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Impact of climate on eel populations of the Northern Hemisphere

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ABSTRACT: Glass eel abundances are declining worldwide. This has mostly been attributed to direct impacts of human activities such as overfishing or habitat loss and degradation, whilst the potential influence of changes in oceanic conditions has received less attention. Eel are characterized by a complex and still enigmatic life cycle that includes a trans-oceanic spawning and larval migration. The apparent synchrony in the decline of eel populations worldwide suggests that the oceanic mechanisms involved are similar for all populations. We analyse the relationships between oceanic conditions in eel spawning areas and glass eel recruitment success of the 3 most commercially important species of the genus *Anguilla*: *A.*

anguilla, *A. rostrata*, and *A. japonica*. We provide evidence that the survival of eel larvae is strongly correlated to food availability during their early life stages. Over the last 4 decades, changes in the marine production related to global warming may have led to the decline of European, American and Japanese eel populations. In the Pacific and Atlantic Oceans, the shifts in the temperature regime detected in the late 1970s were followed by shifts in the recruitment regime of glass eel for the 3 species. The decrease in primary production through climate-driven processes has therefore affected the recruitment of eel populations.

INTRODUCTION

Eel species have always excited a degree of fascination because of their complex and puzzling life cycle. As catadromous fish, they spawn in the open ocean (Fig. 1)—the Sargasso Sea in the case of European and American eels (McCleave 1993), and west of the Mariana Islands in the case of Japanese eels (Tsukamoto 2006). After an oceanic migration that can span thousands of kilometres and last several years (1 to 3 yr for the European eel, Schmidt 1923, Lecomte-Finiger 1994, Tesch 2003; 1 to 2 yr for the American eel, Tesch 2003; 0.5 to 1 yr for the Japanese eel, Kim et al. 2007), eels colonise continental habitats where they grow before migrating back to the open ocean for spawning.

The decline in eel populations of the Northern Hemisphere is alarming (Anonymous 2003, ICES 2006). The European eel has been listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, www.cites.org/common/cop/14/inf/E14i-21.pdf) regarding its current level of abundance. In the Northern Hemisphere, the abundance of juvenile eels has dramatically decreased over the last few decades: in European waters, it is now at historically low levels, i.e. less than 1% of levels in the 1980s for some recruitment time series (ICES 2006). The decline has mostly

been attributed to direct impacts of anthropogenic activities such as dams, pollution and habitat loss, especially in estuaries and continental habitats (McCleave 2001, Feunteun 2002, Dekker 2003, Tatsukawa 2003). Fishing has been proposed as the major factor impacting the European eel population (Dekker 2004). However, although fishing pressure on American glass eel was lower than that on European and Japanese eels before the 1980s, the population exhibited similar signs of declining trends at the same period (Casselman 2003). Notwithstanding stock-specific declining factors, the worldwide synchrony in the decline of eel abundances suggests that common factors such as ocean climate (ocean circulation, temperature or food availability) may have influenced eel population dynamics (Knights 2003, Friedland et al. 2007). As spawning, larval development, feeding, and migration take place in the open ocean, oceanic environmental conditions are believed to be of primary importance for the survival of eel larvae and, therefore, eel recruitment (Knights 2003, Friedland et al. 2007).

Significant negative correlations were found between the North Atlantic Oscillation (NAO) and the catch of glass eels at Den Oever in the Netherlands over the period 1938 to 2005 (Knights 2003, Friedland et al. 2007). Negative relationships have been found between Japanese eel recruitment and the El Niño Southern Oscillation (ENSO; Kimura et al. 2001, Sugimoto et al. 2001, Kim et al. 2007). However, such integrative indices do not allow the elucidation of the precise ecological processes involved, and a novel aspect of our work was to focus on trophic linkage as a key factor for recruitment. No quantitative studies have been carried out to investigate the link between food availability and survival of eel larvae, even though this has been suggested (Castonguay et al. 1994, Désaunay & Guérault 1997).

The temperature of the northern hemisphere has increased more in the 20th century than in any other century during the last 1000 yr, with a main warming period from 1976 onward. The estimate from the Intergovernmental Panel on Climate Change (IPCC) is that the

global average surface temperature has increased by 0.6°C over the last 100 yr (IPCC 2007). This global-scale warming has resulted in increased oceanic temperatures and has strongly affected the spatial and temporal dynamics of a broad range of marine organisms (Beaugrand et al. 2002, Perry et al. 2005). Although responses of marine organisms to climate change have received increasing attention in recent years, the effects of increased sea surface temperature (SST) on the survival of fish larvae and subsequent recruitment, and the resulting impact on fisheries, remain poorly understood. Planktonic food limitation has long been considered to be the dominant factor leading to variability in survival and recruitment of fish larvae (Hjort 1914). Remote sensing observations of the open ocean have revealed that the recent SST increase has triggered large spatial changes in the vertical structure and, consequently, a reduction in the global production of oceanic phytoplankton (Behrenfeld et al. 2006). The increase in temperatures since the early 1980s is also believed to have resulted in a 6% decrease in global primary production (PP), a decline that is mostly due to a pronounced decline in net PP at mid and low latitudes (Gregg et al. 2003), including eel spawning areas.

In the present study, we examined the relationships between the recruitment patterns of European, American, and Japanese eel and patterns of marine PP in their respective spawning areas. These 3 temperate species represent 90% of world eel catches over the 1950 to 2005 period (from FishStat Plus v.2.32, http://www.fao.org/fishery/topic/16073). We tested the hypothesis that recruitment of these eel species is determined by food availability during their early life stages (as leptocephali). Although the diet of eel larvae remains controversial, it has been suggested that they primarily feed on particulate and dissolved organic matter, i.e. at very low trophic levels (Otake et al. 1993, Mochioka & Iwamizu 1996, Pfeiler 1999). Organic matter and PP are strongly correlated in the North Atlantic and North Pacific gyres (e.g. Bates 2001, DuRand et al. 2001, Pilskaln et al. 2005), and PP can therefore be used as a proxy of food availability for leptocephali. It has recently been established that a trophic link

exists between marine PP in the Sargasso Sea and the recruitment of glass eels in European waters: variations in food availability for eel larvae in the spawning area are shown to be strongly positively correlated with fluctuations in recruitment success in subsequent years (Bonhommeau et al. 2008). In this study, we investigate whether this trophic linkage can generally be observed for European, American and Japanese eel populations. Using short- and long term time series and regime shift detection methods, we then analysed the effects of global warming on PP in eel spawning areas and subsequent impacts on eel recruitment.

MATERIALS AND METHODS

Eel recruitment data. For European eel, the recruitment series used for the short-term analysis was the original series from the Loire River over the period 1994 to 2004 selected by Bonhommeau et al. (2008), because it provides the best picture of year-to-year fluctuations. Data used for the long-term analysis were from the 4 longest time-series of glass eel recruitment available from the ICES Working Group on eel (ICES 2006), i.e. from the Ems River (Germany), Den Oever (Netherlands), Loire River (France), and Nalon River (Spain) (Fig. 1). To define a European glass eel recruitment index over the period 1960 to 2005, these time series were averaged after standardization (divided by their mean over the observation period).

American glass eel recruitment data used for short-term analysis are from Sullivan et al. (2006), who studied 2 sampling sites, Little Egg Inlet (New Jersey) and Beaufort Inlet (North Carolina), over the period 1986 to 2004 (Fig. 1). Data used for the long-term analysis were from the index produced from daily passage at the Moses-Saunders dam eel ladder in the upper St. Lawrence River (Ontario, Canada) over the period 1974 to 2001. This index is

fully described in Casselman (2003). This series was 4 yr lagged, since eels were caught an average of 4 yr after the elver stage (Castonguay et al. 1994).

The Japanese recruitment index was the annual catch of glass eels in Japan from 1965 to 2001 and is described in Tatsukawa (2003).

Primary production data. To our knowledge, *in situ* data were only available from Atlantic eel spawning areas and not from the Japanese eel spawning area. We used data provided by the Bermuda Institute of Ocean Sciences (BIOS), which has been carrying out *in situ* sampling of PP during regular cruises since 1988 (Fig. 1). The Bermuda Atlantic Time-series Study (BATS) station is located in the west central Sargasso Sea and can, as a whole, be considered as a representative eel spawning area (Nelson et al. 2004). PP data, together with details of sampling and analytical methods used, are available on the BIOS website (http://bats.bios.edu/bats_form_prod.html). Different sampling events of leptocephali in this region revealed a preferred depth of 160 m during the day and 60 m at night (Schoth & Tesch 1982 1984, Castonguay & McCleave 1987). For this study, PP was integrated over a period of 6 mo, from January to July, to derive an average estimate of the annual productivity in the Sargasso Sea over the spawning period of Atlantic eels. Most of the PP occurs during this period of the year, and averaging over this period also helps to account for the integration time of PP in the first levels of the food chain. Moreover, the hatching periods between March and July for the European eel and between February and April for the American eel are included within these 6 mo (McCleave 1993, Wang & Tzeng 2000).

Temperature data as a proxy for primary production. We used decadal changes in SST in eel spawning areas as a proxy for PP to investigate the impact of warming on recruitment success since the 1960s. Although long-term field measurements of PP are not specifically available for the Sargasso Sea or southwestern North Pacific, it has been shown that, in warm stratified surface waters over decadal time scales, increasing SSTs lead to a

decrease in PP. A clearly identified process in this context is that a rise in SST reduces mixing of the upper part of the water column which, in turn, reduces the upward supply of nutrients (Behrenfeld et al. 2006). In particular, the increased SST in the western North Atlantic and North Pacific (especially at lower latitudes) has been shown to be negatively correlated with PP over decadal time scales (Sugimoto & Tadokoro 1998, Miller & Schneider 2000, Bates 2001, Limsakul et al. 2001, Nelson et al. 2004, Watanabe et al. 2005, Behrenfeld et al. 2006, Aita et al. 2007, Hashioka & Yamanaka 2007). This complex response of PP to changes in SST probably arises because temperature not only affects biota directly—a 1°C increase in temperature is rarely lethal—but also acts as a proxy for other physical processes (i.e. inhibition of nutrient circulation due to enhanced stratification of the water column), thus regulating the size structure, taxonomic composition, and abundance of phytoplankton communities (Li 2002).

The average annual SST during the eel spawning period in the Sargasso Sea (March to July) was computed using SST data from the BATS site over the period of 1960 to 2005 (http://bats.bios.edu/bats_form_ctd.html; Fig. 1). Details on the computation of the Sargasso Sea SST are provided in Bonhommeau et al. (2008).

Data from the Japan Meteorological Agency (JMA) were used to estimate average annual SST in the Japanese eel spawning area for the 1966 to 2001 period. The mean annual SST was computed using 10 d mean SSTs that are available from 1950 until present on the JMA website (http://goos.kishou.go.jp/rrtdb/usr/pub/JMA/wnpsst/). The 10 d mean SSTs were averaged first by month and then by year.

Statistical Analyses.

Relationships between environmental descriptors and eel recruitment indices was determined using 3 different time series analysis methods. Short-term relationships between

PP and recruitment indices were analysed for the 2 Atlantic species (over 11 yr for the European eel and 13 yr for the American eel). Long-term relationships were studied between temperature in eel spawning areas and eel recruitment indices for all 3 species (over 46 yr for the European eel, 28 yr for the American eel, and 36 yr for the Japanese eel). Finally, regime shift detection was used to detect any synchrony between the years of transition in SST and eel recruitment indices for the 3 species.

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

Time lags were included to account for the duration of eel larval migration and to link environmental descriptors to glass eel recruitment. Friedland et al. (2007) used a 1 yr lag, but Knights (2003) and Bonhommeau et al. (2008) used a delay of 2.5 to 3 yr. These discrepancies arise from the use of different methods for the estimation of migration duration, which are discussed below. In this study, we tested different time lags (1 to 3 yr for the European and American eel, 0 to 1 yr for the Japanese eel).

Testing short-term correlations. To assess correlations between interannual variations of PP and recruitment indices, both of the initial length N, we removed autocorrelation by 'prewhitening' the data series, i.e. by first-order differencing prior to statistical testing (Thompson & Page 1989, Pyper & Peterman 1998). The aim is to transform the original data to eliminate autocorrelation whilst retaining the high-frequency signal (Fox et al. 2000). After the transformation, standard correlation tests can be applied to the resultant series. Pearson coefficients were used to assess the linear relationship between the first-order differenced recruitment and environmental time series, and to test correlations. The p-value

was assessed by comparing the Pearson coefficient against its theoretical Student distribution with *(N–1)-2* degrees of freedom (d.f.) where *(N–1)* is the length of the first-differenced time series. We estimated the different correlations between glass eel recruitment indices and environmental descriptors using different lags to take into account the different assumed migration duration. We checked that autocorrelation was correctly removed using the autocorrelation function (ACF).

Testing long-term correlations. To analyse long-term patterns between recruitment indices and SST time series, we first smoothed the data with a 5 yr moving average to analyse low-frequency sources of covariation (Pyper & Peterman 1998). The Pearson coefficient was used to test correlations between the smoothed time series. To compensate for autocorrelation in the smoothed time series of the length N, the d.f. of the Student significance test, denoted N^*-2, was adjusted following the equation proposed by Chelton (1984) and modified by Pyper & Peterman (1998):

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N}\sum_j r_{xx}(jj) \times r_{yy}(j) \qquad (1)$$

where N^* is the corrected sample size interpreted as the number of independent joint observations on the 2 time series x (recruitment data) and y (SST 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 & Jenkins 1976), modified by Chatfield (1989):

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

where $\overline{X}$ is the overall mean.

Pyper & 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 equalled to *N*/5 (Pyper & Peterman 1998).

Regime shift detection. Detection of major changes in glass eel recruitment indices and SST was performed using a sequential regime shift detection (Rodionov & Overland 2005). This method allows estimating the magnitude of the shift by calculating a regime shift index (RSI). The significance level (p) is the level at which the null hypothesis that the mean values of the 2 regimes are equal is rejected by the 2-tailed Student's t-test. The cut-off time scale (*l*) determines the minimum duration of 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, the cut-off length (*l*) was set to 10 yr and the probability level at p = 0.01. We also tested the sensitivity of the results to the parameters by setting *l* to 15 and 20 yr and p to equal 0.05.

RESULTS

Short-term relationships between PP and recruitment indices

We analysed the relationship between PP in eel spawning areas and recruitment of European and American eels over 11 and 13 yr, respectively. For the European and the American eel, only a 2.5 and 1.5 yr lag, respectively, exhibited a significant correlation. Highly significant positive correlations were found between PP and recruitment for European (Pearson's r = 0.74, p = 0.015) and American eel (Pearson's r = 0.71, p = 0.010) (Fig. 2). Thus, more than 50% of the variation in coastal glass eel recruitment success can be explained by fluctuations

in PP in the eel spawning area. The tight link between Sargasso Sea PP and subsequent recruitment of European and American eels suggests that food availability in the Sargasso Sea exerts a major control on eel larval survival, and that such bottom-up control has been driving the recruitment of European and American eels for more than a decade.

Long-term relationships between fluctuations in SST and eel recruitment indices

Fluctuations in Sargasso Sea SSTs followed the same trends as the Northern Hemisphere Temperature (NHT) anomaly, suggesting a direct link between global warming and the increase in SST in these areas (Fig. 3).

Over the past 40 yr, the long-term correlations between Sargasso Sea SST and recruitment indices of Atlantic eel species were the most significant using a 2.5 yr lag for the European eel ($r = -0.88$, $p = 0.03$; Fig. 4a) and a 1.5 yr lag for the American eel ($r = -0.90$, $p = 0.03$; Fig. 4b). The correlation between SST in the Japanese eel spawning area and the Japanese eel recruitment index were most significant using a 0.5 yr lag ($r = -0.84$, $p = 0.01$; Fig. 4c). The decrease in glass eel recruitment appears to be strongly inversely correlated with warming in eel spawning areas.

Regime shifts in eel recruitment indices, SST, and NHT

The regime shift detection method applied to raw time series of recruitment and temperature revealed a negative regime shift in 1982 for the European eel and in 1981 for the American eel, while a positive regime shift in Sargasso Sea SST was shown for 1979 (Fig. 3&5). A negative regime shift was detected for Japanese eel recruitment in 1977, 1 yr after the shift in temperature in the Pacific Ocean detected by Hare & Mantua 2000. For each eel

species, the negative shift in recruitment followed a positive shift in temperature (Fig. 5). In each case, time lags between temperature and recruitment shifts corresponded to lags found previously. These findings reinforce the idea of a strong link between temperature and recruitment.

DISCUSSION

Primary production as a proxy for eel larval food availability and importance during earliest life stages

This study used PP as an indicator of eel larval food supply. This is justified by general considerations (Ware & Thomson 2005) and based on the available knowledge about leptocephalus diet. Two potential sources of nutrition have been proposed for eel 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 & Iwamizu 1996, Pfeiler 1999). Marine snow has also been proposed as a potential source of nutrition (Knights 2003). Since a strong linear relationship between phytoplankton and POM has been described in the Sargasso Sea (DuRand et al. 2001), PP has been considered to be a good proxy for leptocephali food (Bardonnet & Riera 2005). Biological production may directly impact eel larvae because of its characteristics. Eel larvae are qualified as type II larvae based upon their unique developmental strategy. Following a post-hatch period in which the yolk-sac is absorbed, the larval fish show a dramatic increase in size during which up to 40% of the leptocephalus maximum length is attained while only 5 to 7% of the maximum mass is accumulated (Bishop & Torres 2001). This unique strategy allows them to increase rapidly in size while devoting the majority of their energy to metabolism, i.e. nutrition and locomotion, and not to increase in body mass as most other larval fish. Food availability seems critical

during early life stages to determine the capacity of eel larvae to rapidly reach a size that allows them to drift into currents.

The specific location of Japanese eel spawning areas near seamounts may be linked to the functional role of these places in nutrient transport. Seamounts have been shown to induce perturbations in nutrient distributions, leading to enhanced upward transport of nutrients into the euphotic zone (Furuya et al. 1995). This process results in an elevated amount of chl *a* downstream of the seamount. Consequently, seamount ecosystems may be adequate areas to provide eel larvae with a sufficient food supply. The assumed location of these areas relative to frontal systems (e.g. McCleave et al. 1987, Kleckner & McCleave 1988, Kimura et al. 2001) also implies that mixing processes encourage deepening of the mixed depth layers and nutrient circulation.

Food availability in spawning areas seems therefore to be an important factor for eel larval survival during the post-hatch period of these 3 eel species and explains the relationships found between PP and glass eel recruitment. The importance of food availability during the oceanic migration has previously been demonstrated (Désaunay & Guérault 1997, Kettle & Haines 2006).

Global warming effect on eel recruitment

The fluctuations of SST in eel spawning areas are consistent with changes observed for the northern hemisphere temperature. Changes in SST of similar orders of magnitude have been found in other studies dealing with large-scale changes in SST and its impact on marine ecosystems (e.g. Donner et al. 2007, Thresher et al. 2007). Based on our analyses, we did not detect a change or trend in the intra-annual temperature variability over the 4 last decades.

The change in SST has been estimated to lie between 0.4 and 0.8°C (Fig. 3). We hypothesized that an increase in SST has an indirect effect through reinforcement of the vertical thermal stratification of the water column, leading to a decrease in marine production in warm eel spawning areas (Sugimoto & Tadokoro 1998, Bates 2001, Richardson & Schoeman 2004, Watanabe et al. 2005, Behrenfeld et al. 2006). This is strongly supported by the highly positive correlation found between PP and glass eel recruitment, lagged to account for migration duration (i.e. 2.5 yr for the European eel, 1.5 yr for the American eel, and 0.5 yr for the Japanese eel). Global change is known to affect the abundance as well as the size of marine plankton. For instance, Beaugrand et al. (2003) showed that an increasing temperature in the North Sea has led to a decrease by a factor of 2 in the mean size of calanoid copepods after the 1980s, which in turn led to a decrease in cod recruitment. However, the current lack of accurate information on the diet of eel larvae impedes the analysis of such a relationship. The patterns of eel recruitment observed in the present study could be part of longer-term cycles, but the historical data used are not fully reliable. However, the change in abundance detected in the present analysis suggests an abrupt regime shift, rather than a long-term cycle.

The increase in temperature can be relatively small locally. However, when integrated over the whole period of migration, a subtle increase in temperature may have dramatic effects on eel larvae, for instance via the reduction in nutrient supply. It would be interesting to analyse the impact of the food availability along the whole migration routes of leptocephali on eel larva survival. However, the migration duration is not sufficiently well-known to perform such analyses.

To analyse the relationships between eel recruitment and environmental conditions, we tested several lags. For the 3 distinct analyses (short-term relationships of recruitment to PP of Atlantic species, long-term links of recruitment of all 3 eel species to SST, and delays between regime shifts), the most significant correlations were obtained with similar time lags:

2.5 yr for the European eel, 1.5 yr for the American eel and 0.5 yr for the Japanese eel. The 0.5 yr delay used for the Japanese eel is consistent with current available knowledge about its migration duration (Cheng & Tzeng 1996, Kimura et al. 1999). Wang & Tzeng (2000) and Shinoda (2004) also showed that migration of Japanese eel takes between 98 and 227 d.

Migration durations of Atlantic eels remain controversial: ages at recruitment back-calculated by otolith microstructure analysis ranged from 7 to 15 mo (Lecomte-Finiger 1994, Cheng & Tzeng 1996, Arai et al. 2000), but studies based on daily growth increments in glass eel otoliths have been criticized (McCleave et al. 1998, Svedäng et al. 1998, Cieri & McCleave 2000). There is likely a period during metamorphosis when the oceanic eel larvae do not deposit daily rings because of a low metabolic rate. It is also noteworthy that there may be some resorption of otolith chemicals during metamorphosis (Antunes & Tesch 1997). In addition, according to McCleave et al. (1998), European eel leptocephali are unable to swim across the Atlantic Ocean in less than 1 to 2 yr. The ocean circulation model by Kettle & Haines (2006) indicates a migration duration of 2.5 to 3 yr for European eel larvae. Our results appear to contradict approaches based on otolith microstructure analysis, but fit with estimates based on larval drift.

Other factors associated with ocean climate change

The relationships between the Transport index (i.e. the strength of the Gulf Stream; Curry & McCartney 2001), the Gulf Stream Index (i.e. the latitude of the Gulf Stream; Taylor & Stephens 1998) and European glass eel recruitment have not been clearly established (Bonhommeau et al. 2008). However, other studies suggest that leptocephali may be affected by oceanic features because of their long oceanic larval 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 PP, the drift conditions in the

larval transport area, and declining trends in winds have contributed to declining recruitment as well. Friedland et al. (2007) used the Den Oever Index, which is based on regular scientific sampling carried out at Den Oever behind the sluices of a dam at 2 h intervals at night during spring, using a 1 m^2 dipnet in close proximity to one of the closed sluices. They showed that fluctuations of the Den Oever Index are related to fluctuations in the North Atlantic Oscillation (NAO), which indicates that eel recruitment may be influenced by the physical and biological structure of the North Atlantic. It has been suggested that the changes associated with these types of atmospheric forcing could alter the biological characteristics of the surface layer where leptocephali feed (M. Miller et al. unpubl. data). 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 the European 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 of leaving 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 recruitment of European eel.

Similarly, Kimura et al. (2001) showed a certain synchrony between *Anguilla japonica* recruitment and salinity fronts driven by ENSO in the Japanese eel spawning area. If eel eggs hatch south of the salinity front, larvae may be carried away by the southward Mindanao current. By contrast, hatching north of the front, leptocephali may follow the Kuroshio current, which transports them from Taiwan to Japan (Kimura et al. 1999. During the El Niño event in 2002, Kimura & Tsukamoto (2006) noticed that small larvae (<10 mm total length) were collected just south of the salinity front where these young larvae had never been found

in normal years. Kim et al. (2007) also demonstrated that the changing oceanic conditions associated with climate change have resulted in decreased recruitment of Japanese eel.

Trophic conditions in eel spawning areas appear to affect the success of eel recruitment several years later and thousands of kilometres away from the spawning site. Decadal changes in SST have occurred around the Mariana Islands and in the Sargasso Sea; abrupt transitions in the temperature regimes of these regions have occurred in the late 1970s, followed by a period of persistent warming (Hare & Mantua 2000, Bonhommeau et al. 2008). These conditions seem to have induced changes in eel larval survival through bottom-up trophic regulation. The relationships between PP and glass eel recruitment indices in the North Atlantic and North Pacific were found at different nested time scales, i.e. short-term for interannual fluctuations, medium-term for regime shifts and long-term for decadal trends. These consistent and synchronous results at multiple temporal scales provide a general explanatory mechanism for how climate-driven changes in oceanic plankton production can affect eel recruitment in the Atlantic and Pacific Oceans. The destabilization of fish populations due to overfishing leads to higher variability of abundances, associated with higher sensitivity to the environment (Anderson et al. 2008, Stenseth & Rouyer 2008). The multiple anthropogenic effects affecting eel, such as overfishing, may therefore have destabilized eel populations and increased their sensitivity to environmental conditions. We therefore argue that, in conjunction with anthropogenic factors such as overfishing and habitat loss and degradation, global climate variations have resulted in a major bottom-up control contributing to the current decline of eel stocks. Such a combination of negative processes calls for a strict precautionary approach regarding future fisheries management plans.

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1 FIGURE LEGENDS

2

3 **Fig. 1:** (a) Location of American (dashed line) and European (solid line) eel spawning areas
4 (after McCleave 1993). American eel recruitment sampling sites, LEI: Little Egg Inlet, BI:
5 Beaufort Inlet, M-SD: Moses-Saunders Dam (Ontario): European eel recruitment sampling
6 sites, ER: Ems River, DO: Den Oever, LR: Loire River, NR: Nalon River; (triangle):
7 Bermuda Atlantic Time-series Study (BATS) site. (b): Location of Japanese eel spawning
8 area (square; after Tsukamoto, 2006)

9 **Fig. 2:** Short-term time series of European and American eel recruitment indices (no unit),
10 lagged by 1.5 and 2.5 yr, respectively, and integrated primary production (mgC m^{-3} d^{-1}) at the
11 Bermuda Atlantic Time-series Series (BATS) site

12 **Fig. 3:** Sea surface temperature (SST, °C, solid line with circles) in (a) the Sargasso Sea and
13 (b) the spawning area of the Japanese eel, versus Northern Hemisphere Temperature
14 anomalies (°C, available at www.cru.uea.ac.uk/cru/data/temperature; dashed line with
15 diamonds). Vertical dashed lines represent the regime shift in temperature found using the
16 regime shift detection method

17 **Fig. 4:** Long-term relationships (5 yr moving averages) between sea surface temperature
18 (SST, °C) in the eel spawning areas and glass eel recruitment indices for (a) European, (b)
19 American, and (c) Japanese eels, lagged by 2.5, 1.5, and 0.5 yr, respectively, to account for
20 different migration durations. r: correlation coefficient, N^*: degrees of freedom after
21 compensating for serial autocorrelation, p: p-value with N^*–2 degrees of freedom

22 **Fig. 5:** Time series of European, American, and Japanese recruitment indices (solid lines with
23 circles, no unit). Bold lines: regime shift detection, vertical dashed lines: main regime shifts in

24 sea surface temperature (SST) in the North Atlantic (in 1979) and North Pacific (in 1977)

25 oceans

26