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References data on the growth and population parameters of brown trout in siliceous rivers of Galicia (NW Spain)

Javier Sánchez-Hernández[1,2,*], María J. Servia[3], Rufino Vieira[2], Sandra Barca-Bravo[1,2] and Fernando Cobo[1,2]

[1] Department of Zoology and Physical Anthropology, Faculty of Biology. University of Santiago de Compostela. Campus Sur s/n, 15782 Santiago de Compostela, Spain.
[2] Station of Hydrobiology "Encoro do Con", Castroagudín s/n, 36617 Vilagarcía de Arousa, Pontevedra, Spain.
[3] Department of Animal Biology, Vegetal Biology and Ecology. Faculty of Science. University of A Coruña. Campus da Zapateira s/n. 15008 A Coruña, Spain.

[*] Corresponding author: javier.sanchez@usc.es

Received: 15/3/12 Accepted: 22/6/12

ABSTRACT

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Brown trout is an important angling species worldwide, and its morphology, population structure and genetics can be highly variable from one location to another. In this study, we provide data for the establishment of reference range values for several population and growth parameters of brown trout in the Cantabrian-Atlantic siliceous rivers of Galicia (NW Spain). Additionally, this study tests the hypothesis that the population and growth parameters differ among sections of rivers with different exploitation statuses (unexploited, exploited-regulated and exploited-open sections). Our study revealed that such population parameters as biomass and production were higher in unexploited sections, but the differences in growth among the sections with different angling regulations were not consistent. The findings of this study are discussed in light of the present knowledge on the status of trout fisheries, as it is essential for the development of management plans. Additional studies are needed to clarify whether the differences in growth can be correlated to the angling regulations.

Key words: Population parameters, growth, reference categories, angling regulations, Iberian Peninsula, Water Framework Directive.

RESUMEN

Datos de referencia de crecimiento y parámetros poblacionales de trucha común en ríos silíceos de Galicia (NO España)

La trucha común es una especie muy apreciada por los pescadores deportivos en todo el mundo, y su morfología, estructura poblacional y características genéticas pueden variar considerablemente entre áreas geográficas próximas. En este estudio proporcionamos datos para el establecimiento de categorías de referencia de varios parámetros poblacionales y de crecimiento de la trucha común en ríos silíceos Cantábrico-Atlánticos de Galicia (NO España). Además, con la realización de este estudio se pretende verificar la hipótesis de que los parámetros poblacionales y el crecimiento pueden variar entre tramos de ríos con diferente tipo de regulación de pesca deportiva (tramos vedados o inexplotados, tramos de pesca acotados y tramos de pesca libre). Así, nuestro estudio reveló que algunos parámetros poblacionales como la biomasa y la producción fueron más elevados en los tramos vedados, pero las diferencias en el crecimiento entre tramos con diferente regulación de pesca deportiva no fueron consistentes. Los resultados de este trabajo se discuten teniendo en cuenta el conocimiento actual sobre el estado de las poblaciones de trucha común, pues son esenciales para el desarrollo de planes de gestión. No obstante, se requieren de más estudios para aclarar si las diferencias en crecimiento se pueden relacionar con el tipo de regulación de pesca deportiva.

Palabras clave: *Parámetros poblacionales, crecimiento, categorías de referencia, regulación de pesca deportiva, Península Ibérica, Directiva Marco del Agua.*

INTRODUCTION

Limnological studies of the Galician freshwater basins (NW Spain) have shown the homogeneity of the physicochemical characteristics of its watercourses (Membiela *et al*., 1991): the freshwaters in Galicia are generally acid and very soft (Martínez-Ansemil & Membiela, 1992) watersheds draining granite and schist (Membiela *et al*., 1991; Martínez-Ansemil & Membiela, 1992). Moreover, in terms of its freshwater fish biogeography, Galicia has been considered a region that is independent from the rest of the Iberian Peninsula (e.g., Hernando & Soriguer, 1992; Filipe *et al*., 2009). Indeed, as a consequence of the hierarchical characterisation of Spanish rivers for their classification in accordance with the Water Framework Directive of the European Union by González del Tánago & García de Jalón (2006), most of the Galician watercourses have been recently included in a category called "Cantabrian-Atlantic siliceous rivers" by the Spanish Hydrological Plan.

Brown trout (*Salmo trutta* Linnaeus, 1758) is an important angling species worldwide. The fish has an outstanding socio-economic importance, both in commercial and sport fisheries, and brown trout is frequently used as a tourist attraction (Aas *et al*., 2000; Butler *et al*., 2009). Although the management of the wild stocks is the responsibility of the regional governments in Spain, different researchers have proposed some management guidelines to improve the conservation status of the brown trout populations (e.g., Braña *et al*., 1992, 2004; Almodóvar & Nicola, 1998; Alonso-González & García de Jalón, 2001), with the growth and population parameters being the variables usually employed in fishery assessments (e.g., Almodóvar & Nicola, 2004; Oscoz *et al*., 2005). These parameters are well known for the brown trout populations in different regions of Spain and can be highly variable (e.g., García de Jalón *et al*., 1986; Lobón-Cerviá *et al*., 1986; Nicola & Almodóvar, 2004; Parra *et al*., 2009; Lobón-Cerviá, 2010; Alonso *et al*., 2011). Contrastingly, the growth and population parameters of the brown trout populations in the Cantabrian-Atlantic siliceous rivers of Galicia remain poorly investigated, and the limited information available comes mainly from Garcia de Jalón *et al*. (1990) and Hervella & Caballero (1999), thus impeding the comparison of parameters between similar populations or river types.

Density categories have been established for salmonid populations in North America (Joyce *et al*., 1990; Stanfield *et al*., 2006) and Europe (Niemelä, 2004), whereas several authors have standardised the growth parameters of the brown trout populations in some regions of Europe (Kennedy & Fitzmaurice, 1971; Pedicillo *et al*., 2010). Thus, a wider knowledge on the reference categories for the growth and population parameters would improve management plans, as the establishment of these categories for fish populations is essential before meaningful comparisons can be made among rivers (Klemetsen *et al*., 2003). Hence, the aim of this work is the establishment of reference categories for the growth and population parameters of brown trout in the Cantabrian-Atlantic siliceous rivers of Galicia (NW Spain). Additionally, we discuss the effects of angling exploitation on these parameters.

MATERIAL AND METHODS

Study area

For the purpose of this study five annual survey campaigns were conducted in the summer season (from June to September) between 2007 and 2011. A total of 32 siliceous rivers of Galicia (NW Spain) were studied. As shown in Appendix 1 and figure 1, the majority of the rivers were sampled once, but four of the sampling stations for three rivers were sampled twice (Rivers Tamuxe, Hospital and Deva). Thus, the selection of the sampling stations was with the intention of providing an ample spectrum of the temporal and spatial variations in the environmental conditions.

The sampling sites included exploited and unexploited reaches, with three different angling regulations: unexploited sections (fishing activities are forbidden); exploited-regulated sections (sections with a limited in the number of anglers

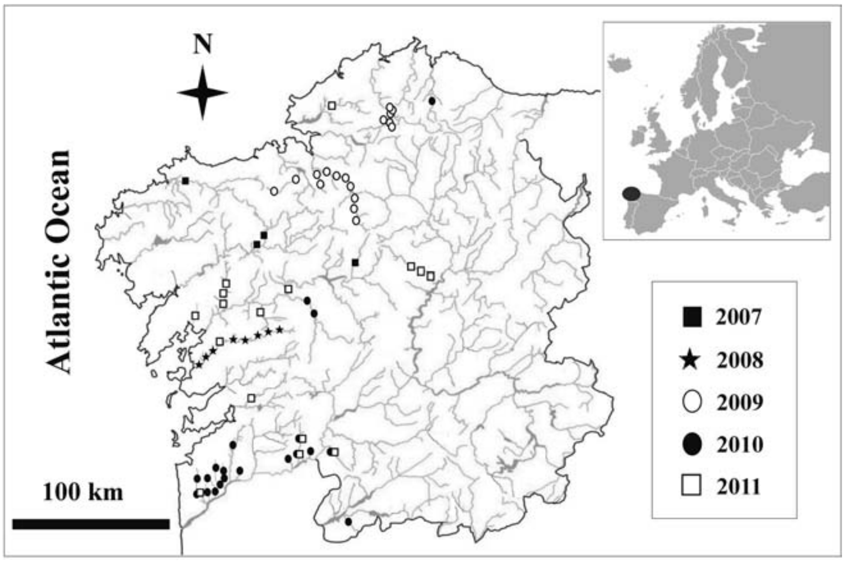

Figure 1. Location of the sampling sites. *Localización de las estaciones de muestreo.*

per day; anglers pay for a special permit for fishing) and exploited-open sections (free sections with no limitation in the number of anglers per day). Detailed information on the sampling sites is provided in Appendix 1 and figure 1.

Fish collection

The protocols used in this study conform to the ethical laws of the country and have been reviewed by the ethics committee of the University of Santiago de Compostela and the regional government (Xunta de Galicia). Fishes were collected using pulsed D.C. backpack electrofishing equipment (Hans Grassl GmbH, ELT60II) and anaesthetised with benzocaine (0.3 ml l^{-1}). The fishes were measured to the nearest 1 mm and weighed to the nearest 0.01 g. Scales were collected only from individuals > 10 cm. The ages of the fish were estimated by scale examination and using the Petersen's length-frequency method (Bagenal & Tesch, 1978). After manipulation, all of the fishes were returned to the river.

Growth and population parameters

Individuals of age-0+ and age-1+ were found in all of the sampling sites, with the exception of four rivers in 2010: River Tripes (only 0+ individuals) and Rivers Deva, Hospital and Tamuxe (only 1+ individuals). Consequently, only the density and biomass were estimated in these rivers. Age-2+ and age-3+ individuals were also present in a high number of populations (in 62 and 34 populations, respectively), but age-4+ individuals were only found in 12 populations. Older specimens were found (one 5+ trout in the River Barcés, one 6+ trout in the River Mandeo and one 7+ trout in the River Barcés), but it was impossible to calculate the specific growth rate (*G*) between these age classes. The condition factor (*CF*) for each fish was calculated according to Granado-Lorencio (1996) using the formula $CF = 100W/L^3$, where W is the wet weight (g) and L is the fork length (cm).

Growth was estimated using several methods. First, the Von Bertalanffy equation (Von Bertalanffy, 1938) assumes that a fish grows toward a theoretical maximum length or weight and that the closer the length is to the maximum, the slower is the rate of the change in size. Thus, the growth parameters L_∞ and k were calculated using the FISAT II (version 1.2.1) software package (Gayanilo *et al.*, 2005). Second, growth was measured as the specific growth rate (*G*) in body weight per year, as follows:

($G = (\ln W_2 - \ln W_1)/(t_2 - t_1)$), where W_1 and W_2 are the mean body weight at times t_1 and t_2 (Jensen *et al.*, 1997). Third, because the comparison of growth among different organisms is often complex, we used the growth performance phi-prime index (Moura *et al.*, 2009). Thus, according to Pedicillo *et al.* (2010), the index of the growth performance phi-prime Φ' was calculated by means of the following equation of Pauly & Munro (1984): $\Phi' = \log 10(k) + 2 \log 10(L_\infty)$, where k and L_∞ are the Von Bertalanffy growth parameters. Fourth, the weight-length relationship was calculated using the equation $W = aL^b$, where W is the total weight in g and L the total length in cm, with a being a coefficient related to the body form and b an exponent indicating isometric growth when equal to 3. The parameters a and b were estimated by the linear regression of the transformed equation: $\log W = \log a + b \log L$. The statistical significance level of r^2 was estimated, and the b-value for *S. trutta* was determined to verify whether the growth was different from the isometric ($b = 3$). When the value of b is other than 3, the weight increase is allometric (positive allometry if $b > 3$, negative allometry if $b < 3$) (Ricker, 1975).

The estimated density of each age class was calculated using the Zippin multiple-pass depletion method (Zippin, 1958; Zamora *et al.*, 2009). The biomass was calculated using the mean weight per age class and the density of each age class. The total density and biomass were calculated as the sum of each age class density and biomass, respectively. According to García de Jalón *et al.* (1993), brown trout juveniles include 0+ and 1+ cohorts, and adults include individuals ≥ 2+. Hence, in this work, the density and biomass are reported for each age class, juveniles, adults and for the total of all of the individuals.

The annual production was estimated as the product of the specific growth rate (G) and biomass (B) using algebraic or graphic techniques, as outlined by Allen (1971). From the calculated estimates of total biomass and annual production, we calculated the turnover ratio (P/B) as the ratio between the production and biomass for the entire fish community.

The specific survival rate (S) for each age class was calculated using the formula $S = N_{t+1}/N_t$, where N_{t+1} and N_t are the number of individuals between consecutive age classes (t). In this work, S was calculated with the values of each age class and was presented as the mean value by sampling site. A graphical representation was used to determine the instantaneous mortality rate (Z). Thus, following Cowx & Frear (2004), we used the linear relationship between the natural logarithm of the number of fishes in each age class ($\ln N_t$) and age (t) to determine Z according to $\ln N_t = \ln N_0 - Z_t$.

Establishment of reference categories

To establish the reference categories for the growth and population parameters in the brown trout populations of the Galician siliceous rivers, all of the variables studied in this work (e.g., density, biomass) were collated and separated by percentiles following Pedicillo *et al.* (2010). Thus, five categories were established: 1) Very poor – when the value of the variable is below the 10th percentile; 2) Poor – when the value of the variable is between the 10th and the 30th percentile; 3) Normal – when the value of the variable is between the 30th and the 70th percentile; 4) High – when the value of the variable is between the 70th and the 90th percentile and 5) Very high – when the value of the variable exceeds the 90th percentile. References categories for the density and biomass of ages 5+, 6+ and 7+ were not calculated because only one individual was obtained for each age class (see above).

Statistical analysis

The statistical analyses were conducted using the programme PASW Statistics 18. The normality of the distribution and homogeneity of the variances were tested using Shapiro-Wilk and Levene's tests, respectively. Kruskal-Wallis tests for non-normal data were used to detect differences among the angling-regulation sections, and the Mann–Whitney U test was used for comparisons *a posteriori*. Additionally, the b-value of the weight–length relationship for each angling-

Table 1. Statistics and reference categories of growth parameters. The *CF* (condition factor), L_∞ and *k* (growth parameters calculated using FISAT II software package), specific growth rate (*G*), index of growth performance phi-prime (Φ′) and *b*-values of the weight-length relationship. *Calculated for one sampling site. Standard error (SE), minimum (Min) and maximum (Max). *Estadísticos y categorías de referencia de los parámetros de crecimiento.* CF *(factor de condición),* L_∞ *y* k *(parámetros de crecimiento calculados usando el software FISAT II), tasa de crecimiento específica* (G)*, índice de crecimiento estándar phi prima* (Φ′) *y* b-*valores de la relación peso-longitud. *Calculados para una estación de muestreo. Error estándar (SE), mínimo (Min) y máximo (Max).*

	Statistics				Reference categories				
	Mean	SE	Min	Max	Very poor	Poor	Normal	High	Very high
CF	1.19	0.007	1.06	1.32	<1.11	1.11–1.16	1.16–1.23	1.23–1.27	> 1.27
k (g $year^{-1}$)	0.21	0.011	0.05	0.41	<0.1	0.1–0.14	0.14–0.27	0.27–0.32	> 0.32
$L\infty$ (cm)	48.15	1.73	29.15	116	<34.42	34.42–41.19	41.19–50.86	50.86–63.38	> 63.38
G_{0+-1+} (g $year^{-1}$)	2.17	0.053	0.97	3.32	<1.73	1.73–1.94	1.94–2.30	2.30–2.83	> 2.83
G_{1+-2+} (g $year^{-1}$)	1.06	0.037	0.64	1.82	<0.72	0.72–0.88	0.88–1.15	1.15–1.49	> 1.49
G_{2+-3+} (g $year^{-1}$)	0.77	0.043	0.36	1.53	<0.48	0.48–0.63	0.63–0.84	0.84–1.09	> 1.09
G_{3+-4+} (g $year^{-1}$)	0.69	0.085	0.36	1.16	<0.36	0.36–0.46	0.46–0.86	0.86–1.14	> 1.14
G_{4+-5+} (g $year^{-1}$)*	0.74	—	—	—	—	—	—	—	—
Mean *G*(g $year^{-1}$)	1.49	0.048	0.95	2.46	<1.10	1.10–1.23	1.23–1.58	1.58–2.12	> 2.12
Φ′	2.61	0.193	2.27	2.94	<2.41	2.41–2.49	2.49–2.72	2.72–2.81	> 2.81
b-values	3.02	0.01	2.83	3.21	<2.90	2.90–2.98	2.98–3.07	3.07–3.12	> 3.12

regulation section was tested using the t-test to verify whether it was significantly different from the isometric ($b = 3$). All of these tests were considered statistically significant at a p level < 0.05.

RESULTS

Growth and population parameters

In the present study, the range of condition factors was 1.06-1.32. We propose a normal category for the Galician populations, with values between 1.16 and 1.23 (Table 1). Differences among the angling regulation types were not significant (Table 2). The mean fork length of each age class varied: 0+ years, 2.3-11 cm; 1+ years, 8.2-21.6 cm; 2+ years, 14.1-26.5 cm; 3+ years 19-40.5 cm and 4+ years, 27-49 cm. Table 3 shows the descriptive statistics of the biometric measurements (size and weight) of all of the age class.

The growth parameters L_∞ and k of the Von Bertalanffy equation for the 66 populations showed an ample range of values: L_∞ varied between 29.15 cm and 116 cm, and k varied between 0.05 and 0.41 g $year^{-1}$ (Table 1). The results for the mean specific growth rate (G) confirm the wide range of data (Table 1). Figure 2 shows the evolution of G in the brown trout populations by age class, being higher in young individuals and decreasing with age. The index of the growth

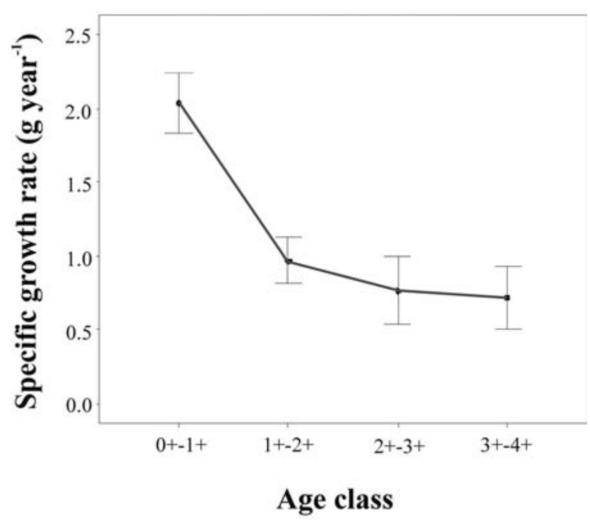

Figure 2. Specific growth rate (g $year^{-1}$) in the brown trout populations of the Cantabrian-Atlantic siliceous rivers of Galicia by age class. Error bars represent 95 % confidence intervals. *Tasa de crecimiento específica (g año^{-1}) en poblaciones de trucha común de ríos silíceos Cantábrico-Atlánticos de Galicia por clase de edad. Las barras de error representan intervalos de confianza del 95 %.*

Table 2. Results of Kruskal-Wallis tests among the sections with different angling regulations. The *CF* (condition factor), L_∞ and *k* (growth parameters calculated using FISAT II software package), specific growth rate (*G*), index of growth performance phi-prime (Φ′) and *b*–values of the weight–length relationship. *Significance <0.05. *Resultados de la prueba Kruskal–Wallis entre secciones con diferente tipo de regulación de pesca deportiva.* CF *(factor de condición),* L_∞ *y* k *(parámetros de crecimiento calculados usando el software FISAT II), tasa de crecimiento específica* (G)*, índice de crecimiento estándar phi prima (Φ′) y* b*-valores de la relación peso-longitud. *Significación <0.05.*

	Kruskal–Wallis test			Kruskal–Wallis test	
	H	*p*		*H*	*p*
Brown trout performance			Density 1+ (trout m^{-2})	3.09	0.213
CF	0.81	0.666	Biomass 1+ (g m^{-2})	5.93	0.052
Growth parameters			Density 2+ (trout m^{-2})	4.49	0.106
k (g $year^{-1}$)	1.40	0.498	Biomass 2+ (g m^{-2})	3.57	0.167
L∞ (cm)	1.02	0.602	Density 3+ (trout m^{-2})	2.43	0.296
G_{0+-1+} (g $year^{-1}$)	2.80	0.247	Biomass 3+ (g m^{-2})	6.00	0.050
G_{1+-2+} (g $year^{-1}$)	1.11	0.573	Density 4+ (trout m^{-2})	0.84	0.657
G_{2+-3+} (g $year^{-1}$)	0.91	0.634	Biomass 4+ (g m^{-2})	2.27	0.321
G_{3+-4+} (g $year^{-1}$)	1.63	0.443	Density juveniles (trout m^{-2})	2.46	0.292
Mean *G*(g $year^{-1}$)	2.51	0.285	Biomass juveniles (g m^{-2})	6.57	0.037*
Φ′	6.52	0.038*	Density adults (trout m^{-2})	3.71	0.156
b–values	0.79	0.675	Biomass adults (g m^{-2})	5.41	0.067
Population parameters			Production (g m^{-2} per year)	8.00	0.018*
Total density (trout m^{-2})	4.02	0.134	Survival (*S*)	1.27	0.529
Total biomass (g m^{-2})	14.79	0.001*	Mortality (*Z*)	1.20	0.942
Density 0+ (trout m^{-2})	0.70	0.703	P/B (per year)	0.88	0.644
Biomass 0+ (g m^{-2})	0.32	0.851			

performance phi-prime (Φ′) varied between 2.27 and 2.94 (Table 1). Statistically significant differences were found among the sections with different types of angling regulation (Kruskal-Wallis test; $H = 6.52$, $p = 0.038$), with the index higher being in unexploited versus exploited-open sections (Mann-Whitney U test; $p = 0.014$). However, no differences were observed between the unexploited and exploited-regulated sections (Mann-Whitney U test; $p = 0.374$) or between the exploited-regulated and exploited-open sections (Mann-Whitney U test; $p = 0.226$).

Regarding the weight–length relationship, all of the estimated *b*-values are within the range 2.83–3.21, but the growth of *S. trutta* was not strictly isometric (t-test, $df = 65$, $t = 2.059$, $p = 0.044$). For each regulated angling section, the brown trout populations of the unexploited and exploited-regulated sections showed isometric growth (t-test, $df = 10$, $t = 0.137$, $p = 0.894$ and t-test, $df = 10$, $t = 0.127$, $p = 0.901$, respectively), with only the exploited-open sections showing no isometric growth (t-test, $df = 43$, $t = 2.477$, $p = 0.017$). Table 1 reports the descriptive statistics and reference categories of the growth parameters.

The population parameters also showed spatial and temporal fluctuations (Table 4); for example, the percentage of juveniles in terms of density varied between 33.35 and 100 % and the biomass between 7.17 and 100 %. The reference categories of the population parameters are given in Table 4.

Effects of fishery management on population parameters

Concerning the effects of angling exploitation on the population parameters, the differences in the biomass, biomass of juveniles and production among the different angling-regulation sections were statistically significant (Table 2 and Fig. 3). The biomass was higher in the unexploited than in the exploited-regulated (Mann-Whitney U test; $p = 0.008$) or exploited-open sections

Table 3. Size and weight data for each age class. *Only one individual was found. *Estadísticos de talla y peso para cada clase de edad. *Sólo capturado un ejemplar.*

	Statistics					Statistics			
	Mean	SE	Min	Max		Mean	SE	Min	Max
0+					4+				
Size (cm)	6.9	0.02	2.3	11	Size (cm)	32.9	1.37	27	49
Weight (g)	4.3	0.04	1	17	Weight (g)	435.0	74.55	208	1422
1+					5+*				
Size (cm)	13.6	0.04	8.2	21.6	Size (cm)	47	—	—	—
Weight (g)	33.0	0.31	3	121.6	Weight (g)	1323	—	—	—
2+					6+*				
Size (cm)	19.1	0.10	14.1	26.5	Size (cm)	50.6	—	—	—
Weight (g)	89.2	1.47	34	222	Weight (g)	2192	—	—	—
3+					7+*				
Size (cm)	25.9	0.35	19	40.5	Size (cm)	58	—	—	—
Weight (g)	210.7	9.22	82	732	Weight (g)	2513	—	—	—

Table 4. Statistics and reference categories of population parameters. Specific survival rate (*S*), instantaneous mortality rate (*Z*) and production/biomass (P/B per year). Standard error (SE) and minimum (Min) and maximum (Max). *Only one individual was found. *Estadísticas y categorías de referencia de los parámetros poblacionales. Tasa de supervivencia específica (S), tasa instantánea de mortalidad (Z), producción/biomasa (P/B por año). Error estándar (SE), mínimo (Min) y máximo (Max). * Sólo capturado un ejemplar.*

	Statistics				Reference categories				
	Mean	SE	Min	Max	Very poor	Poor	Normal	High	Very high
Total density (trout m^{-2})	0.3	0.026	0.04	0.97	<0.07	0.07–0.17	0.17–0.35	0.35–0.56	> 0.56
Total biomass (g m^{-2})	8.62	0.891	1.04	36.74	<2.72	2.72–4.53	4.53–9.69	9.69–16.13	> 16.13
Density 0+ (trout m^{-2})	0.14	0.021	0	0.803	<0.01	0.01–0.04	0.04–0.14	0.14–0.41	> 0.41
Biomass 0+ (g m^{-2})	0.61	0.093	0	3.83	<0.05	0.05–0.12	0.12–0.58	0.58–1.81	> 1.81
Density 1+ (trout m^{-2})	0.12	0.013	0	0.52	<0.02	0.02-0.05	0.05-0.16	0.16-0.29	> 0.29
Biomass 1+ (g m^{-2})	3.88	0.458	0.11	23.13	<0.93	0.93-1.91	1.91-4.67	4.67-8.13	> 8.13
Density 2+ (trout m^{-2})	0.03	0.004	0	0.15	<0.004	0.004-0.01	0.01-0.04	0.04-0.06	> 0.06
Biomass 2+ (g m^{-2})	2.69	0.343	0.2	14.86	<0.48	0.48-1.0	1.0-3.43	3.43-5.49	> 5.49
Density 3+ (trout m^{-2})	0.01	0.002	0.001	0.048	<0.003	0.003-0.004	0.004-0.013	0.013-0.033	> 0.033
Biomass 3+ (g m^{-2})	2.12	0.449	0.03	13.81	<0.41	0.41-0.72	0.72-2.30	2.30-4.33	> 4.33
Density 4+ (trout m^{-2})	0.004	0.0007	0.0001	0.009	<0.007	0.007-0.002	0.002-0.004	0.004-0.008	> 0.008
Biomass 4+ (g m^{-2})	1.53	0.324	0.22	3.17	<0.24	0.24-0.53	0.53-2.59	2.59-3.02	> 3.02
Density 5+ (trout m^{-2})*	0.004	—	—	—	—	—	—	—	—
Biomass 5+ (g m^{-2})*	5.6	—	—	—	—	—	—	—	—
Density 6+ (trout m^{-2})*	0.001	—	—	—	—	—	—	—	—
Biomass 6+ (g m^{-2})*	0.47	—	—	—	—	—	—	—	—
Density 7+ (trout m^{-2})*	0.004	—	—	—	—	—	—	—	—
Biomass 7+ (g m^{-2})*	10.65	—	—	—	—	—	—	—	—
Density juveniles (trout m^{-2})	0.26	0.026	0.03	0.91	<0.06	0.06–0.13	0.13–0.29	0.29–0.53	> 0.53
Biomass juveniles (g m^{-2})	4.42	0.47	0.9	24.53	<1.19	1.19–2.26	2.26–5.34	5.34–8.59	> 8.59
Density adults (trout m^{-2})	0.04	0.005	0	0.18	<0.003	0.003–0.01	0.01–0.04	0.04–0.08	> 0.08
Biomass adults (g m^{-2})	4.2	0.696	0	29.51	<0.44	0.44–1.17	1.17–4.29	4.29–7.91	> 7.91
Production (g m^{-2} per year)	13.28	1.319	1.25	59.52	<4.39	4.39–6.41	6.41–15.79	15.79–27.19	> 27.19
Survival (*S*)	1.33	0.193	0	7.01	<0.18	0.18–0.38	0.38–1.47	1.47–3.01	> 3.01
Mortality (*Z*)	-0.66	0.1	-2.07	1.89	<-1.60	-1.60 and -1.09	-1.09 and -0.30	-0.30–0.20	> 0.20
P/B (per year)	1.62	0.06	0.43	2.59	<1	1–1.28	1.28–1.85	1.85–2.29	> 2.29

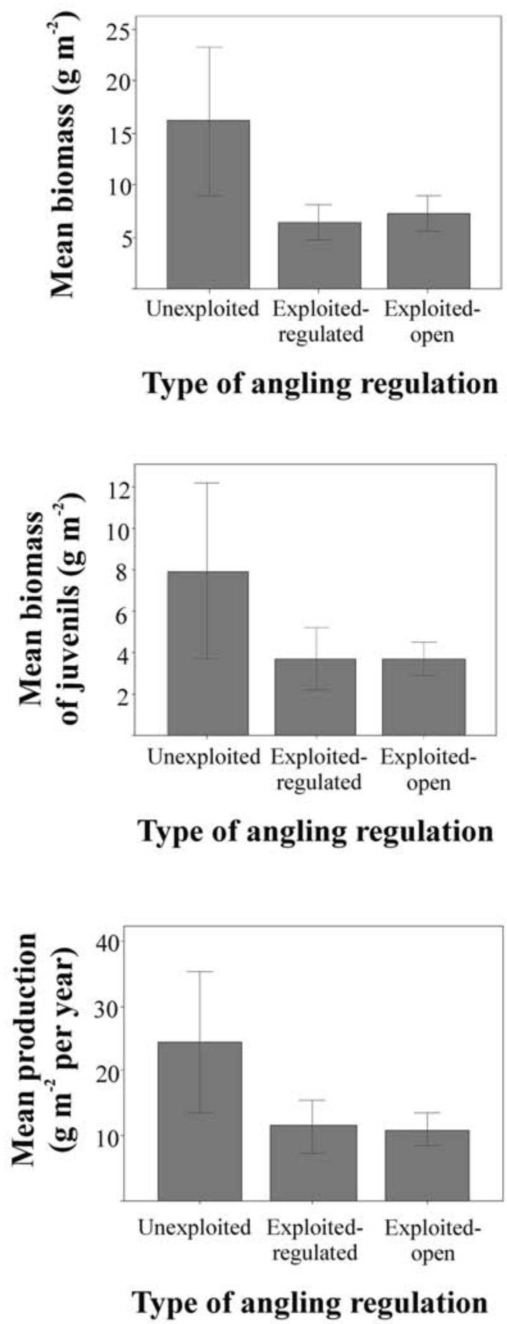

Figure 3. Mean total biomass (g m^{-2}), mean biomass of juveniles (g m^{-2}) and mean production (g m^{-2} per year) in the brown trout populations of the Cantabrian-Atlantic siliceous rivers of Galicia by type of angling regulation. Error bars represent 95 % confidence intervals. *Biomasa total media (g m^{-2}), biomasa de juveniles media (g m^{-2}) y producción media (g m^{-2} por año) en poblaciones de trucha común de ríos silíceos Cantábrico-Atlánticos de Galicia para cada tipo de regulación de pesca deportiva. Las barras de error representan intervalos de confianza del 95 %.*

(Mann-Whitney U test; $p < 0.002$). Similarly, the biomass of juveniles and production were higher in the unexploited than in the exploited-regulated (Mann-Whitney U test; $p = 0.02$ and Mann-Whitney U test; $p = 0.039$, respectively) or exploited-open sections (Mann-Whitney U test; $p = 0.012$ and Mann-Whitney U test; $p = 0.007$, respectively). Table 5 shows the values of the biomass, biomass of juveniles and production for each type of angling regulation.

DISCUSSION

Percentiles have frequently been used for the establishment of reference categories in different freshwater subjects, such as the use of ecological indicator values of freshwater diatoms (Van Dam *et al*., 1994), to test a eutrophication assessment method (Ferreira *et al*., 2007) or growth standards of fish populations (Jackson *et al*., 2008; Pedicillo *et al*., 2010). Within this context, several researchers have recently employed different fish metrics and biotic indices to assess the ecological status of Mediterranean trout-type streams (e.g., Benejam *et al*., 2008; Ayllón *et al*., 2012). However, the establishment of reference categories for the brown trout growth and population parameters is essential before meaningful comparisons can be made among rivers, as the evaluation of the characteristics of a fish population often involves making comparisons with standard reference conditions or among different localities (Pedicillo *et al*., 2010).

For example, the range of growth parameters reported in this study reveals a considerable variability in growth among the 66 sampling sites studied. This variation is normal because growth rates depend on the combination of several factors, such as the water temperature (e.g., Elliott, 1994; Parra *et al*., 2009; 2012), food intake (e.g., Elliott, 1994; Mambrini *et al*., 2006), genetic factors (e.g., Jensen, 1985; McDowall, 1994), social interactions (e.g., Metcalfe, 1994; Lobón-Cerviá, 2007), latitude and altitude (Parra *et al*., 2009) or even alkalinity, with growth being faster in rivers with a high calcium content (Kennedy & Fitzmaurice, 1971). Although our

Table 5. Total biomass, biomass of juveniles, production and index of growth performance phi-prime (Φ′). Data are presented for each angling regulation type. Standard error (SE) minimum (Min), maximum (Max) and sample size (*n*). *Biomasa total, biomasa de juveniles, producción e índice de crecimiento estándar phi-prima (Φ′). Los datos se presentan para cada tipo de regulación de pesca deportiva. Error estándar (SE), mínimo (Min), máximo (Max) y tamaño de la muestra (*n*).*

		Unexploited	Exploited-regulated	Exploited-open
Biomass (g m^{-2})	Min	1.04	2.6	1.7
	Max	37.74	10.06	35.72
	Mean	16.2 ± 3.19	6.5 ± 0.76	7.2 ± 0.87
	n	11	11	44
Biomass juveniles (g m^{-2})	Min	1.0	1.08	0.90
	Max	24.5	8.50	13.06
	Mean	7.96 ± 1.935	3.70 ± 0.665	3.71 ± 0.411
	n	11	11	44
Production (g m^{-2} per year)	Min	2.5	5.1	1.25
	Max	59.5	22.0	41.2
	Mean	24.3 ± 4.91	11.5 ± 1.81	10.9 ± 1.22
	n	10	11	41
Index of growth performance phi-prime (Φ′)	Min	2.42	2.43	2.27
	Max	2.86	2.89	2.94
	Mean	2.70 ± 0.038	2.64 ± 0.047	2.58 ± 0.023
	n	11	11	44

results for the Von Bertalanffy growth parameters (L_∞ and k) appear to be similar to those previously described in other regions of the Iberian Peninsula (e.g., García de Jalón *et al*., 1986; 1990; Lobón-Cerviá *et al*., 1986; Martínez & García de Jalón, 1988; Maia & Valente, 1999), the lack of information about reference categories for growth parameters makes it difficult to determine whether the growth is high or low. In fact, concerning the growth performance phi-prime index, Pedicillo *et al*. (2010) classified the growth rates of *S. trutta* in Central Italy according to the standard growth curves of the Von Bertalanffy equations into five categories (very poor, poor, normal, good and very good). These authors found that the index of growth performance ranged from 2.45 as "very poor" to 2.66 as "very good". Our results are similar to those of Pedicillo *et al*. (2010), except for the last category for which we attained higher values (> 2.81).

The population age structure in *S. trutta* shows within-site variation (Maia & Valente, 1999), with a maximum longevity between 6 and 9 years and a clear dominance of age groups 0+ to 3+ (Maia & Valente, 1999; Parra *et al*., 2009). In this study, the brown trout populations were dominated by groups 0+, 1+ and 2+, a result that was similar to Rodrigues *et al*. (1994) and Nicola & Almodóvar (2002).

Alcaraz-Hernández *et al*. (2007) found that the most relevant variables that explain the density and biomass of brown trout populations in Mediterranean trout-type streams were the stream width and percentage of cobbles. Within this context, the population parameters may also vary substantially within a geographical area (e.g., Joyce *et al*., 1990; Elliott, 1994; Stanfield *et al*., 2006) and are well documented in the Iberian Peninsula (e.g., Lobón-Cerviá & Penczak, 1984; García de Jalón *et al*., 1986; Lobón-Cerviá *et al*., 1986; 2011; Martínez & García de Jalón, 1988; Maia & Valente, 1999; Alonso-González & García de Jalón, 2001, Almodóvar & Nicola, 2004; Alonso-González *et al*., 2008; 2011), with the exception of the NW area. Thus, the scarcely reported densities and biomasses for the rivers of Galicia range from 0.008 trout m^{-2} and 0.026 g m^{-2} in the River Ulla (Garcia de Jalón *et al*., 1990) to 0.864 trout m^{-2} and 17.61 g m^{-2} in the River Miñor (Hervella & Caballero, 1999). More recently, Sánchez-Hernández *et al.* (2011) found that *S. trutta* dominated the fish community in the River Ladra, with a density of 0.077 trout m^{-2}. Using the data of the present work (Table 4), the reported densities would correspond to the very poor category in the River Ulla (Garcia de Jalón *et al.*, 1990), poor category in the River Ladra (Sánchez-Hernández *et al.*, 2011) and very high category in the River Miñor (Hervella & Caballero, 1999).

Production is the best indicator of the quantitative performance of a fish population in any type of habitat (Jones *et al.*, 1996; Minns *et al.*, 1996), and production varies in salmonids according to different parameters, such as the angling regulation, benthos production or environmental factors (Waters 1988; Kwak & Waters, 1997; Almodóvar & Nicola, 2004; Almodóvar *et al.*, 2006). In rivers, the annual production of brown trout usually ranges from 0.14 to 54.70 g m^{-2} per year (Elliott, 1994 and references therein). The published values of this parameter in the Iberian Peninsula vary greatly (Lobón-Cerviá & Penczak, 1984; García de Jalón *et al.*, 1986; 1990; Martínez & García de Jalón, 1988; Lobón-Cerviá *et al.*, 1986; 2011; Lobón-Cerviá, 2003), with extreme values of 46.1 g m^{-2} per year obtained for the River Ucero (Lobón-Cerviá *et al.*, 1986) and 0.8 for the River Jarama (Lobón-Cerviá & Penczak, 1984), both in Central Spain. The only published data we could find for Galician watercourses was that of García de Jalón *et al.* (1990) who found that production ranged from 0.9 g m^{-2} per year in the River Ulla to 29.7 g m^{-2} per year in an affluent, the River Deza. Our range of production values is similar to these, but the normal category we propose is different, as shown in Table 4.

The turnover (P/B) ratio for fish populations is usually below 1 (Cowx, 2003), and the P/B (per year) ratio indicates how quickly the biomass is potentially changing (Randall & Minns, 2000). Moreover, the P/B ratio varies inversely with the fish size-at-maturity and longevity, and it is, therefore, specific for species and populations (Randall & Minns, 2000). For the brown trout populations in the Iberian Peninsula, most of the P/B ratios vary between 0.6 and 3.8 (Lobón-Cerviá & Penczak, 1984; Martínez & García de Jalón, 1988; García de Jalón *et al.*, 1990; Alonso-González & García de Jalón, 2001; Almodóvar & Nicola, 2004; Lobón-Cerviá *et al.*, 2011). Interestingly, the turnover ratios obtained in this study were within this range, but the P/B (per year) ratios for the high and very high categories were above 2, indicating that there were few old individuals, as shown in Table 4.

Different authors have demonstrated that angling exploitation reduces the mean age, age diversity and number of fish exceeding the minimum size in exploited sections (e.g., Braña *et al.*, 1992; Scott *et al.*, 1999; Almodóvar & Nicola, 2004; Jennings & Blanchard, 2004; Hsieh *et al.*, 2006; 2010). Our results are consistent with those obtained in previous works (Coble, 1988; Almodóvar & Nicola, 1998; 2004; Jennings & Blanchard, 2004), as the population parameters (biomass and production) were higher in the unexploited than in the two exploited sections. Moreover, in this study, the density and turnover (P/B) ratio did not seem to be affected by the angling regulation, as had been observed by Almodóvar & Nicola (2004).

The study of the growth of fish populations has been considered to be an important tool in fisheries assessment (e.g., Arslan *et al.*, 2004; Oscoz *et al.*, 2005; Nowak *et al.*, 2009). However, although most researchers agree that the different exploitation status of salmonid populations can affect the growth patterns (Donald & Alger, 1989; Braña *et al.*, 1992; Jenkins, 2003), the exact mechanism is not well understood. For example, Braña *et al.* (1992) stated that, despite the fact that the growth rates were not absolutely consistent, brown trout exhibited faster growth in some exploited sections of rivers. Donald & Alger (1989) found that the growth of *Salvelinus fontinalis* increased when the density of the older cohort of fish was reduced, thus growth was favoured by harvest; however, Jenkins (2003) showed negative effects of catch-and-release angling on the growth of *Oncorhynchus mykiss*. Almodóvar & Nicola (2004) found no differences in the brown trout growth parameters between differently regulated angling sections, but these researchers demonstrated that the fast-growing populations were more susceptible to angling harvest than the slow-growing ones. In our case, we found almost no differences in the growth parameters among the angling-regulation sections, but the index of growth performance phi-prime (Φ′) was higher for the unexploited versus the exploited-open sections, suggesting that differences in growth can occur at different angling regulations, as previously found by Braña *et al*. (1992). According to this index, the brown trout of the Galician rivers showed faster growth in the unexploited sections.

The reported decline of many stocks of *S. trutta* in the Iberian Peninsula has generated a great deal of interest in developing conservation and management plans to protect the brown trout populations. These plans require a deep knowledge of the habitat-specific requirements, distribution and population parameters of the species, as management actions might include habitat restoration or even the restocking of populations. However, this type of information has not been systematically recorded and published, and there is a need of reference values to provide stakeholders with clear guidelines for the design of management plans. We hope our work will trigger further investigations on this subject.

ACKNOWLEDGEMENTS

A portion of this work was performed in the laboratories of the Station of Hydrobiology of USC "Encoro do Con" at Vilagarcía de Arousa. This work was partially supported by the project 10PXIB2111059PR of the Xunta de Galicia and the project MIGRANET of the Interreg IV B SUDOE (South-West Europe) Territorial Cooperation Programme (SOE2/P2/E288). The authors are also grateful to one anonymous reviewer for comments that have improved the manuscript.

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Appendix 1. Date, location, weight–length relationship and angling regulation of the sampling sites. Weight–length relationship (*b*), coefficient of determination (r^2) and sample size (*n*). *Significance <0.05. *Fecha, localización, relación peso-longitud y tipo de regulación de pesca deportiva de las estaciones de muestreo. Coeficiente de determinación* (r^2) *y tamaño de la muestra* (n). **Significación <0.05.*

River	Year	UTM (29T)	Weight–length	r^2	*n*	Angling regulation
Anllóns	2007	509070 4785516	y=2.9605x–1.8817	0.978*	117	Exploited-open
Furelos	2007	580203 4747203	y=3.0964x–2.0543	0.966*	672	Exploited-open
Lengüelle	2007	544138 4762713	y=3.157x–2.1012	0.954*	837	Exploited-open
Tambre	2007	556103 4760391	y=3.1543x–2.0935	0.939*	561	Exploited-open
Umia	2008	528604 4716565	y=2.9863x–1.9128	0.972*	252	Unexploited
Umia	2008	535734 4693212	y=2.9366x–1.8337	0.979*	73	Exploited-open
Umia	2008	540959 4693487	y=3.0405x–1.9404	0.994*	45	Exploited-open
Umia	2008	553395 4696434	y=2.9949x–1.9485	0.991*	101	Exploited-open
Umia	2008	526463 4714746	y=3.0607x–1.9685	0.970*	46	Exploited-open
Umia	2008	522558 4710954	y=3.0226x–1.9458	0.984*	44	Exploited-regulated
Umia	2008	520384 4709255	y=3.0878x–2.0357	0.977*	50	Exploited-regulated
Umia	2008	531419 4717433	y=3.0867x–2.0197	0.969*	115	Exploited-open
Barcés	2009	554535 4786009	y=3.0503x–1.9788	0.990*	106	Exploited-open
Barcés	2009	548212 4781329	y=3.1219x–2.0692	0.961*	122	Exploited-open
Illade	2009	591752 4790431	y=3.064x–1.9918	0.986*	24	Exploited-open
Illade	2009	592122 4791360	y=3.2192x–2.186	0.991*	45	Exploited-open
Illade	2009	593095 4792543	y=2.966x–1.8931	0.987*	31	Exploited-open
Maciñeira	2009	586307 5112862	y=3.2194x–2.1652	0.969*	33	Exploited-open
Maciñeira	2009	587404 4785539	y=2.914x–1.8212	0.991*	63	Exploited-open
Mandeo	2009	578798 4788281	y=2.9845x–1.8845	0.996*	128	Exploited-regulated
Mandeo	2009	567947 4790635	y=2.9453x–1.837	0.996*	98	Exploited-regulated
Mandeo	2009	574451 4789363	y=2.9477x–1.8577	0.995*	197	Exploited-open
Mandeo	2009	580276 4776490	y=3.0308x–1.9552	0.989*	241	Exploited-open
Mandeo	2009	584866 4766623	y=3.0952x–2.0494	0.984*	32	Exploited-open
Mandeo	2009	580338 4786209	y=2.9986x–1.911	0.993*	99	Exploited-open
Mandeo	2009	581904 4780107	y=3.0225x–1.9415	0.991*	111	Exploited-open
Meidelo	2009	580107 5456593	y=2.9601x–1.8748	0.993*	43	Exploited-open
Mendo	2009	567487 4781963	y=3.0698x–1.9806	0.996*	155	Exploited-open
Mendo	2009	565128 4790698	y=3.0185x–1.9237	0.993*	135	Exploited-open
Barxas	2010	567040 4665194	y=3.0392x–1.9552	0.993*	38	Exploited-open
Caselas	2010	537273 4657707	y=2.9662x–1.8666	0.998*	20	Exploited-open
Deva	2010	558660 4667951	y=3.071x–1.9956	0.996*	79	Exploited-regulated
Deva	2010	558230 4663221	y=3.1222x–2.0244	0.997*	11	Unexploited
Deza	2010	562892 4733043	y=2.9649x–1.8851	0.996*	28	Exploited-open
Deza	2010	559186 4735036	y=3.0782x–1.9994	0.994*	32	Exploited-open
Furnia	2010	525576 4649970	y=3.0926x–2.0393	0.997*	21	Exploited-open
Furnia	2010	525328 4652650	y=2.9349x–1.8903	0.966*	62	Exploited-open
Hospital	2010	523227 4648114	y=2.8949x–1.8061	0.994*	10	Exploited-open
Hospital	2010	522505 4650632	y=2.9783x–1.8735	0.979*	35	Exploited-open
Landro	2010	611063 4815914	y=3.1027x–2.0282	0.988*	355	Unexploited
Louro	2010	531881 4670265	y=3.0742x–1.9832	0.977*	91	Exploited-regulated
Pego	2010	520274 4647306	y=3.0188x–1.9151	0.987*	80	Exploited-open
Ribadil	2010	562880 4666272	y=3.1176x–2.0347	0.991*	46	Exploited-open
Tamuxe	2010	515039 4647179	y=3.1357x–2.0824	0.984*	35	Exploited-open
Tamuxe	2010	514098 4642207	y=3.0711x–2.0389	0.993*	9	Exploited-open
Termes	2010	550390 4660358	y=3.0567x–1.9822	0.996*	68	Unexploited

continued

Appendix 1. (continued) Date, location, weight–length relationship and angling regulation of the sampling sites. Weight–length relationship (*b*), coefficient of determination (r^2) and sample size (*n*). *Significance <0.05. *Fecha, localización, relación peso-longitud y tipo de regulación de pesca deportiva de las estaciones de muestreo. Coeficiente de determinación* (r^2) *y tamaño de la muestra* (n). **Significación <0.05.*

River	Year	UTM (29T)	Weight–length	r^2	*n*	Angling regulation
Tripes	2010	527546 4656519	y=2.9723x–1.9236	0.987*	28	Exploited-open
Tripes	2010	529282 4654682	y=2.8654x–1.812	0.913*	41	Exploited-open
Vilameá	2010	574105 4636335	y=3.0281x–1.9825	0.998*	155	Exploited-open
Barral	2011	525115 4715631	y=3.0434x–1.986	0.996*	142	Exploited-open
Deva	2011	558660 4667951	y=3.0104x–1.9238	0.997*	65	Exploited-regulated
Deva	2011	558230 4663221	y=2.8355x–1.7334	0.968*	39	Unexploited
Hospital	2011	522505 4650632	y=3.0152x–1.9549	0.991*	52	Exploited-open
Liñares	2011	543143 4732294	y=2.9962x–1.8791	0.997*	53	Unexploited
Moreda	2011	598524 4728101	y=2.9334x–1.8683	0.979*	54	Unexploited
Moreda	2011	600704 4728715	y=3.0567x–2.0211	0.998*	125	Unexploited
Moreda	2011	601813 4728654	y=3.0315x–1.9979	0.997*	89	Unexploited
Sar	2011	527961 4735192	y=3.02x–1.943	0.995*	50	Exploited-open
Sar	2011	527618 4734039	y=3.0935x–2.062	0.993*	43	Exploited-regulated
Sar	2011	527871 4732466	y=2.8303x–1.7255	0.985*	13	Exploited-regulated
Tamuxe	2011	514098 4642207	y=3.1796x–2.1372	0.984*	32	Exploited-open
Té	2011	515629 4724811	y=3.0157x–1.9281	0.956*	140	Exploited-open
Ulla	2011	554283 4738221	y=3.0323x–1.9313	0.991*	126	Unexploited
Umia	2011	528353 4716218	y=3.1023x–1.9917	0.993*	66	Exploited-regulated
Verdugo	2011	536634 4688658	y=2.878x–1.7799	0.996*	24	Unexploited
Xubia	2011	568821 4819350	y=2.8579x–1.7793	0.986*	23	Exploited-regulated