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A large-scale approach can help detect general processes driving the dynamics of brown trout populations in extensive areas

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Abstract – Most studies on the population dynamics of stream-living salmonids have been conducted at the scale of a reach, a stream or a river basin. This can lead to overestimating the importance of local factors acting on a reduced scale compared to the more general factors that drive the dynamics of several populations. Two models were built on the basis of a data set from 60 sampling stations representing separated populations inhabiting a large heterogeneous area encompassing 18 years of quantifications. Our analyses showed the following: (i) Population growth rate (pgr) of a set of independent brown trout populations can be described by means of a single model; (ii) the youngest and the oldest year classes of these populations seem to be limited by the same constraints; (iii) there is a climatic control of the recruitment because of spring weather conditions, but also the abundance of oldest age class may be controlled by the climate, (iv) there is a nonlinear positive effect of winter North Atlantic Oscillation on pgr; (v) there is a 3-year lagged positive feedback tracing the upward trend of a stock-recruitment curve, and 1-year lagged negative feedback showing the downward trend of the curve; (vi) a strong cohort has a positive effect on the whole population that can be detected throughout the time. Our fitted models allowed to predict the mean population densities at a regional scale with <10% error and shed light onto the main factors and associated ecological processes that control these large-scale dynamics.

Key words: population dynamics; brown trout; North Atlantic Oscillation; synchrony

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Introduction

Understanding the mechanisms underlying the spatio-temporal variation of abundance and demographic variables is a key question in population dynamics. Population regulation and/or limitation is the central concept in studies on these processes; currently, the main objective of researchers in this field is to determine the relative influence of exogenous and endogenous drivers of this fluctuation (Coulson et al. 2008). Among the studies carried out on salmonids, those related to population dynamics have been abundant. Therefore, knowledge on the processes and traits that govern the temporal variation of population abundance in these species is vast; see Milner et al. (2003). Given the territorial behaviour exhibited throughout all their life stages, these species are also ideally suited for studying the importance of density-dependent versus density-independent processes (Vollestad & Olsen 2008).

To express the results on a scale compatible with fishery management strategies, and also owing to the scarcity of large-scale data sets including both biological and environmental information for several years over several basins, most studies on the population dynamics of stream-living salmonids have been

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performed at the scale of a reach, a stream or a river basin (Milner et al. 2003), leaving the dynamics of abundances at other scales, such as those including several basins, little studied (but see Cattanèo et al. 2003 and Zorn & Nuhfer 2007 for two exceptions). At these limited scales, the factors governing populations are, to some extent, local and diverse. This can lead to an overestimation of the importance of local factors acting on a reduced scale compared to more general factors influencing the dynamics of several populations inhabiting larger areas. If common processes driving separated independent populations are found, these are likely to provide wider and more robust knowledge on the autoecology of the species than locally limited process. In addition, models built on this basis are expected to have better explicative and predictive capabilities than those based on more locally relevant variables (Hallett et al. 2004; Stenseth & Mysterud 2005). Furthermore, if several independent populations are found to share a common response to the lumped value of a given population variable, such as the mean density of the whole set of populations, then the effect of an additional synchronising mechanism can be inferred.

The aim of this study is to explore whether the mean density of a set of independent trout populations can be explained by means of a single model. If this is performed in a large and heterogenous area, the resulting model would determine the main processes driving the population dynamics at a large geographical scale, instead of drawing conclusions based on more local effects.

To do this, traditionally a density-dependence-based deterministic model is fitted to the population data prior to the addition of exogenous limitation factors, frequently considered as random environmental noise. Coulson et al. (2001) showed that exogenous drivers act on population dynamics, not only as additive factors, but also through nonadditive processes, influencing the relationship between population density and population growth rates (pgrs). Nonadditive effects of exogenous and endogenous drivers on population dynamics have recently been studied for different taxa (Coulson et al. 2008). Nonadditivity in brown trout abundance dynamics has been studied at a local scale by Vollestad & Olsen (2008).

Therefore, population dynamics models should be fitted giving *a priori* the same importance to exogenous and endogenous drivers and the interaction among them. Because ours is an exploratory approach to large-scale dynamics, a free-of-prejudices approach will be followed. For this reason, an initial set of potential drivers will be tested to find the general factors that govern the interannual variation of the mean density of a set of independent brown trout populations.

Studies specifically determining to what extent exogenous factors influence the temporal dynamics of a given brown trout (*Salmo trutta* L.) population have been widely conducted (Lobón-Cerviá & Mortensen 2005; Budy et al. 2008). Some of these were carried out in the Iberian Peninsula (Lobón-Cerviá & Rincón 2004), producing a good amount of knowledge on this matter at the population scale. Many studies have shown the influence of stream flow regime (Lobón-Cerviá & Mortensen 2005; Alonso-González et al. 2008; see Vollestad & Olsen 2008 for a review) and water temperature (Borgstrøm & Museth 2005) on brown trout population dynamics, so both variables are good candidates to be direct exogenous drivers of brown trout abundance dynamics.

Not only linear effects have been identified, but also nonlinear effects of exogenous drivers have been found to drive brown trout recruitment. Lobón-Cervia & Rincón (2004) found that recruitment was poor when either too high or too low discharge in March occurred.

At a large-scale approach, measures of the natural interannual variation of an ecologically relevant climate variable acting at a scale that involves the whole study area should be used. Such variables would be preferred instead of more local variables, such as flow and temperature regimes, because the main objective of this work is to find the potential factors driving the whole set of independent brown trout populations in the study area. Following Stenseth & Mysterud (2005), climatic variables used as weather packages should fulfil ‘the time window component, the spatial window component and the weather composition component’, meaning temporal, spatial and climatic scales. For this reason, in this study, the North Atlantic Oscillation index (NAO, north-south dipole of anomalies, with one centre located over Greenland and the other centre of opposite sign spanning the central latitudes of the North Atlantic between 35° and 40°N) has been chosen to represent the exogenous drivers.

Since the 1990s, many authors have studied the influence of NAO in ecological processes (Ottersen et al. 2001), both in terrestrial and in marine ecosystems (Stenseth et al. 2002; Mysterud et al. 2003). Straile et al. (2003) provided a good review on the reported effects of NAO in freshwater ecosystems and highlighted the scarcity of evidence for an impact of the NAO on freshwater fish species. In salmonids, the few pieces of evidence of this relationship lay mainly in physiological traits such as size and age of maturity in Atlantic salmon (Jonsson & Jonsson 2004) and emergence date in brown trout (Elliott et al. 2000). However, Borgstrøm & Museth (2005) and Hari et al. (2006) found correlations between NAO and population dynamics traits in brown trout.

A number of studies have recently identified endogenous factors influencing autoecological traits of salmonids, such as survival (see Vollestad & Olsen 2008 for a review) or recruitment (Elliott 1994; Nicola et al. 2008). Some studies have found that density can indirectly control population size by directly affecting other biological parameters such as individual growth (Jenkins et al. 1999; Post et al. 1999; Lobón-Cervia 2007a) or egg size (Gregersen et al. 2006). Intra- and intercohort competition have been identified as processes underlying some of these effects (Nordwall et al. 2001).

Study area

The selected study area had to meet the following conditions:

- To have relatively long time series for population and demographic data sets.
- To include several basins and, if possible, basins showing different environmental characteristics.
- To have a large, minimally disturbed river network.

The study area comprises all rivers and streams where brown trout are present in Navarra (north Spain, long. 0°43′–2°29′W, lat. 41°54′–43°19′N). This area (6420 km^2) is rather heterogeneous, containing two freshwater ecoregions: Cantabric coastal Languedoc (403) and eastern Iberia (414) (Abell et al. 2008), with altitudes ranging from 0 to 2444 m.a.s.l. The largest river basins included in the study area are: Ebro basin (5458 km^2), flowing eastwards to the Mediterranean Sea; Bidasoa (673 km^2), Oria (124 km^2) and Urumea (165 km^2) basins, flowing northwards to the Bay of Biscay in the Atlantic Ocean.

Methods

Brown trout density (individuals·ha^{-1}) and age structure (per cent of fry, juvenile and adult age classes) data have been collected every summer (July–September) by the environmental authority of Gobierno de Navarra and Gestión Ambiental, Viveros y Repoblaciones de Navarra (GAVRN) for the period from 1992 to the present time in a network of 60 sampling sites (see Fig. 1). This sampling network has been designed by the angling management authority of Navarra to represent the natural range of the distribution of brown trout in the whole region, and it has been described elsewhere (Ayllón et al. 2009; Parra et al. 2009; Ayllón et al. 2010). Three sampling stations are located in every river, one in the upper reach, one in the medium reach and a third in the lower reach, plus scattered sites in small tributaries. Mesohabitats included in every sampling site represent the distribution of mesohabitats in the reach where they are located, including at least one riffle-pool sequence. All sampling sites meet the criterion of a minimum sampled area of 0.1 ha. The width of 59 of the 60 sampling sites measured during the 2009 campaign ranged from 2.2 to 18 m (average site width: 8.3 m), with a single site wider than 18 m (35 m). To meet the

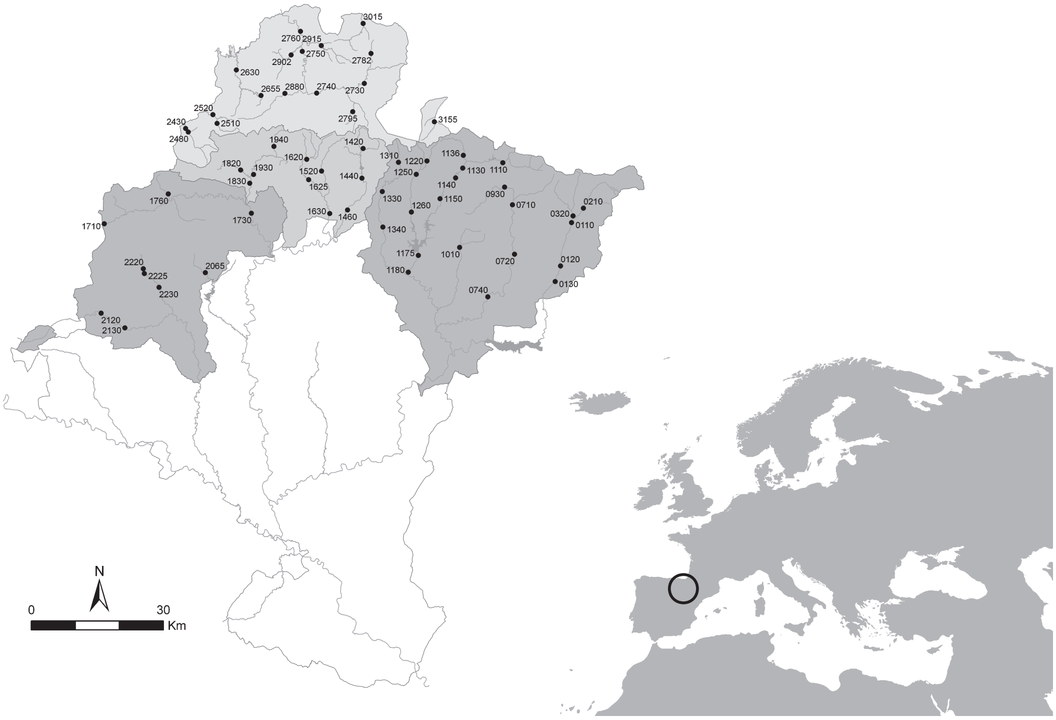

Fig. 1. Study area (shadowed) in the region of Navarra (north Spain) and sampling network (60 sites).

minimum sampled area of 0.1 ha, in that survey campaign site lengths ranged from 49.5 to 172 m (average site length: 107.5 m). The sites were located between natural breaklines or small obstacles and two or three pass-removal – according to Seber & Le Cren (1967) criteria – electrofishing was conducted in all the stream width. One sampling team of six to nine persons, depending on the site width, was required to survey the whole network in 2-month time (July 15th–September 10th). Fork lengths (to the nearest mm) were measured for every captured individual. Trout density (individuals·ha^{-1}) was estimated using the explicit solution of Seber & Le Cren (1967) to the maximum likelihood method with constant effort. Age of the individuals was estimated by means of a combination of scale reading and length frequency distribution analysis.

Because our main goal is to uncover general traits of mean density through time across the whole study area, the mean fry, juvenile, adult and total density from all (60) sampling sites were calculated and used to produce the mean density time series.

Mean monthly NAO data series (1992–2009) were obtained from the Climate Prediction Center, US National Oceanic and Atmospheric Administration (NOAA; http://www.cpc.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table).

We built two types of models to test whether an age-structured model could perform better than a non-structured model. The same procedure was followed to fit both types of models, and, according to Coulson et al. (2008) advice, simple linear models were used prior to testing more complex functional forms.

A model selection was conducted from all multivariate regression models that could be fitted to an initial set of nine potential variables to explain the variation of mean pgr. Both endogenous and exogenous potential drivers were considered to test for additive effects, as well as their interactions to account for nonadditive effects. To test the potential nonlinear effects of exogenous drivers, squared terms of the exogenous variables were also tested. The initial set of independent variables was the following:

- Endogenous drivers: N_t, N_{t-1} and N_{t-2}, mean density (individuals·ha^{-1}) estimated from the Seber & Le Cren (1967) method in all (60) sampling sites in year t, $t-1$ and $t-2$, respectively.
- Exogenous drivers: $\mathrm{NAO}_{w,t+1}$ and $\mathrm{NAO}_{s,t+1}$, mean winter (January, February and March) and spring (April, May and June) values of the North Atlantic Oscillation (NAO) index in year $t + 1$, which is likely to influence the change in the population size between year t, N_t, and year $t + 1$, N_{t+1}.
- Nonlinear effects: $\mathrm{NAO}^2_{w,t+1}$ and $\mathrm{NAO}^2_{s,t+1}$, squared values of mean winter and spring NAO index in year $t + 1$.
- Interactions among variables, nonadditive effects: $N_t \times \mathrm{NAO}_{w,t+1}$ and $N_t \times \mathrm{NAO}_{s,t+1}$, product of population density in year t, and winter and spring NAO in year $t + 1$.

The base time lag has been chosen following Turchin's recommendation that it should generally be set equal to 1 year unless the generation time is much different from 1 year (Turchin 2003).

The possible effects of lagged population sizes (N_{t-2}, N_{t-1}) were tested because N_{t-2} may drive spawning population size in year t, and N_{t-1} can influence survival of 0+ through intercohort competition (Henderson & Letcher 2003). Densities of age classes 0+ ($N_{1,t}$), 1+ ($N_{2,t}$) and ≥2+ ($N_{3,t}$) were not considered in the initial set of variables because total density (N_t) is the linear combination of these values; N_t is highly correlated with $N_{1,t}$; and $N_{1,t}$ is highly correlated with $N_{3,t-1}$.

Seasonal exogenous variables (NAO) were limited to winter and spring because 0+ survival is known to be influenced by water discharge during the incubation (Alonso-González et al. 2008) and the emergence (Lobón-Cerviá & Rincón 2004) periods, which usually take place in winter (January–March) and spring (March–June), respectively, in the study area (Gortázar et al. 2007). No indirect effects such as the influence of lagged NAO were considered, although they can be of importance in influencing N_{t-2}, N_{t-1} and N_t, but these effects are already included in the model.

When interaction terms are included in multiple regression models, lower order terms will usually be highly correlated with their interactions, resulting in inflated variances of estimated coefficients associated with collinearity (Quinn & Keough 2002). To avoid this undesirable effect, all variables were rescaled by centring, i.e., subtracting their mean from each observation, so the interaction would be then the product of the centred values (Aiken & West 1991).

Multiple regression models were then fitted for the complete time series (1992–2008) with the aim of uncovering the driving processes of the pgr, λ_t:

$$\begin{aligned}\lambda_t = f(\lambda_t | N_t, N_{t-1}, N_{t-2}, \mathrm{NAO}_{w,t+1}, \mathrm{NAO}_{s,t+1},\\ \mathrm{NAO}^2_{w,t+1}, \mathrm{NAO}^2_{s,t+1}, N_t \times \mathrm{NAO}_{w,t+1},\\ N_t \times \mathrm{NAO}_{s,t+1})\end{aligned}$$

where the dependent variable, pgr, is calculated as:

$$\lambda_t = N_{t+1}/N_t$$

As the objective of model selection is to find the smallest subset of predictors that provides the best fit to the observed data to avoid 'overfitting', a preselection of models was conducted among different numbers of variables. A single model was selected for every possible subset of the initial set of variables ranging from 1 to 6 variables, thus obtaining six preselected multiple regression models, each with a different number of significant (95% c.l.) independent variables. No higher order (≥7 parameters) models were found significant at the considered confidence level (95%). Among every subset of models, selection criteria were: (i) maximum value of adjusted r^2, which basically uses mean squares instead of sum of squares and is useful to compare models with different numbers of parameters; and (ii) minimum value of Mallow's C_p (Gorman & Toman 1966), which works by comparing a specific reduced model to the full model with all predictors included.

From the six preselected models, the model that provided the 'best fit' to the observed data was selected using Akaike (1978) (AIC) and Bayesian or Schwarz (1978) (BIC) information criteria. Both criteria tend to select models with the smallest number of parameters, but the Bayesian information criterion (BIC) penalises more harshly models with a greater number of predictors than the AIC.

As collinearity can lead to an inflation of the variance of the estimated regression coefficients, correlation among the variables of the selected model was tested and, when it was found to be significant (95%) and with an absolute value of r-Pearson higher than 0.5 among any pair of variables, Ridge Regression was conducted with the selected variables. In this technique, a small biasing constant is added to the normal equations that are solved to estimate the standardised regression coefficients, biasing the estimated regression coefficients but also reducing their variability and hence their standard errors (Quinn & Keough 2002). The chosen value of the constant was the best compromise between reducing the Variation Inflation Factor (VIF) of the variables and minimising the reduction of the adjusted r^2 value.

Once the model was parameterised, observed ($N_{\mathrm{obs},t}$) versus modelled mean densities at time t ($N_{\mathrm{pre},t}$) were compared to represent the descriptive capability of the fitted model.

The predictive capability of the selected model was also tested. For this purpose, 14 different predicted time series were built by iterating the modelled values of N_{t+1} (e.g., to predict $N_{t+1} = N_{2007}$ the observed values of $\mathrm{NAO}_{s,t+1} = \mathrm{NAO}_{s,2007}$ and $\mathrm{NAO}^2_{w,t+1} = \mathrm{NAO}^2_{w,2007}$; and the previously predicted values of $N_t = N_{2006}$; $N_{t-1} = N_{2005}$; $N_{t-2} = N_{2004}$ were used) starting every time series from the observed value of N_t of a different year (1994–2007). Every predicted time series was plotted against the observed time series, and the distributions of the standard error for the forecast of N_{t+1} of the different prediction terms were compared.

A demographic approach was carried out by conducting the same steps described above using each age class per capita growth rate: $\lambda_{1,t}$, $\lambda_{2,t}$ and $\lambda_{3,t}$ as dependent variable. Starting from the definition of per capita pgr:

$$\begin{aligned}\lambda_t &= N_{t+1}/N_t = (N_{1,t+1} + N_{2,t+1} + N_{3,t+1})/N_t \\ &= (N_{1,t+1}/N_t) + (N_{2,t+1}/N_t) + (N_{3,t+1}/N_t) \\ &= \lambda_{1,t} + \lambda_{2,t} + \lambda_{3,t}\end{aligned}$$

therefore:

$$\begin{aligned}\lambda_{1,t} = f(\lambda_{1,t} | &N_t, N_{t-1}, N_{t-2}, \mathrm{NAO}_{w,t+1}, \mathrm{NAO}_{s,t+1}, \\ &\mathrm{NAO}^2_{w,t+1}, \mathrm{NAO}^2_{s,t+1}, N_t \times \mathrm{NAO}_{w,t+1}, \\ &N_t \times \mathrm{NAO}_{s,t+1})\end{aligned}$$

$$\begin{aligned}\lambda_{2,t} = f(\lambda_{2,t} | &N_t, N_{t-1}, N_{t-2}, \mathrm{NAO}_{w,t+1}, \mathrm{NAO}_{s,t+1}, \\ &\mathrm{NAO}^2_{w,t+1}, \mathrm{NAO}^2_{s,t+1}, N_t \times \mathrm{NAO}_{w,t+1}, \\ &N_t \times \mathrm{NAO}_{s,t+1})\end{aligned}$$

$$\begin{aligned}\lambda_{3,t} = f(\lambda_{3,t} | &N_t, N_{t-1}, N_{t-2}, \mathrm{NAO}_{w,t+1}, \mathrm{NAO}_{s,t+1}, \\ &\mathrm{NAO}^2_{w,t+1}, \mathrm{NAO}^2_{s,t+1}, N_t \times \mathrm{NAO}_{w,t+1}, \\ &N_t \times \mathrm{NAO}_{s,t+1})\end{aligned}$$

The model thus obtained is an age-structured model providing a demographic approach to the factors that govern the pgr.

Results

When testing for correlation among the variables in the initial set of potential drivers, nine significant (95% c.l.) correlations were found. After rescaling the variables by centring, significant correlations were reduced to five.

The nonstructured model that scored the best results according to the values of r^2 and adjusted r^2, Mallow's C_p and Akaike (AIC) and Bayesian (BIC) information criteria was the six-parameter model (Table 1), in which endogenous variables N_{t-1}, N_{t-2}, exogenous $\mathrm{NAO}_{w,t+1}$, $\mathrm{NAO}_{s,t+1}$, the nonlinear influence of spring NAO, $\mathrm{NAO}^2_{s,t+1}$, and nonadditive effect of endogenous and exogenous factors $N_t \times \mathrm{NAO}_{s,t+1}$ were significant at 95% c.l. This model originally explained 93% of the observed variability of λ_t. As significant (r-Pearson >0.5; 95% c.l.) collinearity was found among two pairs of its explanative variables, ridge regression (biasing constant = 0.02) had to be conducted to lower the highest value of Variance Inflation Factor (VIF), corresponding to variable $\mathrm{NAO}^2_{s,t+1}$ (VIF = 2.9), below 2.5 – which is half the value usually indicating high collinearity – and thus reducing the r^2 to 89.2% and slightly changing the values of the parameter estimates (i.e., $\lambda_t = -0.0438 + 0.0002 \cdot N_{t-1} + 0.0003 \cdot N_{t-2} - 0.3579 \cdot \mathrm{NAO}_{w,t+1} - 0.2883 \cdot \mathrm{NAO}_{s,t+1} - 0.1998 \cdot \mathrm{NAO}^2{}_{s,t+1} + 0.0002 \cdot N_t \times \mathrm{NAO}_{s,t+1}$). The standard error of the estimate was 0.093. The Durbin–Watson statistic

Table 1. Parameter estimates, P-value (in brackets), coefficient of determination r^2, adjusted r^2, Mallow's C_p, Akaike (AIC) and Bayesian (BIC) information criteria of the nonstructured and the age-structured models of population growth rate.

	Nonstructured model, $\lambda_{1,t}$		Age-structured model, $\Sigma\lambda_{i,t}$		
	5-parameter	6-parameter	$\lambda_{1,t}$	$\lambda_{2,t}$	$\lambda_{3,t}$
Estimates (P-value)					
Constant	−0.2142 (0.002)	−0.0368 (0.347)	−0.1718 (0.007)	−0.0229 (0.038)	−0.0123 (0.0012)
N_t	−0.0003 (0.0002)	–	−0.0003 (0.0003)	–	-2.5×10^{-5} (0.000)
N_{t-1}	0.0001 (0.014)	0.0002 (0.007)	–	4.06×10^{-5} (0.0185)	1.56×10^{-5} (0.0005)
N_{t-2}	0.0004 (0.0002)	0.0003 (0.001)	0.0004 (0.0001)	–	2.01×10^{-5} (0.0002)
$\mathrm{NAO}_{w,t+1}$	–	−0.3613 (0.001)	–	–	–
$\mathrm{NAO}_{s,t+1}$	−0.1612 (0.013)	−0.3179 (0.001)	−0.2141 (0.0054)	–	−0.0190 (0.0004)
$\mathrm{NAO}^2_{w,t+1}$	0.7078 (0.007)	–	0.7827 (0.0032)	–	0.0508 (0.0008)
$\mathrm{NAO}^2_{s,t+1}$	–	−0.2320 (0.018)	–	–	–
$N_t \times \mathrm{NAO}_{w,t+1}$	–	–	–	–	–
$N_t \times \mathrm{NAO}_{s,t+1}$	–	0.0002 (0.002)	–	–	–
Measures of goodness-of-fit					
r^2	0.893	0.930	0.887	0.409	0.966
Adjusted r^2	0.826	0.878	0.830	0.356	0.942
C_p	10.73	7.00	8.07	−2.26	6.56
AIC	−57.91	−62.74	−54.95	−87.27	−133.73
BIC	−54.07	−58.27	−52.12	−86.14	−130.34

showed a P-value slightly higher than 0.05 ($P = 0.0512$), which means that there can be serial autocorrelation in the residuals at 90%.

Table 1 also shows a five-parameter model, which explains up to 89.3% of the observed variability of the pgr. In this case, endogenous factors N_t, N_{t-1}, N_{t-2}, exogenous $\mathrm{NAO}_{s,t+1}$ and the nonlinear influence of winter NAO, $\mathrm{NAO}^2_{w,t+1}$, were found to be significant at 95% c.l. The standard error of the estimate is 0.109. As the Durbin–Watson statistic showed a P-value >0.05 ($P = 0.197$), there is no evidence of serial autocorrelation in the residuals at 95%. No collinearity was found among the explanatory variables.

Because of the lack of collinearity among the variables and serial autocorrelation in the residuals and as parsimony (i.e., using no more complex a model than is absolutely necessary) of the model is a guiding principle in scientific investigations (Mulligan & Wainwrigth 2004), the five-parameter model has been selected to be plotted in Figs 2 and 3. However, the selection criteria (r^2, adjusted r^2, Mallow's C_p, AIC and BIC) found the six-parameter model as the best model; therefore, its variables should be taken into account when explaining the factors that drive brown trout population dynamics in this study.

The estimates of the coefficients and the measures of goodness-of-fit of the models that provided the best fit to the observed data of age classes 0+, 1+ and ≥2+ *per capita* growth rates, $\lambda_{1,t}$, $\lambda_{2,t}$ and $\lambda_{3,t}$, are also shown in Table 1. The summation of modelled $\lambda_{1,t}$, $\lambda_{2,t}$ and $\lambda_{3,t}$, $\sum\lambda_{i,t}$, leads to an age-structured model of the pgr, λ_t, which is in this case modelled following a demographic approach.

The best model of age class 0 + pgr is a four-parameter model in which endogenous variables N_t, and N_{t-2}; exogenous $\mathrm{NAO}_{s,t+1}$ and the nonlinear effect of the winter NAO, $\mathrm{NAO}^2_{w,t+1}$ significantly (95% c.l.) explained up to 89% of the observed variability of $\lambda_{1,t}$. These variables were also significant in the five-parameter nonstructured model and showed the same signs as well. The mean standard error of the estimation is 0.105. The Durbin–Watson statistic ($P = 0.2708$) showed no indication of serial autocorrelation among the residuals, neither collinearity among the variables was found.

The only significant (95%) variable in the best model of age class 1 + pgr was N_{t-1}, explaining 41% of the variability of $\lambda_{2,t}$, with a standard error of the estimation of 0.032.

The variables that were found to significantly explain up to 97% of the variability of mature age classes, $\lambda_{3,t}$, in the best model (according to all selection criteria) were the same, and with the same sign, as in the five-parameter nonstructured model (i.e., N_t, N_{t-1}, N_{t-2}, $\mathrm{NAO}_{s,t+1}$, $\mathrm{NAO}^2_{w,t+1}$). The standard error of the estimation was 0.005, with no serial autocorrelation (Durbin–Watson, $P = 0.171$) among the residuals and no collinearity among the independent variables.

When the modelled values are plotted against the observed densities (N_t) throughout the period of years of this study, it is easier to notice the descriptive capability of both nonstructured and age-structured models (Fig. 2a,b). In this figure, all the time series of the observed values of the explanatory variables have been used to obtain every predicted N_{t+1} (e.g., to predict mean summer density of brown trout $N_{t+1} = N_{2007}$ the observed values of $N_t = N_{2006}$; $N_{t-1} = N_{2005}$; $N_{t-2} = N_{2004}$; $\mathrm{NAO}_{s,t+1} = \mathrm{NAO}_{s,2007}$ and $\mathrm{NAO}^2_{w,t+1} = \mathrm{NAO}^2_{w,2007}$ were used).

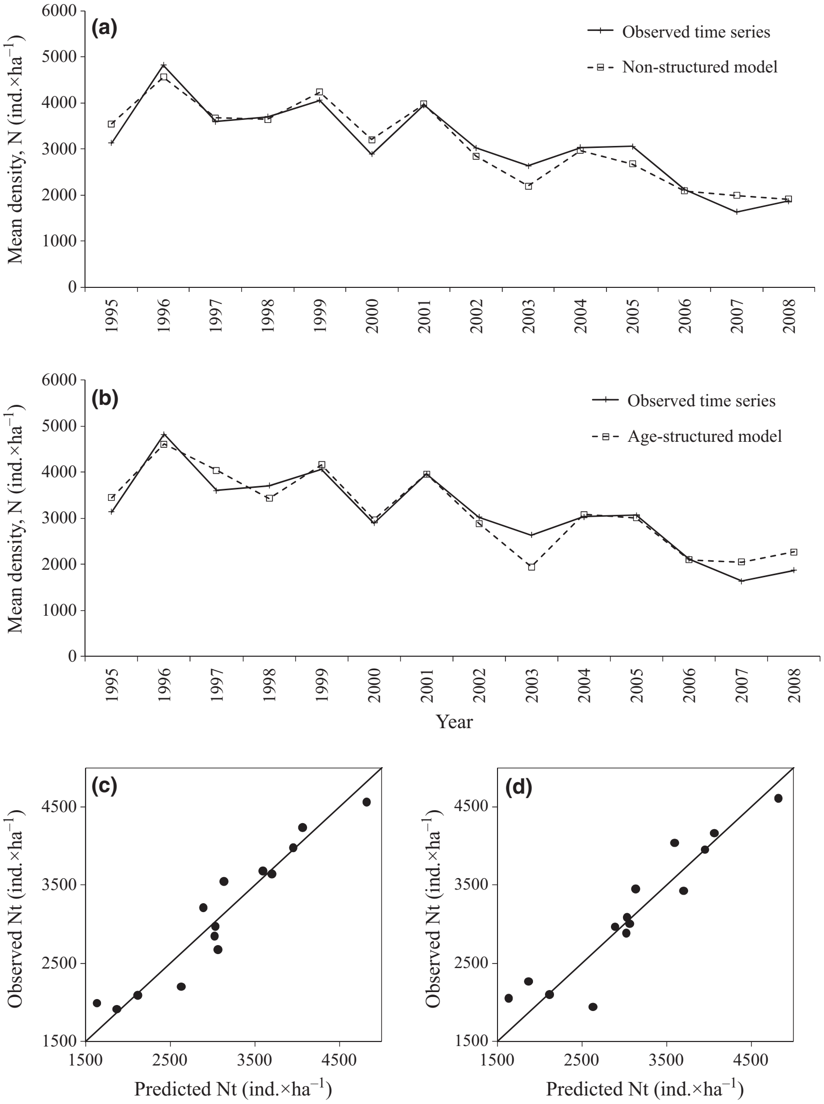

Fig. 2. Results of the fitted nonstructured (a) and age-structured (b) models represented against time; and observed versus modelled graph: nonstructured model (c) and age-structured model (d).

Different predicted time series obtained from the iteration of the selected models starting from different years are presented in Fig. 3(a,b).

The accuracy of predictions was expected to be higher in years near the beginning of every time series than in years far from them because prediction errors are likely to accumulate in each iteration of the model. The absolute value of the standard error for forecasts can be plotted against the number of years lasting from the year whose mean density was used to start the iteration of the model (namely, term of prediction; Fig. 3c,d).

Discussion

The interannual variation of the mean growth rate of a set of independent brown trout populations can be described fairly accurately (i.e., >89% of variance explained) by means of a single multivariate model. This may indicate that the factors included in the model are likely to be the main drivers of the population dynamics of brown trout at a regional scale in the study area.

A set of exogenous and endogenous variables were found to describe the temporal variation of the mean density of the studied populations. Additionally, good predictions can be made using both nonstructured and age-structured (best) approaches for a prediction term equal to 1 year. When increasing the prediction term, error grows slightly faster in age-structured than in nonstructured models. Besides, the sign of error remains more stable in nonstructured than in age-structured model.

The accuracy of long-term predictions largely depends on the number of endogenous variables in

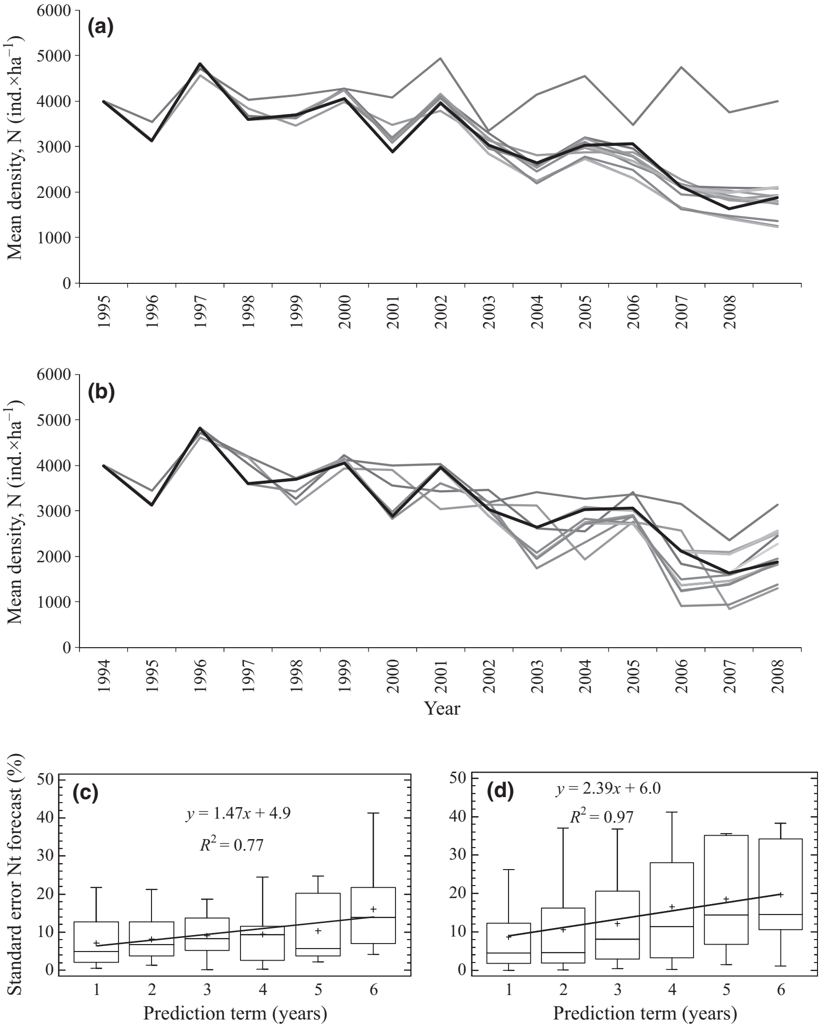

Fig. 3. Observed (black line) and predicted (grey lines) time series of mean densities, N_t, obtained from iteration of the nonstructured (a) and age-structured (b) models starting from observed values of different years. Distributions of the absolute value standard errors for forecast of mean density, N_{t+1}, plotted against the prediction term in years: nonstructured model (c) and age-structured model (d).

the model such that the higher the number of endogenous variables in the model the less accurate predictions are. The reason for this fact arises from the iterative process, which accumulates predicted errors from the years before, and when many endogenous variables are used in the model, the error gets accumulated and becomes bigger. Therefore, as long as an age-structured model has more endogenous variables (it is a summation of three age class partial models) its explicative capability is high, whereas its long-term predictive capability is lower than the nonstructured model (Fig. 3). In addition, predictions made by the nonstructured model are more consistent than those of the age-structured model (Fig. 3a,b).

Factors governing the mean pgr of the whole set of independent populations appeared to be both exogenous (i.e., spring NAO, $\mathrm{NAO}_{s,t+1}$) and endogenous (i.e., N_t, N_{t-1} and N_{t-2}) in an additive form, and also nonlinear effects of exogenous factors have been identified as significant drivers of pgr (i.e., $\mathrm{NAO}^2_{w,t+1}$). Both nonstructured and age-structured selected models showed the same five significant variables.

However, an alternative six-parameter nonstructured model was also found to provide a good fit to the observed data. This model is less parsimonious than the selected five-parameter model, but its good performance can give additional information. In addition to some of the variables that were found significant in the five-parameter model, in this model, winter NAO was found to negatively affect the pgr. A nonlinear negative effect of spring NAO was also detected, indicating that too low (negative) or too high (positive) values of spring NAO may reduce the pgr. A significant nonadditive effect ($N_t \times N_{s,t+1}$) was detected indicating an interaction of density and climate on the pgr. On the basis of our large-scale analysis, it is not straightforward to make an interpretation of these combined effects of exogenous and endogenous factors without falling into speculative conclusions, and deeper analyses must be conducted to understand them. The fact appears to be that the way exogenous factors drive populations is influenced by endogenous determinants. In this sense, Vollestad & Olsen (2008) found that density-dependent effects on brown trout survival predominated when no drought occurred, while density-independent processes were most important when drought occurred.

It is interesting to notice that the factors governing age class 0+ per capita growth rate are the same than those driving age class 2+ and older (Table 1). And also the same factors were found significant in the five-parameter nonstructured model. These results might indicate that the effect of climatic and endogenous drivers is not limited to a single age class, but influences the whole population dynamics. There is an indication that the youngest and the oldest year classes of these populations are limited by the same constraints.

A synthetic finding of this study is that separated populations have a common coordinated response to exogenous factors, suggesting that they fluctuate with a certain degree of synchrony. Because this is a general approach to the dynamics of the studied populations, no specific analyses on synchrony were conducted, but if the observed effect is a consequence of synchrony among populations, then it is likely that exogenous agents (i.e., spring NAO) are responsible for it via the Moran effect (so synchrony among these populations is due mainly to a synchronising exogenous agent).

Exogenous drivers

The five-parameter nonstructured model and also the age-structured models, which are all consistent in their significant explanatory variables, indicate that low negative values of spring NAO in year $t + 1$ tend to reduce the pgr of the year t ($\lambda_t = N_{t+1}/N_t$). This may indicate a climatic control of the recruitment because of spring weather conditions experienced by newly emergent fry, which is to some extent expectable. But also it may highlight that the abundance of the oldest age class is controlled by the climate, as well.

A nonlinear positive effect of winter NAO in year $t + 1$ on pgr of year t means that high or low values of winter NAO lead to an increase in the pgr, while more moderate values will lead to a lower pgr.

Borgstrøm & Museth (2005) linked recruitment and size of the 0+ fish with accumulated snow depth and summer temperatures in Norway, which are variables related to winter NAO. In the same context, Hari et al. (2006) found that an upward shift of the brown trout thermal habitat, which is highly correlated with winter NAO, in combination with temperature-related proliferative kidney disease, explained the decrease in total catch of brown trout in Switzerland.

In general, winter mean value of the NAO index is found to have ecological significance, but some studies have found significant relationships between spring NAO and very different biological events such as bird migration (Hubálek 2003), car-killed deer during spring related to deer condition (Mysterud 2004) and the onset of vegetation in spring and subsequent deer calf performance (Pettorelli et al. 2005). No relationship has been documented before between spring NAO and fish population dynamics, but surprisingly, spring NAO has been found significant in both selected models.

Many studies have demonstrated the relationship between stream flow regime (Lobón-Cerviá & Mortensen 2005; Lobón-Cerviá 2007b; Alonso-González et al. 2008) and water temperature (Borgstrøm & Museth 2005) and brown trout population dynamics, so both variables represent good candidates to be the local exogenous factors through which NAO can drive brown trout abundance dynamics in larger areas. In relation to this, significant negative correlations between the NAO index and local weather variables, such as daily rainfall (Gallego et al. 2005; Rodrigo & Trigo 2007), or river habitat variables, such as stream flow regime (Trigo et al. 2004; Gámiz-Fortis et al. 2008a,b) have been found in the Iberian Peninsula. Mean rainfall in winter has also been negatively related to NAO in the study area (Ebro valley and the eastern Cantabric area; López i Bustins 2007). Exploratory analyses of monthly NAO values versus stream flow have found a negative relationship among these variables that explains up to 17% and 25% of mean flow in March in low reaches of the Bidasoa (Atlantic) and Arga (Mediterranean) rivers, respectively, which are the major catchments in the study area. Mean stream flow in March can be a prior actor in the mechanisms through which winter NAO can influence dynamics of the studied populations, which Lobón-Cerviá (2007a,b) also showed in a Cantabric stream. Supporting Lobón-Cerviá & Rincón (2004) evidences of nonlinear influence of flow in March on trout recruitment, our alternative six-parameter nonstructured model has shown that too low or too high values of spring NAO – and therefore spring flow – would lead to a decrease in pgr. This alternative model also showed a negative relationship between winter NAO and pgr. Winter NAO is negatively related to flow in March ($r^2 = 0.39$) and thus high positive values of winter NAO may lead to low flows in March which may actually limit the habitat available to newly emergent fry, which is a life stage that is known to be characterised by highly territorial behaviour in this species (Elliott 1994).

Endogenous drivers

It has been found a positive effect of density in years $t-1$ and $t-2$ on λ_t. Per capita growth rate of age class 0+ is positively influenced by the density in year $t-2$, which can be identified as a 3-year lagged positive feedback tracing the upward trend of stock-recruitment curve, as was observed by Nicola et al. (2008). The generation time for brown trout is equal to or higher than 2 years, and this fact explains the lagged density dependence $\lambda_{1,t} = f(N_{t-2})$ because trout born in year $t-2$ are the parents of trout born in year $t + 1$, and, as explained above, N_t shows a high correlation with $N_{1,t}$.

There is a positive relation between N_{t-2} and $\lambda_{3,t}$, and, similarly, $\lambda_{2,t}$ is positively affected by N_{t-1}, which may reflect the effect of the presence of a strong cohort in the population. As there is a strong correlation among N_t and $N_{1,t}$, individuals of age class 0+ in year $t-2$ will be 2+ in year t (affecting $\lambda_{3,t}$), and 0+ in year $t-1$ will be 1+ in year t (affecting $\lambda_{2,t}$). Therefore the strength of a cohort has a positive effect on the whole population that can be detected throughout the time.

A negative effect of the population density in year t has been found to drive pgr in the same year, according both to the nonstructured model and to the age-structured model. This 1-year lagged negative feedback shows the downward trend of density dependence. The value of the carrying capacity can be obtained from the fitted models by making $\lambda_t = 1$ and solving N_t. The driving mechanism of this effect can be a type of an intercohort competition by which 1+ density negatively affects 0+ density in a given year t. However, this endogenous factor not only influences the youngest age class but also the oldest one which may indicate the effect of another type of intracohort competition.

Endogenous factors have been found to be the major driving forces in the regulation of populations of anadromous brown trout inhabiting predictable environments such as those described by Elliott (1994). However, evidence for this is scarce for resident brown trout, and existing evidence mainly describes relationships among density and physiological traits such as individual growth (Jenkins et al. 1999; Post et al. 1999; Lobón-Cerviá 2007a). Nicola et al. (2008) searched for evidence of density dependence in recruitment in several exploited brown trout populations in the Iberian Peninsula and found that data of all populations could be fitted to a Ricker stock–recruitment curve, but most of them were in the density-independent part of the curve, suggesting that density was not high enough for negative feedback to operate. When analysing endogenous population regulation from age-structured data, Nordwall et al. (2001) found that when 1+ density was artificially reduced, 0+ and 1+ trout densities increased the following year. They also verified an inverse relationship between 0+ abundance and that of the oldest cohorts for a given year.

The results of this study need to be extended in several ways: (i) the mechanistic explanation to the effects identified in this work has to be addressed; (ii) other climatic interconnection indices should be tested [e.g., Arctic Oscillation (AO), Western Mediterranean Oscillation (WeMO)] that are known to drive European and low Ebro valley (López i Bustins 2007) regional weather to improve the description and prediction capabilities of the models; (iii) specific studies aimed to detect and quantify the synchrony among the studied populations should be conducted; (iv) on the basis of this phenomenological approach, downscaling could lead to finding more local drivers through which NAO influences populations dynamics, thus improving the mechanistic approach to understanding the large-scale dynamics of brown trout populations; (v) this mechanistic approach might also lead us to a sounder interpretation of the observed nonadditive effects of density and spring NAO on the mean growth rate (pgr) of the studied set of populations.

Large-scale population models can be used by fisheries managers to explain fluctuations of the abundance of brown trout in a region, and also to make short-term predictions of the quantitative status of the resource they are managing. Nonstructured models seem to be more appropriate to be used for prediction purposes than age-structured models. Conservation issues also claim for the relevance of large-scale approaches, especially in the Iberian Peninsula where brown trout exhibits a wide variety of phenotypes and five operative conservation units have been proposed. This result highlights the importance of a management scheme based on larger areas.

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