

Fluctuations in European eel (*Anguilla anguilla*) recruitment resulting from environmental changes in the Sargasso Sea

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ABSTRACT

European eel decline is now widely observed and involves a large number of factors such as overfishing, pollution, habitat loss, dam construction, river obstruction, parasitism and environmental changes. In the present study, we analysed the influence of environmental conditions in the Sargasso Sea and Atlantic ocean circulation on European glass eel recruitment success. Over a recent 11-year period, we showed a strong positive correlation between an original index of glass eel recruitment and primary production in eel spawning area. Moreover, primary production was negatively correlated with temperature in the Sargasso Sea. Therefore, we used sea temperature as an inverse proxy of marine production. A close negative relationship has been found over the last four decades between long-term fluctuations in recruitment and in sea temperature. These findings were reinforced by the detection of a regime shift in sea temperature that preceded the start of the decline in glass eel recruitment in the early 1980s. By contrast, variations in integrative indices measuring ocean circulation, i.e. latitude and strength of the Gulf Stream, did not seem to explain variations in glass eel recruitment. Our results support the hypothesis of a strong bottom-up control of leptocephali survival and growth by primary production in the Sargasso Sea on short and long time-scales. We argue that sea warming in the eel spawning area since the early 1980s has modified marine production and eventually affected the survival rate of European eels at early life stages.

Keywords : *Anguilla anguilla*, BATS, glass eel, bottom-up, primary production, regime shift, SST, Sargasso Sea, recruitment.

INTRODUCTION

European eel recruitment (*Anguilla anguilla*) has significantly dropped since the end of the 1970s and the stock is now considered in danger (ICES, 2006). This species has been listed in the red book of endangered species in several European countries (Moriarty and Dekker, 1997; Dekker, 2003a) and its inclusion in Appendix II of the Convention on International Trade in Endangered Species of wild fauna and flora (CITES) was recently proposed (CITES, 2006). A combination of factors are invoked to explain eel stock decline, including overfishing (Dekker, 2003b), anthropogenic impacts such as pollution (Amiard-Triquet *et al.*, 1988; Gony *et al.*, 1988; Feunteun, 2002; McCleave, 2001), habitat loss (Feunteun, 2002), parasites (Aguilar *et al.*, 2005), fluctuations in current speed and ocean circulation patterns (Power & McCleave, 1983, Castonguay *et al.*, 1994; Knights, 2003) and changes in climate features (Knights, 2003). So far, none of these hypotheses has been validated (Dekker *et al.*, 2003), but all are suspected to interact and push the stock downward.

In the present analysis, we investigate whether oceanographic and trophic conditions encountered by eel larvae during their early oceanic life stages may explain the patterns of variability and the decline in glass eel recruitment over several decades.

The European eel is a catadromous fish that goes through one of the longest seaward migrations, more than 6,000 km across the Atlantic Ocean. Adults spawn in the Sargasso Sea. Leptocephali larvae, conveyed by warm currents, come from the Sargasso Sea to settle on African and European shelves, from Mauritania to Polar Circle (Schmidt, 1922). There has been a long history of ecological studies dealing with marine life stages of this species (Dekker, 1998). Evidence now exists showing that oceanic conditions affect the survival of larvae during their migration in the North Atlantic. In particular, Désaunay and Guérault (1997) showed that decreases in biometric characteristics during the oceanic phase, e.g. mean length, were parallel with a decrease in recruitment. Oceanic condition may impact the condition factor of glass eels during their ingress into European estuaries. A recent study of Bureau du Colombier *et al.* (in press) showed the importance of energy state on the glass eel capacity to colonize freshwater watersheds.

It is a challenge to investigate whether major changes observed in North Atlantic marine ecosystems (Planque and Taylor, 1998; Reid *et al.*, 1998; Beaugrand *et al.*, 2002; Drinkwater *et al.*, 2003) could be responsible for fluctuation and/or regime shifts in European glass eel recruitment. This paper investigates and tests two non-exclusive hypotheses on the process by which larvae could be affected during their development and marine migration in the North Atlantic. Firstly, the transport of eel larvae by oceanic currents may play an important part in glass eel recruitment. Leptocephali largely depend on the drift in the current for their trans-oceanic migration. Exact migration duration is still controversial (van Ginneken and Maes, 2005) and is estimated to be comprised between 9 months and 2-3 years depending on methods used to compute it (Lecomte-Finiger, 1994; Tesch, 2003). Unfavorable currents that prolong the duration of oceanic migration, and increase time of exposure to predation are suspected to impact glass eel recruitment (Désaunay and Guérault, 1997; Knights, 2003).

Secondly, food availability during the early life stages may affect eel larvae survival. Although feeding mechanisms and sources of larvae nutrition are still largely debated (Otake *et al.*, 1993; Pfeiler, 1999; Bishop and Torres, 2001), feeding is critical for survival and development of small leptocephali after hatching. Starvation and low prey availability largely affect larvae survival (Cushing, 1995; Werner *et al.*, 1997; Knights, 2003).

Assessing the relative part of these two processes, i.e. transport and food availability, in the variability of glass eel recruitment is of primary importance to improve our knowledge on eel ecology and for the management of this species. To this aim, we examined the relationships between glass eel recruitment indices and different environmental descriptors related to transport and to food availability in the Sargasso Sea. Correlations between recruitment and environmental signals were investigated on two different time-scales, i.e. short-term interannual variability and long-term fluctuations. In particular, we addressed the following questions: (1) Are the recruitment time-series related to physical indices of currents strength and latitude? (2) Can the interannual fluctuations in recruitment of European eel be explained by fluctuations in marine production in the Sargasso Sea? (3) Could long-term changes in food availability in the Sargasso Sea explain the recent decline in eel recruitment?

MATERIALS AND METHODS

Recruitment data

Two recruitment indices were used to examine short and long-term response to marine environment. First, for long-term fluctuations analysis and detection of regime shifts, we used the seven longest time-series of glass eel recruitment available from ICES Working Group on Eel (ICES, 2006), i.e. Ems in Germany, Den Oever and IJmuiden in the Netherlands, IJzer in Belgium, Loire and Vilaine in France and Nalon in Spain (Fig. 1, Table 1). All time-series were standardized (divided by their mean over the period) to define a glass eel recruitment index. All European time-series exhibit similar long-term fluctuations (Dekker *et al.*, 2003). Despite their interest for survey at European scale, these data may suffer from heterogeneity (Dekker, 2004). The first four time-series are derived from scientific surveys while the last three are assessed by fishery-dependent surveys (see ICES, 2006). Data suffer from a certain lack of reliability because of sampling discrepancies. Thus, the decline in European eel population shown by these series may be underestimated due to difficulties in catch data collection prior the 1970s. These indices were only used to describe the general pattern and low frequency variations of European eel recruitment over the last decades but are not fully appropriate to describe recruitment interannual variability.

To investigate short-term interannual variability in glass eel recruitment, we used another original homogeneous time-series of eel recruitment derived from a precise survey of the mean annual catch of glass eel by few fishermen in the Loire river (France) between 1994 and 2004. The series was computed from the financial reports of a French glass eel trader (i.e. 3618 daily catches of 5 fishermen over the period). This company has a long history in glass eel business and in scientific cooperation (e.g. Elie, 1979; Castelnaud *et al.*, 1994) and therefore provides reliable glass eel catch data. We selected fishermen who can be qualified as compliant and regular. "Compliant" includes fishermen who keep on fishing more than five hours per sea trip. "Regular" means that they go fishing each opening day of the season. The mean number of fishing days per fisherman per season was 107.7 with a standard deviation of 11.2 for a mean fishing season of 136 days. Our sample of fishermen fished during 79.2% of authorized time. We averaged catches per year because monthly abundance variability depends on local factors (temperature, winds, rainfall, turbidity and flood) that influence catchability and upstream migration on a very short time-scale (White and Knights, 1997; de Casamajor *et al.*, 1999;

Prouzet *et al.*, 2003; Tesch, 2003; Bouvet *et al.*, 2006). Mean catches of glass eel per fisherman per year were then considered as a reliable recruitment index since fishing methods and effort remained constant during the period and since no change in fishing areas was observed.

Environmental data

Transport Index and Gulf Stream index

Correlation between recruitment data and the Transport Index (TI) and the Gulf Stream Index (GSI) was first investigated to test the hypothesis that recruitment variability was driven by ocean currents variability. TI estimates the strength of the baroclinic gyre circulation in the North Atlantic, i.e. the strength of the Gulf Stream and North Atlantic Current system. It is calculated from the difference of the potential energy anomalies (PEA) between Bermuda and Labrador Basin. Data from 1954 to 2005 were extracted from the website of the Ocean Observations Panel for Climate (OOPC) and with courtesy of Ruth Curry (http://ioc3.unesco.org/oopc/state_of_the_ocean/sub/berm_lab_trans.php).

GSI is a measure of the latitude of the Gulf Stream and is established on monthly charts of its north wall, derived from aircraft, satellite and surface observations (Taylor and Stephens, 1998). Data from 1966 to 2005 were extracted from the website <http://web.pml.ac.uk/gulfstream/data.htm>.

Primary production

We propose to use primary production (PP) as an indicator of eel larvae food. This is sustained by general considerations following Ware and Thomson (2005) and based on the available knowledge about leptocephali diet. Two potential sources of nutrition were indeed proposed for larvae: Dissolved Organic Matter (DOM) and Particulate Organic Matter (POM) in the form of zooplankton fecal pellets and larvacean houses (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler, 1999). PP was considered as a good proxy for leptocephali food as Durand *et al.* (2001) described a strong linear relationship between phytoplankton and POM in the Sargasso Sea. Food availability in the Sargasso Sea can be critical in early life stages to determine larvae capacity to rapidly reach the size that allows them to drift into North Atlantic currents (Knights, 2003). Eel larvae are qualified as type II larvae based upon their unique developmental strategy that allows them to increase rapidly in size while devoting the majority of their energy to metabolism, i.e. nutrition and locomotion, and not to mass increment as in most larval fish. After a post-hatched period in which the yolk-sac is resorbed, the larval fish shows a dramatic increase in size during which up to 40% of the leptocephali maximum length is attained while only 5-7% of the maximum mass is accumulated (Bishop and Torres, 2001). We used data provided by the Bermuda Biological Station for Research which has been carrying out *in situ* sampling of PP by filtering the water column during cruises since 1988. PP data associated with details about methods are available on the Bermuda Biological Station website (<http://bats.bbsr.edu>). A set of 8 standard depths on 20 m intervals from 0 to 140 m is sampled in the area of eel spawning (Southeast of Bermuda, Fig. 1). The Bermuda Atlantic Time-series Study (BATS) station is located in the west central Sargasso Sea and can be considered as a

representative of condition affecting leptocephali as they migrate and begin feeding in the entire Sargasso Sea (Nelson *et al.*, 2004). Different samplings of leptocephali in this region revealed a preferred depth of 160 m during daylight and of 60 m at night (Schoth and Tesch, 1982, 1984; Castonguay and McCleave, 1987). Most of the PP is produced over a 9-month period from November to July. PP was integrated over this period in order to derive an average estimate of the annual production in the Sargasso Sea. Averaging over this period also accounts for the time of transfer of PP in the first levels of the food chain. The hatching period that spans between March and June is included within these 9 months (McCleave, 1993; Wang and Tzeng, 2000). Using these BATS data, we calculated PP time-series over the period 1989-2002.

Sea temperature as a proxy of primary production

In order to investigate long-term regime shift and variations, temperature in the Sargasso Sea was used as an inverse proxy of PP. Indeed, plankton communities dynamics are driven by their physical environment and it has been shown that temperature can be a useful indicator of nutrient availability in thermally stratified waters (Bouman *et al.*, 2003; Behrenfeld *et al.*, 2006; Doney, 2006). The marine production increases with SST in cooler waters of the Northeast Atlantic, but it decreases as SST increases in warmer waters (Richardson and Schoeman, 2004). National Aeronautics and Space Administration (NASA) and McGillicuddy *et al.* (2001) confirmed this inverse relationship exists in the warm waters of the Sargasso Sea (http://daac.gsfc.nasa.gov/oceancolor/locus/tutorial_6.shtml). Warming inhibits indeed vertical mixing, reducing the upward nutrient supply and lowering marine production. Hence, in warm waters of the Sargasso Sea, when sea temperature increases, PP decreases.

Temperature data

Temperature in the Sargasso Sea has been monitored at Hydrostation S of the Bermuda Biological Station since 1955. Since PP was averaged over the 0-140 m layer and we considered that sea temperature impacts PP, we averaged sea temperature over the deepest layer where data were available, i.e. the 0-100 m layer which is above the thermocline. Temperature data were available on a monthly basis but were averaged per year to compute a mean annual time series.

Statistical models

Statistical analyses were performed in two ways: i) First, the correlation between the recruitment and environmental time-series was assessed; ii) Second, the existence of regime shifts in the time-series was investigated.

Recruitment was \log_{10} transformed before each correlation analysis with environmental variables. Because migration duration of larvae is not clearly established and arouses controversy (van Ginneken and Maes, 2005), the correlation between recruitment and environmental time-series was systematically tested considering a time-lag of +1, +2 or +3 year(s). Thus, recruit-

ment indices, X_t , were then correlated with environmental variable, Y_{t-d} , where $d = 1, 2$ or 3 . When considering oceanic indices (TI, GSI) as the environmental variable Y_t , we analysed the correlation between recruitment X_t and $\overline{Y_{t-d}^*}$, where $\overline{Y_{t-d}^*}$ is the average over the years $t - d$ to t .

Testing time-series correlations

Procedures for statistical testing of the degree of correlation between the recruitment and environmental series must account for the autocorrelation in the time-series because it may result in an artificial increase in the statistical significance of the correlation test. Following Pyper and Peterman (1998), we used methods specifically designed to study long-term and short-term correlations in the case of auto-correlated time-series.

Testing short-term correlations

To assess correlations between interannual variations of recruitment index and environmental (TI, GSI, PP, sea temperature) time-series, we removed the autocorrelation by prewhitening the data series prior to statistical testing. The aim is to transform the original data to eliminate statistically significant autocorrelation whilst retaining the high frequency signal (Fox *et al.* 2000). After the transformation, standard correlation tests can then be applied to the resultant series. Prewhitening of the recruitment and environmental time-series, both of initial length N , was performed by first-order differencing (Thompson and Page, 1989). The Pearson coefficients were used to test correlations between the first-order differenced recruitment and environmental time-series. The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with $(N-1)-2$ degrees of freedom (d.f.) where $(N-1)$ is the length of the first-differenced time-series.

Testing long-term correlations

To analyse long-term patterns between recruitment indices and environmental (GSI, TI, sea temperature) time-series, we first smoothed data with a 5-year moving average. Then we adjusted the d.f. in the statistical tests to compensate for autocorrelation in order to analyse low-frequency sources of covariation (Pyper and Peterman, 1998). To adjust d.f., we applied the equation proposed by Chelton (1984) and modified by Pyper and Peterman (1998):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_j r_{xx}(j) \cdot r_{yy}(j) \quad (1)$$

where N^* is the corrected sample size that interprets as the number of independent joint observations on the two time-series X (recruitment data) and Y (environmental data), N is the length of the initial time-series and $r_{xx}(j)$, and $r_{yy}(j)$ are the autocorrelation of X and Y at lag j . Estimators of autocorrelation r are obtained using the Box-Jenkins' equation (Box

and Jenkins, 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{N}{N-j} \frac{\sum_{j=1}^{N-j} (X_t - \bar{X})(X_{t-j} - \bar{X})}{\sum_{j=1}^N (X_t - \bar{X})^2} \quad (2)$$

where \bar{X} is the overall mean. Pyper and Peterman (1998) tested a variety of d.f. adjustment methods and found Eq. 1 to be robust and unbiased compared to other methods. This method is also robust to the number of lags applied in the d.f.-reduction (Eq. 1). In the present analysis, we computed autocorrelations until the 9th lag approximately equal to $N/5$, following Pyper and Peterman (1998). The correlation was then assessed using Pearson coefficients with d.f. correction for autocorrelation as described above (Eq. 1). The p-value was assessed by comparing the Pearson coefficient against its theoretical distribution with $N^* - 2$ degrees of freedom.

Regime shift detection

A sequential regime shift detection method was performed following Rodionov and Overland (2005) to detect major changes in trends of glass eel recruitment indices and sea temperature. Recruitment data were not \log_{10} transformed prior to analysis to maintain a sufficient variance and make the regime shift detection more relevant. This method enables us to estimate the magnitude of the shift through a regime shift index (RSI). The algorithm has user-specified criteria, e.g. cut-off time-scale (l) that determines the minimum duration to qualify as a regime. The key concept is that there must be significant shifts in mean value relative to the within-regime variance in order to detect a new regime. In the present analysis, cut-off length (l) was set to 10 years and probability level at $p = 0.01$. We investigated, however, the sensitivity of the results to the parameters setting l to 15 and 20 years and $p = 0.05$.

RESULTS

No correlation between recruitment and transport-related descriptors

On the short-term, no significant correlation was found between TI or GSI and recruitment time-series whatever the ICES data (not shown) or Loire recruitment index (Table 2) and whatever the time-lag (not shown). On the long-term, no significant correlation was found between TI or GSI and recruitment indices whatever the time-lag (not shown). Thus, this statistical analysis does not reveal any clear linear relationship between the position or the strength of the Gulf Stream and the leptocephali survival rate.

A strong short-term correlation between recruitment in the Loire and PP in the Sargasso Sea

We only reported results of the relation between PP and the Loire recruitment index. Results obtained with other ICES recruitment indices were not significant or much less significant, except for the Loire index from ICES.

Recruitment index in Loire river and PP time-series exhibited a decreasing trend which was more outstanding for our recruitment index (Fig. 2a). Catches dropped from approximately 700 kg per fisherman per year in 1994 to approximately 200 kg in 2004 in the Loire river. Test for synchrony showed a significant positive correlation between Loire recruitment and the 3-year lagged time-series of PP ($r = 0.81$, $p < 0.005$; Table 2, Fig. 2b) whereas no significant correlations were found with 1 or 2-year lagged time series (not shown). High (resp. low) PP during first semester of year t was followed by a high (resp. low) recruitment index in Loire river in winter of year $t+3$.

Long-term relationships between sea temperature and glass eel recruitment

Long-term variations in sea temperature were used as a proxy of PP. The negative relation between sea temperature and PP has been well established for low and mid-latitudes (Behrenfeld *et al.*, 2006). In the Sargasso Sea, this relationship is confirmed by the significant negative relationship between monthly time-series of PP and sea temperature over the period 1989-2002 ($r = -0.54$, $p = 0.02$).

Temperature in the Sargasso Sea decreased from 1960 to the early 1970s and subsequently increased until the most recent records (Fig. 3). Changes in Sargasso Sea temperature resulted in a warming of the upper ocean layer (0-100 m), from less than 21.2 °C in 1971 to more than 22.0 °C in the 2000s, indicating strong environmental changes in the system over the last 40 years. During the colder phase, recruitment indices were high, varying around a long-term average comprised between 2 and 3, whereas it declined markedly during the warming period (after 1980) to reach a value comprised between 0 and 0.5. Glass eel recruitment indices increased in the early 1970s to reach a peak in the beginning of the 1980s. From then on, the recruitment began to decrease. Then, glass eel recruitment indices dropped by more than 90% in less than 25 years. A strong and significant negative relationship was found between fluctuations in sea temperature (3-year lagged) and in recruitment indices over the period 1963-2002 (Fig. 4). Periods of low (resp. high) sea temperature were associated with periods of high (resp. low) glass eel recruitment. Correlations were lower and less significant when using 1 and 2-year time lags between time-series (not shown).

Regime shift in glass eel recruitment indices and in sea temperature in the Sargasso Sea

The results of the regime shift detection show three main phases in the Sargasso Sea temperature, a colder phase before 1980 (mean temperature of 21.4 °C), a warmer phase afterward

(mean temperature of 22 °C), and a third, even warmer, after 1999. The sequential regime shift detection showed a significant positive shift in temperature in 1979 (RSI = 0.98) and a negative shift in glass eel recruitment indices in 1982 for Ems (RSI = -1.44), Den Oever (RSI = -0.94), IJmuiden (RSI = -1.64) and Loire (RSI = -1.92), in 1983 for Vilaine (RSI = -1.41) and Nalon (RSI = -1.42) and in 1979 for IJzer (RSI = -1.93) (Fig. 3). A weaker shift occurred in 1998 for the temperature (RSI = 0.89) but its consequences can not be detected in that analysis as recruitment time-series stopped in 2003 due to the moving average. The shift in 1979 in IJzer recruitment index could be explained by the shortness of the time-series that induced an earlier detection of the shift. Levels of recruitment have dropped again since 2001 for most European recruitment time-series (ICES, 2006) suggesting that another shift is just arising in glass eel recruitment. The main shifts described above were not sensitive to changes in the value of l and p .

DISCUSSION

This study reinforces the hypothesis that marine production within the European eel spawning area affects its earliest life stages and subsequent glass eel recruitment on both short and long time-scales. Based on the analysis of short-term interannual variability for the most recent years (1994-2004) and long-term variations in the last decades (1960-2002), the negative correlation between glass eel recruitment and PP in the Sargasso Sea sustains the hypothesis that variability in glass eel recruitment may be linked to food availability and/or composition in the Sargasso Sea. As PP is negatively correlated with temperature in the Sargasso Sea (Bates, 2001; McGillicuddy *et al.*, 2001), we conjecture that the increase in temperature over the last three decades has led to a decrease in PP and hence to a significant drop in glass eel recruitment. Our findings are reinforced by the detection of a regime shift in temperature that preceded the start of the decline in glass eel recruitment in the early 1980s. By contrast, ocean circulation does not seem to be a major driver of eel larvae survival on the basis of the indices used and of linear relationships.

Recruitment indices

The most significant short-term correlation between recruitment and PP series was obtained using the original recruitment index series in the Loire river assessed from the French glass eel trader. This original recruitment series was particularly relevant for the analysis of interannual variability. Loire river is one of the main glass eel arrival basins in Europe. This index can be considered robust and reliable to analyse interannual variability as fishing methods, fishing wedges of fishermen, fishing date, and duration remained constant over the period 1994-2004. By contrast, other European river indices were calculated using heterogeneous data that cover different time intervals, various sources, and location (ICES, 2006) and their use to analyse interannual variations is debatable. The use of other European series produced less consistent relationships. We attribute these differences to the quality of the European series described above. However, they are of high interest for long-term analysis of recruitment fluctuations over a long period (1960-2003) and were used in several studies (e.g. Dekker, 1998; Knights,

2003).

Migration time

Our results contribute to the study of the migration duration of European eel larvae. Most of the significant correlations were found using a 3-year delay between recruitment and the environmental time-series. In our analysis, this time lag accounts for transatlantic migration, metamorphosis, and estuarine arrival. As PP is calculated from November to July and the fishing season is comprised between December and April, the time lag used is comprised between 2 and 3 years. The time lag of 3 years between the regime shifts in temperature and most of glass eel recruitment indices observed at the beginning of the 1980s also supports the same hypothesis about migration duration. Thus, in a context where uncertainty about migration duration between 1 and 3 years remains high, our results seem to be more consistent with a 2 to 3-year delay between hatching and glass eel recruitment. This is consistent with estimates of several authors (e.g. Schmidt, 1922; McCleave, 1993; Tesch, 2003). In particular, a migration duration longer than 2 years has been validated through Lagrangian modeling in the Atlantic ocean (Kettle and Haines, 2006). Still, this hypothesis of a 2 to 3-year migration duration remains controversial since ages at recruitment back-calculated by otolithometry ranged from 7 to 15 months (Arai *et al.*, 2000; Wang and Tzeng, 2000). However, studies based on daily growth increments in glass eel otoliths have been largely criticized since it may be a period of no deposition of daily rings between hatching and migration of glass eels into estuaries (Svedäng *et al.*, 1998; Cieri and McCleave, 2000).

Impact of transport on glass eel recruitment success

The relationships between TI, GSI and glass eel recruitment were not clearly established. However, other studies suggest that leptocephali may be affected by oceanic features because of their long larvae oceanic phase (Knights, 2003). Recent analysis by Friedland *et al.* (2007) suggested that the influence of ocean parameters such as the shallowing of the mixed layer depth inducing a decrease in primary production, drift conditions in larval transport area, and declining trends in winds have contributed to declining recruitment as well. For instance, they show that fluctuations in Den Oever Index are related to fluctuations in North Atlantic Oscillation (NAO) which indicates recruitment may be influenced by physical and biological structure of the North Atlantic. Miller *et al.* (in prep.) suggested that the changes associated with these type of atmospheric forcing could alter the biological characteristics of the surface layer where leptocephali feed. Although NAO has been widely used to investigate response of marine ecosystems to climatic condition (e.g. Fromentin and Planque, 1996), we did not use this integrative environmental index because it does not allow direct analyses of the responses of plankton communities to their local environment as temperature does. However, large-scale atmospheric forcing by the NAO modifies winds and SST patterns that regulate mixing and stratification and hence phytoplankton abundances (Drinkwater *et al.*, 2003).

Friedland *et al.* (2007) also suggested that fluctuations in latitude of the 22.5°C isotherm which is a useful indicator of the northern limit of eel spawning area, may affect both spawning location and transport of the leptocephali out of the Sargasso Sea by increasing retention within

the Sargasso Sea gyre. Moreover, the possibility to leave the Sargasso Sea may be altered by changes in winds in the northern Sargasso Sea, which have reduced southward Ekman transports and hence contributed to increase larval retention in the Sargasso Sea gyre. Such changes in larval retention might add up to the bottom-up control process suggested by our result and underline the various and potential combined effects of environmental changes on eel recruitment. The mysteries of oceanic life history of eel and the lack of information about eel biology and ecology (e.g. migration duration and routes, larvae diet) hinder to clear up links between eel larvae survival and these environmental changes.

Glass eel recruitment driven by environmental conditions in the Sargasso Sea

Our analysis proposed a focus on the influence of the trophic conditions in the Sargasso Sea on the subsequent recruitment of European glass eels. On the short-term, the highly significant correlation between PP and glass eel recruitment in the Loire river suggests a dynamic relationship between food availability and larvae survival rate. This indicates that a strong bottom-up control may drive the young life stage of European eel. To extend the link between PP and glass eel recruitment on a longer time-scale, we relied on the inverse relationship found between sea temperature and PP and we used variations in temperature in the Sargasso Sea as a proxy of variations in PP in that area (Bates, 2001). Sea temperature is an important manifestation of climate change and can be used as an environmental proxy associated with changes in phytoplankton community structure (Beaugrand *et al.*, 2002). Processes implied include changes in vertical mixing, changes in water mass characteristics, circulation of the subtropical gyre and distribution of mesoscale eddies (Bates, 2001). This complex response of marine production to sea temperature probably arises because temperature not only affects biota directly, but is also a proxy for other physical processes regulating the size structure, taxonomic composition, and abundance of phytoplankton communities (Li *et al.*, 2002). In warmer and more stratified waters with limited nutrients, warming is likely to reduce marine production because increased heating can enhance existing stratification, thereby reducing the availability of nutrients to phytoplankton in the surface layer and leading to a microbial-dominated community (Roemich and McGowan, 1995; Richardson and Schoeman, 2004; Behrenfeld *et al.*, 2006).

We focused on the main patterns of eel recruitment and sea temperature to investigate the synchronism of their fluctuations. The use of robust statistical test for correlation analysis accounts for autocorrelation in time-series. Using linear models allows us to point out the relationships between patterns of eel recruitment and those of sea temperature but the use of other models is beyond the scope of this paper.

The shift in sea temperature in 1979 pointed out the beginning of changes in the Sargasso Sea environment and was followed by a shift in eel recruitment detected in 1982 in most of European rivers we analysed. The drop in recruitment in northern European rivers (e.g. Göta Älv in Sweden) was observed before that year. Our results indicate that temperature may be the main governing factor influencing eel larvae survival by decreasing food availability in the Sargasso Sea.

CONCLUSION

In this study, we focused on the impact of environmental conditions in the Sargasso Sea on glass eel recruitment. Our findings suggest that trophic conditions in the Sargasso Sea may affect glass eel recruitment several years later and thousands of kilometers distant. Further studies have to be engaged to improve our knowledge on the oceanic stages of eel. However, in light of the European stock decline observed for 25 years, many environmental and anthropogenic factors acting at different stages in the life cycle are involved. Moreover, the strong demand of Asian markets has maintained strong harvest pressure on eel stocks. In this context, eel management clearly needs to be integrated within an ecosystem approach in order to account for the different factors impacting eel whether ecological or economic. Further studies must be engaged concerning other eel species to confirm the trophodynamic linkages observed for *A. anguilla*.

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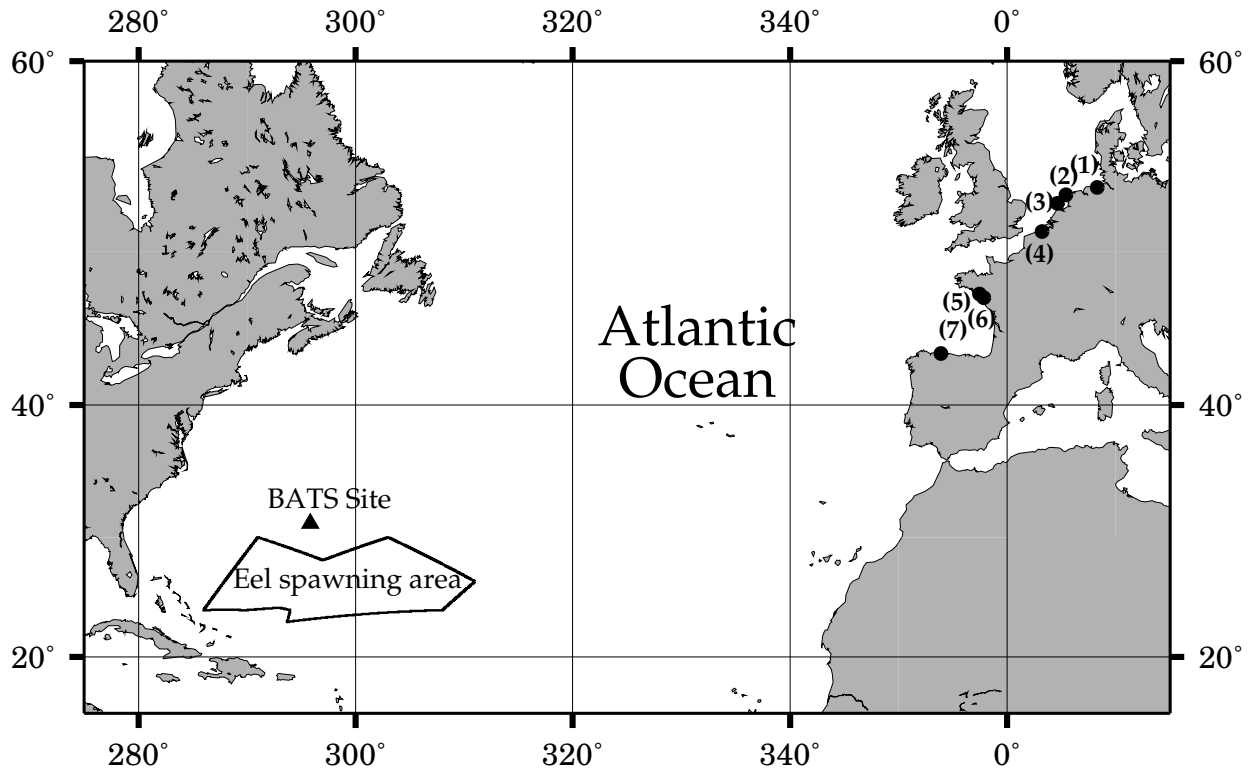


Figure 1: Location of the European eel spawning area (polygon; from McCleave, 1993), Bermuda Atlantic Time-series Study sampling site (black triangle, 32°50'N, 64°10'W) and sampling sites used to calculate recruitment indices (black dot). (1) Ems, (2) Den Oever, (3) IJmuiden, (4) IJzer, (5) Vilaine, (6) Loire, (7) Nalon.

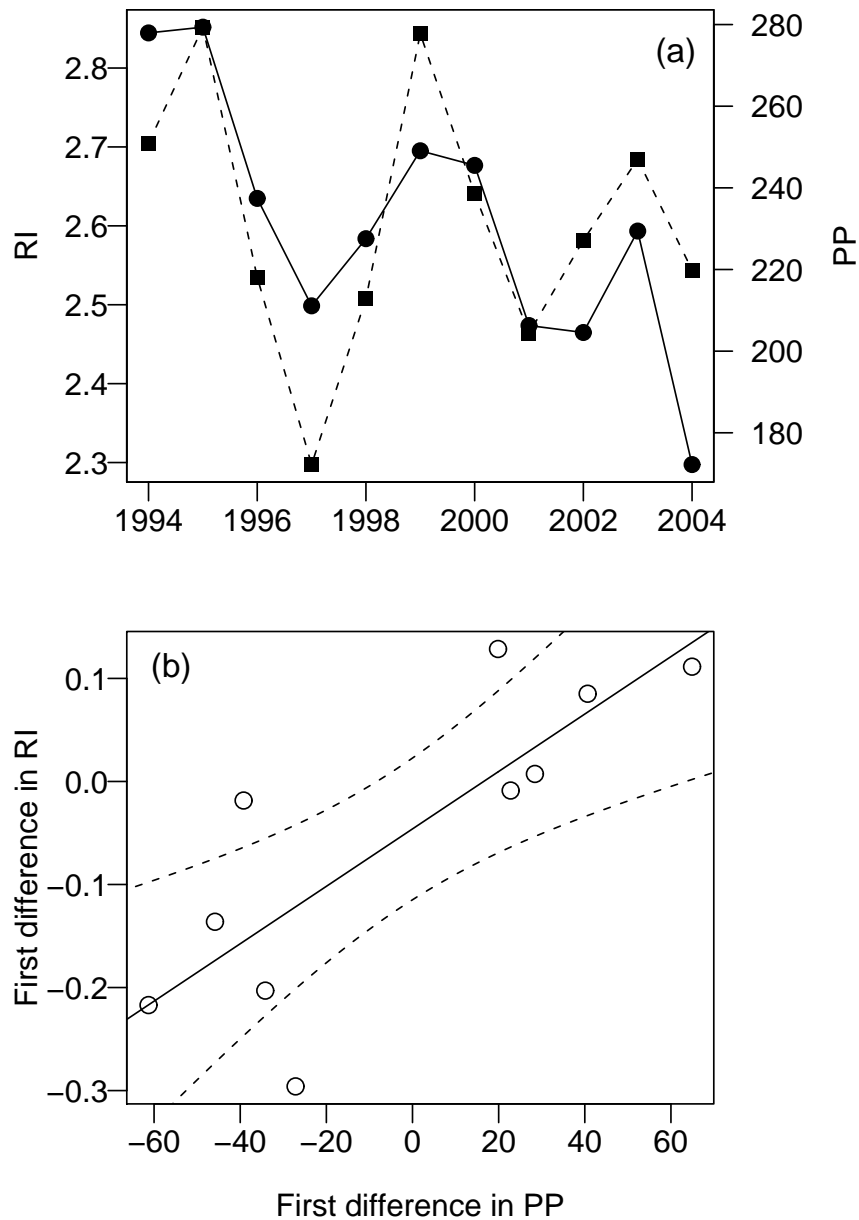


Figure 2: (a) Time-series of log-transformed original recruitment index (RI) (solid line with circles) from season 1994 to 2004 and integrated primary production (PP) 3-year lagged (mgC.m⁻²; dashed line with squares) in the Sargasso Sea from 1991 to 2001 and (b) Correlation between variations in recruitment index and variations in PP lagged by 3 years expressed in first-difference form.

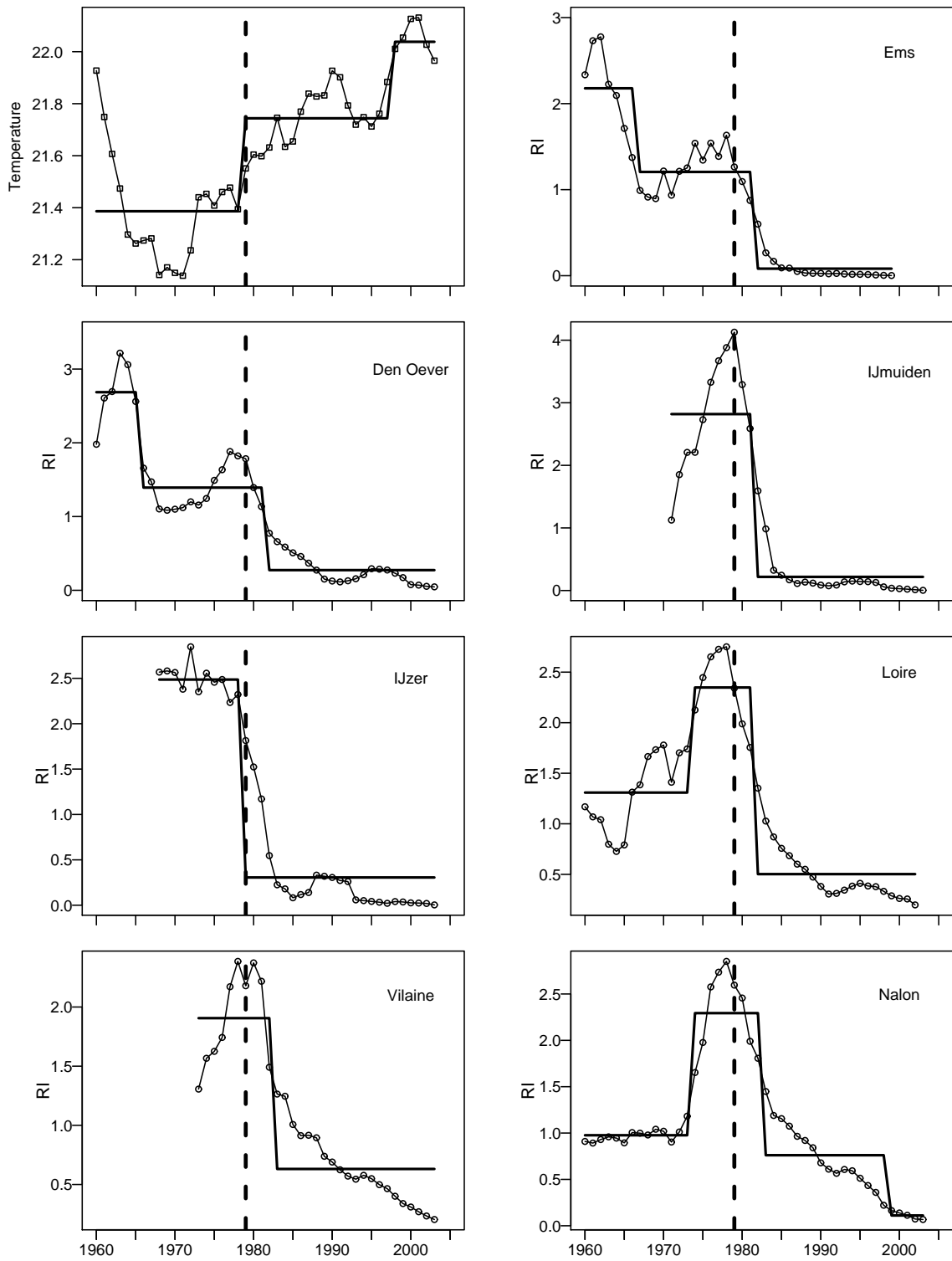


Figure 3: Time-series of ICES recruitment indices (5-year moving average; solid line with circles) and temperature ($\bar{t}C$; 5-year moving average; solid line with squares) in the Sargasso Sea from 1960 to 2003. Bold lines indicate regime shift detection (Rodionov and Overland, 2005) and vertical dashed line indicates the regime shift in temperature in 1979.

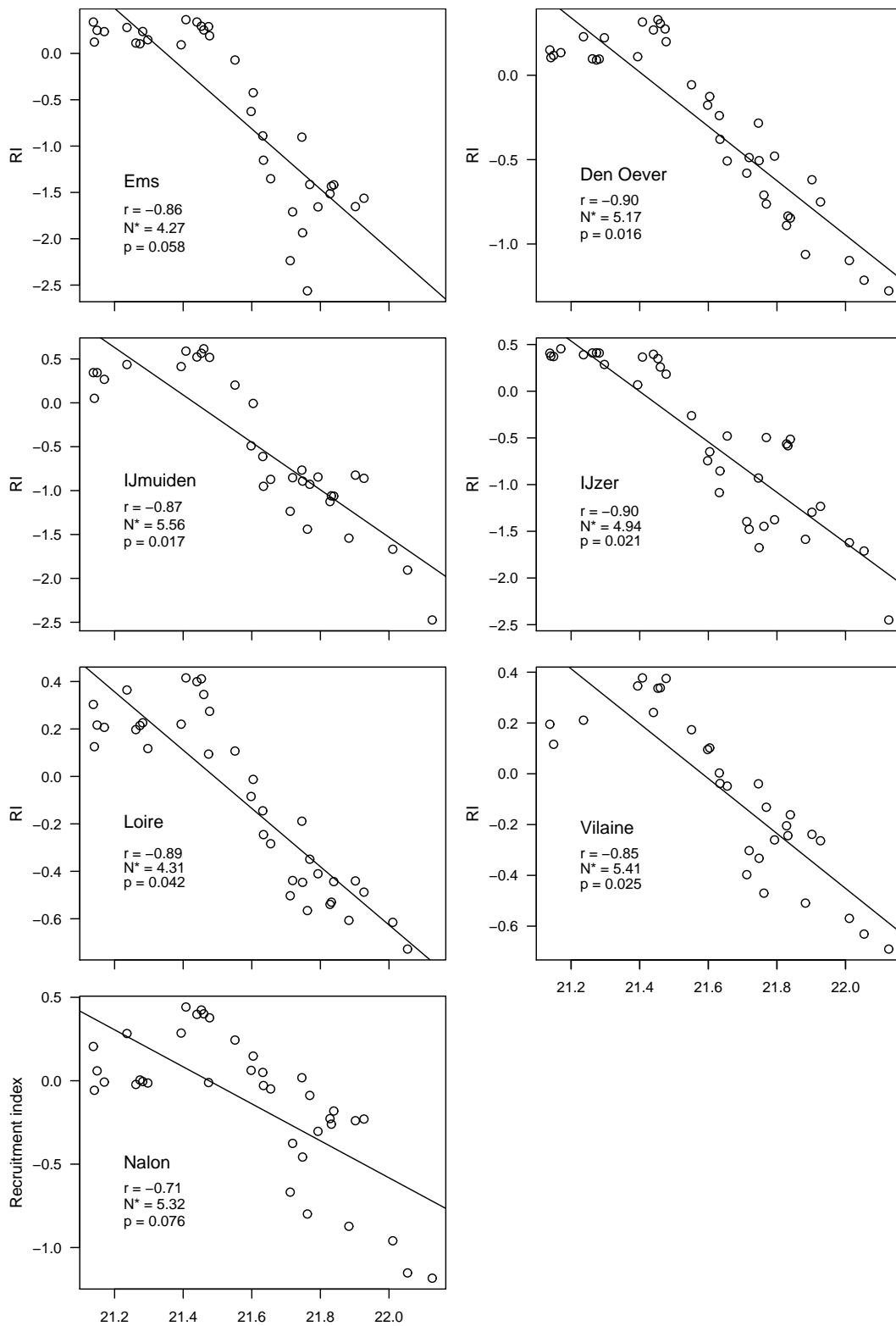


Figure 4: Relationships between temperature in the Sargasso Sea ($^{\circ}\text{C}$; 5-year moving average, 3-year lagged) and the ICES recruitment indices (RI, 5-year moving average) from 1963 to 2003. r indicates the correlation coefficient, N^* , the number of independent joint observations, p , the p-value with N^*-2 d.f.

Table 1: Summary of biological and environmental data. Gulf Stream Index (GSI), Transport Index (TI), Primary Production (PP), Temperature (T), and European sampling sites. Bermuda Atlantic Time-series Study website is <http://bats.bbsr.edu>.

Data	Period	Source	Proxy for:
GSI	1969-2005	scientific (Taylor and Stephens, 1994)	Latitude of Gulf Stream
TI	1958-2005	scientific (Curry and McCartney, 2001)	Intensity of Gulf Stream
PP	1988-2002	scientific (BATS website)	Eel larvae food
T	1958-2005	scientific (BATS website)	Primary Production
Ems	1960-1999	scientific (ICES, 2006)	
Den Oever	1960-2005	scientific (ICES, 2006)	
IJmuiden	1969-2005	scientific (ICES, 2006)	
IJzer	1964-2005	scientific (ICES, 2006)	
Loire	1960-2005	catch data (ICES, 2006)	
Vilaine	1971-2005	catch data (ICES, 2006)	
Nalon	1960-2005	catch data (ICES, 2006)	
Loire	1994-2004	catch data (French trader, pers. comm.)	

Table 2: Summary of relationships between Loire recruitment index and Gulf Stream Index (GSI), Transport Index (TI), Primary Production (PP) and Sargasso Sea Temperature (T) on short-term with a 3-year lag. N indicates the sample size, r the correlation coefficient, p the significance level and N^* the mean corrected sample size.

	N	r	p -value
GSI	11	-0.21	n.s.
TI	11	-0.57	n.s.
PP	10	0.81	<0.005
T	11	0.20	n.s.

Table 3: Summary of relationships between recruitment indices and Transport Index (TI) and Gulf Stream Index (GSI) on long-term with a 3-year lag. r indicates the correlation coefficient, N^* the mean corrected sample size, p the significance level with $N^* - 2$ d.f.

Site	Transport Index (TI)				Gulf Stream Index (GSI)			
	N	N^*	r	p	N	N^*	r	p
Ems	39	6.05	-0.63	0.088	29	5.17	-0.82	0.038
Den Oever	42	5.88	-0.69	>0.1	33	5.94	-0.56	>0.1
IJmuiden	33	4.98	-0.67	>0.1	33	5.90	-0.59	>0.1
IJzer	36	4.90	-0.71	0.092	33	6.00	-0.60	>0.1
Loire	42	5.26	-0.75	0.062	33	5.22	-0.69	0.091
Vilaine	31	4.77	-0.71	>0.1	31	5.15	-0.65	>0.1
Nalon	42	6.20	-0.66	0.07	33	5.92	-0.58	>0.1