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ESTRATEGIAS VITALES DE LA TRUCHA COMÚN *SALMO TRUTTA* EN EL LÍMITE MERIDIONAL DE SU DISTRIBUCIÓN (LIFE HISTORIES OF BROWN TROUT *SALMO TRUTTA* AT THE SOUTHERN EDGE OF ITS DISTRIBUTION)

MEMORIA PARA OPTAR AL GRADO DE DOCTOR
PRESENTADA POR

Irene Parra Montañés

Bajo la dirección de la doctora

Ana Almodóvar Pérez

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Estrategias vitales de la Trucha Común *Salmo trutta* en el límite meridional de su distribución

(Life histories of brown trout *Salmo trutta* at the southern edge of its distribution)

Memoria presentada para optar al grado de Doctor por

Irene Parra Montañés

Bajo la dirección de la Doctora Ana Almodóvar Pérez

y el Doctor Benigno Elvira Payán

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ANA ALMODÓVAR PÉREZ Y BENIGNO ELVIRA PAYÁN, PROFESORES DEL DEPARTAMENTO DE ZOOLOGÍA Y ANTROPOLOGÍA FÍSICA DE LA UNIVERSIDAD COMPLUTENSE DE MADRID,

CERTIFICAN:

Que la presente memoria titulada "**ESTRATEGIAS VITALES DE LA TRUCHA COMÚN *SALMO TRUTTA* EN EL LÍMITE MERIDIONAL DE SU DISTRIBUCIÓN**" que para optar al grado de Doctor presenta **Irene Parra Montañés**, ha sido realizada en el Departamento de Zoología y Antropología Física de la Facultad de Ciencias Biológicas de la Universidad Complutense de Madrid bajo nuestra dirección. Y considerando que representa trabajo de Tesis, autorizamos su presentación a la Junta de Facultad.

Y para que así conste, firmamos el presente certificado,

Madrid, abril de 2012

Fdo. Ana Almodóvar Pérez

Fdo. Benigno Elvira Payán

Fdo.: Irene Parra Montañés

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Que por mayo era, por mayo, cuando hace la calor,
cuando los trigos encañan y están los campos en flor,
cuando canta la calandria y responde el ruiseñor,
cuando los enamorados van a servir al amor.
Sino yo, triste, cuitado, que vivo en esta prisión;
que ni sé cuándo es de día ni cuándo las noches son,
sino por una avecilla que me cantaba al albor.
Matómela un ballestero; déle Dios mal galardón.

Romance del Prisionero (Anónimo).

Índice (Contents)

1. Resumen

Las estrategias vitales son conjuntos de rasgos que determinan el ciclo vital de los organismos, de tal manera que se produce una coevolución de aspectos como la fecundidad, la tasa de crecimiento, la longevidad y la edad y el tamaño en la madurez. La Trucha Común *Salmo trutta* es una especie cuya distribución autóctona incluye la práctica totalidad del continente Europeo y el norte de África. A lo largo de su distribución, se ha descrito una enorme variabilidad en numerosos rasgos biológicos, entre los que destaca el crecimiento dada su íntima asociación con otros rasgos de las estrategias vitales. La amplia diversidad de estrategias vitales de la Trucha Común se debe en gran medida a variaciones espaciales y temporales de los factores que caracterizan el hábitat en el que se encuentra. La temperatura del agua es un factor de gran relevancia y se conocen gran cantidad de sus efectos tanto directos como indirectos en distintos aspectos de la biología y ecología de la Trucha Común. Sin embargo, dentro de los límites térmicos que permiten la presencia de la especie, existen otros factores que determinan su uso del hábitat. El hábitat físico influye en gran medida en el uso que hace de él la Trucha Común y sus características influyen también en el tamaño del territorio y en el nivel de competencia entre individuos, lo que determina en última instancia la densidad máxima que puede alcanzar una población así como el crecimiento que tienen sus individuos. De esta forma, el tamaño de las poblaciones y de los individuos que las componen, varían entre distintos ríos y temporalmente dentro de un mismo río como respuesta ante una gran variedad de factores.

En esta memoria se han estudiado patrones a gran escala, altitudinal y latitudinal, tanto en el crecimiento como en otros rasgos de las estrategias vitales asociados con el crecimiento de poblaciones sedentarias de Trucha Común a lo largo de su rango de distribución. Asimismo, a una escala local se ha analizado el efecto de la densidad sobre el tamaño corporal, considerando los distintos requerimientos de hábitat a lo largo de la ontogenia. Por una parte, se ha estudiado el efecto de la denso-dependencia en el tamaño de los individuos en distintas etapas de la vida de una cohorte. Por otra parte, se han analizado los efectos potenciales de la densidad de las cohortes acompañantes en el crecimiento, y se ha tratado además de esclarecer la

importancia relativa de la temperatura del agua y la densidad sobre el crecimiento. Por último, se ha estudiado cómo varía la abundancia de las distintas clases de edad con respecto a su capacidad de carga. Esto se ha llevado a cabo teniendo en cuenta los distintos requerimientos de hábitat a lo largo de la ontogenia y considerando los efectos potenciales de las condiciones experimentadas durante una etapa en las sucesivas fases del ciclo vital, así como las interacciones con las cohortes que conviven en una población.

Se observó un papel fundamental de la temperatura del agua en la variación espacial del crecimiento, efecto que a pequeña escala se pudo explicar por gradientes altitudinales mientras que a una escala más amplia la variación térmica siguió un gradiente latitudinal. La variación latitudinal del crecimiento, a su vez, tuvo implicaciones en la adopción de distintas estrategias vitales. Así, se detectó una mayor longevidad y mayor edad de madurez en los individuos de poblaciones septentrionales. Sin embargo, el efecto de la latitud sobre la longitud de madurez difirió entre sexos. Por otra parte, se observó que dentro de los límites térmicos para la supervivencia de la especie, la denso-dependencia es un proceso clave en la dinámica de las poblaciones. Sus efectos sobre el crecimiento variaron temporalmente, siguiendo las variaciones del nivel de competencia a lo largo de la ontogenia. Además, las interacciones entre cohortes afectaron al tamaño de los individuos, detectándose efectos de la denso-dependencia en todas las clases de edad. La temperatura del agua y la denso-dependencia afectaron conjuntamente al tamaño corporal, siendo el efecto de la temperatura más marcado en el primer año de vida, mientras que la influencia de la denso-dependencia fue aumentando en los años sucesivos. Por último, la densidad de las distintas clases de edad dependió de la evolución de la capacidad de carga, así como de la competencia entre alevines y juveniles, mientras que no se detectaron efectos de otras cohortes sobre la densidad de individuos adultos. De esta memoria se concluye que la dinámica de las poblaciones de Trucha Común es una compleja red que incluye numerosos efectos. Dentro de los límites establecidos por las condiciones ambientales, las interacciones bióticas llevaron a una gran variedad en el tamaño corporal y en la densidad entre los

distintos ríos estudiados, mientras que las variaciones en tamaño corporal estuvieron íntimamente relacionadas con el hecho de que las distintas poblaciones adopten diversas estrategias vitales.

2. Abstract

Life histories are groups of traits that determine the life cycle of organisms, in a way that there is a coevolution of aspects such as fecundity, growth rate, longevity, and age and size at maturity. Brown trout *Salmo trutta* is a species whose autochthonous distribution includes nearly the whole European continent and Northern Africa. Along its wide distribution, a great variability in numerous traits has been described, growth being remarkable among others because it is tightly linked to other life-history traits. The wide diversity of life histories found in brown trout is mostly due to the spatiotemporal variation of factors which characterise the habitat a population occupies. Water temperature is a factor of huge relevance, and many direct and indirect effects o water temperature have been described on different levels of the biology and ecology of brown trout. Within the thermal limits for the presence of the species, other factors determine brown trout habitat use. Physical habitat influences brown trout habitat use, and its characteristics also influence territory size and competition level, which ultimately determines the maximum density a population can attain, as well as the growth performed by its individuals. Therefore, population size and body size vary within and between rivers as a consequence of the variation of numerous factors.

In this dissertation, global scale patterns considering altitude and latitude have been studied in resident populations of brown trout, to explore their effects on growth as well as on other life-history traits. Moreover, at a smaller scale, the effect of density-dependence on body size at different stages of a cohort life span has been analysed, in addition to the relative importance of water temperature and density on growth. Finally, temporal changes on the abundance of age classes with respect to their carrying capacity have been studied, taking into account the changes in habitat requirements along the ontogeny, as well as potential effects of previously experienced conditions and of interactions with coexisting cohorts in the population.

Water temperature had a pervasive role on spatial variation of growth, this effect being included in altitudinal gradients at a small scale, whereas at a wider scale the thermal variability was incorporated in a latitudinal gradient. Latitudinal variation in growth implied the development of different life histories. In fact, individuals from northern populations in Europe had higher longevity and older age at maturity. The effect of latitude on length at maturity, however, was different between sexes. Furthermore, within the thermal limits for the presence of the species, density dependence was shown as a key process in population dynamics. Its effects on growth changed temporally, shaped by the variations of the level of competition along the ontogeny of a cohort. Besides, intercohort interactions influenced body size of individuals, affecting the final outcome of the effect of density dependence on growth. Water temperature and density dependence concurrently influenced body size, the effect of water temperature being higher on the first year of life of brown trout whereas the influence of density dependence increased as cohorts aged. Finally, density of the age classes tracked the changes in carrying capacity, and also depended on the level of competition between alevins and juveniles, whereas no intercohort effects were detected on the density of adult individuals. In this dissertation it is concluded that population dynamics of brown trout is a complex web which includes numerous effects. Within the limits set by the environmental variables, biotic interactions induced a great variety in body size and density among the studied rivers, while variations in body size were closely linked to the adoption of different life histories.

3. Introducción General y Objetivos

3. 1. Introducción general

3. 1. 1. Estrategias vitales

Las estrategias vitales son conjuntos de rasgos que determinan el ciclo vital de los organismos, de tal manera que se produce una coevolución de aspectos como la fecundidad, la tasa de crecimiento, la longevidad y la edad y el tamaño en la madurez (Stearns 1992). La teoría evolutiva propone que la combinación de rasgos observada en un organismo es el resultado de la selección natural y maximiza el éxito reproductivo en su ambiente (Roff 1984, Stearns 1992).

Los peces son organismos ectotermos, a diferencia de otros grupos de vertebrados como las aves o los mamíferos, y presentan una gran variabilidad de estrategias vitales como consecuencia de la amplísima diversidad de condiciones ambientales que habitan a lo largo de su distribución (Wootton 1998). El hecho de que los recursos sean limitados supone la existencia de un compromiso entre los distintos rasgos de las estrategias vitales, como por ejemplo entre reproducción y supervivencia, o número y calidad de los descendientes. Por su relevancia para el desarrollo de patrones de estrategias vitales, cabe destacar el compromiso existente entre crecimiento y reproducción (Stearns 1992). Por una parte, los peces se caracterizan por tener crecimiento continuo aunque se ralentiza con la edad, por lo que no tienen un tamaño fijo para los adultos (Wootton 1998). Por otra parte, mediante la reproducción los individuos transmiten su material genético a la siguiente generación, por lo que ha de tener lugar en el momento que maximice la supervivencia de la descendencia, además de que requiere recursos para el desarrollo de caracteres sexuales primarios y secundarios (Jonsson & Jonsson 2011). Así, la óptima distribución de los recursos, que primeramente han de cubrir el metabolismo (Ware 1980), entre los caracteres reproductivos y en procesos relacionados con el crecimiento, es fundamental para maximizar el éxito reproductivo (Jonsson *et al.* 1984, Roff 1984, Jonsson 1985). Por ello se encuentra una íntima relación entre la edad y el tamaño en el inicio de la madurez, la fecundidad, la longevidad y el crecimiento.

Los salmónidos son una familia en la que se ha centrado un gran esfuerzo científico a la hora de estudiar las grandes diferencias intraespecíficas e interespecíficas en sus patrones de estrategias vitales, así como los factores que causan dichas diferencias (Klemetsen *et al.* 2003). En concreto la Trucha Común *Salmo trutta*, especie en la que se centra esta memoria, tiene una amplia distribución a lo largo de la cual las poblaciones se ven influidas por una gran variedad espacial y temporal de factores abióticos y bióticos (Jonsson 1977, L'Abée-Lund *et al.* 1989, Elliott 1994, Jonsson & Jonsson 2011). Estos factores, a través de respuestas de plasticidad fenotípica de los distintos rasgos, o bien a través de adaptaciones debidas a la selección natural, determinan la gran diversidad de estrategias vitales descrita para la especie.

3. 1. 2. Variación de estrategias vitales en la Trucha Común

La Trucha Común (Figura 1) es un recurso económico muy importante ya que tiene un gran interés como objeto de pesca en muchos países. De hecho, en España es la especie más importante en pesca deportiva (Almodóvar & Nicola 1998), por lo que el conocimiento exhaustivo de su ecología resulta fundamental a la hora de llevar a cabo una gestión sostenible de las poblaciones.

La distribución geográfica autóctona de la Trucha Común comprende prácticamente la totalidad del continente europeo, desde Islandia y Rusia como límites norte, hasta la costa del Mediterráneo al norte del continente africano y las islas de Córcega, Cerdeña y Sicilia como límite sur. El límite este se localiza aproximadamente en los montes Urales y el mar Caspio (Elliott 1994). Además, debido a las numerosas introducciones en América, África, Asia y Australia, en la actualidad se distribuye por todo el mundo, aunque en esta memoria se considera únicamente su distribución original.

Figura 1. Trucha Común de Navarra.

A lo largo de su distribución, se ha descrito una enorme variabilidad en numerosos rasgos biológicos, entre los que destacan las variaciones en el ciclo vital. Esta especie se reproduce en lechos de grava en las zonas altas de los ríos, pero durante el resto del ciclo puede habitar otras zonas de los ríos, lagos o realizar migraciones al mar en el caso de individuos anádromos (Klemetsen *et al.* 2003, Jonsson & Jonsson 2011). El crecimiento presenta una gran variabilidad interpoblacional, con diferencias en longitud de un orden de magnitud para la misma edad, como el caso de individuos que en su primer año de vida miden 25 mm en Islandia (Steingrímsson & Gíslason 2002) mientras que en poblaciones asturianas llegan a los 107 mm (Braña *et al.* 1992). También se han descrito grandes diferencias de peso de hasta dos órdenes de magnitud, comparando por ejemplo individuos de cuatro años que pesan 20 g en ríos pequeños o hasta de 1 kg en poblaciones anádromas (Jonsson 1985, L'Abée-Lund *et al.* 1989). En parte debido a estas diferencias en el patrón de crecimiento, se han descrito también amplias variaciones en la edad de madurez, que por ejemplo en poblaciones sedentarias abarca desde un año hasta diez años (Klemetsen *et al.* 2003). De manera general, parece que los machos maduran antes y con tamaños más variables que las hembras (Jonsson 1989). La longevidad de los individuos es otro rasgo de gran variabilidad, y aunque se ha llegado a encontrar un individuo de 38 años de edad (Svalastog 1991), por lo general mueren antes de los 10 años (Jonsson *et al.* 1991).

El crecimiento y el tamaño que alcanzan los individuos son atributos de vital importancia dada su íntima asociación con otros rasgos de las estrategias vitales relacionados con la supervivencia, la fecundidad y la longevidad (Jonsson *et al.* 2001, Jonsson & Jonsson 2011). El tamaño de un pez considerado de manera aislada no resulta suficientemente informativo dado que es necesario conocer además la edad de ese individuo, que se puede determinar mediante el análisis de otolitos y de escamas. Ambos tipos de estructuras crecen por deposición de sustancias en círculos concéntricos, que se sitúan más cercanos en invierno, cuando el crecimiento es lento, y más separados en verano (Wootton 1998, Jonsson & Jonsson 2011). Por su influencia sobre otros rasgos de las estrategias vitales, las características de una localidad en cuanto a la potencialidad de crecimiento que ofrece, determinan en gran medida el ciclo vital y la estrategia reproductiva que se observa en los individuos de dicha localidad (Stearns & Koella 1986, Hutchings 1993, Jonsson & Jonsson 2011). Se suele considerar como norma general que individuos que experimentan un crecimiento rápido son capaces de madurar a una edad más temprana e incluso con un tamaño menor (Alm 1959). En cualquier caso, con el aumento de la edad el crecimiento va disminuyendo (Roff 1983). El sexo puede ser otra fuente de variación en las estrategias vitales, ya que diferencias en la inversión energética que realizan ambos sexos en la reproducción (Jonsson & Jonsson 1997) hacen que rasgos como la edad o el tamaño en la madurez puedan diferir entre machos y hembras. En el **capítulo II** de esta memoria se estudian patrones de estrategias vitales, así como posibles diferencias entre las estrategias adoptadas por machos y hembras de Trucha Común.

3. 1. 3. Factores y sus efectos sobre las estrategias vitales de la Trucha Común

El uso del hábitat es fundamental para la ecología de la Trucha Común ya que es el aspecto en el que confluyen la explotación de los recursos y la competencia por ellos, entendiendo como recursos el alimento y el espacio, lo que afecta en última instancia a la supervivencia y la reproducción de los individuos (Jonsson & Jonsson 2011). Así, el uso de distintos hábitats se traduce en variaciones en la tasa de crecimiento y mortalidad de los individuos, con la consiguiente influencia sobre otros rasgos de las estrategias vitales (ver Figura 1). El nicho fundamental (Hutchinson 1957) es un volumen de n dimensiones, factores tanto abióticos como bióticos, que define los rangos de esas dimensiones para los que una especie puede mantener una población viable. Se puede distinguir entre variables que suponen recursos por los cuales los individuos compiten activamente, como el alimento o el espacio, y variables que especifican los límites de tolerancia ante características como la temperatura o el oxígeno disuelto. La amplia variación de estrategias vitales de la Trucha Común se debe en gran medida a variaciones espaciales y temporales de los factores que caracterizan el hábitat en el que se encuentra una población. Haldane (1956) propuso que en poblaciones que habitan áreas con condiciones hostiles tendrán una mayor influencia los factores abióticos, independientes de la densidad, mientras que en poblaciones que habitan zonas con condiciones más favorables, los cambios serán debidos principalmente a factores denso-dependientes. En este sentido, cabe esperar que los efectos de la temperatura del agua, cuya variación responde en gran medida a un gradiente geoclimático, se detecten principalmente en análisis que planteen una amplia área de estudio y, por tanto, abarquen mayor variación potencial de condiciones. Por el contrario, los factores relacionados con la densidad pueden variar a escalas espaciales más pequeñas.

En el caso de los peces, al tratarse de organismos ectotermos, la temperatura del agua es un factor de gran relevancia (Wootton 1998). En concreto con respecto a la Trucha Común, se dispone de vasta literatura que ilustra la gran cantidad de efectos, tanto directos como indirectos, de la temperatura en distintos aspectos de la biología y la ecología de esta especie (por ejemplo, Elliott 1994, Jonsson & Jonsson 2011). La temperatura influye directamente en las reacciones metabólicas (Elliott 1994, Wootton 1998), tiene efectos sobre la locomoción, la tasa de alimentación (Ojanguren *et al.* 2001) y la asimilación del alimento a través de su efecto en el metabolismo (Forseth & Jonsson 1994). Puede tener también un efecto indirecto a través de alteraciones de la productividad de los organismos que utiliza como alimento (Egglishaw & Shackley 1977). Además, desde las primeras etapas del desarrollo, la temperatura puede afectar al número de vértebras que se forman (Tåning 1952) y a la miogénesis (Johnston 2006). Existen límites térmicos para su mera supervivencia, así como para la actividad de la Trucha Común, por lo que la temperatura determina en parte la presencia de la especie en un lugar determinado (Almodóvar *et al.* 2012). Por ejemplo, los embriones tienen una supervivencia máxima entre 8 y 10ºC, y la temperatura crítica se sitúa en 14ºC (Ojanguren *et al.* 2001). En fases más tardías los individuos son menos susceptibles a la temperatura (Elliott 1994) de tal forma que para los alevines el límite superior es de 22ºC y para juveniles 25ºC (Elliott & Elliott 2010). Por lo general, la baja tolerancia de los salmónidos a las altas temperaturas está determinada por sus requerimientos en cuanto a oxígeno disuelto, ya que para mayor temperatura disminuye la cantidad de oxígeno en el agua.

La temperatura del agua tiene un efecto fundamental sobre el crecimiento desde las primeras etapas del ciclo, ya que influye sobre la tasa metabólica de los embriones (Egglishaw & Shackley 1977, Baglinière & Maisse 1990), por lo que determina el momento de eclosión y de emergencia de los alevines (Crisp 1988, Blaxter 1992). Los embriones que se desarrollan a temperaturas más altas ven acelerado su metabolismo, por lo que eclosionan antes y con un tamaño mayor, aunque también han de hacer frente a una conversión de los recursos del huevo menos eficaz (Kamler 1992). Además, una emergencia temprana supone una ventaja competitiva frente a otros alevines (Einum 2003), aunque el excesivo adelantamiento de este momento podría llevar a que los alevines no coincidieran en el tiempo con los recursos alimenticios de los que dependen. La temperatura del agua afecta al crecimiento a través de su influencia sobre la tasa de consumo de alimento (Alm 1959, Ojanguren *et al.* 2001) y la eficacia en la conversión energética de dicho alimento (Forseth & Jonsson 1994, Wootton 1998). El consumo de alimento aumenta con la temperatura hasta un punto en que alcanza su máximo, a un valor de temperatura superior a aquel para el que se encuentra el óptimo de la eficacia en la conversión de alimento. Además, la temperatura óptima para el crecimiento disminuye con la edad (Morita *et al.* 2010), lo que junto con los cambios en la capacidad natatoria y en el tipo de presas que se consumen, provoca cambios ontogenéticos de hábitat. El efecto de la temperatura del agua sobre el crecimiento de la Trucha Común, así como los cambios de este efecto a lo largo de la ontogenia se consideran con detalle en los **capítulos I y IV** de esta memoria.

La temperatura varía a lo largo de gradientes altitudinales y latitudinales. En el caso de organismos endotermos, esto se refleja en un mayor tamaño corporal de los individuos que habitan zonas donde la temperatura es menor a elevadas latitudes, lo que se conoce como la regla de Bergmann. Tradicionalmente, la explicación esgrimida ha sido que un tamaño corporal mayor tiene una menor proporción de superficie frente al volumen, lo que permite una reducción de la pérdida de calor, por lo que previsiblemente se verá favorecido en zonas de baja temperatura. En el caso de organismos ectotermos, como los peces, esta explicación no puede ser aplicada y sin embargo se han llevado a cabo numerosos estudios para comprobar en qué sentido varía el tamaño corporal de organismos ectotermos en un gradiente latitudinal. Los resultados han sido muy variados (por ejemplo, Ray 1960, Belk & Houston 2002), y las explicaciones que se han acuñado para ellos también (Atkinson 1994, Atkinson & Sibly 1997, Blanckenhorn & Demont 2004). Mientras se encuentra una explicación global para estos cambios, las variaciones latitudinales en el tamaño corporal existen y pueden ser debidas a numerosos factores, relacionados o no con la temperatura, que varían con la latitud. En esta memoria se estudia por una parte cómo varía el tamaño corporal en un gradiente latitudinal (considerando además gradientes altitudinales) que cubre prácticamente la distribución autóctona de la especie (**capítulo I**), mientras que en el **capítulo II** se analizan los efectos que ese cambio en el tamaño puede implicar para otros rasgos de las estrategias vitales que están íntimamente unidos con el tamaño corporal.

Tal y como se ha expuesto hasta ahora, el efecto de la temperatura del agua es global, actuando directa o indirectamente a distintos niveles de la ecología de la Trucha Común. Sin embargo, dentro de los límites térmicos que permiten la presencia de la especie, existen otros factores que determinan el uso del hábitat de la especie y que pueden variar temporalmente y a una escala espacial menor, contribuyendo a que se genere una dinámica poblacional y a que ésta sea distinta entre diferentes poblaciones incluso geográficamente cercanas.

Por una parte, el hábitat físico influye en gran medida en el uso que la Trucha Común hace del hábitat, siendo la profundidad, la velocidad del agua, el tipo de sustrato y la disponibilidad de refugio características que marcan dicho uso. Dado que las distintas clases de edad que conviven en una población tienen distintos requerimientos energéticos y preferencias, los individuos cambian de nicho durante la ontogenia. Tras la emergencia, los alevines seleccionan zonas de pequeña profundidad y velocidad, mientras que con la edad van cambiando a zonas de mayor velocidad y profundidad (Ayllón et al. 2009). Además, los individuos seleccionan zonas con sustrato formado por bloques, piedras o grava, que crean intersticios donde los individuos pueden refugiarse de posibles depredadores así como de la corriente, por lo que el gasto energético mientras esperan las partículas de alimento es menor. Por otra parte, dado que la Trucha Común es una especie territorial, el nivel de competencia afectará al crecimiento de los individuos y a su vez estará determinado por la calidad de los territorios que habitan (Newman 1993, Ward *et al.* 2007). Por ello, las características del hábitat físico pueden favorecer la operación de la denso-dependencia sobre el crecimiento. Sin embargo, en muchos estudios hasta la fecha el efecto de la abundancia poblacional sobre el crecimiento se ha analizado utilizando medidas como la densidad o la biomasa totales (Jensen *et al.* 2000, Grant & Imre 2005). La cantidad y la calidad del hábitat disponible, considerando las preferencias de cada clase de edad, determinarán en gran medida el nivel de competencia. Para describir de manera más precisa el nivel de competencia, en esta memoria se emplean medidas de la densidad que la corrigen considerando el hábitat potencial útil para las distintas etapas de una cohorte.

Aunque el tamaño del territorio está principalmente marcado por el tamaño del pez, las características del hábitat físico influyen también en el tamaño del territorio y en el nivel de competencia entre individuos, lo que determina en última instancia la densidad máxima de individuos que puede alcanzar una población. La densidad de las poblaciones cambia a lo largo del tiempo, aunque la magnitud de las fluctuaciones es distinta según la población y la especie de que se trate. El efecto de la densidad de la población sobre el crecimiento parece bastante extendido en distintos grupos animales y, especialmente, en aquellos de crecimiento indeterminado (por ejemplo, Byström & García-Berthou 1999, Ferguson *et al.* 2000, Girish & Saidapur 2003, Etnier 2004, Kawata *et al.* 2005, Wilkin *et al.* 2006). La densidad de una población actúa como factor en su regulación a través de variaciones en la mortalidad y la dispersión de los individuos (Crisp 1993, Keeley 2001). Además, a través de su influencia en el crecimiento de los individuos, la densidad provoca cambios en el tamaño de los individuos (Jenkins *et al.* 1999), la edad de madurez (Hutchings & Jones 1998), la fecundidad y el reclutamiento (Cowan *et al.* 2000). Aunque la denso-dependencia del crecimiento ha generado algo de controversia, principalmente debido a ciertas dificultades en su detección, en la actualidad está ampliamente reconocido que el crecimiento varía en respuesta a las variaciones de la densidad (Crisp, 1993, Jenkins *et al.* 1999, Sundström *et al.* 2004, Grant & Imre 2005, Lobón-Cerviá 2005). Sin embargo, todavía persiste el debate sobre el mecanismo que subyace al efecto de la densidad sobre el crecimiento, ya sea competencia por interferencia, debida a un aumento en el gasto energético en la defensa del territorio a causa de un mayor número de encuentros con otros individuos, o competencia por explotación, debida a que un mayor número de individuos disminuya la disponibilidad de recursos (Ward *et al.* 2007). Si bien el mecanismo puede no ser fácil de determinar, las consecuencias que la competencia entre individuos puede conllevar en cuanto a crecimiento y otras estrategias vitales resultan de gran interés a la hora de establecer medidas de gestión y conservación.

A fin de lograr un conocimiento en detalle del efecto que la densidad ejerce sobre distintos rasgos de la biología de la Trucha Común, existen ciertos aspectos que requieren profundización. Por una parte, tradicionalmente se ha estudiado la denso-dependencia del crecimiento durante el primer año de vida (por ejemplo, Crisp 1993; Keeley 2001, Grant & Imre 2005, Imre *et al.* 2005), pero los cambios ontogenéticos en los requerimientos y el comportamiento de los individuos hacen necesario insistir en el estudio de la competencia a lo largo de las distintas etapas de una misma cohorte. Además, dado que en un mismo río conviven distintas cohortes, es preciso profundizar en el papel que la competencia intercohorte puede tener en el crecimiento y por tanto en la dinámica poblacional. Por otra parte, a pesar de la vasta literatura que recoge los amplios efectos de la temperatura del agua y de la densidad sobre distintos aspectos de la ecología de la Trucha Común, en la actualidad persiste una dificultad a la hora de detectar ambos efectos simultáneamente (por ejemplo, Egglishaw & Shackley 1977, Eliott 1994, Lobón-Cerviá 2005) a fin de establecer la importancia relativa de estos dos factores. Por todo ello, existe una necesidad de estudios que incluyan una amplia escala tanto temporal como espacial y que traten de arrojar luz sobre estos aspectos.

Así, en esta memoria se analiza el efecto de la densidad (expresada como tasa de ocupación del hábitat potencial útil o como densidad en el hábitat útil) sobre el tamaño corporal en distintas etapas de la vida de una cohorte, considerando además la posibilidad de efectos diferidos de las condiciones experimentadas en años anteriores (**capítulo III**). Además, en el **capítulo IV** se han considerado conjuntamente la temperatura del agua y la densidad de la población (teniendo en cuenta los efectos intracohorte así como de las cohortes acompañantes), con el fin de esclarecer la importancia relativa de ambos factores sobre las variaciones espaciales del tamaño corporal.

3. 1. 4. Dinámica poblacional de la Trucha Común

El tamaño de las poblaciones de Trucha Común varía entre distintos ríos y temporalmente dentro de un mismo río. La dinámica de las poblaciones de peces constituye una respuesta compleja ante una gran variedad de factores extrínsecos como son la disponibilidad de alimento, la temperatura y la concentración de oxígeno del agua (Jonsson & Josson 2011). Los factores pueden actuar directamente sobre la población, afectando al crecimiento, a la supervivencia, a la migración y a la fecundidad de los individuos, pero también pueden alterar la disponibilidad de recursos y, por tanto, la capacidad de carga. La capacidad de carga representa el máximo crecimiento que puede alcanzar una población como respuesta ante interrelaciones entre unos recursos limitados y sus consumidores (del Monte-Luna *et al.* 2004). Dado que tanto los recursos como los individuos y sus requerimientos no son estáticos, la capacidad de carga de una población cambia temporalmente, fluctuando alrededor de un valor medio que representa las condiciones ambientales promedio (Jonsson & Jonsson 2011).

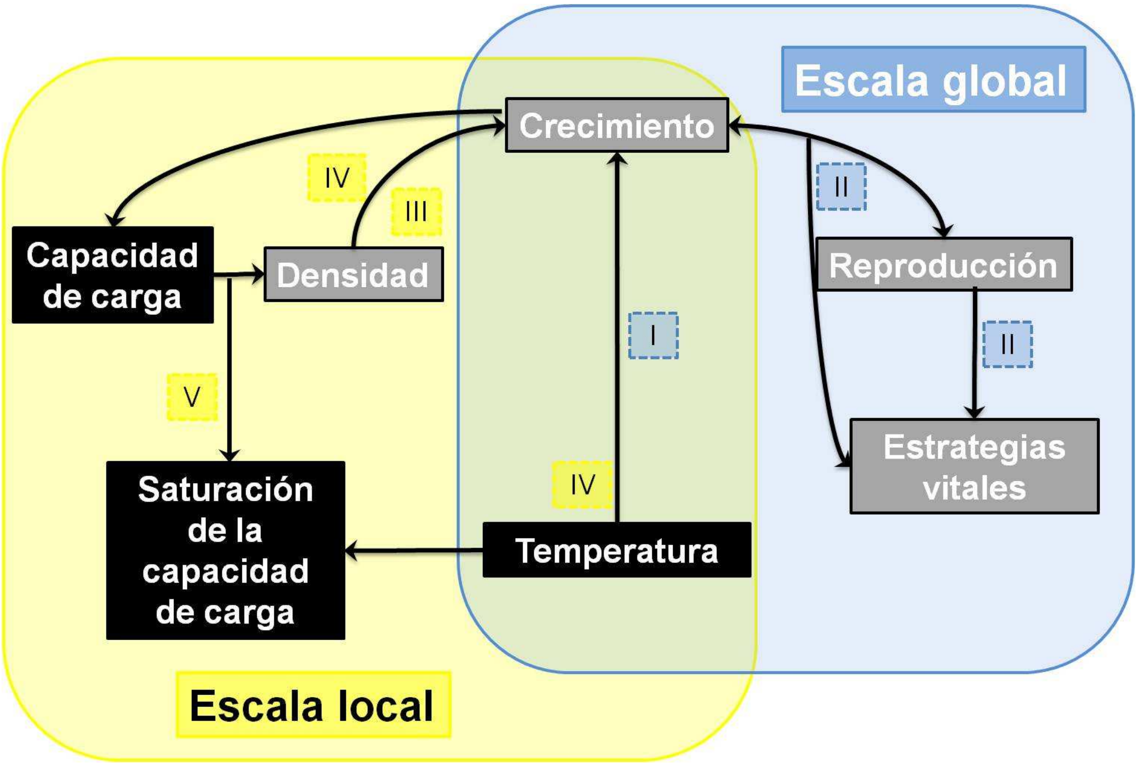
Las causas y consecuencias que rodean a la dinámica poblacional se estudian en parte dentro del marco teórico de la denso-dependencia, que ya se ha tratado previamente a lo largo de esta introducción general. En términos generales, en una población que experimenta denso-dependencia, elevadas densidades hacen que disminuyan aspectos como la supervivencia, la fecundidad y/o el crecimiento de los individuos. Por contra, a bajas densidades estos mismos aspectos aumentan, permitiendo por ejemplo la recuperación de poblaciones después de eventos catastróficos (Jenkins *et al.* 1999). Sin embargo, al considerar altas o bajas densidades no se puede hablar en términos absolutos, sino que el valor ha de relativizarse con respecto a la capacidad de carga de la población.

Aunque existen numerosos factores que potencialmente pueden alterar el crecimiento poblacional o la capacidad de carga, destacan por su importancia el hábitat físico, la disponibilidad de alimento, el clima y las interacciones interespecíficas. En esta memoria se trata la importancia de las variaciones del hábitat físico, por sus implicaciones en la competencia entre individuos. Como se ha comentado anteriormente, la Trucha Común es una especie territorial, de tal forma que los individuos defienden territorios no sólo en el momento de reproducirse, sino también para alimentarse. Por lo general, los salmónidos ocupan posiciones cerca del sustrato desde las que pueden colocarse de cara a la corriente para capturar los invertebrados que van a la deriva (Fausch 1984, Johnson *et al.* 2006). Así, seleccionan un punto o foco con no demasiada velocidad de corriente, pero a la vez situado cerca de zonas de mayor velocidad, para maximizar el acceso a la deriva minimizando el gasto energético de mantenimiento de la posición (Fausch 1984). De esta forma, los individuos pueden competir indirectamente por el alimento (competencia por explotación) o directamente a través de agresiones y defensa de su territorio (competencia por interferencia). En la actualidad no hay consenso acerca del mecanismo que actúa (Ward *et al.* 2007), pero sí acerca de que las consecuencias tienen marcada influencia sobre la dinámica de las poblaciones.

En el momento de la emergencia se suele dar un elevado nivel de mortalidad, por las dificultades para alimentarse y porque emergen en zonas donde se concentraron los nidos en el momento de la reproducción, por lo que las densidades son en general muy elevadas. Desde ese momento, los alevines han de ser capaces de empezar a comer y de encontrar un territorio donde establecerse, lo que en muchos casos implica una dispersión aguas abajo en busca de otras zonas con menor densidad de individuos. La emergencia y el primer año de vida de los individuos, han recibido un gran esfuerzo científico y existe un consenso en cuanto a la importancia de esta fase para la regulación de las poblaciones (ver Elliott 1994). Una vez establecidos en los territorios de alimentación, los alevines van aumentando de tamaño y edad, y ello hace que los recursos que necesitan, en cuanto a espacio y alimento, varíen. Esto conlleva cambios de nicho a lo largo de la ontogenia con importantes implicaciones a la hora de considerar la capacidad de carga, ya que si las distintas clases de edad dependen de recursos diferentes, la capacidad de carga de un río irá cambiando durante la ontogenia. Por ello, es necesario considerar una capacidad de carga asociada a cada clase de edad, que tenga en cuenta los requerimientos de cada etapa. Por otra parte, además de la competencia entre individuos de una misma cohorte, cabe plantearse la posibilidad de que se produzcan interacciones entre individuos de cohortes que conviven en una población. Así, se puede tender a pensar que individuos más viejos y más grandes tendrán una ventaja a la hora de competir por recursos con individuos más jóvenes y más pequeños. Sin embargo, hay una gran carencia de estudios que examinen las consecuencias de la competencia intercohortes en Trucha Común y que permita comprobar esta afirmación.

El conocimiento exhaustivo de la dinámica poblacional y los mecanismos que subyacen puede aportar mucha información de gran utilidad para la conservación y la gestión de poblaciones. En el **capítulo V** de esta memoria se estudia cómo varía la abundancia de las distintas clases de edad con respecto a su capacidad de carga, teniendo en cuenta los distintos requerimientos a lo largo de la ontogenia y considerando además potenciales efectos de las condiciones experimentadas durante una etapa en futuras etapas de una cohorte. Asimismo, se estudian interacciones entre las cohortes que conviven en una población, ya que pueden tener importantes efectos en la dinámica poblacional.

Figura 2. Esquema de las relaciones estudiadas en esta memoria. Los números indican el capítulo en que se aborda cada relación.



3. 2. Objetivos

El objetivo global de esta Tesis es estudiar las estrategias vitales de poblaciones situadas en el límite sur de la distribución de la Trucha Común, a través del análisis de la influencia que la temperatura del agua y la denso-dependencia ejercen sobre las estrategias vitales en general, y especialmente sobre el crecimiento, así como sobre la dinámica poblacional. Asimismo, se pretende encuadrar las poblaciones estudiadas en el contexto de la especie, para lo que se llevarán a cabo análisis a gran escala que permitan la comparación de estrategias vitales a lo largo de la amplia distribución de la Trucha Común (ver Figura 2).

Para lograr este objetivo se plantean los siguientes objetivos parciales:

1. Estudiar la variación espacial del crecimiento y el tamaño corporal en las cuencas de la vertiente cantábrica de Navarra, así como los efectos que sobre el tamaño ejercen la temperatura del agua y la altitud a pequeña escala.
2. Describir la variación del tamaño corporal a lo largo de un gradiente latitudinal que incluya datos de la distribución europea de la especie, a fin de detallar la variación a gran escala del crecimiento y determinar si las poblaciones sedentarias de Trucha Común se ajustan a la regla de Bergmann.
3. Analizar las diferencias espaciales de las estrategias vitales a gran escala, así como poder determinar si las relaciones existentes entre los distintos rasgos que componen esas estrategias varían de manera diferencial a lo largo de gradientes altitudinales y latitudinales, así como entre machos y hembras.
4. Examinar la variación temporal en la influencia de la denso-dependencia sobre el tamaño corporal a lo largo de la ontogenia, a fin de determinar el periodo en el que el efecto de la competencia intraespecífica es mayor.
5. Explorar potenciales efectos denso-dependientes de las cohortes acompañantes sobre el tamaño corporal, para determinar el papel que la competencia intercohorte puede tener en el crecimiento de los individuos y por tanto en la dinámica poblacional.
6. Esclarecer la influencia relativa de la temperatura del agua y la denso-dependencia en el tamaño corporal, considerando las etapas que se dan a lo largo de la vida de una cohorte y sus distintos requerimientos de hábitat.
7. Determinar si la capacidad de carga resulta un parámetro competente para predecir las fluctuaciones que se observan en las distintas clases de edad que componen una población, siendo por tanto una herramienta útil para el estudio de la dinámica poblacional.

4. General Introduction and Aims

4. 1. General Introduction

4. 1. 1. Life histories

Life histories are groups of traits that determine the life cycle of organisms, in a way that there is a coevolution of aspects such as fecundity, growth rate, longevity, and age and size at maturity (Stearns 1992). Life history theory proposes that the combination of traits observed in an organism is the result of natural selection and maximizes its reproductive success in the environment it inhabits (Roff 1984, Stearns 1992).

Unlike other vertebrate groups like birds or mammals, fishes are ectotherms. They show a great variety of life history patterns as a consequence of the wide diversity of environmental conditions they inhabit along their broad distribution (Wootton 1998). Since available resources are limited, there are linkages or trade-offs between life-history traits, such as reproduction and survival, or number and quality of offspring. Given its consequences for the development of life-history patterns, it is of special relevance the trade-off between growth and reproduction (Stearns 1992). In one hand, fishes have indeterminate growth although it slows down with age, so they do not have a characteristic adult size (Wootton 1998). On the other hand, reproduction is the process by which genetic material is transferred to the next generation, so individuals have to mature at the time that maximizes survival of offspring. Besides, it requires resources for the development of primary and secondary sexual characters and other activities that take place during reproduction (Jonsson & Jonsson 2011). Hence, the optimal allocation of resources, which first have to meet the costs of standard and active metabolism (Ware 1980), between reproduction and growth, is essential to maximize reproductive success (Jonsson *et al.* 1984, Roff 1984, Jonsson 1985). Therefore, there is a tight relationship among age and size at the onset of maturity, fecundity, longevity and growth.

Salmonids are a well-studied family with a great research effort focused on intraspecific and interspecific differences in life-history patterns, as well as on the factors underlying these differences (Klemetsen *et al.* 2003). Specifically, this dissertation is focused on brown trout *Salmo trutta*, a wide distributed species with populations inhabiting under a great spatiotemporal variety of abiotic and biotic factors (Jonsson 1977, L'Abée-Lund *et al.* 1989, Elliott 1994, Jonsson & Jonsson 2011). These factors determine the large diversity of life history strategies that has been described for the species, inducing phenotypic plasticity responses or through genetic adaptations of different traits.

4. 1. 2. Life history variation in brown trout

Brown trout (Figure 1) is a very important economic resource since it is of great interest for fishermen in many countries. Actually, it is the most important angling species in Spain (Almodóvar & Nicola 1998) and so a deep understanding of its ecology is essential to achieve a sustainable management of its populations.

Figure 1. Brown trout from Navarra, Northern Spain.

The autochthonous geographic distribution of brown trout essentially covers Europe. Its northern limits are Iceland and Russia, and the islands of Corsica, Sardinia and Sicily, and the northern Mediterranean coast of Africa, are the southern limit. Eastern limits are near the Ural mountains and the Caspian Sea. Besides, due to a large number of introductions in America, Africa, Asia, and Australia, brown trout is now a global species, although in this dissertation only its original distribution is considered.

All over its original area, a great variety in most traits has been described, being of special relevance those related to the life cycle. Brown trout spawn on stone and gravel bottoms, upstream in running waters, but during the life span they may move to other areas in the rivers or lakes, or migrate to the ocean in the case of anadromous populations (Klemetsen *et al.* 2003, Jonsson & Jonsson 2011). Growth varies greatly among populations, with differences in length-at-age that include trout from Iceland attaining 25 mm on their first year (Steingrímsson & Gíslason 2002) in contrast to individuals on their first year attaining 107 mm in populations from Northern Spain (Braña *et al.* 1992). Wide differences in weight have also been described, comparing four year old individuals from small rivers of only 20 g, or almost 1 kg in anadromous populations (Jonsson 1985, L'Abée-Lund *et al.* 1989). Partly because of these differences in growth pattern, variations have also been described for age at maturity, which in resident populations ranges from one to 10 years (Klemetsen *et al.* 2003). As a general rule, males seem to mature earlier and with higher variability in their size with respect to females (Jonsson 1989). Longevity is also variable, and despite a 38-year-old individual has been found (Svalastog 1991), brown tout normally live less than 10 years (Jonsson *et al.* 1991).

Growth and body size are traits of critical importance due to their tight association with other life-history traits related to survival, fecundity and longevity (Jonsson *et al.* 2001, Jonsson & Jonsson 2011). Fish body size is meaningless if it is not associated with the age of the individual, which can be determined by means of the analysis of otholits and scales. Both types of structures grow by accretion at their margins, forming concentric rings which are closer in winter and farther apart in summer, depending on the growth velocity (Wootton 1998, Jonsson & Jonsson 2011). Because of its influence on other life-history traits, the characteristics of a site that set its growing potentiality eventually determine the life cycle and reproductive strategy adopted by the individuals from this site (Stearns & Koella 1986, Hutchings 1993, Jonsson & Jonsson 2011). It is usually considered that individuals experiencing a rapid growth are able to mature earlier and even at a smaller size (Alm 1959). Anyhow, growth slows down with age (Roff 1983). Sex may be another source of variation in life-history strategies, as differences on the energetic investment between sexes (Jonsson & Jonsson 1997) might make age or size at maturity vary between males and females. In **chapter II** from this dissertation, life history strategies are studied, examining trade-offs between some of the studied traits and also potential divergences between the strategies adopted by male and female brown trout.

4. 1. 3. Factors and their effects on life histories of brown trout

Habitat use is an essential aspect of the ecology of brown trout. It is a central feature where resources exploitation and competition for them converge, resources meaning food and space, so it ultimately affects survival and reproduction (Jonsson & Jonsson 2011). Thus, the exploitation of different habitats results in variations in growth rate and mortality of individuals, and consequently in other life-history traits. The fundamental niche is a hypervolume with n dimensions (Hutchinson 1957) which are biotic or abiotic factors, and it defines the ranges of these factors within which a species will maintain a stable population. There are variables that are actual resources individuals have to compete for, like food and space, and variables that set tolerance limits to abiotic characteristics like temperature or oxygen content. The great variety found in life-history traits of brown trout is mostly due to spatiotemporal variations of the factors that characterise the habitat a population occupies. Haldane (1956) proposed that populations from hostile environments would have a greater influence from abiotic density-independent factors, whereas in populations inhabiting more favorable areas changes would be mostly due to density-dependent factors. In this sense, it could be expected that the effects of water temperature, which varies through a geoclimatic gradient, would be mostly detected in analyses covering a wide study area that potentially includes a larger variation in environmental conditions. On the contrary, density-dependent factors are known to vary at a smaller scale.

Water temperature is a pervasive factor for fishes since they are ectotherms (Wootton 1998). Specifically on brown trout there is a vast literature on the great variety of direct and indirect influences that water temperature exerts on several aspects of the biology and the ecology of the species (e.g. Elliott 1994, Jonsson & Jonsson 2011). It has a direct effect on metabolic rate (Elliott 1994, Wootton 1998), it affects locomotion, feeding rate (Ojanguren *et al.* 2001) and food assimilation through its metabolic effect (Forseth & Jonsson 1994). It may also have an indirect influence through alterations of the productivity of the organisms which trout feed on (Egglishaw & Shackley 1977). Furthermore, since the first developmental stages, water temperature affects the number of vertebrae (Tåning 1952) and myogenesis (Johnston 2006). There are thermal limits for brown trout survival and also for its activity, so water temperature somehow determines the presence of the species in a given place (Almodóvar *et al.* 2012). For instance, embryos have a maximum survival between 8 and 10ºC, and their critical temperature is at 14ºC (Ojanguren *et al.* 2001). In later stages, individuals are less vulnerable to temperature (Elliott 1994) so the upper limit for alevins is 22ºC and 25ºC for juveniles (Elliott & Elliott 2010). As a general rule, the low thermal tolerance of salmonids is determined by their oxygen requirements, since the amount of dissolved oxygen decreases with water temperature. Besides, water temperature accelerates the life cycle of fish so maturity is delayed at low temperatures (Alm 1959) partly because of the thermal effect on growth but also because lipid accumulation slows down.

Water temperature has a pervasive effect on growth since the first stages of life cycle, affecting embryo’s metabolic rate (Egglishaw & Shackley 1977, Baglinière & Maisse 1990), so it determines the date of hatching and emergence of fry (Crisp 1988, Blaxter 1992). Embryos developing at higher temperatures have a faster metabolism so they hatch earlier and larger, but they also have to face a less efficient conversion of egg resources (Kamler 1992). Besides, an early emergence is a competitive advantage compared to other individuals (Einum 2003) although they cannot emerge excessively early because it could happen that food resources they use were not available yet. Water temperature also affects growth through its influence on the feeding rate (Alm 1959, Ojanguren *et al.* 2001) and on the efficiency of food energetic conversion (Forseth & Jonsson 1994, Wootton 1998). Food consumption increases with temperature up to a level where it maximises, a value higher than the temperature for optimum efficiency in food conversion. In addition, optimum temperature for growth decreases with age (Morita *et al.* 2010) and this considered together with changes in swimming performance and on the type of prey they ingest, leads to ontogenetic habitat shifts. The effect of water temperature on growth of brown trout, as well as the changes of this effect along ontogeny are explored in detail in **chapters I and IV** of this dissertation.

Temperature varies across altitudinal and latitudinal gradients. In endothermic organisms this induces a larger body size in individuals inhabiting areas with lower temperature in higher latitudes, which is known as the Bergmann’s rule. Traditionally, this has been supported by the fact that a larger body size has a lower surface-volume relationship and this allows a lower heat loss, so it would probably be favoured in low temperature areas. Considering ectothermic organisms, like fishes, this explanation has no place, but still there have been numerous studies to explore how the body size of ectotherms changes in a latitudinal gradient. Results have been varied (e.g. Ray 1960, Belk & Houston 2002) and the proposed explanations too (Atkinson 1994, Atkinson & Sibly 1997, Blanckenhorn & Demont 2004). While a global explanation is found, latitudinal changes in body size exist and may be due to numerous factors, temperature related or not, which vary with latitude. In **chapter I** of this dissertation, variations in body size are studied in a latitudinal gradient that covers most of the entire European distribution of the species (also considering altitudinal gradients), whereas in **chapter IV** the effects that this change in body size may imply on other life-history traits intimately linked to growth are studied.

Just as exposed so far, water temperature has a global effect, acting directly or indirectly on diverse levels of brown trout ecology. Within the thermal limits that allow the presence of the species, however, other factors determine brown trout habitat use. They may vary temporally and at a smaller spatial scale, thus contributing to different population dynamics even between close populations.

In one hand, physical habitat greatly influences habitat use by brown trout, which is especially determined by depth, water velocity, bottom substratum, and shelter availability. Given that the age classes coexisting in a population have different energetic requirements and preferences, there are habitat shifts along ontogeny. After emergence alevins select areas with low depth and water velocity, while as they age they move to areas with higher depth and velocity (Ayllón *et al.* 2009). Besides, a bottom substratum with stones, boulders and gravel is selected because these elements create interstices where individuals can hide from potential predators and also from water velocity, thus lowering the energetic cost while waiting drift particles. On the other hand, brown trout is a territorial species, therefore competition level would affect growth of individuals and would be determined by the quality of the territories they inhabit (Newman 1993, Ward *et al.* 2007). Hence, physical habitat characteristics may favour the operation of density dependence on growth. To date, however, many studies have evaluated the effect of population abundance on growth through total density or total biomass measures (Jensen *et al.* 2000, Grant & Imre 2005). Quantity and quality of available habitat, taking into account the specific preferences of each age class, would greatly determine the level of competition. In this dissertation, measures of density that only include the suitable area for each life stage in a cohort have been used to accurately describe the level of competition.

Although territory size is mostly set by body size of the fish, physical habitat characteristics also influence territory size and the level of competition among individuals, which finally determines the maximum density of individuals a population can attain. Population density changes across time, although the magnitude of those changes is different depending on the population and on the species. A density effect on growth has been detected in different animal groups and especially in animals with indeterminate growth (e.g. Byström & García-Berthou 1999, Ferguson *et al.* 2000, Girish & Saidapur 2003, Etnier 2004, Kawata *et al.* 2005, Wilkin *et al.* 2006). Density acts as a regulatory factor through effects on mortality and migration of individuals (Crisp 1993, Keeley 2001). Moreover, through its influence on individuals' growth, density induces variations in body size (Jenkins *et al.* 1999), age at maturity (Hutchings & Jones 1998), fecundity, and recruitment (Cowan *et al.* 2000). Even though density-dependent growth has been controversial, mostly because of certain detection difficulties, it is widely accepted nowadays that growth varies as a consequence of density variations (Crisp, 1993, Jenkins *et al.* 1999, Sundström *et al.* 2004, Grant & Imre 2005, Lobón-Cerviá 2005). Still persistent is the debate about the mechanism underlying the effect of density on growth, either interference competition due to an increase in the energetic costs of territory defense caused by the higher number of competitive contests, or exploitation competition because of lowered resource availability (Ward *et al.* 2007). Even if the mechanism is not easy to be identified, the consequences that competition may entail in terms of growth and other life histories are of great interest for the design of conservation and management measures.

In order to achieve a profound knowledge on the effect that density exerts on different features of brown trout biology, there are certain aspects that require better understanding. In one hand, density-dependent growth has been traditionally studied on the first year of life (e.g. Crisp 1993; Keeley 2001, Grant & Imre 2005, Imre *et al.* 2005), but ontogenetic changes on habitat requirements and individual behaviour make it necessary to study competition further along the subsequent life stages in a cohort. Furthermore, since several cohorts coexist in a river, a deeper understanding on the role that intercohort competition may have in growth, and thus in population dynamics, is required. On the other hand, despite the vast literature describing the effects of water temperature and density on numerous aspects of brown trout ecology, a simultaneous detection of both effects is still lacking (e.g. Egglishaw & Shackley 1977, Eliott 1994, Lobón-Cerviá 2005) and it would be essential to establish the relative importance of these factors. As a result, there is a need of studies including a wide spatiotemporal scale and meant to enlighten these topics.

Along this dissertation, the effect of density (expressed as habitat occupancy rate or density in suitable habitat) on body size on subsequent life stages in a cohort has been studied, considering also potential delayed effects from the competition conditions experienced on previous years (**chapter III**). Moreover, in **chapter IV** water temperature and density (intracohort and intercohort) effects are studied, in order to enlighten the relative influence of both factors in body size.

4. 1. 4. Population dynamics of brown trout

Population size of brown trout varies among rivers and also temporally within a river. Fish population dynamics represents a complex response to a variety of extrinsic factors such as food availability, water temperature, and oxygen concentration (Jonsson & Jonsson 2011). Factors can act directly on the population, affecting growth, survival, migration and fecundity, but they can also alter resources availability and thus carrying capacity. Carrying capacity is the population growth limit which is shaped by processes and interdependent relationships between finite resources and their consumers (del Monte-Luna *et al.* 2004). Since resources availability, and the abundance and requirements of individuals are not static, carrying capacity of a population fluctuates around an inter-annual mean carrying capacity that reflects the average environmental conditions over the long term (Jonsson & Jonsson 2011).

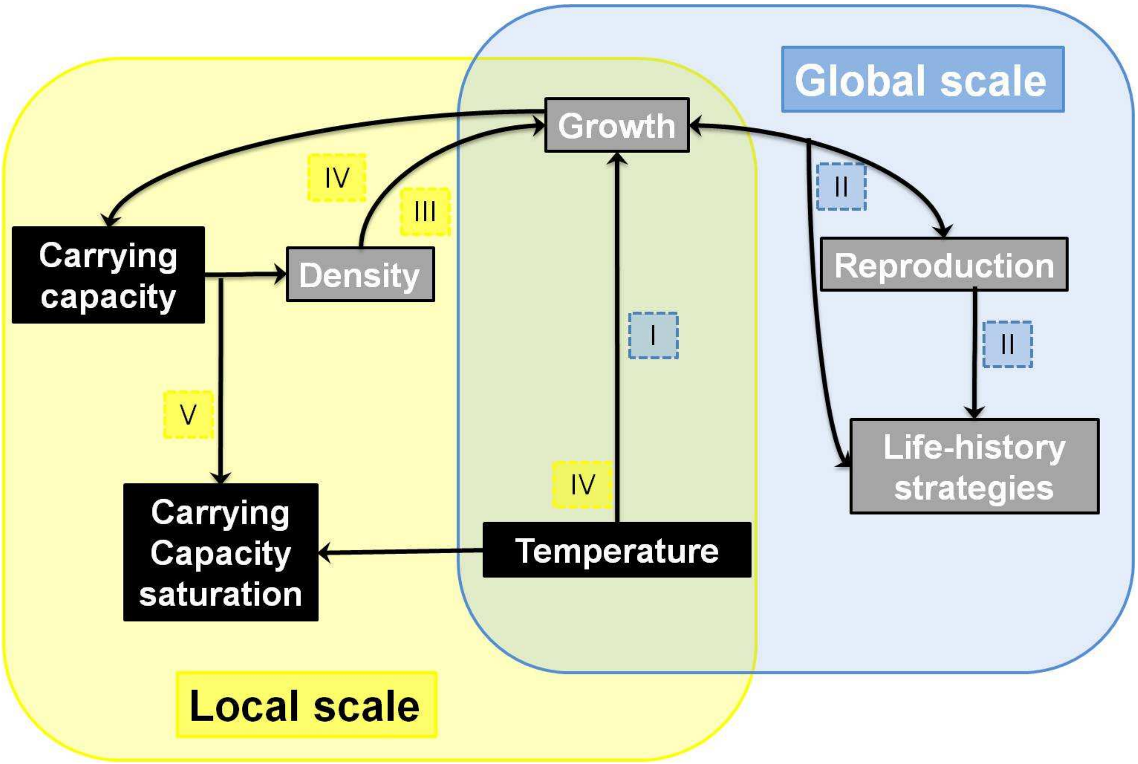
Grounds and consequences surrounding population dynamics are partly studied on the theoretical framework of density dependence, already discussed along this general introduction. In general terms, in a population experiencing density dependence high densities induce a decrease in survival, fecundity and /or growth of individuals. On the contrary, low densities favour an increase in these traits, thus allowing a population to recover from a catastrophic event, for instance (Jenkins *et al.* 1999). When high or low densities are considered, however, they have to be related to the carrying capacity of the population.

Although many factors may potentially alter population growth or its carrying capacity, physical habitat, food availability, climate, and interespecific interactions are among the most important. In this dissertation, the relevance of physical habitat variations on intraspecific competition is discussed. Just as previously mentioned, brown trout is a territorial species, so individuals defend territories for feeding and not only for reproduction. Salmonids tend to hold positions near the bottom from which they can face the current and capture drifting invertebrates (Fausch 1984, Johnson 2006). They select a focal point with low water velocity but with access to nearby areas with higher velocity, thus maximising the access to drift while minimising the energy expended on swimming (Fausch 1984). Hence, individuals may indirectly compete for food (exploitation competition) or directly through contests and territory defense (interference competition). Even though there is still no consensus on the mechanism acting (Ward *et al.* 2007), there is a general agreement about the consequences competition has on population dynamics.

Emergence constitutes a delicate moment where a high level of mortality is reached because of difficulties in feeding and because the areas around redds are overcrowded. Since this moment, alevins have to be able to start feeding and find a suitable territory to set in, which in many cases implies a downstream dispersion to look for less crowded areas. Emergence and the first year of life have been the focus of research as a critical phase for population regulation (see Elliott 1994). Once alevins are established in their territories, they increase their size and age and their requirements of space and food change. This induces habitat shifts along ontogeny, with pervasive implications to calculate carrying capacity since it depends on the individuals' requirements and thus would also change along ontogeny. Carrying capacity has to be considered with respect to an age class and its requirements. Moreover, further than intracohort competition there is a chance that intercohort competition takes place. It could be considered that older, larger individuals would have an advantage when competing with younger, smaller individuals, but a lack of studies examining the consequences of intercohort competition in brown trout prevents from verifying this statement.

A profound knowledge of population dynamics and the underlying mechanisms may provide with useful information for population conservation and management. In **chapter V** from this dissertation, it is examined how the abundance of age classes fluctuates with respect to their carrying capacity, taking into account the changing requirements along ontogeny as well as potential effects of previously experienced conditions on future stages in a cohort. Moreover, intercohort interactions are explored since they may affect population dynamics.

Figure 2. Diagram of the relationships studied in this dissertation. Numbers indicate the chapter where each relationship is discussed.



4. 2. Aims

The overall aim of this Thesis is to study life histories of brown trout populations from the southern limit of its distribution, through the analyses of the effects of water temperature and density dependence on life histories, and especially on growth, as well as further effects on population dynamics. Moreover, it is aimed to study the populations in the context of the whole species and, therefore, large scale approaches would be developed to compare life histories along the wide distribution of brown trout (see Figure 2).

To achieve this goal the following partial objectives are addressed:

1. To study the spatial variation of growth and body size in populations from the Bay of Biscay in Northern Spain, as well as the effects that water temperature and altitude exert on body size at a small scale.
2. To describe the variation of brown trout body size along a latitudinal gradient including data from the European distribution of the species, in order to study growth differences at a large scale and determine whether resident brown trout populations follow Bergmann’s rule.
3. To analyse spatial differences in life-history strategies at a wide scale and to determine whether the interrelationships among life-history traits vary differentially along altitudinal and latitudinal gradients, as well as for males and females.
4. To elucidate the temporal variation in the influence of density dependence on body size along ontogeny, in order to determine the period when the effect of intraspecific competition is highest.
5. To examine potential intercohort effects on the influence of density dependence on body size, to determine the role that intercohort competition may have on growth of individuals, and hence on population dynamics.
6. To unravel the relative influence of water temperature and density dependence on body size, considering the different life stages through a cohort and their different habitat requirements.
7. To determine whether carrying capacity is capable of accounting for the fluctuations in different life stages, and therefore be a useful tool for the study of population dynamics.

5. Capítulos (Chapters)

I. Variación altitudinal y latitudinal del crecimiento

Este capítulo reproduce íntegramente el manuscrito:

I. Parra, A. Almodóvar, G.G. Nicola & B. Elvira. 2009. Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales. *Journal of Fish Biology* 74: 2355-2373.

Se ha explorado la variación espacial del crecimiento en Trucha Común *Salmo trutta* en trece poblaciones y con datos de un estudio a largo plazo (1993-2004) realizado en las cuencas de la vertiente cantábrica de Navarra. La variabilidad encontrada en la longitud furcal (L_F) de *S. trutta* en el área de estudio abarca prácticamente el rango encontrado para la especie en su distribución europea. Así, L_F por clases de edad osciló entre 57,4-100,7 mm para el primer año de vida (0+), 111,6−176,0 mm para el segundo año de vida (1+), 155,6−248,4 mm para el tercer año de vida (2+) y 194,3−290·9 mm para el cuarto año de vida (3+). La longitud furcal media fue mayor en los cauces principales y en las zonas aguas abajo comparada con pequeños afluentes y zonas aguas arriba. Las tasas de crecimiento anual fueron homogéneas espacialmente. Modelos de regresión determinaron que la temperatura del agua y la altitud fueron los principales determinantes de la variación en L_F por clases de edad en el área estudiada. Así, un análisis espacial con una escala más amplia, en el que se utilizaron datos disponibles de poblaciones sedentarias de *S. trutta* a lo largo de Europa, indicó una relación negativa entre la latitud y la L_F, así como una interacción negativa entre la latitud y la altitud. Estos resultados apoyan los obtenidos en estudios previos en cuanto al papel dominante de la temperatura del agua en la determinación de la L_F de esta especie. La altitud actuó como un factor que engloba la variación local de otras variables como la temperatura del agua o la disponibilidad de alimento, mientras que a mayor escala es la latitud el factor que abarcó dichos gradientes ambientales y por tanto explicó las diferencias encontradas en L_F de *S. trutta*. Finalmente, L_F por clases de edad de poblaciones sedentarias de *S. trutta* decrece con la latitud en Europa, siguiendo por tanto la inversa de la regla de Bergmann.

It always seems impossible until it is done.

Nelson Mandela

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Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales

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Spatial variation in growth of stream-dwelling brown trout *Salmo trutta* was explored in 13 populations using a long-term study (1993–2004) in the Bay of Biscay drainage, northern Spain. The high variability in fork length (L_F) of *S. trutta* in the study area was similar to the body-size range found in the entire European distribution of the species. Mean L_F at age varied: 0+ years, 57·4–100·7 mm; 1+ years, 111·6–176·0 mm; 2+ years, 155·6–248·4 mm and 3+ years, 194·3–290·9 mm. Average L_F at age was higher in main courses and lower reaches compared with small tributaries and upper reaches. Annual specific growth rates (G_L) were: 0+ to 1+ years, 0·634–0·825 mm mm^{-1} year^{-1}; 1+ to 2+ years, 0·243–0·342 mm mm^{-1} year^{-1}; 2+ to 3+ years, 0·166–0·222 mm mm^{-1} year^{-1}, showing a great homogeneity. Regression models showed that water temperature and altitude were the major determinants of L_F at age variability within the study area. A broader spatial analysis using available data from stream-dwelling *S. trutta* populations throughout Europe indicated a negative relationship between latitude and L_F of individuals and a negative interaction between latitude and altitude. These findings support previous evidence of the pervasive role of water temperature on the L_F of this species. Altitude appeared as the overall factor that includes the local variation of other variables, such as water temperature or food availability. At a larger scale, latitude was the factor that encompassed these environmental gradients and explained the differences in L_F of *S. trutta*. In summary, L_F at age in stream-dwelling *S. trutta* decreases with latitude in Europe, the converse of Bergmann's rule.

Key words: Europe; growth variation; latitude; altitude; temperature.

INTRODUCTION

Growth is a major life-history trait strongly linked to other features dependent on size, such as survival, longevity and reproduction (Wootton, 1998; Hendry & Stearns, 2004). Salmonids show a high interpopulation variability in mean body size, mainly as a response to different environmental conditions (Elliott, 1994; Lobón-Cerviá, 2000; Nislow, 2001; Nicola & Almodóvar, 2004).

Brown trout *Salmo trutta* L. is an important angling species in Spain, currently threatened by pollution, habitat destruction, introduction of exotic species, overfishing

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and introgression of foreign genes caused by restocking (Elvira, 1995; Almodóvar & Nicola, 1998, 1999, 2004; Almodóvar *et al.*, 2001, 2002, 2006*a*; Elvira & Almodóvar, 2001). Moreover, it is a widespread species in Europe, showing large variations of its growth pattern among populations (L'Abée-Lund *et al.*, 1989; Elliott, 1994; Jonsson *et al.*, 2001; Klemetsen *et al.*, 2003). A wider knowledge of the factors that influence growth and produce this spatial variability could be a useful tool to achieve conservation and management plans, which involves comparative studies on contrasting populations at a large scale.

Water temperature is considered the most pervasive environmental factor affecting growth of *S. trutta* (Elliott, 1994). There have been various attempts to establish the optimum temperature for growth, but authors have found different values at diverse latitudes (Elliott, 1975*a*, *b*; Jensen, 1990; Forseth & Jonsson, 1994; Elliott *et al.*, 1995). Similarly, the thermal range that permits growth seems to vary between populations (Elliott *et al.*, 1995; Ojanguren *et al.*, 2001; Vøllestad *et al.*, 2002). This suggests that adaptations to local thermal conditions can occur, although there is still a lack of evidence of whether this variation has a genetic basis or is based on the phenotypic plasticity of the species (Forseth & Jonsson, 1994; Lobón-Cerviá & Rincón, 1998; Jensen *et al.*, 2000; Vøllestad *et al.*, 2002; Nicola & Almodóvar, 2004).

Along the Bay of Biscay drainage, *S. trutta* inhabit rivers with a wide variation of environmental conditions. This situation may be a favourable situation to identify factors affecting growth. The primary objective of this study was to describe the spatial variation in growth pattern of *S. trutta* in the Bay of Biscay drainage, and its relation to water temperature and altitude. The different thermal regimes of the streams were expected to affect growth, so growth would be slow in populations with lower water temperatures and shorter growing seasons, as compared with populations experiencing more optimal temperatures for growth. To test this prediction, mean fork length (L_F) at the end of the growing season as well as annual specific growth rate (G_L) were compared among 13 rivers, using a data set compiled over 12 years (1993–2004).

Finally, a broader study of L_F at age was used to compare available data for stream-dwelling *S. trutta* from European populations over the range of 37–70° N. This approach permitted an expansion of the spatial scale of the analysis and the understanding of factors influencing body size of *S. trutta* geographically.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in 13 rivers (Fig. 1), River Urumea and its tributary Zumarrezta, River Araxes and its tributary Errekagorri, River Leitzarán and its tributary Erasote, River Orabidea, and River Bidasoa and its tributaries Aranea, Zoko, Ezkurra, Arrata and Tximista. One sampling site was selected for each river, except for River Bidasoa, which is the longest, where four sampling sites were located (Bidasoa 1–4). The selection of sites was made to cover the range of environmental conditions within the area. Sampling sites corresponded to first to fifth-order streams and were located from 43°03′ to 43°16′ N and from 1°29′ to 2° W, at an altitude ranging from 40 to 490 m. Altitudes were measured directly from topographic maps. Mean altitude and other characteristics of rivers are shown in Table I. Water quality was in accordance with the limits proposed by the European Directive (EU, 2006). Ionic content was similar among the rivers, although the lowest values were found in River Urumea and its

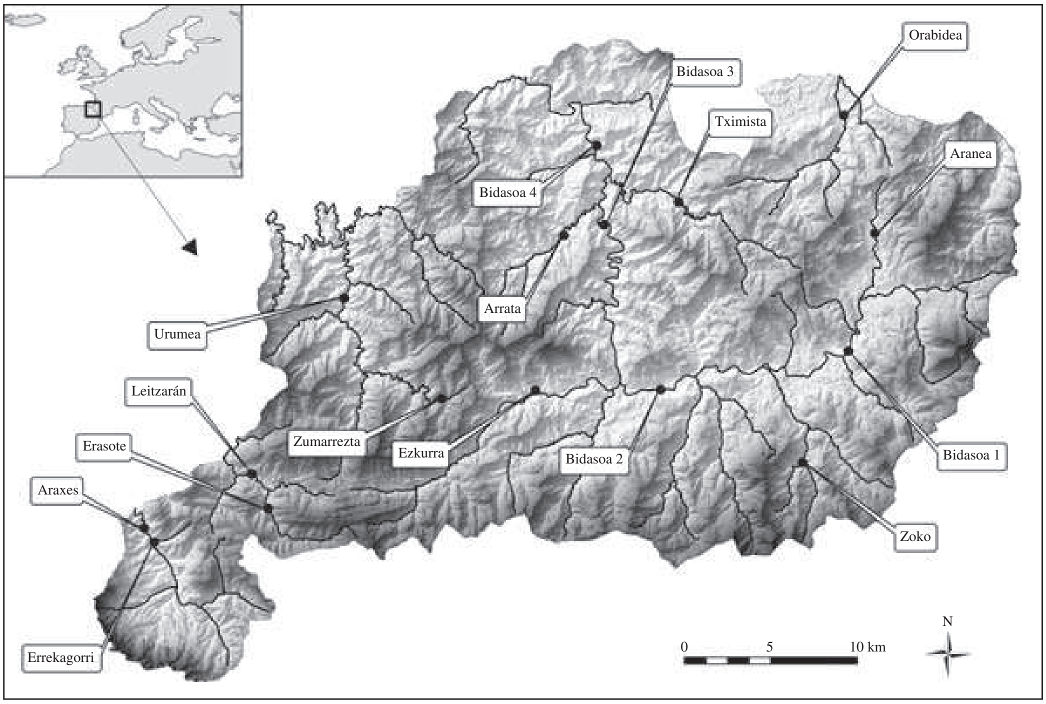

FIG. 1. Map of the study area in northern Spain, showing the location of the sampling sites.

tributary, River Zumarrezta, whereas the highest figures were found in River Araxes. Water mineral content has been considered as one of the factors affecting growth of *S. trutta* (Kelly-Quinn & Bracken, 1988; Mann *et al*., 1989; Nicola & Almodóvar, 2004). The rivers in the present study, however, flow in a small area and the differences in water mineral ionic content do not cover a range wide enough to induce differences in L_F. This meant that the present study was focused on other abiotic variables.

Salmo trutta is the prevailing fish species throughout the area and its populations only comprise freshwater resident individuals. Less common species are European eel *Anguilla anguilla* (L.), Pyrenean gudgeon *Gobio lozanoi* Doadrio & Madeira, Ebro nase *Parachondrostoma miegii* (Steindachner), Pyrenean minnow *Phoxinus bigerri* Kottelat, Pyrenean stoneloach *Barbatula quignardi* (Bacescu-Mester) and Atlantic salmon *Salmo salar* L., while Ebro barbel *Luciobarbus graellsii* (Steindachner), rainbow trout *Oncorhynchus mykis*s (Walbaum) and Adour sculpin *Cottus aturi* Freyhof, Kottelat & Nolte are rare. The streams are open to recreational angling except for some reaches, which are preserved sections. The scattered presence of power stations and dams on the lower reaches are the main anthropogenic pressures in the study area. In addition, industrial areas and alterations of the riparian habitat are found in Rivers Leitzarán and Bidasoa.

Water temperature was measured with data loggers (Minilog Vemco, Ltd; www.vemco.com) permanently placed in each river between July 2004 and October 2005. Mean daily temperature was the average of the maximum and the minimum readings in each 24 h period. Historical data series of temperatures were used. For other years, linear regression was used to estimate water temperature from air temperature readings at local meteorological stations (Elliott, 1984; Crisp, 1992). From the data, mean, minimum and maximum daily temperatures (T_M, T_{min} and T_{max}, respectively, in ° C) were calculated. The values were typical of temperate rivers. Rivers Urumea, Araxes, Leitzarán and their tributaries (Rivers Zumarrezta, Errekagorri and Erasote, respectively) had lower temperatures, with mean annual values between 10·4 and 11·2° C and minimum and maximum annual temperatures between 4·6–5·3° and 15·6–16·3° C, respectively. Recorded values were higher for the remaining rivers, River Bidasoa and its tributaries Aranea, Zoko, Ezkurra, Arrata and Tximista, and

TABLE I. Location and some physico-chemical characteristics from the 16 sampling sites in 13 rivers from the Bay of Biscay drainage, Spain. Mean summer discharge was calculated for each sampling site during 1993–2004. Water temperature was measured with data loggers between July 2004 and October 2005 and these data together with historical data series were used to calculate annual water temperature (Annual T) and mean temperature during the growing season (T_{GS}, estimated for March to September) for the period 1993–2004. Conductivity data were obtained from databases held by the Northern Hydrographical Confederation (www.chn.es) and the Government of Navarre (www.navarra.es)

River	Latitude N	Longitude W	Altitude (m)	Width (m)	Depth (m)	Summer discharge (m^3 s^{-1})	Annual T (°C)	T_{GS} (°C)	Conductivity ($\mu S\,cm^{-1}$)
Urumea	43°10′57″	1°51′34″	145	8·7	0·292	1·883	11·20	12·61	103·5
Zumarrezta	43°07′45″	1°47′29″	470	4·8	0·227	0·094	—	—	71·2
Araxes	43°03′49″	2°00′14″	185	8·2	0·437	0·532	11·29	12·38	424·9
Errekagorri	43°03′23″	1°59′48″	210	2·5	0·123	0·053	—	—	304·0
Erasote	43°04′24″	1°54′57″	490	6·1	0·210	0·438	10·41	12·14	262·9
Leitzarán	43°05′29″	1°55′37″	440	7·6	0·302	1·238	10·39	12·08	262·9
Bidasoa 1	43°09′02″	1°30′05″	205	12·4	0·293	1·421	13·59	15·61	175·0
Bidasoa 2	43°07′56″	1°38′07″	130	16·7	0·353	2·769	13·61	15·59	237·5
Bidasoa 3	43°13′07″	1°40′26″	60	21·6	—	—	—	—	234·3
Bidasoa 4	43°15′36″	1°40′41″	40	22·2	0·251	3·539	—	—	234·3
Aranea	43°12′43″	1°28′52″	300	5·4	0·258	0·425	13·59	15·42	197·3
Zoko	43°05′35″	1°32′07″	340	4·5	0·170	0·170	13·36	15·78	192·8
Ezkurra	43°07′58″	1°43′28″	175	8·7	0·202	0·703	13·61	15·59	210·3
Arrata	43°12′48″	1°42′09″	115	6·1	0·218	0·329	14·03	16·06	242·0
Tximista	43°13′47″	1°37′14″	115	6·1	0·248	0·291	13·67	15·54	126·6
Orabidea	43°16′25″	1°30′06″	85	7·3	0·317	—	14·25	16·01	298·0

River Orabidea. They had mean annual temperatures oscillating between 13·4 and 14·3° C, whereas minimum and maximum values ranged 1·7–6·2° and 18·9–25·4° C, respectively.

SALMO TRUTTA POPULATIONS

Electrofishing with a 2200 W DC generator took place every year at the end of the growing period from 1993 to 2004. *Salmo trutta* individuals were anaesthetized with MS-222 (tricaine methanesulphonate), measured (L_F, to the nearest mm), and scales were taken for age determination. Then, the individuals were returned alive into the river. G_L was calculated as $G_L = (\ln L_{F2} - \ln L_{F1})(t_2 - t_1)^{-1}$, where L_{F1} and L_{F2} are mean L_F at age at times t_1 and t_2, that correspond to the month of September of 2 consecutive years, when the samplings took place.

DATA ANALYSIS

The total of individuals analysed was 36353. L_F at age and G_L were compared between populations using multifactor ANOVA, with subsequent Tukey's tests for comparison of means. Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro-Wilk and Levene's tests, respectively. The significance level α for all statistical tests was set at 0·05.

Pair-wise correlations (Pearson r) were used to explore relationships of L_F and G_L with environmental factors. Forward stepwise multiple regression analyses were performed with L_F and G_L as dependent variables, while those environmental variables significantly correlated with growth were employed as independent variables. Finally, a factorial multiple-regression analysis was employed to address the relationship between L_F and both altitude and latitude of *S. trutta* European populations. These linear regressions were selected applying an information–theoretic approach based on Akaike's information criteria (AIC; Burnham & Anderson, 2002; Motulsky & Christopoulos, 2003). In all cases, and in both small-scale and large-scale approaches, the lowest AIC values corresponded to the linear models compared to the values obtained with non-linear models ($y = ax^b$, $y = ae^{xb}$ and $y = a + bx + cx^2$). The obtained ΔAIC values indicated a 99·9% probability that linear models were the correct choice in overall analyses.

Statistical analyses were performed using the STATISTICA 6·1 computer package (StatSoft, Inc; www.statsoft.com).

RESULTS

SALMO TRUTTA POPULATIONS

Salmo trutta populations were long-lived, with a maximum longevity between 6 and 9 years and a clear dominance of age groups 0+ to 3+ years. These age classes were selected for the analyses because they were well represented in all the rivers.

There were marked differences between rivers in mean L_F of 0+ to 3+ year age classes at the end of the growing period, which were established in the first year of life (Table II). Populations from main streams and lower reaches had a higher mean L_F, whereas populations from small tributaries and upper reaches had a lower mean L_F. Thus, L_F defined a gradient where the highest values were found on the main course of River Bidasoa, then decreasing gradually in Rivers Leitzarán, Arrata, Orabidea, Tximista, Araxes, Ezkurra, Urumea, Aranea, Errekagorri, Zoko, Zumarrezta and Erasote.

Despite the wide differences found in mean L_F, the minimum size limit for angling is set at 200 or 230 mm, depending on the type of stream. Thus, *S. trutta* attains the recruitment age between 2+ and 3+ years. Taking into account that age at maturity

TABLE II. Fork length (L_F) at age (mean ± S.D.) of *Salmo trutta* from 16 sampling sites in 13 rivers from the Bay of Biscay drainage, Spain, during 1993–2004. The results of the one-way ANOVA tests are given and the significant differences are denoted as *** ($P < 0·001$)

	Mean L_F 0+years (mm)	*n*	Mean L_F 1+years (mm)	*n*	Mean L_F 2+years (mm)	*n*	Mean L_F 3+years (mm)	*n*
Erasote	57·4 ± 9·1	2369	117·2 ± 10·6	1208	162·6 ± 13·3	1181	198·3 ± 9·5	303
Zumarrezta	57·9 ± 7·4	1298	111·6 ± 15·0	1330	155·6 ± 11·5	466	196·2 ± 12·6	107
Zoko	58·3 ± 9·0	1255	113·1 ± 17·4	1231	160·3 ± 11·2	335	201·5 ± 8·0	19
Errekagorri	60·4 ± 9·8	1468	114·1 ± 13·8	563	160·2 ± 11·1	185	194·3 ± 10·6	59
Aranea	66·9 ± 10·6	1634	131·5 ± 14·2	1668	179·2 ± 13·0	628	223·0 ± 11·7	105
Urumea	69·4 ± 10·6	1070	143·5 ± 12·9	574	159·5 ± 14·1	318	232·9 ± 13·2	81
Ezkurra	70·0 ± 10·3	1708	145·4 ± 14·9	757	190·8 ± 13·6	370	229·4 ± 11·3	92
Araxes	71·2 ± 10·7	1482	148·6 ± 14·7	568	191·6 ± 15·5	385	223·6 ± 21·8	227
Tximista	71·9 ± 9·3	333	153·4 ± 20·6	481	211·4 ± 12·7	77	259·4 ± 11·9	8
Orabidea	72·6 ± 11·1	1403	157·2 ± 19·3	813	216·4 ± 13·4	209	255·5 ± 11·5	51
Arrata	73·8 ± 10·5	778	156·4 ± 19·9	425	212·3 ± 11·6	62	254·7 ± 10·5	7
Leitzarán	76·8 ± 11·6	291	158·8 ± 20·1	658	223·4 ± 13·5	237	272·9 ± 12·8	129
Bidasoa 3	84·1 ± 13·2	47	176·0 ± 20·2	74	248·4 ± 26·0	13	290·9 ± 23·6	25
Bidasoa 1	84·5 ± 12·5	837	162·1 ± 19·3	1341	220·3 ± 11·9	239	265·6 ± 14·7	48
Bidasoa 4	92·6 ± 19·4	56	169·8 ± 19·7	476	239·7 ± 13·8	113	280·6 ± 12·4	42
Bidasoa 2	100·7 ± 13·9	627	166·4 ± 21·3	649	226·9 ± 13·4	155	272·6 ± 13·5	90
Mean	67·8 ± 14·3	16653	139·0 ± 26·5	12815	183·2 ± 27·7	4973	229·0 ± 33·0	1393
ANOVA	$F_{15,16637} = 1040·11$	***	$F_{15,12799} = 1298·33$	***	$F_{15,4957} = 1146·61$	***	$F_{15,1377} = 414·68$	***

(age at which 50% of a cohort is mature) of females varies in the studied rivers between 1+ and 2+ years, it is expected that some of the harvested females do not reproduce even once in their life.

Salmo trutta growth varied during the life span, reaching a peak in the first year of life, decreasing sharply in the second year and gradually diminishing thereafter. Populations showed little variation in G_L, in spite of the broad differences described in L_F. During the first annual interval (0+ to 1+ years), G_L was similar among the study sites, shaping a gradient where the only significant differences were observed between the extreme values (ANOVA, d.f. = 15, 161, $P < 0{\cdot}001$). Thus, the lowest rate found in River Errekagorri (0·634 mm mm^{-1} year^{-1}) contrasted with that of River Leitzarán (0·825 mm mm^{-1} year^{-1}). The trend of G_L during the second annual period (1+ to 2+ years) was similar to that described in the former interval, with significant differences among rivers (ANOVA, d.f. = 15, 161, $P < 0{\cdot}01$). Comparisons of means, however, only revealed significant differences between the highest values in River Zoko (0·333 mm mm^{-1} year^{-1}) and River Bidasoa at site 4 (0·342 mm mm^{-1} year^{-1}) and the remaining rivers. Conversely, the next annual period (2+ to 3+ years) had no significant differences in G_L among rivers (ANOVA, d.f. = 15, 143, $P > 0{\cdot}05$). The lowest value was found in River Bidasoa 4 (0·166 mm mm^{-1} year^{-1}), whereas the highest rate was found in River Zumarrezta (0·221 mm mm^{-1} year^{-1}).

INFLUENCE OF ENVIRONMENTAL FACTORS ON L_F OF *SALMO TRUTTA*

The correlation analysis revealed significant relationships of L_F of *S. trutta* with water temperature and altitude. There was a positive relationship between L_F at age and maximum water temperature, whereas altitude was negatively related to L_F at age (Table III).

The L_F at age variability within the study area was determined by a combination of altitude and water temperature, whose respective influences seemed to depend on the life stage. Thus, altitude was the variable with the greatest effect on L_F at the beginning of life (0+ and 1+ year age classes, Fig. 2), accounting for 28–44% of the variance explained by the model (Table IV). Maximum water temperature, however, was the variable with the greatest effect on L_F variability of older individuals (2+ and 3+ year age classes), explaining between 33 and 37% of the variance (Table IV).

A wider spatial analysis was carried out based on the present data and a review of other European studies (Table V), showing a large L_F at age variability (L_F 0+ years, range: 25·0–107·5 mm; L_F 1+ years, range: 57·0–192·3 mm). L_F was negatively related to latitude in 0+ and 1+ year age classes (Fig. 3), whereas the interaction of latitude and altitude (latitude × altitude) had effects on L_F in their second year of life (1+ years, Table VI). The interaction term showed that the effect of latitude was magnified by altitude, *i.e.* the negative effect of latitude on L_F of *S. trutta* was more pronounced for high altitudes, whereas for low altitudes the slope of L_F related to latitude was lower.

TABLE III. Correlation coefficients (Pearson r) and their probabilities for comparisons of fork length (L_F) at age of *Salmo trutta* with altitude and variables measuring water temperature (mean, T_M; maximum, T_{max}; minimum, T_{min})

	L_F 0 + years	L_F 1 + years	L_F 2 + years	L_F 3 + years
Altitude	−0·57*	−0·69**	−0·63*	−0·59*
T_M	0·40	0·40	0·43	0·42
T_{max}	0·54*	0·58*	0·65*	0·62*
T_{min}	−0·39	−0·44	−0·53	−0·49

Significant correlations are shown as; $^*P < 0.05$ and $^{**}P < 0.01$

DISCUSSION

The present study shows that the variability in L_F of *S. trutta* in the study area is similar to that found in the entire European distribution of the species. For example, 0+ year individuals range from 25·0 mm in Iceland (Steingrímsson & Gíslason, 2002) to 107·5 mm in Spain (Braña *et al*., 1992), whereas in the study area, 0+ year individuals vary between 57·4 and 100·7 mm. Further, growth pattern was different even within the same river, as other authors have previously described (Otto, 1976; Nicola, 1999; Baglinière & Maisse, 2002; Hesthagen *et al*., 2004). An increase in L_F was found from tributaries to main courses (*e.g*. from River Erasote to River Leitzarán) and seawards within a main course (*e.g*. River Bidasoa).

The observed negative relationship between altitude and L_F at age may indicate a response of *S. trutta* to changes in environmental factors related to an altitudinal gradient, such as stream width, stream depth, water temperature, nutrients concentration or food abundance, which clearly influence growth of *S. trutta* and the availability of

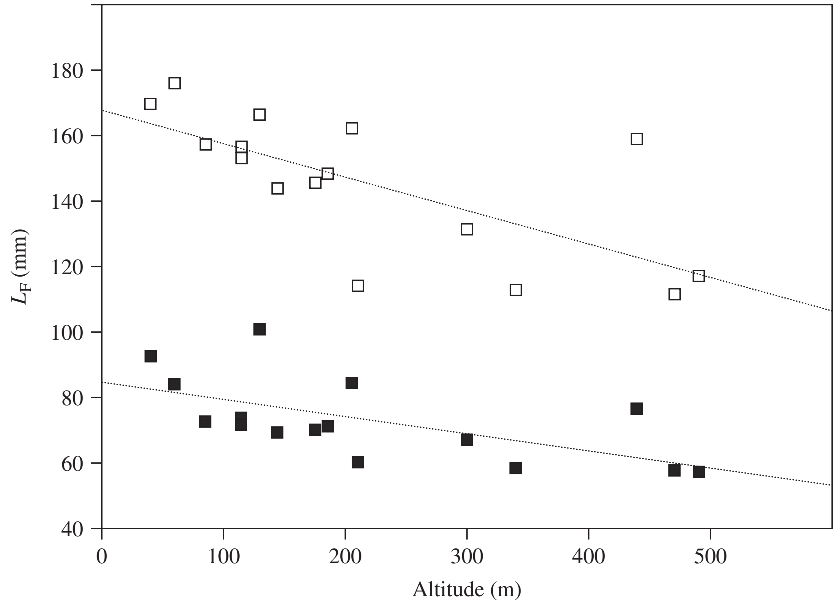

FIG. 2. Relationship between fork length (L_F) and altitude for populations of *Salmo trutta* in the studied rivers in northern Spain. Data are split into 0+ (■) and 1+ (□) year age classes (see Table IV).

TABLE IV. Results of regression analyses of fork length (L_F) at age in relation to maximum water temperature (T_{max}) and altitude of 16 sampling sites on 13 rivers discharging to the Bay of Biscay, Spain

Model	Dependent variables	Independent variables	Coefficient	(95% CI)	*P*
Adjusted $r^2 = 0{\cdot}28$,	L_F 0+years	Altitude	−0·005	(−0·009 to −0·0009)	<0·001
d.f. = 1, 12; $P < 0{\cdot}05$		Intercept	8·50	(7·42 to 9·58)	<0·05
Adjusted $r^2 = 0{\cdot}44$,	L_F 1+years	Altitude	−0·009	(−0·015 to −0·003)	<0·001
d.f. = 1, 12; $P < 0{\cdot}01$		Intercept	16·87	(15·52 to 18·21)	<0·01
Adjusted $r^2 = 0{\cdot}37$,	L_F 2+years	T_{max}	0·559	(0·142 to 0·976)	<0·05
d.f. = 1, 12; $P < 0{\cdot}05$		Intercept	9·48	(1·15 to 17·80)	< 0·05
Adjusted $r^2 = 0{\cdot}33$,	L_F 3+years	T_{max}	0·583	(0·119 to 1·046)	<0·01
d.f. = 1, 12; $P < 0{\cdot}05$		Intercept	13·21	(3·94 to 22·47)	<0·05

TABLE V. Summary of selected mean fork length (L_F) at age from the literature for European stream-dwelling populations of *Salmo trutta* at different altitudinal and latitudinal locations. The number of streams is indicated, and when data are given for different areas in a stream the number of sections is indicated in parentheses

Latitude (°N)	Altitude (m)	L_F 0+years (mm)	L_F 1+years (mm)	Number of streams	Country	Reference
70·6	77	—	61	1	Norway	Power, 1973
69·8	57	43	—	1	Norway	Hesthagen, 1989
65·6	200	25	57	1	Iceland	Steingrímsson & Gíslason, 2002
63·1–66·2	45–380	41·4–60·5	86·6–111·1	3	Sweden	Näslund *et al*., 1998
61·9–62·0	450–720	35–43	76–78	1 (2)	Norway	Hesthagen *et al*., 2004
61·2–61·3	400–479	61·8	90·0–118·0	3	Norway	Jonsson & Sandlund, 1979
58·7	106	63·7	127·5	1	Norway	Bergheim & Hesthagen, 1990
56·3	400	49	97	1	Scotland	Egglishaw & Shackley, 1977
54·7–55·9	85–150	82·8–91·1	162·5–167·9	23	Lithuania	Skrupskelis *et al*., 2006
54·6–55·7	0–36	67–88	—	1 (2)	Sweden	Otto, 1976
54·7	460–550	52–69	86–110	17	England	Crisp *et al*., 1974
54·7	564	52–56	87–107	2	England	Crisp *et al*., 1975
54·6	430	61	102	1	England	Crisp & Cubby, 1978
53·5	125	72	142	1	Poland	Mortensen & Penczak, 1988
52·4–53·9	18–100	49–73	102–146	4 (13)	Ireland	Lobón-Cerviá & Fitzmaurice, 1988
53·3	46–167	55·5–76·0	114·4–130·5	1 (5)	Ireland	Kelly-Quinn & Bracken, 1988
52·1–52·4	130–360	75·2–82·6	128·6–148·2	4 (11)	Wales	Milner *et al*., 1978
51·9	200–250	63·5–65·0	117·5–122·8	3	Wales	Bembo *et al*., 1993
50·8	59	48	102	1	England	Elliott, 1988
48·33	125	96·3–96·5	183·5–192·3	2	France	Baglinière, 1981
43·9	40–150	70–90	117·5–175·0	3 (4)	France	Baglinière & Maisse, 1990
43·4	167–267	69–91	107–168	4	Spain	Lobón-Cerviá *et al*., 1997
43·1	460–1380	60–95	115–183	1 (5)	Spain	García & Braña, 1988
43·0	553–858	82·3–107·5	116·0–175·0	1 (6)	Spain	Braña *et al*., 1992

TABLE V. continued

Latitude (°N)	Altitude (m)	L_F 0+years (mm)	L_F 1+years (mm)	Number of streams	Country	Reference
42·2–42·9	695–1291	—	116·5–135·3	8 (19)	Spain	García de Jalón & Serrano, 1985
42·3	1000	72·0–82·1	133·0–157·3	2	Spain	García de Jalón *et al*., 1986
42·1	1050–1400	—	84–101	1 (3)	Bulgaria	Jankov, 1986
41·7	40	66	120	1	Portugal	Valente, 1988
41·7	980	80	185	4 (9)	Spain	Lobón-Cerviá *et al*., 1986
41·4–41·8	1010–1360	69·3–94·0	132·5–152·0	3	Spain	Almodóvar & Nicola, 2004
40·6–41·9	885–1340	57·4–99·3	107·2–176·6	7	Spain	Nicola & Almodóvar, 2002
40·8	770–810	80·3–85·0	164·5–175·6	1 (2)	Spain	Lobón-Cerviá & Penczak, 1984
39·7	946	79	121	1	Greece	Papageorgiou *et al*., 1983–1984
37·8	1300	92·2	118·2	1	Turkey	Alp *et al*., 2005

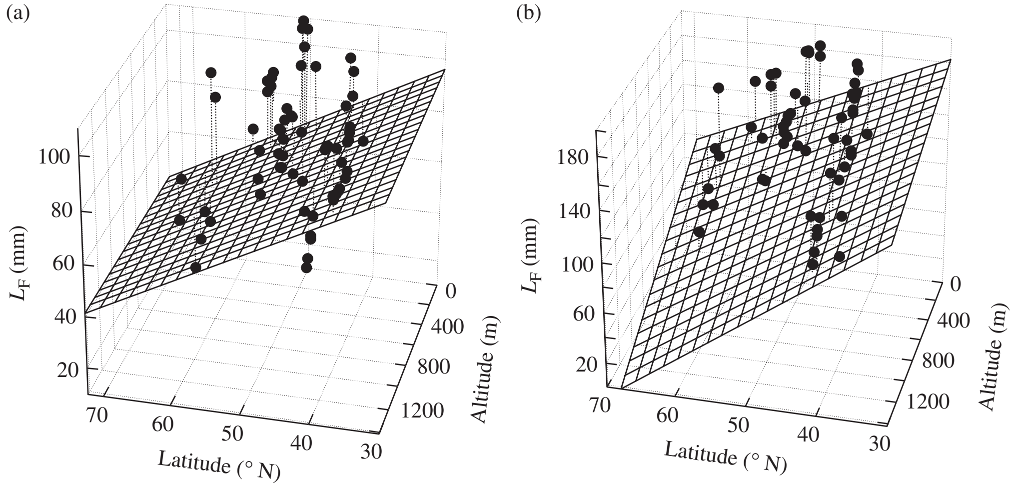

FIG. 3. Relationship between fork length (L_F; y) of (a) 0+ year and (b) 1+ year age classes with latitude (x) and altitude (z) for the studied European populations of *Salmo trutta*. The curves were fitted by: (a) $y = 13{\cdot}53 - 0{\cdot}130x$ and (b) $y = 25{\cdot}25 - 0{\cdot}230x - 0{\cdot}00006xz$.

suitable habitat for larger individuals (Reyes-Gavilán *et al.*, 1995; Almodóvar *et al.*, 2006*b*; Ayllón *et al.*, 2009). Other life-history features related to growth have been found to differ with altitude. Vøllestad *et al.* (1993) found that altitude was a good descriptor of the variation in both length at maturity and estimated asymptotic length.

The local thermal regime was also observed to be positively related to L_F variability. Water temperature is known to have a strong effect on size of *S. trutta*. Growth is controlled by enzymatic activities, so *S. trutta* only grow at a given range of temperatures (3·6–19·5° C; Elliott *et al.*, 1995). In addition, water temperature can exert an indirect influence on growth, affecting other features such as metabolic rate (Forseth & Jonsson, 1994; Wootton, 1998), embryonic development (Ojanguren & Braña, 2003), feeding activity (Elliott, 1989; Ojanguren *et al.*, 2001) and food availability, as temperature increases reproduction, diversity and abundance of invertebrates (Egglishaw & Shackley, 1977; Baglinière & Maisse, 2002).

G_L decreased with age, as has been observed in other populations of this species (Jonsson, 1977, 1985; Mortensen, 1977, 1982; Papageorgiou *et al.*, 1983–1984; Elliott, 1994; Forseth & Jonsson, 1994; Wootton, 1998; Baglinière & Maisse, 2002; Nicola & Almodóvar, 2002, 2004). Growth of fishes is indeterminate and asymptotic, and several factors influence this decrease in growth intensity, *e.g.* the relationship between stomach surface area and body size (Wootton, 1998) and the relative size of gill area (Forseth & Jonsson, 1994). Maturity, however, is considered the main cause of the growth reduction, since the energetic investment in reproduction depends on and influences the allocation of resources into somatic growth (Elliott, 1994; Jonsson *et al.*, 2001; Lagarrigue *et al.*, 2001; Baglinière & Maisse, 2002; Nicola & Almodóvar, 2002, 2004). On the other hand, G_L was homogeneous among the rivers studied, contrasting with the differences found in L_F at age. For instance, there were no differences in G_L between the main course of River Bidasoa and its tributaries, whereas wide differences were detected in L_F at age. There is a negative relationship between the date of fry emergence from the stream bed and water temperature (Elliott

TABLE VI. Results of regression analyses of fork length (L_F) at age in relation to altitude and latitude from literature data on the European distribution of *Salmo trutta*

Model	Dependent variables	Independent variables	Coefficient	(95% CI)	*P*
Adjusted $r^2 = 0{\cdot}33$, d.f. = 1, 99; $P < 0{\cdot}001$	L_F 0+years	Latitude	−0·130	(−0·166 to −0·094)	<0·001
		Intercept	13·53	(11·80–15·26)	<0·001
Adjusted $r^2 = 0{\cdot}34$, d.f. = 2, 119; $P < 0{\cdot}001$	L_F 1+years	Latitude	−0·230	(−0·289 to −0·171)	<0·001
		Latitude × altitude	−0·00006	(−0·00009 to −0·00004)	<0·001
		Intercept	25·25	(22·19–28·31)	<0·001

& Hurley, 1998; Ojanguren & Braña, 2003). The thermal regime varied among the studied rivers and this probably led to interpopulation differences in emergence times. The date of emergence finally determines the length of the first growing period and therefore the L_F attained by 0+ year individuals (Ojanguren & Braña, 2003). The L_F variation among populations was therefore established in the first year of life and continued during following years due to similar G_L. The findings highlight the effect of growth of 0+ year individuals on their size at older ages.

Finally, G_L in the populations from the Bay of Biscay drainage showed higher values for the first growing period than observed in previous studies on *S. trutta* from the centre of the Iberian Peninsula (Almodóvar & Nicola, 1998; Nicola & Almodóvar, 2004). These differences in the intensity of growth could be due to the higher altitude in the centre of the Peninsula and the colder thermal regime, but at similar latitudes. A similar comparison with European populations of *S. trutta* could not be undertaken due to the scarcity of available data of G_L on stream-dwelling populations.

Altitude was the major factor affecting L_F at age of *S. trutta* at a local scale. When considering a broader scale with data from all over Europe, however, the differences among populations resulted from variations in latitude. Nevertheless, latitude determined a large part of the geographic variation in L_F of young individuals, whereas altitude only magnified the effect of latitude (*i.e.* the decrease in L_F with latitude was steeper for high altitudes). Some of the environmental factors previously mentioned to fluctuate with altitude are also highly correlated with latitude (Jensen *et al*., 2000). When the spatial scale of the study became wider, latitude rather than altitude came out as the overall factor that encompassed those environmental gradients and would explain spatial differences in L_F of *S. trutta*.

One of the most well-known patterns of latitudinal variation in animal body size is Bergmann's rule (Belk & Houston, 2002). It holds that within endothermic animals, body size increases with increasing latitude (or decreasing temperature). Application of this rule in ectotherms is controversial. Belk & Houston (2002) and Millien *et al.* (2006) showed that, considering size at age, most North American freshwater fishes analysed followed the converse of Bergmann's rule.

Latitudinal trends in body size of *S. trutta* have been further studied in anadromous stocks of this species. *Salmo trutta* tend to be anadromous in northern regions and resident to the south, but migratory and resident individuals can occur even within a single population. Anadromous *S. trutta* grow faster and attain greater body size than resident fish (Jonsson, 1985; Klemetsen *et al*., 2003). Moreover, an increase in longevity with latitude due to a later maturity has been described for anadromous populations. This higher longevity could imply a larger maximum size with latitude (Jonsson & L'Abée-Lund, 1993).

The results of the present study showed that stream-dwelling *S. trutta* populations follow the converse of Bergmann's rule, as reported in other European freshwater fishes including common dace *Leuciscus leuciscus* (L.) (Lobón-Cerviá *et al*., 1996) and perch *Perca fluviatilis* L. (Heibo *et al*., 2005). Temperature is perhaps the most important environmental factor for fishes growth. Since water temperature decreases with latitude, it would be expected that L_F at age is strongly negatively correlated with latitude.

The present study underscores several key points of interest to fishery managers, which could help in the sustainable exploitation of the populations. The minimum size limit established on the studied rivers does not ensure the reproduction of a proportion of the females at least once before being harvested. Besides, fast-growing populations have fewer potential chances for future spawning as a consequence of a higher adult mortality by angling (Almodóvar & Nicola, 2004). Thus, it is recommended to establish higher minimum size levels according to the situation of each population instead of using more generalized limits.

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II. Variación altitudinal y latitudinal de las estrategias vitales

Este capítulo reproduce íntegramente el manuscrito:

I. Parra, A. Almodóvar, G.G. Nicola, L.A. Vøllestad & B. Elvira. 2012. Life-history strategies of brown trout along altitudinal and latitudinal gradients. *Evolutionary Ecology* (enviado).

Las estrategias vitales dependen del ambiente que habitan los organismos, y están interrelacionadas a través de equilibrios o “trade-offs”. Las condiciones ambientales podrían tener una influencia más fuerte en poblaciones sedentarias de Trucha Común, pero se conoce muy poco acerca de la variación de los patrones de estrategias vitales a lo largo de gradientes altitudinales y latitudinales. En este estudio se han empleado dos aproximaciones, incluyendo dos niveles de organización y dos escalas espaciales, para explorar la variación altitudinal y latitudinal de las estrategias vitales de poblaciones sedentarias de Trucha Común. En primer lugar, se estudiaron los factores que influyen sobre la decisión de madurez de individuos de poblaciones españolas, en Navarra. En segundo lugar, se exploraron los efectos de la altitud y la latitud en la longevidad, la longitud máxima, la longitud y la edad en la madurez y la fecundidad, comparando poblaciones de los límites norte y sur de la distribución europea de la Trucha Común. La madurez individual estuvo determinada por la longitud, la edad y el sexo, y para una longitud y edad dadas, la probabilidad de madurez fue mayor en altas altitudes. Umbrales de madurez menores con la altitud pueden resultar adaptativos, ya que la madurez reflejaría las oportunidades de crecimiento del río. Las truchas fueron más longevas pero alcanzaron menores tallas con la latitud. Tanto machos como hembras maduraron con mayor edad con la latitud pero, aparte de esto, la latitud afectó de manera diferencial a las estrategias vitales adoptadas por ambos sexos. Los machos maduraron con tallas menores con la latitud, lo que apoya la idea de que su decisión de madurez refleja el potencial de crecimiento del río. No se detectó ese efecto en la longitud mínima de las hembras, ya que si su fecundidad aumenta con el tamaño probablemente han de alcanzar una talla umbral que haga que la madurez sea energéticamente rentable. La Trucha Común tiene está caracterizada por una gran plasticidad fenotípica que le permite habitar en ambientes muy diversos y la importancia de estudios latitudinales radica en que pueden ayudar a predecir potenciales efectos del cambio climático, especialmente en el límite sur de su distribución.

It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organisms, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction

R.A. Fisher

Life-history strategies of brown trout along altitudinal and latitudinal clines

Irene Parra · Ana Almodóvar · Graciela G. Nicola · L. Asbjørn Vøllestad · Benigno Elvira

Abstract Life-history traits are modulated by the environmental conditions where an organism lives and are interrelated by means of trade-offs. Local environment conditions may have a particularly strong influence on stream-dwelling organisms such as populations of brown trout *Salmo trutta*, but little is known about the variation of its life-history patterns over altitudinal and latitudinal clines. Besides, the environment may induce different strategies in males and females depending on the mating system. To explore altitudinal and latitudinal variation in life histories of stream-dwelling brown trout we used two different approaches involving two organizational levels and spatial scales. First, we studied the factors influencing the maturation decision of individuals from populations in Northern Spain. Second, we explored the effects of altitude and latitude in longevity, maximum length, length and age at maturity, and fecundity, comparing populations across Europe. Individual maturation was determined by length, age, and sex, and at a given size and age individuals were more likely mature at higher altitudes. Lower maturation thresholds with altitude may be adaptive since maturation reflects growth opportunities of the river. Brown trout lived longer but attained smaller sizes at higher latitudes. Both males and females matured at older age with increasing latitude, but latitude affected differentially their life-history strategies. Males matured at smaller sizes with increasing latitude, which supports that their maturation decision depends on the growth potential of the river. No such effect was detected in females. Since female fecundity increases strongly with size there may be a threshold size below which maturation is too energetically costly and have strong fitness costs. Brown trout has an extraordinary phenotypic plasticity which allows the species to inhabit a great variety of environments, and latitudinally based studies are important to predict potential effects of climate change especially on the southern edge of its distribution.

Keywords Sex divergences · Body size · Salmonids · Latitude · Altitude

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Introduction

Life history theory proposes that natural selection shapes the timing and duration of various key events in an organism’s life in order to maximize the number of surviving offspring (Roff 1992; Stearns 1992). These events are related to growth, reproduction and survivorship, depend on the environmental conditions where an organism lives and are interrelated by means of trade-offs. Among the most studied trade-offs are those relating reproduction and growth, reproduction and survival and current and future reproduction (Stearns 1992). The need of optimality in the schedule of growth and reproduction leads to adjustments of age and size at maturity considering growth rate and life expectancy (Kozłowski and Uchmański 1987). Besides, species with indeterminate growth must also optimize the distribution between growth, current reproduction and residual reproductive value (Kozłowski and Uchmański 1987).

There are a number of relationships among key life-history traits that can be considered to be constant within major taxa such as mammals, birds or fish (called “dimensionless numbers”, e.g., Charnov and Berrigan 1991; Charnov et al. 1993; Charnov et al. 2001). Dimensionless numbers are patterns that relate aspects of life histories such as the ratio between length at maturity and the von Bertalanffy asymptotic length (i.e., relative size at maturity; L_α/L_∞). The dimensionless numbers are suggested to be constant within groups of species or populations within a species (Charnov and Berrigan 1991). These theories were first applied to fish by Berverton and Holt (1959) and later by other authors (Pauly 1980; Roff 1984), confirming the constancy of these dimensionless numbers within different fish groups. Looking for generality, theories about life-history strategies are normally focused on broad groups of related species, in which the intragroup variation is less than that between groups. This approach can certainly be very informative when looking for general patterns. Within a single species, however, it may seem possible that individuals from different environments adopt different strategies. Actually, Vøllestad et al. (1993) found that dimensionless numbers are not constant in brown trout *Salmo trutta* populations from Norway, and encouraged further research on these interrelations between life-history traits. Constant or variable, the study of relations between key traits appears as a useful tool for the description and comparison of life-history strategies adopted by populations or individuals in a population.

A great variety of different life histories has been described for brown trout along its wide geographic distribution (Klemetsen et al. 2003; Cucherousset et al. 2005; Jonsson and Jonsson 2011). Latitudinal variation in life histories has been studied in migrant brown trout, especially in northern areas of its European distribution (Jonsson and L'Abée-Lund 1993). Smolt age, sea-age at maturity, and longevity are known to be influenced by clinal variations in environmental factors (L'Abée-Lund et al. 1989; Jonsson and L'Abée-Lund 1993). In addition, sex is a source of life-history variation driven by both natural and sexual selection. Males and females invest differently in reproduction (Hendry et al. 2004), and their size is selected by different mechanisms (see Serbezov et al 2010). Male size is strongly affected by sexual selection, which has favoured the existence of alternative reproductive tactics in anadromous populations where males can mature as parr or migrate because they can both be reproductively successful (Jonsson & Jonsson 1993). On the contrary, females in anadromous populations usually migrate to the ocean to increase their size because female fecundity is dependent on body size (Elliott 1995). Besides, large females normally get better spawning territories and defend them more successfully (van den Berghe and Gross 1989) and they may be more attractive spawners to males (Sargent et al. 1986). Therefore, optimal age and size at maturity may differ between sexes in a population. However, when river conditions are favourable for growth and/or migration is prevented, populations are usually stream-dwelling leading to different selection processes. Furthermore, environmental conditions may have a stronger influence on the life history of stream-dwelling fish (Nicola and Almodóvar 2002) since they cannot move to more productive areas (Jonsson and Jonsson 1993). In a previous study, Parra et al. (2009) described the spatial variation in growth of brown trout in southern European populations. The variation in growth was mainly driven by an altitudinal cline. A further comparison at a larger latitudinal scale revealed that length-at-age in stream-dwelling brown trout decreases with latitude, the converse of Bergman's rule. This growth variability among populations may lead to differences in other life-history traits that are interrelated through trade-offs. Hence, environmental changes through altitudinal and latitudinal gradients influencing growth and development may lead to clinal variations in life histories that may differ for males and females. But, to date, these differences have not been described.

Here, we aimed to determine the factors driving spatial variation in stream-dwelling brown trout life history traits along altitudinal and latitudinal gradients. To achieve this goal we used two different approaches involving distinct organizational levels and spatial scales.

Firstly, we focused on individual variability in life-history traits at a regional scale to investigate which factors influence the maturation decision of individuals from populations in Northern Spain. Differences in growth opportunity set by altitudinal gradients may lead to different life-history strategies. In a second approach, we studied the effects of large-scale altitudinal and latitudinal gradients on life-history traits of stream-dwelling brown trout populations, comparing populations inhabiting in the southern periphery of the distribution (Latitude 40-43º) with northern stocks from Norway (Latitude 61º). In the theoretical context of dimensionless numbers, we aimed to determine whether the interrelationships between life-history traits vary differentially with altitude and latitude for male and female brown trout.

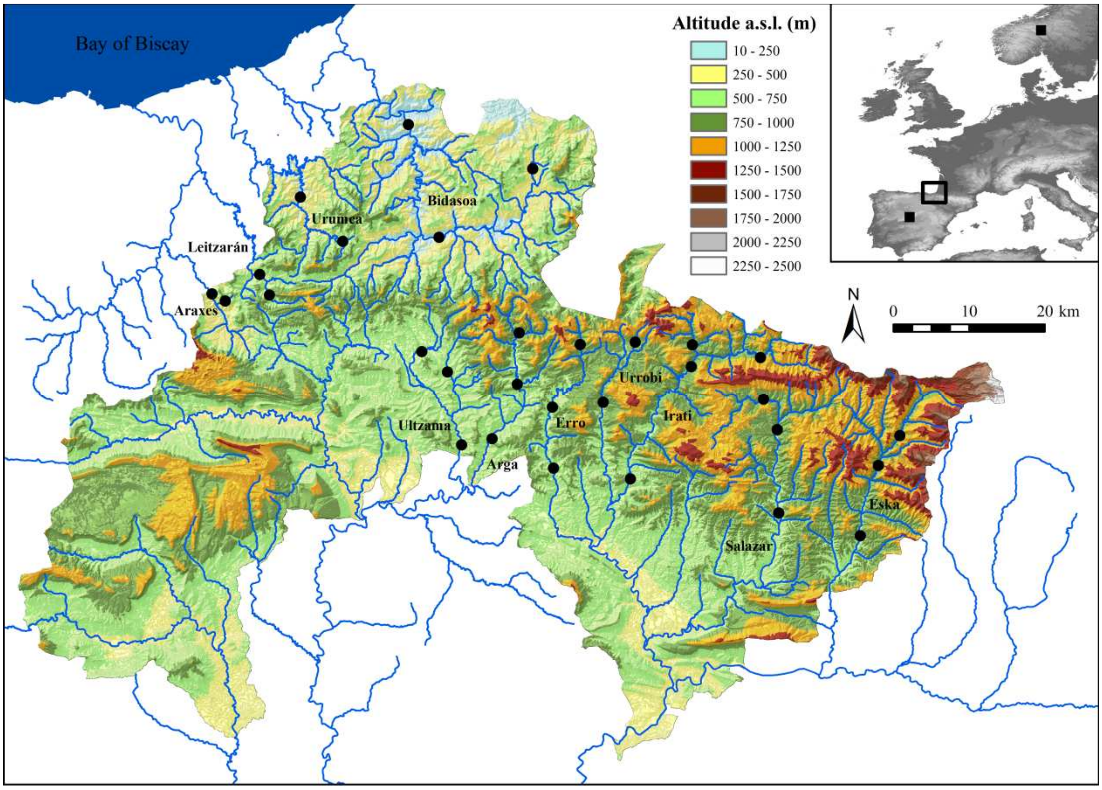
Materials and methods

Study area

The analysis of maturation was carried out with individual data from four basins from the Bay of Biscay drainage (Araxes, Leitzarán, Urumea, and Bidasoa) and seven basins from the Mediterranean Ebro River drainage (Erro, Urrobi, Irati, Salazar, Eska, Ultzama, and Arga) (Fig. 1, Table 1). Between four and 17 sampling sites were selected in each basin, depending on its size and number of tributaries. Sampling sites corresponded to first to fifth-order rivers and were located at an altitude ranging from 40 to 895 m. Median summer discharge ranged from 0.05 to 3.70 $m^3 s^{-1}$ and mean daily summer temperature ranged between 11.6 and 17.4ºC (for further details see Ayllón et al. 2010).

For the analysis of latitudinal variation in life-history patterns we used averaged population data from the above mentioned basins and also data from populations at the southern and northern limits of brown trout distribution. In one hand, seven basins belonging to two Atlantic drainages from the centre of the Iberian Peninsula, Tagus River drainage (Jarama, Dulce, Gallo, Cabrillas, and Hoz Seca) and Douro River drainage (Cega and Eresma), fully described in Nicola and Almodóvar (2002). On the other hand, we used data from five Norwegian rivers (Bellbekken, Gjesa, Ulvåa, Søre Osa, and Nordre Bjøråa, see Olsen and Vøllestad 2003 for further details).

Fig. 1 Map of the study area in Northern Spain, showing the location of sampling sites in Bay of Biscay and Ebro drainages. The situation of the rivers in Europe is also shown (open square), as well as that from the rivers in Central Spain and Norway (solid squares)



Sampling

Electrofishing with a 2200W DC generator took place every year at the end of the growing season from 1993 to 2004. Fish were anaesthetized with MS-222 (tricaine methanesulphonate), fork length (L, to the nearest mm) and weight (to the nearest g) were measured, and scales were taken for age determination. During the summer of 1996, reproductive traits were studied, so caught individuals were immediately frozen on dry ice at -80ºC until their subsequent analysis in the laboratory, where they were dissected and eviscerated, and sex and maturity stage determined. Counting the total number of ripe eggs (stage IV to V) gave the individual fecundity of females.

Then, we calculated several reproductive traits for the studied basins:

- A_{matF} and A_{matM}: age at maturity was the age when 50% of a cohort was mature, calculated for females (F) and males (M) separately.

- L_{minF} and L_{minM}: minimum length at maturity (mm) was the minimum length of a mature individual in the population, considering females and males separately.
- Fecundity: we calculated the fecundity-length relationship ($F=aL^b$). Finally we used the power b (the slope of the log-log regression) for the between populations comparison.

We also wanted to study the longevity of trout in the studied populations by means of the size and age they reach at the end of their lives. Because observed maximum length and observed maximum age come from individual data, they may be biased and hardly comparable between populations (see Rochet 1998), so we calculated:

- A_{max}: maximum age was the age when 10-15% of a cohort is still alive.
- L_{max}: maximum length was the mean length of the age-class correspondent with A_{max}.

Finally, following the idea of dimensionless number (relative size at maturity, L_α/L_∞; Charnov and Berrigan 1991a, 1991b), we used two of the parameters calculated above to locate the size at which the event of maturity (considering minimum size at maturity) takes place with respect to the maximum size reached by the individuals in the population:

- $RelL_{matF}$ and $RelL_{matM}$: relative length at maturity, calculated as L_{minF}/L_{max} for females or L_{minM}/ L_{max} for males.

Table 1 Summary of mean (range) population characteristics of the brown trout populations used to study latitudinal and altitudinal clines in life history traits. Individual data from Ebro and Bay of Biscay drainages were used in the analysis of factors affecting maturation. b is the exponent of the length-fecundity relationship, L_{0+} (mm) is mean length the first year of life, L_{minM} and L_{minF} (mm) are minimum length at maturity of males and females, respectively, A_{matM} and A_{matF} are age at maturity (50% of a cohort) of males and females, A_{max} is age when 10-15% of a cohort is still alive, and L_{max} (mm) is the mean length of the age-class correspondent to A_{max}

Area	Ebro drainage	Northern Spain	Central Spain	Norway
No. basins	8	4	6	5
Altitude	693 (460-895)	269.4 (40-490)	1207.3 (885.0-1340.0)	349.1 (276.0-472.0)
Latitude	42.9 (42.8-43.0)	43.1 (43.1-43.3)	41.4 (40.6-41.9)	61.3 (61.1-61.7)
b	2.7 (1.1-3.4)	2.0 (1.2-2.8)	2.3 (1.5-3.0)	1.88 (1.77-1.96)
L_{0+}	73.2 (60.1-94.3)	69.1 (57.4-92.6)	75.2 (57.0-99.0)	48.6 (40.8-57.7)
L_{minM}	155.5 (102.0-230.0)	158.3 (120.0-231.0)	133.5 (123.2-141.4)	123.4 (96.0-165.0)
L_{minF}	165.2 (123.0-235.0)	150.2 (122.0-183.0)	150.7 (133.0-167.3)	146.1 (106.0-178.0)
A_{matM}	1.3 (1.0-2.0)	1.5 (1.0-2.0)	1.5 (1.0-2.0)	2.0 (1.0-3.0)
A_{matF}	1.6 (1.0-2.0)	1.6 (1.0-2.0)	1.8 (1.0-2.0)	3.1 (2.0-5.0)
A_{max}	2.9 (2.0-3.9)	3.2 (2.0-5.0)	3.3 (3.0-4.0)	4.3 (3.0-6.0)
L_{max}	255.0 (183.0-312.0)	239.6 (167.0-363.0)	244.1 (181.1-330.7)	178.7 (157.0-192.0)

Data analyses

First, to study the maturation pattern of brown trout in Northern Spain (Bay of Biscay and Ebro drainages, see Table 1) we analysed individual data by means of multiple logistic regression performed with the glmulti package in R (Calcagno 2012). It generates all possible model formulas from the main effects, including their pairwise interactions, and returns a list of the best models based on information criterion (Calcagno and Mazancourt 2010). Fork length, age, sex, and altitude were used as fixed effects, while maturation stage (1=mature, 0=immature) was used as dependent variable, and the link function was specified to be binomial. Altitude was included as a proxy for growth opportunity with potential implications on other life-history traits including maturation (see Baum *et al.* 2004). Fifty competing models were compared by means of Akaike's Information Criterion adjusted for small samples (AICc, Burnham and Anderson 2002) to select the best model. Finally, correct classification rate (CCR) was calculated based on the optimum prediction threshold, where the model sensitivity equalled specificity.

Second, to analyse the large-scale spatial variation of the different traits, we employed data from the above mentioned drainages, and also included population data from Central Spain and Norway. As for the individual analysis, the models were fitted using the glmulti package in R (Calcagno 2012), to obtain a list of models and select the best by means of AICc, and if competing models were equally supported (i.e., ΔAIC < 2, Burnham and Anderson 2002) we picked the one with the higher Akaike weight. We separately regressed A_{matF}, A_{matM}, L_{minF}, L_{minM}, A_{max}, L_{max}, $RelL_{matF}$, $RelL_{matM}$, and b, as dependent variables, and latitude and altitude as main effects. Latitude and altitude were standardized, and dependent variables were log-transformed in those cases where it was needed to achieve normality.

Results

Regarding the study of the maturation pattern of brown trout individuals from Northern Spain, the best model for the logistic regression analysis showed that the maturation probability of a brown trout individual increased with increasing length, age, and altitude. The magnitude of these effects was different by sex, with an increase in the probability of maturity for male with respect to female brown trout (Table 2). Several interactions modified these main effects, as the probability of maturity rose less steeply with length for high altitude rivers and for older individuals. Besides, a negative interaction with age counteracted the increase in probability of maturity for older males, whereas a positive interaction increased the probability of a male being mature in high altitude rivers. Sensitivity equalled specificity at approximately 0.53, where the CCR of the model was 83%.

In the large-scale analysis, the impact of latitude and altitude varied depending on the various life-history traits, and there were also differences between male and female strategies (Table 3, Fig. 2). The best models showed that L_{max} decreased with latitude, whereas A_{max} increased with latitude. Age at maturity also varied with the environmental gradients studied, A_{matM} increased with latitude and A_{matF} was higher with both altitude and latitude. Length at maturity responded differently to the clines in males and females. In the case of males, L_{minM} decreased with both altitude and latitude, but when it was considered with respect to L_{max} ($RelL_{matM}$) it showed no relationship with either of the studied gradients. Conversely, when considering females, L_{minF} showed no altitudinal or latitudinal changes, whereas $RelL_{matF}$ increased with latitude. Finally, the exponent of the length-fecundity relationship, b, decreased with latitude.

Discussion

Life-history traits in brown trout showed a great spatial variation related to changes in altitude and latitude. Maturation probability from Northern Spain was determined by length, age, and sex of an individual, but also by altitude. At a wider European scale, altitude and latitude drove the variation in life-history traits, influencing both longevity and maximum length. Male and female traits such as length and age at maturity were also influenced by the studied gradients, but the outcome differed between sexes.

In Northern Spain, where maturation was assessed, a negative interaction between age and length supports the idea that maturity is not determined by a specific age or size but that it results from a combination of both traits, as suggested by Jonsson et al. (1984) for cutthroat trout *Oncorhynchus clarkii* and Dolly Varden charr *Salvelinus malma*. Age has been described to affect the size-maturity relationship in Atlantic salmon (Baum et al. 2004) and white-spotted charr (Morita and Morita 2002), resulting in different threshold sizes for maturity. Given that reproduction implies growth and survival costs, maturation at a specific age would make slow-growing individuals mature at a size with lower fecundity, whereas maturation at a fixed length may delay maturation and thus increase pre-reproductive mortality for slow-growing individuals (Morita and Morita 2002).

Table 2 Models fit to maturation status (0 immature, 1 mature). The 20 first models are ordered by ΔAIC value with respect to the best model. Akaike weights (w_i) are also shown. sex(M) refers to males, L is length of an individual, age is age of an individual, alt is altitude of the river and x indicates interaction between two variables

model	ΔAICc	w_i
state = 1 + sex(M) + L + age + alt + age x L + alt x L + sex(M) x age + sex(M) x alt	**0**	**0.17**
state = 1 + sex(M) + L + age + alt + age x L + sex(M) x age + sex(M) x alt	0.46	0.14
state = 1 + sex(M) + L + age + age x L + sex(M) x age	0.60	0.13
state = 1 + sex(M) + L + age + alt + age x L + sex(M) x L + sex(M) x age + sex(M) x alt	1.78	0.07
state = 1 + sex(M) + L + age + alt + age x L + alt x age + sex(M) x age + sex(M) x alt	1.99	0.06
state = 1 + sex(M) + L + age + alt + age x L + alt x L + alt x age + sex(M) x age + sex(M) x alt	2.07	0.06
state = 1 + sex(M) + L + age + age x L + sex(M) x L + sex(M) x age	2.16	0.06
state = 1 + sex(M) + L + age + alt + age x L + alt x L + sex(M) x L + sex(M) x age + sex(M) x alt	2.31	0.05
state = 1 + sex(M) + L + age + alt + age x L + sex(M) x age	2.32	0.05
state = 1 + sex(M) + L + age + alt + age x L + alt x L + sex(M) x age	3.14	0.04
state = 1 + sex(M) + L + age + alt + age x L + alt x age + sex(M) x L + sex(M) x age + sex(M) x alt	3.78	0.03
state = 1 + sex(M) + L + age + alt + age x L + alt x L + alt x age + sex(M) x L + sex(M) x age + sex(M) x alt	3.78	0.03
state = 1 + sex(M) + L + age + alt + age x L + sex(M) x L + sex(M) x age	3.99	0.02
state = 1 + sex(M) + L + age + alt + age x L + alt x age + sex(M) x age	4.23	0.02
state = 1 + sex(M) + L + age + alt + age x L + alt x L + alt x age + sex(M) x age	4.44	0.02
state = 1 + sex(M) + L + age + alt + age x L + alt x L + sex(M) x L + sex(M) x age	4.77	0.02
state = 1 + sex(M) + L + age + alt + age x L + alt x age + sex(M) x L + sex(M) x age	5.92	0.01
state = 1 + sex(M) + L + age + alt + age x L + alt x L + alt x age + sex(M) x L + sex(M) x age	6.09	0.01
state = 1 + sex(M) + L + age + alt + sex(M) x age + sex(M) x alt	8.73	0.00
state = 1 + sex(M) + L + age + sex(M) x age	9.31	0.00

Environmental (Parra et al. 2009) as well as biotic (Parra et al. 2011) factors entail a high spatiotemporal variability in growth of brown trout in this area from Northern Spain. Conditions, however, are generally favourable for growth of this species, as water temperature is normally high below the upper limit for growth during the growing season, a period that can last for more than three months at these latitudes. Given that the decision to mature the subsequent breeding season is made based on growth history (Jonsson and Jonsson 2011), and that contrary to anadromous populations there is no conflict with smolt transformation, maturity can be attained as young as the second or the third year of life. So, the studied populations are generally short-lived and young maturing, as described in stream-dwelling brown trout populations from the southern edge of the distribution of the species (e.g. Nicola and Almodóvar 2002).

At a given size and age, individuals were more likely to be mature at high altitude sites. Lower thresholds for maturation with altitude may be adaptive, in agreement with the idea that maturation thresholds reflect growth opportunities of the river (Baum et al. 2005; Jonsson and Jonsson 2011). This increase in the probability of maturation with altitude was more marked for small individuals, as indicated by the negative interaction between altitude and length. Especially males had a higher likelihood of maturation at high altitude sites at a given size and age. Gonadal investment is much lower for males than for females, as testes require less energy than the ovaries (Jonsson and Jonsson 1997) and sperm production is not limited by body size (Hendry et al. 2004). Hence, male fitness is probably not as strongly determined by body size as it is in females (but see Serbezov et al 2010). On the contrary, male reproductive success decreases with the number of competitors (Baum et al. 2005), which are expected to be smaller in sites with low growth opportunity. The maturation decision of males should therefore be highly influenced by the potentiality for growth, as supported by the positive influence of altitude on the likelihood of maturity. In this sense, as males mature earlier than females, they experienced a lower effect of age on their probability of maturity.

Metabolism, which is governed by temperature (Atkinson 1994; Wootton 1998), so decreased rates of physiological processes occur as temperature decreasing northwards and/or upwards. This thermal variation leads to differences in growth and in other traits that co-evolve with growth, as has been described for many fish species (Blanck and Lamouroux 2007). Specifically, anadromous brown trout are larger, live longer and mature older in northern than in southern rivers (Jonsson et al. 1991; Jonsson and L'Abée-Lund 1993). Conversely, in stream-dwelling brown trout body size decreases with latitude (Parra et al. 2009). In this study, brown trout lived longer but attained smaller size at higher latitude. Besides, male fish matured older with latitude and smaller with both altitude and latitude. Since male reproductive success is not as strongly linked to body size as it is in females, environmental changes associated with altitude and latitude would be expected to influence minimum length at maturity of males at a higher extent. For the same reason, the relative length at maturity of males was not influenced by geographical gradients, indicating that the decision to mature is taken at a similar point along the growing trajectory in places with different growing opportunities. On the other hand, females matured at older ages with increasing altitude and latitude. There was, however, no geographical gradient in their minimum size at maturity. But relative size at maturity varied with latitude, increasing with increasing latitude. In contrast with males, spawning competition among females is relatively weak (Jonsson and Jonsson 2006), whereas fecundity is mostly determined by body size (Jonsson and Jonsson 1993). We acknowledge that both L_{min} and L_{max} are both estimates dependent on sample size, so these results have to be considered cautiously. However, Vøllestad et al. (1993) pointed out that decreasing constancy of L_{α}/L_{∞} might be related to an increase in life history complexity, with potential importance of traits such as habitat complexity or parental care, that may affect life history elements. In this study we show that also differences in the allocation of energy may induce differences between sexes within a species. The thermal variation along altitudinal and latitudinal axes not only slows down physiology but also delays emergence (Elliott et al. 2000) and shortens the growing season (Dmitriew 2011). Thus, in a shorter growing season northern brown trout have to accumulate reserve tissue to survive a longer winter and since growth and reproduction compete directly for the energy, northern and high-altitude conditions limit the opportunity for early maturation. Northern female trout would have to invest in growth for a longer period and so mature older, also delaying maturity with respect to the growing trajectory along a life span. Since growth rate, maximum size and longevity are partially determined by environmental conditions, life history traits including age at maturity are adjusted accordingly to maintain evolutionary fitness (Jennings and Beverton 1991).

Variables	Population	
	Altitude	Latitude
b	=	⬇
Amax	=	⬆
Lmax	=	⬇

	Female		Male	
	Altitude	Latitude	Altitude	Latitude
Amat	⬆	⬆	=	⬆
Lmin	=	=	⬇	⬇
RelLmin	=	⬆	=	=

Fig. 2 Summary chart of the altitudinal and latitudinal changes of the analysed life-history traits

Table 3 Results of regression analyses testing the variation of mean life-history traits with altitude, latitude and their interaction. The 5 possible models are ordered by ΔAICc and Akaike weights (w_i) value with respect to the best model. b is the exponent of the length-fecundity relationship, L_{minM} and L_{minF} are minimum length at maturity of males and females, respectively, A_{matM} and A_{matF} are age at maturity (50% of a cohort) of males and females, A_{max} is age when 10-15% of a cohort is still alive, and L_{max} is the mean length of the age-class correspondent to A_{max}. Rel_{LmatM} and Rel_{LmatF} are relative length at maturity of males and females

Variable	Model	ΔAICc	w_i
b	**b = lat**	**0**	**0.453**
	b = intercept	1.94	0.171
	b = alt	1.97	0.169
	b = lat + alt	2.13	0.156
	b = lat + alt + alt x lat	4.42	0.05
L_{minM}	**L_{minM} = lat + alt**	**0**	**0.533**
	L_{minM} = lat	1.7	0.228
	L_{minM} = lat + alt + alt x lat	1.94	0.202
	L_{minM} = intercept	6	0.027
	L_{minM} = alt	7.79	0.011
L_{minF}	**L_{minF} = intercept**	**0**	**0.338**
	L_{minF} = lat	0.74	0.233
	L_{minF} = lat + alt + alt x lat	0.85	0.221
	L_{minF} = alt	1.8	0.138
	L_{minF} = lat + alt	3.12	0.071
A_{matM}	**A_{matM} = lat**	**0**	**0.421**
	A_{matM} = lat + alt	0.54	0.323
	A_{matM} = lat + alt + alt x lat	1.39	0.211
	A_{matM} = intercept	5.05	0.034
	A_{matM} = alt	7.34	0.011
A_{matF}	**A_{matF} = lat + alt**	**0**	**0.567**
	A_{matF} = lat + alt + alt x lat	1.24	0.304
	A_{matF} = lat	2.97	0.128
	A_{matF} = intercept	26.91	<0.0001
	A_{matF} = alt	29.18	<0.0001
A_{maX}	**$A_{max10-15\%}$ = lat**	**0**	**0.399**
	$A_{max10-15\%}$ = lat + alt	0.1	0.378
	$A_{max10-15\%}$ = lat + alt + alt x lat	1.17	0.222
	$A_{max10-15\%}$ = intercept	13.51	0.0005
	$A_{max10-15\%}$ = alt	15.75	0.0002
L_{max}	**$L_{max10-15\%}$ = lat**	**0**	**0.703**
	$L_{max10-15\%}$ = lat + alt	2.29	0.223
	$L_{max10-15\%}$ = lat + alt + alt x lat	4.52	0.073
	$L_{max10-15\%}$ = intercept	16.19	0.0002
	$L_{max10-15\%}$ = alt	16.94	0.0001
Rel_{LmatM}	**Rel_{LmatM} = intercept**	**0**	**0.358**
	Rel_{LmatM} = alt	0.79	0.251
	Rel_{LmatM} = lat	1.6	0.182
	Rel_{LmatM} = lat + alt	1.83	0.162
	Rel_{LmatM} = lat + alt + alt x lat	4.36	0.046
Rel_{LmatF}	**Rel_{LmatF} = lat**	**0**	**0.589**
	Rel_{LmatF} = lat + alt	1.92	0.226
	Rel_{LmatF} = lat + alt + alt x lat	2.44	0.174
	Rel_{LmatF} = intercept	8.71	0.008
	Rel_{LmatF} = alt	10.61	0.003

Longevity increased with latitude, which has been shown in other fish species (Mills 1988; Colby and Nepszy 1981; Mann et al. 1984; Heibo et al. 2005; Blanck and Lamouroux 2007). In anadromous brown trout, a latitudinal increase in longevity was linked to the decrease in water temperature in the river (Jonsson et al. 1991), which is associated with the reduction in metabolic rate explained above. Increased longevity is linked to the older age at maturity at higher latitudes, since age at maturity should be adjusted to survival rate, but maturity and reproduction may raise mortality (Jonsson and L'Abée-Lund 1993). Hence, by delaying age at maturity northern trout are able to dedicate all the surplus energy to grow for a longer period with the subsequent relative increase in fecundity, but they can also increase their total fitness by means of a longer life span. The slope of the length-fecundity relationship decreased with latitude. Williams (1966) predicted a lower reproductive effort per reproductive time for longer-lived individuals. Charnov et al. (2007) refined this concept to the "Lifetime Reproductive Effort" that considers the reproductive effort by unit time multiplied by the average adult life span and is supposed to be constant among different species. Since reproduction in fishes is a trade off between current and future reproduction (Stearns 1992), in those populations where riverine growth is limited as in the north of Europe, the slope might be less steep so that more energy can be assigned to growth for as long as possible. This might appear to decrease lifetime fecundity with respect to southern populations, but in combination with an older age at maturity and higher longevity, it may increase the potential maximum length and the number of reproductive events, with the resulting increase in lifetime total fecundity.

To conclude, two contrasting life-history patterns were found in stream-dwelling populations from very distant areas within the species distribution, and altitude was also shown to induce spatial variability in life history. Male and female traits were differentially influenced by latitude. An extraordinary phenotypic plasticity has been attributed to brown trout, which allows the species to inhabit a great variety of environments. Present day climate change intensifies the environmental constraints that already affect many thermally sensitive species, especially in the southern edge of their distribution (e.g., Root et al. 2003; Almodóvar et al. 2012). Latitudinally based studies are therefore important for the prediction of potential effects of global warming because of the latitudinal variation of key environmental parameters, which may be representative of climate-driven changes in life history traits over time (Power et al. 2005).

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III. Variación de la denso-dependencia del crecimiento a lo largo de la ontogenia

Este capítulo reproduce íntegramente el manuscrito:

I. Parra, A. Almodóvar, D. Ayllón, G.G. Nicola & B. Elvira. 2011. Ontogenetic variation in density-dependent growth of brown trout through habitat competition. *Freshwater Biology* 56: 530-540.

La denso-dependencia del crecimiento ha sido ampliamente detectada en peces de agua dulce, pero la evolución de la competencia durante la ontogenia, así como sus posteriores efectos sobre el crecimiento a lo largo de la vida, aún se desconocen. Los patrones de competencia se pueden describir integrando datos de abundancia de la población con resultados de la modelización del hábitat. Las curvas de hábitat potencial útil (*weighted usable area*, m^2 WUA ha^{-1}) se obtienen para cada valor de caudal y se combinan con datos demográficos para obtener las tasas de ocupación (truchas m^{-2} WUA) del WUA para cada clase de edad, año y localidad. Se ha estudiado una serie larga de datos para estudiar la variación temporal que tiene la tasa de ocupación sobre el crecimiento de la Trucha Común *Salmo trutta*. En concreto, se ha examinado si (i) la tasa de ocupación experimentada durante la vida de una cohorte se ve afectada por la masa media de una cohorte; (ii) la tasa de ocupación experimentada por los individuos a distintas edades influye sobre su tamaño corporal medio. Se observó una relación potencial y negativa entre la masa media de una cohorte y la tasa de ocupación media experimentada durante la vida, indicando que cohortes más numerosas están asociadas con un menor crecimiento corporal, lo que puede tener consecuencias para el éxito reproductor de los individuos. Los efectos de la tasa de ocupación en la longitud por clases de edad se detectaron principalmente en el tamaño alcanzado el segundo año de vida, aunque son debidos a la competencia experimentada en distintos momentos. Así, el nivel de competencia varió durante la ontogenia, de tal forma que en algunos ríos afectó al crecimiento desde el primer año de vida, mientras que en la mayoría de los ríos los mayores efectos sobre el tamaño corporal fueron el resultado de la competencia experimentada el segundo año de vida. Se propone el uso de la tasa de ocupación como una medida más ajustada que la densidad a la hora de evaluar la competencia por el hábitat en peces de agua dulce, ya que incluye las diferencias en calidad y en cantidad del hábitat disponible adecuado para los individuos de cada clase de edad. Este estudio destaca la importancia de la denso-dependencia del crecimiento como proceso clave en la dinámica de las poblaciones. La variación a lo largo del tiempo de este proceso depende de los cambios temporales en la densidad y de la variación de la competencia asociada a la capacidad del hábitat para cada clase de edad.

Knowing ingnorance is strength
Ignoring knowledge is sickness

Lao Tse

Freshwater Biology

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Ontogenetic variation in density-dependent growth of brown trout through habitat competition

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SUMMARY

1. Density-dependent growth has been widely reported in freshwater fishes, but the ontogenetic evolution of competition and its subsequent effects on growth through a life span remains unclear.
2. Patterns of competition can be described by integrating population abundance data with habitat-modelling results. Weighted usable area (WUA; m^2 WUA ha^{-1}) curves are obtained for each flow value and are then coupled with demographic data to obtain the occupancy rates (trout m^{-2} WUA, the density of a given age class related to its suitable habitat) of the WUA for every age class, year and site.
3. We examined a long-term data series searching for temporal variation in the influence of habitat occupancy rate on the growth of brown trout *Salmo trutta*. We tested whether (i) mean cohort mass (mean mass of the cohort during the first 3 years of life) is affected by the occupancy rate experienced across a life span; and (ii) the occupancy rate experienced at different ages influenced mean body size.
4. We observed a consistent negative power relationship between average cohort mass and mean occupancy rate through a life span, indicating that stronger cohorts were related to a reduced growth, with likely consequences for individual fitness.
5. The effects of occupancy rate on size-at-age were mainly detected in the size attained at the second year of life, but they were because of the competition at different times. Thus, the level of competition varied through ontogeny, in some of the rivers affecting growth since the first year of life, whereas in most of the rivers the main effects on body size resulted from the competition during the second year of life.
6. Occupancy rate appears more appropriate than density for assessing the occurrence of habitat competition in freshwater fishes, since it encompasses the differences in quantity and quality of suitable habitat for each age class.
7. Our study highlights the importance of density-dependent growth as a key process in the dynamics of brown trout populations, its temporal variation depending on the temporal changes of density and the variation of competition associated with the habitat capacity for each life stage.

Keywords: density dependence, life history, physical habitat simulation, population dynamics, Salmonids

Introduction

Density-dependent growth has been described in both marine (Lorenzen & Enberg, 2002) and freshwater fishes (e.g. Byström & García-Berthou, 1999; Jenkins

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IV. Estudio de la importancia relativa de la temperatura del agua y la denso-dependencia en la variación espacial del tamaño corporal de la Trucha Común

Este capítulo reproduce íntegramente el manuscrito:

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Este estudio se centra en la influencia relativa de la temperatura del agua y la denso-dependencia en la variación espacial del tamaño corporal en 126 cohortes de Trucha Común (Salmo trutta) de 12 ríos ibéricos durante un período de 12 años. La masa media de las cohortes y la longitud de las clases de edad 0+ a 2+ varió significativamente entre localidades debido al efecto conjunto de la temperatura del agua y la denso-dependencia. La densidad en el hábitat adecuado ejerció un papel limitante que influyó sobre el crecimiento potencial máximo de las cohortes y la temperatura del agua diferenció dichas cohortes en dos grupos de localidades, de alto y bajo potencial de crecimiento máximo. La temperatura del agua tuvo un efecto positivo y acumulativo en el tamaño corporal de todas las clases de edad. Sin embargo, el tamaño alcanzado por las truchas el primer año estuvo influido no linealmente por las exposiciones de corta duración a temperaturas extremas. Por lo tanto, dichas temperaturas extremas se tornaron en un factor limitante que tuvo efectos perjudiciales para el crecimiento. Se observaron efectos de la denso-dependencia intracohorte e intercohorte a lo largo de la vida, que fueron debidos fundamentalmente a la densidad en el hábitat adecuado disponible que experimentaron las truchas de mayor o igual clase de edad. El presente estudio apoya la hipótesis de que factores tanto denso-dependientes como denso-independientes son cruciales para la comprensión de la dinámica poblacional, siendo su importancia relativa variable a lo largo de escalas temporales y espaciales.

I am a firm believer that, without speculation
there is no original observation.

Letter from C. Darwin to A.R. Wallace, 22nd Dec 1987

Unravelling the effects of water temperature and density dependence on the spatial variation of brown trout (*Salmo trutta*) body size

Irene Parra, Ana Almodóvar, Daniel Ayllón, Graciela G. Nicola, and Benigno Elvira

Abstract: This study looks at the relative influence of water temperature and density dependence on the spatial variation in body size of 126 brown trout (*Salmo trutta*) cohorts from 12 Iberian rivers over a 12-year period. Mean cohort mass and length of age groups 0+ to 2+ varied significantly among sampling sites because of the concurrent effect of water temperature and density dependence. Density in suitable habitat had a limiting role that influenced potential maximum growth of cohorts, and water temperature differentiated these cohorts in two groups of sites with high and low potential maximum growth. Water temperature had a positive cumulative effect on body size of all age classes. However, body size of age-0 trout was nonlinearly influenced by short-term exposure to extreme water temperature. Thus, extremely high temperatures became a limiting factor and had deleterious effects on growth. There were intracohort and intercohort effects of density dependence throughout the life span, which were mainly due to the density in the available suitable habitat of trout of the same age or older. The present study supports the hypothesis that both density-dependent and density-independent processes are crucial for the understanding of population dynamics and that their relative importance varies across scales of space and time.

Résumé : L'étude s'intéresse à l'influence relative de la température de l'eau et de la dépendance de la densité sur les variations spatiales de la taille du corps pour 126 cohortes de truite brune (*Salmo trutta*) de 12 rivières ibériennes, sur une période de 12 ans. La masse des cohortes et la longueur moyenne des groupes d'âge de 0+ an et 2+ ans variaient de manière significative selon le site de prélèvement, en raison des effets concomitants de la température de l'eau et de la dépendance de la densité. La densité dans les habitats convenables, jouait un rôle limitant qui influait sur la croissance maximum potentielle des cohortes, alors que la température de l'eau différenciait ces cohortes selon deux groupes de localités, qui présentaient des croissances maximums potentielles élevée et faible, respectivement. La température de l'eau avait un effet cumulatif positif sur la taille du corps pour toutes les classes d'âges. Toutefois, l'exposition de courte durée à des températures d'eau extrêmes avait un effet non linéaire sur la taille du corps des truites de 0 an. Les températures extrêmement élevées devenaient ainsi un facteur limitant et avaient des effets néfastes sur la croissance. Des effets intracohorte et intercohorte de la dépendance de la densité étaient présents tout au long de la durée de vie, ces effets étant principalement dus à la densité dans l'habitat convenable disponible de truites du même âge ou plus vieilles. L'étude appuie l'hypothèse voulant que des processus dépendants et indépendants de la densité soient nécessaires pour expliquer la dynamique des populations et que l'importance relative de ces deux types de processus varie en fonction de l'échelle spatiale et temporelle.

[Traduit par la Rédaction]

Introduction

Fish growth is inherently linked to population dynamics, and therefore, its study and the elucidation of the numerous factors underlying body size variation is a central topic in fish ecology research (Lorenzen 2008). Body size of salmonids is limited by diverse factors that operate across space and time and induce variations in size within and among populations (Davidson et al. 2010; Bal et al. 2011; Jonsson and Jonsson 2011). However, these factors do not operate at all times or places, so their effects cannot be easily isolated (Dunham et al. 2002). In fact, they may be interrelated, and one factor may reduce the influence of others. Consequently, a clear understanding of the effects of the factors that have the greatest influence on fish body size requires analysis of data over a wide spatial and temporal scale.

Brown trout (*Salmo trutta*) is widely distributed geographically and exhibits large interpopulation variations in body size (Nislow 2001; Vøllestad et al. 2002; Nicola and Almodóvar 2004), making it an excellent target for research on spatial variability in body size. Water temperature is considered the key environmental factor determining the variation

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V. Modelización de la dinámica de la capacidad de carga para la conservación y la gestión de salmónidos territoriales

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Inherente al concepto de capacidad de carga es la idea de la población máxima que un nivel concreto de recursos es capaz de sustentar durante un periodo de tiempo. El conocimiento de la capacidad de carga es esencial para la conservación de poblaciones silvestres, ya que determina en gran medida cuánto hábitat ha de ser conservado para mantener poblaciones en condiciones adecuadas. Además, este concepto ha sido la piedra angular para la gestión de poblaciones explotadas de animales y plantas. Sin embargo, la cuestión acerca de qué determina la capacidad de carga para especies territoriales y cómo puede ser cuantificada todavía no ha sido abordada en profundidad en la investigación ecológica. En este estudio se propone un método novedoso para la modelización de la capacidad de carga para salmónidos territoriales, que puede ser aplicado además en otras especies territoriales siempre que estén fundamentalmente limitadas por las condiciones del hábitat. En el modelo, la abundancia máxima está limitada por condiciones del hábitat que fluctúan a causa de variaciones ambientales, y regulada a través del comportamiento territorial. Se analizó si el modelo era capaz de explicar las variaciones espacio-temporales en la densidad de Trucha Común *Salmo trutta* de 12 poblaciones mediterráneas durante un periodo de 12 años. Se observó que la densidad de las distintas clases de edad seguía la misma trayectoria que la dinámica de la capacidad de carga, así como que el funcionamiento final de una cohorte depende del nivel de competencia con las cohortes con las que convive y de la competencia intracohorte experimentada el año anterior. Asimismo, el reclutamiento dependió de los niveles de saturación de la capacidad de carga experimentados por el stock de individuos adultos el año anterior. En todo caso, la resiliencia disminuyó al aumentar la capacidad de carga. Estos resultados sugieren que aquellas medidas de restauración que traten de incrementar la abundancia de una población a través de repoblaciones, de aumentar la dispersión en el momento de la puesta o de incrementar la supervivencia de una cohorte, puede afectar negativamente tanto a la cohorte tratada como a las que conviven y compiten con ella. Además, tasas de explotación elevadas pueden llevar a la extinción a poblaciones que se dan en zonas de baja capacidad de carga.

If I have been able to see further than others,
it is because I have stood on the shoulders of giants.

Sir Isaac Newton

Modelling carrying capacity dynamics for the conservation and management of territorial salmonids

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ABSTRACT

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Habitat modeling
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Population regulation
Brown trout

Inherent in the carrying capacity notion is the basic idea of a maximum population a particular level of resources can support over a period of time. Knowledge of carrying capacity is essential for wildlife conservation since it is intrinsic in determining how much habitat must be conserved to maintain healthy populations. Further, this concept has been the cornerstone of the management of exploited animal and plant populations. Yet the question about what determines carrying capacity for territorial species and how it can be quantified has been long neglected by ecological research. We propose a novel method to model carrying capacity dynamics for territorial salmonids, which can be further applied to any territorial species as long as they are principally limited by habitat conditions. In our model, maximum abundance is limited by environmentally-induced fluctuating habitat conditions and regulated through territorial behaviour. We tested whether the model was capable of explaining the spatio-temporal fluctuations in densities of brown trout *Salmo trutta* from twelve Mediterranean populations for a twelve-year study period. We observed that density of the different life stages tracked carrying capacity dynamics, but also that the eventual cohort performance was affected by both intercohort competition and intensity of intracohort competition experienced the previous year. Likewise, recruitment depended on the levels of carrying capacity saturation experienced by adult stock the year before. In any case, resilience decreased with carrying capacity. Such results suggest that restoration measures attempting to increase population abundance through stocking, increased breeding dispersion or cohort survival may reduce the performance of both the enhanced and competing cohorts. Further, high exploitation rates may lead populations occurring at low carrying capacities to extinction.

6. Discusión General y Conclusiones

6. 1. Discusión general

A lo largo de la presente memoria se han abordado numerosos aspectos relacionados con el crecimiento y otros rasgos de las estrategias vitales de la Trucha Común, centrándose especialmente en factores abióticos y bióticos que pueden afectar a estos rasgos. En esta sección, los resultados obtenidos en los distintos capítulos se expondrán en conjunto (ver Figura 3) para tratar de llegar a una mejor comprensión de las relaciones entre efectos dentro de la compleja red de interacciones que compone la ecología de la Trucha Común.

En primer lugar, en poblaciones de Trucha Común de un área relativamente pequeña como son las cuencas de la vertiente cantábrica de Navarra, se observó una variación espacial en longitud que prácticamente es equiparable a la variabilidad descrita para la distribución europea de la especie (**capítulo I**). Esto pone de relieve la influencia determinante que ejercen las condiciones locales, tanto abióticas como bióticas, en el tamaño alcanzado por los individuos. El patrón de crecimiento observado mostró una deceleración general en la tasa de crecimiento con la edad (**capítulo I**), tal y como se ha descrito previamente para otras poblaciones de la especie (Jonsson 1977, 1985, Mortensen 1977, 1982, Papageorgiou *et al.* 1983-84, Elliott 1994, Forseth & Jonsson 1994, Baglinière & Maisse 2002, Nicola & Almodóvar 2002, 2004). Se han sugerido varias explicaciones para este patrón de crecimiento continuo pero asintótico. La madurez se ha propuesto como la principal causa de la ralentización del crecimiento, ya que aquellas reservas de energía que se invierten en reproducción dejan de estar disponibles para el crecimiento, y viceversa (Stearns 1992). También se ha sugerido que la disminución del crecimiento sea debida a cambios de comportamiento, como una disminución de la actividad de alimentación para evitar la exposición excesiva ante depredadores (Roff 1983). Otra explicación alternativa es que las posibilidades de crecimiento disminuyan con la edad, debido a que la tasa de consumo de alimento experimente un menor incremento con el tamaño que el que se da en la ración de mantenimiento (Elliott 1994). Esto a su vez puede ser debido a que el consumo de oxígeno, necesario para metabolizar el alimento, resulte limitante al aumentar el tamaño del individuo, ya que la superficie relativa de las branquias disminuye con el tamaño del pez (Forseth & Jonsson 1994). Por último, una disminución en la superficie relativa del estómago y el intestino con respecto al tamaño corporal, podría influir en la ralentización del crecimiento (Wootton 1998).

Aunque se conocen muchos factores que afectan al crecimiento y a otros rasgos de las estrategias vitales de la Trucha Común, muchos de esos factores varían con gradientes geográficos como la altitud y la latitud. Por ello, cambios en la altitud indujeron diferencias en el tamaño corporal y en la decisión de madurez entre ríos de Navarra. Cuando la escala del estudio fue mayor, la latitud fue el factor que englobó las variaciones en gradiente de otros factores, por lo que explicó las diferencias observadas en el tamaño corporal (**capítulo I**), así como las complejas variaciones en las estrategias vitales, que fueron además distintas entre sexos (**capítulo II**).

La temperatura del agua es considerada como el principal factor que subyace a los gradientes ambientales altitudinales y latitudinales. Ello es debido a sus efectos sobre el tamaño corporal a través de su influencia sobre la tasa metabólica (Forseth & Jonsson 1994), el desarrollo embrionario (Ojanguren & Braña 2003), la actividad de alimentación (Ojanguren *et al.* 2001), así como la disponibilidad de alimento, ya que la reproducción, diversidad y abundancia de invertebrados aumentan con la temperatura (Egglishaw & Shackley 1977, Baglinière & Maisse 2002). De hecho, el efecto de la temperatura en el desarrollo embrionario puede llevar a diferencias entre poblaciones en la fecha de emergencia, lo que determina en última instancia el periodo de tiempo de que disponen los alevines para crecer antes de la llegada del primer invierno (Ojanguren & Braña 2003). El tamaño corporal que se alcanza tras ese primer periodo de crecimiento tiene una gran influencia sobre la trayectoria de crecimiento que seguirán los individuos durante el resto de su vida, por lo que también afecta a otros rasgos de las estrategias vitales que están relacionados con el crecimiento y el tamaño corporal. Así, a igualdad del resto de factores, los individuos tuvieron mayor probabilidad de estar maduros en sitios de elevada altitud, especialmente los machos. Dado que la producción de esperma no está tan asociada al tamaño corporal (Hendry *et al.* 2004), el éxito reproductivo de los machos se ve afectado por el nivel de competencia. Por tanto, los machos tendrán que ajustar su tamaño con respecto al del resto de machos en la población (Baum *et al.* 2005) por lo que su decisión de madurar reflejaría la potencialidad de crecimiento del río, madurando así a menores tamaños en elevadas altitudes. Sin embargo, en el caso de las hembras la fecundidad depende en gran medida del tamaño corporal (Elliott 1995), por lo que su madurez está determinada por la talla. Un periodo más largo para alcanzar la talla necesaria para madurar pudo causar que las hembras maduraran con mayor edad a mayores altitudes.

Cuando la escala espacial se amplió para tener en cuenta un gradiente latitudinal, las diferencias en el tamaño corporal entre poblaciones fueron más marcadas, con las consiguientes consecuencias sobre los rasgos de las estrategias vitales que están relacionados con el tamaño corporal. Los individuos de las poblaciones más septentrionales alcanzaron longitudes máximas más pequeñas, a pesar de que fueron más longevos. Además, tanto machos como hembras maduraron con mayor edad al aumentar la latitud. Aparte de eso, el efecto de la latitud fue distinto para las estrategias adoptadas por los dos sexos. Por un lado, los machos maduraron a tallas menores con la latitud, dato que apoya el argumento utilizado previamente al explicar el gradiente altitudinal. Así, la decisión de madurez de los machos dependería de la potencialidad de crecimiento en el río, por lo que maduran más pequeños en ríos con menor crecimiento potencial. De hecho, no se detectó influencia latitudinal en la relación entre su longitud de madurez y la longitud máxima, por lo que maduraron en el mismo punto de su trayectoria de crecimiento en poblaciones del norte y del sur de la distribución. Por otro lado, en las hembras no se encontraron los mismos efectos, ya que no se detectó variación latitudinal en su longitud mínima de madurez. Dado que su fecundidad aumenta con el tamaño corporal (Elliott 1995), es probable que tengan que alcanzar una talla umbral que haga que la madurez sea rentable en términos de costes energéticos y beneficios energéticos. En las condiciones de las poblaciones más al norte, con periodos de crecimiento más cortos e inviernos más largos, las hembras tendrían que invertir energía en crecimiento por más tiempo para alcanzar esa talla mínima. Esto podría haber causado la madurez más tardía observada, que a su vez tuvo lugar más tarde con respecto a su trayectoria total de crecimiento en poblaciones de mayor latitud.

La Trucha Común vivió más tiempo a mayores latitudes, lo que puede estar asociado con una reducción de la tasa metabólica debida a la temperatura. Un aumento de la longevidad con la latitud se ha observado en otras especies de peces (por ejemplo, Mills 1988, Blanck & Lamouroux 2007), y se ha descrito también en poblaciones anádromas de Trucha Común (Jonsson *et al.* 1991). El retraso de la madurez está asociado a vidas más largas, ya que la edad de madurez se ajusta por la tasa de supervivencia. Sin embargo la madurez y la reproducción tienen costes que pueden incrementar la mortalidad (Jonsson & L'Abée-Lund 1993). De esta forma, las truchas de poblaciones más septentrionales podrían dedicar la energía disponible para crecer durante más tiempo de tal manera que maximizarían su éxito reproductivo potencial, aunque el incremento de su fecundidad con el tamaño sea menos acusado que en poblaciones más meridionales debido a una menor pendiente de la relación fecundidad-tamaño. Así, aunque su inversión reproductiva en cada evento fuera menor, se podría compensar con una vida más larga con mayor número de eventos reproductivos, lo que incrementaría el esfuerzo reproductivo total (*Lifetime Reproductive Effort*, Charnov *et al.* 2007).

La variación latitudinal en el tamaño corporal es la base para uno de los patrones ecológicos más conocidos, la regla de Bergmann. Esta regla señala que el tamaño corporal dentro de una especie decrece al aumentar la temperatura, por lo que tiende a disminuir con la latitud. El argumento clásico se basa en que en los animales endotermos, los de mayor tamaño son más capaces de conservar el calor (por ejemplo, Atkinson 1994). Sin embargo, la gran mayoría de las especies animales son ectotermos, por lo que no es esperable que sigan esta pauta, o al menos no que lo hagan por razones relacionadas con la conservación del calor. De hecho, cada vez más estudios apuntan que tanto la regla de Bergmann como su inversa se dan entre los ectotermos (por ejemplo, Ashton & Feldman 2003). En esta memoria se ha visto que las poblaciones sedentarias de Trucha Común siguen la relación inversa a la regla de Bergmann (**capítulo I**). Blanckenhorn & Demont (2004) propusieron que la existencia de dos gradientes hacia el norte, de temperatura del agua y de duración del periodo de crecimiento, podrían explicar la gran variedad de tendencias que se han encontrado en distintas especies de animales ectotermos. Así, periodos más cortos para alimentarse, crecer y desarrollarse podrían resultar en el tamaño corporal menor observado en poblaciones de Trucha Común a elevadas latitudes.

Hasta este punto, se ha puesto de manifiesto la gran influencia que la temperatura del agua ejerce en diversos aspectos de la ecología de la Trucha Común, lo que provoca una amplia variedad de estrategias vitales a lo largo de su distribución. A una escala menor, sin embargo, otros factores pueden alterar el ambiente en el que los individuos se desarrollan, crecen y se reproducen, por lo que podrían inducir cambios en las estrategias adoptadas. En primer lugar, a la vista de los resultados obtenidos, los individuos de una cohorte experimentaron a lo largo de su vida numerosos efectos (ver Figura 3), que se van a exponer a continuación para ver cómo su tamaño, su densidad y la capacidad de carga que encontraron en el río estuvieron íntimamente relacionados de manera que finalmente determinaron el funcionamiento de esa cohorte. Como esquema general se puede describir un ciclo que relaciona la densidad con el tamaño corporal que alcanzan los individuos de una determinada clase de edad (**capítulo III**), mientras que al mismo tiempo la densidad se verá determinada por la capacidad de carga del río para esa clase de edad (**capítulo V**).

La saturación de la capacidad de carga experimentada por los individuos adultos el año anterior determinó parcialmente la densidad que se encontraron los individuos 0+ que fundaron una cohorte, que también estuvo influida por la capacidad de carga del río para alevines. Una vez establecidos, la densidad en el hábitat útil para estos alevines pudo afectar directamente al tamaño corporal que alcanzaron al final del periodo de crecimiento, aunque en la mayor parte de los ríos la densidad de alevines influyó sobre la talla a la que llegaron al año siguiente como juveniles. A pesar de que se han descrito efectos muy tempranos de la denso-dependencia en el crecimiento (por ejemplo, Crisp 1993, Grant & Imre 2005), estos resultados apuntarían a que los alevines están regulados principalmente por la mortalidad denso-dependiente, ya que son más susceptibles a la inanición (Bohlin *et al.* 2002, Einum *et al.* 2006). Sin embargo, más tarde en la ontogenia, los individuos tienen una mayor capacidad para sobrevivir a periodos de escasez de comida, por lo que es más probable que estén regulados por crecimiento denso-dependiente (Einum *et al.* 2006). Además, se han descrito con anterioridad efectos retardados de la limitación de recursos, esgrimidos como explicación en situaciones en las que no se detectaba denso-dependencia en la supervivencia (Byström & García-Berthou 1999). No obstante, esta parece ser la primera vez que se describen estos efectos retardados sobre el tamaño corporal.

Continuando con la cohorte, en su segundo año de vida los juveniles alcanzaron una talla que pudo estar determinada por el nivel de competencia experimentado el año previo, como se ha explicado anteriormente, pero también pudo responder al nivel de competencia en el año considerado. Además, su densidad siguió las variaciones de la capacidad de carga del sistema, considerando los requerimientos que tienen los individuos de esta clase de edad. También se observó un efecto no lineal de la saturación de la capacidad de carga experimentada en la fase de alevín, de tal forma que la densidad de los juveniles aumentó con incrementos de esta saturación hasta un punto en que la competencia intracohorte provocaría mortalidad denso-dependiente. Una relación similar se encontró entre las etapas de juveniles y adultos, de tal manera que la saturación de la capacidad de carga de los juveniles influyó no linealmente en la densidad que se encontraron al año siguiente como adultos. En ese momento, en su tercer año de vida, los individuos adultos alcanzaron un tamaño corporal que estuvo determinado parcialmente por el nivel de competencia experimentado el año anterior, o bien por el nivel de competencia actual. Finalmente, este efecto generalizado de la densidad en el hábitat útil sobre el tamaño corporal de los individuos a lo largo de las etapas de una cohorte se puso de manifiesto al analizar las cohortes completas con datos medios, destacando la gran influencia que puede ejercer la competencia sobre la talla que alcanzan los individuos de una cohorte. Así, las fluctuaciones de las condiciones que experimentan las cohortes conllevan la alternancia de cohortes más o menos abundantes, que oscilan a lo largo del tiempo alrededor de un valor medio de capacidad de carga.

Desde una perspectiva más amplia, una cohorte nunca se encontrará aislada en un río, sino que coexistirá con otras cohortes. De hecho, una comparación entre ríos con distintos niveles de competencia puso de manifiesto que las interacciones con las cohortes acompañantes tienen un papel muy importante en el funcionamiento de una cohorte a lo largo de la vida. Este papel se da a través de efectos del nivel de competencia que experimentan bien sobre la densidad de la clase de edad estudiada (**capítulo V**) o sobre el tamaño de los individuos de la clase de edad estudiada (**capítulo IV**).

Por una parte, el tamaño corporal se vio negativamente afectado por elevadas densidades en el hábitat útil para las distintas clases de edad. El efecto se detectó tanto intra como intercohorte, y fue especialmente debido a la densidad de individuos de la misma edad o de mayor edad, aunque también se detectaron efectos de clases de edad más jóvenes. De estos efectos, la influencia que parece más esperable es el efecto negativo de individuos más viejos sobre el tamaño corporal de individuos más jóvenes, ya que el tamaño y la experiencia favorecen a los individuos más grandes y de mayor edad en los encuentros agresivos (por ejemplo, Jenkins *et al.* 1999, Nordwall *et al.* 2001, Lobón-Cerviá 2005). El efecto opuesto, una influencia negativa de individuos jóvenes sobre las clases de edad mayores podría ser explicado a través de mecanismos de competencia por interferencia. Aunque las preferencias de hábitat cambian a lo largo de la ontogenia, hay un cierto grado de solapamiento (ver Ayllón *et al.* 2009, 2010) de tal manera que algunos hábitats son útiles para varias clases de edad simultáneamente. Cuando dichos hábitats son más adecuados para los individuos más jóvenes, los de mayor edad sólo los ocuparán siempre y cuando la densidad de jóvenes sea pequeña, ya que en caso contrario los costes de vigilancia y defensa podrían causar disminuciones en el crecimiento de los individuos mayores. Además, la competencia por explotación podría hacer que con elevadas densidades de las clases de menor edad, estas consuman presas que de otro modo habrían estado disponibles para las de mayor edad, con el consiguiente efecto para su crecimiento.

Por otra parte, las interacciones entre cohortes influyeron sobre la densidad de las distintas clases de edad, aunque de manera distinta a lo explicado con respecto al tamaño corporal. Así, niveles elevados de saturación de la capacidad de carga, tanto de juveniles como de adultos, tuvieron efectos negativos sobre la densidad de individuos en su primer año de vida. Con densidades altas de las clases de edad mayores, estos individuos ocuparán no sólo los hábitats de mayor calidad, sino también los subóptimos, por lo que disminuirán el hábitat disponible para los alevines. Además, se detectó un efecto de la saturación de la capacidad de carga de los alevines sobre la densidad de juveniles, revelando la existencia de competencia por explotación o por interferencia que podría incrementar los costes energéticos de algunos hábitats. Esto haría que dichos hábitats no fueran rentables para los juveniles, tal y como se explicó en el caso de los efectos intercohorte sobre el tamaño corporal, por lo que disminuiría su densidad a través de mortalidad y/o migración a hábitats más rentables. En el caso de los adultos, sin embargo, no se detectaron efectos intercohorte en su densidad. Esto podría contrastar de alguna manera con los resultados expuestos anteriormente para el tamaño corporal, ya que hubo interacciones entre todas las clases de edad e incluso la densidad de alevines influyó sobre el tamaño de los adultos. Sin embargo, una mayor capacidad de los individuos mayores para resistir periodos de escasez de alimento podría hacer más factible una regulación a través de crecimiento denso-dependiente en vez de mortalidad denso-dependiente (Einum *et al.* 2006).

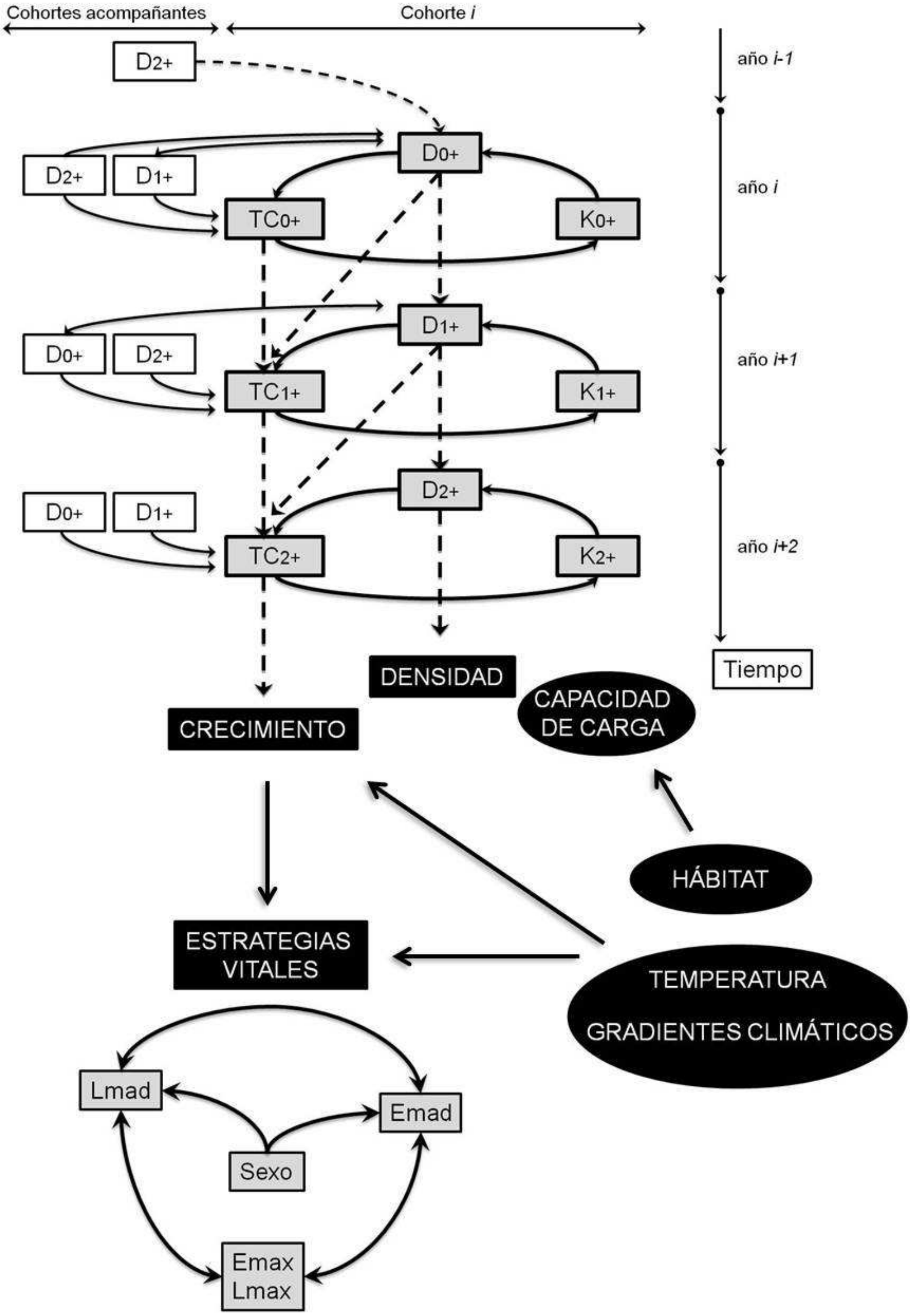
Todas estas interacciones entre cohortes tuvieron lugar con la temperatura del agua afectando al resultado final. Así, se trató de determinar la contribución relativa de procesos denso-dependientes y un factor denso-independiente como la temperatura del agua. La temperatura del agua ejerció una influencia positiva sobre el tamaño corporal a lo largo de toda la vida, aunque el efecto fue mayor el primer año de vida y luego fue decreciendo en favor de la influencia de la densidad, siendo la denso-dependencia el proceso con mayor efecto sobre el crecimiento de los adultos. Una mayor relevancia de la temperatura del agua el primer año de vida podría deberse al gran efecto que tiene la temperatura sobre la fecha de emergencia (Elliott & Hurley 1998, Ojanguren & Braña 2003, Nicola *et al.* 2009) y, por tanto, sobre la duración del primer periodo de crecimiento. Teniendo en cuenta el equilibrio regulador que existe entre la densidad y el tamaño corporal, el efecto positivo de la temperatura del agua sobre la talla de los individuos causará una disminución de la densidad en favor de un incremento en biomasa y producción acumulada en individuos más grandes. Por otra parte, los alevines se vieron afectados por un efecto no lineal de exposiciones cortas a temperaturas máximas, de tal forma que incrementos en la temperatura favorecieron el crecimiento hasta llegar a valores en los que resultó limitante y llegó a reducir el crecimiento. La mayor susceptibilidad de los individuos más jóvenes a las temperaturas máximas puede ser debida a la relación alométrica entre el volumen y la superficie del pez (Brett 1952). Además, las clases de edad de menor edad sufren en mayor medida los efectos de las fluctuaciones de temperatura (Elliott 1994) y carecen de la capacidad natatoria que permite a juveniles y adultos moverse a zonas más frescas en caso de eventos con temperaturas extremas. Estos resultados resultan de gran importancia en el escenario actual de cambio climático, ya que se prevé que las condiciones empeoren hacia temperaturas más elevadas y sequías más prolongadas (IPCC 2007). Esto podría llegar a ser una limitación para especies estenotermas como la Trucha Común, resultando de especial relevancia en la zona meridional de su distribución (Jonsson & Jonsson 2009, Almodóvar *et al.* 2012) donde se encuentran las poblaciones estudiadas. El calentamiento global podría inducir cambios en las estrategias vitales de poblaciones del límite sur, y causar en última instancia su extinción.

Por lo tanto, se ha observado que factores tanto denso-dependientes como denso-independientes afectaron a la dinámica poblacional de la Trucha Común. La temperatura del agua, como principal factor ambiental, afectó en gran medida al tamaño corporal. Además, este efecto fue de especial importancia para las truchas en su primer año de vida debido al efecto de la temperatura sobre la fecha de emergencia, que establece a su vez la duración del primer periodo de crecimiento. También resulta destacable el efecto limitante de temperaturas máximas extremas que se detectó en los alevines, probablemente debido a una mayor susceptibilidad de los individuos más jóvenes a las temperaturas altas y fluctuantes. Por otra parte, la influencia térmica estableció un escenario en el que la denso-dependencia influyó sobre distintos aspectos de las poblaciones de Trucha Común. Se observó que el tamaño corporal a lo largo de una cohorte está influido por la densidad de esa cohorte, que a su vez está determinada por la capacidad de carga del río para la clase de edad considerada. También se describieron efectos retardados de la competencia experimentada el año anterior sobre el tamaño corporal y la densidad de una clase de edad. Asimismo, efectos intercohorte determinaron el tamaño corporal alcanzado por las distintas clases de edad, ya que el nivel de competencia en todas las cohortes que coexistieron en un río influyó en el tamaño corporal alcanzado por el resto de cohortes, e incluso la densidad de jóvenes afectó al tamaño corporal de las de mayor edad. Igualmente, se detectaron efectos intercohorte con respecto a la densidad, de tal manera que la densidad de los alevines se vio negativamente influida por su capacidad de carga pero también por la saturación de la capacidad de carga de los individuos mayores. La densidad de juveniles se vio a su vez negativamente afectada por la densidad de alevines, mientras que en los adultos no se detectaron efectos intercohorte en su densidad.

Para concluir, se ha observado que la dinámica de poblaciones de Trucha Común es una compleja red que incluye numerosos efectos. Dentro de los límites establecidos por las condiciones ambientales, las interacciones bióticas llevaron a grandes diferencias en el tamaño corporal y en la densidad entre los distintos ríos estudiados. Las diferencias en el tamaño corporal están íntimamente relacionadas con el hecho de que las distintas poblaciones adopten diversas estrategias vitales. Por tanto, todas estas interrelaciones afectan a distintos aspectos de la ecología de la

Trucha Común y en conjunto favorecen que las poblaciones vayan siguiendo las fluctuaciones de la capacidad de carga a lo largo del tiempo, por lo que permiten la persistencia de dichas poblaciones. Estos resultados pueden tener importantes implicaciones a la hora de diseñar medidas de conservación y gestión. Por ejemplo, aquellas medidas que tratan de aumentar la abundancia a través de repoblaciones pueden llevar a que la clase de edad repoblada exceda la capacidad de carga. Eso influiría directamente en la producción de esa clase de edad a través de efectos negativos en el crecimiento y la supervivencia de los individuos, pero además podría tener efectos negativos en el funcionamiento de las cohortes acompañantes en el río. En última instancia, una influencia continua en el tamaño corporal causada por medidas de repoblación, podría inducir variaciones en otros rasgos de las estrategias vitales, con las profundas implicaciones que esto podría conllevar en las estrategias vitales adoptadas por las poblaciones de Trucha Común.

Figura 3. Esquema de las relaciones descritas en este apartado. *D* es densidad, referida al nivel de competencia. *TC* es el tamaño corporal y *K* es la capacidad de carga. *Lmad* es la longitud mínima de madurez, *Emad* la edad de madurez y *Lmax* y *Emax* son la longitud máxima y la edad máxima respectivamente.



6. 2. Conclusiones

1. La temperatura del agua tuvo un papel determinante en la variación espacial de la longitud furcal de la Trucha Común por clases de edad. La influencia de la temperatura en el desarrollo embrionario determina la fecha de emergencia, por lo que establece la duración del primer periodo de crecimiento, etapa en la que se establecieron las diferencias en tamaño corporal en el área de estudio. A pequeña escala, el efecto de la temperatura fue incorporado por la altitud, un factor que engloba la variación local de la temperatura y otras variables a lo largo del gradiente altitudinal. A una escala más amplia, la variación latitudinal de las variables climáticas explicó las diferencias espaciales en longitud furcal por clases de edad de la Trucha Común a lo largo de su distribución europea. El tamaño corporal disminuyó con la latitud, siguiendo la inversa de la regla de Bergmann.

2. La Trucha Común de poblaciones del norte de Europa alcanzó tamaños menores a pesar de vivir durante más tiempo en comparación con las poblaciones del sur de la distribución de la especie. Tanto machos como hembras maduraron con mayor edad en elevadas latitudes. Sin embargo, los machos maduraron con menor talla según aumentó la latitud, apoyando la idea de que la decisión de madurez en los machos depende de la potencialidad de crecimiento del río. No se detectó dicho efecto latitudinal en la longitud de madurez de las hembras, ya que probablemente tienen que alcanzar una talla mínima para optimizar su fecundidad, que depende íntimamente del tamaño.

3. La denso-dependencia del tamaño fue un proceso clave en la dinámica de las poblaciones de Trucha Común. La variación temporal de sus efectos dependió de las variaciones del nivel de competencia a lo largo de la ontogenia. Asimismo, se detectaron efectos retardados de las condiciones de competencia experimentadas por los individuos de una clase de edad sobre el tamaño que dichos individuos alcanzaron el año siguiente.

4. Interacciones intracohorte e intercohorte modelaron los efectos de la denso-dependencia en el tamaño corporal de la Trucha Común, ya que la densidad de todas las clases de edad que coexistieron en el río afectó negativamente al tamaño corporal alcanzado por el resto de clases de edad.

5. La temperatura del agua y la denso-dependencia actuaron conjuntamente sobre el tamaño corporal. Los efectos de la temperatura fueron más marcados en el primer año de vida, probablemente debido a la influencia que ejerce sobre la fecha de emergencia. Los alevines se vieron afectados además por temperaturas máximas extremas, que resultaron limitantes para el tamaño corporal alcanzado el primer año de vida.

6. La densidad de las distintas clases de edad a lo largo de la vida siguió la dinámica de la capacidad de carga y reflejó además los efectos de competencia intracohorte experimentada el año anterior. La competencia entre alevines y juveniles afectó también a la dinámica de las poblaciones.

7. General Discussion and Conclusions

7. 1. General Discussion

All along the present dissertation, many aspects related to growth and other life histories of brown trout, especially focusing on abiotic and biotic effects that can affect these traits, have been studied. In this section, all these findings are put together to accomplish a better comprehension of the interrelationships among single effects in the whole net of interactions that is the ecology of brown trout (see Figure 3).

First of all, brown trout from a relatively small area such as Bay of Biscay drainages from Navarra showed a spatial variability in length that almost equalled the range described for the entire European distribution of the species (**chapter I**). This clearly emphasises the pervasive effect of local conditions, either abiotic or biotic, on the size attained by the individuals. The observed growth pattern illustrated a general decrease in growth rate with age (**chapter I**), as previously described for other populations of the species (Jonsson 1977, 1985, Mortensen 1977, 1982, Papageorgiou *et al.* 1983-84, Elliott 1994, Forseth & Jonsson 1994, Baglinière & Maisse 2002, Nicola & Almodóvar 2002, 2004). Several reasons have been pointed out as potential explanations for this pattern, as growth in fish is continuous but asymptotic. Maturation has been frequently put forward as the main cause of growth slowing down, since those energy reserves invested in reproduction are no longer available for growth and vice versa (Stearns 1992). It also has been suggested that behavioural changes may be behind growth slowing down, like a decrease in feeding activity to avoid being exposed and thus decrease predation risk (Roff 1983). Another alternative explanation is that the scope for growth declines with size, as the rate of food consumption experiments a lower increase with size than maintenance ration (Elliott 1994). This may rely on that oxygen is needed to metabolising the food, and its consumption may have an increased limiting effect with size since the relative surface of gills decreases with the size of the fish (Forseth & Jonsson 1994). Finally, a decrease in the relationship of stomach and intestine surface area and body size may also influence the decrease in growth intensity (Wootton 1998).

Although many factors are known to influence growth and other life histories of brown trout, a great part of these factors are known to vary with geographical gradients such as altitude and latitude. Thus, changes in altitude induced variations in body size and in the maturation decision among rivers from Northern Spain. When the spatial scale of the study became wider, latitude was the overall factor that encompassed other environmental gradients and explained the observed differences in body size (**chapter I**) and also the complex variations in life-history traits, which differed between sexes (**chapter II**).

Water temperature is considered the main factor underlying these altitudinal and latitudinal gradients. It influences body size through its effects on metabolic rate (Forseth & Jonsson 1994), embryonic development (Ojanguren & Braña 2003), feeding activity (Ojanguren *et al.* 2001) and food availability, since reproduction, diversity and abundance of invertebrate increase with temperature (Egglishaw & Shackley 1977, Baglinière & Maisse 2002). Actually, the effect of thermal conditions on embryonic development probably leads to interpopulation differences in emergence time, which finally determines the time window available for alevins to grow before the first winter arrives (Ojanguren & Braña 2003). The size attained after this first growing period has a great influence on the growing trajectory followed by individuals on the rest of their life span, thus affecting other life-history traits related to growth and size. In fact, all else being equal, individuals were more likely to be mature at higher altitude sites, especially males. As sperm production is not limited by body size (Hendry *et al.* 2004) reproductive success of males would be determined by the level of competition. Hence, males would have to assess their size with respect to that of the rest of males in the population (Baum *et al.* 2005), so their maturation decision would therefore reflect the potentiality for growth of the river, thus maturing at a smaller length at higher altitudes. Females' fecundity, however, depends tightly on body size (Elliott 1995), so maturity would be determined by size in females. A longer period would be necessary to attain a minimum size to mature, so females matured older with altitude.

When the spatial scale of the study broadened to a latitudinal gradient, the differences in body size among populations were much larger, with subsequent consequences on the related life-history traits. Individuals from northern populations attained shorter maximum lengths, even though they lived longer. Besides, both male and female brown trout matured older with increasing latitude. Apart from that, latitude affected differentially the life history strategies adopted by both sexes. Males matured smaller at higher latitudes, which supports the argument stated with the altitudinal gradient: maturation decision in males depends on the growing potential of the river, thus they mature smaller in rivers with lower growth potential. Actually, they matured at the same point of their growing trajectory as shown by the lack of latitudinal effect on the relation between length at maturity and maximum length. No such effect was detected in females, since no latitudinal effect was revealed in their minimum length at maturity. Given that their fecundity increases with body size (Elliott 1995) they probably have to reach a threshold size that makes maturation worthy in terms of energetic costs and benefits. Thus, in a shorter growing season northern brown trout would have to accumulate reserve tissue to survive a longer winter. Northern female trout would have to invest in growth for a longer period and consequently they matured older, also delaying maturity with respect to the growing trajectory along a life span in northern populations.

Brown trout lived longer with latitude, which could be associated with a reduction in metabolic rate with temperature. Increased longevity with increasing latitude has been observed in other fish species (e.g. Mills 1988, Blanck & Lamouroux 2007), and has also been described for anadromous brown trout (Jonsson *et al.* 1991). A delay in maturity is related to a longer life span, since age at maturity is adjusted by survival rate but the maturation and reproduction costs may raise mortality (Jonsson & L’Abée-Lund 1993). Therefore, northern brown trout would be able to invest their surplus energy to growth for a longer period so they would maximise their potential fitness, although their increase in fecundity with size is smoother due to a lower slope of the fecundity-length relationship. Thus, even though their reproductive effort per reproductive time might be lower, they would balance it with a longer life span with more reproductive events, which would increase the final “Lifetime Reproductive Effort” defined by Charnov *et al.* (2007).

Latitudinal variation in body size is the ground for one of the most well-known ecological patterns, Bergmann’s rule. It holds that body size decreases intraspecifically with average ambient temperature, thus tending to increase with latitude. The original explanation is based on that within endothermic animals, large-bodied individuals are more able to conserve heat (e.g. Atkinson 1994). However, the vast majority of species on Earth are ectothermic, so they are not supposed to follow this trend or at least not for heat conservation reasons. Actually, an increasing body of literature shows that both Bergmann’s pattern and the converse exist within ectothermic animals (e.g. Ashton & Feldman 2003). Stream-dwelling brown trout was shown to follow the converse of Bergmann’s rule (**chapter I**). Blanckenhorn & Demont (2004) proposed that two different but non-mutually exclusive environmental variables decreasing towards the North, water temperature and length of the growing season, could explain the variety of trends found in different ectothermic species. Hence, shorter periods for foraging, growth and development would result in smaller body size in northern populations as observed for brown trout.

So far, it has been highlighted the pervasive effect that water temperature exerts on diverse aspects of the ecology of brown trout, leading to a great variety of life-history strategies along its wide distribution. At a smaller scale, however, other factors may alter the environment where individuals develop, grow and reproduce, and thus may induce changes in the strategies they adopt. To begin with, and based on the obtained results, individuals in a cohort experience numerous effects along their life span. These effects will be exposed below to see how their size, their density and the carrying capacity they find in the river are linked and eventually determine the performance of this cohort (see Figure 3). As a general scheme, a cycle could be described that relates density with the body size attained by the individuals at a given age (**chapter III**), whereas at the same time density would be determined by the carrying capacity of the river for this life stage (**chapter V**).

Carrying capacity saturation experienced the previous year by adult trout somehow set the density that was found on the 0+ individuals founding a cohort, which was also determined by the carrying capacity of the river for alevins. Once established, the density on suitable habitat of these alevins could affect directly the body size attained by them by the end of the season or, most frequently, this effect was detected on the size they reached next year as juveniles. Although an early effect of competition on growth has been commonly described in the literature (e.g. Crisp 1993, Grant & Imre 2005), these findings may suggest that alevins would be primarily regulated by density-dependent mortality, since they are more susceptible to starvation (Bohlin *et al.* 2002, Einum *et al.* 2006). Later in ontogeny, however, individuals are more able to survive to periods of food shortage and are thus more likely to be regulated by density-dependent growth (Einum *et al.* 2006). Such a delayed effect of resource limitations has been previously put forward as a potential explanation in situations with lack of density dependence in survival (Byström & García-Berthou 1999), but this might happen to be the first evidence of delayed effects on body size.

Going on with the cohort, on their second year of life juveniles had a body size that could be related to the level of competition experienced the previous year, as explained above, but it was also determined by the present level of competition. In addition, their density tracked the carrying capacity of the system considering the requirements of this age class. A nonlinear effect of carrying capacity saturation on the alevin stage was also detected to influence density of juveniles, showing that this density increased with increasing saturation levels experienced the previous year up to a level where intracohort competition would induce density-dependent mortality. A similar effect was found between juvenile and adult trout, with carrying capacity saturation of juveniles nonlinearly influencing the density they found next year as adults. By this time, on their third year of life, adult individuals attained a body size which was also partially determined by the level of competition experienced the previous year, or by the level of competition on the present year. Finally, this widespread effect of density in suitable habitat on body size of the individuals through a life span was also manifest when analysing a whole cohort, highlighting the strong influence that competition exerts on the body size of the individuals conforming a cohort. Natural fluctuations in the conditions experienced by cohorts would induce an alternation of strong and weak cohorts that would oscillate through time around an average value of carrying capacity.

From a wider perspective, a cohort will never be isolated in a river but will coexist with other cohorts. In fact, a comparison among rivers with differing competitive conditions showed that interactions with accompanying cohorts have an important role on the performance of a cohort through a life span, through effects of the competition levels they are experiencing either on the density of the studied age class (**chapter V**) or on the body size attained by the individuals of the studied age class (**chapter IV**).

Body size was negatively affected by increased intracohort and intercohort density in suitable habitats, especially of trout of the same age or older, but also of younger age classes. From these influences, negative effects of older individuals on the body size of younger ones would be the expected outcome of size and experience favouring older, larger individuals in competitive contests (e.g. Jenkins *et al.* 1999, Nordwall *et al.* 2001, Lobón-Cerviá 2005). The overturned effect showing a negative influence of younger over older age classes could be explained by interference competition mechanisms. Although habitat preferences change through ontogeny, there is a certain degree of overlapping (see Ayllón *et al.* 2009, 2010) so that some habitats are simultaneously suitable for several age classes. When these habitats are better suited for younger trout, older individuals would only occupy them if the density of younger individuals is low, due to increased guarding and defending costs that could otherwise reduce growth of older individuals. In addition, increased exploitative competition could induce that increased densities of younger age classes depress growth of older ones, since younger individuals can consume preys that would have been available to older individuals.

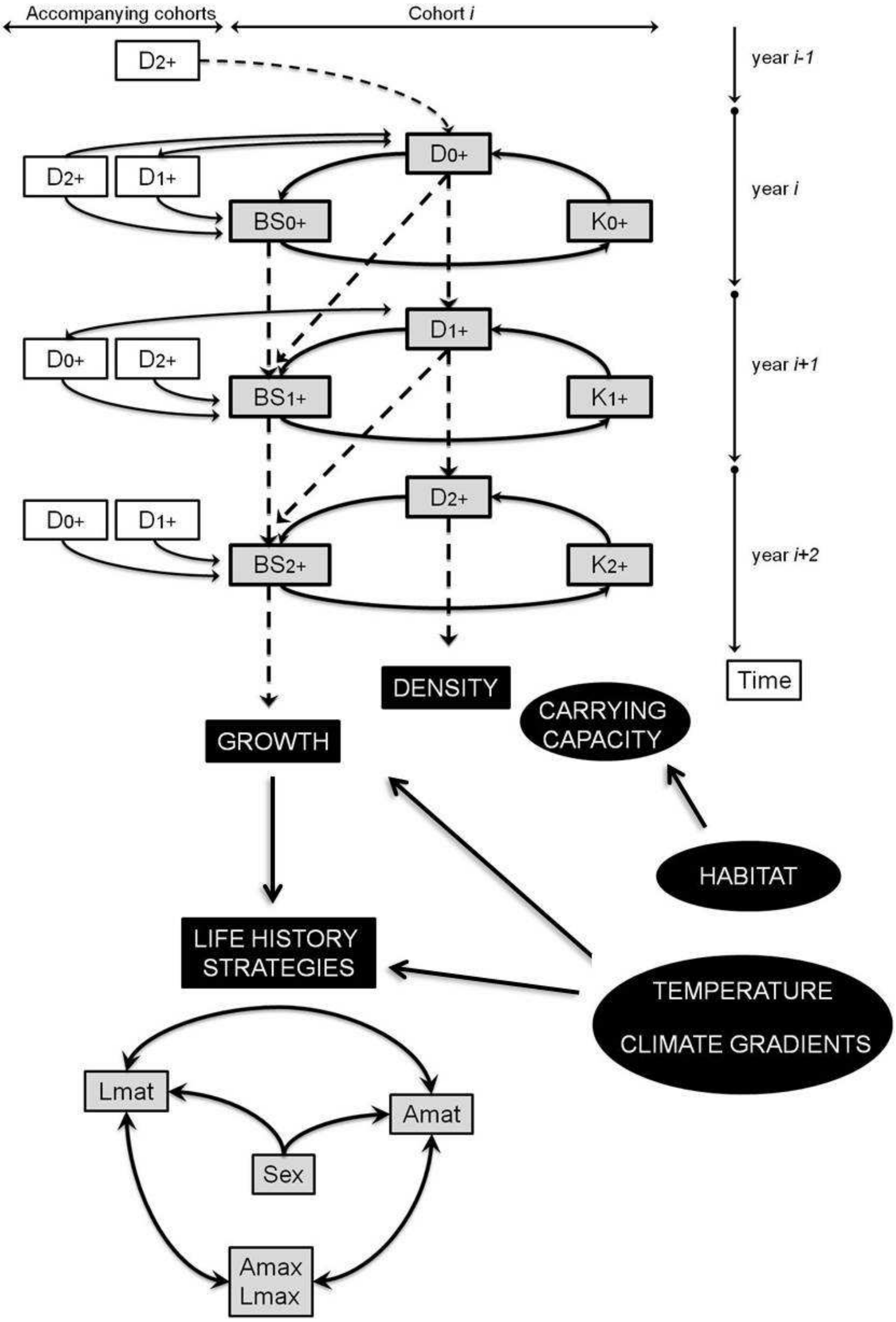
Intercohort interactions also influenced the density of the successive age classes, although somehow differently compared to the effects described for body size. Density on the first year of life was negatively affected by increased levels of carrying capacity saturation of juvenile and adult trout. With increasing densities of older age classes, older individuals would occupy not only high quality habitats but also suboptimal habitats, decreasing the available habitat for alevins. Besides, an effect of saturation of the carrying capacity of the youngest individuals was detected on the density of juveniles, showing exploitative or interference competition that would increase the energetic costs of certain habitats. This could turn them non-profitable for juvenile individuals, as explained above with the intercohort effects on body size, thus affecting their density through mortality and/or emigration towards more profitable habitats. When considering adult individuals, however, no negative effects of intercohort interactions were detected on their density. This fact somehow contrasts with the exposed figures for body size, since there were interactions among all age classes and even the density of alevins negatively affected the body size attained by adults. However, a greater capacity of older individuals to resist periods of food shortage may promote a regulation through density-dependent growth instead of density-dependent mortality (Einum *et al.* 2006).

All those intercohort interactions took place with water temperature influencing the final outcome. There was an interest in determining the relative contribution of density-dependent processes and a density-independent factor such as water temperature. It was revealed that water temperature exerted a positive influence on body size throughout a life span, although the effect was highest on the first year of life and then decreased in favour of density dependence growth as the main process affecting growth of adults. A higher influence of water temperature on the first year of life could originate on the pervasive effect of incubation temperature in determining the date of emergence (Elliott & Hurley 1998, Ojanguren & Braña 2003, Nicola *et al.* 2009) and thus the length of the first growing season. Considering the regulatory trade-off between density and body size, the positive effect of water temperature on body size would promote a decrease in density towards an increase in biomass and production packed in larger individuals. Moreover, alevins were also affected by a nonlinear effect of maximum water temperature, so that increasing temperature favored growth up to values where it became limiting and constrained growth. A higher susceptibility of younger individuals to extreme maximum temperature could rely on the allometric relationship between volume and fish surface area (Brett 1952). Besides, younger age classes are more affected by temperature fluctuations (Elliott 1994) and they lack the increased swimming performance that allows juveniles and adults to move toward cooler areas in case of extreme temperature events. These findings are of remarkable importance under the current scenario of climate change. Freshwater conditions are projected to worsen towards higher temperatures and longer droughts (IPCC 2007). This could turn into an environmental constraint for thermally sensitive species such as brown trout, being especially critical at the southern edge of its distribution (Jonsson & Jonsson 2009, Almodóvar *et al.* 2012) where the studied populations are located. Global warming could induce changes in life history traits of brown trout populations from southern areas, and eventually increase the risk of extinction.

Therefore, it was revealed that both density-dependent and density-independent factors affect brown trout population dynamics. Water temperature, as the main environmental factor influencing brown trout, was described to outstandingly influence body size of brown trout. Besides, this effect was especially critical for trout on their first year of life through the thermal effect on the date of emergence, which would establish the duration of the first growing season. Also remarkable was the limiting effect of extreme maximum temperatures on body size of alevins, probably due to a higher susceptibility of younger individuals to higher and fluctuating temperatures. On the other hand, this thermal influence established a scenario for density dependence to influence several important aspects of brown trout populations. It was observed that body size of a cohort through a life span was influenced by its density, which was in turn determined by carrying capacity for the considered life stage. There was also room for delayed effects on both body size and density from the level of competition experienced the previous year. Furthermore, intercohort effects determined body size attained by the subsequent age classes, since the density of coexisting cohorts influenced body size of each other, even the density of younger age classes negatively influenced body size of older ones. There were also intercohort effects with respect to density, so that alevin density was negatively influenced by the carrying capacity for its own age class but also by the saturation of carrying capacity of older individuals. Intercohort competition between alevins and juveniles also determined population dynamics, whereas no intercohort effects were detected on adult density.

To conclude, it was observed that a complex web of effects shapes the dynamics of brown trout populations. Within the limits set by the variation of environmental conditions, biotic interactions led to a great variety in body size and density across rivers. Differences in body size were tightly related to populations adopting different life history strategies. Hence, all these interrelationships influence different aspects of the ecology of brown trout and in the end drive populations to follow the fluctuations of carrying capacity though time, thus allowing the persistence of brown trout populations. These findings entail important implications for the design of conservation and management measures. Attempts to enhance populations through stocking could lead to stocked fish exceeding the carrying capacity, which could directly influence the future production of the stocked cohort through deleterious effects on growth and survival, but also could have detrimental effects on the performance of coexisting cohorts in the river. Furthermore, a continuous influence on body size through stocking measures could finally induce variations in other life-history traits, with deep implications on the life-history strategies adopted by brown trout populations.

Figure 3. Diagram of the described relationships. *D* means density, in the sense of competition level. BS means body size, and K means carrying capacity. *Lmat* means minimum length at maturity, *Amat* means age at maturity, and *Lmax* and *Amax* are maximum length and age, respectively.



7. 2. Conclusions

1. Water temperature had a pervasive role on length-at-age spatial variation in brown trout. The influence of water temperature on embryonic development likely determined the date of emergence and thus ultimately set the duration of the first growing period, when spatial variations in body size were mainly established in the study area. At a smaller spatial scale, the thermal effect was accounted for by altitude, an overall factor that includes the local variation of temperature and other variables through the altitudinal gradient. At a broader scale, latitudinal variation in climatic factors explained the spatial differences in length-at-age of brown trout through the European distribution of the species. Body size of brown trout decreased with latitude, following the converse of Bergmann's rule.

2. Brown trout from northern populations attained shorter maximum lengths, even though they lived longer. Both male and female brown trout matured older with increasing latitude. However, males matured smaller at higher latitudes, supporting the idea that maturation decision in males depends on the growing potential of the river. No such latitudinal effect was detected on the minimum length at maturity of females, since they probably have to reach a threshold size to optimize fecundity, which depends tightly on body size.

3. Density dependence of body size was a key process in the dynamics of brown trout populations. The temporal variation of its effects depended on the variations of the level of competition through ontogeny. There was also potentiality for delayed effects of the crowdedness conditions experienced by individuals constituting an age class on the size they attained the following year.

4. Intracohort and intercohort interactions shaped the effects of density dependence on body size of brown trout, with the density of all coexisting age classes negatively affecting the body size attained by the rest of age classes.

5. Water temperature acted on body size concurrently with density dependence. Its effects were higher on the first year of life, probably due to the influence it exerts on the date of emergence. Alevins were also affected by extremely high temperatures which became limiting and had deleterious effects on body size attained on the first year of life.
6. Density of the different age classes through a life span tracked the dynamics of carrying capacity and also reflected the effects of intracohort competition experienced the previous year. Intercohort competition between alevins and juveniles also determined population dynamics.

8. Bibliografía (References)

Nota: en este apartado sólo figuran las citas correspondientes a la Introducción General y la Discusión General. La bibliografía de cada uno de los capítulos se encuentra al final de los mismos.

Note: in this section only references from the General Introduction and General Discussion are included. References from the chapters are at the end of the corresponding chapter.

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