

# Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel

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Anguillid eel recruitment in the North Atlantic has declined in recent decades, raising concerns that climatic changes in the Sargasso Sea may be influencing oceanic reproduction and larval survival. There is a significant negative correlation between the North Atlantic Oscillation and long-term variations in catches of glass eel stages of the European eel *Anguilla anguilla* recorded by the fishery independent Den Oever recruitment index (DOI) in the Netherlands, lagged by one year. Ocean-atmospheric changes in the Sargasso Sea may affect the location of spawning areas by silver eels and the survival of leptocephali during the key period when they are transported towards the Gulf Stream. A northward shift in a key isotherm (22.5°C), defining the northern boundary of the spawning area, a declining trend in winds and transport conditions in larval transport areas, and a shallowing of the mixed layer depth could affect primary productivity in areas where leptocephali feed. The relationships between these ocean parameters and the DOI suggest that these changing ocean conditions could be contributing to declining recruitment of the European eel and probably also of the American eel (*A. rostrata*), but anthropogenic factors during their continental life stage must also be considered.

**Keywords:** American eel, European eel, North Atlantic Oscillation, ocean climate, recruitment.

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## Introduction

The declining recruitment of anguillid eels documented on both sides of the Atlantic Ocean in recent decades (Haro *et al.*, 2000; Casselman, 2003; Dekker *et al.*, 2003) has been hypothesized by Castonguay *et al.* (1994) and Knights (2003) to be related to changes in ocean conditions affecting the survival of leptocephali, their transparent leaf-like larvae that are born in the Sargasso Sea (Schmidt, 1923). These declines may also be related to reductions in the size of the spawning population of each species (Dekker, 2003, 2004), driven by anthropogenic factors such as habitat loss, pollution, parasite introductions, and overfishing (Haro *et al.*, 2000; Feunteun, 2002). However, anguillid eels are facultatively catadromous fish that leave their freshwater and estuarine juvenile growth habitats to spawn in the open ocean, so most of the key life history events associated with reproduction and recruitment take place during the marine phase. It has been difficult to study the possible mechanistic links between changes in ocean conditions and reproduction and recruitment in eels because of an almost complete lack of information on key factors such as spawner escapement, egg production, and survival of larvae.

Maturing European, *Anguilla anguilla*, American, *A. rostrata*, and Japanese, *A. japonica*, silver eels make long migrations to spawn in the subtropical gyres of the North Atlantic or North Pacific oceans (McCleave *et al.*, 1987; Tsukamoto, 1992).

The distribution of the youngest larvae suggests that spawning takes place in specific areas that may facilitate mating and help place larvae in the appropriate west-flowing currents (Kleckner and McCleave, 1988; McCleave, 1993; Tsukamoto *et al.*, 2002; Tsukamoto, 2006). In the case of the two Atlantic species, distinct temperature fronts present in winter and spring in the Sargasso Sea (Weller, 1991) form the northern boundary of the spawning area (Kleckner *et al.*, 1983; Kleckner and McCleave, 1988; Tesch and Wegner, 1990); these fronts may be used as cues to help eels locate the spawning area (McCleave, 1987).

During the spawning season of Atlantic eels in winter and spring (Schoth and Tesch, 1982; Kleckner and McCleave, 1985, 1988; Wipplehauser *et al.*, 1985; Tesch and Wegner, 1990) and in subsequent larval migration in summer and early autumn (Boëtius and Harding, 1985; Kleckner and McCleave, 1985; McCleave and Kleckner, 1987), the leptocephali of *A. anguilla* and *A. rostrata* are widely distributed in overlapping areas of the Sargasso Sea. After hatching, the leptocephali are present primarily in the upper 250 m of the ocean and are generally most abundant in the upper 100 m, although the degree of vertical migration is difficult to evaluate owing to net avoidance by day (Schoth and Tesch, 1984; Castonguay and McCleave, 1987). Leptocephali grow larger and have a longer larval duration than most fish larvae, the northern temperate species taking up to a year or

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longer before recruiting to estuarine and freshwater habitats as glass eels or elvers.

This long larval duration probably makes the larvae particularly vulnerable to changes in ocean currents and the availability of food. The dominant climate-forcing signal in the North Atlantic, the North Atlantic Oscillation (NAO), has been associated with a wide range of oceanographic and biological changes (Curry and McCartney, 2001; Parsons and Lear, 2001; Weijerman *et al.*, 2005), including eel recruitment (Knights, 2003). However, it remains to be determined how alterations of the ocean-atmospheric system signalled by regime shifts in the NAO influence eel reproduction or larval survival. This is in part because many aspects of spawning and the early life histories of the species are poorly understood. Anguillid leptocephali appear to be adapted to grow in low-productivity open ocean environments as they drift west towards western boundary currents such as the Gulf Stream and Kuroshio, which transport them to their continental habitats (McCleave, 1993; Tsukamoto *et al.*, 2002). They appear to feed at a very low trophic level, utilizing particulate organic matter (POM) such as marine snow, including discarded larvacean houses (Urochordata), faecal pellets, and possibly even dissolved organic matter (DOM) (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996; Pfeiler 1999). Availability of POM and DOM and the formation of marine snow are dependent on primary and secondary production, and their availability is strongly coupled to phytoplankton blooms in the Sargasso Sea and other regions of the North Atlantic (Turner, 2002).

Because anguillid leptocephali live primarily in the surface layers of the oceans, their growth, transport, and eventual recruitment are likely to be affected by variability in the biological and physical processes in the upper few hundred metres. Changes in oceanographic conditions caused by ocean-atmospheric regime shifts signalled by the NAO in the Atlantic (Knights, 2003) or *El Niño* in the Pacific (Kimura *et al.*, 2001; Kimura and Tsukamoto, 2006) have been hypothesized as possible factors contributing to the recent declines in northern temperate species of anguillid eels such as the European eel. Although the authors cited above found correlations between recruitment of glass eels and the NAO and ENSO indices, respectively, they were not able directly to determine the mechanisms controlling recruitment success. Developing and testing hypotheses about which specific oceanic factors have the greatest effect on recruitment success in anguillid eels requires exploratory and experimental research. Therefore, the objective of the present study was to determine whether decade-scale changes and regime shifts in key thermal, wind, oceanic currents, and productivity associated with the NAO are correlated with European eel recruitment and to hypothesize how these changes may have contributed to the observed declines in recruitment of glass eels.

## Material and methods

The year-class strength or recruitment success of the European eel has been assessed in various ways, but the index of standardized catches of glass eels at Den Oever in the Netherlands [Den Oever recruitment index, DOI] is an important time-series because it is based on fishery-independent sampling, which makes it particularly useful in studies of multi-decade climate signals (Dekker, 1998). Glass eels have been collected each year since 1938 (except during World War II) at Den Oever, which is located at the outflow from Lake IJsselmeer (52°56'20"N 05°02'70"E) into the Wadden Sea. The eels are collected at night

at 2-h intervals in spring with a 1-m<sup>2</sup> dipnet with 1 mm mesh. The DOI data were log-transformed to approximate normality (ICES, 2005).

The temporal changes in the DOI were compared with the NAO using time-series techniques and a regime shift indicator. The NAO winter index (December through March) was used in the analysis (Hurrell *et al.*, 2001); NAO is defined as the difference in normalized sea level pressure between Lisbon, Portugal, and Stykkisholmus/Reykjavik, Iceland, since 1864. Comparisons between NAO and DOI were made at a 1-y lag (NAO<sub>*t*</sub> vs. DOI<sub>*t+1*</sub>) to account for the duration of the leptocephalus stage. Trends in DOI and NAO indices were analysed with a smoothing filter. The smoothing filter was a Fast Fourier Transform filter that removes Fourier components with frequencies higher than a cut-off frequency of

$$F_{\text{cut-off}} = \frac{1}{n\Delta t},$$

where *n* is the number of data points specified by the user and  $\Delta t$  is the time (or more generally the abscissa) spacing between two adjacent data points. Larger values of *n* result in lower cut-off frequencies, and therefore a greater degree of smoothing. The function used to clip out the high-frequency components is a parabola with a maximum of 1 at zero frequency, falling to zero at the cut-off frequency defined above. We used a value of *n* = 5.

The regime shift indicator of Rodionov (2004) was used to assess whether there had been major changes in trends of the DOI and NAO in particular years. The method is based on sequential *t*-test analysis of regime shifts where, with each step of a time-series, it is determined whether the new values represent a significant deviation from the mean value of the current regime. If the test indicates a significant difference, the year is marked as one showing a potential regime change, and subsequent observations are used to confirm or reject the hypothesis. The hypothesis is tested using the regime shift index (RSI), which is calculated for each change point:

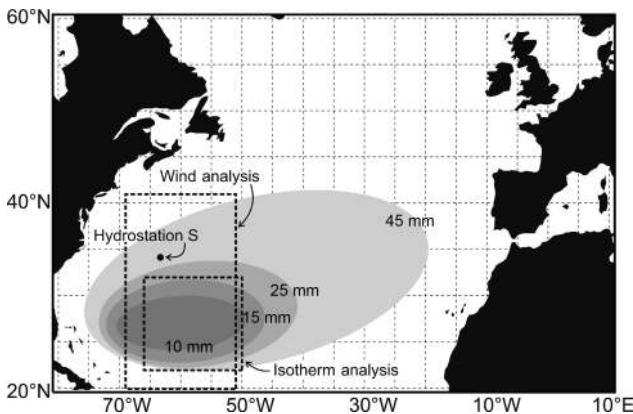
$$\text{RSI} = \sum_i^{i+m} \frac{x_i^*}{1\sigma_1},$$

where *m* is the number of years since the start of a new regime, *l* being the cut-off length of the regimes to be tested, and  $\sigma_1$  is the average standard deviation for all one-year intervals in the time-series. RSI represents a cumulative sum of normalized deviations  $x_i^*$  from the hypothetical mean level for the new regime, for which the difference from the mean level for the current regime is statistically significant according to a Student's *t*-test. We also applied red noise estimation to account for time-series autocorrelation (Rodionov, 2006). The relationship between the DOI and NAO was tested using Pearson product-moment correlation at a 1-y time lag, because it takes leptocephali at least one year to migrate from the spawning area to Europe (McCleave, 1993). The temporal relationship between regime shifts was further examined by calculating a cross-correlation function between DOI and NAO over  $\pm 15$  lags.

The temporal variation in the DOI was then compared with ocean-atmospheric parameters in the region of the Sargasso Sea encompassing most of the likely spawning area of the European eel. These parameters were sea surface temperature

(SST) distributions on the spawning grounds, wind in the larval transport area, currents in the larval transport area, and mixed layer depth (MLD) in the early larval development area. The longitudinal zone analysed is located on the eastern side of where the smallest sized leptocephali have been collected (McCleave *et al.*, 1987), based on the assumption that spawning takes place slightly to the east of where larvae are actually collected, so allowing for some westward drift.

During the time period covered by the DOI, there have been changes in the distribution of SST in the North Atlantic and southern Sargasso Sea (Grey *et al.*, 2000; Polyakov *et al.*, 2005), where both European and American eels spawn. Temperature fronts in the Sargasso Sea may act as cues that help adult eels locate the spawning area (McCleave, 1987; Kleckner and McCleave, 1988). Therefore, we analysed the latitude of the surface expression of the 22.5°C isotherm, which is typically near the frontal zone at the northern limit of eel spawning (Kleckner and McCleave, 1988; Tesch and Wegner, 1990). The 22.5°C isotherm was selected because it has been located near the northernmost temperature front observed to form at the same water density in all previous studies of the region prior to 1994 (Kleckner and McCleave, 1988; Tesch and Wegner, 1990, Miller and McCleave, 1994). An “Isotherm Analysis” was conducted over a range of longitudes that encompass the spawning area (Figure 1) during the months of December–March to bracket the time of spawning (Kleckner and McCleave, 1988; Tesch and Wegner, 1990). Specifically, the analysis was carried out using the extended reconstructed SST data set of Smith and Reynolds (2003, 2004) for 22–32°N and 50–66°W. The latitude of the 22.5°C isotherm was determined for each of eight 2° longitude bins for each of the four months. The time-series was restricted to 1947–2004 to avoid problems with the DOI (missing values and the war years). Correlations were then calculated between the DOI and the latitude of the 22.5°C isotherm for



**Figure 1.** Map of the North Atlantic Ocean showing the general distribution of size ranges of leptocephali of the European eel (based on Schmidt, 1923) and the locations used for the ocean-atmospheric data analyses. The darkest grey shape shows the approximate area where 10 mm leptocephali were collected, which would be relatively close to the spawning grounds. Progressively lighter grey areas show the regions where larger, older larvae were found. The two rectangles show where data were obtained for the Isotherm Analysis and Wind Analysis, and the location of Hydrostation S near Bermuda, where the mixed layer depth was calculated.

each 2° longitude bin for each month from December to March. Correlations were made at a 1-y lag, as with the NAO data.

Variations in the winds in the Sargasso Sea were also compared with the DOI at a 1-y lag. Winds can affect larval transport or other conditions in the Sargasso Sea, so influencing recruitment. Wind data for the months February–May for the years 1949–2003 over an area that includes the spawning and early stage larval transport area were used. This area includes part of the Gulf Stream through which many older leptocephali probably pass (Figure 1). Wind data were obtained from the NCEP/NCAR (National Centers for Environmental Prediction/National Center for Atmospheric Research) re-analysis (Kalnay *et al.*, 1996). The vector wind velocities ( $u$  and  $v$  vectors) were compared with the DOI. To evaluate the directional effect of wind on larvae, Ekman volume transports were calculated for selected time periods for both zonal and meridional transport vectors:

$$Q_x = \frac{1}{\rho_0} M_x = \frac{1}{\rho_0 f} \tau_w^y,$$

$$Q_y = \frac{1}{\rho_0} M_y = -\frac{1}{\rho_0 f} \tau_w^x,$$

where  $f$  is the Coriolis parameter,  $\rho_0$  the density of seawater ( $1028 \text{ kg m}^{-3}$ ), and  $\tau_w$  the wind stress. The absolute value of zonal and meridional wind stress was computed as

$$|\tau_w| = \rho_a C_d U_{10}^2,$$

where  $\rho_a$  is the density of air ( $1.29 \text{ kg m}^{-3}$ ),  $C_d$  the drag coefficient, and  $U_{10}$  the zonal or meridional winds at 10 m. Drag coefficient was parameterized as a non-linear function of wind speed rather than a constant, based on Large and Pond (1981), and further modified for low wind speeds following Trenberth *et al.* (1990):

$$C_d = 0.00218 \quad \text{for } U_{10} \leq 1 \text{ m s}^{-1}$$

$$= \left(0.62 + \frac{1.56}{U_{10}}\right) 0.001 \quad \text{for } 1 \text{ m s}^{-1} < U_{10} < 3 \text{ m s}^{-1}$$

$$= 0.00114 \quad \text{for } 3 \text{ m s}^{-1} \leq U_{10} < 10 \text{ m s}^{-1}$$

$$= (0.49 + 0.65 U_{10}) 0.001 \quad \text{for } U_{10} \geq 10 \text{ m s}^{-1}$$

For the same time periods, Ekman depth was calculated as

$$D_E = \frac{7.6}{\sqrt{\sin(\Phi)}} U_{10},$$

where  $\Phi$  is the latitude in radians.

In addition to examining the time-series of Ekman transports for the Sargasso region, we also considered the climatological currents for the area using the US Coastguard’s Mariano Global Surface Velocity Analysis (MGSVA) 1.0 (Mariano *et al.*, 1995). The data have a monthly temporal resolution and a spatial resolution of 1° of longitude and latitude. The currents are derived from ship-drift estimates made by merchant and military ships. Our intention was to evaluate how variation in wind-driven transport may affect the movement of larvae into the major geostrophic transport currents.

MLD was also compared with the DOI because it is associated with nutrient circulation, which could have an effect on productivity in the Sargasso Sea and subsequently on growth and survival of larvae. We calculated the MLD at Hydrostation S located southeast of Bermuda (Figure 1), using temperature at depth data monitored at approximately bimonthly intervals by the Bermuda Biological Station for Research (<http://www.bbsr.edu/>). MLD was calculated for the two contrasting periods of eel recruitment, pre- and post-1985, as guided by the regime shift analysis (see above). Two different computational algorithms were used to account for deficiencies in the data. The  $\Delta$ -criterion method (Kara *et al.*, 2003) is based on a change in temperature ( $\Delta T = 0.8^\circ\text{C}$ ) from the temperature at a reference depth (10 m). The  $H_{\text{mix}}$ -criterion (Lorbacher *et al.*, 2005) method is based on an estimate of the shallowest extreme curvature of a near-surface temperature profile and has the added benefit of providing a goodness-of-fit criterion.

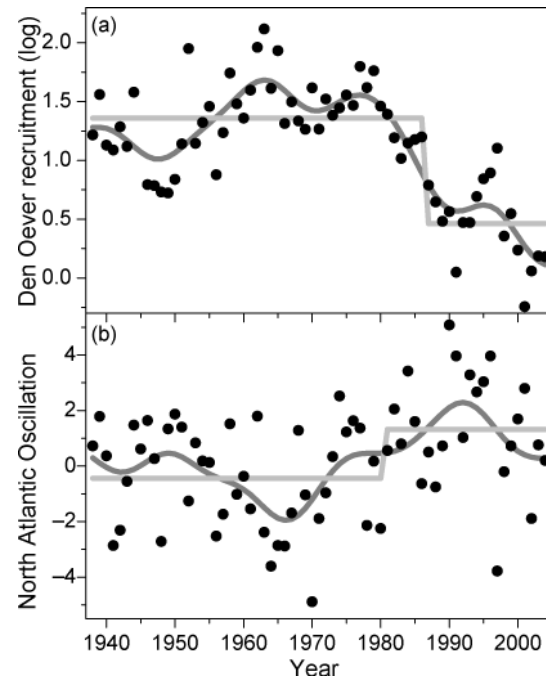
The time-series we compared in this study had varying degrees of autocorrelation. We sought to account for this autocorrelation in our correlation analyses (Pearson product-moment correlation) by adjusting the effective degrees of freedom of each test according to the procedure suggested by Pyper and Peterman (1998). The effective degree of freedom ( $N^*$ ) of a correlation between two time-series, in notation series  $X$  and  $Y$ , was estimated by

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N} \sum_{j=1}^{N/5} \frac{(N-j)}{N} \rho_{xx}(j) \rho_{yy}(j),$$

where  $N$  is the sample size and  $\rho_{xx}(j)$  and  $\rho_{yy}(j)$  are the autocorrelations of  $X$  and  $Y$  at lag  $j$ . Following Garrett and Petrie (1981), we took the autocorrelation at lag  $j$  of the cross-products of standardized time-series of  $X$  and  $Y$ . The probability associated with a correlation coefficient is designated as  $p$ , and as  $p^*$  for a test with degrees of freedom based on  $N^*$ .

## Results

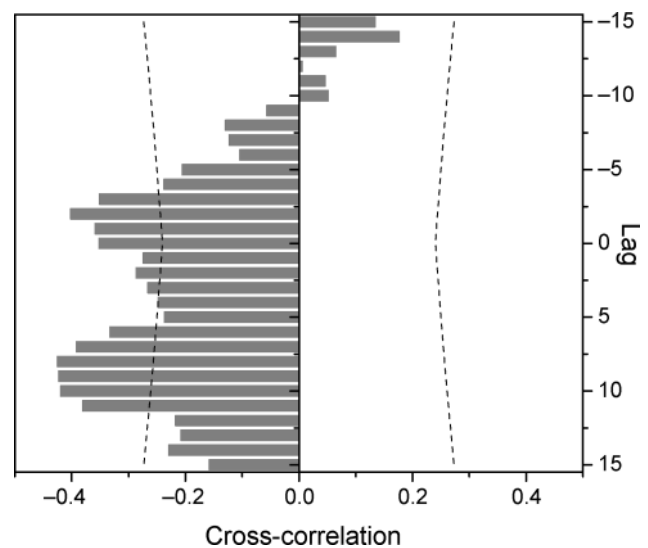
Recruitment of the European eel, as represented by the DOI since 1938, has exhibited a multi-decadal pattern of change that is inversely related to the NAO winter index. The DOI was low during the 1940s and 1950s, followed by a sustained period of high index values that suggest favourable recruitment through the 1970s (Figure 2a). The DOI began to decline in the 1980s, reaching its lowest level in the last few years of the time-series. Although the decline in recruitment appeared to have begun several years earlier, the most prominent regime shift in the DOI to a low, but relatively stable, level appears to have begun around 1987. The NAO trend changed from positive to negative and back to a prolonged period of high positive values between 1938 and 2005 (Figure 2b). The most prominent positive regime shift in the NAO appears to have begun around 1981, coinciding with apparent initial decreases in the DOI. There was significant cross-correlation between the DOI and the NAO around lag 0 and interestingly around 8, which would support the lag between regime transitions in the two time-series (Figure 3). The cross-correlation at lag 0 would correspond to the correlation reported by Knights (2003) of a long-term negative relationship between the DOI and the NAO using a 1-y lag, and this relationship was reaffirmed in the present study ( $r = -0.352$ ;  $p = 0.003$ ,  $p^* = 0.010$ ). This correlation, we believe, may be related to a NAO effect on larvae of that year. The cross-correlation at the



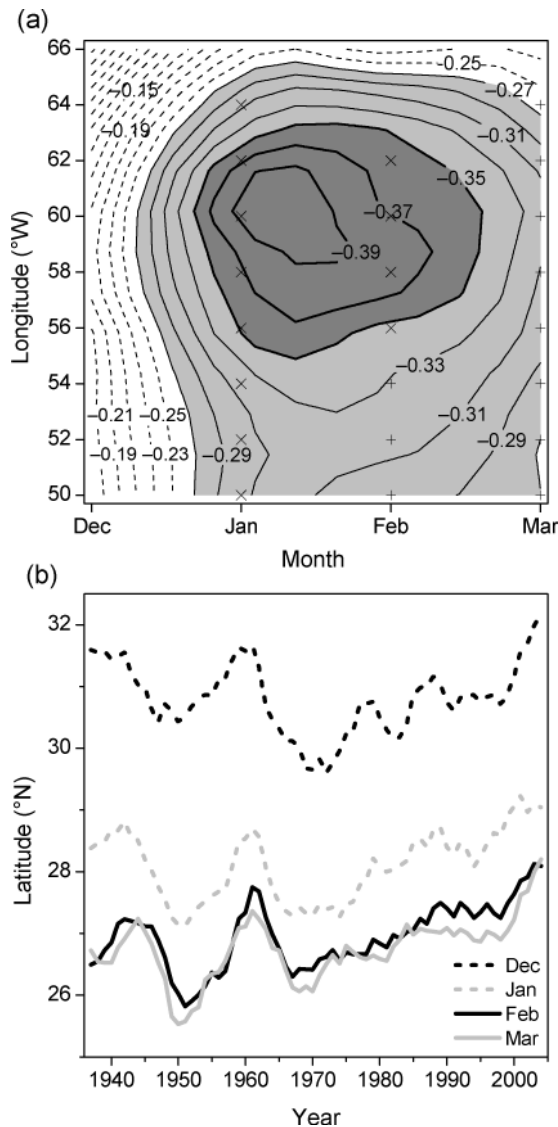
**Figure 2.** Time-series of (a) the Den Oever recruitment (DOI), and (b) the North Atlantic Oscillation (NAO) indices. The DOI is a fisheries-independent index of glass eel catches in the Netherlands. The NAO is the winter index at a 1-y lag to the recruitment year. Fast Fourier transform filter smoothing (dark grey) and sequential regime shift detection (light grey) lines are added.

8-y lag would suggest a different mechanism and would be consistent with the idea that the NAO effect on recruitment is delayed by the approximate time between larval recruitment and spawning.

The distribution of SST in the spawning area of eels in the Atlantic has changed over time, reflecting a general warming trend (Knights, 2003). The iso-correlate surface of correlation between the DOI and the latitude of the key  $22.5^\circ\text{C}$  isotherm shows that negative correlation peaked in January and February



**Figure 3.** Cross-correlation function between DOI and NAO indices.



**Figure 4.** Correlation between (a) the DOI and the latitude of the surface expression of the 22.5°C isotherm in the Sargasso Sea. Correlations are calculated by 2° longitudinal bins and month. The latitude data are at a 1-y lag to the recruitment index. The significance levels of uncorrected and autocorrelation-corrected correlations are shown: solid lines and light grey shading marks uncorrected correlation at  $p = 0.05$ ; heavy solid lines and dark grey shading marks uncorrected correlations at  $p = 0.01$ ; crosses mark a coordinate where corrected correlation is significant at  $p^* = 0.1$ ; plus signs mark a coordinate where corrected correlation is significant at  $p^* = 0.05$ ; symbols omitted for  $p^* > 0.1$ . (b) Plot of the changes in latitude of the 22.5°C isotherm at 60°W in the North Atlantic, as 5-point moving averages, during the period December–March to encompass the spawning season.

in an area centred at 60°W (Figure 4a). However, this region of the correlation surface was also associated with a high degree of autocorrelation in both the recruitment and latitude time-series. Although correlations in other regions of the response surface are significant in both uncorrected and autocorrelation-corrected significance tests, this region is not significant at the conventional 95% confidence level in the autocorrelation-corrected test. In

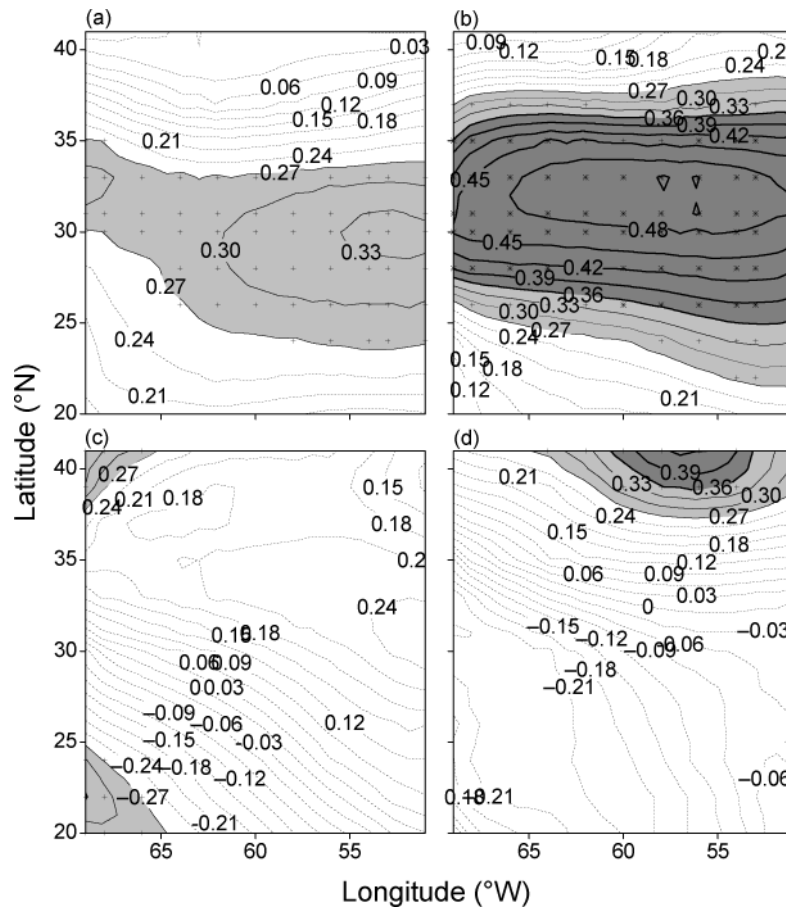
looking at the correlation probabilities in closer detail, we are limited to stating that the correlations associated with January and February in the area centred at 60°W are significant at about a 93–94% confidence level (Table 1). The January and February isotherms moved from as far south as 27°N and 26°N during the 1950s to as far north as 29°N and 28°N in the most recent years of the time-series, respectively (Figure 4b). Therefore, the northward shift in the 22.5°C isotherm since about 1970 may have caused a northward shift in the spawning area, and this trend is correlated with decreases in recruitment.

Wind speed and direction over the Sargasso Sea were also correlated with recruitment of the European eel. The  $u$ -vector velocities, especially those in March at latitudes 27–36°N, and to a lesser degree in February, suggest the importance the east–west aspect of the winds in the area (Figure 5). Uncorrected and autocorrelation-corrected correlation probabilities were virtually the same in these data, largely because of the lack of autocorrelation in the wind-speed data. The  $v$ -vector velocities were generally weakly correlated with the DOI (Figure 6). Moreover, autocorrelation-corrected probabilities associated with the March  $v$ -vector velocities were mostly non-significant at the 95% confidence level. The wind speed of  $u$ -vector winds decreased from  $6 \text{ m s}^{-1}$  to  $< 3 \text{ m s}^{-1}$ , whereas  $v$ -vector wind speed increased slightly over the period. These correlations reflect a weakening of southwest winds over the northern Sargasso Sea (the latitudinal extent of the Sargasso Sea is taken to be 25–35°N) in recent decades. Ekman transports of near-surface waters of the northern Sargasso during March declined to negligible levels in a comparison of mean transports by decade (Figure 7a–f). Ekman transports during the 1950s and continuing through the 1970s were to the south and southeast, whereas transports during the 1980s through to the period 2000–2005 became more to the southeast and eventually declined to negligible transports. Ekman mixing depths also decreased, as shown by a similar analysis of mean depth during March by decade (Figure 8a–f). Waters of the northern Sargasso had Ekman depths on the order of 30–50 m during the first three decades of the time-series, whereas the values shallowed to 10–20 m in recent years.

Climatological current data for the Sargasso Sea and surrounding ocean area during March show that the weak currents of the

**Table 1.** Uncorrected and autocorrelation-corrected probabilities of correlations between the Den Oever recruitment index (DOI) and the latitudes of the surface expression of the 22.5°C isotherm in the Sargasso Sea, limited to significant uncorrected correlations. Correlations are calculated by 2° longitudinal bins and month. The latitude data are at a 1-y lag to the recruitment index. Emboldened numbers denote significance at the 95% confidence level.

Longitude (°W)	January		February		March	
	$p$	$p^*$	$p$	$p^*$	$p$	$p^*$
50	<b>0.019</b>	0.093	<b>0.023</b>	<b>0.024</b>	<b>0.036</b>	<b>0.036</b>
52	<b>0.017</b>	0.093	<b>0.017</b>	<b>0.037</b>	<b>0.032</b>	<b>0.035</b>
54	<b>0.012</b>	0.083	<b>0.013</b>	<b>0.050</b>	<b>0.026</b>	<b>0.026</b>
56	<b>0.006</b>	0.079	<b>0.008</b>	0.063	<b>0.019</b>	<b>0.021</b>
58	<b>0.002</b>	0.071	<b>0.005</b>	0.073	<b>0.013</b>	<b>0.021</b>
60	<b>0.001</b>	0.065	<b>0.004</b>	0.083	<b>0.012</b>	<b>0.022</b>
62	<b>0.002</b>	0.064	<b>0.007</b>	0.095	<b>0.016</b>	<b>0.019</b>
64	<b>0.010</b>	0.070	<b>0.020</b>	0.123	<b>0.032</b>	<b>0.032</b>



**Figure 5.** Correlation between the DOI and  $u$ -vector wind speed during (a) February, (b) March, (c) April, and (d) May. Correlations are plotted by latitude and longitude and by month. The wind data are at a 1-y lag to the recruitment index. The significance levels of uncorrected and autocorrelation corrected correlations are shown: solid lines and light grey shading marks uncorrected correlations at  $p = 0.05$ ; heavy solid lines and dark grey shading marks uncorrected correlations at  $p = 0.01$ ; plus signs mark a coordinate where corrected correlation is significant at  $p^* = 0.05$ ; the asterisk marks a coordinate where corrected correlation is significant at  $p^* = 0.01$ ; symbols omitted for  $p^* > 0.05$ .

Sargasso Sea are bracketed by the west-flowing Antilles Current to the south and the east-flowing Gulf Stream to the north (Figure 9). Although most current vectors of the Sargasso Sea are very small, it is apparent that the currents of the southern Sargasso Sea (25–30°N) tend to the west whereas the vectors of the northern Sargasso (30–35°N) tend to the east and southeast.

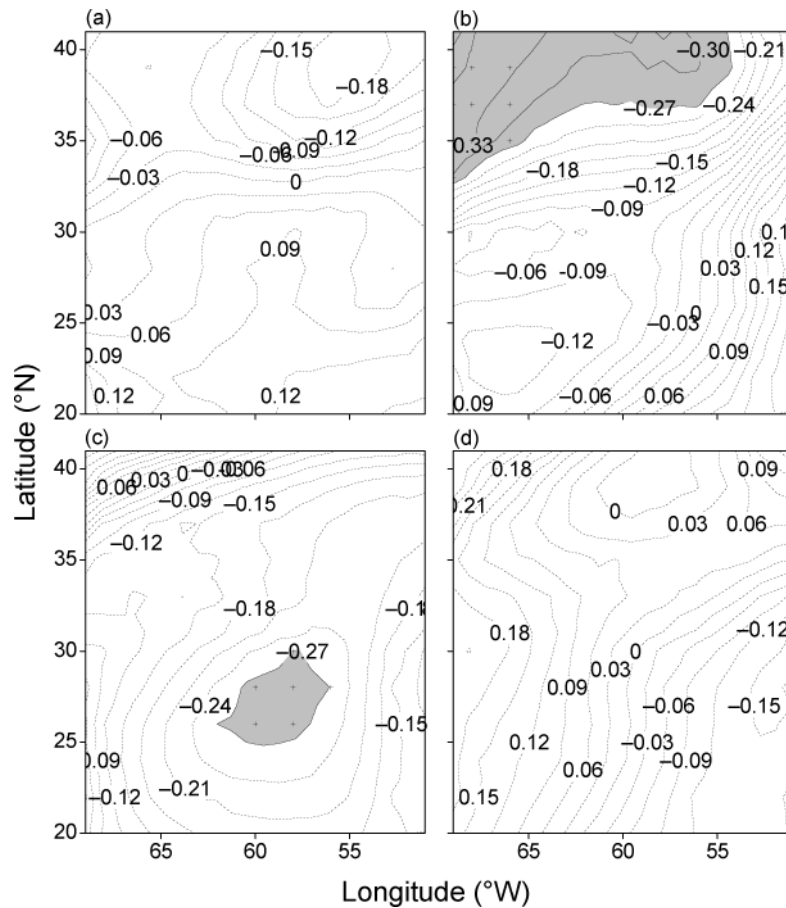
Spring MLD has shallowed in the Sargasso Sea, suggesting that related changes in transport and the nutrient dynamics of leptocephalus habitats have also occurred. Owing to the elimination of some MLD estimates because of poor model fits, we compared MLD before and after the DOI regime shift demarcated by the year 1985 (Figure 2). These comparisons indicate that the MLD during the period February–May has decreased since 1985 (Figure 10) and, for the spring months of March, April, and May, the decrease has been on the order of 50–100 m. Therefore, the regime of low DOI and high NAO is associated with decreased MLD.

## Discussion

Our findings provide evidence of linkages between declines in recruitment of the European eel and specific environmental changes within the spawning and early larval development areas of eels in the Sargasso Sea. European eels may be responding to

NAO-forced changes in fronts and currents affecting spawning and the survival of leptocephali in a similar manner to that proposed for the Japanese eel *A. japonica*, which are linked to *El Niño* forcing (Kimura *et al.*, 2001; Kimura and Tsukamoto, 2006). Japanese eel migration in the North Pacific is believed to be affected by the salinity front associated with the North Equatorial Current, which has moved north in recent years, resulting in poor transport conditions for leptocephali. The northward displacement of thermal fronts in the southern Sargasso Sea would be expected to have similar ramifications for the migration and transport of European eels. However, our analysis suggests that a number of ocean condition parameters have changed in the Sargasso Sea, which in combination form a more complex set of factors that may influence recruitment. Such changes could also have affected recruitment of the American eel because of the proximity of its spawning area to that of the European eel and similarities in the early migration pathways of both species.

Because of the many factors that could be involved, the finding of a correlation between the DOI and the NAO does not resolve the issue of what is causing the declines of the northern temperate anguillids. However, there is mounting evidence that the NAO is related to significant changes in the physical and biological



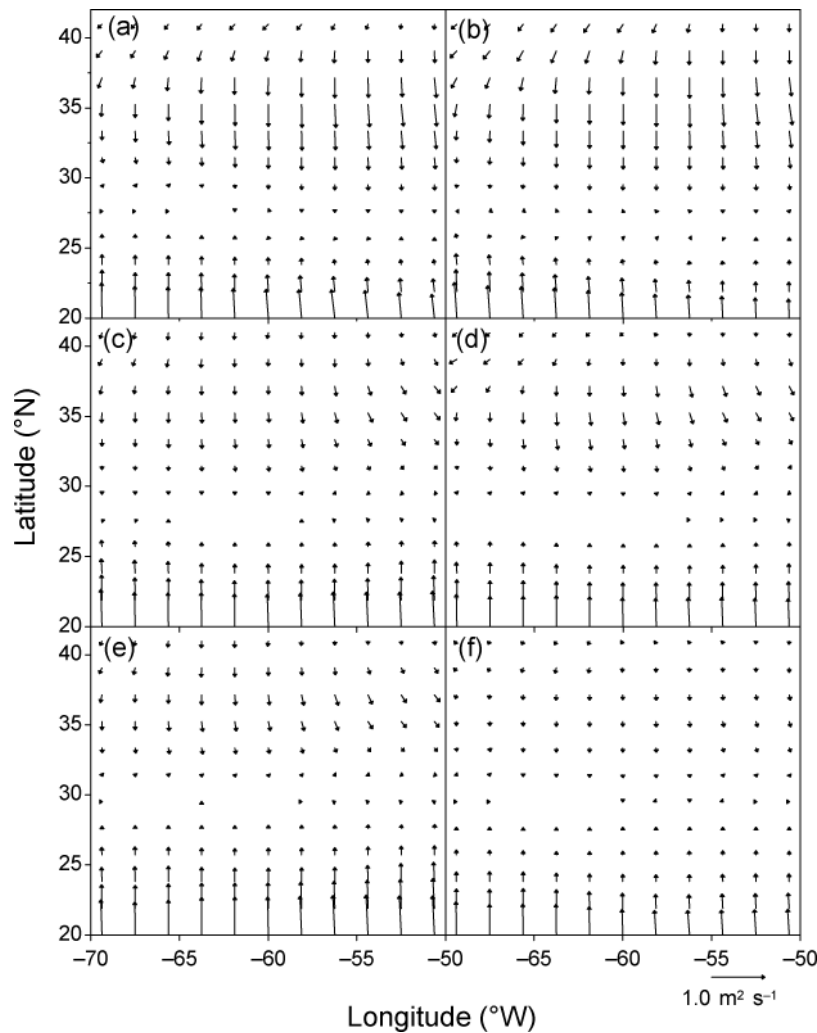
**Figure 6.** Correlation between the DOI and  $\nu$ -vector wind speed during (a) February, (b) March, (c) April, and (d) May. Correlations are plotted by latitude and longitude and by month. The wind data are at a 1-y lag to the recruitment index. The significance levels of uncorrected and autocorrelation corrected correlations are shown: solid lines and light grey shading marks uncorrected correlations at  $p = 0.05$ ; heavy solid lines and dark grey shading marks uncorrected correlations at  $p = 0.01$ ; plus signs mark a coordinate where corrected correlation is significant at  $p^* = 0.05$ ; symbols omitted for  $p^* > 0.05$ .

structure of the North Atlantic, affecting a wide range of marine organisms, from zooplankton to fish (Parsons and Lear, 2001; Weijerman *et al.*, 2005). In the northern Sargasso Sea, specifically the Bermuda Atlantic Time-Series site, SST, MLD, salinity, primary productivity, new production, and TCO<sub>2</sub> appear to be related to the NAO in recent years (Bates, 2001; Nelson *et al.*, 2004). In our analysis, we detect associations between eel recruitment and thermal, wind, and mixing parameters in areas of the Sargasso that correspond spatially to eel spawning and larval ecology. These parameters co-vary with the NAO and with each other, suggesting that they may be acting synergistically on eel recruitment.

Changes in the temperature structure of the Sargasso Sea could alter thermal and density features that affect the oceanic stages of the eels of the Atlantic. Our analysis of the location of the 22.5°C isotherm during the early spawning season indicates that there has been a gradual warming trend of surface waters of the region that began around 1970. Warming trends in the global oceans have been reported (Levitus *et al.*, 2000), and both warming and cooling periods have been noted in the upper layer of the North Atlantic region, including the southern Sargasso Sea (Molinari *et al.*, 1997; Grey *et al.*, 2000; Polyakov *et al.*, 2005). The latitude of the 22.5°C isotherm reaches its southernmost position

sometime during the period January–April (Halliwell *et al.*, 1991), which corresponds to the spawning season, before moving north and eventually going subsurface as the SST rises across the whole basin in summer (Steinberg *et al.*, 2001). That isotherm fluctuated to the north and to the south several times between 1940 and 1970, but in the last few years of the analysis, the latitudes during each of the four months have been farther north than in any year since 1940 (Figure 4b). Knights (2003) also showed positive correlations between Sargasso Sea temperature anomalies at 100–250 m and the DOI between 1952 and 1995, which may be related to the same trends of warming in the region.

The 22.5°C isotherm is located within the most distinct portion of the fronts that consistently form at the 25.6 density isopycnal in the Sargasso Sea (Kleckner and McCleave, 1988; Eriksen *et al.*, 1991; Pollard and Regier, 1992; Miller and McCleave 1994). It is a useful indicator of the northern limit of spawning by both species of eels in the Atlantic, because studies on the distributions of the leptocephali of both species indicate that they spawn south of the isotherm (Kleckner and McCleave, 1988; Tesch and Wegner, 1990; McCleave, 1993). Frontal jets also form in association with these fronts (Eriksen *et al.*, 1991), which appear to transport a variety of leptocephali species eastwards (Miller and McCleave, 1994).



**Figure 7.** Mean decadal Ekman volume transports for March, data for (a) the 1950s, (b) the 1960s, (c) the 1970s, (d) the 1980s, (e) the 1990s, and (f) 2000–2005.

Therefore, changes in the latitude or intensity of these fronts may affect both the spawning location and the subsequent transport of the leptocephali to continental habitats, if transport out of the Sargasso Sea is more efficient with more southerly spawning. If this is true, a northward movement of the fronts that form the northern boundary of spawning may have resulted in increased retention of leptocephali within the Sargasso Sea gyre, which could reduce the number of successful recruits each year.

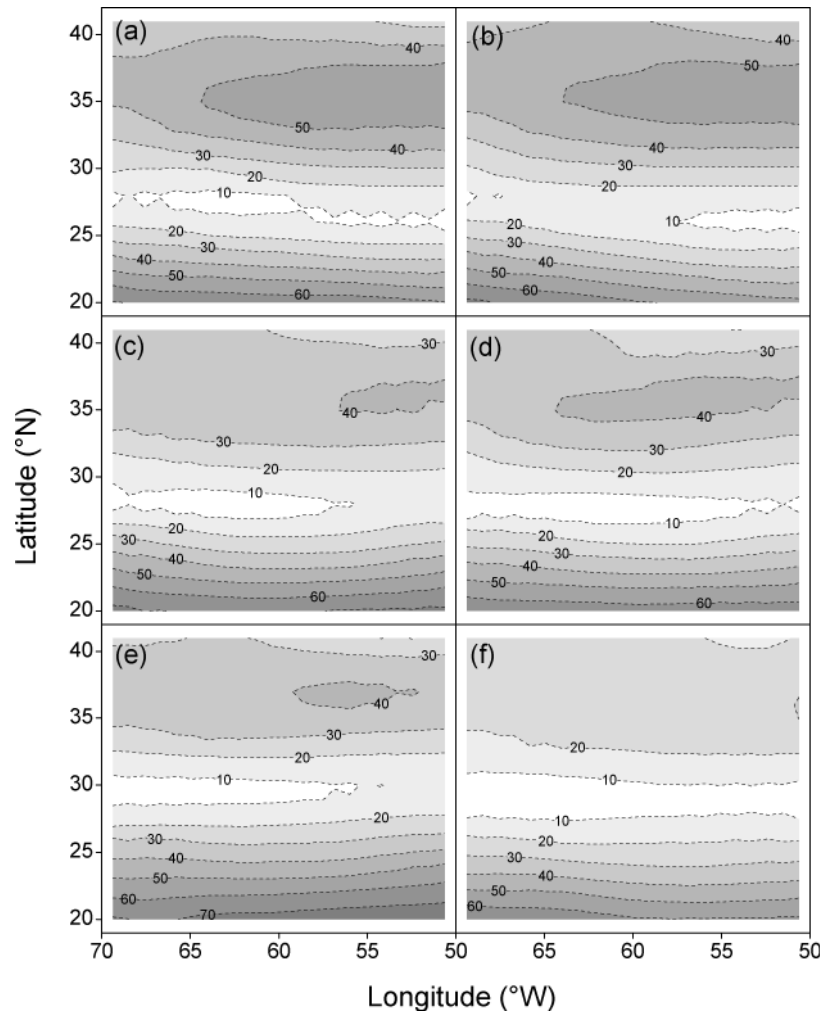
Changes in the winds and wind-driven Ekman transports in the Sargasso Sea could also have an effect on larval transport out of the Sargasso Sea. We found a reduction of  $u$ -vector winds during late winter, in particular during March, which was highly correlated with the pattern of decline of the DOI. Any reductions in easterly winds in the southern Sargasso might slow the rate of westward transport of leptocephali toward the Florida Current or into the Gulf Stream, or increase the likelihood of some being retained in the Sargasso Sea gyre by eddies if these winds are important in maintaining the westward Antilles Current in the southern Sargasso Sea. Transport in the Antilles Current would help leptocephali reach the Gulf Stream, which transports European eel leptocephali into the North Atlantic Drift that carries them towards continental waters (McCleave, 1993). American eel leptocephali must also reach the

Florida Current or Gulf Stream, but they later have to detrain from that current system to recruit to North America.

Although the Antilles Current probably transports recently spawned leptocephali westwards, leptocephali become widely distributed in summer as the surface layer warms in the Sargasso Sea (Boëtius and Harding, 1985; Kleckner and McCleave, 1985; McCleave and Kleckner, 1987). This suggests that the transport of many leptocephali is not direct. The flow structure in the southwestern Sargasso, through which anguillid leptocephali must pass to enter the Florida Current, is complex, but the Antilles Current northeast of the northern Bahamas appears to be present throughout most of the year (Amos *et al.*, 1971; Ingham, 1975; Gunn and Watts, 1982; Fiadeiro and Veronis 1983; Olson *et al.*, 1984; Reverdin *et al.*, 2003; Meinen *et al.*, 2004). Anguillid leptocephali are abundant in this region in October (Kleckner and McCleave, 1982), so it may be important in transporting leptocephali out of the Sargasso Sea.

Changes in the winds in the northern Sargasso Sea, which have reduced southward Ekman transports, could also be contributing to increased larval retention in the Sargasso Sea gyre. Southward Ekman transports could tend to move leptocephali that detrain from the southern edge of the Gulf Stream in eddies towards the





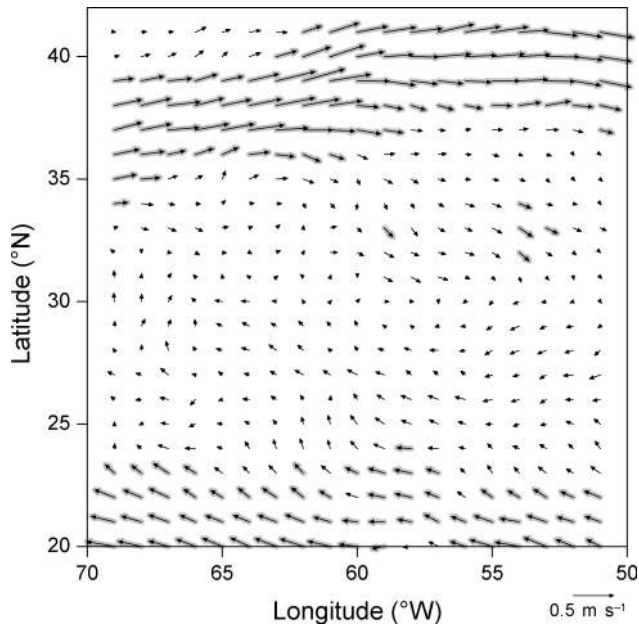
**Figure 8.** Mean decadal Ekman mixing depth (m) for March, data for (a) the 1950s, (b) the 1960s, (c) the 1970s, (d) the 1980s, (e) the 1990s, and (f) 2000–2005.

westward flow farther south in the Sargasso Sea. A reduction in this transport in summer and autumn when leptocephali leave the Sargasso Sea could affect the transport of some, resulting in increased retention in the northern Sargasso Sea. These possible factors, coupled with the potential for changes in current velocities, directions, or recirculation patterns (Curry and McCartney, 2001; Bersch, 2002; Molinari, 2004) influencing the transport of leptocephali across the North Atlantic basin to Europe, could contribute to the declines in European eel recruitment. Modelling exercises of the transport of European eel leptocephali suggest that after spring spawning, leptocephalus migration trajectories may ensure a degree of synchronization with later spring/summer plankton blooms (Kettle and Haines, 2006). Hence, changes in the speed or the pathway of transport, or reductions in primary productivity in the northern and eastern regions of the extensive larval migration could reduce the growth and survival of leptocephali.

Interannual changes in the productivity and temperature structure of the surface layer in the larval development area of eels in the Atlantic could be influenced by the recent reductions in the MLD of the northern Sargasso Sea observed here and previously (Palter *et al.*, 2005). Decreases in the MLD could be associated with reductions in upward mixing of deeper nutrient-rich water,

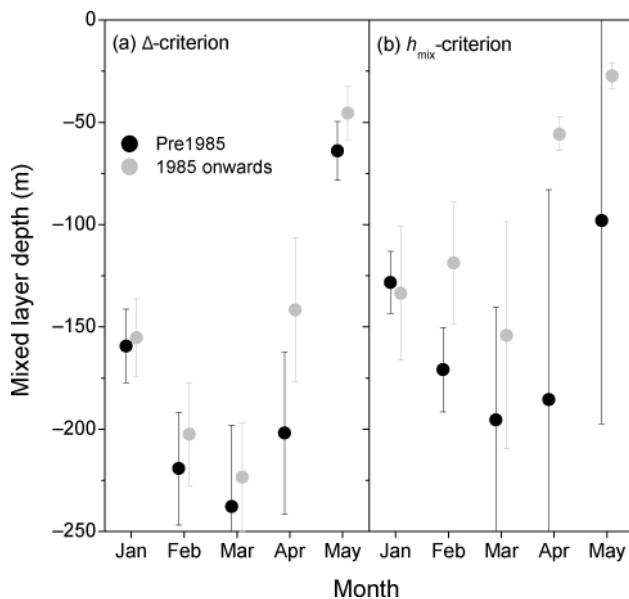
resulting in less primary production in the surface layer, especially during spring thermocline overturns (Kimura *et al.*, 2001; Knights, 2003). Although the factors influencing the upward flux of nutrients into the euphotic zone are complex and poorly understood, the strength of winds and the actions of eddies have been proposed as important mechanisms in the mixing of nutrients into the surface layer (McGillicuddy and Robinson, 1997; McGillicuddy *et al.*, 1998; Stammer *et al.*, 2001; Palter *et al.*, 2005). These types of factors have been associated with increased primary productivity after hurricanes have traversed the Sargasso Sea (Babin *et al.*, 2004).

If changes in the MLD significantly influence the primary productivity or community structure of the Sargasso Sea, then the growth or survival of anguillid leptocephali may have been affected. The feeding ecology of leptocephali is poorly understood, but they appear to feed on POM such as marine snow, including discarded larvacean houses (Otake *et al.*, 1993; Mochioka and Iwamizu, 1996), and gain their nutrition at the microbial trophic level (Otake *et al.*, 1993; Pfeiler, 1999). Therefore, changes in water column structure that influence primary productivity and the production of marine snow in the Sargasso Sea could affect the availability of food for leptocephali during their critical first months of feeding and for growth during their larval migration.



**Figure 9.** Climatologically derived surface currents for March. Highlighted current vectors are of a velocity of  $0.2 \text{ m s}^{-1}$  or greater. The current at the northern end of the plot is the Gulf Stream, and that at the southern end of the plot is the Antilles Current.

There is also some evidence that larval growth or the duration of larval migration may influence the timing and size of glass eels upon arrival, suggesting that oceanic conditions may be affecting recruitment on a long-term or seasonal basis. Dekker (2004) suggested that leptocephalus size has changed on a multi-decadal



**Figure 10.** Estimates of MLD for two time periods and by two procedures for data from Hydrostation S near Bermuda. MLD is computed using (a) the  $\Delta$ -criterion and (b) the  $h_{\text{mix}}$ -criterion methods for the months January through May, separated into two time periods associated with regime shifts in the DOI (1954–1984 and 1985–2003). Error bars are 95% confidence intervals.

scale, and except for the last part of the time-series, glass eel size may have declined along with recruitment. Desaunay and Gueraud (1997) analysed these patterns and also examined the otolith microstructure of glass eels to estimate their hatching dates and migration histories. These findings are intriguing in relation to the findings of the present study, but many questions about the early life history of the European eel complicate interpretations of the causal mechanisms of these types of observations (McCleave *et al.*, 1998). Reductions in growth rates or lengthening of the duration of larval migration could result from the oceanic changes described here, but more basic life history information is needed to help resolve the questions about larval duration, migratory behaviour, and routes of migration of eels in the Atlantic before links can be made with changes in oceanic conditions.

The correlations we have found between key environmental factors acting in the spawning and larval development areas of eels in the Atlantic provide preliminary evidence that oceanic factors may have contributed to the recent declines in recruitment of European and American eels. These correlations with specific factors in the ocean provide the first conceptual basis for linking recruitment to ocean-atmosphere changes in the Sargasso Sea, but the lack of knowledge about the marine phase of the eels makes it currently impossible to determine the importance of the correlations. Our general lack of knowledge about eels is not limited to the early larval stages however, and oceanic changes may act on later larval stages as they approach or cross continental shelves. For example, Knights (2003) suggested that unfavourable changes in wind-driven coastal currents could be important in the transport and survival of glass eels and juveniles in the North and Baltic seas.

In addition, complex ocean-atmosphere changes and anthropogenic factors may be acting simultaneously and interactively to control eel recruitment. Many anthropogenic factors have been listed as likely to reduce eel population sizes or to reduce the number of spawners each year (Haro *et al.*, 2000; Feunteun, 2002; Casselman, 2003; Dekker *et al.*, 2003; Dekker, 2003, 2004), so the causes of the declines of northern temperate eel species cannot be attributed simply to any single cause. Determining cause-effect relationships is complicated by a lack of basic information on silver eel escapement and on the spawning and survival of eggs and larvae. More long-term research on specific changes in the Sargasso Sea and North Atlantic, and on the biology, reproductive ecology, and recruitment patterns of eels in the Atlantic is needed. The potential causal mechanisms proposed here, however, provide a framework for future studies to examine the relationships between ocean-atmosphere changes and recruitment of anguillid eels.

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