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Semblanzas Ictiológicas Iberoamericanas
Francisco Javier Lobón Cerviá

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y
Justina Ponte Gómez

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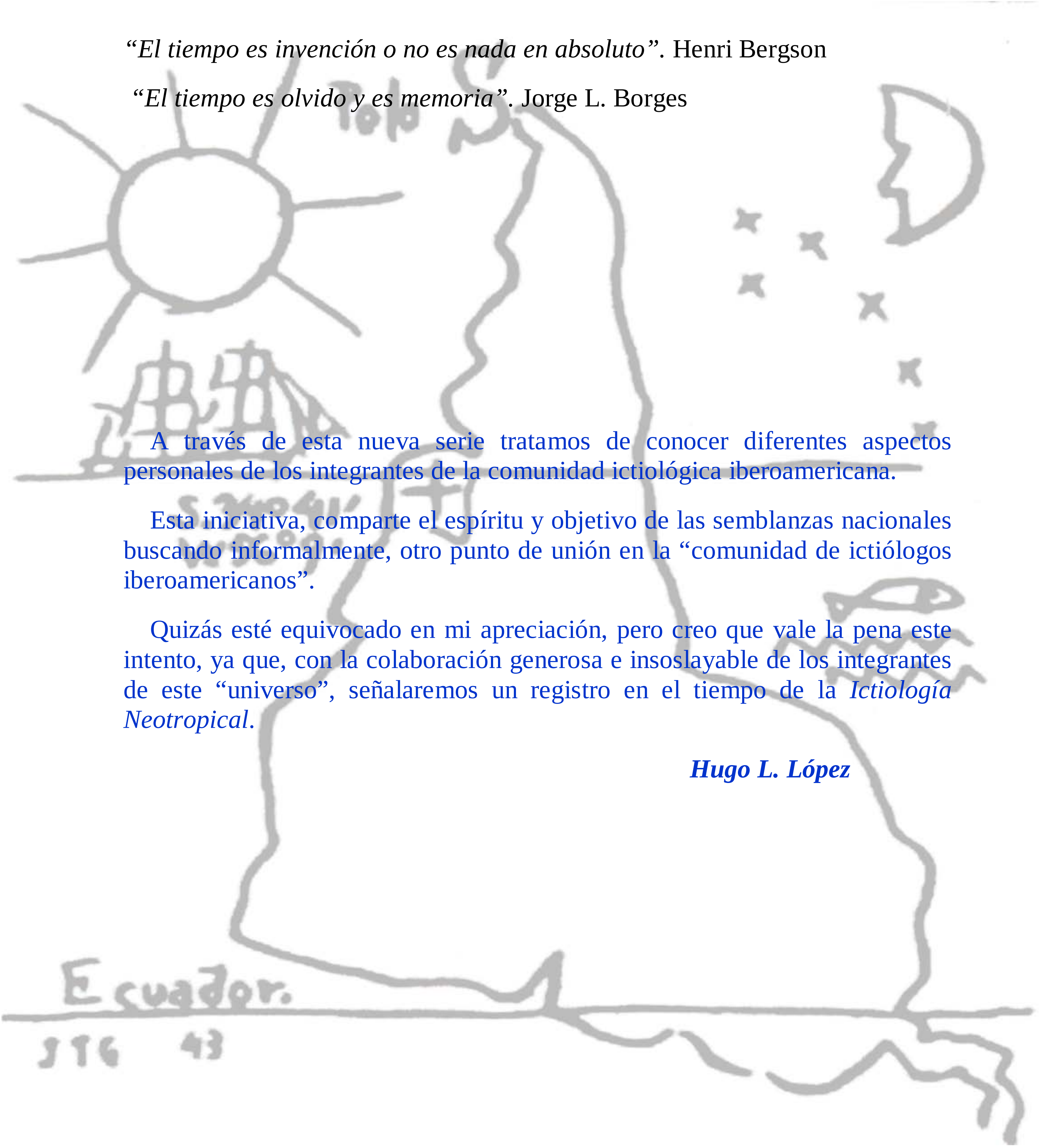

“El tiempo es invención o no es nada en absoluto”. Henri Bergson

“El tiempo es olvido y es memoria”. Jorge L. Borges

A través de esta nueva serie tratamos de conocer diferentes aspectos personales de los integrantes de la comunidad ictiológica iberoamericana.

Esta iniciativa, comparte el espíritu y objetivo de las semblanzas nacionales buscando informalmente, otro punto de unión en la “comunidad de ictiólogos iberoamericanos”.

Quizás esté equivocado en mi apreciación, pero creo que vale la pena este intento, ya que, con la colaboración generosa e insoslayable de los integrantes de este “universo”, señalaremos un registro en el tiempo de la *Ictiología Neotropical*.

Hugo L. López

Semblanzas Ictiológicas Iberoamericanas

Francisco Javier Lobón Cerviá

En algún lugar remoto del Amazonas Colombiano, 2011

Hugo L. López y Justina Ponte Gómez

ProBiota
División Zoología Vertebrados
Museo de La Plata
FCNyM, UNLP

Agosto, 2014

Imagen de Tapa
Javier Lobón Cerviá en algún lugar remoto del Amazonas Colombiano, 2010

Imagen de fondo de la Introducción
Porque en realidad nuestro norte es el sur, dibujo de Joaquín Torres García

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Cuestionario

-**Un libro**: *El Nombre de la Rosa*
-**Una película**: *Papillon*
-**Un tema musical**: *Yesterday*, The Beatles
-**Un artista**: Dalí
-**Un deporte**: casi todos (lo tengo asumido como el nuevo opio del pueblo)
-**Un color**: todos los del Arco Iris y sus infinitas combinaciones
-**Una comida**: cualquiera que esté bien cocinada
-**Un animal**: el Pirarucú (*Arapaima gigas*)
-**Una palabra**: vida
-**Un número**: el que sea tan grande (o tan pequeño) que yo no pueda comprender
-**Una imagen**: el Amazonas visto desde el aire
-**Un lugar**: A Serra do Mar do Brazil
-**Una estación del año**: cualquiera en la que no haga frio
-**Un nombre**: cualquiera que NO esté en el Santuario católico
-**Un hombre**: Hernan Cortés
-**Una mujer**: Isabel de Castilla (Isabel I); Bien… quiza Naomí Campbell
-**Un ictiólogo/a del pasado**: William Ricker
-**Un ictiólogo/a del presente**: todos los que contribuyen al conocimiento
-**Un personaje de ficción**: Don Quijote y Don Sancho, hermanados en la eternidad por D. Miguel de Cervantes
-**Un superhéroe**: super-heroína, la mamá de Superman

Lobón Cerviá con su nieta Daniela en Villanueva del Pardillo, Madrid, España, marzo del 2014

Lobón Cerviá (en cuclillas) participando de una ceremonia en la Comunidad Indígena Huitoto cercana a Leticia, Colombia, 2011

Lobón Cerviá en la margenes del río Esva a donde va con frecuencia-E.C.
Tomada de *Se puede pescar en el Narcea un salmón que sea del Esva*, ELCOMERCIO.es, octubre de 2014

ECOGRAPHY 23: 588–602. Copenhagen 2000

Longitudinal structure, density and production rates of a neotropical stream fish assemblage: the river Ubatiba in the Serra do Mar, southeast Brazil

Rosana Mazzoni and Javier Lobón-Cerviá

Mazzoni, R. and Lobón-Cerviá, J. 2000. Longitudinal structure, density and production rates of a neotropical stream fish assemblage: the river Ubatiba to the Serra do Mar, southeast Brazil. – Ecography 23: 588–602.

Spatio-temporal variations in the structure, density, biomass and production rates of fish were assessed in the neotropical River Ubatiba (Serra do Mar, southeast Brazil). Electrofishing techniques and the length-frequency method were shown to be reliable for the assessment of fish numbers and production rates in these running waters of medium conductivity. Eighteen fish species of small size and prolonged spawning period were broadly distributed throughout the river catchment. Over the year, the assemblage structure was persistent along the river. Water column omnivore and algae/detritivore species dominated in density (15086–70330 ind. ha^{-1}), whereas three omnivores and a piscivorous species accounted for 70% of the production (51.5–250.4 kg ha^{-1} yr^{-1}). Comparison of production rates among, tropical, temperate and Mediterranean stream fish assemblages indicate lower rates in tropical streams and an inverse relationship between production and species diversity, lower production rates in high-diversity tropical streams vs higher rates in low-diversity Mediterranean streams, with intermediate rates in temperate streams of intermediate diversity.

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Fish production (Ivlev 1945) as a major pathway of energy flow (Waters 1977) at population and assemblage levels has been intensively studied in Holarctic streams (Mann and Penczak 1986) and lakes (Randall et al. 1995) but only a few, scattered reports deal with production rates of stream fish from other zoogeographical regions (Hopkins 1971, Bishop 1973, Watson and Balon 1984, Penczak and Lasso 1991, Agostinho and Penczak 1995). The neotropics are of particular interest because they did lose species through glaciation, but acted as refuges for fish speciation incorporating extremely high numbers of species within complex trophic webs in all-season warm waters.

Within the neotropics, the relatively abundant literature on large river fish populations such as on the Rivers Amazonas, Madeira and Paraná (Goulding 1981, Goulding et al. 1988, Junk et al. 1989, Agostinho and Zalewski 1996) contrasts with the scarce information available for the 3000 km long eastern corridor of the Brazilian coast. This corridor contains a complex net of coastal streams rising in the high altitudes of the Serra do Mar, flowing east through Mata Atlantica forest, towards the Atlantic Ocean. The presence of extensive urban areas (Sao Paulo, Rio de Janeiro, Belo Horizonte, Curitiba, etc.) surrounding all these, small coastal rivers together with the recent human settle-

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Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*

Javier Lobón-Cerviá and Pedro A. Rincón

Lobón-Cerviá, J. and Rincón, P. A. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-living brown trout *Salmo trutta*. – Oikos 105: 641–646.

The relative importance of endogenous feedback mechanism vs environmental factors in the dynamics of animal populations is a long-standing, but not fully resolved yet, issue in ecology. We have addressed this subject by examining the dynamics of a stream-resident population of *Salmo trutta* in a northwestern Spain stream. Recruitment was the major determinant of population size and the abundance of recruits resulted from a combination of regional and local environmental factors. Stream discharge in March determined the amount of stream area suitable for newly emerged trout ($r^2 = 0.59$–0.79%), that in turn determined the abundance of recruits at each site ($r^2 = 0.51$–0.77%). Stream discharge determines the overall strength of annual recruitment. Discharge, however, combines with stream morphology at the site scale to result in a site-specific area suitable for juveniles and, hence, site-specific recruitment. Thus, our study exemplifies how an environmentally driven animal population may persist on time with little or no operation of endogenous regulatory mechanisms.

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Identifying the causes of spatio-temporal variations in the abundance of animal populations has long been at the core of ecological research (Nicholson 1933, Andrewartha and Birch 1954) and can acquire great practical importance (exploited species, pests, etc.). Much attention has been focused on the role of density-dependent processes that might regulate population size through negative feedbacks between population abundance and demographic parameters (i.e. mortality and fecundity). Endogenous regulation has been considered self-evidently necessary for population persistence and temporal stability, and empirical evidence of its occurrence in wild populations has been steadily accumulating (Sinclair 1989, Turchin 1995, 1999). In contrast, the role of density-independent factors (e.g. environmental variability) is less well understood (Ricklefs and Miller 2000). However, density-dependent and density-independent factors need not be mutually exclusive but their relative importance might be context-dependent (Harrison and Cappuccino 1995). This emergent notion appears akin to the classical view that density-dependent mechanisms would predominate in benign environments whereas density-independent processes would predominate in harsh environments (Haldane 1953, Huffaker and Messenger 1964).

In fishes and other aquatic organisms with complex life histories, population size is frequently determined by the abundance of recruits incorporating to the population (Victor 1983, Roughgarden et al. 1988, Doherty and Fowler 1994, Caley et al. 1996, Noda and Nakao 1996, Menge 2000). Fueled mostly by practical interest (e.g. forecast of fishery harvest), substantial efforts have been devoted to assess the effects of parental stocks and environmental factors on the recruitment dynamics of fish populations. The function linking the parental population and recruit abundance is known as a stock-

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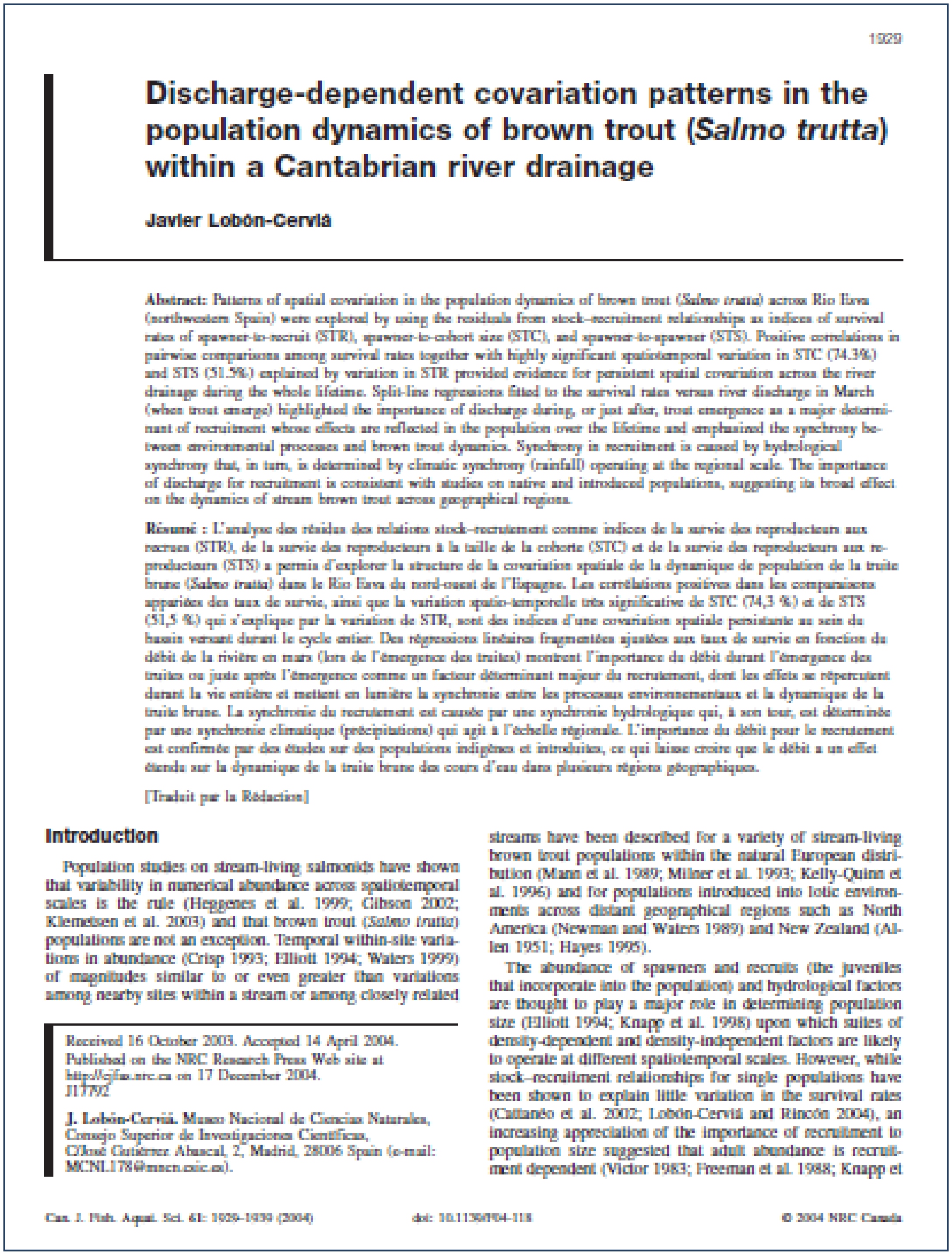

Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage

Javier Lobón-Cerviá

Abstract: Patterns of spatial covariation in the population dynamics of brown trout (*Salmo trutta*) across Río Esva (northwestern Spain) were explored by using the residuals from stock–recruitment relationships as indices of survival rates of spawner-to-recruit (STR), spawner-to-cohort size (STC), and spawner-to-spawner (STS). Positive correlations in pairwise comparisons among survival rates together with highly significant spatiotemporal variation in STC (74.3%) and STS (51.5%) explained by variation in STR provided evidence for persistent spatial covariation across the river drainage during the whole lifetime. Split-line regressions fitted to the survival rates versus river discharge in March (when trout emerge) highlighted the importance of discharge during, or just after, trout emergence as a major determinant of recruitment whose effects are reflected in the population over the lifetime and emphasized the synchrony between environmental processes and brown trout dynamics. Synchrony in recruitment is caused by hydrological synchrony that, in turn, is determined by climatic synchrony (rainfall) operating at the regional scale. The importance of discharge for recruitment is consistent with studies on native and introduced populations, suggesting its broad effect on the dynamics of stream brown trout across geographical regions.

Résumé : L'analyse des résidus des relations stock–recrutement comme indices de la survie des reproducteurs aux recrues (STR), de la survie des reproducteurs à la taille de la cohorte (STC) et de la survie des reproducteurs aux reproducteurs (STS) a permis d'explorer la structure de la covariation spatiale de la dynamique de population de la truite brune (*Salmo trutta*) dans le Río Esva du nord-ouest de l'Espagne. Les corrélations positives dans les comparaisons appariées des taux de survie, ainsi que la variation spatio-temporelle très significative de STC (74,3 %) et de STS (51,5 %) qui s'explique par la variation de STR, sont des indices d'une covariation spatiale persistante au sein du bassin versant durant le cycle entier. Des régressions linéaires fragmentées ajustées aux taux de survie en fonction du débit de la rivière en mars (lors de l'émergence des truites) montrent l'importance du débit durant l'émergence des truites ou juste après l'émergence comme un facteur déterminant majeur du recrutement, dont les effets se répercutent durant la vie entière et mettent en lumière la synchronie entre les processus environnementaux et la dynamique de la truite brune. La synchronie du recrutement est causée par une synchronie hydrologique qui, à son tour, est déterminée par une synchronie climatique (précipitations) qui agit à l'échelle régionale. L'importance du débit pour le recrutement est confirmée par des études sur des populations indigènes et introduites, ce qui laisse croire que le débit a un effet étendu sur la dynamique de la truite brune des cours d'eau dans plusieurs régions géographiques.

[Traduit par la Rédaction]

Introduction

Population studies on stream-living salmonids have shown that variability in numerical abundance across spatiotemporal scales is the rule (Heggenes et al. 1999; Gibson 2002; Klemetsen et al. 2003) and that brown trout (*Salmo trutta*) populations are not an exception. Temporal within-site variations in abundance (Crisp 1993; Elliott 1994; Waters 1999) of magnitudes similar to or even greater than variations among nearby sites within a stream or among closely related streams have been described for a variety of stream-living brown trout populations within the natural European distribution (Mann et al. 1989; Milner et al. 1993; Kelly-Quinn et al. 1996) and for populations introduced into lotic environments across distant geographical regions such as North America (Newman and Waters 1989) and New Zealand (Allen 1951; Hayes 1995).

The abundance of spawners and recruits (the juveniles that incorporate into the population) and hydrological factors are thought to play a major role in determining population size (Elliott 1994; Knapp et al. 1998) upon which suites of density-dependent and density-independent factors are likely to operate at different spatiotemporal scales. However, while stock–recruitment relationships for single populations have been shown to explain little variation in the survival rates (Cattanéo et al. 2002; Lobón-Cerviá and Rincón 2004), an increasing appreciation of the importance of recruitment to population size suggested that adult abundance is recruitment dependent (Victor 1983; Freeman et al. 1988; Knapp et

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21, 117–124

Density-dependent growth in stream-living Brown Trout *Salmo trutta* L.

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Summary

1. Several studies have offered evidence for the occurrence of density-dependent growth in stream-living Brown Trout. However, such evidence has been gleaned for low-density populations, whereas studies on persistently high-density populations have claimed that growth is density-independent. Such a paradoxical observation is shared with other salmonids and has been assumed by several authors to suggest that stream salmonid populations may be regulated by two different mechanisms: density-dependent growth at low densities and density-dependent mortality, in the absence of density-dependent growth, at high densities.

2. This comparative long-term study explored the occurrence of density-dependent growth by examining growth during the lifetime across cohorts in three stream-living Brown Trout populations representing the opposite extremes of growth and density documented throughout the species' distributional range.

3. This comparison highlighted identical growth–recruitment patterns in a high-density population with low potential for growth, in a low-density population with high potential for growth and in a population with intermediate traits. In the three populations, growth declined with increased recruitment describing negative power trajectories. These observations are consistent with there being a single, negative power relationship between growth and density where the effects of density dependence are stronger at low densities and become negligibly low at high densities.

4. Stream-living Brown Trout populations may be regulated by the continuous operation of density dependence on growth and mortality. In poorly recruited cohorts density dependence may operate on growth but not on mortality during a time period after which density dependence operates on both growth and mortality. In highly recruited cohorts, density dependence operates simultaneously on growth and mortality from the youngest life stages.

Key words: regulation, density-dependence, growth, stream, *Salmo trutta*

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Introduction

The negative feedback nature of density-dependent growth along with its overwhelming effects on major life-history traits such as age at maturity and fecundity (Rose *et al.* 2001) and its potential to be translated into density-dependent mortality is deemed to be a major mechanism underlying the numerical regulation of fish populations (Lorenzen & Enberg 2001). Succinctly, among the numerous factors that may affect growth throughout the lifetime (Lobón-Cerviá 2005a), the operation of density dependence predicts depressed growth at high densities caused by decreased food intake due to competition when resources become depleted by the increased abundance of individuals (Heath 1992).

Density-dependent growth has been documented in marine (Lorenzen & Enberg 2001) and freshwater fishes, including salmonids (Crisp 1993; Jenkins *et al.* 1999; Lobón-Cerviá 2005a; Imre, Grant & Cunjak 2005) and nonsalmonids (Le Cren 1958; Backiel & Le Cren 1967; Pivnicka & Svatora 1988; Wootton & Smith 2000), and experimental designs in the field (Nordwall, Naslund & Degerman 2001; Bohlin *et al.* 2002) and laboratory (Rodriguez-Muñoz, Nicieza & Braña 2003) have corroborated these patterns. In the wild, however, detecting the operation of density dependence on growth has proved to be difficult (Walters & Post 1993). Therefore, the generality of mechanistic issues and their relative

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Habitat quality enhances spatial variation in the self-thinning patterns of stream-resident brown trout (*Salmo trutta*)

Javier Lobón-Cerviá

Abstract: This study explored the extent to which variation in habitat factors related to growth and density influence self-thinning patterns in stream-living brown trout (*Salmo trutta*). Analysis of 110 cohorts at 12 sites of four contrasting streams revealed density–mass relationships in two phases. Density of survivors decreased little during the first half of their lifetime. A second phase commenced as individuals attained a threshold mass upon which density declined linearly with increased mass. The slopes of the second phase were greater than predicted by space and food demands. Among sites, these slopes were related to threshold densities at the beginning of the second phase. In turn, elevations, threshold densities, and slopes depicted concave trajectories against site depth, whereas threshold masses increased linearly. Apparently, cohorts remain below the carrying capacity during the first half of their lifetime and self-thin during the second half. Space-limited habitats impose site-specific carrying capacities and site-specific self-thinning coefficients, suggesting a common mechanism underlying self-thinning and an unanticipated, emerging property: two-phase patterns with far more variation in self-thinning coefficients. Variability in growth and density exhibited by brown trout and other salmonids across regions suggests that two-phase patterns may occur broadly, and self-thinning coefficients may vary widely.

Résumé : La présente étude explore dans quelle mesure la variation des facteurs de l'habitat reliés à la croissance et la densité influence les patrons d'auto-éclaircie chez des truites brunes (*Salmo trutta*) vivant en eau courante. L'analyse de 110 cohortes à 12 sites dans quatre cours d'eau bien différents indique deux phases dans les relations densité–masse. La densité des survivants diminue peu durant la première moitié de la vie des poissons. Une deuxième phase débute lorsque les individus atteignent une masse seuil au-delà de laquelle la densité diminue en fonction linéaire de l'accroissement de masse. Les pentes de cette seconde phase sont plus fortes que ne permettent de le prédire les besoins en espace et en nourriture. Parmi les sites, ces pentes sont reliées aux densités seuils au début de la seconde phase. En séquence, l'altitude, la densité seuil et la pente décrivent des trajectoires concaves en fonction de la profondeur du site, alors que la masse seuil augmente de façon linéaire. Il semble que les cohortes demeurent sous le stock limite durant la première moitié de leur cycle et procèdent à une auto-éclaircie durant la seconde moitié. Les habitats limités en espace imposent des stocks limites et des coefficients d'auto-éclaircie spécifiques au site, ce qui laisse croire à un mécanisme commun sous-jacent à l'auto-éclaircie et une caractéristique émergente inattendue, soit des patrons biphasiques avec beaucoup plus de variation dans les coefficients d'auto-éclaircie. La variabilité de la croissance et de la densité observée chez la truite brune et d'autres salmonidés dans les diverses régions indique que les patrons biphasiques peuvent se produire sur une grande échelle et que les coefficients d'auto-éclaircie peuvent varier considérablement.

[Traduit par la Rédaction]

Introduction

The importance and implications of body size to the structure and dynamics of populations composed of individuals with indeterminate and flexible growth have been well documented (Peters 1983; Lomicki 1988). Self-thinning refers to the allometric relationship between density (N) and body size (W) caused by intraspecific competition when a crowed population reaches the carrying capacity of the habitat. This relationship takes the form $N = aW - b$ or

$$(1) \qquad \log(N) = a - b\log(W)$$

Self-thinning is the ultimate expression of competition for limited resources and eq. 1 relates density and mass to define the carrying capacity of the habitat. In eq. 1, the significance of the intercept (a) is uncertain but is likely related to the habitat quality, whereas the slope (b) is the self-thinning coefficient and is thought to be determined by the demands of space and food. Following studies by Yoda et al. (1963) on intraspecific competition among higher plants, substantial evidence has been presented in support of this rule in sessile (Damuth 1998) and mobile (Fréchette and Lefaivre 1995) organisms, including invertebrate species (Begon 1986; Latto 1994; Guiñez et al. 2005) and vertebrate populations of birds (Juanes 1986), mammals (Silva and Downing 1995), and fishes (Grant 1993; Steingrímsson and Grant 1999). In addition, experimental studies on fishes

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Freshwater Biology

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Factors driving spatial and temporal variation in production and production/biomass ratio of stream-resident brown trout (*Salmo trutta*) in Cantabrian streams

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SUMMARY

1. The objective was to identify the factors driving spatial and temporal variation in annual production (P_A) and turnover (production/biomass) ratio (P/B_A) of resident brown trout *Salmo trutta* in tributaries of the Rio Esva (Cantabrian Mountains, Asturias, north-western Spain). We examined annual production (total production of all age-classes over a year) (P_A) and turnover (P/B_A) ratios, in relation to year-class production (production over the entire life time of a year-class) (P_T) and turnover (P/B_T) ratio, over 14 years at a total of 12 sites along the length of four contrasting tributaries. In addition, we explored whether the importance of recruitment and site depth for spatial and temporal variations in year-class production (P_T), elucidated in previous studies, extends to annual production.

2. Large spatial (among sites) and temporal (among years) variation in annual production (range 1.9–40.3 g m^{-2} per year) and P/B_A ratio (range 0.76–2.4 per year) typified these populations, values reported here including all the variation reported globally for salmonids streams inhabited by one or several species.

3. Despite substantial differences among streams and sites in all production attributes, when all data were pooled, annual (P_A) and year-class production (P_T) and annual (P/B_A) and year-class P/B_T ratios were tightly linked. Annual (P_A) and year-class production (P_T) were similar but not identical, i.e. $P_T = 0.94\ P_A$, whereas the P/B_T ratios were $4 + P/B_A$ ratios.

4. Recruitment (Rc) and mean annual density (N_A) were major density-dependent drivers of production and their relationships were described by simple mathematical models. While year-class production (P_T) was determined ($R^2 = 70.1\%$) by recruitment (Rc), annual production (P_A) was determined ($R^2 = 60.3\%$) by mean annual density (N_A). In turn, variation in recruitment explained $R^2 = 55.2\%$ of variation in year-class P/B_T ratios, the latter attaining an asymptote at $P/B_T = 6$ at progressively higher levels of recruitment. Similarly, variations in mean annual density (N_A) explained $R^2 = 52.1\%$ of variation in annual P/B_A, the latter reaching an asymptote at $P/B_A = 2.1$. This explained why P/B_T is equal to P/B_A plus the number of year-classes at high but not at low densities.

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Why Fishing Does Not Magnify Temporal Fluctuations in the Population Abundance of Stream-Living Salmonids

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The hypothesis that size-selective fishing induces magnified temporal variations in recruitment of fished, relative to unfished, populations is explored by comparing the recruitment of two stream-resident populations of brown trout Salmo trutta *inhabiting two tributaries of Rio Esva drainage (northwestern Spain). One population is exploited by angling; the other has never been fished. Fishing truncated the length structure of the fished population. In some years, fishing extirpated the two older reproductive year-classes (age 2 and 3), and the reproductive potential was limited to the age 1 spawners. Nevertheless, the temporal variation in recruitment over a 20-year period was lower in the fished population. The inter-annual variation in recruitment of the two populations closely tracked inter-annual environmental variation with a parabolic relationship between recruitment and stream discharge. Year-to-year variation in the carrying capacity to sustain recruits implies that annual recruitment only requires the survival of a few spawners to buffer the combined effect of environmental variability and fishing-induced mortality. Conventional fishing theory is not compatible with such processes, suggesting that new strategies are required to make fisheries and conservation goals compatible, with the importance of environmental stochasticity replacing the deterministic character of density-dependent population growth rates inherent to conventional fishery models.*

Keywords fishing effects; population truncation; recruitment; temporal variability; environmental control; fisheries and conservation goals

INTRODUCTION

Formulating effective harvesting and conservation goals for animal populations requires the identification of sources and ranges of natural variability over temporal scales and the extent to which human interventions may modify natural variability. Numerous studies have long recognized that fishing (the harvesting of aquatic wildlife; Pauly et al., 2002), as a source of density-independent mortality deemed to exceed natural mortality by orders of magnitude (Metz and Myers, 1998), may destabilize population abundance, generate boom-and-bust patterns, and increase extinction risks (Beddington and May, 1977; Jonzén et al., 2002). Several studies have documented ranges of temporal variability in wild and exploited populations of marine (Cushing, 1996) and freshwater fishes (Lobón-Cerviá and Mortensen, 2005; Elliott and Elliott, 2007). However, the separation of the fishing effects from the overwhelming natural variability that typifies fish populations and the elucidation of the mechanisms that permit these populations to withstand severe mortalities caused by fishing remain challenging.

Intensive investigations on marine fish populations have recurrently reported detrimental effects of fishing through the so-called "age truncation effect," where size-selective fishing truncates the age and length distributions of the populations, reduces life expectancy (Longhurst, 2002) and the abundance of larger females (Green, 2008), and may induce changes in life history traits (Thériault et al., 2008) of major ecological (Venturelli et al., 2009), genetic (Lewin et al., 2006), and evolutionary consequences (Law, 2000; Olsen et al., 2004; Jorgensen et al., 2007; Hard et al., 2008). Recently, Hsieh et al. (2006), based on the

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Freshwater Biology

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Patterns of natural mortality in stream-living brown trout (*Salmo trutta*)

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SUMMARY

1. We tested the hypothesis that lifetime mortality patterns and their corresponding rates and causal factors differ among populations of stream-living salmonids. To this end, we examined the lifetime mortality patterns of several successive cohorts of two stream-living brown trout (*Salmo trutta*) populations in Spain and Denmark.

2. In the southern population, we observed a consistent two-phase pattern, in which mortality was negligible during the first half of the lifetime and severe during the rest of the lifetime. In contrast, the northern population demonstrated a three-phase pattern with an earlier phase varying from negligible to severe, followed by a second stage of weak mortality, and lastly by a third life stage of severe mortality.

3. Despite substantial differences in the mortality patterns between the two populations, the combined effect of recruitment (as a proxy of the density-dependent processes occurring during the lifetime) and mean body mass (as a proxy of growth experienced by individuals in a given cohort) explained *c.* 89% of the total lifetime mortality rates across cohorts and populations.

4. A comparison with other published data on populations of stream-living brown trout within its native range highlighted lifetime mortality patterns of one, two, three and four phases, but also suggested that common patterns may occur in populations that experience similar individual growth and population density.

Keywords: density, growth, mortality rates, recruitment, stream-living salmonids

Introduction

The elucidation of mortality patterns across the lifetime and their corresponding rates and their causal factors is central in fish ecology research and critical for the effective design of management and conservation strategies. Across the lifetime, a wide array of factors may cause mortality including intrinsic factors such as lethal alleles in genotypes (Wootton, 1990), constraints in body size and temperature on metabolism (Pepin, 1991; McCoy & Gillooly, 2008) and age, sex and reproduction (Gunderson & Dygert, 1988; Hutchings, 1994). Extrinsic factors are also influential and may include the availability of space and food, parasites, predation, diseases and harsh environmental conditions such as extremes of temperature, discharge, oxygen depletion, winter conditions (Hurst, 2007) and climatic changes (Biró, Post & Booth, 2007). Moreover, both intrinsic and extrinsic factors may act in combination with fishing-induced mortality in exploited populations.

However, identifying mortality patterns in the wild and their causal factors has proved difficult for both marine and freshwater fish populations. Such difficulties have led to the development of a variety of predictive models through theoretical approaches involving metabolic (Brown *et al.*, 2004) and size spectrum theories (Peterson & Wroblewski, 1984; Kerr & Dickie, 2001), mathematical inferences (Wang, 1999) and empirical models relating mortality rates with other life history traits (Beverton &

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ARTICLE

Recruitment and survival rate variability in fish populations: density-dependent regulation or further evidence of environmental determinants?

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Abstract: Recently, Minto et al. (2008), based on a fishery data set including marine, estuarine, and freshwater fishes, described higher variability in the survival rates of juveniles at low rather than at high parental density in an inversely density-dependent fashion and suggested density-dependent mechanisms underpinning those patterns. This study, based on a long-term study of brown trout (*Salmo trutta*; a species and habitat not included in the Minto et al. (2008) analysis), documents that survival rates in these stream-living populations exhibit a pattern that matches exactly those reported by Minto et al. (2008). Nevertheless, hypothesis testing rejected the occurrence of stock–recruitment relationships and the operation of density-dependent recruitment regulation. The patterns elucidated for these brown trout populations can be entirely explained by the operation of two single environmental factors, namely, stream discharge in March determining annual survival rates across streams and sites and site-specific depth determining site-specific survival rates. It is open to question that exactly the same patterns can be generated by two sets of opposing factors, density-dependent (i.e., Minto et al. 2008) and environmental factors (i.e., this study). The consistency of this pattern suggests that survival rates and recruitment are probably determined by environmental factors across fish populations and habitats.

Résumé : Minto et al. (2008) ont récemment décrit, à la lumière d'un ensemble de données sur les pêches incluant des poissons de mer, d'estuaire et d'eau douce, une plus grande variabilité des taux de survie de juvéniles à faible, plutôt qu'à forte, densité parentale (relation de dépendance inverse avec la densité) et suggéré que des mécanismes dépendant de la densité sous-tendraient ces observations. Notre étude reposant sur le suivi à long terme de truites brunes (*Salmo trutta*; une espèce et un habitat non inclus dans l'analyse de Minto et al. (2008)) révèle des taux de survie, dans ces populations de cours d'eau, dont la distribution est identique à celles signalées par Minto et al. (2008). Un test d'hypothèse a toutefois permis d'exclure la présence de relations stock–recrutement et d'une régulation du recrutement dépendant de la densité. Deux facteurs environnementaux peuvent entièrement expliquer les patrons obtenus pour les populations de truite brune, à savoir le débit du cours d'eau en mars, qui détermine les taux de survie annuels d'un cours d'eau et d'un site à l'autre, et la profondeur en un site donné, qui détermine le taux de survie propre à ce site. Il semble douteux que des patrons exactement identiques puissent être produits par deux ensembles de facteurs s'opposant, à savoir des facteurs dépendant de la densité (Minto et al. 2008) et des facteurs environnementaux (la présente étude). La cohérence de ces patrons porte à croire que les taux de survie et de recrutement caractérisant différentes populations de poissons et différents habitats sont probablement déterminés par des facteurs environnementaux. [Traduit par la Rédaction]

Introduction

Fluctuations in density across temporal scales typify the numerical dynamics of wild animal populations. Identifying the mechanisms underlying such variation is a fundamental goal of ecology research and critical for population management. Specifically, ecological research has attempted to elucidate the relative importance of density-dependent feedback loops underpinning population size (Nicholson 1933) versus the operation of density-independent factors under which populations fluctuate over time tracking environmental randomness (Andrewartha and Birch 1954). This central problem is critical in fishery research and, more specifically, in the design of management strategies for exploited fish populations.

Unlike other vertebrates, fish populations are characterized by severe mortalities during the first few weeks of life (Elliott 1994; Bradford and Cabana 1997), and recruitment (the abundance of the youngest juveniles surviving to commence a new year class) is deemed to be set during or soon after that time period. "At its simplest, recruitment is the survival from the eggs that were laid." (Cushing 1996) Decades-long efforts to identify the factors causing mortality vis-à-vis the setting of recruitment magnitudes have fostered considerable insight into the dynamics of fish populations (Chambers and Trippel 1997) and its application to fishery management (Hilborn and Walters 1992; Walters and Martell 2004). Nevertheless, unequivocal identifications of the relative roles of density-dependent versus density-independent factors underlying recruitment variations remain sufficiently elusive to have been considered an "enigma" (Frank and Leggett 1994).

As a consequence, the development of management strategies for fisheries and conservation purposes undergo two differing and opposing approaches. On the one hand, fish populations are assumed to be regulated by density-dependent processes. Under this assumption, a core hypothesis relates recruitment to the abundance of the parental stock. Such links, in the form of stock–recruitment relationships, as a major expression of density-dependent recruitment regulation, are expected to occur across fish populations and habitats. These relationships imply that beyond the operation of any factor causing mortality from the egg

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