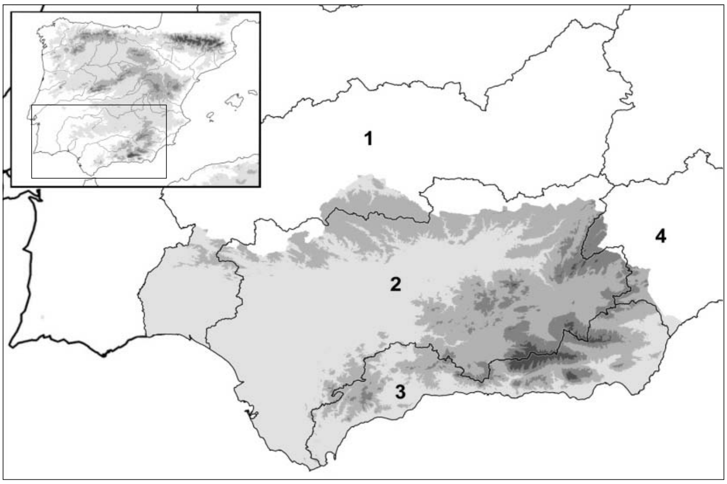

Figura 2.1. Localización del área de estudio. Relieve y vertientes hidrográficas: 1) Guadiana, 2) Guadalquivir, 3) Mediterráneas, 4) Segura.

2.2. Material y métodos

Los trabajos de campo fueron llevados a cabo entre los años 2005 y 2014, dentro de diversos programas de gestión y conservación de ecosistemas fluviales en general, y de la trucha común en particular, desarrollados por la Consejería de Medio Ambiente de la Junta de Andalucía. En todos ellos el doctorando trabajó desde un principio como Técnico en Biodiversidad, y posteriormente como Técnico responsable y colaborador de estos proyectos:

- Restauración de las poblaciones de trucha común en Andalucía (1589/2007/M/00)
- Seguimiento de los efectos del Cambio Global en Sierra Nevada: 2010-2014 (562/2010/M/00)
- Erradicación de poblaciones naturalizadas de trucha arcoíris en Andalucía
- Censo andaluz de pesca

La ubicación de las estaciones de muestreo utilizadas para el censo anual de pesca (Figura 2.2) fue seleccionada de acuerdo a varios criterios (Consejería de Medio Ambiente de la Junta de Andalucía, 2006), entre los que destacan el grado de introgresión genética, la presencia de cotos de pesca o la densidad de trucha en los ríos, todo ello de acuerdo a escasos estudios técnicos previos realizados hasta esa fecha en la región (García de Jalón *et al*., 2003; Machordom *et al*., 2003).

La metodología empleada para los estudios realizados en cada uno de los capítulos que componen esta Tesis se expone detalladamente en cada uno de ellos, si bien, y a modo de resumen, a continuación se señalan los aspectos metodológicos generales de cada investigación.

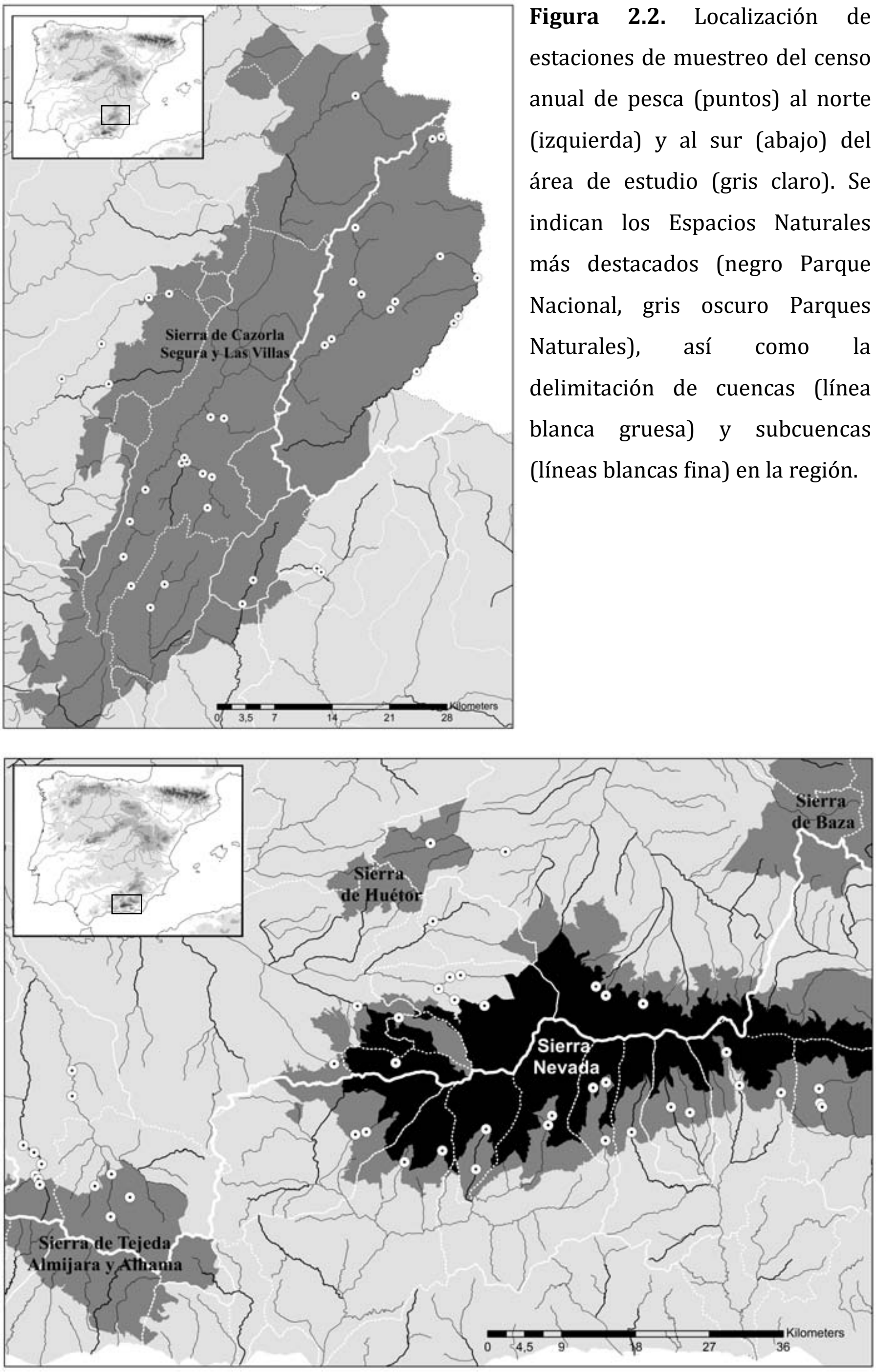

Figura 2.2. Localización de estaciones de muestreo del censo anual de pesca (puntos) al norte (izquierda) y al sur (abajo) del área de estudio (gris claro). Se indican los Espacios Naturales más destacados (negro Parque Nacional, gris oscuro Parques Naturales), así como la delimitación de cuencas (línea blanca gruesa) y subcuencas (líneas blancas fina) en la región.

Capítulo I. *Distribución de la trucha común (*Salmo trutta *Linnaeus, 1758) (Teleostei: Salmonidae) en su límite europeo más suroccidental: posibles causas.*

En primer lugar, utilizando información relativa a distribución histórica de la trucha común (Menor y Prenda 2006; Sáez Gómez 2010), bibliografía actual (*inventario de especies terrestres y de agua dulce*, Real Decreto 556/2011) y entrevistas personales (agentes forestales, pescadores, pastores, etc.), se identificaron las masas de agua con *presencia segura* y *presencia probable* de la especie en la región de estudio: a) todos los ríos pertenecientes a las cuencas mediterráneas del sur, b) la cuenca del río Guadalquivir y b) en aquellos cursos fluviales de la cuenca del río Segura que discurren por Andalucía. Durante 2008 y 2009 se llevaron a cabo muestreos cualitativos con pesca eléctrica en todas esas masas de agua previamente identificadas, lo que permitió determinar 1) la presencia/ausencia de la especie en cada una de ellas, 2) los límites superiores e inferiores de cada población y 3) los factores naturales (*temperatura del agua*, *salto natural infranqueable*, *sequía estival* o *poblaciones con imposibilidad de ascender más por llegar hasta el nacimiento del río*) o antropogénicos (utilizamos los factores señalados por Clavero *et al*., [2010]) que implicaban el comienzo o el fin de las poblaciones en cada uno de los límites. Además, se consideraron otros factores que podrían haber influido a la distribución actual de la especie: a) la orografía de la región de estudio y b) la distribución de espacios naturales protegidos (EENNPP) en ella.

Todo ello ha permitido obtener el mapa de distribución de la trucha común en Andalucía y la distancia total (km) de cursos fluviales habitados en la región de estudio, así como la distancia parcial que discurre por el interior de EENNPP.

Capítulo II. *Freza extendida en poblaciones de trucha común (*Salmo trutta*) del sur de la península ibérica: el papel de la variabilidad climática.*

Ante la imposibilidad de aplicar de forma homogénea una sencilla metodología de observación de frezaderos (Dunham *et al*., 2001) para determinar el periodo reproductivo de la trucha común en la región de estudio (*causas justificadas en el capítulo*), se decidió aplicar una metodología que aunase pesca eléctrica y masajes abdominales, con la intención de determinar 1) el género de los individuos, 2) el estado de maduración de los gametos y 3) las fechas de comienzo y fin del periodo reproductivo de estas poblaciones.

Esta metodología fue aplicada durante seis campañas consecutivas (2008 a 2013; entre los meses de septiembre a junio) sobre 12 poblaciones residentes en las tres cuencas fluviales habitadas (Figura 2.2). Los resultados obtenidos durante los dos primeros años permitieron determinar un periodo de freza general y el resto de campañas fue invertido en afinar las fechas de comienzo y fin de cada etapa reproductiva.

En cada ocasión de muestreo se procuró analizar un mínimo de 30 truchas adultas (ejemplares ≥ 2 años; identificación de clases de edad por medio de sus longitudes furcales) por punto. Todos los ejemplares analizados fueron pesados, medidos y masajeados ligeramente para determinar su sexo y estado de maduración. Tras su manipulación se devolvieron al mismo tramo de río donde fueron capturados.

Las hembras determinaron la duración del periodo reproductivo (los machos producen esperma de forma previa y posterior al desarrollo de huevos por parte de las hembras). Los ejemplares sexados como hembras fueron clasificados en tres categorías: a) hembra formando huevos, b) hembra con huevos maduros, o c) hembra recién frezada (con abdomen laxo y/o restos de huevos).

Una población se encontraba en un momento reproductivamente activo si durante esa ocasión de muestreo se detectaban a) hembras de “categoría b”, o b) hembras de “categoría a y c” a la vez. De este modo se determinaron “periodos de freza seguros”, periodos de freza probable” y “periodos de freza total” (suma de periodos seguros y probables). Además se calculó la duración total del periodo reproductivo (en días) y la fecha media de reproducción para cada población.

Todos estos resultados se compararon con los obtenidos por Gortázar *et al.* (2007) con respecto a las fechas de freza detectadas en numerosas poblaciones europeas, así como con la tendencia latitudinal en la freza (*la fecha de freza se retrasa cuanto más al sur se encuentran las poblaciones*) descrita por Klemetsen et al. (2003).

Además, se determinó el régimen de lluvias estacional y anual durante el periodo 1980 – 2009 en los ríos estudiados con la intención de comprobar si la extrema variabilidad de flujo característica de los ecosistemas mediterráneos pudiera haber promovido el desarrollo de periodos de freza particulares en las poblaciones de trucha común que habitan la región de estudio.

Capítulo III. *Driving factors of synchronous dynamics in brown trout populations at the rear edge native distribution*

La dinámica de abundancias en cada estación se describió mediante las series temporales de densidad de cada clase de edad: 0+, 1+ y 2++, en adelante ‘adultos’, Ad.

Con el fin de hacer nuestros resultados comparables con los obtenidos por Bret *et al.* (2016) en Francia, usamos variables similares. Para ello se tomaron los logaritmos de los datos de densidad, añadiéndoles una unidad, para normalizar su distribución aprovechando las observaciones con densidad cero. Luego se ajustaron modelos lineales para tener en cuenta el efecto de la cohorte y del stock de reproductores en la densidad de cada grupo de edad, y para reducir la correlación serial. Los análisis de las series temporales de densidad se hicieron con los residuos de estos modelos globales (uno para cada clase de edad).

Se calculó la media estacional (e.g. invierno: enero-febrero-marzo) de la precipitación total y la temperatura media diaria del aire para cada estación para ser empleadas como factores exógenos potencialmente explicativos.

Se contrastaron tres hipótesis auxiliares:

1ª hipótesis auxiliar: *La variación interanual de las densidades de los grupos de edad está determinada por la variación de las condiciones físicas del hábitat*. Variables ambientales como el caudal y la temperatura del agua determinan la variabilidad de las condiciones físicas del hábitat. Estas variables ambientales están, a su vez, dirigidas por factores climáticos como el régimen de precipitaciones y temperaturas del aire, respectivamente. Como la respuesta del caudal y la temperatura del agua a la precipitación y la temperatura del aire está modulada por las características del hábitat a escala de la cuenca vertiente, hay un retardo entre los episodios climáticos y la respuesta del hábitat fluvial. Para sobrellevar este efecto retardado se puede usar una ventana temporal que sintetice las condiciones climáticas predominantes que han inducido una condición general del hábitat físico en un período del año.

Se llevó a cabo un análisis de las variables mediante un modelo linear de efectos mixtos (LME) permitiendo efectos aleatorios del río anidado en la cuenca (*catchment/stream*), para evitar la pseudorreplicación. Las variables explicativas se seleccionaron mediante un procedimiento por pasos hacia atrás, eliminando sucesivamente variables potenciales hasta que quedaron en cada modelo las variables climáticas con p-valor<0.05.

2ª hipótesis auxiliar: *La distancia euclídea entre series temporales de una variable entre dos sitios puede usarse como un indicador de la sincronía* *de dicha variable entre ambos sitios*. Cuanto menor sea esa distancia, mayor será la sincronía. Si la sincronía de la densidad de truchas entre dos sitios está producida por un efecto Moran, estará significativamente correlacionada con la sincronía de una o varias variables ambientales entre ambos sitios.

De forma similar a Bret *et al*. (2016), la asincronía entre pares de estaciones se describió mediante matrices 14 × 14 cuyos elementos son índices de disimilaridad. La sincronía de la densidad fue correlacionada con la sincronía ambiental y distancia geográfica mediante tests de Mantel. El efecto de la conectividad entre poblaciones sobre la sincronía de la densidad se analizó mediante modelos lineales generalizados (GLM).

3ª hipótesis auxiliar: *La respuesta de una determinada población a los factores climáticos está modulada por las características físicas del hábitat del tramo que habita*. Aquí comprobamos si hay una relación significativa entre la similitud de la respuesta de la densidad de pares de poblaciones a las variables climáticas y la similitud de características físicas del hábitat fluvial entre el par de estaciones que habitan.

La respuesta de una variable poblacional a una variable climática se expresó por un vector de 4 dimensiones, cuyas componentes son los estimadores y el valor de p del ajuste de dicha variable poblacional a los factores climáticos. La matriz de respuesta está formada por 14 vectores de respuesta de las correspondientes 14 estaciones de muestreo. Sólo se consideraron en el análisis aquellas relaciones significativas obtenidas del contraste de la 2ª hipótesis auxiliar. Para buscar relaciones entre la disimilaridad de respuestas y las características del hábitat se llevaron a cabo tests de Mantel entre las matrices de disimilaridad de: (1) respuesta, (2) características del hábitat y (3) distancias geográficas.

Capítulo IV. *Cómo prevenir la extinción de poblaciones amenazadas viviendo en un borde de distribución: propuestas de gestión para las poblaciones más meridionales de trucha común (*Salmo trutta*) en Europa.*

Para la elaboración de este capítulo se partió de toda la información obtenida en el Capítulo I (distribución de la trucha en Andalucía, causas que delimitan sus poblaciones, presencia de trucha arcoíris en la región de estudio), a la cual se unió información relativa a las figuras administrativas que regulan los tramos trucheros en Andalucía (cotos de pesca, aguas libres, cotos intensivos, refugios de pesca y excepciones). Todo ello fue digitalizado utilizando ArcGIS y constituyó la base sobre la cual se proponen medidas de gestión administrativa y medidas de gestión adaptativa que permitan conservar las poblaciones de trucha común más meridionales de Europa (una especie catalogada como amenazada en la región de estudio).

Además se hace hincapié en medidas concretas para erradicar poblaciones naturalizadas (con capacidad reproductiva) de trucha arcoíris (*Oncorhynchus mykiss*), de modo que esos cursos fluviales puedan ser repoblados con poblaciones de trucha autóctona, considerando para ello los haplotipos propios de la región (Almodóvar *et al*. 2010).

Todas las propuestas se basan en bibliografía científica relacionada con la conservación de ecosistemas fluviales y peces continentales, así como en las particularidades políticas, climáticas y de gestión del agua características del área de estudio.

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3. CHAPTER I

Distribution of brown trout (Salmo trutta Linnaeus, 1758) (Teleostei: Salmonidae) in its southwesternmost European limit: possible causes

*Distribución de la trucha común (*Salmo trutta *Linnaeus, 1758) (Teleostei: Salmonidae) en su límite de distribución europeo más suroccidental: posibles causas*

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3. CHAPTER I. DISTRIBUTION OF BROWN TROUT (SALMO TRUTTA LINNAEUS, 1758) (TELEOSTEI: SALMONIDAE) IN ITS SOUTHWESTERNMOST EUROPEAN LIMIT: POSSIBLE CAUSES

3.1. Abstract

Andalusian brown trout populations represent the southwestern limit of this species in Europe, show a high genetic diversity, are subjected to extreme habitat conditions and environmental alterations, and are very sensitive to extinction. However, there is a lack of scientific studies on them. A necessary first step to preserve them is to describe their spatial distribution. We detected the species in eastern Andalusia along almost 710 km of rivers, finding 38 populations inhabiting streams and reservoirs in the upper reaches of three basins (Guadalquivir, Segura and South) in an altitude range between 200 and 2200 m above sea level. Populations are constrained by natural causes in their upper limits, and by anthropogenic causes in their lower limits (mainly related to water management). Currently, the populations are very isolated in protected areas (62% of their distribution) or downstream of those areas (32%), and a range displacement towards higher altitudes compared with their distribution in the nineteenth century is observed.

3.2. Introduction

Brown trout (*Salmo trutta* Linnaeus, 1758) is a species native to Europe, showing a high genetic, ecological and morphological variability throughout its wide distribution area (Jonsson and Jonsson, 2011). In the Iberian Peninsula, it is naturally located at the headwaters of almost all rivers, except some rivers in the east and south of Spain, and the Guadiana basin (Doadrio, 2001).

South Iberian populations together with those of North Africa represent the southwestern limit in the natural distribution of the species. In the southernmost region of the Iberian Peninsula, Andalusia, this species is the only endemic salmonid. Andalusian brown trout populations include two of the six evolutionarily significant units (ESUs) present in the Iberian Peninsula (Machordom *et al*., 2000), with five new worldwide haplotypes recently discovered (Almodóvar *et al*., 2010). Thus, preserving the integrity of these populations is crucial for the conservation of the entire genetic diversity of the species (Almodóvar *et al*., 2006).

Deleterious effects of overfishing (Almodóvar and Nicola, 2004; Johnston *et al*., 2012), problems associated with habitat loss, alteration and fragmentation (e.g. Gosset *et al*., 2006; Maceda-Veiga and De Sostoa, 2011), introduction of exotic species (e.g. Elvira and Almodóvar, 2001; Leunda, 2010; De Silva, 2012) and introgression of foreign genes (e.g. Laikre, 1999; Madeira *et al*., 2005; Almodóvar *et al*., 2006) on the brown trout populations are problems that have been intensively studied by many authors in all the wide distribution range of this species. Although overfishing has affected its current distribution and conservation status in some Spanish rivers (García de Jalón and Schmidt, 1995), since 2005, brown trout in Andalusia may be fished only in the modality of catch and release. Hence, this problem does not affect trout populations in the study area.

Moreover, it is noteworthy that human civilizations have shown an intense and historic predilection for settling in areas of the Mediterranean basin, so that the rivers flowing in Mediterranean climate regions have suffered the largest anthropogenic interventions on Earth (Blondel *et al*., 2010). This high impact has resulted mainly in pollution, water abstraction and droughts, restricted distribution ranges of species or limited dispersal of taxa. Thus, in the Mediterranean rivers, 36% of freshwater fish species can be included as threatened (critically endangered, endangered or vulnerable), seven species are extinct and one is extinct in the wild (Tierno de Figueroa *et al*., 2013). This situation is even more worrying when considering only Mediterranean endemic species, with 56% of them threatened (Smith and Darwall, 2006). In Andalusia, 19 of the 22 native freshwater fishes (more than half being Iberian endemisms) are under some degree of threat. Thus, while brown trout in Europe is catalogued as "least concern, LC" (Freyhof, 2011) and in Spain as "vulnerable, VU" (criterion 1cde; Doadrio, 2001), in Andalusia it is catalogued as "endangered, EN" (criterion A1e; Franco Ruíz and Rodríguez de los Santos, 2001).

All of these previous data show the importance of conservation of Andalusian brown trout populations. However, only two studies on historical distribution in the nineteenth century (Menor and Prenda, 2006; Sáez Gómez, 2010), and another on genetic analysis (Almodóvar *et al*., 2010), have been published regarding brown trout conservation in the study area.

Thus, the aims of the present study are (1) to identify external factors responsible for the current distribution of brown trout in the study area, which is crucial for the future conservation of the species and its habitats; and (2) to determine the number and distribution of brown trout populations that inhabit the fresh waters of Andalusia, establishing their limits of distribution and identifying the factors that set those limits.

3.3. Materials and methods

3.3.1. Study area

Andalusia is the southwesternmost region of the European continent (Figure 3.1), and is the second largest region of Spain (17.3% of the surface of the country). Noteworthy is the fact that it has the largest network of protected natural areas in Europe, which constitute 30% of the entire protected areas in Spain.

Figure 3.1. Location of Andalusia (in gray shading). The Iberian Peninsula basins are delimited in the figure. Four of them form part of Andalusia: (1) Guadiana, (2) Segura, (3) Guadalquivir and (4) South.

Andalusia has 46,415 km of water courses within four basins: Guadalquivir, South Mediterranean (hereafter South), Guadiana and Segura (Figure 3.1.; Table 3.1).

Table 3.1. Overview of the four Andalusian basins and results obtained for brown trout in them.

	Guadalquivir	South	Segura	Guadiana
Total surface in Spain (Km^2)	631930	179921	189866	601615
Presence in Andalusia	91%	100%	9%	17%
River length in Andalusia (Km)	28852	11025	827	5645
Representation in Andalusia	62%	24%	2%	12%
River length inhabited by *S. trutta* in Andalusia (km)	497.23	143.94	68.39	0
% basin inhabited by *S. trutta*	1.7	1.3	8.3	0
% Andalusian populations in the basin	70.1	20.3	9.6	0

3.3.2. Methods

Historical information was obtained from: (1) the distribution of brown trout in Andalusia in the nineteenth century (Menor and Prenda, 2006; Sáez Gómez, 2010); (2) a Spanish inventory of terrestrial and freshwater species (Spanish law, *Real Decreto 556/2011*); and (3) interviews with people related to the aquatic environment (environmental agents, local fishermen, shepherds, etc.).

This information allowed us to identify the rivers where the presence of the species was known in the past, and rivers where their presence could be likely, being next to reaches of inhabited rivers, tributaries with permanent water or isolated reaches of difficult access.

To set the current limits of the distribution range, field sampling was conducted by means of electrofishing qualitative surveys (presence/absence) during the summers of 2008 and 2009. To minimize fish mortality, electric current intensity was regulated depending on water conductivity (Johnson *et al.*, 2007) at every sampling site.

Single-pass electrofishing surveys were conducted at each sampling site (maximum length 400 m). If the species was detected, the following sampling station was located 1 km upstream or downstream, depending on whether we were delimiting the upper or lower limit in that river, respectively. This procedure was repeated until no brown trout was detected at the following sampling station. In such cases, one more sampling was performed 500 m away from the former site to corroborate the limit.

The geographical distribution of the brown trout populations was defined by the limits of the presence of brown trout in a continuous river network (Berryman, 1999). Each population was characterized by the geographical coordinates and the altitude of its limits. Subsequently, the type of factors (natural or anthropogenic) and the causes that prevented the expansion of the species were identified.

Natural factors (NA) were classified into four categories (causes): (1) water temperature (Te); (2) the limit is the source of the stream (Rs); (3) impassable waterfall (Iw); and (4) naturally dry in summer (Sd). Six main sources of perturbation on biodiversity and ecology of freshwater rivers pointed out by Clavero *et al*. (2010) were considered as anthropogenic factors (AN): (1) reservoirs and channel construction (Da); (2) agriculture (leading to agricultural water pollution, Ag); (3) water abstraction (Wa); (4) invasive species (Is); (5) overfishing (Of); and (6) pollution (Po). Moreover, an additional category was considered, multiple (Mu), when more than one cause acted. Furthermore, other factors that may be relevant to the current distribution of the species in this area were considered: (1) the distribution of mountain systems in Andalusia and (2) the location of its protected natural areas.

To obtain inhabited total distances in the study area and identify how much of them were located within protected areas, the limits of trout populations were digitalized using ArcGIS 9.3.1. and the boundaries of protected natural areas were obtained from the Environmental

Information Network of Andalusia (REDIAM, http://www.juntadeandalucia.es/medioambiente/site/web/rediam)

3.4. Results

Eighty-one water courses, including main rivers and tributaries, were sampled. It should be noted that a population may have one or more upper limits (as many as there are tributaries), but only one lower limit after all the inhabited tributaries converge. Thereby, 38 isolated populations, 64 upper limits and 37 lower limits have been identified.

Brown trout distribution is currently concentrated in the east of the Andalusian region (Figure 3.2B). The species has been detected along almost 710 km of rivers, streams and reservoirs in the upper reaches of the Guadalquivir, Segura and South basins (Figures 3.1 and 3.2; see also supplementary data 3.1): 70.1, 20.3 and 9.6%, respectively.

The altitudinal ranges of brown trout populations in Andalusia, the causes of population limits, both upper and lower, and different natural reserves where the species is present are summarized in Figure 3.3 (more details in the supplementary data 3.1). The highest amplitude of altitude ranges (from 2200 to 200 m above sea level, a.s.l.) have been detected in populations whose upper limits are located in the Sierra Nevada National Park within the Guadalquivir and South basins.

Brown trout is present is Sierra Nevada National Park and it also inhabits some natural parks: Tejeda–Alhama–Almijara, Castril, Cazorla–Segura–Las Villas and Sierra Nevada (Figure 3.2). The upper limits of all populations are located in these protected areas, except in rivers 16, 17, 30, 31, 32 and 39 (supplementary data 3.1), that are completely outside of the natural reserves and account for 6% of the total distribution of the species in the region.

The remaining inhabited reaches outside the natural reserves (32% of the Andalusian distribution) are the downstream continuation of populations inhabiting those areas (Figure 3.3; supplementary data 3.1) and more than half of them (21% of the Andalusian distribution) are characterized by the species' reduced population size and fragile demographic status (unpublished data). Thus, currently the species inhabits both protected areas (62%) and unprotected ones (38%) (Table 3.2).

In general, populations are delimited by natural causes in their upper limits, and by anthropogenic causes in their lower limits (Table 3.3). In 33 cases, brown trout inhabits from the headwaters of the rivers, in another 13 cases they arrive at the highest possible altitude, above which the low temperatures prevent survival, and in nine cases they are limited by impassable waterfalls. The remaining eight populations are fragmented populations located downstream of reservoirs, whose upper limits are found in the dams. Regarding the 37 lower limits detected, 17 of them are due to the presence of impassable dams to create reservoirs, and 12 to water abstraction for irrigation and human consumption.

Finally, the strong alteration of watercourses due to the synergistic effects of agriculture, water diversion, deterioration of water quality (pollution) and habitat fragmentation (reservoirs), causes the disappearance of the species in another seven rivers (Mu in Table 3.3). In only one lower limit does the cause of the disappearance have a natural origin, i.e. drying in summer due to the natural flow reduction characteristic of the Mediterranean region and the geological characteristics of the substrate (high porosity).

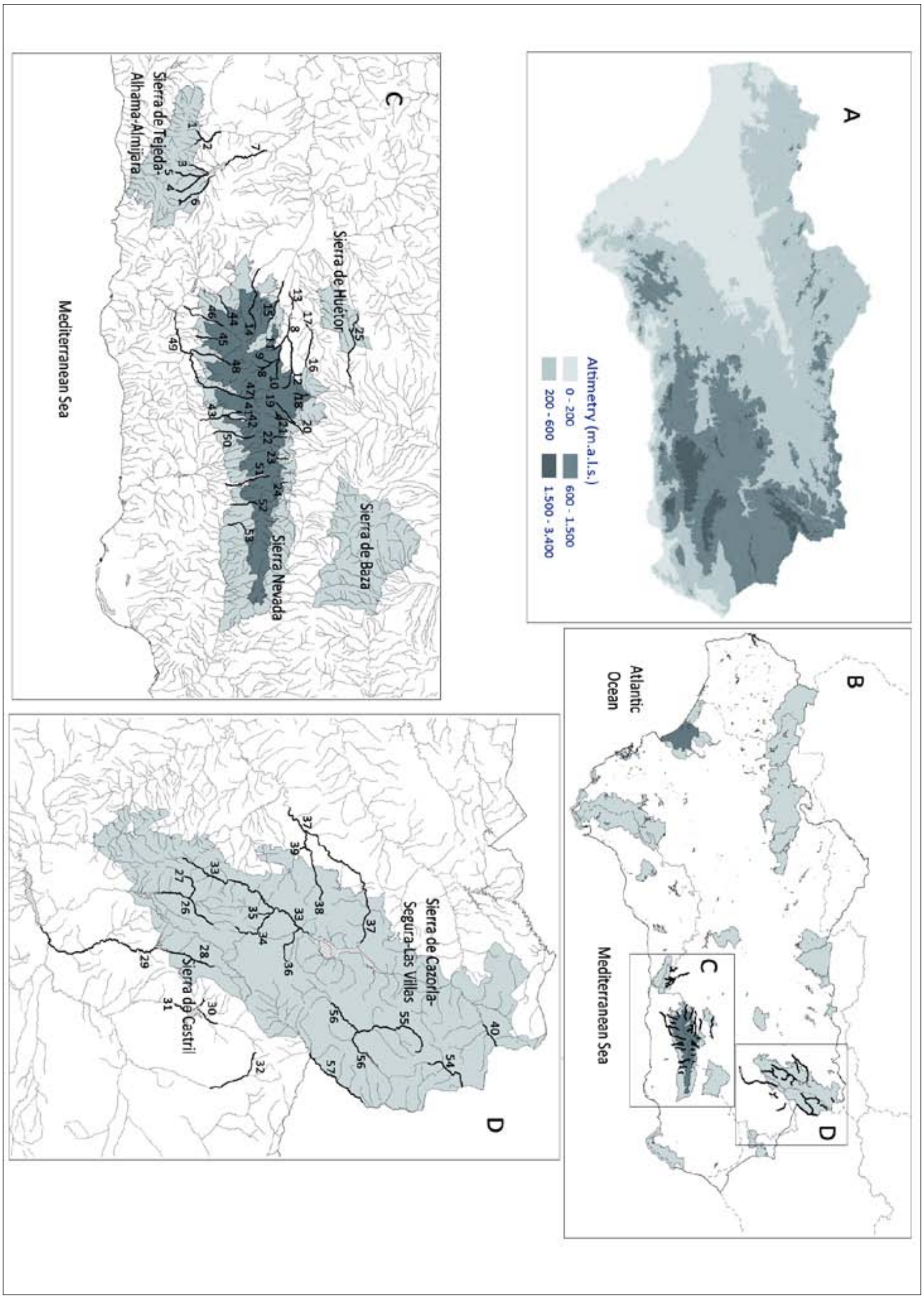

Figure 3.2. (A) Altimetry of the study region (meters above sea level, m a.s.l.); (B) distribution of the brown trout in Andalusia: thick lines delimit Andalusia, shaded lines demarcate the basins (see Figure 3.1) and the boxes show the areas where brown trout populations are present; (C, D) detailed distributions. The light gray surfaces are natural parks and the dark gray surfaces are national parks. These natural reserves are named, and the inhabiting rivers are numbered, according to the codes in the supplemental online data.

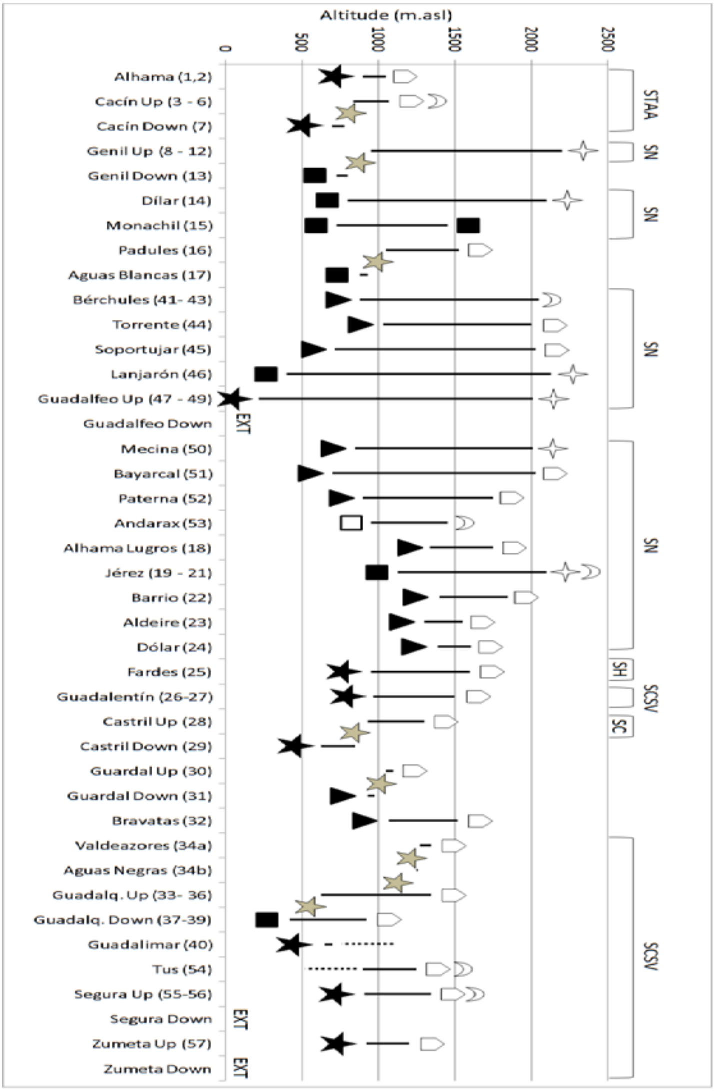

Figure 3.3. Altitudinal ranges (meters above sea level, m a.s.l.) inhabited by each population (reaches codes in brackets are as listed in the supplemental data), causes of their upper and lower limits (natural indicated with empty symbols, and anthropogenic with solid symbols) and natural reserves containing all, or part, of the reaches inhabited by the population. Causes of the limits: ★ Dam causing lower limits, ☆ dam fragmenting ancestral populations; ▲ water abstraction; ■ multiple; □ summer drought; ⌂ population reaches the source; ∩ impassable waterfall; ✧ temperature. Natural reserves are named at the top of the figure (EXT: extinct population; STAA: Sierras de Tejeda–Alhama–Almijara; SN: Sierra Nevada (Natural and National Park); SH: Sierra de Huétor; SCSV: Sierras de Cazorla–Segura–Las Villas; SC: Sierra de Castril). Dotted lines indicate reaches outside the administrative boundaries of Andalusia.

Table 3.2. Kilometers of river inhabited by brown trout in the Andalusian basins, and inhabited partial percentages in each basin. Distribution inside and outside of natural reserves is shown. Gray cells indicate where the trout is managed as a fishing resource (Andalusian law, *Orden 6 de mayo de 2014*).

		Guadalquivir		Sur		Segura	
		%	Km	%	Km	%	Km
% Andalusian population		70.08	497.23	20.29	143.94	9.64	68.39
Natural reserve	National Park	9.03	64.09	4.29	30.41	0	0
	Natural Park	30.30	214.97	8.80	62.41	9.64	68.39
Outside of nature reserves		30.75	218.17	7.21	51.13	0	0

Table 3.3. Causes delimiting the brown trout populations in Andalusia in their upper and lower limits. The types of factors and particular causes are shown.

Type of factor	Particular cause	Frequency	
		Upper limits	Lower limits
Natural (NA)	Temperature (Te)	13	0
	Population reaches the source (Rs)	33	0
	Impassable waterfall (Iw)	9	0
	Summer drought (Sd)	0	1
Anthropogenic (AN)	Dam and channel construction (Da)	8	17
	Water abstractions (Wa)	0	12
	Agriculture (Ag)	0	0
	Invasive species (Is)	0	0
	Pollution (Po)	0	0
	Overfishing (Of)	0	0
	Multiple (Mu)	1	7

Table 3.4 summarizes all reaches inhabited by rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) close to or within the current distribution of the native species. All of these sections are or were inhabited by brown trout in the past. Some naturalized rainbow trout populations (with reproductive capacity) have been detected.

Table 3.4. Reaches inhabited by rainbow trout coinciding with reaches currently or historically inhabited by the brown trout in Andalusia. Only reaches close to the current distribution of the native salmonid are considered. Rivers designated as "*Oncorhynchus mykiss*" were inhabited by brown trout in the past (Sáez Gomez 2010). The current administrative figure (Andalusian law, Orden 6 de mayo 2014), its length, reaches to which they belong (codes in the supplemental online data) and salmonids detected in each case are indicated. NLFA: non-limited access fishing areas; SFA: stocked fishing areas (some in reaches inhabited by brown trout). Asterisks (*) indicate reaches where rainbow trout reproduction has been confirmed. Shading cells in the "*Salmo trutta* & *Oncorhynchus mykiss*" column indicate that both species are present in these reaches; shading cells in the "*Oncorhynchus mykiss*" column indicate that this species is the only one present in those reaches.

				Salmonids detected	
Current figure	Name	Code	Length (m)	*S. trutta* & *O. mykiss*	*O. mykiss*
SFA	Charco de la cuna	33 – 34	1218	▨	
SFA	El Duende	37	3821	▨	
SFA	Embalse de la Bolera	26	6862	▨	
SFA	Embalse San Clemente	30	5563	▨	
SFA	Embalse La Vieja	57	850	▨	
SFA	Puente del Hacha	33	3314	▨	
SFA	Embalse Quéntar	16	3279	▨	
NLAFA	Aguascebas Grande	38	8483	▨ *	
NLAFA	Guardal	30	8490	▨	
NLAFA	Jérez	19 - 20	7431	▨ *	
NLAFA	Padules	16	10264	▨ *	
NLAFA	Guadalquivir	33	9371	▨	
NLAFA	Laroles	-	9940		▨ *
NLAFA	Nacimiento	-	21242		▨ *
NLAFA	Ohanes	-	2916		▨ *
NLAFA	Nechite	-	11056		▨ *
NLAFA	Válor	-	13372		▨ *
NLAFA	Lanteira	-	10500		▨ *
NLAFA	Aguas Blancas	-	7040		▨

3.5. Discussion

3.5.1. Geographical distribution, mountain systems and natural reserves

Brown trout inhabits cold waters (Kottelat and Freyhof, 2007) and in the Iberian Peninsula is located in mountain streams and upper reaches of the rivers (Nieto *et al.*, 2006).

Comparing the current Andalusian distribution of the species (Figure 3.2B) with its distribution in the nineteenth century (Menor and Prenda, 2006; Sáez Gómez, 2010), we observed a range contraction and a displacement towards higher altitudes, the western populations having disappeared, closer to the great valley of the Guadalquivir River, where the average water temperature is higher. Its current distribution is associated with rivers whose sources are in the eastern mountain systems, the only ones with areas above 1500 m a.s.l. (Figure 3.2A) and temperature and flow regimens (REDIAM 2014) that can sustain optimum ecological conditions for the species. Hence, the eastern Andalusian mountain systems are the last habitat available for the species in its southwestern European distribution edge. In the absence of metapopulation studies, it can be noted that this species in Andalusia is represented by resident populations with a high degree of population isolation between basins and even among rivers (Figure 3.2).

On the other hand, the organisms living at the edge of their distribution range are subjected to intense habitat pressures that increase their vulnerability to threats: they often persist in small isolated populations, facing ecological conditions very different from those of the main distribution area and from those considered optimum (Sanz *et al.*, 2006).

A lack of protection measures in the middle and lower reaches of rivers (urbanized, fragmented and used in agriculture) has endangered many endemic species of these areas, and has eliminated river connectivity between nearby mountain ranges, removing the natural corridors that kept relatively distant brown trout populations connected. Therefore, brown trout populations in Andalusia are isolated in rivers and streams from protected natural spaces (62% of the distribution) and downstream of those watercourses (32%). Very few populations inhabit areas completely out of them (6% of the distribution). Furthermore, the inhabited river reaches outside of protected natural areas present impacts by damming, water extraction and invasive species, and trout densities are much lower than those detected in the interior of the natural reserves (unpublished data).

It is also known that freshwater biodiversity is being lost at an alarming rate, even more rapidly than terrestrial biodiversity (Moyle and Yoshiyama, 1994; Cowx and Collares-Pereira, 2002). Moreover, most current reserves were designed for preserving terrestrial organisms, based on insufficient criteria for adequate management of freshwater biodiversity. Also, there is an urgent need to protect native fish species in light of the ongoing anthropogenic degradation of aquatic environments (Filipe *et al.*, 2004).

3.5.2. Causes and typologies of the distribution limits

The fact that the upper limits in the fluvial networks have a natural origin, while the lower limits are anthropogenic (Table 3.3), means that the geographical range of the species under undisturbed conditions would be larger downstream than currently observed. These lower limits are mainly disturbances related to the management of water (reservoirs and water abstraction), a resource that is often scarce in the study area.

Generally, the lower limits at Sierra Nevada are more related to the presence of urban settlements and water management (ditches/untreated discharges), while in other areas the dams and the arrival at lower altitudes more suitable for cyprinid species are the limit factors (Figure 3.3). Also, in the Guadalquivir basin, there is a strong impact of olive farming on the riverbed by increased turbidity and runoff, as well as by the current and historical presence of stocked fishing areas (SFA): reaches established by the regional administration where specimens of fishable size of rainbow trout are or were introduced (Table 3.4).

Upper limits

In 33 upper limits, the species was detected to the source of the water course (Table 3.3). Due to the high interannual variability that characterizes the Mediterranean climate, rivers may suffer sharp declines in flow during summer (Tierno de Figueroa *et al*., 2013). During the field work, we detected several times how the natural retractions were so intense that the sources in summer were displaced up to hundreds of meters downstream, forcing fish communities to restrict their range temporarily. The rains of spring and autumn increased again the altitude of the sources and favored the upstream spawning migration of the adults during late fall and early winter.

In 13 cases, the upper limits had an ecological component related to water temperature, and all of them were located in the Sierra Nevada Mountains. This mountain massif has some of the highest peaks of the Iberian Peninsula, and is the southernmost refuge for many species of higher latitudes (Molero Mesa *et al*., 1992).

Temperature has pervasive influences on rates of chemical and physiological reactions of fish, affecting metabolic rate, swimming, feeding, growth and reproduction (Jonsson and Jonsson, 2011). It is assumed that the lower lethal temperature for brown trout is at, or slightly below, 0°C (Ojanguren and Braña, 2003; Elliott and Elliott, 2010), and in these 13 limits, the species reaches the highest level (about 2100 to 2200 m a.s.l.) at which the winter temperature allows it to survive in these latitudes.

In another nine cases, the populations reach up to impassable waterfalls (Table 3.3), although above them the optimal habitat is maintained. It is possible that the trout have never inhabited above these waterfalls.

One only population presents an anthropogenic upper limit, due to the synergistic interaction of water extraction and fragmentation of habitat (water diversion associated with a dam for the production of hydroelectric power).

The eight cases noted as Da in Table 3.3 are populations inhabiting downstream of reservoirs (Figure 3.3). These barriers are also the lower limits of the isolated populations upstream. The effects of damming will be discussed below, in the lower limits section.

Lower limits

The rivers of Mediterranean regions tend to be more heavily impounded than rivers in humid climates, because the demand for water is greater (Kondolf and Batalla, 2005; Grantham *et al.*, 2010). Water abstraction has been a cause described in numerous studies analyzing anthropogenic impacts on river ecosystems and fish populations in different Mediterranean climate regions (e.g. in Australia: Kingsford, 2000; in California: Moyle *et al.*, 2011; in Chile: Habit *et al.*, 2007). Dewatering by diversion reduces the habitat available in streams and sometimes renders it entirely hostile (e.g. through warming) or serves as a barrier to fish passage (e.g. loss of surface flow through riffle crests) (Williams, 2006). In the study area, the 12 cases of water abstraction are associated with irrigation ditches, mainly for agriculture and human consumption. The extractions are so intense that the water flow decreases strongly all year round, and in summer drying is complete. In addition, in these and other rivers, numerous ditches were detected along their entire length, regardless of the ditches that cause the lower limits. These ditches tend to decrease the flow in summer, drying up some reaches, fragmenting the populations and threatening the survival of individuals that become isolated in pools. We observed how the first 100 m inside some of these ditches are used for spawning by trout, as noted by Williams (2006) in the Columbia River Basin, because the granulometry and the laminar flow inside ditches are very suitable to the egg incubation. However, they can become death traps for adults and fry that die in irrigation ponds or farmland.

There are a large number of reservoirs in the headwaters of the rivers inhabited by brown trout (Figure 3.3). Thus, 17 lower limits are due to the presence of dams (Table 3.3). Downstream of them, nine trout populations disappear, while on eight occasions the ancestral populations have been fragmented. Dams are one of the greatest threats to river biodiversity worldwide (Poff *et al*., 2007) and one of the major problems described in the European Water Framework Directive (2000/60/CE). Dams produce drastic changes in river courses: they change the natural flow regimes (e.g. Kingsford, 2000; Alonso-González *et al*., 2008), alter the dynamics of the whole catchment basin and the periodic patterns of temperature, sediment grain size and composition of the rivers (e.g. Shieh *et al*., 2007; Maddock *et al*., 2008; Kishi and Maekawa, 2009) and promote the invasion of exotic species (Clavero *et al*., 2004; Johnson *et al*., 2008), modifying their structure and the natural dynamics of the biota (Bunn and Arthington, 2002). Thus, damming is a cataclysmic event in the life of a riverine system (Ligon *et al*., 1995). Many authors have studied the effects of damming on river ecosystems and fish populations (e.g. Hart and Poff, 2002), with more than twice as many studies being conducted on salmonids than on any other fish family (Murchie *et al.*, 2008). Alteration of natural flow regimes modifies the natural rates of growth, development, habitat use, reproduction or size (Yrjänä *et al.*, 2002; Kishi and Maekawa, 2009) and the construction of hydrological barriers fragments populations into discrete units regardless of historical connections, and causes genetic isolation (Rieman and Dunham, 2000; Gosset *et al.*, 2006; Heggenes and Røed, 2006). To these general effects we have to join the high natural stochasticity of the Mediterranean systems, due to the highly unpredictable interannual flow variations associated with natural seasonal events (Gortázar *et al.*, 2007). Thus, the isolation of Mediterranean fishes has devastating effects: the resilience of patchy populations decreases when facing stochastic events, particularly when carrying capacity is low (Morita and Yokota, 2002). For this reason, isolated brown trout populations in the study area are subjected to high stress and the processes of extinction could be intensified in these peripheral populations.

Currently, the eight populations located downstream of reservoirs (Table 3.3) have much lower densities than upstream populations (unpublished data). Considering both adverse effects of fragmentation and their current low densities, we can assume that these populations are severely endangered (16% of current distribution). In fact, during the realization of a previous study, three populations located downstream of dams have recently disappeared (Figure 3.3).

Severe droughts have marked effects on salmonid populations by reducing the volume of water available to the fish, impeding their migration and adversely affecting water quality, especially water temperature and dissolved oxygen (Elliott, 2000), causing increased mortality and decreased growth of the trout (Elliott *et al.*, 1997). Thus, summer drought is the only natural cause detected in one of the lower limits in the study area (53), due both to the natural flow retracting and the river bed permeability. In periods of strong increases in flow, this river can connect with a small reach, 10 km downstream, where water remains throughout the year and a remnant population inhabits, which could behave as sink within a metapopulation structure.

Sometimes many factors contribute to the extinction of a species, and often it is difficult to identify a single cause (Allan and Flecker, 1993). Furthermore, in freshwater fishes, it has been demonstrated that some factors acts more synergistically than additively (Leuven and Poudevigne, 2002). This is the case of seven lower limits (named “multiple” in Table 3.3). In them, agriculture, pollution, water abstraction and invasive species interact with different intensity. They are worldwide proven causes of declines and extinctions of riverine communities in general, and of fish populations in particularly (e.g. Malmqvist and Rundle, 2002; Smith and Darwall, 2006).

Mediterranean climate regions have an unpredictable annual precipitation and limited water availability during the dry season (Grantham *et al*., 2010), so intensive agriculture threatens the conservation of natural inland waters in the study area. This threat may be indirect, by water infrastructure development (e.g. reservoirs or water extractions) or direct, due to crop expansion and traditional land management. The lower Guadalquivir population (37 to 39 in the supplementary data 3.1) is the only case detected in Andalusia where a brown trout population is directly affected by agriculture, due to intensive olive monoculture widely distributed throughout the affected subbasin. The land is highly plowed, without vegetation cover, and large amounts of silts and fine sands flow into streams by runoff from farmland, even when the intensity of rainfall is very low, resulting in a reduction of both the redd permeability and the oxygen supply to incubate eggs, inhibiting the emergence of fry (Acornley and Sear, 1999; Moyle *et al*., 2011). This runoff increases the water turbidity, which reduces in brown trout its ability of capturing food, and modifies its feeding (Stuart-Smith *et al.*, 2004). It is also known (Maceda-Veiga, 2013) that the use of pesticides and herbicides affects fish populations, and especially brown trout (Rodríguez-Cea *et al.*, 2003). Furthermore, this population is also affected by the presence of a reservoir, upstream, and one SFA, downstream, so that the probability of local extinction in this case increases.

On the other hand, brown trout stand as symbols of clean, cold water from the northern hemisphere (Jonsson and Jonsson, 2011). In the study area, the species is found from the upper reaches of rivers until the appearance of the first urban settlements, where water management carried out by its inhabitants often causes a sharp reduction in flow (water abstraction or damming in particular; Table 3.3). Moreover, sometimes these villages discharge their untreated waste water into the rivers. Pollution has deleterious effects for the survival of this species, but being mountain villages with few inhabitants, the small size of their discharges does not cause the disappearance of the species by itself. However, the deleterious effect of discharges increases under low-flow conditions (Gasith and Resh, 1999), acting synergistically.

It is known (Clavero *et al.*, 2004) that in Mediterranean systems, the number of introduced species is positively related to the presence of reservoirs. In fact, in most of the reservoirs included in the distribution area of trout in Andalusia (Figure 3.3), invasive species can be found (e.g. *Esox lucius* Linnaeus, 1758, *Cyprinus carpio* Linnaeus, 1758, *Micropterus salmoides* Lacépède, 1802, etc.). Moreover, since the late nineteenth century, rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) has been stocked in Spain for angling purposes (Elvira and Almodóvar, 2001), in agreement with the "human activity" hypothesis for the species invasions (Leprieur *et al.*, 2008). We detected this alien species cohabiting with brown trout along almost 69 km of rivers (Table 3.4), which represents 9.7% of the current distribution of the native species in Andalusia.

Furthermore, rainbow trout was the only fish detected in another 76 km of rivers (Table 3.4), in reaches that had harbored indigenous trout populations in the past (Sáez Gómez, 2010). Of these 145 km invaded, 32 km correspond to SFA in reaches inhabited by brown trout, or very close to the current range of the native species. The remaining alien populations come from deliberate introductions made in the past (uncontrolled genetic stocks for infertility) or from escapes of rainbow trout detected in all Andalusian river reaches located downstream of fish farms. In many of these reaches (including some SFAs), the alien species has become naturalized, and we detected active reproduction and representation of all age classes (Table 3.4).

In this way, acclimatization of exotic freshwater fishes in Iberian rivers is probably one of the most important negative factors affecting the survival of the native species (Elvira and Almodóvar, 2001), because they may cause predation, competition, disease transmissions, hybridization and behavioral interference (Crawford and Muir, 2008; Leunda, 2010). Thus, rainbow trout affects brown trout habitat selection and survival (Blanchet *et al*., 2007; Fausch, 2007), and its spawn destroy native trout spawning redds (Landergren, 1999). When the spawning space is limited, the interspecific competitive pressure due to redd superimposition can eliminate native populations of trout (Scott and Irvine, 2000). It seems likely that these phenomena have taken place in the "*Oncorhynchus mykiss*" reaches reported in Table 3.4.

3.6. References

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Supplementary data 3.1

Table S.3.1. Characteristics of brown trout populations in the study area. Basins (GU: Guadalquivir; S: South; SE Segura) and subbasins (Al: Almijara; Ge: Genil; Gm: Guadiana Menor; Gu: Guadalquivir; Gf: Guadalfeo; Ad: Adra; An: Andarax; Se: Segura), names of the principal rivers, populations and tributaries inhabited by brown trout in the study area, and their codes (graphically showed in figure 2), indicating “EXT” for populations that have become extinct within the last three years. Partial length (of the tributaries) and total length (of each complete population), UTM, type of factors (NA: Natural; AN: Anthropogenic), particular cause (Te: Temperature; Rs: Population reaches the source; Iw: Impassable waterfall; Sd: Summer drought; Da: Dam construction; Wa: Water abstraction; Mu: Multiple) and altitude of the upper and lower limits are shown. Shaded cells in the “cause” column indicate reservoirs (by damming) located inside the inhabited rivers isolating ancestrally continuous populations (grey starts in Figure 3). “OA” is used for those stretches that remain inhabited outside of Andalusia whose limits have not been identified. Finally, for each of the stretches, length inhabited in Natural and National Parks, as well as the name (STAA: Sierras de Tejeda–Alhama–Almijara; SN: Sierra Nevada; SH: Sierra de Huétor; SCSV: Sierras de Cazorla–Segura–Las Villas; SC: Sierra de Castril) are shown.

Basin (subbasin)	Principal River	Population	Tributary		Length population (m)		Upper limits			Lower limits			Stretch length in Nature Reserve (m)		
			Code	Name	Partial	Total	UTM Top	Cause	Altitude (m a.s.l.)	UTM end	Cause	Altitude (m a.s.l.)	Natural Park	National Park	Name nature reserve
GU (Al)	Alhama	Alhama	1	Cerezal	3101	14230	413677/4088265	NA(Rs)	1050	412116/4087192	Tributary of 2	980	2442	0	STAA
GU (Al)			2	Alhama	11129		412481/4093952	NA(Rs)	1050	415518/4086805	AN(Da)	900	1895	0	STAA
GU (Al)	Cacín	Cacín Upstream	3	Añales	6140	50580	420714/4085366	NA(Rs)	950	422665/4090442	Tributary of 5	836	1189	0	STAA
GU (Al)			4	Cebollón	9499		426919/4081692	NA(Iw)	1070	423502/4088231	Tributary of 5	860	9499	0	STAA

Basin (subbasin)	Principal River	Population	Tributary		Length population (m)		Upper limits			Lower limits			Stretch length in Nature Reserve (m)		
			Code	Name	Partial	Total	UTM Top	Cause	Altitude (m a.s.l.)	UTM end	Cause	Altitude (m a.s.l.)	Natural Park	National Park	Name nature reserve
GU (Al)			5	Cacín Alto	16821		422589/4081594	NA(Rs)	1050	420592/4095016	AN(Da)$_1$	836	10426	0	STAA
GU (Al)			6	Río Grande	15778		429714/4082982	a + b	1050	423379/4091559	Tributary of 5	836	12442	0	STAA
GU (Al)			6a	Ayo. Almijara	1029		430430/4082647	NA(Rs)	1070	429714/4082982	Tributary of 6	1060	1029	0	STAA
GU (Al)			6b	Golondrinas	1313		429554/4082305	NA(Rs)	1070		Tributary of 6		1313	0	STAA
GU (Al)		Cacín	7	Cacín Bajo		14263	420592/4095016	AN(Da)$_1$	780	417076/4106295	AN(Da)	699	0	0	
GU (Ge)	Genil	Genil Upstream	8	Genil Alto	18775	48072	471002/4105636	a + b	1690	457450/4112987	AN(Da)$_2$	950	0	8848	SN
GU (Ge)			8a	Valdecasillas	1140		471546/4104732	NA(Te)	1900	471002/4105636	Tributary of 8	1690	0	1140	SN
GU (Ge)			8b	Valdeinfierno	2058		470698/4103913	NA(Te)	1950		Tributary of 8		0	2058	SN
GU (Ge)			9	Guarnón	2016		469028/4105477	NA(Te)	1900	469822/4107275	Tributary of 8	1460	0	2016	SN
GU (Ge)			10	Vadillo	4827		472877/4108896	NA(Te)	2100	468539/4109573	Tributary of 8	1300	0	4827	SN
GU (Ge)			11	San Juan	2882		466651/4107549	NA(Te)	1700	465444/4110013	Tributary of 8	1160	0	2882	SN
GU (Ge)			12	Maitena	16374		475936/4110519	NA(Te)	2200	463088/4111720	Tributary of 8	1010	0	6484	SN
GU (Ge)		Genil Downstream	13			4907	456418/4113128	AN(Da)$_2$	800	452098/4112446	AN(Mu)	730	0	0	
GU (Ge)	Dílar	Dílar	14			18941	461633/4103009	NA(Te)	2100	446368/4104500	AN(Mu)	800	1421	12374	SN

Basin (subbasin)	Principal River	Population	Tributary		Length population (m)		Upper limits			Lower limits			Stretch length in Nature Reserve (m)		
			Code	Name	Partial	Total	UTM Top	Cause	Altitude (m a.s.l.)	UTM end	Cause	Altitude (m a.s.l.)	Natural Park	National Park	Name nature reserve
GU (Ge)	Monachil	Monachil	15		12819		459744/4106670	AN(Mu)	1450	449520/4110753	AN(Mu)	730	2926	5480	SN
GU (Ge)	Aguas Blancas	Padules	16		11188		470583/4116881	NA(Rs)	1530	461241/4117704	AN(Da)$_3$	1050	0	0	
GU (Ge)		Aguas Blancas	17		818		461241/4117704	AN(Da)$_3$	930	460182/4117025	AN(Mu)	880	0	0	
GU (Gm)	Lugros	Lugros	18		4103		477396/4113730	NA(Rs)	1750	478345/4120299	AN(Wa)	1340	0	4103	SN
GU (Gm)	Jérez	Jérez	19	Alhorí	7937	22647	479694/4108796	NA(Te)	2100	483656/4112664	Tributary of 20	1280	3588	4260	SN
GU (Gm)			20	Jérez	3754		483656/4112664	19 + 21	1280	487414/4116178	AN(Mu)	1130	0	0	
GU (Gm)			21	Alcázar	3981		483631/4110525	a + b + c	1500	485107/4113913	Tributary of 20	1280	3698	41	SN
GU (Gm)			21a	Sabinar	2416		483270/4108489	NA(Iw)	1750	483631/4110525	Tributary of 21	1500	0	2416	SN
GU (Gm)			21b	Cabañuela	2900		481921/4108627	NA(Iw)	1870		Tributary of 21		0	2900	SN
GU (Gm)			21c	Casas Nuevas	1659		482710/4108800	NA(Iw)	1700	483712/4109899	Tributary of a	1550	0	1659	SN
GU (Gm)	Barrio	Barrio	22	Barrio	3030	4084	487939/4108819	Bajo a	1690	488276/4111614	AN(Wa)	1400	2081	949	SN
GU (Gm)			22a	Toril	1054		488347/4107961	NA(Rs)	1850	487939/4108819	Tributary of 22	1690	0	1054	SN
GU (Gm)	Aldeire	Aldeire	23	Aldeire	2841	4242	493483/4109416	a + b	1440	493595/4112139	AN(Wa)	1300	1083	0	SN

Basin (subbasin)	Principal River	Population	Tributary		Length population (m)		Upper limits			Lower limits			Stretch length in Nature Reserve (m)		
			Code	Name	Partial	Total	UTM Top	Cause	Altitude (m a.s.l.)	UTM end	Cause	Altitude (m a.s.l.)	Natural Park	National Park	Name nature reserve
GU (Gm)			23a	Pasillos	589		493665/4108899	NA(Rs)	1550	493483/4109416	Tributaries of 23	1440	589	0	SN
GU (Gm)			23b	Tejos	812		493195/4108667	NA(Rs)	1550				812	0	SN
GU (Gm)	Dólar	Dólar	24		2389		499835/4109821	NA(Rs)	1610	499351/4111788	AN(Wa)	1390	2389	0	SN
GU (Gm)	Fardes	Fardes	25a	Prado Negro	6132	26381	457563/4130525	NA(Rs)	1600	462422/4129053	Tributaries of 25	1200	6132	0	SH
GU (Gm)			25b	Perdices	1246		461332/4128618	NA(Rs)	1230				1246	0	SH
GU (Gm)			25	Fardes	19003		462422/4129053	a + b	1200	477647/4129857	AN(Da)	950	6483	0	SH
GU (Gm)	Guadalentín	Guadalentín	26	Guadalentín	21172	27342	514574/4195472	NA(Rs)	1350	508636/4179630	AN(Da)	970	21194	0	SCSV
GU (Gm)			27	Tornillos Gualay	6170		505631/4189690	NA(Rs)	1500	509759/4190612	Tributary of 26	1070	6170	0	SCSV
GU (Gm)	Castril	Castril Upstream	28		14837	63460	522243/4195767	NA(Rs)	1300	518813/4184270	AN(Da)$_4$	930	14837	0	SC
GU (Gm)		Castril Downstream	29		48623		518813/4184270	AN(Da)$_4$	850	504118/4157334	AN(Da)	630	0	0	
GU (Gm)	Guardal	Guardal Upstream	30a	Raigadas	2426	11446	532912/4196333	NA(Rs)	1100	530521/4191946	AN(Da)$_5$	1050	0	0	
GU (Gm)			30b	Fuentes	3306		528364/4193373	NA(Rs)	1100	530521/4191946		1050	0	0	
GU (Gm)			30	Guardal alto	5714		530521/4191946	a + b	1050	530986/4190330		1050	0	0	
GU (Gm)		Guardal Downstream	31		4300		530687/4189894	AN(Da)$_5$	980	529432/4187696	AN(Wa)	930	0	0	
GU (Gm)	Bravatas	Bravatas	32		14019		538334/4204184	NA(Rs)	1520	544960/4194937	AN(Wa)	1070	0	0	

Basin (subbasin)	**Principal River**	**Population**	**Tributary**		**Length population (m)**		**Upper limits**			**Lower limits**			**Stretch length in Nature Reserve (m)**		
			Code	**Name**	**Partial**	**Total**	**UTM Top**	**Cause**	**Altitude (m a.s.l.)**	**UTM end**	**Cause**	**Altitude (m a.s.l.)**	**Natural Park**	**National Park**	**Name nature reserve**
GU (Gu)	Guadalquivir	Valdeazores	34a	Valdeazores	1603		514949/4199991	NA(Rs)	1350	516069/4201039	AN(Da)$_6$	1270	1603	0	SCSV
GU (Gu)		Aguas Negras	34b	Aguas Negras	1215		516069/4201039	AN(Da)$_6$	1260	516300/4202110	AN(Da)$_7$	1250	1215	0	SCSV
GU (Gu)		Guadalquivir Upstream	33	Guadalquivir alto	50806	72041	502214/4189328	NA(Rs)	1250	517985/4225386	AN(Da)$_8$	630	50806	0	SCSV
GU (Gu)			34	Borosa	9487		516300/4202110	AN(Da)$_7$	1220	511675/4207849	Tributary of 33	660	9487	0	SCSV
GU (Gu)			35	Ayo. Truchas	2381		512467/4204721	NA(Rs)	800	512552/4206945	Tributary of 34	680	2381	0	SCSV
GU (Gu)			36	Aguamulas	9367		521513/4210530	NA(Rs)	1350	515248/4213285	Tributary of 33	630	9367	0	SCSV
GU (Gu)		Guadalquivir Downstream	37	Guadalquivir bajo	39037	56733	517985/4225386	AN(Da)$_8$	560	492779/4210991	AN(Mu)	420	12949	0	SCSV
GU (Gu)			38	Aguascebas grande	16431		510049/4217224	NA(Rs)	920	497128/4214172	Tributary of 37	430	7139	0	SCSV
GU (Gu)			39	Aguascebas chico	1265		500602/4213133	NA(Rs)	500	500193/4214126	Tributary of 38	450	0	0	
GU (Gu)	Guadalimar	Guadalimar	40		5403		537118/4253040	OA	700	533154/4250214	AN(Da)	650	5403	0	SCSV
S (Gf)	Bérchules	Bérchules	41	Chico Berchules	4860	19257	482139/4099741	NA(Iw)	2050	483061/4095911	Tributary of 43	1450	4459	401	SN
S (Gf)			42	Grande de Berchules	6315		483890/4100824	NA(Iw)	2000	483069/4095905	Tributary of 43	1450	2470	3845	SN
S (Gf)			43	Berchules	5506		483069/4095905	41 + 42	1450	483554/4090648	Tributary of 44	1000	2404	1523	SN
S (Gf)			43a	Cádiar	2576		483554/4090648	Bajo 43	1000	484043/4088290	AN(Wa)	880	0	0	

Basin (subbasin)	**Principal River**	**Population**	**Tributary**		**Length population (m)**		**Upper limits**			**Lower limits**			**Stretch length in Nature Reserve (m)**		
			Code	**Name**	**Partial**	**Total**	**UTM Top**	**Cause**	**Altitude (m a.s.l.)**	**UTM end**	**Cause**	**Altitude (m a.s.l.)**	**Natural Park**	**National Park**	**Name nature reserve**
S (Gf)	Torrente	Torrente	44			6366	458495/4095874	NA(Rs)	2000	453103/4093586	AN(Wa)	1030	3723	2643	SN
S (Gf)	Soportujar	Soportujar	45			6306	463939/4092956	NA(Rs)	2030	463115/4087019	AN(Wa)	720	4827	1374	SN
S (Gf)	Lanjarón	Lanjarón	46			13372	460541/4094393	NA(Te)	2130	455731/4083960	AN(Mu)	400	2257	2861	SN
S (Gf)	Guadalfeo	Guadalfeo Upstream	47a	Trevelez	28494	57446	478452/4102316	a + b	1980	467294/4084152	Tributary of 50	380	13826	5913	SN
S (Gf)			47b	Juntillas	339		478219/4102539	NA(Te)	2010	478452/4102316	Tributary of 48	1980	0	339	SN
S (Gf)			47	Puerto de Jerez	208		478606/4102454	NA(Te)	2010		Tributary of 48		0	208	SN
S (Gf)			48	Poqueira	13356		470207/4096483	NA(Te)	1900	467309/4085467	Tributary of 50	400	10429	2927	SN
S (Gf)			49	Guadalfeo alto	15049		467294/4084152	48 + 49	380	455872/4079561	AN(Da)	220	0	0	
S (Gf)		Guadalfeo Downstream	EXT			0	455872/4079561	AN(Da)	150	-	-	-	-	-	-
S (Ad)	Mecina	Mecina	50			13056	487842/4102752	NA(Te)	2010	487288/4091826	AN(Wa)	850	8832	1845	SN
S (Ad)	Bayarcal	Bayarcal	51			13769	497768/4106955	NA(Rs)	2030	499844/4095011	AN(Wa)	700	0	3656	SN
S (Ad)	Paterna	Paterna	52			8407	504820/4103740	NA(Rs)	1750	504886/4096266	AN(Wa)	900	3271	2611	SN
S (An)	Andarax	Andarax	53			5964	511200/4100284	NA(Iw)	1450	509867/4095713	NA(Sd)	950	5964		SN
SE (Se)	Tus	Tus	54a	Ayo. de la fuente	3454	11917	540369/4239029	NA(Rs)	1250	540256/4241979	Tributary of 55	1010	3454	0	SCSV

Basin (subbasin)	**Principal River**	**Population**	**Tributary**		**Length population (m)**		**Upper limits**			**Lower limits**			**Stretch length in Nature Reserve (m)**		
			Code	**Name**	**Partial**	**Total**	**UTM Top**	**Cause**	**Altitude (m a.s.l.)**	**UTM end**	**Cause**	**Altitude (m a.s.l.)**	**Natural Park**	**National Park**	**Name nature reserve**
SE (Se)			54b	Ayo. Andres	116		540151/4242024	NA(Iw)	1130		Tributary of 55		116	0	SCSV
SE (Se)			54	Tus	8347		540256/4241979	a + b	1010	544854/4245917	OA	900	8347	0	SCSV
SE (Se)	Segura	Segura Upstream	55	Madera	19833	39386	538141/4236562	NA(Rs)	1350	534610/4224933	Tributary of 57	1010	19833	0	SCSV
SE (Se)			56	Segura alto	19553		529239/4219355	NA(Iw)	1320	541114/4228817	AN(Da)	910	19553	0	SCSV
SE (Se)		Segura Downstream	EXT			0	541114/4228817	AN(Da)	870	-	-	-	-	-	-
SE (Se)	Zumeta	Zumeta Upstream	57			17082	538441/4215190	NA(Rs)	1200	547607/4225776	AN(Da)	920	17082	0	SCSV
SE (Se)		Zumeta Downstream	EXT			0	547607/4225776	AN(Da)	890	-	-	-	-	-	-

4. CHAPTER II

Extended spawning in brown trout (Salmo trutta) populations from the Southern Iberian Peninsula: the role of climate variability

Freza extendida en poblaciones de trucha común al sur de la península Ibérica: el papel de la variabilidad climática

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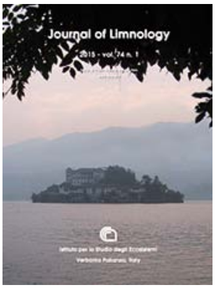

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4. CHAPTER II. EXTENDED SPAWNING IN BROWN TROUT (*Salmo trutta*) POPULATIONS FROM THE SOUTHERN IBERIAN PENINSULA: THE ROLE OF CLIMATE VARIABILITY

4.1. Abstract

The reproductive periods of brown trout (*Salmo trutta*) populations in 12 rivers in the Baetic Mountains in southern Spain were studied from 2008 to 2013. This area is an ecological and geographical limit for the distribution of this species in Europe. We found that the spawning period has been markedly extended in these fish. The mean spawning dates in the studied populations are consistent with the European trend at this latitude, but our data suggest that females from most of the populations that we studied are able to produce eggs from early October through late April or early May, yielding a reproductive period of between 150 and 170 days, the longest and most delayed brown trout reproduction periods that have been reported in the literature. We believe that such expanded spawning periods result primarily from the unpredictability of the Mediterranean climate, although it is possible that other factors may have contributed to the development of this reproductive behaviour. This hypothesis is discussed in the context of a comparison of our results with those found for other European *S. trutta* populations.

4.2. Introduction

The brown trout (*Salmo trutta* Linnaeus, 1758) is a Palaearctic species that exhibits high genetic, ecological and morphological variability (Bernatchez *et al.*, 1992; Klemetsen *et al.*, 2003) within its native area, which extends from Norway and Russia (71°N) in the north to the Atlas Mountains (30°N) in the south (Jonsson and Jonsson, 2011; Snoj *et al.*, 2011).

The Baetic Mountains (latitude 36°-38° N) in the Iberian Peninsula are the south western boundary of this species' habitat in Europe and thus represent an ecological limit for the distribution of *S. trutta*. In this area there is great topographical diversity with elevations ranging from 0 to 3482 m asl; this diversity permits the presence of rivers with rainfall, snowmelt and rain-on-snow hydrological regimes. Moreover, this region has a Mediterranean climate, with a cool, wet season followed by a warm, dry season; this climate pattern causes a sequence of often extreme floods and droughts (Gasith and Resh, 1999; Tierno de Figueroa *et al*., 2013).

Over the past century, brown trout have experienced range contraction and displacement toward higher elevations in these mountains (Menor and Prenda, 2006; Sáez Gómez, 2010). Currently, the species is distributed in isolated resident populations that generally occupy small areas. The connectivity among these populations appears to have never been very strong, but anthropogenic factors have reduced connectivity among these populations further. Almodóvar *et al*. (2010) showed that these populations are genetically distinct and possess haplotypes that have not been described previously.

In habitats at the limit of the ecological niche for a given species, environmental pressures driving selection may be stronger and hence of greater adaptive significance for this species (Lesica and Allendorf, 1995; Antunes *et al*., 2006). Thus, Iberian rivers could have acted as a refuge for *S. trutta* during the last ice age of the Quaternary (García-Marín *et al*., 1999; Sanz *et al*., 2000; Suárez *et al*., 2001), allowing uninterrupted speciation processes to occur for a longer period in this region than elsewhere in the native area of this species. In this way, the high phenotypic and ecological plasticity of this species (Elliot, 1994; Ayllón *et al*., 2010; Valiente *et al*., 2010), together with the specific characteristics of the distribution of *S. trutta* populations and of the topography and climate of this region, could have allowed the appearance of particular adaptive traits, such as those reported in Cyprinidae (Carmona *et al*., 1997) or aquatic invertebrates (Giller and Malmqvist, 1998) inhabiting similar environments.

Along its wide geographical native range, *S. trutta* exhibits a continuum of life history tactics (Cucherousset *et al*., 2005) that range from anadromy to residence. The reproductive traits of *S. trutta* are likely to exhibit a similarly wide range of variation. For example, significant latitudinal variations in the mean spawning date and in the duration of the spawning period have been observed. The effects of latitude on brown trout spawning have been shown to be related to water temperatures (Elliott, 1982; Jonsson and L'Abée-Lund, 1993; Ojanguren and Braña, 2003); lower water temperatures require a longer incubation period (Crisp 1988; Elliott and Hurley, 1998; Klemetsen *et al*., 2003). Consequently, a cline in spawning periods is observed: spawning occurs from October through December in northern Europe and from January through March in more southern populations. Therefore, in general, it has been assumed that *S. trutta* spawning periods rarely last for more than 1 or 2 months. On the other hand, this widespread reproductive behaviour, which is influenced by latitude, may also vary due to specific genetic or environmental factors. Thus, a population of sea trout (*S. trutta*, anadromous form) in a stream in Denmark spawned from October to February in the same breeding season (Aarestrup and Jepsen, 1998). However, examples of variation in the cline in spawning time are more frequently observed in populations inhabiting the southernmost boundary of this species' habitat. In the Metauro River in Italy (43°N), Caputo *et al*. (2010) observed early spawning (November-January) typical in populations at northern latitudes. These authors linked this anomaly in the latitudinal cline to genetic introgression because the population had been highly stocked with Atlantic strains since at least the beginning of the 20th century. At more southern latitudes, Gortázar *et al*. (2007) observed longer spawning periods (from December to April) to occur in populations in the Castril River in Spain (37°N). These authors hypothesized that this phenomenon may be a response to catastrophic events (floods and droughts) in populations connected to a reservoir.

The present study had three aims: i) to describe regional and local patterns of the reproductive phenology of *S. trutta* populations from the Baetic Mountains; ii) to compare spawning data among populations inhabiting different rivers in the study area and between the study area and other European areas; and iii) to discuss the effects of climatic variability or other possible factors on spawning dates and durations. The conclusions of this work will increase our knowledge of the local adaptations to climatic drivers of life history traits.

4.3. Material and methods

4.3.1. Study area

The study populations inhabit the upper reaches of several rivers originating in the Baetic Mountains. These rivers belong to three basins: the Guadalquivir, South Mediterranean and Segura river basins (Figure 4.1). The sampling sites that were studied are located between the coordinates 38°03’- 36°30’ N and 03°51’- 02°45’ W.

Twelve populations were studied. These populations were distributed in three different mountain systems: the Sierra de Alhama - Tejeda - Almijara in the west, the Sierra Nevada in the southeast and the Sierras de Cazorla – Segura - Las Villas y Castril in the north (Figure 4.1). All of the populations studied are resident populations that are completely isolated and exhibit no connectivity within the same mountain system. The sampling locations were at very diverse elevations, particularly in Sierra Nevada (Table 4.1).

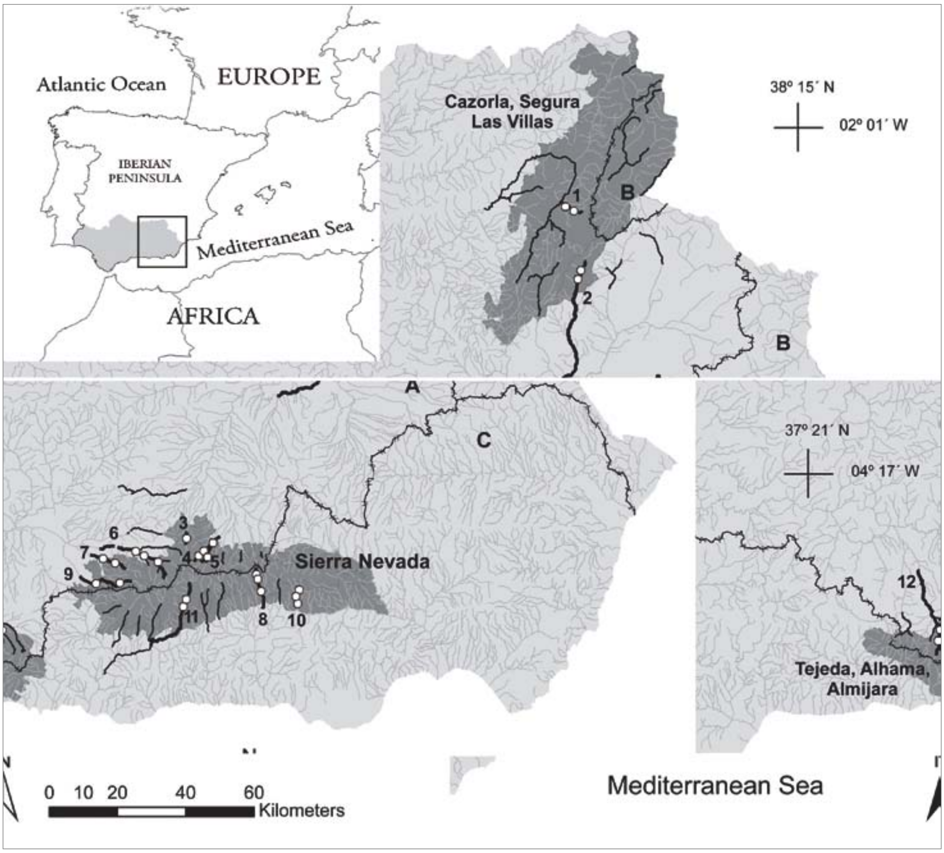

Figure 4.1. Location of the study area. Basins delimited: Guadalquivir (A), Segura (B) and South Mediterranean (C). Fluvial network (gray lines), rivers inhabited by *Salmo trutta* (thin and thick black lines), the rivers that were studied (thick black lines) and sampling sites are also shown. The river numbers shown in this figure match those listed in Table 4.1.

4.3.2. Methods

Female salmonids lay their eggs in pits that they dig in gravel beds, and the series of nests that are usually placed in a row by a female is known as redd (Jonsson and Jonsson, 2011). Redd counts are accepted as an effective, economical and non-invasive method for identifying spawning periods (Dunham *et al*., 2001). However, this method was not used in this study because the sampling sites were at high elevations and was difficult to access because of the rugged terrain; the widths of the sampling sites typically did not exceed 3 metres, and dense forests were present on the riverbanks. In addition, due to the high slope and low order of the rivers that were studied (primarily orders 1 and 2), a large number of large rocks were frequently found in the riverbed. Thus, the hydrogeomorphology of the rivers examined in this study is characterised by frequent rapids that produce turbulent water surfaces and by pools that prevent the formation of large spawning areas. It is also known (Al-Chokhachy and Budy, 2005) that difficulties in detecting redds constructed by small resident fish may prevent accurate monitoring of a reproductive population. In previous demographic studies (Supplementary data 4.1), we showed that adults in the trout populations analysed in this study did were not usually more than 3 years old (3+) and were primarily 2+ females (usually 18-25 cm Lf), which cannot displace a considerable amount of substrate during redd construction. Hence, in these rivers, counting redds is not the recommended method for identifying spawning periods; thus, electrofishing and stripping are allowed. These methods generate the most consistent results in the study area.

Between one and three sampling sites in each of the twelve selected rivers were chosen (Table 4.1). For six consecutive sampling periods (from 2008 to 2013), surveys were conducted using single-pass electrofishing between September and June. Each spawning period includes the autumn of the previous year and the winter and spring of the indicated year (e.g., the 2008 spawning period includes the period from autumn 2007 to spring 2008).

During the first two years of the study period, surveys were conducted monthly to determine when spawning periods occurred in general. In the final years of the study, the sites were sampled every two weeks, at the beginning and the end of the spawning period, to refine our knowledge of the start and end of the reproductive period in each river.

Table 4.1. Summary of surveys conducted over 6 years and of the spawning periods determined for the 12 *Salmo trutta* populations examined in this study. Nss: Number of sample sites. Ns: Number of surveys during the study period. Nt: Total number of trout over 15 cm (L_f) which were gently stripped in that river during the study period. Nf: Total number of females over 15 cm (L_f) detected. Spawning period: grey bars indicate confirmed spawning periods. White bars indicate probable spawning periods. The dates indicate the first and last date of detection of females with mature eggs in this river. The *dates indicate the survey in which all females had obvious signs of having recently spawned. In river Castril, the last redd observed by Gortázar *et al.* (2007) is noted like #date. Days: confirmed spawning days / total probable spawning days (sum of confirmed and probable spawning days). The * indicates inaccuracy due to lack of surveys.

River	River	Latitude (north)	Nss	Altitude (m.a.s.l.)	Sampled years	Ns	Nt	Nf	Spawning period (days)		Mean spawning date
									Conf	Prob	
Aguasmulas	1	38º 03´	2	729 | 826	2008 | 2009 | 2011 | 2012 | 2013	16	441	41	42	≈49*	25-Feb
Castril	2	37º51´	2	1014 | 1104	2009 | 2011 | 2012 | 2013	21	339	32	78	≈142	8-Feb
Lugros	3	37º 10´	1	1798	2010 | 2013	6	175	43	21	≈154	9-Feb
Alhorí	4	37º 09´	2	1525 | 1752	2009 | 2010 | 2011 | 2012 | 2013	22	593	128	89	≈167	1-Feb
Alcázar	5	37º 08´	2	1622 | 1743	2008 | 2009 | 2010 | 2012 | 2013	15	169	40	96	≈211	19-Jan
Genil	6	37º 08´	3	1196 |1299 | 1493	2008 | 2009 | 2010 | 2011 | 2012 | 2013	36	949	95	140	≈154	20-Jan
Monachil	7	37º 06´	2	911 | 1476	2008 | 2009 | 2010 | 2011 | 2012 | 2013	21	521	55	146	≈160	18-Jan
Bayárcal	8	37º 04´	3	1354 | 1815 | 1883	2009 | 2010 | 2011 | 2012 | 2013	31	789	113	145	≈159	5-Feb
Dílar	9	37º 3´	2	1048 | 1797	2008 | 2009 | 2010 | 2011 | 2012 | 2013	18	355	41	13	≈147	21-Jan
Andarax	10	37º 01´	3	1058 | 1106 | 1237	2008 | 2009 | 2010 | 2011 | 2012 | 2013	34	710	77	127	≈168	21-Jan
Trevélez	11	37º 00´	2	1513 | 1777	2008 | 2009 | 2010 | 2011 | 2012 | 2013	27	730	89	129	≈172	5-Feb
Cacín	12	36º 54'	2	970 | 1009	2008 | 2009 | 2011 | 2012 | 2013	19	446	62	141	≈155	11-Feb

Thus, when females with mature eggs were detected for the first time each year, we did not sample again until the beginning of the following spring. In the spring, surveys were conducted every two weeks until either all females that were examined had spawned, no females were forming eggs or no females with mature eggs were observed.

Because of our previous analyses of individual growth in the study region, we were able to estimate the ages of trout by their body size (fork length, henceforth Lf; Supplementary data 4.1). In each survey, we collected a minimum of 30 adult trout (2 or more years old). The length of every individual was measured (to the nearest 1 mm), every individual was weighed (to the nearest 0.01 g), and the status of each individual´s gonads was evaluated after gently stripping them. When a mature individual was detected, only a small quantity of gametes was extracted to identify the sex of the individual. Because males produce sperm longer than females produce eggs, only females were used to define active spawning periods. The maturation status of every female was examined, and all of the females were classified into three categories: females forming eggs, females with mature eggs and recently spawned females (females with loose abdomens). After data collection, all specimens were returned to the same reach of the sampling site.

A population was considered to be spawning when females with mature eggs or both females maturing eggs and spawned females were detected in the same survey. A *confirmed spawning period* (grey bar in Figure 4.2) for a particular river was determined by aggregating all of the dates on which spawning trout were observed in all of the studied years. There were sometimes obvious evidences that a spawning period may have been longer than the confirmed spawning period. Thus, we defined a *probable spawning period* (white bar in Figure 4.2) based on the occurrence of any of the following: i) females with mature eggs were detected in the first survey in the confirmed period; this implies that spawning very likely occurred in the days before the survey; ii) females with mature eggs were detected in the last survey in the confirmed period; this implies that spawning females were present in the days after the survey; and iii) females in a survey conducted after the confirmed period had obvious signs of having recently spawned; these females must have spawned in the days before the survey. The *total spawning period* was defined as the sum of confirmed spawning period and the probable spawning period. In addition, the *confirmed spawning duration* (the number of days in a confirmed spawning period), *total spawning duration* (the number of days in a total spawning period) and the *mean spawning date* (within the total spawning period) were calculated for each river (Table 4.1).

The mean spawning date was used to determine (by means of simple regression analysis using STATISTICA software version 8.0; StatSoft, Tulsa, OK, USA) whether our results for the southernmost brown trout populations in Europe agreed with the latitudinal trend in spawning dates observed in northern populations (Klemetsen *et al*., 2003). Mean spawning dates calculated in this study were compared with mean spawning dates reported in the literature, as reviewed by Gortázar *et al*. (2007), to achieve this goal.

In addition, the rainfall regime during the period 1980-2009 was calculated for 4 rivers in the study area (Figure 4.4) to observe the natural variability in flow regimes. The estimates given were calculated for the reaches inhabited by *S. trutta* in these rivers and their tributaries. The Watershed function of Spatial Analyst extension of ArcGIS 9.3.1. software (ESRI 2009) was used to set the boundaries of the watersheds of the inhabited reaches. Monthly rainfall in each watershed was determined using the Zonal statistics as table function of the Spatial Analyst extension. Monthly rainfall date were obtained from the REDIAM (Environmental Information Network of Andalusian Government). Finally, with the aim of including all data in a simpler graph, seasonal rainfall was calculated for each year, based on the average litres per square metre that were measured in winter (January + February + March), spring (April + May + June), summer (July + August + September) and autumn (October + November + December).

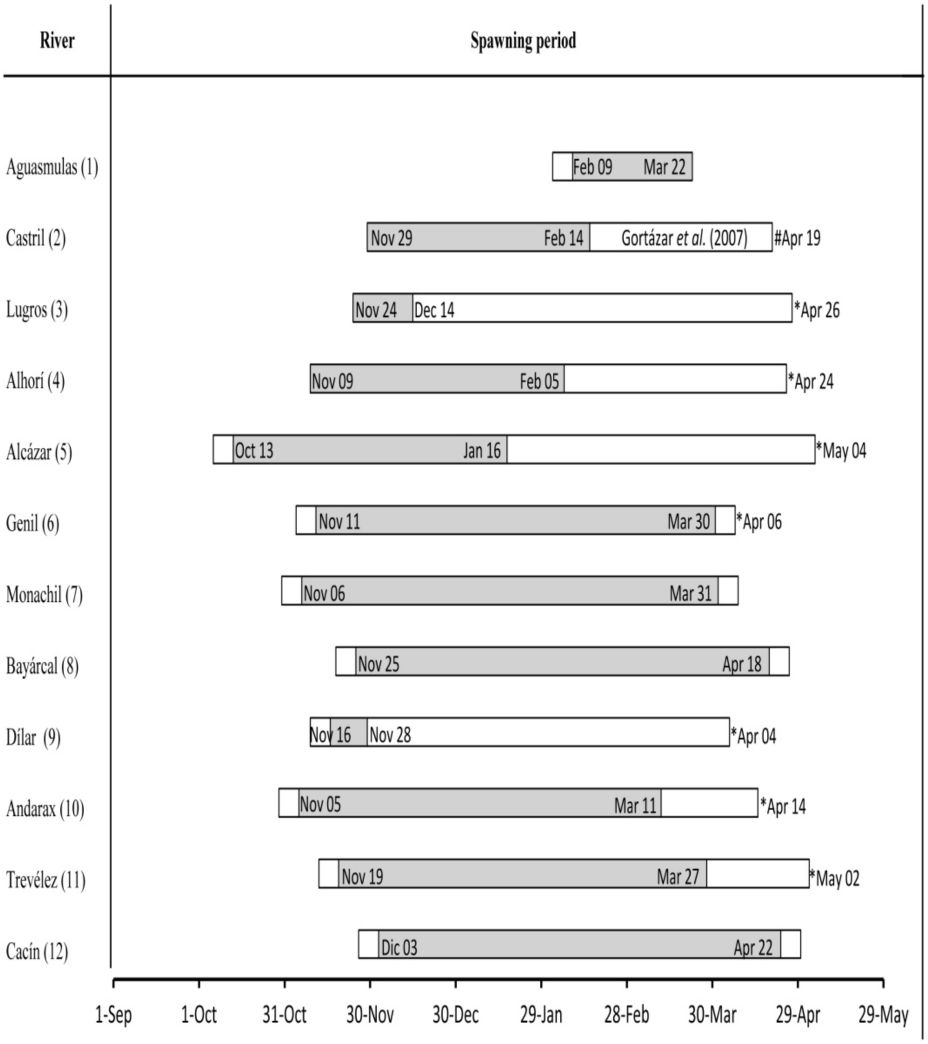

Figure 4.2. Spawning periods. Grey bars indicate confirmed spawning periods. White bars indicate probable spawning periods. The dates indicate the first and last dates on which females with mature eggs were observed in a given river. The dates marked with an asterisk indicate that all females surveyed on that date exhibited obvious signs of having recently spawned. In the Castril River, the last redd observed by Gortázar *et al*. (2007) is indicated as #date. The river numbers shown in this figure match those listed in Table 4.1.

4.4. Results

Data were obtained for 26 sampling points in 12 rivers belonging to two different river basins (Guadalquivir, rivers 1, 2, 3, 4, 5, 6, 7, 9 and 12; and South Mediterranean, rivers 8, 10 and 11; Figure 4.1) and analysed. During the sampling period, which was distributed in six campaigns from 2008 through 2013, 266 surveys were conducted, 6217 *S. trutta* were stripped and 816 of them were sexed as females (Table 4.1).

The lengths of the spawning seasons in the studied rivers were determined (Table 4.1). The longest confirmed spawning period lasted 211 days (in the Alhorí River), and all of the probable spawning periods lasted longer than 142 days (except in the Aguasmulas River, most likely due to the limited number of surveys conducted in this river). The data obtained in this study suggest that the sets of females present in some of the rivers that were studied can produce eggs from early October through late April or early May, for a period of between 150 and 170 days (i.e., between 5 and nearly 6 months). The period in which males produced sperm was even more extended, but this period was not considered here because females define the spawning periods (see the Methods section).

The mean spawning dates in all of the studied rivers agreed with European latitudinal trends [Figure 4.3; $y=-4.04 \bullet x+267.76$; R^2 adjusted=0.755, $P<0.05$; residuals of the fitted model satisfies the assumptions of normality and homoscedasticity; as dependent variable we used the mean spawning date in days since September 30, which is the first date of mean spawning in Europe compiled by Gortázar *et al.* (2007)]. Rainfall regime in the study area exhibited high interannual variability (Figure 4.4), as expected in a Mediterranean-climate zone.

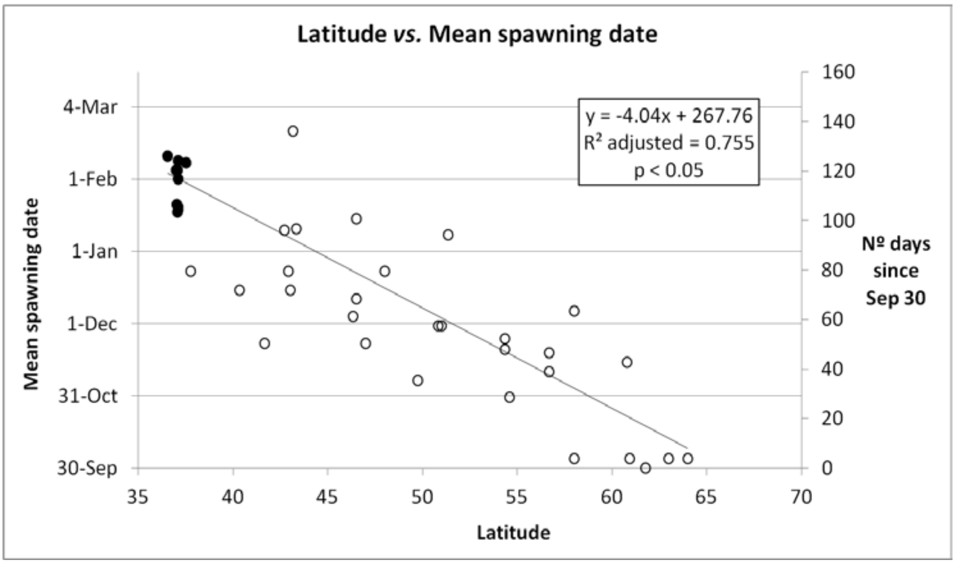

Figure 4.3. Simple regression analysis examining the relationship between latitude and mean spawning date. Solid circles represent data collected in this study. Open circles represent previously published data (in Gortázar *et al.*, 2007).

4.5. Discussion

S. trutta is known to exhibit high phenotypic plasticity throughout its extensive area of distribution (Elliot, 1994; Ayllón *et al.*, 2010; Valiente *et al.*, 2010). At the same time, the reproductive rhythms in salmonids have a strong genetic basis, as a consequence of adaptation to particular environmental conditions in geographic isolation (Northcote, 1992; Elliott, 1994). This fact may be particularly relevant for the populations inhabiting the study area, which have been isolated since the last glacial retreat (ca. 13,000 years ago). Several factors could have acted separately or together to affect the development of the reproductive behaviour observed in the trout populations that were studied (Table 4.1, Figure 4.2). Considering the geographical location of the studied populations (Figure 4.1), we believe that such prolonged spawning periods (extended spawning) are primarily conditioned by characteristics of the Mediterranean climate, particularly rainfall variability. These and other possible factors are discussed below.

Temperature is an important parameter in the life cycle (Gillooly *et al.*, 2001). Several aspects of ontogenetic development and reproductive success in salmonids are governed by temperature-dependent processes: the number and sizes of eggs, the duration of embryonic development, the duration of the hatching periods, survival rates before and after hatching and fry emergence (Ojanguren and Braña, 2003; Lobón-Cerviá and Mortensen, 2005; Lahnsteiner and Leitner, 2013). Similarly, the duration of the incubation period and the duration of endogenous larval feeding are temperature-dependent: the lower the temperature, the longer the duration. Moreover, several investigators have found that the start date of spawning exhibits a latitudinal trend; the start date is delayed in southern populations compared with northern populations (Jonsson and L'Abée-Lund, 1993; Klemetsen *et al.*, 2003; Gortázar *et al.*, 2007).

In addition to latitude, elevation is another factor capable of modulating the water temperature as it can mimic the effect of latitude on temperatures. In fact, it is often assumed that elevation gradients can be used as a proxy for understanding ecological processes along latitudinal gradients (Hansen *et al.*, 1997; Körner, 2007; Halbritter *et al.*, 2013). Given the modulating effects of latitude and elevation on water temperatures, the spawning periods of *S. trutta* populations located in high mountain systems at lower latitudes could be similar to those of populations inhabiting lower elevations at higher latitudes. Gortázar *et al.* (2007) thus investigated the relationship between latitude and elevation in the spawning date of European *S. trutta* populations. However, these investigators failed to find any significant effect of elevation using data extracted from previous publications, and this relationship thus had to be removed from the model. In fact, little is known about habitat conditions at spawning sites in rivers at higher elevations (Riedl and Peter, 2013).

The mean spawning dates in the populations examined in this study (Table 4.1) are in agreement with the latitudinal trend in mean spawning dates (Figure 4.3) (Gortázar *et al*., 2007; Klemetsen *et al*., 2003). Nevertheless, the lengths of the spawning period of *S. trutta* populations located in the study area are considerably longer than any other reported spawning periods. Gortázar *et al*. (2007) reviewed the durations of spawning periods in different European brown trout populations and reported that no spawning period lasted longer than 100 days. By contrast, several populations in our study started their reproductive periods in October, and their reproductive periods extended to late April or early May (Figure 4.2).

Variation in the reproductive periods among the populations in the rivers that were studied may be due to differences in temperature and hydrological regimes (rain-on-snow and snowmelt). Thus, all of the *S. trutta* populations studied in the Sierra Nevada (rivers 3, 4, 5, 6, 7, 8, 9, 10 and 11 in Figure 4.1), which populations inhabit rivers originating in the highest elevations of the Iberian Peninsula (above 3000 m asl) and are greatly influenced by snow (snowmelt and rain-on-snow regimes), begin spawning early (Figure 4.2). Other populations that inhabit rivers originating in lower-elevation mountain systems that are less influenced by snow (rain-on-snow and main rainfall regimes; e.g., the Cacín River and the Castril River, rivers 12 and 2 in Figure 4.1, respectively) exhibit a slightly delayed spawning start relative to the populations of the Sierra Nevada (Figure 4.2). On the other hand, in the Aguasmulas River (river 1 in Figure 4.1), which is a typical mid-mountain Mediterranean river that is little influenced by snow (i.e., in a rainfall regime) and runs at lower elevations, water temperatures fluctuate more than in the other rivers studied, and the spawning period appears to start later than in the other rivers studied. Nevertheless, the relative lack of surveys in this river may have affected these findings (Figure 4.2). Thus, the results of this study suggest that higher elevations, greater snowfall amounts, and consequently lower temperatures could affect the beginning of spawning periods at local scales.

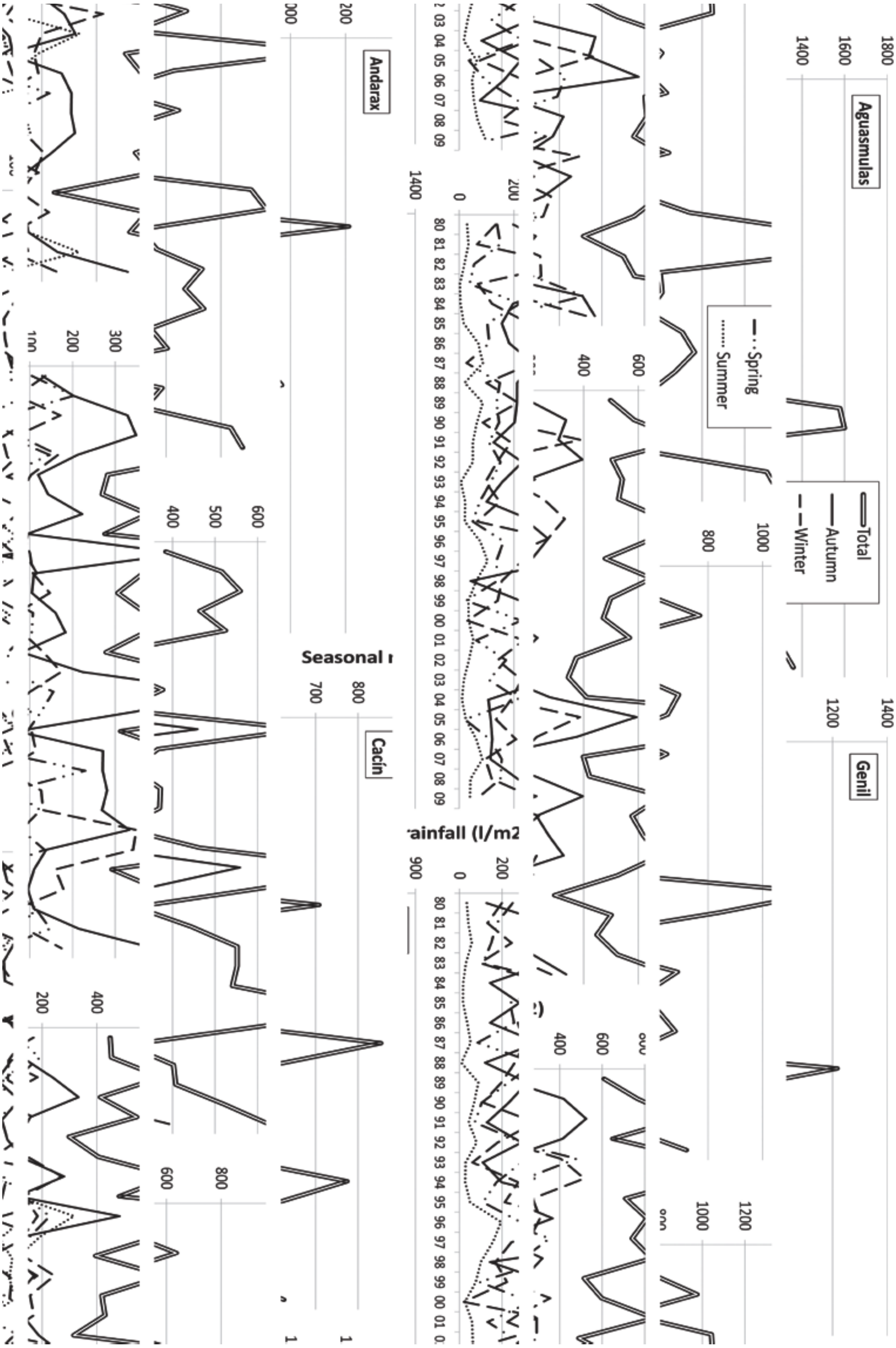

Figure 4.4. Time series of accumulated rainfall by seasons for three decades (1980-2009) in the rivers Aguasmulas, Genil, Andarax and Cacín (1, 6, 10 and 12 in Figs. 1 and 2), showing the interannual unpredictability of the study area.

Furthermore, the Mediterranean climate is widely recognised to be unpredictable (Gasith and Resh, 1999; Tierno de Figueroa *et al*., 2013). This unpredictability, which is related to the seasonality of the Mediterranean climate, directly affects water flows and causes periods of drought and flooding that can occasionally be extreme (Figure 4.4). In summer, the flows in the rivers examined in this study decrease, and the water temperatures increase. Because *S. trutta* populations in the study area permanently inhabit high-middle reaches of rivers, drought periods seldom become extreme, and the water temperature threshold for the survival of the species (Jonsson and Jonsson, 2011) is rarely reached. Nevertheless, extreme flow decreases in the lower-elevation limits of the species distribution are sometimes observed, and such decreases can directly cause population disappearance in these locations (personal observations).

Likewise, increases in flow also greatly influence river communities in the studied reaches. For example, torrential spring rains can produce devastating effects in Mediterranean river ecosystems by altering the morphological structure of rivers and dragging plant and animal communities downstream (Gasith and Resh, 1999). In the study area increases in flows during winter and spring can be gradual or torrential, and the flows can increase repeatedly. Repeatedly increased flows are much more harmful to *S. trutta* populations (Jensen and Johnsen, 1999) because a high intensity of floods during the incubation and emergence periods may limit recruitment (Cattaneo *et al*., 2002; Lobón-Cerviá and Rincón, 2004; Unfer *et al*., 2011). Thus, mechanisms to avoid the detrimental effect of either or both drought and floods, which are stochastic events, could potentially be selectable features of species that inhabit unpredictable ecosystems. Aquatic insects, for example, exhibit important adaptations to unpredictable flow regimes (Giller and Malmqvist, 1998); egg diapause and delayed hatching are adaptations used by mayfly and stonefly species in temporary and desert streams, and some of these species may extend their hatching for up to 5-7 months (Dieterich and Anderson, 1995; Jacobi and Cary, 1996). Plasticity in life history allows the eggs of these species to remain in the substrate during summer droughts, so that development can be resumed when water flows again. Since trout have not developed these ecological adaptations, extended spawning may be an adaptive strategy with similar purposes.

Figure 4.2 shows that females in the studied populations mature their eggs asynchronously, so that the reproductive period is able to last from five to more than six months. In other Mediterranean trout populations with extended spawning periods (Gibertini *et al.*, 1990; Gortázar *et al.*, 2007; Caputo *et al.*, 2010), the spawning intensity (understood as the number of females spawning at a given time) is not constant throughout the reproductive period but does exhibit a temporal peak in intensity. It is known that spawning times have evolved to match offspring emergence with optimal seasonal environmental conditions (Heggberget, 1988; Jonsson and Jonsson, 2011). However, the presence of actively reproducing individuals before and after the spawning peak increases the chances of reproductive success for populations inhabiting rivers with interannually variable environmental conditions. Therefore, individuals within the same populations may exhibit differences in the timing of reproductive behaviours. With such variability in the reproductive strategies of a given population, the longer the spawning period, the greater the capacity of the population to avoid negative consequences of stochastic phenomena. Thus, the ecological advantages provided by extended spawning in the context of the unpredictability of the Mediterranean climate may have allowed the *S. trutta* populations that inhabit the study area to develop the largest known reproductive periods of any trout population.

In general, freshwater fishes exhibit prolonged spawning periods in tropical and subtropical regions, while this strategy is uncommon in temperate areas (Nikolsky, 1963; Jonsson and Jonsson, 1993). Thus, the extended spawning period observed in this study is not an expected reproductive mechanism in freshwater fishes inhabiting European latitudes. Nevertheless, longer-than-expected spawning periods have been observed in fish populations inhabiting environments with uniform water temperatures and food supplies available throughout the year (Sigler and Sigler, 1990), but these conditions are far from those observed in our study. A small number of Salmonid populations with longer spawning periods have been observed previously; the longer spawning periods in these populations have been thought to be related to the presence of a reservoir (Gortázar *et al*., 2007), to heavy introgression with Atlantic haplotypes (Caputo *et al*., 2010), or to altered photoperiods in *Salmo fibreni* (Zerunian *et al*., 1996). However, in our study area, most populations inhabit river sections that are not connected with reservoirs, the annual effect of the photoperiod is not altered and the percentage of genetic introgression is extremely low or zero (Almodóvar *et al*., 2010). Moreover, it is known (Leggett and Carscadden, 1978) that the fine-tuning of reproductive strategies to local environmental conditions may be widespread among fish and may be the ultimate basis for the evolution of homing. Thus, migratory salmonids such as anadromous *S. trutta* populations or Atlantic salmon (*Salmo salar* L. 1758) exhibit a latitudinal cline in their spawning activities. However, the salmonid populations that have exhibited extended spawning in Southern Europe (*S. fibreni* in Lake Posta Fibreno and the *S. trutta* populations studied in this paper) are resident populations. It is likely that the disconnection of the life cycles of resident populations from phenomena associated with ocean dynamics and the need to have lower energy expenditures during migration (populations sometimes ascend only tens or hundreds of metres to spawn) has been an enabling factor in the development of the extended spawning periods that have been observed in resident populations.

4.6. Conclusions

The intra-populational asynchrony observed during the spawning period in the populations examined in this study could act as a reproductive mechanism that provides advantages within the framework of the unpredictability of the Mediterranean climate, which can cause stochastic events such as drought, floods or heavy rains that can affect the reproductive success of these populations. Furthermore, it is likely that the water temperature acts as a local modulating factor at the beginning of the breeding period and that local variations in water temperature could thus explain the differences observed among the populations in the mountain systems investigated in this study. We thus suggest that variations in water temperature (occurring as a result of local interaction between latitude, elevation and hydrological regime), unpredictable climatic factors and the life history tactics (migratory versus resident forms) of a given population should be considered to be the main drivers of the reproductive periods of *S. trutta*.

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Supplementary data 4.1

Growth equations of the Studied brown trout populations

The growth equations for brown trout [*Salmo trutta* (Linnaeus, 1758)] populations were calculated from the surveys made during 2005-2013 period. Sampling sites were distributed in the nine sub-basins present in the distribution area of the species in the region (Figure S.1 and Table S.1). Surveys were made by electrofishing, using three successive passes without replacement and with a constant effort (DeLury, 1947). Fishes were placed into holding boxes to be measured (furcal length, LF, 1 mm accuracy) and weighed (0.01 g accuracy). Finally they were recovered and returned back to the sampled section.

For each sub-basin the growth equation was obtained (Table S.2) by means of Von Bertalanffy's method (1938), complemented by the combined study of frequency distribution of lengths in the sample and scalimetry (Pauly and Caddy 1985; Steinmetz and Müller 1991; Hining and West 2000).

Table S.4.1. Sampling sites in the study area. * Numbers in "River" column refer to the rivers where spawning was studied (see Figure 1 and Table 1 of Chapter II).

Basin	Subbasin	River/Reach*	Code Sampling site	UTM X	UTM Y
Guadalquivir	Almijara	Alhama	81	414498	4088169
		Alhama	82	414684	4087523
		Alhama	83	413988	4091434
		Alhama	84	414151	4088661
		Alhama	85	414903	4090028
		Alhama	86	412676	4092325
		Cacín	91	425668	4085989
		Cacín (11)	92	423419	4088808
		Cacín (11)	93	423312	4083608
		Añales	94	421396	4087349
		Cacín	96	418628	4098320
		Cacín	97	418608	4101439

Basin	Subbasin	River/Reach*	Code Sampling site	UTM X	UTM Y
	Genil	Dílar (12)	105	450541	4102247
		Genil (6)	114	465214	4110044
		Genil (6)	115	463264	4111387
		Maitena	121	466963	4113015
		Maitena	122	464618	4112816
		Monachil (7)	132	453368	4109287
	Guadalquivir I	Aguasmulas (1)	211	517726	4211633
		Aguasmulas (1)	212	516094	4211778
		Ayo. Valdeazores	231	515714	4200750
		Borosa	241	512612	4206109
		Borosa	242	513204	4206322
		Borosa	243	516254	4204488
		Borosa	244	515143	4204913
		Borosa	245	512911	4206841
		Guadalquivir I	253	505474	4194778
		Guadalquivir I	255	506258	4199069
		Guadalquivir I	261	508158	4202950
	Guadalquivir II	Aguascebas Grande	221	503687	4215813
		Guadalquivir II	262	511043	4226794
		Guadalquivir II	263	509669	4226626
		Guadalquivir II	264	502804	4220679
		Guadalquivir II	265	497956	4216410
		Guadalimar	271	533749	4250891
	Guadiana Menor I	Fardes	311	462269	4129150
		Fardes	312	471394	4128096
		Alhama de Lugros (3)	461	477961	4116224
		Alhorí (4)	401	482425	4111683
		Alcázar (5)	391	483630	4110575
		Bco. del Barrio	411	488168	4109578
	Guadiana Menor II	Castril (2)	301	521286	4191944
		Castril (2)	302	519965	4189046
		Guadalentín	323	510486	4191428
		Guadalentín	324	506417	4191227
		Guadalentín	326	508701	4188639
		Guadalentín	327	508764	4188609
		Guardal	331	529022	4193388
		Guardal	332	529570	4192921
South Mediterranean	Sª Nª Oriental	Andarax (9)	62	509601	4099225
		Andarax (9)	63	509711	4097438
		Andarax (9)	64	509981	4096994
		Bayárcal (8)	11	498324	4103668
		Bayárcal (8)	13	499893	4099610
		Mecina	31	486769	4093919
		Paterna	41	504957	4098742
	Guadalfeo	Bérchules	151	482081	4099328
		Bérchules	152	483650	4099986
		Bérchules	153	483582	4092905
		Lanjarón	161	459112	4090279
		Poqueira	171	469044	4094273
		Poqueira	172	467797	4089401
		Torrente	181	454444	4093948

Basin	Subbasin	River/Reach*	Code Sampling site	UTM X	UTM Y
		Torrente	182	453134	4093631
		Trevélez (10)	192	477088	4095939
		Trevélez (10)	193	476596	4094765
		Chico de Soportújar	291	463712	4091657
Segura	Segura	Madera	351	533734	4234833
		Madera	352	533469	4228249
		Madera	354	534457	4226694
		Segura	361	544057	4231363
		Segura	362	530002	4220543
		Segura	363	530826	4221279
		Segura	366	538011	4224890
		Segura	367	538572	4225846
		Tus	372	543136	4245630
		Tus	373	544191	4245905
		Zumeta	383	541203	4217322
		Zumeta	384	545718	4223207
		Zumeta	385	546275	4224062
		Zumeta	386	548588	4228730

Table S.4.2. Parameters of the Von Bertalanffy's growth equations in the nine sub-basins inhabited by the brown trout in Andalusia. Age = t0 – [Ln (1 - (LF / L∞)) / K]; t0: age at which the organisms would have had zero size; LF: Fork length; L∞: asymptotic length at which growth is zero; K: growth rate.

Sub-basin	t_0	L∞	K
Almijara	-0,176	61,935	0,167
Genil	-0,205	107,253	0,083
Guadalfeo	-0,39	69,996	0,115
Guadalquivir I	-0,126	45,62	0,32
Guadalquivir II	0,109	38,286	0,442
Guadiana Menor I	-0,182	81,2	0,123
Guadiana Menor II	-0,157	40,154	0,292
Segura	-0,157	40,154	0,292
Sª Nª Oriental	-0,145	64,657	0,194

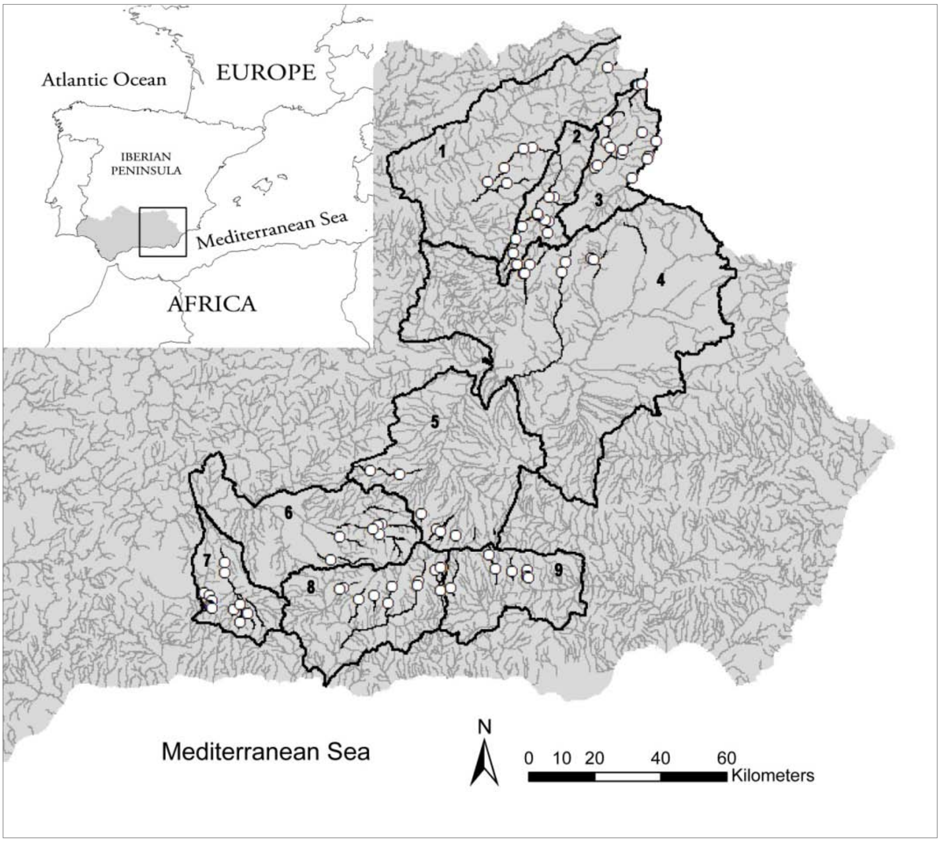

Figure S.4.1. Fluvial network (gray lines), rivers inhabited by Salmo trutta (thin black lines), location of the subbasins (thick black lines) in Andalucía (shaded region in gray) and sampling sites (white circules). Numbers indicat the subbasins: Guadalquivir II (1), Guadaliquivir I (1), Segura (3), Guadiana Menor II (4), Guadiana Menor I (5), Genil (6), Almijara (7), Guadalfeo (8), Sierra Nevada oriental (9).

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5. CHAPTER III

Driving factors of synchronous dynamics in brown trout populations at the rear edge of their native distribution

Factores reguladores de las dinámicas síncronas en poblaciones de trucha común en el borde trasero de su distribución nativa.

5. CHAPTER III. DRIVING FACTORS OF SYNCHRONOUS DYNAMICS IN BROWN TROUT POPULATIONS AT THE REAR EDGE OF THEIR NATIVE DISTRIBUTION

5.1. Abstract

This study aims at filling the gap of knowledge between the processes governing population regulation and synchrony in brown trout populations from southern Spain. For this purpose, analyses include the size of all age classes (0+, 1+, and adults), trying to detect drivers of the whole population dynamics. From 2005 to 2014, population (density) and environmental (water temperature and precipitation) trends in 18 sampling stations distributed in two peripheral different catchments were analysed. Results indicated that juveniles and adults did not show exogenous regulation, while recruitment was negatively related to winter rainfall and positively to spring rainfall. Besides, a clear cohort effect was detected affecting the density of juvenile age class. However, effect of the density of juveniles during the previous year on the density of adults at a given year was not detected. Thus, adults were only positively related to adult abundance in the previous year. Moreover, winter rainfall was the main environmental factor causing synchrony on recruitment through a Moran effect. In addition, the greater the difference among their altitude, distance to upper limit (DUL), Fluvial Habitat Index (IHF) and geographical position, the lower the similarity of response to winter rainfall, and consequently the lower the Moran effect. To disentangle driving factors the dynamic of populations living in rear edges of distribution will allow to give another step forward in the proposal for new adaptive management measures in metapopulations threatened by Global Change.

5.2. Introduction

Temporal variation of density of a population is the result of the variation of abundances of the different cohorts of the population. Recruitment is directly responsible for the increases and decreases in the density of brown trout [*Salmo trutta* (Linnaeus, 1758)] populations (Elliott 1984a, Elliott 1984b , Cattanéo *et al*. 2002 , Lobón-Cerviá 2003 , Lobón-Cerviá and Rincón 2004, Lobón-Cerviá and Mortensen 2005 , Zorn and Nuhfer 2007 , Lobón-Cerviá 2009b, Lobón-Cerviá *et al*. 2011) (see Lobón-Cerviá 2005 for a detailed revision of the causes), since there is a strong correlation between densities of a cohort throughout all the years of its life (Knapp *et al*. 1998 , Alonso *et al*. 2011). Besides, the recruitment processes prevail over post-recruitment processes as the main determinants of density (Knapp *et al*. 1998, Cattanéo *et al*. 2002, after Lobón-Cerviá 2005). The co-existence of several cohorts enables trout populations to overcome annual fluctuations of recruitment. However, if conditions reducing recruitment last for several years, the population structure, size and biomass may become altered (Belica 2007). Consequently, recruitment modeling is a vital component of the stock assessment focused on the fisheries strategic management (Needle 2002) and many studies have identified factors that drive recruitment at the local scale.

Factors controlling brown trout [*Salmo trutta* (Linnaeus, 1758)] recruitment in the Mediterranean area are not yet well known (Nicola *et al*. 2009), and the existence of generalized mechanisms still remain controversial. The classical debate between density-dependent (endogenous factors) and density-independent (external drivers) regulation has still recently produced interesting debates. To some authors, density-dependent recruitment would be responsible for population growth rate to fluctuate around zero due to other causes but pure chance (Einum 2005). Whereas to other authors, density-dependent recruitment would be an epiphenomenon or a lagged density-dependent factor that adjusts excessive abundances to a habitat limited abundance (Lobón-Cerviá 2007), which is in turn determined by temporal variability of weather conditions. In fact, recruitment may exhibit strong fluctuations among years, responding to specific flow patterns. High flows before and during the spawning season are positively correlated, whereas high flows during incubation and emergence are negatively correlated to recruitment (Jensen and Johnsen 1999, Unfer *et al*. 2011), and consequently, to the cohort strength. Another example is the water temperature, which may impact salmonid biology – thus regulating their populations – in some cases even more than flow, particularly in relation to temperature dependent metabolic costs, spawning timing and fecundity (Moore *et al*. 2012). It has also been suggested that the effect of flow and temperature on the early life stages may occur in a very short period, acting on two developmental stages related, although differentiated: flow acts shortly after emergence; and temperature acts during the stages of egg, at the hatching and shortly before or during emergence (Lobón-Cerviá and Mortensen 2005).

On the other hand, these external drivers may homogeneously act at large scales so as to affect synchronously to several separate populations (i.e. "Moran effect", Royama 1992; Cattanéo et al., 2003). When two separate populations share a common response to a large-scale-acting external driver, they might likely exhibit synchronous dynamics (Moran 1953). So the lack of a synchrony among separate populations affected by a large-scale-acting external factor may be produced by significant differences among the responses to this common external factor. These different responses might be produced by significant differences in their respective habitat characteristics, which might have relevant effect in the conservation of species at the metapopulation level (Palmqvist and Lundberg, 1998; Earn *et al*., 1998; Bret *et al*. 2016). Heino *et al.* (1997) observed a positive correlation between global extinction rate and the level of synchrony in dynamics among subpopulations. They also concluded that it is asynchrony, not chaos, what reduces the probability of global extinctions.

Spatial autocorrelation in environmental stochasticity (i.e. temporal fluctuations in the probability of mortality and the reproductive rate of all individuals in a population in the same or similar fashion) is a major determinant of spatial autocorrelation in population size. Since the impact of environmental stochasticity is roughly the same for small and large populations, it constitutes an important risk of population decline in all populations regardless of their abundance at a given location. If environmental stochasticity is weakly correlated among spatial locations wide geographic range can reduce the risk of population decline (Lande *et al*. 2003). Therefore, asynchrony among the dynamics of the demes of a single metapopulation might prevent local extinction processes to become irreversible, thus increasing the resilience of the metapopulation. This asynchrony may prevail as long as there is no homogenizing processes that reduce the differences among habitats. It is therefore of high interest to detect which habitat features are responsible of these observed different responses. Once identified, this asynchronizing habitat features should be preserved (or restored) in order to guarantee the lack of demographic syncrony among demes within a given metapopulation. This might be specially crucial in the metapopulations located at what Hampe and Petit (2005) call 'the rear edge' of the species native range, where local extinction rates might become more frequent in the near future. In this work it is the dynamics of these rear edge populations what will be disentangled.

Is in this context where this study aims at filling the gap of knowledge between the processes governing population regulation and synchrony. Since detected synchrony of a given age group can be inherited from previous age classes (Bret *et al.* 2016), analyses include the size of previous age classes in previous years when trying to detect drivers of the whole population dynamics. The residuals of the endogenous models can then be analysed in order to find the effect of external drivers, namely rainfall and temperature regimes. Once the global population dynamics are described as a function of endogenous and exogenous mechanisms, the synchrony among age group abundance dynamics is quantified, and the presence of Moran effect checked. Finally, the study looks for habitat features that are responsible for the observed synchrony of age class density among sites.

To reach these goals three subsidiary hypotheses have to be tested:

1st subsidiary hypothesis: Interannual variation of age group densities is determined by variation of physical habitat conditions.

Environmental variables such as stream flow and water temperature directly affect physical habitat. This environmental variables are, in turn, driven by climatic drivers such as rainfall distribution and air temperature, respectively. Since the response of flow and water temperature to rainfall and air temperature is mediated by features at the catchment scale, there is a lag between climatic events and stream habitat responses. To cope with these lagged effect, a seasonal window can be used to synthesizing the prevailing climatic conditions that induce a generalized stream habitat condition.

2nd subsidiary hypothesis: Euclidean distance among time series of a given variable at two sites can be used as an indicator of synchrony of that variable among both sites. The lower the distance, the higher the synchrony. If trout density synchrony among a pair of sites is produced by Moran effect, it would be significantly correlated to environmental synchrony among both sites.

3rd subsidiary hypothesis: The response of a given population to climatic drivers is mediated by physical habitat features that characterize the reach where it lives. Here we test whether there is a significant relationship among the similarity of population density responses to climatic conditions and the similarity of habitat characteristics among a pair of sites.

5.3. Material and methods

5.3.1. Study species

Brown trout is a Paleartic species whose southern distribution range reaches some regions of north Morocco (Kottelat and Freyhof, 2007; Snoj *et al.*, 2011). In front of the Atlantic coasts of the Iberian Peninsula it is located that known as limit of anadromy (Antunes *et al.*, 2001, 2006).

Brown trout populations studied in this work are the most southerly in Europe and show exclusively resident forms (Chapter I). They have been classified as endangered (Franco Ruíz and Rodríguez de los Santos, 2001) and show exceptional local characteristics: 1) high genetic diversity with new haplotypes of recent discovery (Almodóvar *et al*. 2010), 2) high degree of population isolation between basins and even among rivers (Chapter I), as well as 3) the most extensive spawning period described for this species to date (Chapter II). According to the authors, these characteristics would be due to the fact that these populations remain isolated since the last glacial period, evolving in parallel with the development of the current Mediterranean climate. These characteristics are in agreement with those exhibited by populations that inhabit the rear edge of the species distribution (Hampe and Petit 2005).

5.3.2. Study region

The study area included two subsets of sampling sites, located in separate catchments: Segura basin, draining to the Mediterranean, and Genil basin draining to the Atlantic Ocean.

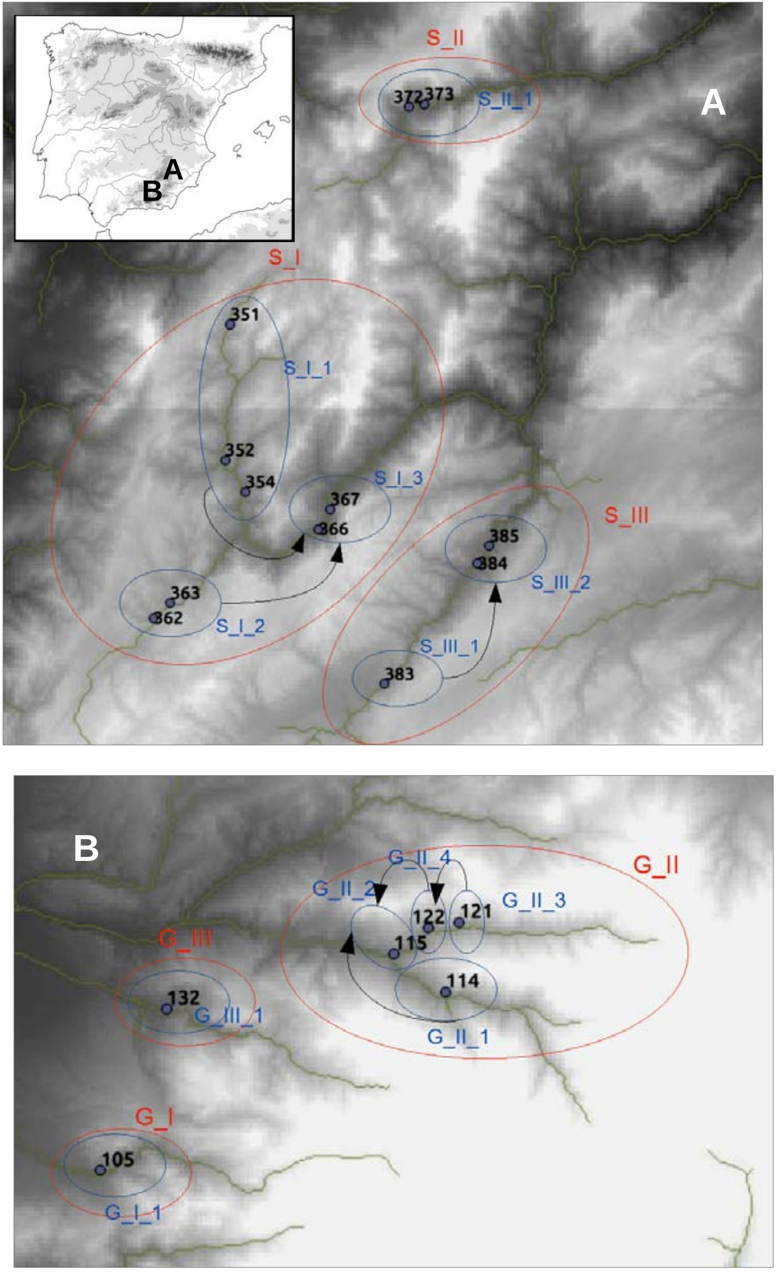

Figure 5.1. Location of the sampling sites (numbers = codes in Table S.4.1.) within metapopulations (red) and demes (blue, connections and their direction represented by black arrows) of brown trout populations inhabiting Segura (A) and Genil (B) basins.

From the distribution limits of brown trout in the southernmost basins of Iberian Peninsula (Chapter I), the spatial structure of metapopulations and demes in the study region was identified (Figure 5.1) through a detailed field study looking for any physiographic feature that prevents the population connection between watercourses inhabited by the species (Supplementary data 5.1).

5.3.3. Study data

To fulfill the goals of this work three types of data were collected in the sampling sites: (1) age class density and meteorological time series, (2) site habitat features, (3) fluvial connectivity.

Time series

Time series included both demographic (i.e. 0+ density) and meteorological (i.e. rainfall, ppt, and air temperature, tem) data.

The demographic series come from previous own studies (Chapter II). Eighteen sites were analysed annually between 2005 and 2014 in the basins of study. However, data quality control involved the removal of every site with less than 7 years of available data, as well as the years with less than 13 sites, or surveys conducted out of the July to October period. Finally the starting demographic series was composed of 98 surveys distributed among 14 sampling sites, between the years 2006 and 2014 (Supplementary data 5.2) (Table 5.1, Figure 5.1).

Meteorological conditions were characterized by the mean annual and seasonal (i.e. winter: January, February, and March) values of total daily rainfall (mm) and mean daily air temperature. For this purpose, first the study basins were delimited (watershed function, ArcGIS 9.3.1). Thereafter both monthly precipitation and temperature were determined over 2003-2015 period (zonal statistics as table function, ArcGIS 9.3.1) using the monthly series of rainfall and air temperatures (Ministry of Agriculture, Fisheries and Environment. 2014a, 2014b), as well as the digital elevation model (Spanish Ministry of Environment, 2004).

Table 5.1. Sampling sites. Name, code and location of all sampling sites analised. In gray are indicated the 4 stations removed of the analyses for failing in the data quality control.

Basin	Subbasin	River/Reach	Sampling site	Code	Coordinates	
					UTM X	*UTM Y*
Guadalquivir	Genil	Dílar	Dilar	105	450541	4102247
		Genil	Genil_I	114	465343	4110023
		Genil	Genil_II	115	463116	4111673
		Maitena	Maitena_I	121	465938	4113051
		Maitena	Maitena_II	122	464618	4112816
		Monachil	Monachil	132	453368	4109287
Segura	Segura	Madera	Madera_I	351	533734	4234833
		Madera	Madera_II	352	533469	4228249
		Madera	Madera_III	354	534457	4226694
		Segura	Segura_I	362	530002	4220543
		Segura	Segura_II	363	530826	4221279
		Segura	Segura_III	366	538011	4224890
		Segura	Segura_IV	367	538572	4225846
		Tus	Tus_I	372	542366	4245441
		Tus	Tus_II	373	543130	4245583
		Zumeta	Zumeta_I	383	541203	4217322
		Zumeta	Tobos_I	384	545718	4223207
		Zumeta	Tobos_II	385	546275	4224062

However, the summer environmental conditions were not considered, since the methodology of fish sampling for Mediterranean regions requires that the censuses be carried out in that season. Because 70% of the samples were taken before September (Table 5.2), the effects of summer (July, August and September) precipitation and temperature were not analysed in this work.

Site habitat characteristics

Site habitat characteristics were annually recorded at each sampling station by applying specific sampling techniques for each case. These features included physiogeographic, and values for quality indices (CI, HIS, QBR and IHF) (Table 5.3). Raw data of the site features may be consulted in Supplementary data 5.3.

Table 5.2. Temporal distribution of samplings between 2005 and 2014

Month	Frequency	Cumulative	Cumulative %
July	27	27	28%
August	40	67	70%
September	19	86	90%
October	10	96	100%

Fluvial connectivity

During 2008 and 2009 an intense habitat mapping was conducted on foot with the aims of locating: a) upper and lower limits reached by trout populations in the studied rivers (Chapter I) and b) impassable obstacles (waterfalls, dams, etc.) present in their channels (Supplementary data 5.1).

Table 5.3. Site features analysed. All features are quantitative except catchment geology. DUL: *distance to upper limit* (average length of inhabited sections upstream of the sampling station, considering tributaries).

Type	Noun	Unids	Acronym
Physiogeographic	Altitude	m asl	Alt
	Distance to upper limit	m	DUL
	River width	m	RW
	Water depth	m	WD
	Conductivity	µS/cm	C
	Catchment geology	Calcareous or Siliceous	Geology
Cover Index	According to García de Jalón and Schmidt (1995)		CI
Habitat Suitability Index	See Supplementary data 5.4		HSI
Riparian Quality Index	According to Jáimez-Cuéllar *et al.* (2002)		QBR
Fluvial Habitat Index			IHF

The results allowed to calculate: 1) DUL (Table 5.3) and 2) fluvial connectivity in the study area (Figure 5.1). The latter result was used to determine whether the detection of a possible Moran effect (hypothesis 2) might be due to metapopulation connectivity or external drivers.

5.3.4. Statistical analysis

Abundance dynamics were described by the density of every age class: 0+, 1+ and 2++, henceforth 'adults', Ad, at a given year, y.

In order to make our results comparable to those obtained by Bret *et al.* (2016) in France, we used similar variables. To do this we log(x+1)-transformed the density data to normalize their distributions while keeping zero-density observations. Then we fitted linear models to account for the cohort effect and spawners stock on density of age groups, and to reduce serial correlation. Linear regressions were fitted relating $\log(D_{0+,y}+1)$; $\log(D_{1+,y}+1)$ and $\log(D_{\mathrm{Ad},y}+1)$ to $\log(D_{\mathrm{Ad},y-1}+1)$; $\log(D_{0+,y-1}+1)$, and $\log(D_{1+,y-1}+1)$ and $\log(D_{\mathrm{Ad},y-1}+1)$, respectively. Synchrony analyses were conducted on residuals (observed minus predicted) of these models: r_{0+}, r_{1+} and r_{Ad}. All analyses were done in R (R Core Team, 2015).

Daily rainfall, R (mm), and air temperature, T (ºC), data were totaled and averaged, respectively, for the season (i.e. autumn: October-November-December) preceding every fish sampling occasion, thus obtaining the potential explanatory climatic variables: $R_{\mathrm{aut},y}$; $R_{\mathrm{win},y}$; $R_{\mathrm{spr},y}$; $T_{\mathrm{aut},y}$; $T_{\mathrm{win},y}$; and $T_{\mathrm{spr},y}$.

1st subsidiary hypothesis

The null hypothesis to be tested is H_0^1: 'Total rainfall and average air temperature for each season preceding fish sampling do not significantly ($p<0.05$) explain observed age group densities'.

All potential explanatory variables were uncorrelated to each other (|r-Pearson| <0.7) but $T_{\mathrm{aut},y}$,which was removed from the analyses in order to avoid collinearity.

To avoid pseudoreplication mixed effect linear models (LME, lme function of the package 'nlme') were fitted allowing for nested random effects (catchment/stream). Significant variables were selected, starting with the complete set of potential explanatory variables and removing them stepwise until all remaining variables had p-values lower than 0.05. To visually perceive the relation among explanatory and explained variables, a generalized additive model (GAM) was plotted to every set of significant variables for every explained variable.

2nd subsidiary hypothesis

The null hypothesis here tested is H_0^2: 'There is not significant ($p<0.05$) relationship among environmental synchrony and density synchrony for all the possible pairs of sites'.

Similarly to Bret *et al.* (2016), asynchrony between pairs of reaches was described by 14 × 14 matrices, whose elements were dissimilarity indices calculated by vegdist function of package 'vegan' (Oksanen *et al.* 2013), using partial match to Euclidean method. Density synchrony was correlated to environmental synchrony by means of Mantel tests for all possible relationships between r_{0+}, r_{1+} and r_{Ad}; and $R_{\mathrm{aut},y}$; $R_{\mathrm{win},y}$; $R_{\mathrm{spr},y}$; $T_{\mathrm{aut},y}$; $T_{\mathrm{win},y}$; and $T_{\mathrm{spr},y}$; and geographic distance (dissimilarity). Mantel tests find the matrix correlation (Mantel statistic, r) between two dissimilarity matrices. The significance of the statistic tests whether the relationship is occurring randomly, and it is evaluated by permuting rows and columns of the first dissimilarity matrix (4000 random permutations).

The effect of connectivity among sites on the synchrony of age class densities was tested by means of GLM. The dependent variables and the predictors were somewhat different than in the previous analyses. Dissimilarities among sites were calculated as ρ = 1-r-Pearson, where r-Pearson is the correlation coefficient among the variable time series for a pair of sites. As many variables as potential pairs of site were considered (N=91 pairs). Then the analysed model became: ρ0+ = ρ_Ppt_win + ρ_Ppt_spr + ρ_Ppt_aut + ρ_Tem_win + ρ_Tem_spr + euclidean_UTM + connect_qual, thus taking into account the dissimilarities of climatic regimes, the geographical distance and the connectivity among every pair of sites. Connectivity was considered as a semi-quantitative variable (*unconnected*; *partially connected* -only upstream to downstream; and *connected*).

3rd subsidiary hypothesis

The null hypothesis to be tested is H_0^3: 'There is not a significant ($p<0.05$) relationship among physical habitat similarity and similarity of density response to climatic drivers among pairs of sites'.

The response of a population variable to a climatic driver is expressed by a 4-dimensional vector whose dimensions are the estimates and p-values of the fitting of that variable to the climatic drivers. The matrix of response is formed by the 14 vectors of response of the corresponding 14 sites. Only those relationships that were found significant from the 2st subsidiary hypothesis test were considered at this stage.

To look for relationships between the dissimilarities of responses and habitat characteristics, Mantel test among dissimilarity matrices of response, habitat and geographical distances were conducted (4000 permutations).

5.4. Results

The values observed (individuals/ha) for the total population ranged from 0 to 10568, with a mean value of 1116 and standard deviation of 1498. For recruitment, these values were of 0 to 3356 (range), 565 (mean value) and 770 (standard deviation) individuals/ha.

1st subsidiary hypothesis

In order to obtain the residuals of the adjusted global linear model that controls for the cohort effect and endogenous mechanisms, (r0, r1 and rAd; *sensu* Bret *et al*. 2016), the following linear models were fitted (Table 5.4):

Table 5.4. Results of the model coefficients [±standard deviation]. R^2 shows the variance explained by each model: (1) Fry, (2) Juveniles, (3) Adults.

(1) $$\boxed{\log(0{+}y + 1) = 1.69\ [\pm 0.36] + 0.11\ [\pm 0.18]\bullet\log(Ady{-}1{+}1)}$$

$(R^2 = 0.005)$

p-value (Ady-1+1)= 0.56

(2) $$\boxed{\log(1{+}y + 1) = 0.45\ [\pm 0.14] + 0.71\ [\pm 0.06]\bullet\log(1{+}y{-}1{+}1)}$$

$(R^2 = 0.645)$

p-value (1+y-1+1) = $2\bullet 10^{-16}$

(3) $$\boxed{\log(Ad{+}y + 1) = 1.03\ [\pm 0.26] + 0.13\ [\pm 0.09]\bullet\log(1{+}dy{-}1{+}1) + 0.28\ [\pm 0.12]\bullet\log(Ady{-}1{+}1)}$$

$(R^2 = 0.131)$

p-value (1+dy-1+1) = 0.17

p-value (Ady-1+1) = 0.02

A clear cohort effect was detected affecting the density of juvenile age class (1+) (eq. 2), being weaker for adults (eq. 3). There is not a significant effect of spawners density during the previous year on the density of 0+ age class (eq. 1). Up to 64% of the juvenile density variability was explained by the density of young-of-the-year during the preceding year; whereas recruitment does not exhibit any significant effect of density-dependent mechanisms, not even a positive feedback (produced by the increasing section of a classical Ricker stock-recruitment curve). In the case of adults, the cohort effect lay on the influence of adult density during the previous year (p=0.01), with no significant influence of the juvenile density (p=0.17).

Recruitment is negatively related to winter rainfall, and positively to spring rainfall (Table 5.5, Figure 5.2)

Table 5.5. Results of linear mixed effect models (LME) fitted to the residuals of the 0+, 1+ and 2++ age class density, r0+, r1+ rAd, with catchment/stream as nested random categories.

r0 ~ Ppt_win_t + Ppt_spr_t						
		Value	*Std.Error*	*DF*	*t-value*	*p-value*
	(Intercept)	0.064	0.438	58	0.146	0.884
Explanatory variables	**Ppt_win_t**	-0.014	0.002	58	-6.614	0.000
	Ppt_spr_t	0.027	0.006	58	4.441	0.000
r1 ~ Not related to environmental variables						
rAd ~ Not related to environmental variables						

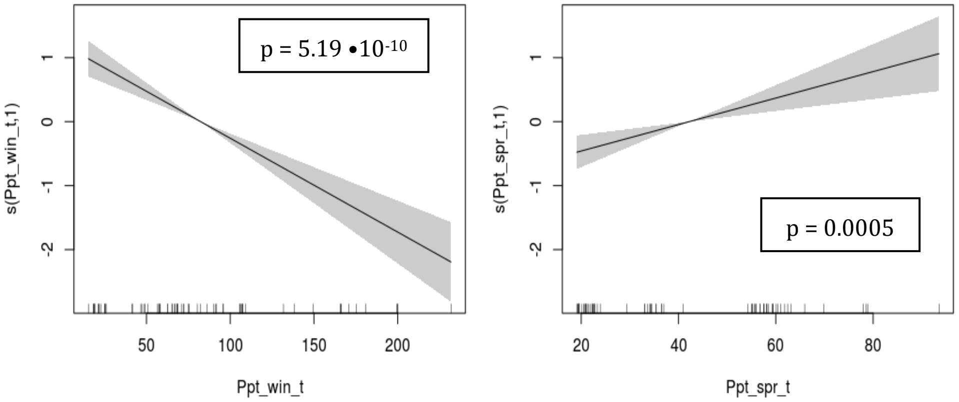

Figure 5.2. Generalized additive model fitted for residual of recruitment (r0+) as a function of significant explanatory climatic variables.

2nd subsidiary hypothesis

The most frequent r-Pearson value of 0+ age class density time series among pairs of sites lays between 0.8 and 1 (37 pairs). This indicates that 40% of all the pairs of sites show synchronous recruitment time series. This proportion raises up to 70% if pairs of sites with r-Pearson > 0.6 are accounted. Synchrony is less frequent among juvenile or adult density time series (Figure 5.3).

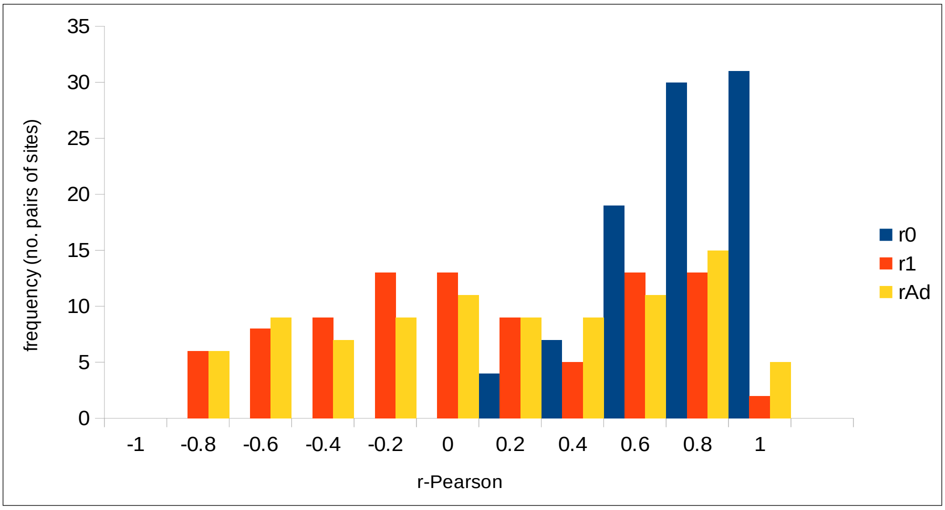

Figure 5.3. Frequency distribution of r-Pearson values for 0+, 1+ and 2++ age class density time series among avery pair of sites (N=91).

The dissimilarity of precipitation in winter, temperature in spring and autumn, and the geographic distance (Table 5.6) were marginally significant ($0.05<p<0.1$) with respect to recruitment synchrony, even though the first was almost significant (Ppt_win.dist Significance: 0.057). However the winter precipitation GAM was the only significant of the 4 exogenous drivers selective by the Mantel statistics (Figure 5.4).

Table 5.6. Mantel statistics based on Pearson's product-moment correlation: *mantel (permutations = 4000)*

xdis	ydis	Mantel statistic (r)	Significance
r0.dist	*Ppt_win.dist*	0.194	0.057
	Tem_spr.dist	0.157	0.095
	Tem_aut.dist	0.156	0.092
	geographic.dist	0.161	0.087
r1.dist	No synchronizing factors		
rAd.dist			

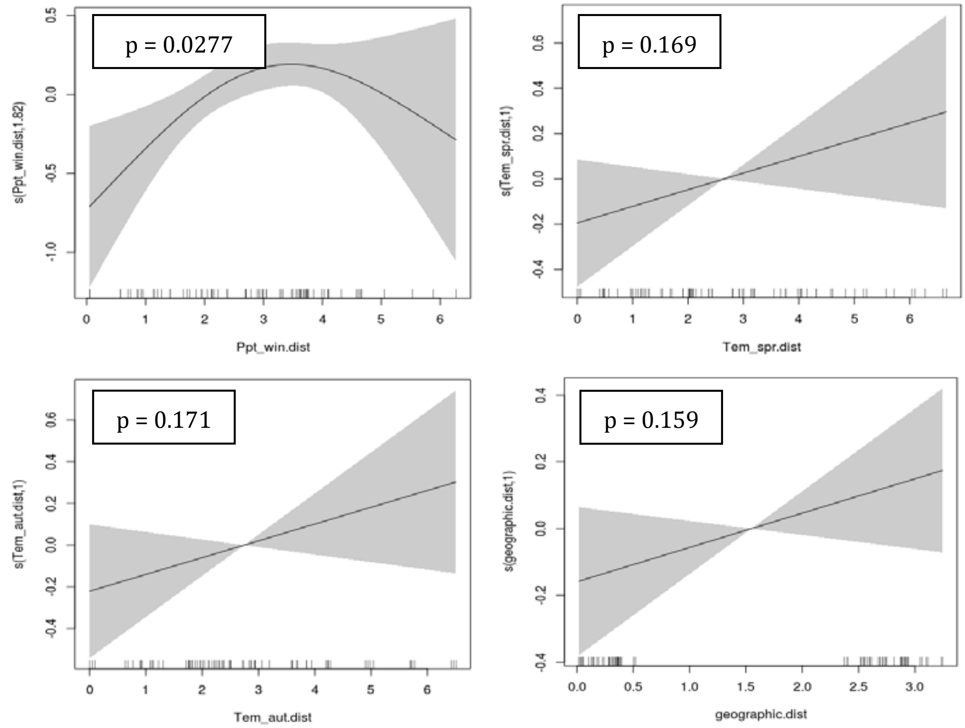

Figure 5.4. Generalized additive model fitted for residual of recruitment dissimilarity among pairs of sites, and dissimilarity of significant climatic variables among the same pairs of sites (Left to right and top to bottom: Ppt_win.dist, Tem_spr.dist, Tem_aut.dist, and geographic.dis).

3rd subsidiary hypothesis

The relationship among dissimilarities of IHF and altitude, and recruitment response to spring and autumn temperature, respectively, were marginally significant ($0.05<p<0.1$) (Table 5.7, Figure 5.5).

Dissimilarities of the variables altitude, DUL and IHF significantly strengthened ($p<0.05$) the asynchrony of the recruitment response to winter precipitation between pairs of sampling sites (Table 5.7, Figure 5.6). Habitat feature was marginally significant ($p = 0.066$) for the same response.

Table 5.7. Mantel statistics based on Pearson's product-moment correlation: *mantel (xdis, ydis, permutations = 4000)*

xdis	Ydis	Mantel statistic (r)	Significance
r0 (response_Ppt_win.dist)	*habitat.dist*	0.250	0.066
	Alt.dist	0.396	0.021
	DUL.dist	0.364	0.046
	IHF.dist	0.341	0.020
r0 (response_Tem_spr.dist)	*IHF.dist*	0.178	0.069
r0 (response_Tem_aut.dist)	*Alt.dist*	0.163	0.096

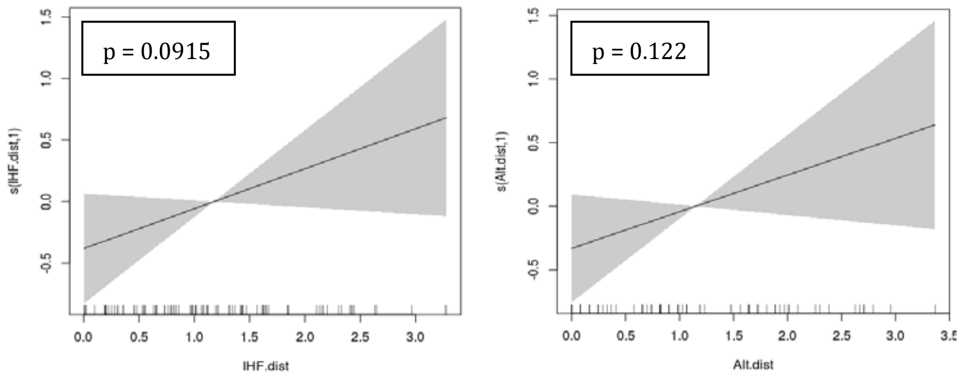

Figure 5.5. GAM fitting the dissimilarities of response of r0+ to Tem_spr (left) and Tem_aut (right) among pairs of sites as a function of dissimilarities of several habitat characteristics (IHF.dist and Alt.dist, respectively) among the same pairs of sites.

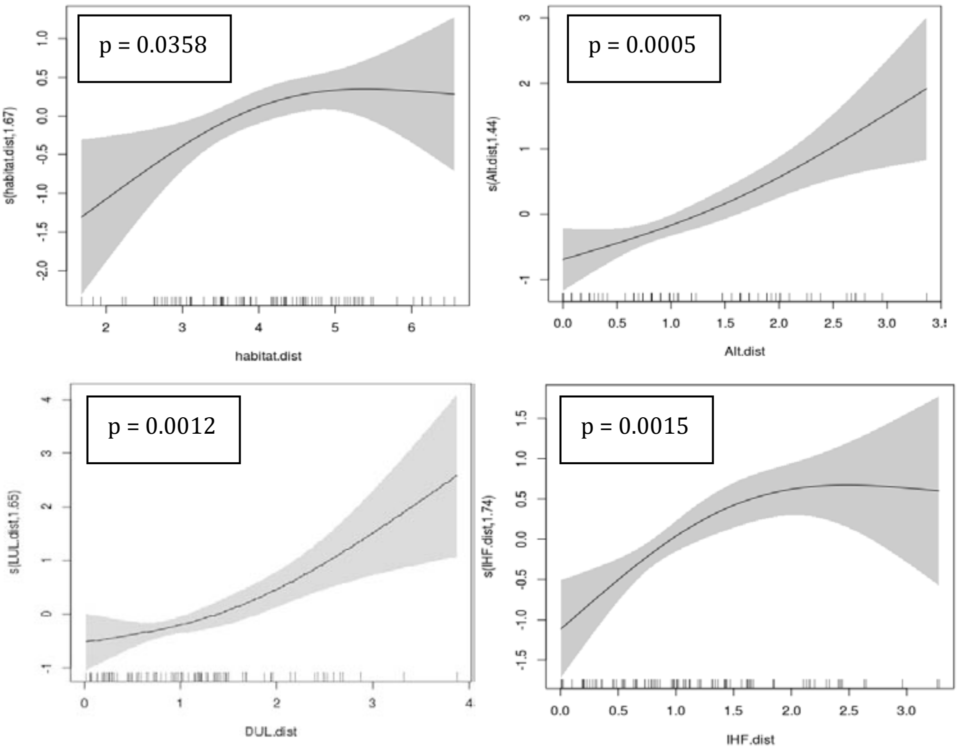

Figure 5.6. GAM fitting the dissimilarities of response of r0+ to Ppt_win among pairs of sites as a function of dissimilarities of several habitat characteristics among the same pairs of sites (Left to right and top to bottom: habitat.dist, Alt.dist, Tem_aut.dist, DUL.dis., and IHF.dist)

5.5. Discussion

5.5.1. Population regulatory factors

Population density in benign environments is higher than in harsh ones. The reason for the development of these density gradients lies in the conditions of ecological niche: extreme conditions at the distribution edges prevent populations from reaching carrying capacity, which can be more easily achieved in central regions (Lobón-Cerviá *et al*. 2011). Hence, the role of exogenous and endogenous regulatory processes that drive temporal fluctuations of animal populations do not equally affect populations of a same species throughout its range of distribution (Guo *et al*. 2005, Antonovics *et al*. 2006). Thus, in peripheral populations density-dependent mechanisms do not usually get to be developed (Haldane 1956, Lawton 1993; Brown et al. 1996; Case and Taper 2000) and in the case of populations inhabiting high mountain peripheral streams (such as those studied in this work, see Chapter I) the low densities (Barquín *et al*. 2010) may become even more significant (Elliott 1987, Gibson 1988, Jonsson *et al*. 1998). Therefore, populations located in geographically marginal areas are subjected more intensely to external drivers, whereas biotic processes (governed by density-dependent factors) modulate central populations (Mehlman 1997, Williams *et al*. 2003, Einum, 2005, Giralt and Valera 2006, Vøllestad and Olsen 2008). In this sense, if recruitment is directly responsible for variations in population density of brown trout (Lobón-Cerviá 2005), in a particular way in the study area the fry density should be influenced by exogenous factors, at least in part.

Our results are in agreement to these previous ideas, as well as to other works conducted so far in the Iberian peninsula (Lobón-Cerviá 2003, 2007; Lobón-Cerviá and Rincón 2004; Alonso and Gortázar 2014). In our study, recruitment regulation is not density-dependent (Table 5.4), in agreement to other studies (Shepherd and Cushing 1990; Lobón-Cerviá 2009a), showing no significant evidence of negative feedbacks. There is not even a positive effect of reproductive stock (Kanno *et at*. 2015b). In addition, for the juvenile and adult age classes exogenous regulation was not detected. But the strength of the cohort is transmitted throughout its life (Knapp *et al*. 1998, Grenouillet *et al*. 2001, Lobón-Cerviá 2009a, Alonso *et al*. 2011): the slopes of eqs. 1 and 2 and the sum of slopes in eq. 3 were significantly less than 1, suggesting some degree of apparent density dependence regulation in age group successions (*sensu* Bret *et al*. 2016) (Table 5.4). Thus, juvenile density is determined by the density of young-of-the-year (0+) during the previous year (R^2=0.65). The density of the adult age group is less dependent (R^2=0.13) on the density of adults during the previous year, yet remaining significantly related (p=0.017). However, there is not any significant effect of the density of juveniles during the previous year on the density of adults at a given year. This might be produced by a negative feedback effect of adults on juvenile density: the lack of specific mesohabitat (Armstrong *et al*. 2003; Ayllón *et al*. 2010) for both age groups might produce intercohort competence, resulting in a displacement of the juvenile age group.

Rainfall is the only external driver that significantly explains the recruitment dynamics in the study area (Table 5.5), which partly agrees with other studies conducted in the Iberian peninsula (Lobón-Cerviá 2003, 2007; Lobón-Cerviá and Rincón 2004; Alonso and Gortázar 2014). According to these works, both stream flow and water temperature are the drivers of recruitment inter-annual variability. This fact agrees, in turn, with conclusions on salmonid population dynamics (Jonsson and Jonsson, 2011; Unfer *et al*., 2011). However, in the present work significant (p<0.05) influence of temperature on any age group was not detected. (Tabla 5.5).

Specifically, in our study area recruitment is negatively affected by winter rainfall (Ppt_win_t) and positively by spring rainfall (Ppt_spr_t). It is known that extreme flow conditions during egg incubation and fry emergence stages (directly linked to Ppt_win) reduce recruitment (Cattanéo *et al*. 2002, Jensen and Johnsen 1999, Zorn and Nuhfer 2007, Unfer *et al*. 2011), due to the expected effects of gravel-scouring flows on eggs and newly hatched individuals (Kanno *et at*. 2015a). These are sessile stages of the trout life cycle, in which individuals cannot relocate (eggs and eleuteroembryos) or exhibit an intense territorial behaviour (first weeks after emergence). Therefore, winter (January to March) is an extremely critical period in which flow increments (or extreme droughts) may be the cause of high mortalities.

On the other hand, an increase in spring rainfall produces a positive effect on recruitment. A recent study (Alonso and Gortázar 2014, Alonso *et* *al.* 2015) on the general regulation of brown trout populations in the Iberian peninsula showed that extreme flows (both high and low flows) in spring (April to June) produce lower recruitments. In the study area, where spring stream flows are usually low (Lorenzo-Lacruz *et al.*, 2013), an increase over the average value of rainfall might increase the base flow. Under these circumstances, shore habitats, which are positively selected by trout young-of-the-year (submerged roots, aquatic plants, *Chara* spp., etc.) (Barquín *et al*. 2015), might remain functionally active during the first weeks after emergence.

5.5.2. Synchrony and Moran effect

Three general causes are attributed to synchrony: the 'Moran effect' (the synchronizing effect of an environmental forcing), dispersal of individuals or shared nomadic predators among populations (Koenig 1999; Ripa 2000). In our case: (1) trout populations in the study area are highly isolated (Chapter I); (2) according to our results, connectivity among sites does not significantly explain the degree of synchrony; and (3) studied trout populations lack a common specialized predator, and extractive angling is not permitted (Andalusian Law, *Orden 25 de febrero 2005*) due to its conservation status (Franco Ruíz and Rodríguez de los Santos 2001). Therefore, population synchrony has to be produced by Moran effect.

Regarding synchrony, our results are similar to those obtained by Bret *et al.* (2016). The Mantel tests performed provided only valid results for possible recruitment synchrony (Table 5.6). Neither juveniles nor adults provided significant results. This is in agreement to the fact that young-of-the-year was the only age group found to be determined by an external driver (Table 5.5), as well as evidences of synchrony (Figure 5.4).

Results show that recruitment asynchrony among pairs of sites is related to dissimilarity of meteorological variables: Ppt_win.dist, Tem_spr.dist, Tem_aut.dist and geographic distance among pairs of sites, being this relationship at least marginally significant ($0.05<p<0.1$). The greater the difference among meteorological variables time series of a pair of sites, the lower the degree of recruitment synchrony among that pair of sites. Of them all, only winter rainfall (Ppt_win) is one of the global external drivers of recruitment that were found in the study area (Table 5.5). Therefore, spring rainfall is a variable that regulates recruitment (Table 5.5) but does not generate synchrony (Table 5.6). Besides, among the variables that produce synchrony, winter rainfall (Ppt_win) is the most significant ($p=0.057$) and the only one that yields significant GLM fitting (Figure 5.4). Therefore, we can conclude that sites with synchronous winter rainfall time series are likely to exhibit synchronous recruitment time series, thus evidences Moran effect. This synchrony seems to be greater when sites are geographically close to each other ($p=0.087$). Spring and autumn air temperature show weak signals of producing recruitment synchrony (p-values 0.095 and 0.092, respectively. See Table 5.6). Similar results were found by Cattanéo *et al*. (2003) for French populations of this species.

5.5.3. Synchrony modulating factors

The most important physiographical factors that determine the common response of population dynamics to external drives, which in turn is responsible for the observed synchrony among sites are: Alt, DUL and IHF (Table 5.7), along with the global distance among pairs of sites of the whole set of habitat variables (named 'habitat.dist'). Thus, dissimilarity of Alt, DUL and IHF between pairs of sites significantly ($p<0.05$) explains the dissimilarity of responses of recruitment to Ppt_win among pairs of sites. The same can be said of IHF and Alt regarding dissimilarities of responses to Tem_spr and Tem_aut, respectivelly; though marginally significant ($0.05<p<0.1$).

Therefore, given two sites in the study area, the greater the difference among their altitude, DUL, IHF and geographical position, the lower the similarity of response to winter rainfall, and consequently the lower the Moran effect. Altitude synthesizes several hydrologic variables that are driven by rainfall, namely: (1) catchment area (the higher the altitude the smaller the catchment and thus lower discharge); (2) type of rainfall regime (nival at high altitude, pluvial at lower altitudes); (3) general suitability of spawning areas (higher suitability in upper reaches). Besides, distance to upper limit (DUL) is directly linked to catchment characteristics of the site, and therefore to the discharge. IHF index quantitatively characterize hydrogeomorphological conditions and thus it is closely linked to hydraulic conditions as perceived by trout: velocity and depth distribution, substrate and shelter, principally.

5.5.4. Management measures for the conservation of the species at its distribution edges

Given the characteristic isolation of populations inhabiting edges distribution (Hampe and Petit, 2005) metapopulation dynamics and structure have to be considered, since in case of synchrony the resilience of the species in peripheral areas may be reduced. Therefore, to identify what habitat factors modulate population synchrony (3rd hypothesis), as well as to promote their heterogeneity between the demes, should be a key objective for the conservation of these populations.

In our particular case, this heteorogeneity of responses of recruitment to external drivers might be preserved by means of assuring that trout populations inhabit a wide range of altitudes (high values of Alt.dist), with long continuous inhabited reaches (high DUL.dist) and heterogeneous habitat characteristics (diverse values of IHF, not only low values, which might be quite obvious, but also high values). Besides, the preservation of geographically distant populations (large habitat.dist values) may be another key factor to avoid homogeneous responses to global common external drivers.

Nevertheless, since the external drivers (rainfall and temperature) are factors of vital importance for the survival of these populations (modulating the population dynamics and their synchrony), the alteration of their dynamics could cause substantial modifications in the structure and dynamics of brown trout populations. Thus, the future scenarios of climate change are not at all optimistic, especially in regions such as the one studied in this work. In particular, in the Mediterranean basins water flow reductions, summer drought periods, increases in water temperature and greater intensity of heavy rainfall are events severely expected (Ulbrich *et al.*, 2006; Giorgi and Lionello, 2008). Its effects on trout populations will be devastating.

Further, from the nineteenth century a decrease in the area of distribution of the studied populations, as well as a range displacement towards higher altitudes, have been observed (Saéz Gómez, 2010). In addition, apart from the high degree of isolation of brown trout populations in the study area, their upper limits have a natural origin while the lower ones are anthropogenic (Chapter I). Constriction of the river sections inhabited by the populations (DUL), whether by the ascent of the lower limits or by the descent of the superiors, could have direct consequences on the effects of the synchronous recruitment response to Ppt_win. Therefore preserve at least the current population limits must be another adaptive management measures adopted in the study region.

Finally, future works should investigate the importance of the different variables that make up the IHF index. These results will determine which specific variables of the habitat might be modulating to a greater or lesser extent the synchronous effect caused by the detected external drivers. This will be another step forward in the proposal for new adaptive management measures.

5.6. References

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Supplementary data 5.1.

Table S.5.1. Field study results about physiographic features that impact on watercourses inhabited by brown trout in Segura and Genil basins. All obstacles were photographed, and the azudes were characterized by the Index of Fluvial Connectivity, ICF (ACA, 2006; Solà *et al.*, 2011). Their individual analysis allowed to detect the obstacules that prevent the connection between populations (see metapopulations in Figure 5.1). "Colum Date" refers to the date of detection of the obstacle.

Date	Basin	River	Type of obstacule	X	Y
10/05/2007	Genil	Bco. San Juan	NIO	466506	4107809
10/05/2007	Genil	Bco. San Juan	NIO	466457	4107862
10/05/2007	Genil	Bco. San Juan	NIO	466422	4107921
10/05/2007	Genil	Bco. San Juan	NIO	466342	4108055
10/05/2007	Genil	Bco. San Juan	NIO	466330	4108070
10/05/2007	Genil	Bco. San Juan	NIO	466309	4108136
10/05/2007	Genil	Bco. San Juan	NIO	466310	4108145
10/05/2007	Genil	Bco. San Juan	NIO	466200	4108380
10/05/2007	Genil	Bco. San Juan	NIO	466160	4108600
10/05/2007	Genil	Bco. San Juan	NIO	465553	4109563
10/05/2007	Genil	Bco. San Juan	WACh	465941	4108925
10/05/2007	Genil	Bco. San Juan	Weir	465743	4109289
23/04/2007	Genil	Maitena	NIO	464401	4112418
23/04/2007	Genil	Maitena	NIO	464491	4112622
23/04/2007	Genil	Maitena	NIO	464509	4112646
23/04/2007	Genil	Maitena	NIO	464531	4112695
03/05/2007	Genil	Maitena	NIO	469964	4112951
24/04/2007	Genil	Maitena	NIO	465798	4112967
23/04/2007	Genil	Maitena	Weir	463365	4111991
03/05/2007	Genil	Maitena	Weir	470457	4112842
24/04/2007	Genil	Maitena	Weir	465212	4112946
23/05/2007	Genil	Dílar	NIO	457641	4101773
09/05/2007	Genil	Dílar	NIO	455645	4102399
15/05/2007	Genil	Dílar	NIO	454606	4102828
15/05/2007	Genil	Dílar	NIO	460243	4103061
08/05/2007	Genil	Dílar	NIO	460917	4103068
15/05/2007	Genil	Dílar	NIO	460572	4103133
23/05/2007	Genil	Dílar	Weir	457893	4102302
23/05/2007	Genil	Dílar	Weir	456046	4102318
07/05/2007	Genil	Dílar	Weir	455762	4102377
08/05/2007	Genil	Dílar	Weir	451772	4102989

Date	Basin	River	Type of obstacule	X	Y
19/04/2007	Genil	Genil	Dam	464158	4110848
19/04/2007	Genil	Genil	Dam	457440	4112986
19/04/2007	Genil	Genil	Dam	453722	4113069
26/04/2007	Genil	Genil	NIO	470564	4106359
26/04/2007	Genil	Genil	NIO	470596	4106507
26/04/2007	Genil	Genil	NIO	470246	4107025
26/04/2007	Genil	Genil	NIO	470215	4107058
26/04/2007	Genil	Genil	NIO	470215	4107059
20/04/2007	Genil	Genil	NIO	463064	4111745
19/04/2007	Genil	Genil	Weir	465113	4110058
20/04/2007	Genil	Genil	Weir	463526	4111074
20/04/2007	Genil	Genil	Weir	461518	4112289
19/04/2007	Genil	Genil	Weir	456420	4113062
19/04/2007	Genil	Genil	Weir	454991	4113131
13/06/2007	Genil	Guarnón	NIO	469424	4106502
13/06/2007	Genil	Guarnón	NIO	469449	4106534
13/06/2007	Genil	Guarnón	NIO	469471	4106565
13/06/2007	Genil	Guarnón	NIO	469543	4106671
13/06/2007	Genil	Guarnón	NIO	469574	4106705
13/06/2007	Genil	Guarnón	NIO	469599	4106733
13/06/2007	Genil	Guarnón	NIO	469633	4106843
13/06/2007	Genil	Guarnón	NIO	469640	4106899
13/06/2007	Genil	Guarnón	NIO	469685	4107059
13/06/2007	Genil	Guarnón	NIO	469722	4107111
13/06/2007	Genil	Monachil	NIO	458440	4107882
13/06/2007	Genil	Monachil	NIO	458134	4107950
13/06/2007	Genil	Monachil	NIO	454014	4109366
13/06/2007	Genil	Monachil	Weir	459694	4106671
13/06/2007	Genil	Monachil	Weir	460031	4106684
13/06/2007	Genil	Monachil	Weir	459918	4106717
13/06/2007	Genil	Monachil	Weir	458558	4107877
13/06/2007	Genil	Monachil	Weir	455688	4108491
13/06/2007	Genil	Monachil	Weir	455685	4108497
13/06/2007	Genil	Monachil	Weir	454079	4109344
14/05/2007	Genil	Vadillo	NIO	474020	4107943
14/05/2007	Genil	Vadillo	NIO	473849	4107965
14/05/2007	Genil	Vadillo	NIO	473741	4107989
14/05/2007	Genil	Vadillo	NIO	473343	4108428
14/05/2007	Genil	Vadillo	NIO	472940	4108838
26/04/2007	Genil	Valdecasillas	NIO	471288	4105136
26/04/2007	Genil	Valdecasillas	NIO	471292	4105233

Date	Basin	River	Type of obstacule	X	Y
26/04/2007	Genil	Valdecasillas	NIO	471166	4105398
11/05/2007	Genil	Valdeinfierno	NIO	470871	4104008
11/05/2007	Genil	Valdeinfierno	NIO	470886	4104023
11/05/2007	Genil	Valdeinfierno	NIO	470913	4104098
11/05/2007	Genil	Valdeinfierno	NIO	470920	4104136
11/05/2007	Genil	Valdeinfierno	NIO	470938	4104307
11/05/2007	Genil	Valdeinfierno	NIO	470960	4104360
11/05/2007	Genil	Valdeinfierno	NIO	470979	4104412
02/04/2007	Segura	Madera	NIO	537355	423771
14/03/2007	Segura	Madera	Weir	534381	422586
10/04/2007	Segura	Segura	Dam	541105	422881
11/05/2007	Segura	Segura	NIO	531623	422173
11/05/2007	Segura	Segura	NIO	532344	422216
11/05/2007	Segura	Segura	NIO	532430	422245
11/05/2007	Segura	Segura	NIO	532444	422264
14/05/2007	Segura	Segura	NIO	534618	422467
10/04/2007	Segura	Segura	WACh	541259	422887
10/04/2007	Segura	Segura	WACh	544043	423135
14/05/2007	Segura	Segura	Weir	543597	423114
19/06/2007	Segura	Zumeta	Dam	545373	422283
20/06/2007	Segura	Zumeta	Dam	546917	422537
20/06/2007	Segura	Zumeta	Dam	547608	422578
19/06/2007	Segura	Zumeta	NIO	543541	422049
19/06/2007	Segura	Zumeta	NIO	543946	422064
16/04/2007	Segura	Zumeta	WACh	548555	422712
19/06/2007	Segura	Zumeta	Weir	541133	421731

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Supplementary data 5.2.

Table S.5.2. Demographic series finally analyzed between the years 2006 and 2014 (the 4 stations removed from the analysis due to failure in data quality control are not considered).

Year	Code	River	Month	Basin	Name	dens0t	dens1t	dens2t
2006	105	Dilar	9	Genil	Dilar	2928,2	1427,5	219,6
2009	105	Dilar	10	Genil	Dilar	0,0	25,3	202,6
2010	105	Dilar	10	Genil	Dilar	0,0	0,0	25,0
2011	105	Dilar	9	Genil	Dilar	496,5	0,0	78,4
2012	105	Dílar	8	Genil	Dilar	1163,6	202,4	50,6
2013	105	Dílar	8	Genil	Dilar	102,2	638,8	0,0
2014	105	Dílar	8	Genil	Dilar	543,8	233,1	310,8
2006	114	Genil	9	Genil	Genil_I	670,7	540,3	316,7
2009	114	Genil	10	Genil	Genil_I	191,0	883,3	716,2
2010	114	Genil	10	Genil	Genil_I	225,7	200,6	301,0
2011	114	Genil	9	Genil	Genil_I	1266,8	304,0	228,0
2012	114	Genil	9	Genil	Genil_I	746,3	1261,0	334,6
2013	114	Genil	8	Genil	Genil_I	25,6	383,3	153,3
2014	114	Genil	8	Genil	Genil_I	485,7	377,8	350,8
2006	115	Genil	9	Genil	Genil_II	546,1	191,2	218,5
2009	115	Genil	10	Genil	Genil_II	253,9	228,5	279,3
2010	115	Genil	10	Genil	Genil_II	77,7	181,3	51,8
2011	115	Genil	9	Genil	Genil_II	1645,4	48,4	96,8
2012	115	Genil	9	Genil	Genil_II	2612,3	1090,6	101,5
2013	115	Genil	8	Genil	Genil_II	252,2	504,5	75,7
2014	115	Genil	8	Genil	Genil_II	152,6	254,4	228,9
2006	122	Maitena	9	Genil	Maitena_II	1182,5	430,0	0,0
2009	122	Maitena	10	Genil	Maitena_II	200,6	501,4	50,1
2010	122	Maitena	9	Genil	Maitena_II	0,0	200,9	150,7
2011	122	Maitena	9	Genil	Maitena_II	2039,0	0,0	100,7
2012	122	Maitena	8	Genil	Maitena_II	1084,6	1084,6	100,9
2013	122	Maitena	8	Genil	Maitena_II	231,7	875,4	437,7
2014	122	Maitena	8	Genil	Maitena_II	318,2	450,8	424,3
2006	132	Monachil	9	Genil	Monachil	408,0	578,0	374,0
2009	132	Monachil	10	Genil	Monachil	0,0	258,0	412,8
2010	132	Monachil	10	Genil	Monachil	25,6	0,0	512,1
2011	132	Monachil	10	Genil	Monachil	2478,3	25,8	258,2
2012	132	Monachil	8	Genil	Monachil	2854,2	6017,0	1697,1
2013	132	Monachil	8	Genil	Monachil	0,0	274,7	793,6
2014	132	Monachil	8	Genil	Monachil	0,0	0,0	175,0
2006	351	Madera	8	Segura	Madera_I	121,1	403,6	0,0

Year	Code	River	Month	Basin	Name	dens0t	dens1t	dens2t
2009	351	Madera	NA	Segura	Madera_I	NA	NA	NA
2010	351	Madera	8	Segura	Madera_I	76,6	306,5	51,1
2011	351	Madera	8	Segura	Madera_I	1411,3	302,4	151,2
2012	351	Madera	7	Segura	Madera_I	1063,3	202,5	75,9
2013	351	Madera	7	Segura	Madera_I	25,5	459,0	25,5
2014	351	Madera	7	Segura	Madera_I	102,2	204,5	51,1
2006	352	Madera	8	Segura	Madera_II	880,5	33,9	0,0
2009	352	Madera	9	Segura	Madera_II	578,7	251,6	0,0
2010	352	Madera	8	Segura	Madera_II	0,0	201,4	0,0
2011	352	Madera	8	Segura	Madera_II	529,1	72,1	24,0
2012	352	Madera	7	Segura	Madera_II	191,4	23,9	71,8
2013	352	Madera	7	Segura	Madera_II	100,0	100,0	0,0
2014	352	Madera	7	Segura	Madera_II	0,0	75,0	0,0
2006	354	Madera	8	Segura	Madera_III	417,3	160,5	32,1
2009	354	Madera	9	Segura	Madera_III	75,7	176,7	25,2
2010	354	Madera	8	Segura	Madera_III	0,0	283,8	51,6
2011	354	Madera	8	Segura	Madera_III	876,1	0,0	27,4
2012	354	Madera	7	Segura	Madera_III	225,0	0,0	75,0
2013	354	Madera	7	Segura	Madera_III	130,8	78,5	78,5
2014	354	Madera	7	Segura	Madera_III	0,0	25,1	0,0
2006	362	Segura	8	Segura	Segura_I	1963,9	2031,6	101,6
2009	362	Segura	9	Segura	Segura_I	267,3	908,8	347,5
2010	362	Segura	8	Segura	Segura_I	73,8	393,4	172,1
2011	362	Segura	8	Segura	Segura_I	1811,2	122,4	122,4
2012	362	Segura	7	Segura	Segura_I	889,9	1310,2	247,2
2013	362	Segura	7	Segura	Segura_I	0,0	625,8	104,3
2014	362	Segura	7	Segura	Segura_I	0,0	109,0	245,2
2006	367	Segura	8	Segura	Segura_IV	1223,8	840,5	88,5
2009	367	Segura	9	Segura	Segura_IV	25,7	128,4	436,7
2010	367	Segura	8	Segura	Segura_IV	0,0	31,3	93,8
2011	367	Segura	8	Segura	Segura_IV	1373,4	0,0	0,0
2012	367	Segura	7	Segura	Segura_IV	2128,5	499,3	262,8
2013	367	Segura	7	Segura	Segura_IV	0,0	179,4	0,0
2014	367	Segura	7	Segura	Segura_IV	25,0	0,0	75,0
2006	372	Tus	8	Segura	Tus_I	743,2	357,8	110,1
2009	372	Tus	9	Segura	Tus_I	400,2	275,2	100,1
2010	372	Tus	8	Segura	Tus_I	0,0	126,3	75,8
2011	372	Tus	8	Segura	Tus_I	961,8	0,0	52,0
2012	372	Tus	7	Segura	Tus_I	584,7	661,0	0,0
2013	372	Tus	7	Segura	Tus_I	114,0	227,9	57,0
2014	372	Tus	7	Segura	Tus_I	0,0	0,0	50,0

Year	Code	River	Month	Basin	Name	dens0t	dens1t	dens2t
2006	373	Tus	NA	Segura	Tus_II	NA	NA	NA
2009	373	Tus	9	Segura	Tus_II	24,9	124,4	0,0
2010	373	Tus	8	Segura	Tus_II	0,0	77,9	26,0
2011	373	Tus	8	Segura	Tus_II	893,2	0,0	22,9
2012	373	Tus	7	Segura	Tus_II	281,3	93,8	0,0
2013	373	Tus	7	Segura	Tus_II	0,0	175,0	25,0
2014	373	Tus	7	Segura	Tus_II	25,0	75,0	75,0
2006	384	Zumeta	8	Segura	Tobos_I	452,6	696,2	243,7
2009	384	Zumeta	9	Segura	Tobos_I	0,0	0,0	100,5
2010	384	Zumeta	8	Segura	Tobos_I	0,0	0,0	151,5
2011	384	Zumeta	8	Segura	Tobos_I	2273,9	23,9	167,5
2012	384	Zumeta	7	Segura	Tobos_I	3355,8	2510,6	2038,3
2013	384	Zumeta	7	Segura	Tobos_I	382,5	969,0	153,0
2014	384	Zumeta	7	Segura	Tobos_I	513,4	256,7	308,0
2006	385	Zumeta	8	Segura	Tobos_II	261,0	559,2	223,7
2009	385	Zumeta	8	Segura	Tobos_II	0,0	0,0	25,1
2010	385	Zumeta	8	Segura	Tobos_II	0,0	0,0	24,9
2011	385	Zumeta	8	Segura	Tobos_II	601,7	0,0	0,0
2012	385	Zumeta	7	Segura	Tobos_II	471,1	297,5	148,8
2013	385	Zumeta	7	Segura	Tobos_II	0,0	207,4	103,7
2014	385	Zumeta	7	Segura	Tobos_II	75,2	0,0	75,2

Supplementary data 5.3

Table S.5.3. Raw data of the site features (meaning of abbreviation in Table 5.3). In "geology" column, S: siliceous; C: calcareous.

Subbasin	Code	Geology	Alt	DUL	RW	WD	C	CI	HSI	QBR	IHF
Genil	105	S	950	13905	3,98	0,23	213,13	4,42	67,00	56,11	72,22
	114	S	1150	22024	7,64	0,39	108,71	4,83	74,89	83,33	78,44
	115	S	1050	24729	6,54	0,28	122,86	4,50	67,26	70,56	73,78
	122	S	1160	14183	3,00	0,18	115,00	3,85	58,69	45,00	72,20
	132	S	870	8450	3,85	0,33	369,33	4,95	68,47	50,00	78,50
Segura	351	C	1195	7479	2,50	0,21	504,57	4,25	71,39	78,33	71,38
	352	C	1070	15541	5,15	0,34	408,25	4,28	67,78	82,00	67,89
	354	C	1050	17701	6,03	0,44	442,13	3,75	65,11	77,00	64,11
	362	C	1280	1848	5,21	0,38	317,25	4,22	71,50	70,56	77,13
	367	C	950	34838	9,25	0,44	336,25	3,08	67,00	87,00	67,78
	372	C	940	8747	6,01	0,23	401,00	4,42	59,43	55,00	66,89
	373	C	920	9853	6,64	0,21	408,43	4,28	62,59	73,89	69,00
	384	C	960	13279	6,52	0,42	396,13	5,75	74,22	76,50	74,22
	385	C	950	14514	7,35	0,34	365,43	4,47	66,78	86,00	71,33

Supplementary data 5.4.

Table S.5.4. Values of the parameters evaluated by the HSI

Habitat Suitability Index (HSI)					
	Very good	**Good**	**Acceptable**	**Deficient**	**Poor**
Habitat refuge	Habitat unchanged. Abundant refuge	Important presence of refuge	Habitat with capacity to maintain stable populations	Habitat reduced or greatly altered	Without refuges
Suitability	10/9	8/7	6/5	4/3	2/1/0
Mesohabitat diversity	Deep & Shallow pools, glides and rapids	Shallow pools, glides and rapids	Lack of a single mesohabitat	Predominate one over the others	A single mesohabitat
Suitability	10/9	8/7	6/5	4/3	2/1/0
Mesohabitat distribution	Deep rapids dominate	Shallow rapids dominate	Without predominances	Deep glides dominate	Shallow glides dominate
Suitability	10/9	8/7	6/5	4/3	2/1/0
Redds	Plenty of optimum areas	Plenty of suitable areas	Shortage of potential redds	Spawning very difficult	No possibility of spawning. Total clogging
Suitability	10/9	8/7	6/5	4/3	2/1/0
Channeling	Natural channel, unaltered	Channel punctual alterations	Old Channeling. Only on one of the banks	Partial channeling of the two banks	Almost total channeling
Suitability	10/9	8/7	6/5	4/3	2/1/0
Water level	Whole rivebed submerged	> 75% submerged < 25% emerged	25-75% submerged > 25% emerged	Very low level	Only isolated pools
Suitability	10/9	8/7	6/5	4/3	2/1/0
Clogging	Without clogging	< 25% clogging	20 - 50%	50 - 75%	> 75%
Suitability	10/9	8/7	6/5	4/3	2/1/0

Riberbank erosion	Stable riverbanks. No erosion factors	Possible erosion o < 5%	5 - 30% affected	Unstable margins, great potential erosion, floods. 30 - 60%	Riverbanks collapsed. <60% affected
Suitability	10/9	8/7	6/5	4/3	2/1/0
Aquatic macrophytes	> 50% covered. High diversity	> 50% covered. Moderate diversity	Patch distribution	Presence of macrophytes	Absence of macrophytes
Suitability	10/9	8/7	6/5	4/3	2/1/0
Vegetation - Shadow riparian cover	> 75% shadow in various strata	50- 75% shadow in various strata	50- 75% shadow. One stratum. Plantations. Discontinuous gallery forest	25 - 50% shadow	< 25 shadow
Suitability	10/9	8/7	6/5	4/3	2/1/0
Riparian vegetation width	Unmodified	Wide banks. Small alterations	Reduced banks. Moderate alteration	Banks very limited. Alterated vegetation	No vegetation due to anthropic cause
Suitability	10/9	8/7	6/5	4/3	2/1/0

6. CHAPTER IV

How to prevent extinction of endangered populations living on the edge: management proposals for the southernmost populations of brown trout (*Salmo trutta*) in Europe

Cómo prevenir la extinción de poblaciones amenazadas viviendo en un borde de distribución: propuestas de gestión para las poblaciones más meridionales de trucha común (Salmo trutta) en Europa.

6. CHAPTER IV. HOW TO PREVENT EXTINCTION OF ENDANGERED POPULATIONS LIVING ON THE EDGE: MANAGEMENT PROPOSALS FOR THE SOUTHERNMOST POPULATIONS OF BROWN TROUT (*SALMO TRUTTA*) IN EUROPE

6.1. Abstract

The southeastern mountain ranges of the Iberian Peninsula are one of the geographical and ecological distribution limits of brown trout (*Salmo trutta*) in Europe. The historic anthropogenic impact suffered by the watercourses in Mediterranean areas has been intensified in the last century, causing a strong spatial and population regression of the species in this distribution edge. These latest residual and resident brown trout populations have endangered status and they have been relegated to the higher mountain areas. They are highly isolated and fragmented by anthropogenic factors and subjected to a complex administrative situation regulating them as fishery resource. In addition, the reproduction of rainbow trout (*Oncorhynchus mykiss*) has been widely observed in the study area. These non-native populations have displaced completely several brown trout historic populations and threat currently to brown trout populations cohabiting with them. However, these peripheral populations of brown trout have shown worldwide unique haplotypes and the most extended reproductive periods observed to date, perhaps as a Mediterranean climate adaptation of populations living in geographic isolation since the last glacial period. To preserve their peculiar traits, to conserve the potential of the Paleartic species as a whole and to increase the capacity of resilience of populations facing Global Change, numerous management measures are proposed in this paper. In this sense, direct interventions on habitat, specific modifications to the current law that regulate fishing in the three southernmost basins inhabited by the species in Europe, as well as a phased restoration in reaches inhabited by rainbow

trout (as well as their inclusion in the list of invasive alien species), are among the recommended measures. Along with these actions, reintroductions with endemic haplotypes of the subbasins to which these populations belong are proposed.

6.2. Introduction

South Iberian populations of brown trout (*Salmo trutta* Linnaeus, 1758), together with those of North Africa, represent the south–western limit in the natural distribution of this species (Sanz *et al*., 2006). In Andalusia region (S Iberian Peninsula), below the limit of anadromy (SNPRCN, 1991), all the brown trout populations have resident status and they are located in one of its geographical and ecological distribution edges (*sensu* Hampe and Petit, 2005).

It is known that the populations inhabiting at the periphery of a species' range are subject to a higher degree of stress and extinction events (Soule, 1973), but at the same time these regions may be active sites of natural selection, and hence of adaptive significance (Lesica and Allendorf, 1995). The last fact can be reinforced when the plasticity of the species is high (West–Eberhard, 2005), as occurs in brown trout, which high genetic, ecological and morphological variability (Bernatchez *et al*., 1992; Klemetsen *et al*., 2003) has allowed it to inhabit a wide range of marine and fluvial habitats (Jonsson and Jonsson, 2011).

In this regard, on one hand, peripheral populations inhabiting the Andalucía region have been able to generate evolutionary diversity and to diverge from central populations (*sensu* Lesica and Allendorf, 1995). Thus, they have shown the existence of five unique worldwide haplotypes (Almodóvar *et al*., 2010) as well as the most extended spawning period, as adaptation to the variability of the Mediterranean climate, reported to date (Chapter 2). On the other hand, an increase in the extinction risk of brown trout populations is observed when descending in latitude and scaling size of considered area: in Europe the species is catalogued as “least concern LC” (Freyhof, 2011), in Spain as “vulnerable VU” (Doadrio, 2001), and in Andalusia as “endangered, EN” (Franco Ruíz and Rodríguez de los Santos, 2001).

Moreover, current anthropogenic impact on the species range restricts the natural boundaries that once had, especially in Mediterranean systems (Blondel *et al.*, 2010, Clavero *et al.*, 2010). Chapter 1 described in detail the distribution of all brown trout populations in Andalusia (Figure 6.1), the causes that limit their distribution ranges (Figure 6.2), as well as the presence of the exotic rainbow trout (*Oncorhynchus mykiss* Walbaum, 1972) introduced in rivers where native brown trout inhabit currently or dwelled in the past (Table 6.1, left side). Comparing with the Andalusian brown trout distribution in the 19th century (Sáez Gómez, 2010), nowadays a range displacement towards protected areas located in higher altitudes has been observed. Thus, their populations only inhabit river reaches of eastern Andalusia (Figure 6.1), in an altitudinal range of 200 - 2200 m a.s.l., with a high degree of isolation, and whose upper limits have a natural origin while the lower ones are anthropogenic (Figure 6.2). Over half of the 38 populations detected in the region ascend to the headwaters of its rivers; in 9 cases the populations reached the basis of impassable waterfalls; and in Sierra Nevada National Park, where there are some of the highest mountains in Iberian peninsula, 13 populations have their upper limits in sections where low winter temperature prevents the survival of the species. Regarding the anthropogenic lower limits, most are related to water management, a resource often scarce in Mediterranean climate areas (Grantham *et al.*, 2010). On 17 occasions the ancient populations were fragmented by dams and currently only 8 of the populations located downstream of these infrastructures have survived. In the other 9 cases, populations relegated downstream of reservoirs have disappeared. In other 12 occasions the excessive water extraction dries out watercourses and prevents the maintenance of stable populations of fishes. Finally, the multiple interactions of water extraction, pollution and agriculture involve the disappearance of 7 populations.

Although the brown trout populations in Andalusia are threatened, this salmonid is one of the most important species for sport fisheries (Laikre *et al*. 1999) and the Andalusian Government only permits its fishing in catch and release modality (hereafter C&R) (Andalusian Law, *Orden 25 de febrero 2005*) using different administrative figures to manage this fishery resource (Andalusian law, *Orden 6 de mayo de 2014*): a) LAFA: Limited access fishing areas, fishable in open season with a permit; b) NLAFA: Non–limited access fishing area, fishable in open season without a permit; c) SFA: Stocked fishing areas: reaches where specimens with fishable size of the alien species rainbow trout are or were introduced; d) FR: Fish refuges, prohibited fishing all year; and e) E: Exceptions, some Andalusian reservoirs with special regulations.

Antunes *et al*. (2006) suggested the need to protect peripheral populations of brown trout to conserve the future potential of the species as a whole. In this sense, the peripheral studied populations show unique haplotypes, extended reproductive period and endangered status. Moreover, they are highly isolated by anthropogenic factors and subjected to a complex administrative situation regulating them as fishery resource. Thus, protecting these populations and their fluvial habitats means protecting evolutionary processes, and Andalusia region could even be an important site for events of speciation, particularly considering that there is no definitive scientific consensus about taxonomy of *Salmo trutta* (Kottelat and Freyhof, 2007; Jonsson and Jonsson, 2011).

Therefore, the goal of this work is twofold: 1) to propose administrative management measures at local scale aimed to improve the conservation status of this endangered fish at its southernmost distribution limit in Europe and 2) to propose anticipatory adaptation measures after discussing how the current causes that limit the distribution of the populations inhabiting the region of study will be affected in the Global Change frame reported by IPCC (2013).

6.3. Material and methods

6.3.1. Study area

Andalusia is the south-westernmost region of the European continent whose rivers flowing through four basins: Guadalquivir, South Mediterranean, Segura and Guadiana; brown trout populations inhabit the upper reaches of the first three ones (Figure 6.1).

6.3.2. Methods

This paper delves into the conservation of brown trout in the study region from the information reported in Chapter 1 in which the distribution of Andalusian brown trout populations (Figure 6.1), the causes that limit these populations (Figure 6.2), as well as the salmonid species detected in the rivers belonging to the current or historical distribution of brown trout (Table 6.1, left side) were described.

To find out which part of the reaches inhabited by brown trout were regulated for fishing, both the reaches inhabited by the species (Figure 6.1) and the limits of the administrative figures used by Andalusian Government to manage the fishery resources (LAFA, NLAFA,SFA, FR, and E) were digitalized using ArcGIS 9.3.1.

From this information, both administrative measures and anticipatory management measures are proposed, aimed to improve fisheries policy and to deal with the effects of Global Change by acting on current causes limiting populations, respectively. Regarding the latter, emphasis on concrete measures to eradicate naturalized rainbow trout populations that gravely threaten the conservation of native trout populations is made. All proposed measures are based on prior scientific knowledge related to the conservation of river ecosystems and freshwater fishes, which is especially wide in salmonid management, as well as regional particularities of the study area (policy, water management and climate).

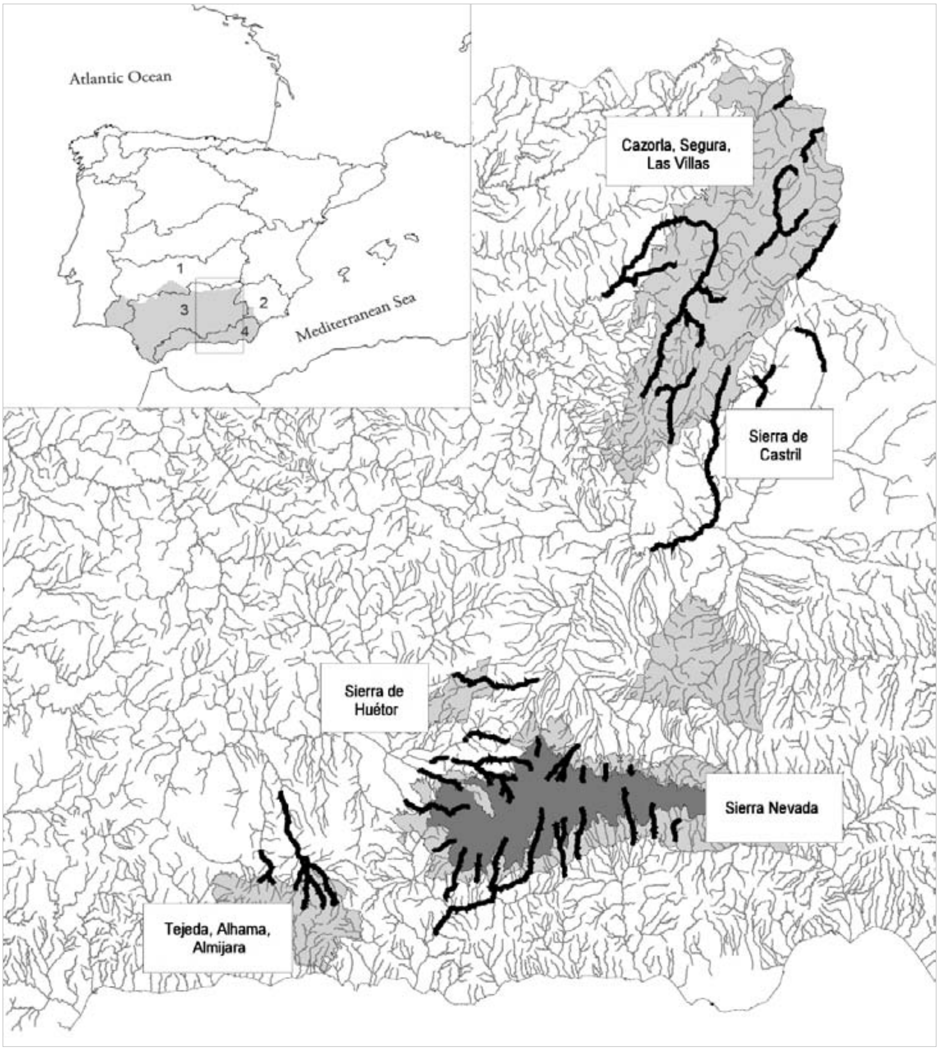

Figure 6.1. General map showing Spanish River basins, Andalusian region (shaded) and its numbered basins: Guadiana (1), Segura (2), Guadalquivir (3) and South (4). Detailed map shows Andalusian river network (thin lines), distribution of the brown trout (thick lines) and the natural reserves (light gray surfaces: Natural Parks; dark gray surfaces: National Park).

6.4. Results

The species is found in 3 of the 4 Andalusian basins: Guadalquivir, Segura and South. In each of them the administrative figures that regulate fisheries resources vary (Figure 6.3). Thus, fishing is not allowed throughout the year neither in NP (Sierra Nevada) nor in FR reaches, while in other sections fishing can be practiced with various degrees of regulation (NLAFA, LAFA, SFA and E). For the whole range of brown trout, NLAFA sections are the most abundant (nearly 40%) followed by FR (23.5%). With less presence, LAFA and NP show similar surface (15% roughly). Exceptions (E) correspond to 7% of the distribution of brown trout in the study area. Finally, 3.3% of the sections inhabited by the species are intended for fishing rainbow trout (SFA).

Within the SFA it should be differentiated between those sections recently created where the exotic species is introduced without reproductive capacity, and those historical introductions in sections where uncontrolled stocks of rainbow trout have become naturalized (Table 6.1, left side), facilitating the development of processes of intensive competition and displacement over the native trout. To conserve stocks of the brown trout a phased restoration is suggested and each of the affected sections is allocated to different objectives: Genetic Refuge, NLAFA *S. trutta*, LAFA *S. trutta*, or corridor for the dispersion of this native species (Table 6.1, right side).

In view of the causes that currently limit these populations, the specific effects that Global Change might have on them have been schematized. In addition, particular adaptive management measures to mitigate those effects in the study area have been proposed (Figure 6.4).

STUDIED REACHES			SALMONIDS DETECTED			MANAGEMENT PROPOSAL		
Current figure	Name	Length (m)	None	S.t. & O.m	O. m	Initial stage	Intermediate stage	Final stage
NLAFA	Dúrcal	15218	▨			P. R. W.	Studies of potentiality	Genetic Refuge
NLAFA	Huéneja	14609	▨			P. R. W.	Studies of potentiality	Genetic Refuge
SFA	Charco de la cuna	1218		▨		P. R. W.	Eradication	LAFA *S. trutta*
SFA	Don Marcos	4571		▨		P. R. W.	Stop introduction *O.m* & Eradication	LAFA *S. trutta*
SFA	El Duende	3821		▨		P. R. W.	Stop introduction *O.m* & Eradication	LAFA *S. trutta*
SFA	Bolera Reservoir	6862		▨		P. W.	Stop introduction *O.m* & *Eradication	LAFA *S. trutta*
SFA	San Clemente Reservoir	5563		▨		P. W.	Stop introduction *O.m* & *Eradication	LAFA *S. trutta*
SFA	La Vieja Reservoir	850		▨		P. W.	*Eradication	LAFA *S. trutta*
SFA	Puente del Hacha	3314		▨		P. R. W.	Eradication	LAFA *S. trutta*
SFA	Quéntar Reservoir	3279		▨		P. W.	Stop introduction *O.m* & *Eradication	LAFA *S. trutta*
NLAFA	Aguascebas Grande	8483		▨ *		P. R. W.	Eradication	NLAFA *S. trutta*
NLAFA	Guardal	8490		▨		P. R. W.	Eradication	NLAFA *S. trutta*
NLAFA	Jérez	7431		▨ *		P. R. W.	Eradication	NLAFA *S. trutta*
NLAFA	Padules	10264		▨ *		P. R. W.	Eradication	NLAFA *S. trutta*
-	Guadalquivir	9371		▨		P. R. W.	Eradication	Dispersal corridor
NLAFA	Laroles	9940			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Nacimiento	21242			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Ohanes	2916			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Nechite	11056			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Válor	13372			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Lanteira	10500			▨ *	P. R. W.	Eradication	Genetic Refuge
NLAFA	Aguas Blancas	7040			▨	P. R. W.	Eradication	LAFA *S. trutta*

Table 6.1. Management measures on 1) some reaches where does not live any salmonid after the recent disappearance of brown trout, 2) in sections where this native species cohabits with rainbow trout and 3) in sections where the native species has been extirpated after the introduction of the exotic one. **Left side**: "Studied reaches" and "Salmonids detected" columns. Only the reaches currently (Chapter I) or historically inhabited (Sáez Gómez 2010) by brown trout in Andalusia are considered. For each reach, its length, the administrative figure that currently regulates over it (Andalusian law, *Orden 6 de mayo 2014*; see Fig. 6.3) and salmonids detected (shading cells) are indicated. "None": rivers without salmonids. "S.t. & O.m": reach where *Salmo trutta* and *Oncorhynchus mykiss* cohabit. "O. m.": reach exclusively inhabited by rainbow trout at the present. SFA (underlined): SFA where the last law reform (*Orden 6 de mayo 2014*) prevents the release of rainbow trout. Asterisks (✻): rivers where reproduction of rainbow trout has been confirmed. **Right side**: Phased restoration proposal for the recovery of the river reaches with native brown trout populations. "Initial stage" for the new administrative declaration of the river reaches. P. R. W.: Potentially recoverable water (reaches where the probability of success during the intermediate stage is high); P.W.: Potential water (reservoirs where the probability of success during the intermediate stage is lower). "Intermediate stage" for studies of potentiality, to stop introductions of O. mykiss and to implement eradications. Eradication (*underlined*): In 2008, Environmental Counsel of the Government of Andalusia began to eradicate these rainbow trout populations; *Eradication (*with asterisk*): Reservoirs, where eradication it is only possible with drastic methods (we recommend the complete desiccation of the reservoir, but in some cases will be an unfeasible method). "Final stage" for the final administrative declaration of the river reaches, once the reintroduction with native haplotypes has succeeded.

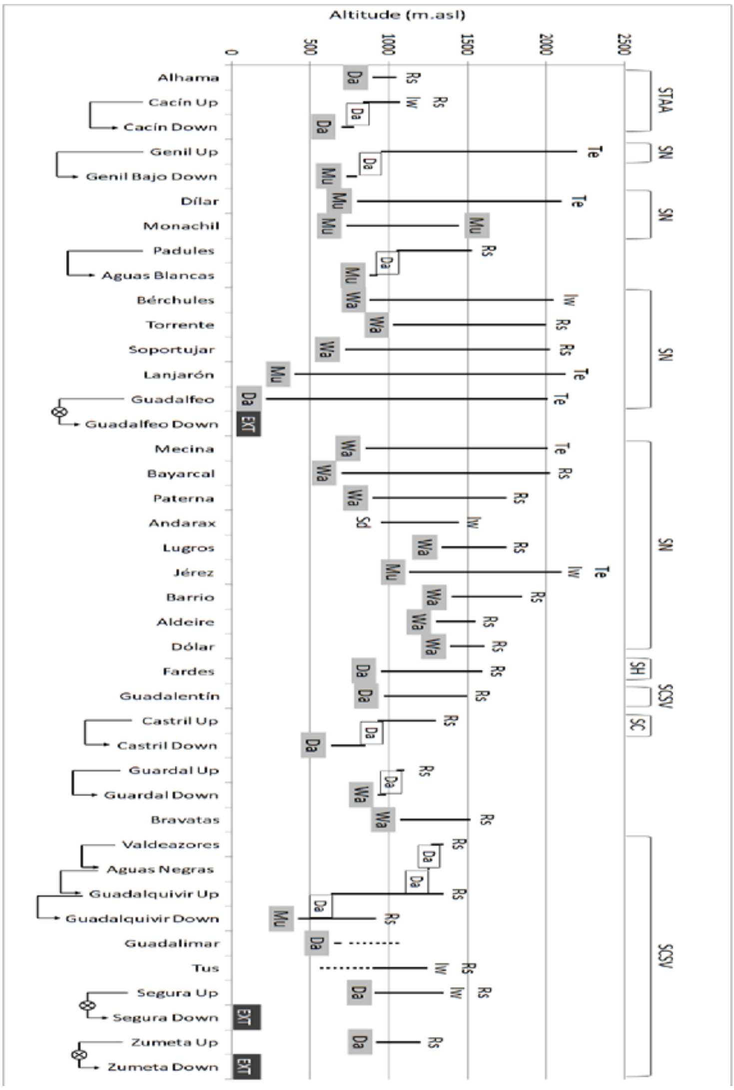

Figure 6.2. Altitudinal ranges inhabited by all populations of brown trout of the study area and causes of their upper and lower limits (natural causes are indicated with empty acronyms and anthropogenic causes with grey ones). Da: Damming; Wa: Water abstraction; Mu: Multiple; Sd: Summer drought; Rs: Population reaches the source; Iw: Impassable waterfall; Te: Temperature; Da in boxes represents dams fragmenting populations. The populational connections are indicated with arrows linking their names. Recently extinct populations located downstream reservoirs are indicated (EXT). Natural reserves containing all, or part, of the populations are named: STAA: Sierras de Tejeda–Alhama–Almijara; SN: Sierra Nevada (Natural and National Park); SH: Sierra de Huétor; SCSV: Sierras de Cazorla–Segura–Las Villas; SC: Sierra de Castril. Dotted lines (in Guadalimar and Tus Rivers) indicate reaches outside the administrative boundaries of Andalusia. (see also Chapter I).

6.5. Discussion

The uneven spatial distribution of threats across the Mediterranean basins requires different strategies to conserve freshwater biodiversity (Hermoso and Clavero, 2011). The knowledge on the impacts fragmenting and delimiting all Andalusian brown trout populations (Figure 6.2) as well as the fishery administrative figures present in those trout reaches (Figure 6.3) provide valuable information to implement a correct management of the species, to foresee the effects of Global Change and, consequently, to propose for particular measures to conserve the brown trout populations in the study region (Figure 6.4).

6.5.1. Proposal for the administrative management of brown trout

Sport fishing is a forbidden activity inside Spanish National Parks. Therefore, the declaration of FR is an administrative tool to designate areas without fishing impact outside of these protected areas. Approximately 40% distribution of the species in the study area has non fishing impact (inhabited reaches in Sierra Nevada National Park [NP], and FR ones), while in the remaining 60% fishing is allowed at some time of year (NLFA, LAFA, SFA and some E) (Figure 6.3).

These percentages for the whole Andalusia (40/60, approximately) are maintained in two of the three basins inhabited by brown trout, Guadalquivir and Segura basins, but with some differences between them. The 40% non-fishable reaches in Segura flows only through FR, while in Guadalquivir basin its 40% non-fishable is divided into 13% for NP and 27% for FR. Because of both the worrying population status of brown trout in Andalusia and that 70% of the reaches inhabited by this species in the study region are located in the Guadalquivir basin, it would be appropriate to increase the number of reaches designated as FR in this basin, to the detriment of other administrative figures in which fishing is allowed.

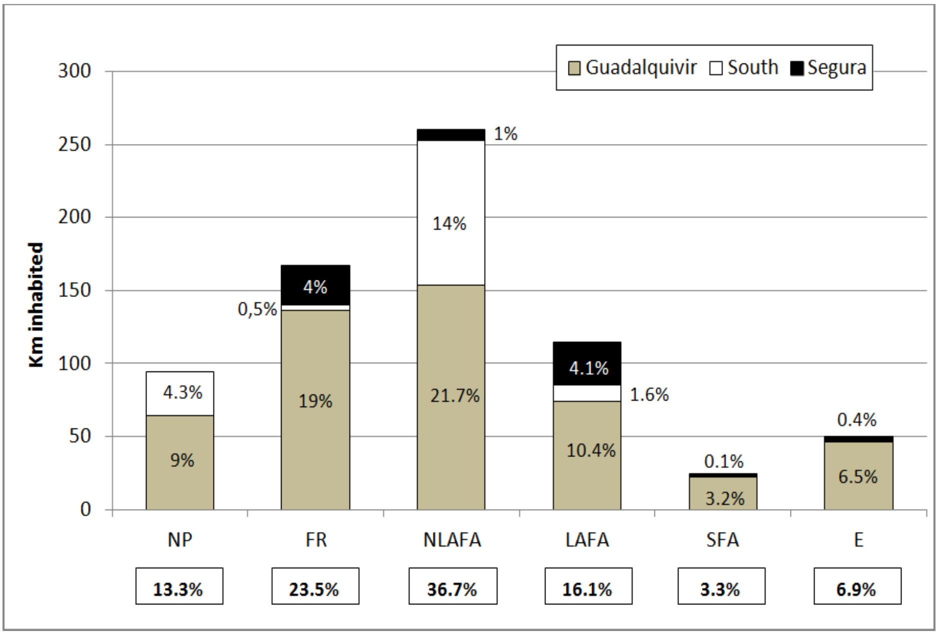

Figure 6.3. Kilometers and percentages (totals for the study region, and partials for the basins) of the area inhabited by brown trout in Andalusia occupying administrative reaches (Andalusian law *Orden 6 de mayo 2014*). NP: National Park; FR: Fish refuge, fishing is prohibited throughout the year; LAFA: Limited access fishing areas, fishable in open season with a permit (C&R for *S. trutta*); NLAFA: Non–limited access fishing area, fishable in open season without a permit (C&R for *S. trutta*); SFA: Stocked fishing areas: reaches where specimens with fishable size of the alien species rainbow trout are or were introduced; E: Exceptions (some Andalusian reservoirs with special regulations).

Regarding the South basin, the southernmost region of the species distribution in Europe with a high degree of isolation between populations (Chapter 1) and where several endemic Mediterranean haplotypes have been described (Almodóvar *et al.*, 2010), the 80% of their inhabited reaches are fishable. Therefore, in South basin it would be very necessary reduce the reaches designed to NLAFA, and expand the FR (nowadays 70% and 2%, respectively).

Generally, the increase in non-fishable reaches promotes a greater protection of watercourses inhabited by brown trout through the reduction of the access of fishermen to the inhabited reaches and hence the diminution of their potential impact on the species and fluvial ecosystems. It is known (O´Toole *et al.*, 2009) that angling activities can produce damage to the ecologic integrity of riparian ecosystems (soil compaction by trampling, and lower terrestrial and aquatic macrophyte density, height and diversity), as well as that the wading by fishermen can damage spawning sites of fishes in low order rivers (Arlinghaus *et al.*, 2002). Regarding the latter reproductive aspect, breeding periods of brown trout in Europe are characterized by beginning in November and finishing in January. This generality agrees with the single spawning season defined by Doadrio *et al*. (2011) for the Spanish populations, but in some Andalusian brown trout populations a longer spawning period, from October to May, has been recently detected (Chapter 2). Nevertheless, the current Andalusian law delimits the fishing periods from late March to late September in the best of cases. This fact should be considered to readjust the fishing periods in the study area, because in rivers where the extended spawning occurs, between March and May the active spawning sites remain unprotected against trampling.

On the other hand, nowadays overfishing cannot be the cause the disappearance of brown trout in the study area, because since 2005 this salmonid only can be fished in C&R modality in study region. Nevertheless, one of the assumptions associated with C&R is that the fishes returned after catching survive with negligible long–term impact on their fitness, but this assumption is not always true (Muoneke and Childress, 1994; Arlinghaus *et al.*, 2007; Cooke *et al.*, 2013). C&R has effects on behavior, growth or reproduction of fish (Policansky, 2002) and has been questioned in several countries (Arlinghaus *et al.*, 2002). However, even considering these factors, C&R has the potential to be used successfully as a management practice that conserves populations (Arlinghaus *et al.*, 2007) in areas where fishing is a deeply rooted traditional practice.

Besides, in the upper Guadalquivir basin (Guadalquivir, Borosa and Aguasmulas Rivers) there is a long reach not classified by the Andalusian law, but in which the detection of brown trout is punctual (Table 6.1). It is one of the fundamental axes of distribution of this species in Andalusia, a natural corridor of more than 9 km, whose preservation is of great importance to prevent habitat fragmentation, enable connectivity of remote demes and maintain the metapopulation dynamics. It is therefore necessary to modify its current classification. Its designation as FR should be proposed, which will allow it to act as a natural corridor, a similar action to the proposed by Hermoso *et al*. (2011b) in rivers of other Iberian basin for the conservation of endemic freshwater fish.

Finally, it should be noted that the recent law reform (Andalusian law, *Orden 6 de mayo de 2014*) provides some protection measures towards the indigenous populations of brown trout, hitherto not considered in previous laws. It has been forbidden the release of rainbow trout in three SFA (Table 6.1), and since 2008 the Environmental Council of the Andalusian Government has begun to eradicate rainbow trout populations in some reaches historically inhabited by brown trout and other reaches where both species still coexist (Table 6.1). Moreover, in one river (Lanteira River), after eradication, brown trout individuals of haplotype characteristic of the area were successfully introduced. These measures follow the working line proposed in Table 6.1 and the results to date are very promising.

6.5.2. Global Change and brown trout in Andalusia

There are five essential components of Global Change: climate change, introduction of invasive species, changes in land use, pollution (water, soil, air) and overexploitation of resources (Groom *et al*., 2006). At present, all of them are factors that constrain the distribution of brown trout populations in the study region (Chapter 1) (Figure 6.2) and their effects will be enhanced in the future (IPCC, 2013). Therefore, it could be predicted that if no action is taken, the current locations of the upper and lower limits of brown trout in Andalusia will continue being modified by effects related to Global Change (Figure 6.4).

On the one hand, direct exploitation has ceased to be a problem for the brown trout conservation in this region (fishing at C&R modality). Regarding climate change, over the past century, the average global temperature increased faster than previously recorded (Lobell *et al*., 2008) and even further increases are to be expected (IPCC, 2013). Temperature affects fish at all levels of biological organization (Graham and Harrod, 2009) and the temperature changes expected will affect river ecosystems with impacts on the hydrology, morphology, physicochemistry, food webs and production, with different results among cold, temperate or warm ecoregions (Kernan *et al*., 2010). Besides, these temperature changes also will alter the European rainfall patterns (IPPC, 2013) which could trigger chain effects: the amount of precipitation will decrease, the summers will be warmer and dryer, and the winters will be longer, milder, wetter and stormier. There will be changes in the snow dynamics, the precipitation will fall more frequently as rain instead of snow and the snow–line will rise. Periods with extreme weather will become more frequent, and the extreme events (e.g., floods or droughts) will be more recurrent and intense. Furthermore, runoff and earlier spring discharge peaks will increase in snow–fed rivers. Therefore, in this framework of Climate Change the current distribution limits of the species will be modified (Jonsson and Jonsson, 2009). Cold water fish populations will be positively affect at their cooler boundaries and negatively at the warmer ones (Rahel *et al*., 1996; O'Brien *et al*., 2000; Reid *et al*., 2001), and from a global perspective, the most favored salmonids will be the populations inhabiting sub–Arctic regions (Babaluk *et al*., 2000; Stephenson, 2006). Thus, the result of the interaction between water temperature and flow will be one of the keys to understand future distribution changes in freshwater fish populations.

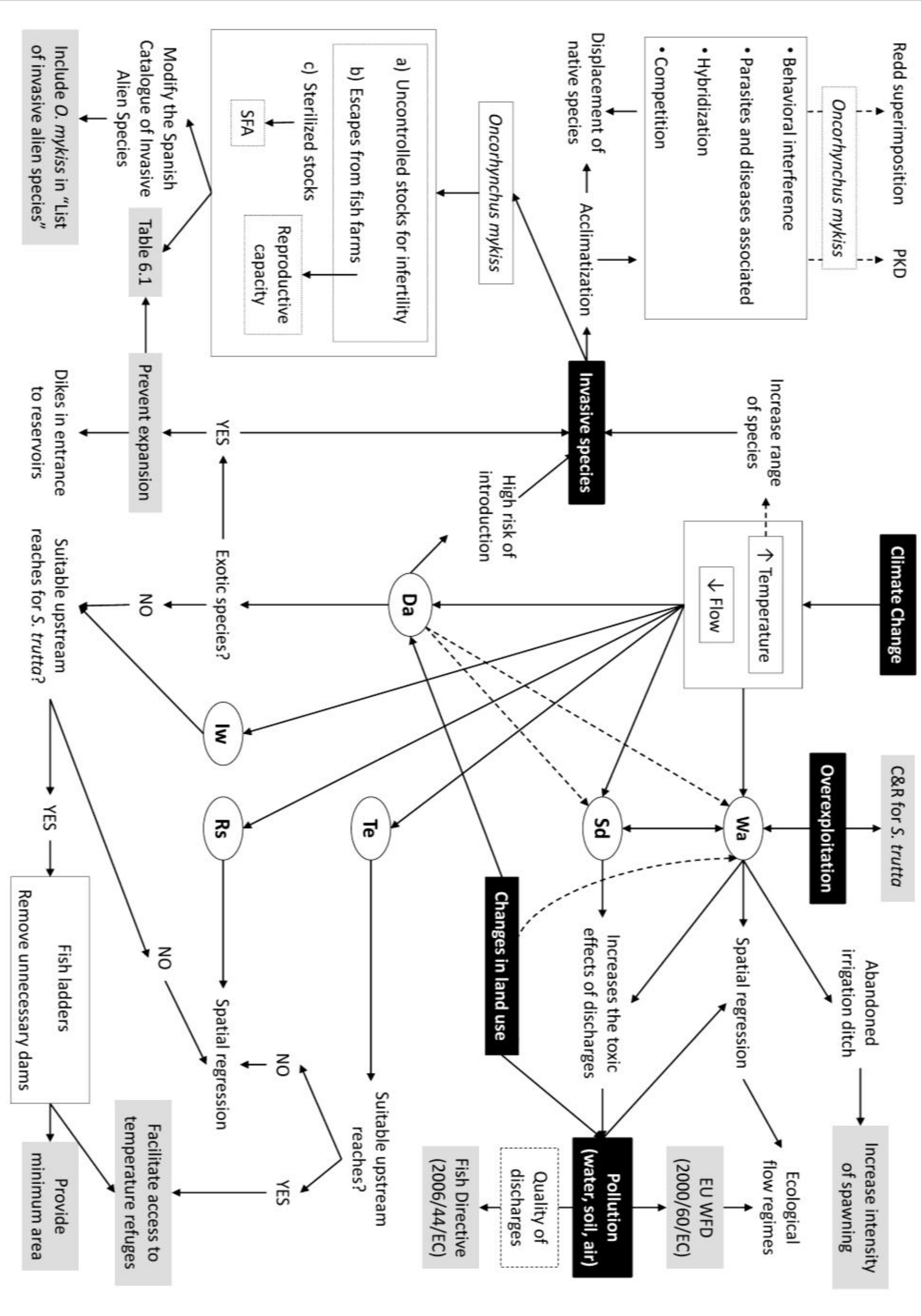

Figure 6.4. Flowchart for possible future effects of the five components of Global Change (black boxes) on populations of brown trout in Andalusia, considering the natural and anthropogenic factors (circular boxes) that currently delimit to these populations (Da: damming; Wa: water abstraction; Sd: summer drought; Rs: population reaches the source; Iw: impassable waterfall; Te: low temperature), as well as some of the main measures proposed (grey boxes).

This general scenario could be particularly drastic in mid–latitude regions, where impacts aforementioned could be more severe. In particular, in the Mediterranean basins water flow reductions, summer drought periods, increases in water temperature and greater intensity of heavy rainfall are events severely expected (Ulbrich *et al*., 2006; Giorgi and Lionello, 2008). Therefore, the loss of suitable thermal habitat for brown trout predicted for the whole of Spain (Clavero *et al*., 2017), and specifically for the north (Almodóvar *et al*., 2012; Ayllón *et al*., 2016) and center (Santiago *et al*., 2016) of the country, could be even more intense in Andalusia. However, since the altitudinal effect can soften the latitudinal effect (Körner, 2007), a delay in the range of contraction of populations located in high Mediterranean mountain systems, which are also usually protected natural areas with less anthropogenic impact, would be expected. In this sense, in the last century the populations located in warmer regions of Andalusia disappeared (Sáez Gómez, 2010), leaving the current populations relegated to the highest mountain ranges (Figure 6.1), some of which are the higher peaks of the Iberian Peninsula. Thus, it is probable that trout populations located at lower altitude in the study region lose faster their optimal habitat in favor of cyprinids populations that nowadays cohabit with them, even with higher density (e.g., *Luciobarbus sclateri* Günther 1868, *Squalius pyrenaicus* Günther 1868, or *Pseudochondrostoma willkommii* Steindachner, 1866, own data). Therefore, the active search for thermal refugia should be one of the measures to be taken in order to cope to Climate Change (Santiago *et al*., 2017).

Furthermore, it is noteworthy that during the study period two extreme and stochastic processes characteristic of Mediterranean climate (Gasith and Resh, 1999) were observed: heavy rainfall events and summer drought periods. The former caused effects of washing out (*sensu* Heggenes and Traaen, 1988; Jensen and Johnsen, 1999) and the latter increased the temperature and dried the habitat. The result in both cases was a high reduction in densities of brown trout and disappearance of the species in certain river sections. However, in the following years the populations of brown trout were recovered in the absence of new impacts. Thus, the high capacity of resilience of brown trout populations against stochastic events, principally annual unpredictability in rainfall pattern, should be highlighted.

Moreover, certain ectothermic organisms show behavioral thermoregulation seeking temperature refuges when they detect increase in water temperature. In the case of salmonids these refuges could be cool–water sites created by inflowing tributaries, groundwater seeps or, in most cases, the upper river reaches (Berman and Quinn, 1991; Baird and Krueger, 2003; Breau *et al*., 2011). However, the upward shift of the thermal habitat not always will involve the upstream shift of populations, since the latter depends on the ability of individuals to reach upper suitable sections as well as the fluvial connectivity. In this way, the small populations of resident brown trout in the study area are highly fragmented by dams (Da) and their upper limits are in a) impassable waterfalls (Iw), b) the source of the river (Rs) or c) they have an ecological limit because of low winter temperature at high altitude (Te) (Figure 6.2).

In the latter case (situation identified only in Sierra Nevada), a water warming could promote the ascent of populations, provided that the new habitats generated upstream are suitable for their survival and there are no impassable barriers preventing it. In this sense, physical barriers posed by Iw and Da (natural and anthropogenic limiting cause, respectively) restricts the longitudinal migration (*sensu* Hari *et al*., 2006) and removes the adaptation ability to climate change, although there are suitable habitat upstream. In addition to allow the arrival to temperature refuges, connectivity also favors the availability of a minimum size of habitat, since it is necessary that the size of the fragments where the isolated Andalusian populations inhabit is larger or equal than the minimum area needed to complete its life cycle (*sensu* Koizumi, 2011). Thus, increasing river connectivity is one of the most effective mitigation measures (Morita and Morita, 2009). Therefore, in case of not adopt any measures a range contraction could be predicted in populations whose upper limits are Da, Rs or Iw. However, in Da and Iw, adaptive management measures could prevent the spatial regression (Figure 6.4). Thus, to reduce the likelihood of local extinctions reconnecting fragmented rivers by installing efficient fish ladders in dams in use or new construction, as well as removing currently unnecessary impassable dams (Marchamalo *et al*., 2000; Hart and Poff, 2002; Alonso–González *et al*., 2009), should be measures proposed in the study region, as long as the impact generated do not endanger the persistence of another species inhabiting upper reaches (Tierno de Figueroa *et al*., 2010). If this is not done, populations relegated under reservoirs will be the first to go extinct, as recently happened in three Andalusian populations fragmented by Da (Figure 6.2).

Besides, the expected increase of water withdrawals for civilian population supply in Mediterranean regions (Bates *et al*., 2008) will increase the risk and severity of climate change impacts on stream communities. Their effects will be more noticeable at the lower limits of the brown trout populations in study region (Figure 6.2). In addition, water warming coupled with the flow reduction, increases the toxic effects of discharges (Bates *et al*., 2008; Kernan *et al*., 2010). Therefore, in the future it will become increasingly difficult to discriminate a single cause as the origin of the lower limits, and the presence of multiple causes (Mu) delimiting populations will be more frequent (Figure 6.2). Regarding water extractions (Wa), it is necessary to regulate fluvial disconnection produced by dykes associated with water diversions, to prevent the entry of fishes into irrigation ditches, and to preserve the ecological flow regimes in the reaches located downstream the water extraction points. In this sense, as Williams (2006) noted in the Columbia River Basin, during the work for the delimitation of brown trout populations in the study area (Chapter 1) it was found how irrigation ditches can act as very active artificial spawning sites. Most likely this is due to that the grain size, depth and flow velocity are parameters more constants and extensive into the ditches than in the upper reaches of rivers where the spawning sites are usually punctual and smaller size (personal observation). Thus, the numerous irrigation ditches abandoned (currently characterized by their substrate composed by gravels) in the upper trout reaches could be used to increase the intensity of spawning of the species in Andalusia. This management would require its restoration and conditioning, as well as the creation of bypass circuits that return water to the river, in order to that trout do not reach farmlands or irrigation ponds. Additionally, the provision of suitable deep pools should be an essential part of the strategy for successfully managing populations of *S. trutta* during summer droughts (Elliott and Elliott, 2010).

On the other hand, in populations inhabiting Alpine rivers increases in the incidence of temperature–dependent Proliferative Kidney Disease (PKD), related to Global Change, have been observed (Hari *et al*., 2006). Nevertheless, PKD has not yet been detected in study region, which does not mean that it is not a problem in the future, because the stress associated with water warming facilitates the input of invasive species (Dukes and Mooney, 1999; Walther *et al*., 2009), as well as parasites and diseases associated to them (Fausch, 2007; Leunda, 2010; De Silva, 2012). Thus, the current scenario of Global Change potencies unintentional or deliberate introductions and increase of range of non native species through of global warming (Dukes and Mooney, 1999; Walther *et al*., 2009; Cobo *et al*., 2010; De Silva, 2012). The arrival of exotic freshwater species could result a serious threat to the integrity of Mediterranean ecosystems, affecting the survival of the native species, mostly endemic (Elvira and Almodóvar, 2001). The impacts of introductions and translocations on the native fishes are multiple, highlighting predation, competition (for trophic or habitat resources), disease transmission, hybridization and behavioral interference (Leunda, 2010; Figure 6.4). These threats have been already observed in almost all rivers of medium and low mountains of Andalusia, where native Mediterranean species cohabit with exotic fishes (e.g. *Alburnus alburnus* Linnaeus, 1758; *Cyprinus carpio* Linnaeus, 1758; *Gobio gobio* Linnaeus, 1758; *Esox lucius* Linnaeus, 1758; *Gambusia holbrooki* Agassiz, 1859; *Lepomis gibbosus* Linnaeus, 1758; *Micropterus salmoides* (Lacépède, 1802); Elvira, 1995; Hermoso *et al*., 2011a), which have become a large stock of future invaders threatening the upper reaches currently inhabited only by native species. Furthermore, many of these exotic species inhabit lentic ecosystems and the intensive construction of dams in the study region, originating new lentic habitat, enhances their invasive potential (Almeida and Grossman, 2014; Clavero *et al*., 2004; Johnson *et al*., 2008).

For all these reasons, it is probable that the harmful effects of Global Change on worldwide range of brown trout distribution may be maximum in the southernmost populations in Europe. Moreover, over the next 50 years major changes in fish communities are expected (Graham and Harrod, 2009), so it is of great importance to initiate adaptive management measures to mitigate the effects of Global Change, being a fundamental priority to maintain both optimal flow and connectivity in trout rivers throughout all year. To protect the river biodiversity it is necessary to act in the whole catchment, which implies carrying out more drastic changes of those made to preserve land areas (Likens *et al*., 2009). It must be maintained the quality of freshwaters, doing them suitable for fish life (Fish Directive, 2006/44/EC) and promoting the objectives specified in the Water Framework Directive (2000/60/EC). In addition, it is necessary to develop management programs for the recovery of resident fishes and routes of migrant fishes (Muhlfeld *et al*., 2011). Some of these programs are already underway by the Environmental Council of the Andalusian Government, among them, the Conservation Program for brown trout, to which belong the results of this work.

The case of rainbow trout

Rainbow trout is probably the most widely introduced fish in the world (Crawford and Muir, 2008). In Spain it was introduced in the late 19th century for angling, although escapes from fish farms are currently another identified cause (Elvira and Almodóvar, 2001; Doadrio, 2001; Consuegra *et al*., 2011). In the study region there are rainbow trout populations cohabiting with brown trout populations or occupying rivers where autochthonous species has been displaced by the exotic one (Table 6.1). The origin of these exotic populations in Andalusia is triple, according to the "human activity" hypothesis (Leprieur *et al*., 2008). First, in the 60's and 70's, uncontrolled genetic stocks for infertility of rainbow trout were introduced in some rivers of the range of brown trout (Table 6.1). Second, more recently, Regional Administration designated SFA (driven by repeated authorized introductions of large numbers of sterilized stocks of rainbow trout), as a fishery resource to reduce the impact of fishermen on native populations of brown trout. These SFA are distributed throughout Andalusia, but should be highlighted that eight of them are located in reaches inhabited by brown trout, or very close to the current range of the native species. These SFA are located mainly in the Guadalquivir basin and they are absent in South basin (Figure 6.3). Finally, as third cause escapes of rainbow trouts in all Andalusian river reaches located downstream of fish farms, and in several reservoirs in the range of distribution of brown trout in Andalusia, have been detected (Table 6.1).

Rainbow trout affect to native trout habitat selection and survival (Blanchet *et al*., 2007; Fausch, 2007). This alien species interferes with brown trout for territorial space and food resource, and when the spawning space is limited, the interspecific competitive pressure due to redd superimposition can eliminate the native populations (Landergren, 1999; Scott and Irvine, 2000). Interestingly few populations have acclimated and reproduced outside the native area, but in some cases *O.*

mykiss can constitute stable populations able to survive and to colonize areas that naturally lack other salmonids. Reproduction of rainbow trout had been observed in northern Europe (Norway, Sweden or Denmark) and in alpine streams of Austria, Slovenia or Italy (Landergren, 1999; Kottelat and Freyhof, 2007; Candiotto *et al*., 2011). Doadrio *et al*. (2011) accept that, despite of the little knowledge, in the Iberian Peninsula rainbow trout reproduce sporadically and punctually in freedom. Thus, to date in Spain the rainbow trout has been listed in scientific literature (Doadrio, 2001; Leunda, 2010; Maceda–Veiga, 2013) and state laws (*Real Decreto 1628/2011*) as a naturalized species and potentially invasive. However, in the present study it has been observed that this reproductive capacity is extended to the three basins inhabited by declivous or extinct brown trout populations in Andalusia (Table 6.1), compared to the increase or stability observed in the alien species populations. In this regard, to allow unrestricted stocking, certain species introduced for recreational fisheries (e.g. rainbow trout and *C. carpio*) have even been declared native in several European countries (Freyhof and Brooks, 2011). However, this statement should never be approved, since the stocking of alien salmonid species for recreational and commercial purposes is the most important problem for salmonid conservation (Kottelat and Freyhof, 2007). Thus, Crawford and Muir (2008) recognized the need to terminate ongoing stocking programs for introduced salmonids worldwide and Consuegra *et al*. (2011) that the escapes from fish farms facilitate establishment of non–native rainbow trout. Furthermore, the presence of invasive alien species in river basins threatens the fulfillment of the Water Framework Directive (*2000/60/CE*).

Thereby, it would be necessary to remove the SFA located in reaches inhabited by brown trout and in reaches potentially recoverable waters (Table 6.1), and to execute the laws currently in place to prevent the introduction of the exotic species (*Real Decreto 630/2013*) in reaches currently inhabited by native trout or reaches potentially recoverable (historically inhabited by them). In the case of reservoirs, where eradication is impossible, it would be necessary create dikes in the entrance of the tributaries of the reservoir (Figure 6.4) to prevent access of alien species to the restored upper reaches. In addition, due to the reproductive capacity described, as well as the adverse effects that this exotic species have and had on historic Andalusian brown trout populations, the Spanish Catalogue of Invasive Alien Species (*Real Decreto 630/2013*) should be modified to include rainbow trout in the list of invasive alien species. It would also be necessary to control the escapes of fish farms, to prohibit the establishment of new hatcheries that drain into to reaches inhabited by brown trout, and even to eliminate farms currently located in reaches inhabited or potentially habitable for brown trout. In this way, modifications to the Andalusian law about fishery resources (Andalusian law, *Orden 6 de mayo de 2014*) aimed to facilitate the restoration of brown trout populations are proposed in Table 6.1 (some of these modifications already have been initiated by Environmental Council of the Andalusian Government).

In the study area, rainbow trout cohabits with native species along almost 69 km (Table 6.1), which represents 9.7% of brown trout distribution in Andalusia. Moreover, 76 km inhabited almost exclusively by this non–native species, in reaches which harbored brown trout populations in the past (Sáez Gómez, 2010), have been detected. In case of eradicate exotic species of these sections and subsequently reintroduce the native trout, the distribution area of brown trout in Andalusia would increase by 15% (more than 105 km of watercourses). These reintroductions should be made with endemic haplotypes characteristics of the subbasins to which these rivers belong (Almodóvar *et al*., 2010), and the receptors reaches should be regulated mostly as Brown Trout Genetic Refuges (Araguas *et al*., 2009) to preserve the integrity of brown trout gene pools (Caudron *et al*., 2012) in this region (Table 6.1). Thus, the analysis of the spatial distribution of the brown trout genetic variation in Andalusia should be used to define management units in conservation (Vilas *et al*., 2010), and generate a demogenetic model (Frank *et al*., 2011).

6.6. References

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7. DISCUSIÓN GENERAL

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Las severas condiciones climáticas impuestas en latitudes elevadas durante el último periodo glacial (hace unos 18.000 años) supusieron la extinción de todas aquellas especies que no mostraron mecanismos de escape hacia latitudes menores. En el caso de Europa, algunos territorios circumediterráneos mantuvieron condiciones microclimáticas apropiadas para la supervivencia de un gran número de especies (Bianco *et al*., 1990; Petit *et al*., 2003), especialmente la península ibérica Bennett *et al*., 1991; Hewitt, 2004). En particular, la región de estudio constituyó un refugio poblacional para varias especies piscícolas, entre ellas la trucha común (*Salmo trutta* Linnaeus, 1758) (Machordom *et al*. 2000; Suárez *et al*. 2001; Antunes *et al*. 2002; Sanz *et al*. 2002; Cortey *et al*. 2004). Con la retracción de los polos (hace unos 13.000 años) y la consiguiente colonización (o recolonización) de regiones septentrionales por parte de numerosas especies (Doadrio y Carmona, 2003; Bennett y Provan, 2008), las poblaciones de trucha común mantuvieron estrategias residentes en el área de estudio. La pérdida de la anadromia supuso su aislamiento, y desde entonces su proceso evolutivo ha seguido un curso independiente.

El elevado grado de plasticidad ecológica y fenotípica que muestra la especie (Elliot, 1994; Ayllón *et al*., 2010; Valiente *et al*., 2010) en toda su área de distribución (Figura 1.3, página 30) ha permitido su adaptación al paulatino desarrollo del clima mediterráneo. En particular, la presencia conjunta de factores como aislamiento poblacional, estatus residente y clima mediterráneo, favorecieron el desarrollo de ciertas características particulares en las poblaciones analizadas en esta Tesis: (1) haplotipos genéticos autóctonos (Almodóvar *et al*., 2010), (2) periodos reproductivos extendidos (aspecto abordado en el Capítulo II), y (3) tallas mínimas de freza muy bajas (observaciones personales).

Sin embargo, el histórico impacto antropogénico que han sufrido los cursos de agua de las regiones mediterráneas, intensificado en los últimos siglos (Blondel *et al*., 2010, Clavero *et al*., 2010), ha provocado en las poblaciones de trucha andaluzas un acelerado proceso de regresión espacial y poblacional (Sáez Gómez, 2010). Esto ha supuesto su catalogación como *en peligro de extinción* “EN” (Franco Ruíz and Rodríguez de los Santos, 2001) y desde el año 2005 su pesca deportiva únicamente puede ser realizada en la modalidad de captura y suelta (*Orden 25 de febrero 2005*, Ley Andaluza). Además, el cambio climático, y de forma particular en los sistemas mediterráneos (Ulbrich *et al*., 2006; Giorgi and Lionello, 2008) como el estudiado, podría tener efectos devastadores para el desarrollo y supervivencia de las poblaciones de estudio; más aún cuando la especie que se trata es ectoterma y dependiente de aguas frías (Santiago *et al*. 2017).

Todas estas singularidades locales descritas (genéticas, reproductivas, retracción poblacional, poblaciones amenazadas, etc.) coinciden con las características teóricas que potencialmente podrían observarse en poblaciones habitando en lo que Hampe y Petit (2005) denominan “bordes traseros de distribución” (“*rear edge of distribution*”). Las poblaciones de trucha aquí estudiadas habitan en uno de ellos.

Por todo ello, así como ante la carencia en la región de estudio de trabajos científicos previos sobre una especie pescable y apreciada como es la trucha común, en la presente Tesis se ha aportado un abundante conocimiento científico nuevo. En primer lugar se ha determinado la distribución exacta de la trucha en Andalucía, las causas que limitan sus poblaciones, así como los cursos fluviales habitados por la exótica trucha arcoíris (*Oncorhynchus mykiss* Walbaum, 1972) (Capítulo I). Asimismo, se ha delimitado el periodo reproductivo de las poblaciones de trucha común en las diferentes cuencas de captación que habita, ya que conocer la fenología reproductiva de una especie es un rasgo fundamental para la correcta propuesta de medidas de gestión de sus poblaciones (Capítulo II). También se han identificado qué procesos dependientes y/o independientes de la densidad regulan la dinámica de las poblaciones de estudio, así como qué características físicas del hábitat podrían estar modulando un posible fenómeno sincrónico en sus poblaciones ("Efecto Moran"; Moran, 1953) (Capítulo III). Por último, considerando las conclusiones obtenidas en los capítulos previos, se han propuesto medidas de gestión concretas y específicas para las poblaciones de trucha en Andalucía (Capítulo IV).

Los resultados muestran cómo las poblaciones actuales de trucha común en la región de estudio son un reducto poblacional de las presentes en el s. XIX, habiendo desaparecido de las regiones occidentales descritas por Menor y Prenda (2006) y Sáez Gómez (2010). En la actualidad la especie sólo es detectada en sistemas montañosos orientales con altitudes superiores a los 1500 m.s.n.m., donde viven en cursos fluviales altos de las cuencas del Guadalquivir, Segura y Mediterráneas del Sur (Figura 3.2.B, página 69). Habita fundamentalmente en ríos que circulan por el interior de Espacios Naturales Protegidos (62% de la distribución) y en ríos que salen de estas reservas (32%): Tejeda-Almijara-Alhama, Sierra Nevada, Sierra de Huétor, Castril y Cazorla-Segura-Las Villas (Figura 7.1). Las escasas poblaciones detectadas sin conexión con Espacios Naturales Protegidos (6%) muestran densidades mucho más bajas que las mostradas por las poblaciones que habitan en el interior de los espacios protegidos. Además, suelen estar aisladas aguas arriba de embalses y afectadas en mayor medida por extracciones de agua y especies invasoras.

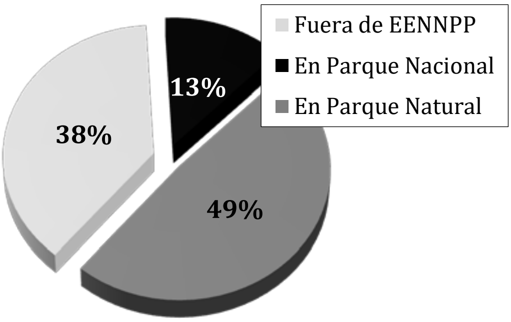
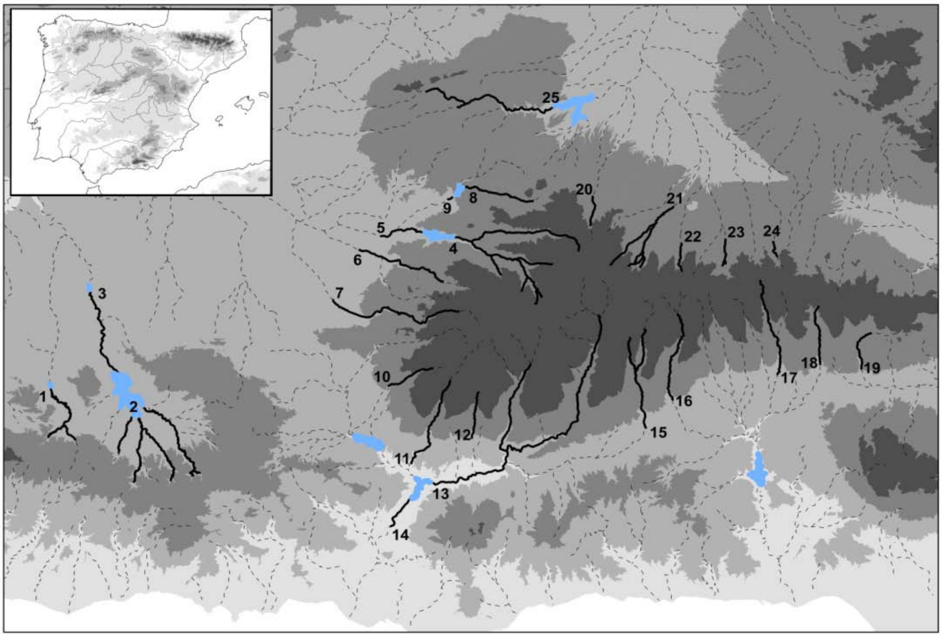


Figura 7.1. Distribución de la trucha en Andalucía: tramos que discurren por EENNPP y fuera de ellos. Del 38% fuera de EENNPP, el 32% son ríos que nacen en ellos, mientras el 6% son cursos fluviales no relacionados con EENNPP.

En total, se han identificado 38 poblaciones con un elevado grado de aislamiento interpoblacional, mostrando en su mayoría una estructura metapoblacional (Figura 7.2). Los rangos altitudinales más elevados se observan en Sierra Nevada, donde la trucha puede ser localizada desde los 2200 hasta los 200 m. de altitud. Que en la actualidad la cota altitudinal máxima detectada y compartida por numerosas poblaciones en Sierra Nevada sea 2200 m. podría estar indicando la existencia de un límite ecológico en la región de estudio. Este límite altitudinal deberá ser considerado en futuros trabajos, ya que su variación podría revelar efectos relacionados con el Cambio Climático.

Las poblaciones de trucha en Andalucía se encuentran limitadas superiormente por causas naturales, mientras que los límites inferiores son debidos a factores antropogénicos, en su mayoría relacionados con la gestión del agua (recurso escaso en la región de estudio). Por tanto, el rango de distribución, así como la superficie habitada por la especie podría aumentar en caso de eliminar los impactos que actualmente limitan aguas abajo a sus poblaciones.

Con respecto a los límites superiores, en 33 ocasiones las poblaciones andaluzas alcanzan el nacimiento de sus cuencas vertientes, sin posibilidad de más ascenso. En otras 13 el límite superior lo marca el límite ecológico-altitudinal antes mencionado, por encima del cual, aun habiendo agua fluyendo, no se detectan ejemplares de trucha. Sin embargo, 9 límites superiores son debidos a la presencia de saltos naturales infranqueables (cascadas), por encima de los cuales el hábitat continúa siendo apropiado para la especie. Por tanto, estos tramos potencialmente habitables deberán ser considerados a la hora de proponer medidas de gestión adaptativa en un futuro.



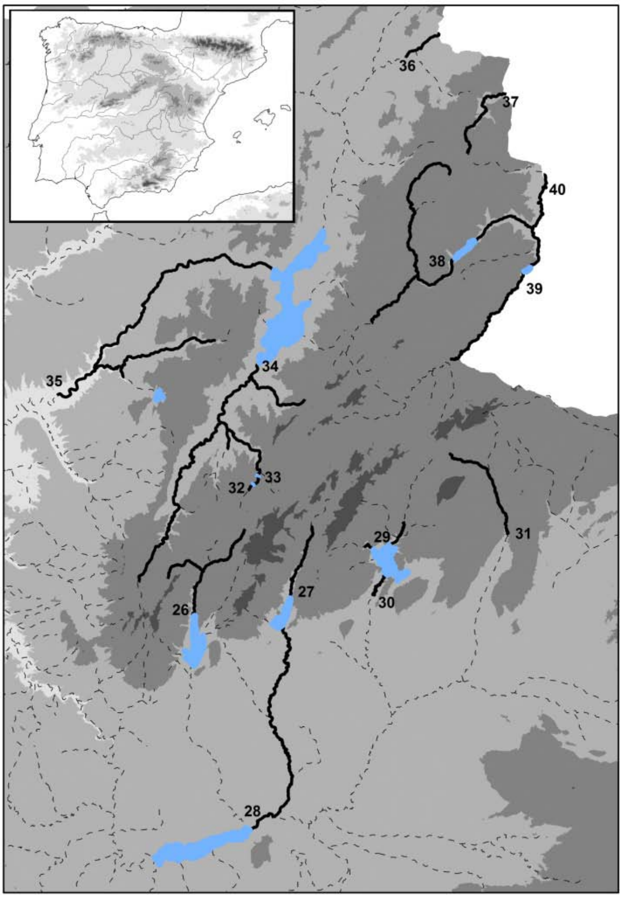


Figura 7.2. Poblaciones delimitadas en región sur (arriba) y norte (abajo) del área de estudio: 1. Alhama; 2, Cacín alto; 3. Cacín bajo; 4. Genil alto; 5. Genil bajo; 6. Monachil; 7. Dílar; 8. Padules; 9. Aguas Blancas; 10. Torrente; 11. Lanjarón; 12. Chico de Soportújar; 13. Guadalfeo alto; 14. Guadalfeo bajo; 15. Bérchules; 16. Bayárcal; 17. Paterna; 18. Mecina; 19. Andarax; 20. Lugros; 21. Jérez; 22. Barrio; 23. Aldeire; 24. Dólar; 25. Fardes; 26. Guadalentín; 27. Castril alto; 28. Castril bajo; 29. Guardal alto; 30. Guardal bajo; 31. Bravatas; 32. Valdeazores; 33. Aguas Negras; 34. Guadalquivir alto; 35. Guadalquivir bajo; 36. Guadalimar. 37. Tus; 38. Segura alto; 39. Zumeta alto; 40. Segura/Zumeta bajo (extinta).

Con respecto a los límites inferiores, en 12 poblaciones se establece al llegar a puntos con extracciones de agua incontroladas (acequias) que desecan por completo los cursos fluviales. Por otro lado, la contaminación del agua (vertidos) unida a (a) la disminución de caudales (lo cual potencia el efecto tóxico de los vertidos, ver Gasith y Resh, 1999) y/o (b) a la introducción de especies exóticas, supone la aparición del límite inferior en otras 7 poblaciones. La solución a estos 19 límites inferiores artificiales pasa por el cumplimiento de las normas establecidas en lo que respecta a (1) caudales ecológicos (Consejería de Medio Ambiente y Ordenación del Territorio, *Orden de 23 de febrero de 2016*), (2) vertidos (*Directiva 2006/44/CE del Parlamento Europeo y del Consejo*, relativa a la calidad de las aguas continentales que requieren protección o mejora para ser aptas para la vida de los peces) y (3) especies exóticas (Catálogo Español de Especies Exóticas Invasoras, *Real Decreto 630/2013*). Su cumplimiento aumentaría el área de distribución de la especie y permitiría la conexión de poblaciones actualmente aisladas a causa de estos factores antropogénicos.

Por otro lado, la causa artificial que con más frecuencia supone la desaparición de las poblaciones de trucha que habitan la región de estudio es la construcción de embalses. Estas grandes obras hidráulicas suponen la aparición de 17 límites inferiores. En 8 de esos casos fragmentan poblaciones antaño conectadas: Cacín, Genil, Castril, Guardal, Guadalquivir, Guadalfeo, Segura y Zumeta (Supplementary data 3.1). Además, durante los trabajos de campo se observó la desaparición de dos poblaciones de trucha en los tramos situados bajo los embalses de los ríos Segura (embalse de Anchuricas) y Zumeta (embalse de la Vieja).

Llegado este punto se hace necesario hacer una reseña sobre el impacto que genera la construcción de embalses, al tratarse de las mayores amenazas para la biodiversidad asociada a ecosistemas fluviales (Poff *et al*. 2007), tal y como refleja la Directiva Marco del Agua (2000/60/ CE). Los embalses causan drásticos cambios en los cursos de los ríos. Modifican los regímenes naturales de flujo y temperatura (Kingsford 2000; Alonso *et al*. 2008), la geodinámica de toda la cuenca de captación (tamaño de partículas, procesos de sedimentación, etc.) (e.g. Shieh *et al*. 2007; Maddock *et al*. 2008; Kishi y Maekawa 2009) y la estructura y dinámica natural de la biota (Bunn y Arthington 2002). De hecho favorecen la invasión de especies exóticas (Almeida y Grossman, 2014; Clavero *et al*., 2004; Johnson *et al*. 2008), llegando a constituir grandes reservorios de futuros invasores, lo que amenaza los tramos superiores históricamente habitados de forma exclusiva por especies nativas (Clavero *et al*., 2015). Tal y como lo definió Ligon *et al*. (1995), la creación de un embalse es un evento catastrófico en la vida de un sistema fluvial.

En el caso de los salmónidos, los embalses alteran sus tasas de crecimiento, desarrollo, uso de hábitat y reproducción (Yrjänä *et al*. 2002; Kishi y Maekawa 2009). Además, suponen la creación de barreras que aíslan y fragmentan poblaciones (Rieman y Dunham 2000; Gosset *et al*. 2006; Heggenes y Røed 2006), fenómeno descrito en la región de estudio (Supplementary data 3.1). Si a todos estos efectos sumamos la estocasticidad propia de los sistemas mediterráneos (elevada impredecibilidad anual de flujo), el aislamiento de las poblaciones puede tener efectos devastadores en su resiliencia, de forma particular cuando la capacidad de carga es baja (Morita y Yokota, 2002), un hecho frecuente en poblaciones habitando regiones periféricas como las estudiadas en esta Tesis.

Por otro lado, durante los trabajos de campo se observó un fenómeno relativamente frecuente en la región de estudio: una vez que la especie ya ha sido sustituida aguas abajo por otros taxones (ciprínidos en nuestra región), se detecta la reaparición de poblaciones de trucha común aguas abajo de algunos embalses. La explicación se encuentra en varios de los impactos ambientales que producen los embalses. En primer lugar, aguas arriba de la presa, la modificación de los regímenes térmicos y de velocidad del agua provocan la desaparición de la trucha. En su lugar, surgen especies termófilas y lénticas habitando ese nuevo ecosistema (en muchas ocasiones exóticas). Sin embargo, aguas abajo, el agua liberada procede del hipolimnion. Se trata de un agua más fría que corre libremente, generando de nuevo un sistema de rápidos más apto para la trucha común. Este fenómeno de "reaparición" ha sido detectado en los ríos Guadalfeo (embalse de Rules), Guadalquivir (embalse del Tranco), Cacín (embalse de los Bermejales) y Genil (embalse de Canales; población reintroducida aguas abajo en el año 2005). A continuación se señalan ciertas particularidades detectadas en tres de ellos, que deben ser consideradas de un modo especial:

a. El dato de altitud más baja detectado en toda la distribución de la especie (200 m.s.n.m.) se corresponde con la captura de unos pocos ejemplares de trucha, pertenecientes a diferentes clases de edad (incluidos juveniles), en el tramo bajo del Guadalfeo (aguas abajo del embalse de Rules). Una población muy reducida, pero con capacidad reproductora, que se mantenía con dificultades tras la construcción y puesta en marcha de dicho embalse. En el momento de la detección (año 2006) se trataba de un reducto poblacional inviable, por la presencia de caudales invertidos y una gestión del agua incompatible con la especie. Sin embargo, la Consejería de Medio Ambiente de la Junta de Andalucía ha llevado a cabo en los últimos años trabajos de reforzamiento poblacional en este tramo. Es probable que la densidad poblacional haya aumentado, pero los resultados de estas sueltas deberán ser valorados a largo plazo, ante el no cese de los impactos que recibe el tramo de acogida.
b. Las obras llevadas a cabo en el río Guadalimar durante el año 2008 para la construcción de un embalse inundaron una antigua estación de muestreo en la que la densidad de trucha común (y trucha arcoíris) ya era escasa. En la actualidad puede que este fenómeno de reaparición haya aumentado la densidad de salmónidos aguas

abajo del embalse. Esta hipótesis deberá ser constatada, ya que supondría la aparición de un nuevo tramo óptimo sobre el que llevar a cabo medidas de gestión para la conservación de la especie.

c. El río Aguas Blancas, afluente del río Genil en su tramo truchero bajo, está seccionado en su mitad por la presa de Quéntar. Aguas arriba han sido detectados escasos adultos de trucha común con elevada introgresión genética (procedentes de introducción) (Almodóvar *et al.* 2010), compartiendo hábitat con un elevado número de ejemplares de trucha arcoíris procedentes de introducciones realizadas para alimentar un coto intensivo de pesca. Sin embargo, aguas abajo de la presa, se detectó un pequeño reducto poblacional que parece haberse mantenido inalterado en un tramo muy corto de dificultoso acceso. La importancia de esta población radica en sus peculiaridades genéticas, ya que no muestra introgresión y ha mantenido los haplotipos autóctonos de la cuenca del Genil (Almodóvar *et al.* 2010).

Los cursos de agua habitados o potencialmente habitables por la trucha común en Andalucía están regulados por figuras administrativas (Figura 6.3, pág 179). El 40% de ellos no poseen impacto pesquero (discurren por el interior del Parque Nacional de Sierra Nevada, o por "Refugios de Pesca"), mientras que en el 60% restante la pesca es permitida en la modalidad de captura y suelta en algún momento del año ("Aguas Libres", "Cotos de pesca", "Cotos intensivos" y "Excepciones") (Ley Andaluza, *Orden 6 de mayo 2014*).

Aunque se trata de una pesca no extractiva, el aumento de los tramos no pescables promovería una mayor protección de los tramos habitados, y en definitiva de las poblaciones, ya que:

- El acceso de los pescadores a los cursos de agua altera la integridad del ecosistema fluvial (compactaciones del terreno, disminución en la densidad y diversidad de macrófitas, etc.)

(O´Toole *et al*., 2009), y de los frezaderos, principalmente en ríos de bajo orden (Arlinghaus *et al*., 2002) como los estudiados. *A priori*, la declaración de periodos de veda reduce el impacto sobre los frezaderos. Sin embargo, en la región de estudio esto no tiene por qué ser así: la existencia de periodos de freza extendida (y anualmente variable) en las poblaciones de estudio (desde octubre hasta mayo, Capítulo II) impide evitar por completo la afección sobre los frezaderos cuando la veda de pesca es abierta (en marzo). La remoción del lecho durante los periodos más críticos para la supervivencia de la especie (periodos sésiles de incubación y primeras semanas tras la emergencia) puede tener consecuencias fatales sobre el éxito reproductivo de las poblaciones. Por tanto, reajustar los periodos de veda en función del periodo de freza tan particular que presentan las poblaciones andaluzas, deberá ser otra de las medidas de gestión a adoptar a corto plazo.

- Aunque la pesca de la trucha común en Andalucía se realiza de modo no extractivo, la modalidad de captura y suelta ha sido cuestionada en numerosas ocasiones por sus teóricos efectos inocuos. Ya no solo por la posible muerte de los ejemplares (Muoneke y Childress, 1994; Arlinghaus *et al*., 2007; Cooke *et al*., 2013), sino también por afectar al comportamiento, crecimiento y reproducción de los peces (Policansky, 2002).

Por todo ello, se propone el incremento de los tramos catalogados como “Refugios de Pesca”, especialmente en las cuencas del Guadalquivir y Cuencas Mediterráneas del Sur. En el caso de la cuenca del Guadalquivir, el 40% de sus tramos son “no pescables” (13% Parque Nacional y 27% “Refugios de Pesca”). En el caso de las Cuencas Mediterráneas del Sur, el 80% de sus tramos habitados son pescables (sólo un 2% son “Refugios de Pesca”). Considerando estos datos, y sabiendo que el 70% de los tramos habitados por la trucha en Andalucía discurren por la cuenca del

Guadalquivir, así como el elevado grado de aislamiento (Figura 7.2) y presencia de haplotipos únicos en las Cuencas Mediterráneas del Sur (Almodóvar *et al*. 2010), se observa la necesidad de aumentar los "Refugios de Pesca" en ambas cuencas. Los efectos de esta medida, a medio plazo, serán muy positivos.

Otra de las propuestas está encaminada a la recuperación de un tramo alto del Guadalquivir no catalogado en la actualidad administrativamente. Concretamente los nueve kilómetros situados entre las desembocaduras de los afluentes Borosa y Aguasmulas. Ambos poseen poblaciones bien conservadas de trucha, sin embargo, el tramo de conexión del Guadalquivir apenas conserva truchas comunes y posee un "Coto Intensivo" (de trucha arcoíris) en su mitad. La recuperación de este tramo supondría la presencia de un corredor natural que favorecería la conexión entre sus afluentes, preservando el carácter metapoblacional del tramo alto del Guadalquivir, y mejorando por tanto la capacidad de resiliencia de sus poblaciones. Para ello es necesario eliminar el coto intensivo, erradicar los ejemplares de trucha arcoíris y declarar este tramo como "Refugio de Pesca".

Como se aprecia, el impacto que ocasiona la trucha arcoíris sobre las poblaciones de trucha común en Andalucía es notable. Su invasión en la región de estudio (Tabla 3.4, página 72) puede entenderse a la luz de los dos mecanismos principales que esta especie exótica ha seguido para su establecimiento en todo el mundo, y en la península ibérica en particular: (a) la introducción deliberada desde el siglo XIX para su pesca deportiva (Elvira y Almodóvar 2001), así como (b) los escapes desde piscifactorías (Doadrio, 2001; Consuegra *et al*., 2011). Concretamente, tras los diferentes estudios realizados en esta Tesis, se puede afirmar que la trucha arcoíris ha seguido tres vías para alcanzar los cursos fluviales andaluces:

1) En un primero momento (años ´70 y ´80) fueron introducidos stocks incontrolados en su fertilidad en algunos ríos habitados por la trucha común.

2) Otra de las vías ha sido la suelta de gran número de ejemplares infertilizados como recurso pesquero en los "Cotos intensivos". Sin embargo, ocho de ellos se acotaron en tramos habitados por la trucha común, o muy cerca de su área de distribución (Figura 6.1, página 176). Estas introducciones, realizadas por la propia Administración hasta 2016, tenían la intención de disminuir el impacto de la pesca sobre la trucha común. Pero en la actualidad sus efectos dificultarán la puesta en marcha de medidas de gestión adaptativa en los tramos afectados.
3) Finalmente los escapes desde piscifactorías son otra de las causas identificadas en la región de estudio. Este fenómeno ha sido detectado dentro de la actual distribución de la trucha (ríos Aguas Blancas, Guardal y Aguasmulas), así como en otras regiones de su distribución histórica (río Majaceite, en Parque Natural de la Sierra de Grazalema).

De este modo, las poblaciones de trucha arcoíris detectadas en esta Tesis (a) cohabitan con poblaciones de trucha autóctona en 69 km de ríos (9,7% de la distribución total de la trucha común), (b) han desplazado y sustituido a esta especie nativa en 76 km de ríos históricamente habitados y (c) han sido introducidas en 32 km de ríos declarados "Cotos Intensivos", pero situados dentro, o muy cerca, del área de distribución actual y potencial de la trucha común (Tabla 6.3., página 179). Es importante anotar, que estos datos hacen referencia exclusiva a los tramos situados en el área de influencia de la trucha común en la región de estudio, y no a todos los cursos fluviales habitados por la trucha arcoíris en Andalucía, los cuales son considerablemente mucho más numerosos a los descritos en este trabajo.

La trucha arcoíris afecta a la selección de hábitat y supervivencia de la trucha común (Blanchet *et al*., 2007; Fausch, 2007) al competir con esta por los mismos territorios y recursos alimenticios, pudiendo llegar a producirse fenómenos de hibridación interespecífica entre ambas especies (Ayllón *et al*., 2004; Castillo *et al*., 2008). Además, cuando la presencia de frezaderos óptimos es escasa, se desarrolla una presión competitiva en la que la superimposición puede llegar a eliminar poblaciones nativas (Landergren, 1999; Scott and Irvine, 2000). En este sentido, en muchos de los tramos invadidos la trucha arcoíris se ha naturalizado: ha sido observada reproducción activa (machos y hembras con producción de gametos) y ejemplares de todas las clases de edad (Tabla 6.1, pág 176). Este fenómeno muy poco frecuente en la península ibérica (Doadrio *et al*., 2011), pero descrito en países del norte de Europa (Landergren, 1999; Kottelat and Freyhof, 2007; Candiotto *et al*., 2011), ha sido detectado en ríos de las tres cuencas de captación habitadas por la trucha común en Andalucía. Debido a la capacidad reproductiva detectada, así como a sus efectos nocivos sobre especies autóctonas, se hace necesario mantener a la trucha arcoíris en el Catálogo Español de Especies Exóticas Invasoras (*Real Decreto 630/2013*), independientemente de las presiones ejercidas hacia el Tribunal Supremo en los últimos años por parte de organizaciones interesadas en su descatalogación. Esta medida prevendrá nuevas introducciones en tramos habitados o potencialmente recuperables para la trucha común, u otras especies nativas.

Además, debería iniciarse un estricto control para evitar el escape de ejemplares desde piscifactorías, prohibir el establecimiento de instalaciones nuevas que se alimenten y drenen hacia cursos fluviales habitados por la trucha común e incluso proponer el traslado de algunas ya existentes en su área de distribución. Por otro lado, deben ejecutarse planes de erradicación de trucha arcoíris acoplados a reintroducciones de trucha común con haplotipos característicos de esos tramos. Ejemplo de ello son los trabajos de erradicación iniciados por la Administración andaluza en 2008 (Tabla 6.1, pág 176) en algunos ríos de la cara norte de Sierra Nevada (Lanteira y Jérez). Los resultados, aún no publicados, han sido muy esperanzadores (observaciones personales).

Por otro lado, se han obtenido resultados interesantes sobre el periodo reproductivo de la trucha común en la región de estudio (Capítulo II). De forma general las poblaciones de trucha en toda su área de distribución muestran periodos activos de freza durante 1 ó 2 meses. Sin embargo la fecha de inicio muestra una tendencia latitudinal (Jonsson y L'Abée-Lund, 1993; Klemetsen *et al*., 2003; Gortázar *et al*., 2007, Gortázar, 2015), ya que temperaturas del agua más bajas requieren periodos de incubación más largos (Crisp, 1988; Elliott y Hurley, 1998). Así, la freza sucede desde octubre hasta diciembre en poblaciones norteñas, y desde enero a marzo en poblaciones meridionales. Por tanto, sería previsible que las poblaciones de trucha andaluzas tuvieran periodos de freza tardíos similares a estos últimos.

Sin embargo, los resultados obtenidos muestran cómo el conjunto de hembras en algunos ríos andaluces posee la capacidad de producir huevos desde principios de octubre hasta finales de abril/principios de mayo, durante un periodo de casi 6 meses, manteniendo la fecha media del periodo reproductivo en concordancia con la tendencia latitudinal descrita previamente. Este fenómeno ha sido comprobado de forma generalizada en distintas poblaciones no conectadas, habitando cuencas de captación diferentes en la región de estudio.

La presencia de un periodo reproductivo anticipado, extendido y retrasado con respecto a lo esperado, podría proporcionar una ventaja a la especie dentro del marco de la impredecibilidad característica del clima mediterráneo, el cual puede causar eventos estocásticos (sequías/inundaciones) que afectan al éxito reproductivo de las poblaciones estudiadas. La posibilidad de puesta en diferentes momentos permite a las poblaciones (1) disponer de la capacidad de frezar tras un episodio de crecida torrencial que haya eliminado las puestas previas, y (2) poseer diferentes grados de desarrollo en la cohorte de alevines llegado el periodo de crecidas primaverales y posterior estiaje estival. Un estiaje cada vez más frecuente y drástico en la península ibérica (Lorenzo-Lacruz *et al*., 2013).

Además, es probable que la temperatura actúe como un factor modulador del inicio de la freza, lo cual podría explicar las diferencias observadas entre poblaciones que habitan bajo regímenes pluviales o nivales en la región de estudio. Así, el tipo de precipitación (agua o nieve), que influye en la temperatura del agua, está asociado a la altitud en la que se hallan las poblaciones (Hansen *et al*., 1997; Körner, 2007; Halbritter *et al*., 2013). De este modo poblaciones que habitan cursos fluviales provenientes de sistemas montañosos elevados se desarrollan en aguas más frías que poblaciones que viven en sistemas montañosos bajos, aunque ambas se encuentren a la misma altitud. Esto podría explicar el comienzo más temprano del periodo reproductivo detectado en Sierra Nevada (ríos que nacen en algunos de los picos más elevados de la península ibérica), en comparación con poblaciones que habitan cursos fluviales en sistemas montañosos más bajos (v.g. Sierra de Tejeda-Almijara-Alhama o Sierra de Cazorla-Segura-Las Villas).

Por otro lado, las poblaciones anádromas de trucha deben sincronizar el periodo reproductivo de sus poblaciones y sus rutas migratorias son energéticamente muy costosas. Sin embargo, el estatus residente de las poblaciones de estudio facilitaría el desarrollo de los periodos de freza extendidos descritos: (a) los ejemplares están presentes durante todo el año en las masas de agua donde frezan y (b) el gasto energético es muy bajo en comparación con el de las formas anádromas (en ocasiones ascienden pocos cientos de metros en busca de las cabeceras).

Por todo ello, los resultados obtenidos sugieren que la variación en la temperatura del agua (resultado de la interacción entre latitud, altitud y régimen hidrológico), la presencia de factores climáticos impredecibles, así como el estatus (residente *versus* anádroma) de una población dada, deberían ser considerados los principales factores reguladores del periodo reproductivo de *Salmo trutta*.

Otro de los aspectos estudiados en esta Tesis han sido los factores que regulan las dinámicas de las poblaciones de trucha en Andalucía. Se sabe (Elliott, 1984a; Elliott, 1984b; Cattanéo *et al*. 2002; Lobón-Cerviá, 2003; Lobón-Cerviá y Rincón, 2004; Lobón-Cerviá y Mortensen, 2005; Zorn y Nuhfer, 2007; Lobón-Cerviá, 2009; Lobón-Cerviá *et al*., 2011) que el reclutamiento es el responsable de las variaciones en la densidad poblacional en esta especie. Por tanto, conocer qué factores dirigen su éxito reproductivo anual es un aspecto clave a la hora de gestionar sus poblaciones.

Así, se ha comprobado cómo el reclutamiento de la trucha en Andalucía es un parámetro poblacional modulado de forma exclusiva, y significativamente, por factores ambientales. Concretamente de forma negativa por las precipitaciones totales de invierno y positivamente por las de primavera.

Debido a que la región de estudio constituye un borde de distribución natural de la especie, las condiciones extremas de nicho ecológico impiden alcanzar la capacidad de carga. De este modo los procesos densodependientes no llegan a desarrollarse, a diferencia de lo que sucede en poblaciones que habitan regiones centrales de su distribución natural, donde las densidades son más elevadas (Mehlman, 1997; Williams *et al*., 2003; Giralt y Valera, 2006; Thingstad *et al*., 2006; Vøllestad y Olsen, 2008). Además, la fuerte desestructuración poblacional que muestran las poblaciones andaluzas (Consejería de Medio Ambiente, 2010) retroalimenta la densoindependencia: la baja densidad de juveniles y escasa presencia de adultos de clases de edad elevada≥ (3+) fomenta la inexistencia de procesos de retroalimentación negativa sobre la cohorte de alevines.

Además, no se han detectado factores externos modulando las clases de edad juvenil ni adulto. Sin embargo, sí se detecta reforzamiento de la cohorte en juveniles y un efecto positivo de la presencia de adultos del año anterior sobre la densidad de adultos en este. Esto último, junto a la no detección de reforzamiento de la cohorte en adultos por parte de los juveniles, podría deberse a la escasez de hábitats potenciales para la segregación de juveniles y adultos en mesohábitats diferentes. El resultado sería el desarrollo de un fenómeno de competencia entre juveniles y adultos, el cual favorecería a los últimos.

La relación negativa de la precipitación de invierno con el reclutamiento detectada en las poblaciones de estudio ha sido observada en otras poblaciones ibéricas (Lobón-Cerviá 2003, 2007; Lobón-Cerviá y Rincón, 2004; Alonso y Gortázar, 2014). Durante esta estación los alevines se encuentran todavía en fase sésil (en el interior del huevo, incubando dentro de los frezaderos), o bien en las primeras semanas tras la eclosión y emergencia de los frezaderos, momento en el que los alevines son muy territoriales y defienden posiciones muy concretas del río. Se trata por tanto de un periodo crítico en el que la remoción del fondo o el desarrollo de procesos de deriva fluvial asociados al incremento de caudales tienen consecuencias nefastas para el éxito reproductivo.

Por otro lado, los hábitats preferenciales para los alevines en la región de estudio (Barquín *et al*. 2010, 2015) están asociados a características fisiográficas relacionadas con las orillas (poca profundidad, presencia de raíces sumergidas, macrófitas acuáticas, etc.). En caso de disminuir el caudal, estos mesohábitats serán los primeros en desaparecer, obligando a todos los ejemplares de trucha a circular por regiones batimétricas más profundas, seleccionadas (y defendidas) preferencialmente por los adultos. Esto genera interacciones alevines-adultos, cuyo resultado puede ser desde el desplazamiento de los primeros hasta el canibalismo por parte de los segundos (Vik *et al*., 2001; Klemetsen *et al*., 2003). Por tanto, durante la estación primaveral (primeros meses de actividad en alevines) el reclutamiento se ve favorecido por la presencia de caudales elevados que mantengan la presencia de orillas sumergidas. Esta puede ser la explicación de la relación positiva detectada entre la precipitación de primavera y la tasa de reclutamiento.

Asimismo, se ha detectado un fenómeno muy significativo de sincronía en el reclutamiento. De este modo, la densidad anual de alevines en poblaciones inconexas dentro de la región de estudio responde del mismo modo a la precipitación de invierno, y con menor intensidad a las temperaturas de primavera y otoño (Cattanéo *et al*. 2003). Además, el efecto sincrónico aumenta con la proximidad geográfica. Este fenómeno juega en contra de las poblaciones de estudio. Si la dinámica poblacional es reflejo del éxito reproductivo y el reclutamiento se encuentra regulado exclusivamente por factores ambientales, que además generan un efecto sincrónico, en caso de desarrollarse un fenómeno estocástico homogéneo en la región de estudio (tan habitual en climas mediterráneos), este podría provocar una reducción poblacional generalizada en todo el área. Si a esto le unimos el carácter metapoblacional de la especie en Andalucía (Figura 7.2), la resiliencia de la trucha en esta región periférica puede verse gravemente afectada, aún más ante un marco de Cambio Climático.

Para conocer en qué sentido han de llevarse a cabo trabajos de gestión adaptativa que eviten o minimicen este problema, se han investigado qué factores concretos del hábitat reducen o promueven la sincronía. De este modo, se ha comprobado que cuanto mayor sean las diferencias entre dos localidades dadas para los valores de altitud, distancia hasta la cabecera e índice IHF, menor será la sincronía. Por tanto, promover la heterogeneidad de estos parámetros permitirá que las respuestas de las poblaciones sean diferentes ante unas condiciones climáticas homogéneas. De este modo se conseguirá aumentar la resiliencia de las poblaciones de trucha en Andalucía.

Ante los resultados expuestos hasta el momento en esta discusión puede comprenderse cómo los cinco factores que componen el Cambio Global [a) cambio climático, b) introducción de especies exóticas, c) cambios en el uso del terreno, d) contaminación y e) sobreexplotación (*sensu* Groom *et al*., 2006)] son fenómenos susceptibles de amenazar la supervivencia de las poblaciones de trucha común en el borde de distribución aquí estudiado. De hecho, todos ellos (excepto la sobreexplotación por estar prohibida la pesca extractiva de la trucha en la actualidad) son factores que limitan hoy en día a las poblaciones de estudio (Tabla 3.3, pag 71) y sus efectos se verán incrementados en el futuro (IPCC, 2013), alterando la distribución de los peces de agua dulce en general (Jonsson y Jonsson, 2009; Comte *et al*., 2013; Ruiz-Navarro *et al*., 2016) y de los sistemas mediterráneos en particular (Ulbrich *et al*., 2006; Giorgi and Lionello, 2008).

El aumento generalizado de temperatura asociado al Cambio Climático supondrá la pérdida de hábitat térmico para la trucha común (Almodóvar *et al*., 2012, Santiago *et al*., 2016), especialmente en poblaciones que habitan bordes traseros de distribución (Santiago *et al*., 2017), como las analizadas en esta Tesis. Además, las poblaciones que viven en sistemas montañosos menos elevados serán las primeras en verse afectadas (Williams *et al*., 2015; Santiago *et al*., 2016). Así, en la región de estudio, las poblaciones de trucha que habitan las sierras de Tejeda-Almijara-Alhama y sierra de Huétor serán las más amenazadas. Asimismo el aumento generalizado de la temperatura podría provocar variaciones directas en la temporalización de los periodos de freza (Makhrov *et al*., 2011) detectados en estas poblaciones (Capítulo II). Ante esta amenaza, se hace necesario llevar a cabo trabajos a escala local que aborden la predicción de los efectos del Cambio Climático en la región de estudio. Trabajos parecidos a los realizados por Almodóvar *et al*. (2012) o Ayllón *et al*. (2016) al norte de España, por Santiago *et al*. (2017) en el centro, o por Clavero *et al*. (2017) para toda la península. El resultado de un trabajo parecido en Andalucía, permitiría (1) identificar el estado de riesgo de las poblaciones de trucha que actualmente habitan en la región de estudio (Capítulo I), (2) detectar futuros refugios térmicos (Santiago *et al*. 2017), y (3) jerarquizar, de modo racional, la inversión económica que suponen las actuaciones de restauración fluvial. De este modo se invertiría de forma lógica en tramos y cursos fluviales que en un futuro podrían mantener poblaciones de trucha común.

Por otro lado, la reducción de las precipitaciones en forma de nieve, así como el aumento altitudinal en su cota (IPPC, 2013), tendrán un efecto directo sobre los cursos fluviales actualmente regidos por una dinámica pluvionival (Sierra Nevada y Sierra de Cazorla-Segura-Las Villas). La disminución del agua procedente de deshielo (a) reducirá los caudales primaverales y (b) producirá el adelanto, dentro del año hidrológico, de los picos de caudal característicos de esta estación (Morán-Tejeda *et al*. 2014). Así, el efecto positivo que ejerce el caudal de primavera sobre el reclutamiento (fenómeno detectado en esta Tesis, ver Tabla 5.5, página 141) se verá disminuido o incluso anulado. El resultado será transmitido, en años posteriores, a las clases de edad superiores mediante un previsible menor reforzamiento de las cohortes (Knapp *et al*., 1998, Alonso *et al*., 2011), alterando finalmente la dinámica y estructura poblacional.

Al mismo tiempo, los inviernos serán más largos, húmedos y tormentosos (IPPC, 2013). Si la predicción es correcta estas tormentas serán recurrentes e intensas, aún más en los sistemas mediterráneos (Ulbrich *et al*., 2006; Giorgi y Lionello, 2008), por lo que el daño sobre las poblaciones de peces será mayor: las especies piscícolas son menos sensibles a las inundaciones cuando éstas suceden dentro, y no fuera, del régimen natural de crecidas. Sin embargo, inundaciones extremadamente elevadas tienen la capacidad de reducir clases de edad completas en la trucha común (Jensen and Johnsen, 1999).

Finalmente, ha de considerarse el elevado grado de aislamiento entre las poblaciones que habitan el área de estudio, así como el hecho constatado que sus límites superiores se deben a causas naturales mientras que los inferiores poseen un origen antropogénico (Capítulo I). En este sentido, los efectos del Cambio Global relacionados con la introducción de especies exóticas, cambios en el uso del terreno y contaminación podrían provocar la constricción de las poblaciones debido a un ascenso altitudinal en sus actuales límites inferiores (Tabla 3.3, página 71). Esto supondría la disminución de la distancia de las poblaciones hasta la cabecera, y por tanto la modificación de la respuesta sincrónica del reclutamiento ante la precipitación de invierno.

Por tanto, el Cambio Climático provocará alteraciones climáticas con la capacidad de modificar los patrones de regulación exógena detectados en esta Tesis para el reclutamiento y su sincronía (Capítulo III). En caso de no ejecutar medidas de gestión adaptativa como las aquí propuestas (Figura 6.4, página 183), que conserven, e incluso mejoren, los actuales límites superiores e inferiores detectados para las 38 poblaciones de trucha común en Andalucía (Figura 7.2), los efectos de los factores externos que sincronizan las poblaciones podrían dar lugar a cuellos de botella y extinciones generalizadas. Esto supondría la pérdida de todas las singularidades locales que muestran las poblaciones de trucha en la región de estudio (haplotipos autóctonos únicos, periodos de freza extendida, tallas de freza pequeñas), lo cual reduciría la capacidad de resiliencia global de la especie ante el Cambio Global.

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8. PROPUESTAS DE LÍNEAS DE INVESTIGACIÓN FUTURAS

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- Modelizar el efecto del Cambio Climático sobre la distribución actual de la trucha (Capítulo I), tal y como otros autores han realizado para otras poblaciones menos periféricas de la península ibérica (Almodóvar *et al*., 2012; Ayllón *et al*., 2016; Clavero et al., 2017; Santiago *et al*., 2017). A partir de esta previsión, se podrá jerarquizar el orden de importancia en la ejecución de medidas de gestión adaptativa en los límites superiores e inferiores descritos en esta Tesis.

- Iniciar trabajos para la detección de tramos fluviales concretos que podrían comportarse como refugios térmicos (Elliott, 2000) ante el Cambio Climático (Brewitt y Danner, 2014; Daigle *et al*., 2014; Santiago *et al*., 2016). En este sentido será necesario determinar la capacidad de albergar poblaciones de trucha de los tramos situados aguas arriba de saltos infranqueables que suponen, en la actualidad, el límite superior de algunas poblaciones.

- Generar un modelo de respuesta del reclutamiento ante la Oscilación Atlántico Norte (NAO). Se sabe que la precipitación en la región de estudio está fuertemente asociada con la NAO, la cual muestra un marcada influencia sobre la variabilidad de caudales de invierno y primavera (López-Moreno *et al*., 2011; Lorenzo-Lacruz *et al*., 2011), siendo precisamente éstos los dos factores exógenos detectados en esta Tesis que regulan en mayor medida el éxito reproductivo de las poblaciones de trucha estudiadas (Capítulo III). Obtener un modelo que relacione reclutamiento con NAO podría tener un poder predictivo de las dinámicas poblacionales de la trucha en la región de estudio.

- Investigar el efecto de la precipitación y temperatura de verano sobre la dinámica poblacional en la región de estudio, ya que los periodos de estiaje estival muestran un aumento en su duración, magnitud y cobertura espacial – desde mediados del último siglo – en la península ibérica (Lorenzo-Lacruz *et al.*, 2013). Para ello será necesario plantear una metodología de muestreo anual, y a largo plazo, durante los primeros días de otoño (finales de septiembre/principios de octubre), de modo que no se interfiera con el comienzo del periodo reproductivo (Capítulo II). Los resultados podrán unirse a los ya obtenidos en esta Tesis sobre la regulación exógena que ejercen la precipitación de invierno y las temperaturas de primavera y otoño sobre la dinámica de las poblaciones andaluzas de trucha común (Capítulo IV).

- Comprobar si el inicio de la freza muestra diferencias intrapoblacionales (a nivel de individuo). La diferencia temporal en la puesta de las hembras podría ser un carácter genético que mantuviera la existencia de frezas extendidas (Capítulo II). Para ello será necesario, entre otras cosas, la determinación de haplotipos genéticos en individuales concretos y llevar a cabo una metodología de muestreos de captura-recaptura (marcaje) a medio plazo.

- Comprobar si (1) la variación en la temperatura del agua (Makhrov *et al.*, 2011), (2) la presencia de factores climáticos impredecibles (Gortázar, 2015), así como (3) el estrategia reproductiva (residente *versus* anádroma) de una población dada, son los principales factores que conjuntamente regulan el periodo reproductivo de *Salmo trutta* en todo su rango de distribución natural.

- Identificar las relaciones específicas de cada uno de los valores determinados por el IHF sobre la sincronía poblacional en el área de estudio (Capítulo III). Ampliar este trabajo a otros parámetros físicos del hábitat no considerados en la presente Tesis.

- Investigar los efectos de la pesca sin muerte en las poblaciones de trucha común andaluzas. Determinar si esta práctica debe ser mantenida o bien endurecer las políticas de gestión actuales (Capítulo IV) y catalogar a la especie como "no pescable" en Andalucía.

- Localizar todos los tramos habitados por la trucha arcoíris en Andalucía, plantear trabajos para su erradicación y posterior introducción de truchas comunes con haplotipos característicos de esas cuencas.

- Caracterizar las poblaciones de invertebrados terrestres susceptibles de formar parte de la alimentación de la trucha en la región de estudio. Los resultados obtenidos complementarían los previamente descritos sobre preferencias tróficas de la especie en Andalucía (Barquín *et al*., 2015).

- Dadas las peculiaridades genéticas, de fenología reproductiva (Capítulo II) y el carácter periférico tan extremo de las poblaciones de trucha en Andalucía (Capítulo I), desarrollar nuevos estudios que abarquen aspectos novedosos de su biología, ecología y fisiología: estado nutricional y oxidativo (Bayir *et al*., 2011; Lushchak, 2011), competencia intraespecífica (Courchamp *et al*., 1999; Rodríguez, 2002; Yakubu y Fogarty, 2006; Lobón-Cerviá, 2012) e interespecífica (Case y Taper, 2000; Hanski, 2008), etc. Los resultados obtenidos serán de gran utilidad para la correcta propuesta de medidas de gestión de sus poblaciones.

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9. CONCLUSIONES

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1) El área de distribución actual de la trucha común en Andalucía se restringe a tan sólo 38 poblaciones acantonadas en algunos cursos de agua de los Sistemas Béticos Orientales, en su mayor parte incluidos en Espacios Naturales Protegidos y sistemas fluviales que nacen en ellos. Además, muestran un elevado grado de aislamiento poblacional, en algunos casos con estructuras metapoblacionales. Estos hechos, junto con el desplazamiento detectado de sus límites inferiores aguas arriba, confirma el estatus de amenaza que posee la especie en la región.

2) Los límites superiores de distribución de estas poblaciones son de origen natural, mientras que los inferiores se deben a causas antropogénicas. Particularmente grave es la situación de las poblaciones fragmentadas por embalses. Los reductos que habitan aguas abajo de ellos muestran un elevado grado de amenaza, confirmándose la extinción de dos poblaciones (Segura bajo y Zumeta bajo) durante los trabajos de campo, así como el estado crítico de otras (Cacín bajo, Guadalfeo bajo, etc.).

3) La presencia de poblaciones de trucha arcoíris en 20 tramos habitados, o históricamente habitados, por la trucha común supone un importante riesgo para la supervivencia de la especie autóctona en el área de estudio. La detección de capacidad reproductiva en nueve de esas poblaciones de trucha arcoíris aumenta aún más este riesgo y respalda la inclusión de esta especie exótica en la Lista de Especies Invasoras de España.

4) El periodo reproductivo de las poblaciones más meridionales de trucha en Europa es consistente en su fecha media con la tendencia latitudinal de la especie en el continente, pero tiene una duración de

150 a 170 días, lo que lo convierte en el periodo de freza más extendido descrito para la especie en toda su área de distribución. La capacidad de desove desde primeros de octubre hasta finales de abril o principios de mayo es una adaptación de la especie en la región de estudio. Este hecho está relacionado con la inexistencia de anadromía, la impredecibilidad climática característica de los sistemas mediterráneos y el rango de temperaturas que muestran los cursos fluviales habitados.

5) El reclutamiento de las poblacionales de trucha en la región de estudio es un parámetro densoindependiente, regulado de forma negativa por la precipitación total de invierno y positivamente por la precipitación total de primavera. Las dinámicas poblacionales de juveniles y adultos no muestran regulación exógena.

6) El reclutamiento está sincronizado mediante un Efecto Moran. Esta sincronía aumenta con la proximidad geográfica y está regulada principalmente por la precipitación de invierno y, en menor medida, por las temperaturas de primavera y otoño. Cuanto mayor sean las diferencias altitudinales, de IHF y distancia a la cabecera entre estaciones, menor será la sincronía de sus poblaciones y, por tanto, mayor la resiliencia de la especie en su conjunto ante fenómenos ambientales homogéneos.

7) Dada la situación actual de las poblaciones de trucha en Andalucía, se hace necesaria la aplicación de medidas de gestión adaptativa para asegurar su conservación futura. Así, intervenciones directas sobre el hábitat, modificaciones específicas de las actuales leyes que regulan la pesca de la especie en la región, restauraciones por fases en los tramos habitados por la trucha arcoíris y la reintroducción de ejemplares con

haplotipos endémicos característicos de cada subcuenca permitirán conservar gran parte de las poblaciones actuales.

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