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ARTICLE

Increasing Regional Temperatures Associated with Delays in Atlantic Salmon Sea-Run Timing at the Southern Edge of the European Distribution

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Abstract
Populations of Atlantic salmon *Salmo salar* at the edge of the species' distribution are the most vulnerable to environmental changes. Those inhabiting southern European rivers are expected to be particularly affected by global warming. However, they are exploited as a very valuable resource for the region, attracting tourism and generating substantial income. In the central part of northern Spain (Asturias), there is a long tradition of sport fisheries (angling). The first salmon caught in a river each year is called the "campanu." Analysis of a 50-year time series demonstrates that the run timing of the Asturian Atlantic salmon has changed over this period, as inferred from significant delays in the date of capture of the campanu. Average campanu weight has experienced a parallel significant decrease but age has not changed, indicating diminution of salmon condition. These changes are statistically associated with an increase in regional temperature, there being a minor effect of the global climate North Atlantic Oscillation index. Negative effects of high temperatures on salmon run and feeding, together with long migratory routes, may explain these results.

Climate change has varied consequences for animal species, including variation in the reproductive performance of marine birds (Croxall et al. 2002; Gjerdrum et al. 2003) and changes in the abundance, mortality, and distribution of fishes (Finney et al. 2000; McFarlane et al. 2000; Parson and Lear 2001; MacKenzie and Koster 2004). One effect of global warming with a high potential impact in ecosystems is asynchronization of migrations, as reported for birds (Both and Visser 2001), fish (Drinkwater 2006), and others. Delayed or premature arrival of a species to a temporary habitat affects its interactions with prey and predators as well as the community of species sharing the common space and resources. Populations at the edge of species distributions are particularly vulnerable to environmental changes (Walther et al. 2002; Thomas et al. 2004). These populations are more vulnerable because they are adapted to limiting, non-optimal environments. Among the species potentially sensitive to global warming (De Young et al. 2004), the migratory Atlantic salmon *Salmo salar* provides an opportunity for a case study because of its broad distribution on both sides of the Atlantic Ocean and its sensitivity to environmental effects, particularly temperature (Mills 1991).

Atlantic salmon populations located in the southern part of the species' distribution are declining or extirpated (Parrish et al. 1998; Valiente et al. 2010), and recent stock declines have been

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attributed, in part, to global climate change (Friedland et al. 2003). The southernmost European populations are located in North Iberia (Spain), at 42–43°N (Mills 1991); being at the edge of the native range, they are thus expected to be the most vulnerable to global warming.

Asturian rivers are short and steep and have high discharge due to the proximity of the Cantabrian Cordillera to the coast and the high frequency of precipitation in the region. Although small, Atlantic salmon populations are very appreciated for sport fisheries in Spain, where there is a long tradition of angling (i.e., Larios 1930; García de Leániz and Martinez 1988; De la Hoz 2001). Since the Spanish Civil War (1936–1939), the first salmon caught in Asturias (the central coastal region in northern Spain; see Figure 1), called "campanu" in the old regional language, is subjected to public auction. It can reach a very high price (3,000 euros/kg in 2008). When the rod angling season opens (traditionally the first Sunday in March), anglers crowd into Asturian rivers to catch the first salmon returning to the region to spawn in freshwater. The campanu is celebrated and widely publicized in the Spanish media. Delays in the first catch have been reported by the media the last few years, perhaps related to changes in climate conditions (e.g., García de Leániz et al. 2001).

In this study, we quantified the changes in sea-run times and tested their association with local and global climate conditions for wild Spanish populations, potentially the most vulnerable to environmental warming among all Atlantic salmon populations in Europe.

METHODS

The date of the first angling catch (campanu date in Asturias) was used as a proxy for population return time (Juanes et al. 2004). The intense and unique fishery for the campanu in these relatively small rivers and its consistency year after year has resulted in a long-term database that extends back prior to the existence of scientific sampling, and is thus ideally suited for our analyses. During the time period studied, fishing effort (number of rods per river and day) did not vary in this region (Braña et al. 1995).

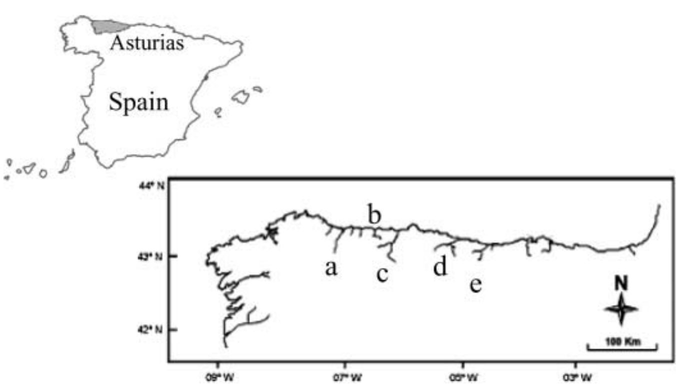

FIGURE 1. Map of the study area. Specific rivers in which Atlantic salmon spawn are as follows: (a) Eo, (b) Esva, (c) Narcea, (d) Sella, and (e) Cares.

The dates and weights of the campanu catch were compiled for each river from Asturian regional and Spanish national media. The data can be found recorded in compact disc files at the Hemeroteca Digital de la Nueva España, available upon request in the Asturian Regional Library (Oviedo, Spain).

For some campanu individuals caught before 1996, as well as for the entire run during the last 11 years, scale samples were made available by the Asturian regional government (the organization in charge of salmonid management in the region). Scales were employed for campanu age determination following Baglinière (1985).

Air temperatures, as an index of local climatic conditions, recorded in stations located near the mouth of the rivers (suitable records of water flow and temperature do not exist prior to 1990), were obtained from the official files of the Instituto de Meteorología de España. The five Asturian rivers considered, from west to east, were the Eo, Esva, Narcea, Sella, and Cares (Figure 1). The Eo River population has suffered a dramatic decline during the last decade (De la Hoz 2001) and should be considered with caution.

Values of the North Atlantic Oscillation index (NAOI) were fluctuations in sea-level air pressure between the Atlantic subpolar, low-pressure zone centered around Iceland and the subtropic, high-pressure zone centered around the Azores (Hurrell 1995).

We used the normalized Lisbon-minus-Stykkisholmur December–March average single-locus probe anomalies (obtained from www.cgd.ucar.edu/∼jhurrell). We used the winter index because it is during this season that the NAOI has its greatest effect on sea temperatures and hydrographic variability (Marshall et al. 2001; Ottersen et al. 2001; MacKenzie and Koster 2004).

Principal components analysis (PCA) and other statistical procedures (e.g., linear r correlations) were performed with the program PAST, version 1.88 (Hammer et al. 2001). This software was used for finding hypothetical variables (components) that account for as much of the variance in these multidimensional data sets as possible, through a PCA of the data with default settings, choosing the "correlation matrix" option for variables measured in different units.

RESULTS

In the absence of salmon traps or counters in this region, catch data seem to be a possible source of information for investigating Atlantic salmon return timing. Significant linear regression of date of campanu angling versus percent of annual catch obtained during the first month of the fishing season (by river, except for the Esva) supports the use of the angling date as a proxy for the average return date ($r = -0.75$, -0.42, -0.50, -0.60, and -0.74 for the Eo, Esva, Narcea, Sella, and Cares rivers, respectively; $P = 0.001$, 0.102, 0.05, 0.023, and 0.003).

Reliable data (date of angling, weight) on the campanu were found in Spanish national and local newspapers from 1956 (Figure 2). Before this date, only sporadic and often incomplete information existed for some years and rivers. The mouth of the Esva River was closed with a sand barrier until its removal in 1962. The first anadromous salmon entered the river, probably coming from neighboring populations, in 1963. Local temperature data were available for different time periods in the Cares (only 6 years between 1984 and 2003), Sella (1956–2003), Narcea (1967–2002), Esva (1962–2000), and Eo (1977–2002) rivers. Although local temperatures oscillated during the study period, minimum annual temperatures continuously increased ($P < 0.05$) from the beginning of the existing records, except for the Eo River (Figure 3; linear regression lines of

(a)

(b)

FIGURE 2. (a) Old (9.3 kg; 1956) and (b) recent (4.2 kg; 2004) campanu captured in the Narcea River. Photographs courtesy of *La Nueva España*.

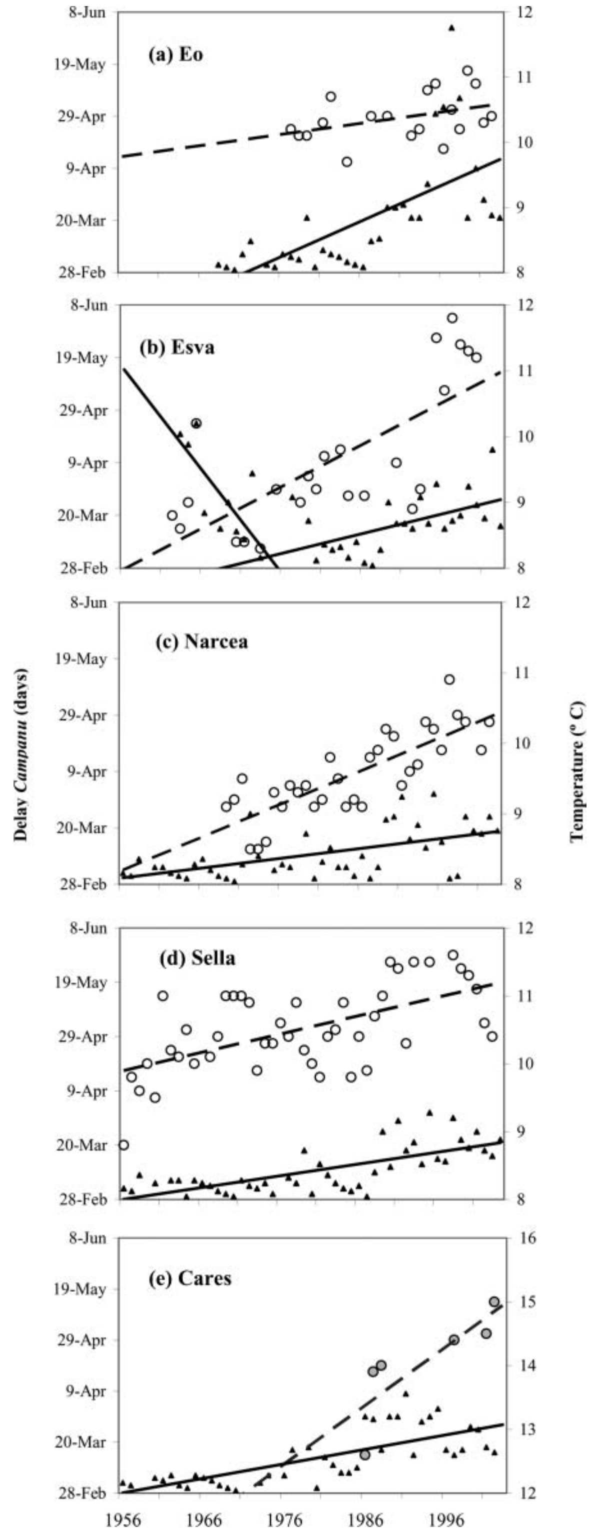

FIGURE 3. First-catch dates and local temperatures, by river. Circles indicate the mean annual minimum temperatures (mean annual temperatures for the Cares River), triangles the campanu delays. Linear regressions for the two data series are indicated by the dashed and solid lines, respectively. The mouth of the Esva River was opened in 1962 and salmon runs were irregular until approximately 1977. Therefore, two solid regression lines are shown, one for before 1977 and one for after.

$y = 0.06x–116.34$ [$r = 0.73$, df $= 22$], $y = 0.05x–83.95$ [$r = 0.8$, df $= 31$], $y = 0.03x–42.84$ [$r = 0.59$, df $= 42$], and $y = 0.09x–169.38$ [$r = 0.83$, df $= 4$] for minimum annual temperatures of the Esva, Narcea, and Sella rivers, and mean annual temperatures of the Cares River, respectively). The mean annual maximum temperatures patterns also increased significantly for the Esva, Narcea, and Sella rivers since 1968 (slope = 0.05 and 0.04, $P < 0.001$ and $P = 0.002$, df = 31 and 30, respectively), as it did for the Esva River since 1972 (slope = 0.02, df = 18, $P = 0.037$).

We found a significant delay in the date of campanu angling for all the rivers ($y = 1.69x–3{,}338.7$ [$r = 0.63$, df $= 27$], $y = 0.35x–678.61$ [$r = 0.57$, df $= 43$], $y = 0.43x–840.09$ [$r = 0.70$, df $= 43$], and $y = 0.57x–1{,}113.1$ [$r = 0.74$, df $= 39$] for the Eo, Narcea, Sella, and Cares rivers, respectively [$P < 0.001$ in all cases]), except the Esva River (Figure 3). For this river, the campanu delay increased significantly only since 1977 ($y = 0.97x–1{,}907.3$; $r = 0.63$; df $= 23$; $P < 0.001$). Due to annual variations in the opening date of the angling season (up to 10 d, in some cases), these data cannot be considered direct indicators of real first-catch delays. Another indication of delayed angling is the mean number of days existing between the opening of the sport angling season and the first catch in each river in the first and the second half of the time period studied (Table 1). We excluded the pre-1980 Esva River data from this analysis because until then its salmon population was stabilizing (De la Hoz 2001). Before 1980, most campanu were caught the opening day of each angling season. Since 1980, the average delay in catching the campanu ranges from three (Narcea River) to more than eight (Eo River) days.

The average campanu delay in the region (averaging campanu delays for all the rivers) was independent of sea age return (Figure 4). The campanu was multi–sea winter in 96% cases, without variation across years since 1956; therefore, a change in the campanu age can be excluded as a cause of sea-run delays. The weight, however, has significantly decreased in the period time considered ($r = 0.74$, $P < 0.001$).

A more global approach can be taken by exploring associations between local campanu characteristics (date of angling, weight) and indicators of climate change, considering both the global NAOI and average regional temperatures (annual maximum and minimum). Principal components analysis identified two main components (Table 2). Component 1 contributed to almost 50% variance, and the two main factors were weight and annual minimum temperature (Table 3), which were negatively associated ($r = -0.555$, $P < 0.001$). Component 2, accounting for 21% variance, included regional maximum annual temperature and campanu delay. These two factors were not significantly associated ($r = 0.004$, $P > 0.05$). The NAOI appeared as main contributor only to component 3 (which was less significant), indicating that this global indicator had only marginal effect in the data set variance. North Atlantic Oscillation Index was significantly negatively correlated with campanu weight ($r = -0.305$, $P = 0.003$) but not with the campanu delay ($r = 0.262$, $P > 0.05$). Consistently, the scatter diagram of the data set (Figure 5) showed NAOI as the less-important factor for explaining the variance. In the same diagram, both global (NAOI) and regional (annual) temperatures, which are climate indicators, were positively associated with campanu delays and negatively associated with the campanu weight.

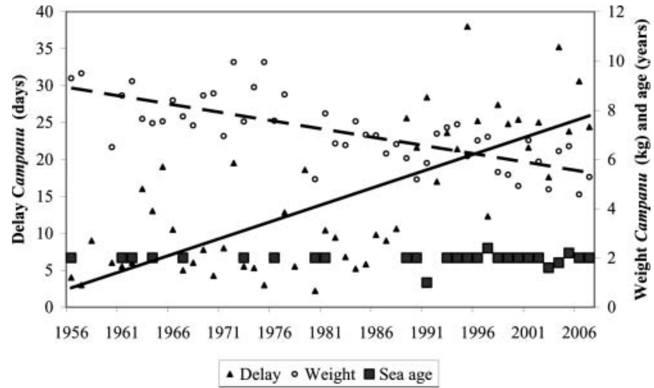

FIGURE 4. Data and linear regressions for campanu delay (solid line; $y = 0.45x–874.12$; $r = 0.72$, df $= 48$, $P < 0.001$), weight (dashed line: $y = -0.67x + 140.53$; $r = 0.74$, df $= 46$, $P < 0.001$), and years at sea in the period considered averaged across the five rivers studied.

DISCUSSION

Our results unequivocally point out the influence of climate change in southern European Atlantic salmon populations. Both local (local temperatures) and global (NAOI) factors affect return dates of Atlantic salmon, but local temperatures seem to be stronger determinants for the date of entering the rivers. Sea-run migration timing seems to be in synchronization with local

TABLE 1. Average (SD) number of days between the opening of the Atlantic salmon fishery and the first angling catch.

River	Before 1980	After 1980
Cares	1.000 (2.666)	7.208 (7.360)
Sella	0.714 (1.383)	4.957 (7.326)
Narcea	1.545 (4.383)	3.130 (5.371)
Esva		5.217 (6.802)
Eo	0.636 (2.110)	8.348 (10.768)

TABLE 2. Eigenvalues and percentages of total variance attributed to each PCA component. Jolliffe's (1986) cutoff eigenvalue was 0.7.

Component	Eigenvalue	% Variance
1	246.928	49.386
2	10.736	21.472
3	0.796441	15.929
4	0.443853	8.877
5	0.216827	4.336

TABLE 3. Coefficients for each trait considered, by principal component. The highest coefficients (bold italics) are for the traits that contribute most to the variance.

Trait	Component 1	Component 2	Component 3
Delay	0.4726	***−0.4379***	−0.3096
Weight	***−0.5015***	0.2227	0.2114
NAOI	0.3491	−0.1427	0.9205
Tmax	0.2924	***0.8297***	−0.0335
Tmin	***0.5637***	0.2232	−0.1051

freshwater conditions for Spanish populations, as it occurs in other latitudes (Scarnecchia 1983; Dahl et al. 2004; Jonsson et al. 2007). The intensity of warming seems to be well reflected in the Atlantic salmon populations analyzed: the delay in campanu angling showed a stronger trend for the time period after 1980 versus the entire time period (Table 1), in agreement with indications that the period 1970 onward is a distinct period of warming, increases in temperature occurring at a rate nearly double that of the previous period (Houghton et al. 2001; Gian-Reto et al. 2002). It is most likely that the southernmost populations are more affected by climate change than others inhabiting the middle portion of the distribution range, as they are in higher extinction risk (Thomas et al. 2004).

Our results indicate a delay in return timing for southern European Atlantic salmon. However, the change in average return date (the date of campanu angling is a proxy for it; see Juanes et al. 2004) seems to be the opposite of that expected. Since increasing temperatures advance maturity (Meerburg 1986; Jonsson and Jonsson 2004; References *in* Jonsson and Jonsson 2004), return dates should be advanced, not delayed, as is consistently found in Spanish populations (see, e.g., García de Leániz et al. 1992, 2001). High local temperatures at their arrival to the river mouth can, at least partially, explain delays. Anadromous fish enter rivers when water temperatures reach a triggering threshold (Leggett and Whitney 1972), but too-high freshwater temperature may make the way upstream difficult (Glebe and Leggett 1981; Enders et al. 2005; Salinger and Anderson 2006). Other within-river factors—such as discharge rates that are, in turn, affected by man-made barriers aimed at obtaining electricity or water supply (Thorstad et al. 1998)—are also affected by climate change and could be influencing the timing of the runs. Another possible cause that could contribute to delayed returns could be the presence of hatchery-reared individuals. A common feature of both hatchery-reared and escaped, farmed salmon seems to be their late river entry compared with that of wild salmon (Jonsson et al. 1990, 1991, 1994; Heggberget et al. 1993; Carr et al. 1997; Thorstad et al. 1998), resulting in upstream migration and entering of spawning areas later in the season. Although there are no salmon farms in the region and, therefore, escapes are not a problem, the Spanish rivers have been heavily stocked in the decades 1980–1990 (e.g., Moran et al. 2005; Ayllon et al. 2006). Hatchery-reared individuals could have contributed to increase delays in those decades; however, this does not exclude climate as a cause of delays, given the clear association of run timing and temperature obtained also before and after the stocking period.

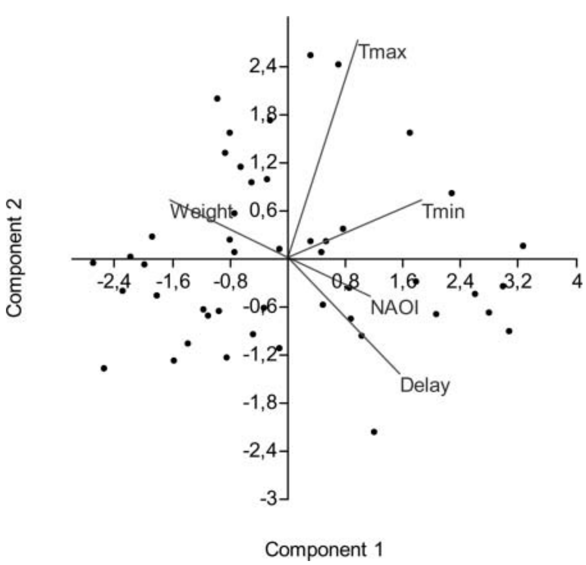

FIGURE 5. Scatterplots for the PCA showing the relative weights of the five traits considered (diagonals): campanu delay, campanu weight, NAOI, and mean annual maximum and minimum temperatures (Tmax and Tmin, respectively).

Another factor contributing to delayed arrival could be poor salmon condition at sea. Mean weight has significantly decreased for campanu, but age has not (Figure 4); therefore, the average condition factor has declined. Low water temperature stimulates lipid storage relative to protein production (Jonsson and Jonsson 2004); thus less lipid reserves are expected in salmon growing in warm conditions. Atlantic salmon feeding behavior is also affected by high temperatures, which tend to reduce appetite in this species (Elliott 1991; Grande and Andersen 1991). Other concomitant factors at sea—such as depletion of abundance of salmon prey (Atlantic herring *Clupea harengus*, pink shrimp *Farfantepenaeus duorarum*, white shrimp *Litopenaeus setiferus*, and *Pandalus* spp., and other species) associated with NAOI, fisheries (e.g., Buch 2004; Guijarro 2007; Lajus et al. 2007), or both—may also significantly contribute to weight reduction. Poor condition factor would cause lower swimming stamina and delays in arrival to the natal river, enhanced by the fact that these salmon run the longest distance from feeding grounds of all European Atlantic salmon.

The results of this study may also be used for management. As Atlantic salmon are a traditional resource of importance in the region (e.g., De la Hoz 2001), delayed returns are a serious concern for sport fishermen because they perceive a loss of real fishing days if the season is open when there are no salmon in the river. Our results could aid to planning the date of opening, revising and adjusting it periodically according to climate trends.

A final remark concerns the need of global perspectives when analyzing the effect of climate change. Both local and global changes can be evidenced in populations at the edge of the species distribution because warming is relatively recent (Walther et al. 2002). Two or three decades is a short time period for a vertebrate species. On the other hand, significant changes in migration times for this species in only four decades are probably a signal that the whole ecosystem is being affected, at least the species that interact with Atlantic salmon. Similar to birds (Saether et al. 2000; Both and Visser 2001) and other key species (Wuethrich 2000), both short- and long-term changes are expected in the rest of the freshwater and estuarine species that share Atlantic salmon habitat.

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