

Influence of oceanic factors on *Anguilla anguilla* (L.) over the twentieth century in coastal habitats of the Skagerrak, southern Norway

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The European eel (*Anguilla anguilla* L.) is distributed in coastal and inland habitats all over Europe, but spawns in the Sargasso Sea and is thus affected by both continental and oceanic factors. Since the 1980s a steady decline has been observed in the recruitment of glass eels to freshwater and in total eel landings. The eel is considered as critically endangered on the International Union for the Conservation of Nature and Natural Resources Red List of species. The Skagerrak beach seine survey from Norway constitutes the longest fishery-independent dataset on yellow/silver eels (starting in 1904). The Skagerrak coastal region receives larvae born in the Sargasso Sea spawning areas that have followed the Gulf Stream/North Atlantic Drift before they penetrate far into the North Sea. The Skagerrak coastal time series is therefore particularly valuable for exploring the impacts of oceanic factors on fluctuations in eel recruitment abundance. Analyses showed that Sargasso Sea surface temperature was negatively correlated with eel abundance, with a lag of 12 years revealing a cyclic and detrimental effect of high temperatures on the newly hatched larvae. The North Atlantic Oscillation index and inflow of North Atlantic water into the North Sea were negatively correlated with eel abundance, with a lag of 11 years. Increased currents towards the North Atlantic during high North Atlantic Oscillation years may send larvae into the subpolar gyre before they are ready to metamorphose and settle, resulting in low recruitment in the northern part of the distribution area for these years. The Skagerrak time series was compared with glass eel recruitment to freshwater in the Netherlands (Den Oever glass eel time series), and similar patterns were found revealing a cycle linked to changes in oceanic factors affecting glass eel recruitment. The recent decline of eels in the Skagerrak also coincided with previously documented shifts in environmental conditions of the North Sea ecosystem.

Keywords: European eel; *Anguilla anguilla*; time series; oceanic factors; population decline

1. INTRODUCTION

The European eel (*Anguilla anguilla*) is distributed all over Europe, from Iceland and the North Cape in Norway, around the Mediterranean, down to northwest Africa. Its tolerance to different salinity environments is exceptional and thus it is found in all kinds of habitats: rivers and lakes, marshes, brackish water, fjord systems and marine coastal waters. Although their adaptability is outstanding, eels are seriously threatened, as inferred from declines over recent decades in recruitment and fishery yields in Northern Hemisphere species [1]. Since 2008 they have been included in the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of threatened species as critically endangered. In 2009, information on freshwater recruitment, freshwater stock and fisheries reviewed by the International Council for the Exploration of the Sea (ICES) Working Group on Eels [2] confirmed the view that the stock is outside safe biological limits.

Many factors are suspected as the cause of the decline: overfishing, limited access to upper reaches of the watershed owing to dams and other obstructions to migration, entrainment of downstream migrating silver eels in turbines of hydroelectric power plants, pollution and parasites (e.g. the nematode *Anguillicoloides crassus*) found in freshwater [3]. Because eels have marine spawning grounds in the Sargasso Sea area [4] and a long transatlantic migration as leptocephalus larvae drifting with the Gulf Stream, oceanic factors may well be involved in the decline [5–9]. Glass eel recruitment to freshwater (observations based mostly on fishery-dependent data) is related to some oceanic factors such as the North Atlantic Oscillation (NAO) and Sargasso Sea temperature [8,10–12]. Mechanisms behind the correlations are unknown, but these factors are related to ocean currents and influence the ocean productivity (and thus food availability) for migrating leptocephalus larvae [7,11].

In Norway, the European eel is present in all coastal areas and low-elevation watersheds. Abundance was thought to gradually decline towards the north, based

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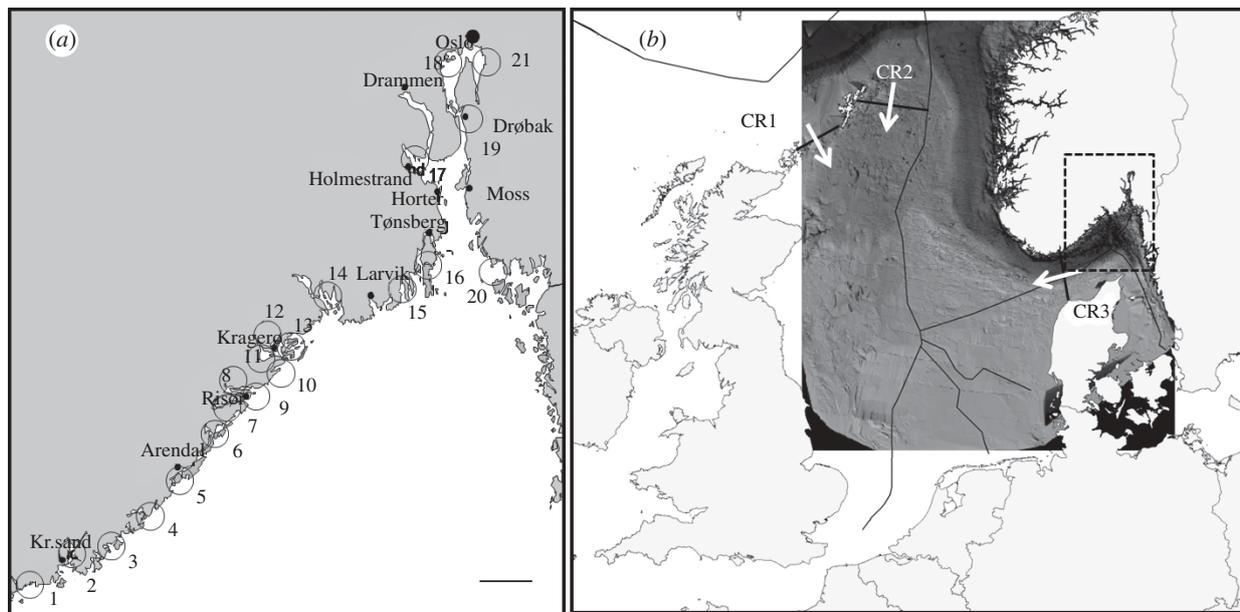


Figure 1. (a) The distribution of sampling sites. Only areas still sampled are shown. (b) Positions of the sections chosen from the NORWECOM model for flux calculations in the North Sea. The shaded area corresponds to the area covered by the model. CR1: Orkney–Shetland; CR2: Feie–Shetland western part; and CR3: Oksøy–Hanstholm. White arrows indicate the direction of the flow used in the study. (a) scale bar, 20 km; 1, Torvefjord; 2, Tøpdalsfjord; 3, Høvåg–Steindalsfjord; 4, Bufjorden–Grimstad; 5, Flødevigen; 6, Lyngør–Dypvåg; 7, Sandenesfjord; 8, Søndeledfjord; 9, Risør skerries; 10, Stølefjord; 11, Kilsfjord; 12, Hellefjord; 13, Soppekkilen; 14, Grenlandsfjords; 15, Sandefjord; 16, Nøtterø–Tjørne; 17, Holmestrand area; 18, Vestfjord; 19, Drøbak area; 20, Hvaler; 21, Bunnefjord.

on the presence of eel fisheries [13,14]. There has, however, historically been a low interest for eels in Norway, but according to investigations, there are significant occurrences of eels in rivers at high latitudes to 68° – 70° N [15,16]. Eels are very common further south in the fjords and around the coastal islands, therefore in brackish to marine areas.

The Norwegian Skagerrak beach seine survey constitutes the longest fishery-independent set of data on eel abundance (started in 1904). Every year in autumn, close to a hundred stations are sampled along the Norwegian Skagerrak coast in 21 different areas (figure 1a). Fish are caught with standardized beach seines, identified and counted. Eels have been inventoried since the beginning of the survey. Most of them are yellow eels living in the eel grass beds along the coast and have probably not entered or spent significant periods of time in freshwater. This time series, to our knowledge, is the only one available for a coastal eel population and is therefore ideal to examine influences of oceanic factors on eel fluctuation.

The objectives of this study were to compare the fluctuations of a marine subpopulation of eels (having a predominantly marine life cycle) with a long-term time series for recruitment of glass eels from the North Sea into freshwater, and to investigate links with environmental factors (NAO, Sargasso Sea temperature, currents in the North Sea) potentially having an effect on the oceanic phase of this species.

2. METHODS

(a) Biological data

The Skagerrak beach seine data are the result of a unique monitoring programme that was initiated in 1904 by Gunder Mathiesen Dannevig (1841–1911) and the great

pioneer in marine research Johan Hjort (1869–1948) as a way to survey cod releases along the Norwegian Skagerrak coast. Based on the initial results from these hauls, the monitoring programme was established and reached its present form in 1919 [17–20].

More than 250 stations between Kristiansand and the Norwegian–Swedish border have been sampled in September/October since 1919. The present number of stations sampled each year is about 120 (since 1987). Stations are grouped into 21 sampling areas (figure 1a), each area containing between two and eight stations. Since 1987, eels have been found in 16.5 per cent of the stations. Since 1919, all species of fish have been identified, but we analysed data from 1925 onwards, as the quality of the data before that time was less reliable (Tore Johannessen, Institute of Marine Research, Norway, 2009, personal communication).

The standardized beach seines are 40 m long and 3.7 m deep, with a 20–30 m long rope and a stretched mesh size of 1.5 cm. Each haul covers an area of up to 700 m². Depth ranges between 3 and 15 m. Hauls are performed during daytime in a standardized manner, every year at the same season (September and October). Additional details on the gear and hauling technique can be found in [18].

The selectivity of the beach seine for eels is not known. For a 1.5 mm stretched mesh the modal length retained can be estimated around 23 cm [21]. Dekker [22] estimated the size distributions of eels caught with 1 and 2 cm mesh sizes. The modal lengths (or length under which the number of eels decreases) are, respectively, 24 and 28 cm. Therefore, eels smaller than approximately 25 cm are probably under-represented in the data.

In addition to escaping through the mesh, fish may escape under or above the net. However, the net is equipped with weights at the bottom rope, and it is hauled in a way to avoid lifting from the bottom. Underwater video recordings

have shown that few fishes escape under the net (Institute of Marine Research, unpublished video recordings). Most demersal and littoral fishes react to dangers by going down towards the bottom. It is therefore unlikely that they will escape above the net.

To compare the fluctuations of Skagerrak eels with those of recruitment to a catadromous subpopulation, we chose another well-documented fishery independent dataset from the northern part of the distribution area: the recruitment time series from Den Oever in the Netherlands, where the abundance of glass eels has been monitored since 1938 [23]. This time series is representative of temporal fluctuations in glass eel recruitment in the rest of the distribution area [12,24]. These data were obtained by courtesy of Dr Willem Dekker (Swedish Board of Fisheries, Institute of Freshwater Research, Stångholmsvägen 2, Drottningholm, SE-178 93, Sweden).

(b) Eels from the Skagerrak coast

Body length of eels has been measured since 1993 and ranged from 20 to 90 cm. Previous studies in the Oslo fjord (Drøbak area: area 19, figure 1a) have shown that eels in the same size range (from 37 to 85 cm, mean around 45 cm) were estimated to be aged between 3 and 12 years (since arrival as a glass eel), with a mean of 6 years [25,26]. The mean age of silver eels from the river Imsa (located on the western shore of southern Norway, approximately 200 km west of the first station of the survey) is 9 years [27]. From 1958 to 1965, 69 per cent of samples were classified into yellow and silver eels, and of these eels 58 per cent were yellow (resident) and 42 per cent silver (migratory). The remaining 31 per cent were mostly small yellow eels (Tore Johannessen, Institute of Marine Research, Norway, 2009, personal communication).

(c) Environmental data

Eel time series were compared with several series of environmental data: sea surface temperatures in the Sargasso Sea, the NAO index and North Sea fluxes. Sargasso Sea temperatures (from 1955 on) were obtained from the Bermuda Atlantic Time Series study (BATS: <http://bats.bios.edu/>). Sargasso Sea temperatures from March to June (supposed period of spawning [28]) were averaged per year and over the first 300 m, for the mixed layer (300–1000 m, determined from the temperature/depth profiles) and for the bottom layer (1000–3900 m).

NAO Index Data were provided by the Climate Analysis Section, UCAR, Boulder, USA (<http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html> [29]).

North Sea currents between 1955 and 2004 were obtained from the Norwegian Ecological Model system (NORWECOM) [30,31]. This model has been validated by comparison with field data in the North Sea/Skagerrak [32–34]. Most of the inflow into the North Sea comes from the northern boundary (95%). About half of the inflow across the northern boundary comes over the plateau, via the Orkney–Shetland section and the western part of the Feie–Shetland section, the other half following the Norwegian Trench (figure 1b). The flows through three sections were investigated as these showed significant correlations with eel abundance in a preliminary analysis (insignificant analyses are not presented here): net flow into the North Sea from the North Atlantic: Orkney–Shetland (inflow) and Feie–Shetland western part (inflow); and along the

Skagerrak coast: Oksoy–Hansthalm section (outflow). In the rest of the manuscript, these three currents will be referred to as CR1, CR2 and CR3, respectively. Figure 1b shows the position of the sections as well as the direction of the flows. Because seasonal variability of currents is higher than annual variability (Hein Rune Skjoldal, Institute of Marine Research, Norway, 2009, personal communication), quarterly means were calculated (as three-month periods) and correlated individually to the biological data, with Q1 designated January–March, Q2 April–June, Q3 July–September and Q4 October–December.

(d) Time-series analysis

Stations are grouped into sampling areas. The number of eels is given for each of the 21 sampling areas (figure 1a). Between 1925 and 2007, 1898 eels were caught during the survey. The maximum number of eels caught in one area was 27 individuals. Only data from sampling areas where eels have represented at least 4 per cent of the grand total were analysed. These were areas 2, 3, 7, 8, 14, 17, 18 and 20. These data were standardized according to

$$SSC_{i,j} = \frac{x_{i,j} - \mu_j}{\sigma_j},$$

where x is the mean catch per sampling area, SSC the standardized Skagerrak catch, i the year and j the sampling area, μ the mean and σ the standard deviation.

Average values per year were then calculated according to

$$SSC_i = \frac{SSC_{i,j}}{n_j},$$

where n is the number of sampling areas.

Trends were calculated using the cumulative sums method (CUSUM [35,36]). A cumulative sum represents the running total of the deviations of the first observations from a mean based on the same interval [35,37]. The CUSUM approach to detecting change points performs well, has been well-documented and is relatively easy to implement [37]. Change points that may not be possible to detect in the original data often become easier to detect when the CUSUM is plotted.

For a time series with data x_t sampled for each t , a reference value k is chosen (here we chose the standardized mean catch per area over the entire time series: SSC_j). After subtracting k from each data point, the residuals are added successively to calculate the cumulative sums:

$$CS = \sum_{t=1}^n (x_t - k),$$

where n is the total number of years.

The successive values of CS are plotted versus time (in this study, years) to produce the so-called CUSUM chart. The plot allows one to determine t when the change occurred. The local mean between two change points can be calculated and is equal to the slope of the cumulative sum curve between the two points, plus the reference value k . Changes in the average level of the process are reflected as changes in the slope of the CUSUM plot. For successive values equal to k , the slope will be horizontal, and for successive values lower than k , the slope will be negative and proportional, and *vice versa*.

The year of the change in the slope of the CUSUM is the year that a shift occurs. Change points were visually identified on the CUSUM trajectories, as indicated by abrupt changes (as opposed to a gradual change) in direction of

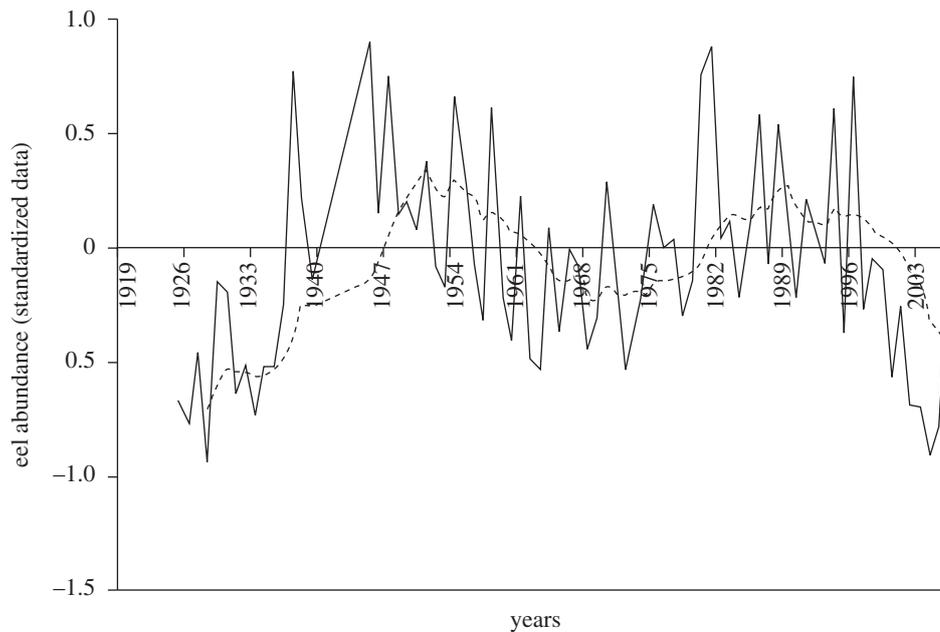


Figure 2. Skagerrak eel standardized mean catch versus time (years). Dotted line is a moving average (period of 10 years).

slope for over a period of 10 years, as this is the scale of events we were looking for.

Pearson's correlations between the time series and environmental factors were calculated on the SSC and on the original environmental time series. Some of the data were autocorrelated and this violates the assumption required for inference tests. One approach is to remove the autocorrelation by detrending the data. However, this will remove much of the covariance [38]. A second approach, suggested by Pyper & Peterman [38], is to modify the hypothesis testing procedure by adjusting the degree of freedom for the sample correlation. The adjusted sample size N^* was calculated following modifications recommended by Pyper & Peterman [38] as

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

where N is the sample size, and $\rho_{xx}(l)$ and $\rho_{yy}(l)$ are the autocorrelations of time series x and y at lag l . Autocorrelations were estimated over the first $N/5$, using the Box Jenkins estimator modified by Chatfield [39], as recommended by Pyper & Peterman [38].

3. RESULTS

(a) Biological data

SSC has fluctuated substantially since 1925. A moving average (period of 10 years) shows what seems to be a cycle, with two seemingly equivalent peaks, one in the 1950s and one in the 1980s (figure 2). The CUSUM function reveals a slightly more complex trajectory with four change points: years 1936, 1958, 1979 and 1996 (figure 3), defining five periods (table 1). The minimum point is in 1936 and the highest in 1996. Each regime lasts for approximately 20 years. The two periods of increasing abundance—1937–1958 and 1980–1996—are very similar: they last for 22 and 16 years, respectively, and have identical slopes and similar means (table 1). A slightly decreasing phase (negative slope of -0.08) of 21 years separates these two periods. The last

period (from 1997 to 2007) is very similar to the first one (table 1).

The CUSUM trajectory of the recruitment data from Den Oever shows two periods of decline (beginning and end of time series) and a long period of increase (figure 3). A short, more or less stable period can be detected between 1965 and 1976, although these years are not true change points as the sign of the slope does not change. The lowest local mean is in 1951 while the highest is in 1980. Correlations between the two time series (Skagerrak standardized catch and Den Oever index) were significant when a lag of 18 years was applied (table 2). Events at Den Oever occurred before events in the Skagerrak.

(b) The North Atlantic oscillation

The CUSUM trajectory of the NAO index shows four major periods: 1919–1950 (relatively high NAO index but stable), 1951–1970 (decreasing), 1971–1995 (increasing) and 1996–2007 (relatively high but stable; figure 4). SSC and NAO index were negatively correlated with a lag of 11 years: a positive NAO index results in a low SSC 11 years later (table 2).

(c) Sargasso sea temperature

Sargasso Sea surface temperature (SSST) CUSUMs show three major periods: a period of stability from the beginning of the time series in 1955 until 1961, a declining trend between 1962 and 1980, and an increasing trend from 1981 to 2007 (figure 4). Significant negative correlations were found between SSC and SSST (between 0 and 300 m) at lag 12 years (table 2). No significant correlations were found with average temperature calculated for either the mixed layer (300–1000 m) or the bottom layer (1000–3900 m).

(d) Currents

Correlations between SSC and winter means (Q1, January–March) from the CR1 (northern North Sea) and CR3 (Skagerrak coast) sections were significant,

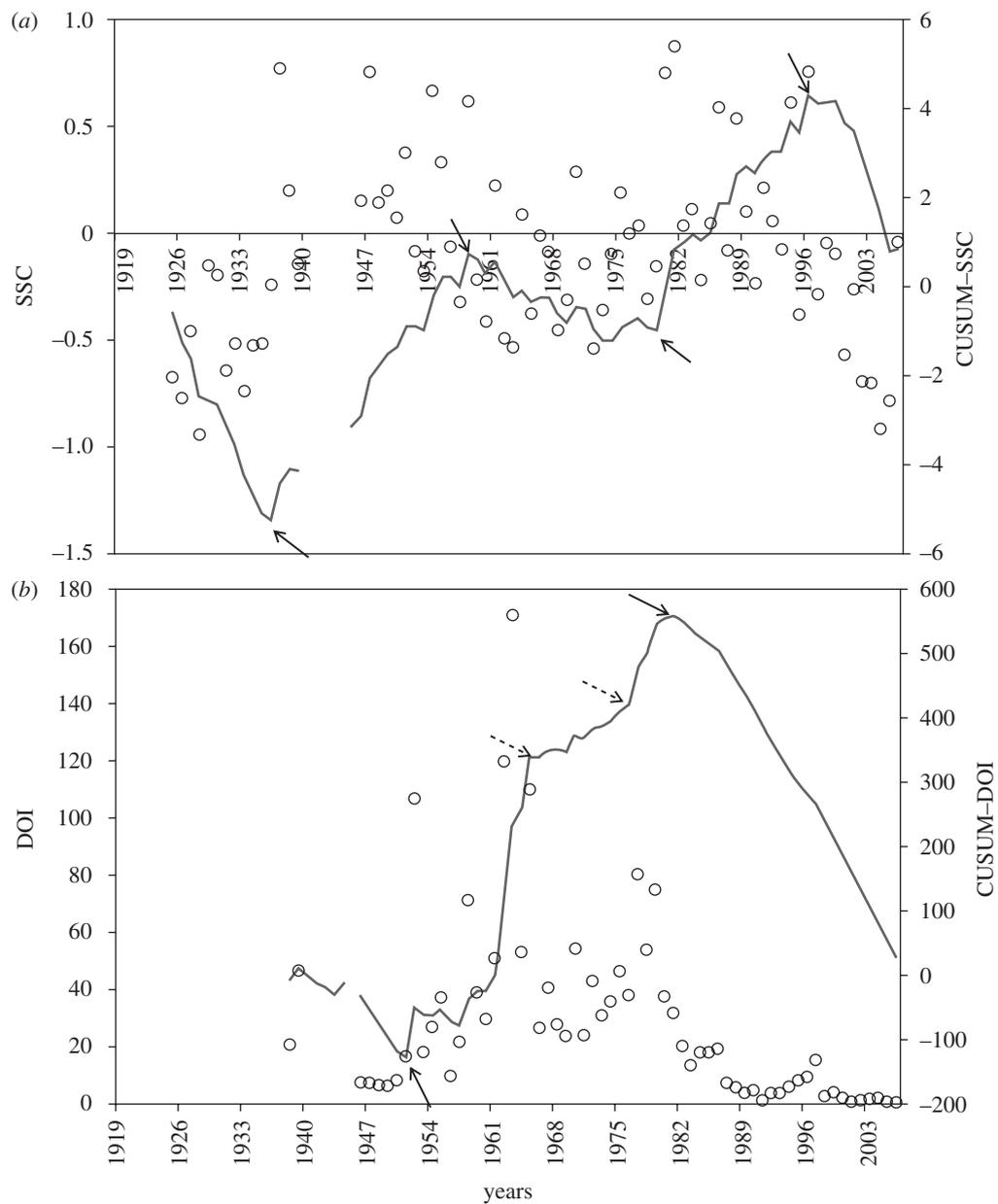


Figure 3. Cumulative sums (CUSUM) trajectories of (a) Skagerrak eel standardized catches (SSC) and (b) Den Oever glass eel index (DOI) versus time (years). The original data are represented by circles. A negative slope indicates a period of below-average anomalies; a positive slope indicates a period of above-average anomalies. Abrupt changes in slope indicate change points; these are marked with solid arrows, pointing downwards for decreases and upward for increases. Dashed arrows do not represent true change points but reveal important changes in the slope of the trend. (a) Open circles, SSC; solid line, CUSUM-SSC. (b) Open circles, DOI; solid line, CUSUM-DOI.

Table 1. Characteristics of change points identified on the Skagerrak eel CUSUM trajectory. Change direction: plus symbol, increases; minus symbol, decreases.

| date of initiation | change point (date of termination) | duration of period (years) | change direction | slope | mean of standardized catch |
|--------------------|------------------------------------|----------------------------|------------------|-------|----------------------------|
| 1925 | 1936 | 12 | - | -0.43 | -0.53 |
| 1937 | 1958 | 22 | + | 0.24 | 0.26 |
| 1959 | 1979 | 21 | - | -0.08 | -0.17 |
| 1980 | 1996 | 16 | + | 0.24 | 0.19 |
| 1997 | (2007) ^a | 12 | - | -0.39 | -0.38 |

^aThis is not a change point but the last point of the series.

when lags of 11 and 9 years, respectively, were applied (table 2). Correlations were positive with inflows into the North Sea (CR1) and negative with the westward

transport along the Skagerrak coast (CR3). In spring (Q2), only the CR1 inflow was significantly correlated with SSC, with a lag of 1 year (table 2). No statistically

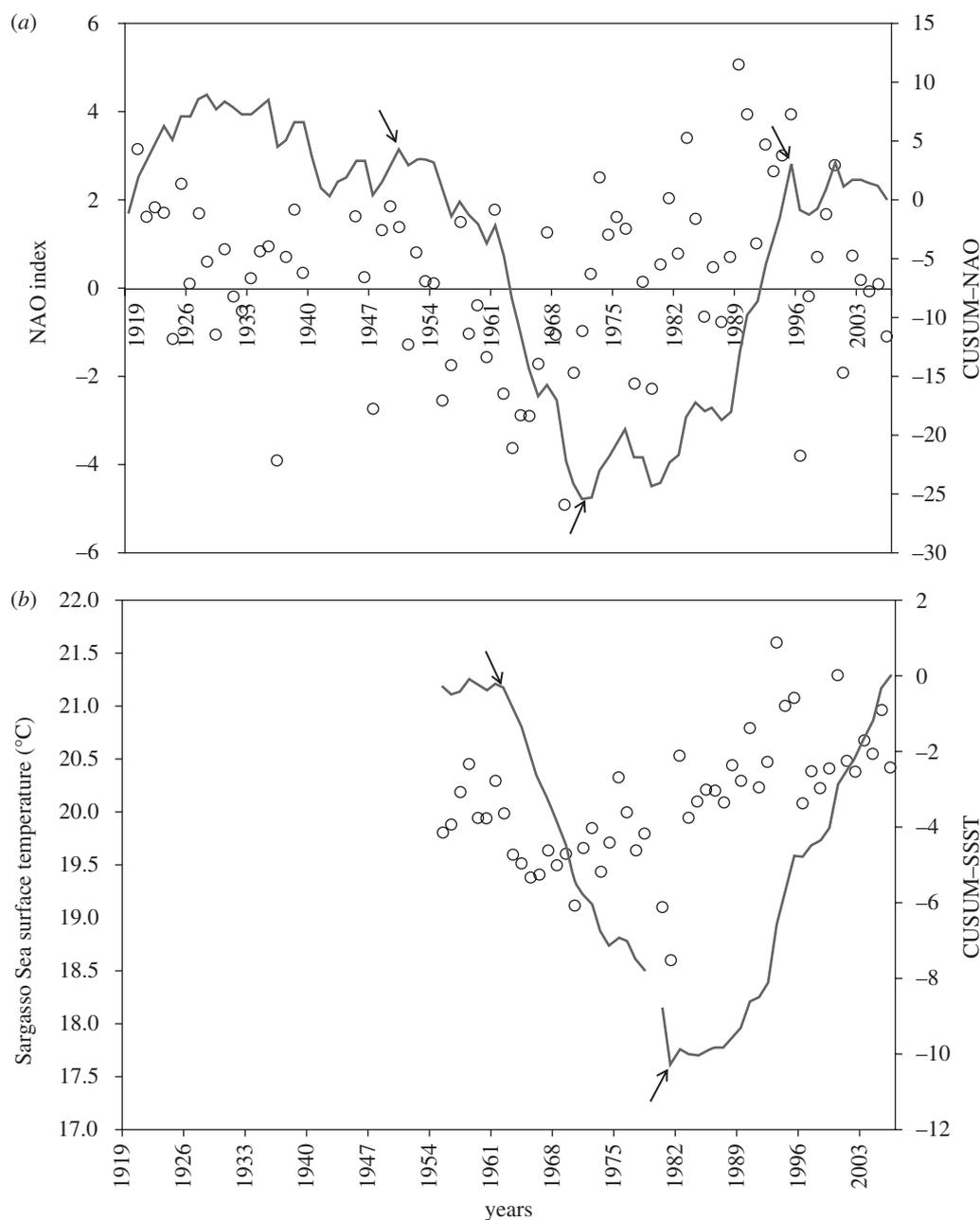


Figure 4. CUSUMs of (a) NAO index and (b) Sargasso Sea surface temperature (SSST) versus time (years). Original data are represented by circles. (a) Open circles, NAO index; solid line, CUSUM-NAO. (b) Open circles, SSST; solid line, CUSUM-SSST.

significant correlations were found with the summer means of flows (Q3). All autumn current values (Q4; table 2) were significantly correlated with SSC. However, signs of correlations were opposite. Thus, reduced inflow through the CR1 and CR2 sections (northern North Sea) and increased westward coastal current along the Skagerrak (CR3) were favourable to SSC, with lags of either 2 or 8 years.

4. DISCUSSION

(a) *Long-term fluctuations of *Anguilla anguilla**

Long-term time series, such as the Skagerrak beach seine data, are extremely valuable to understand the population dynamics and relationship with environmental factors. The beach seine data show that eel abundance in the Skagerrak fluctuates following a cycle. The abundance is currently undergoing a severe decline, but a comparable

decline also occurred at the beginning (as well as a slight decrease in the middle) of the last century.

This cycle is clearly influenced by oceanic factors, as seen through the correlation between SSC, SSST, NAO index and northern North Sea inflow (CR1). Correlations were consistent between all three factors in terms of lags, which were significant when differences of 11–12 years were applied; this suggests that most of the eels caught during the survey are up to 11–12 years old. This is consistent with the 60–70 cm mode of the length distribution measured since 1993 and of previous age estimations from the same area [25,26]. It is also consistent with oceanic factors affecting recruitment at the time of spawning and/or larval migration. Our analysis also confirms the presence of eel larvae in the first 300 m of the water column [28], as only surface temperatures in the Sargasso Sea showed significant correlations with SSC, as opposed to temperatures below the thermocline.

Table 2. Statistics of cross-correlation analyses between the SSC (standardized Skagerrak catch) and statistically significantly related factors (biological and environmental). DOI, Den Oever index (glass eel recruitment in the Netherlands); SSST, Sargasso Sea surface temperature (between 0 and 300 m); currents: CR1, Orkney–Shetland section; CR2, Feie–Shetland western part; CR3, Oksøy–Hanstholm section. Q1–Q4 designate the quarterly periods over which the mean was calculated: Q1, January–March; Q2, April–June; Q3, July–September; Q4, October–December. N , sample size; N^* , corrected sample size based on autocorrelation of the series; lag, number of years that the series was lagged for a significant correlation; r , Pearson's correlation coefficient; p^* , critical value of the correlation coefficient adjusted for N^* for a 5% significance level.

| time series | N | N^* | lag (years) | r (with SSC) | p^* |
|----------------|-----|-----------------|-------------|----------------|-------|
| DOI | 69 | 29 | –18 | 0.33 | 0.31 |
| NAO index | 78 | 44 | –11 | –0.29 | 0.25 |
| SSST (0–300 m) | 51 | 21 | –12 | –0.39 | 0.37 |
| CR1_Q1 | 50 | 28 | –11 | 0.37 | 0.31 |
| CR3_Q1 | 50 | 37 | –9 | –0.31 | 0.27 |
| CR1_Q2 | 50 | 50 ^a | –1 | 0.34 | 0.23 |
| CR1_Q4 | 50 | 50 ^a | –2 | –0.32 | 0.23 |
| CR2_Q4 | 50 | 35 | –8 | –0.39 | 0.28 |
| CR3_Q4 | 50 | 50 ^a | –2 | 0.35 | 0.23 |
| | 50 | 50 ^a | –8 | 0.31 | 0.23 |

^aThere was no significant autocorrelation for these series.

(b) The influence of oceanic factors

High abundance in the Skagerrak was associated with low SSST, low NAO index and increased inflow from northern North Sea (CR1). These three parameters are linked by their physical and chemical properties, and we can only speculate about the causal mechanisms underlying the correlations with eel abundance.

There was a 1-year difference in significant lags between effects of SSST (12 years) and NAO–CR1 (11 years). Thus, SSST affects eels earlier than NAO and CR1, probably at the spawning grounds. Temperature determines the rate at which phytoplankton cells divide, and subsequently affects zooplankton, and thus food for eel larvae. High temperatures at the spawning grounds can also prevent the spring thermocline mixing and hence decrease primary and secondary productions [7,10,11]. The effect of NAO is concurrent with the effect of CR1: it affects larvae during their trans-Atlantic drift and upon their arrival into the North Sea rather than at the spawning grounds. The NAO is a climatic phenomenon in the North Atlantic ocean, which results from the difference in atmospheric pressure at sea level between the Icelandic low and the Azores high [40]. Positive NAO index years are associated with stronger-than-average westerly winds [41]. Strong variations in climate driven by the NAO exert a major impact on the distribution and seasonal development of temperature and nutrients, as well as influencing the time of onset and the rate of the plankton succession [41–43]. High NAO years were associated with lower eel abundance in the Skagerrak. Faster transport within the Gulf Stream (high NAO index) results in a shorter migration and stronger currents towards southern Europe. A shorter

migration time would bring the larvae too early when they reach the upper limit of their distribution area to metamorphose and colonize northern coastal and inland waters. Whether these larvae will be lost or be preferentially distributed towards the southern part of the distribution can be questioned. Thus, positive NAO years may profit southern Europe in terms of recruitment, while negative NAO years would favour the northern part. The NAO shows the same negative correlation with the Den Oever glass eel index [8]. Kettle *et al.* [12] found both negative and positive correlations between NAO and fishery-dependent data about Food and Agricultural Organization (FAO) landings from clusters of European countries. But there was no obvious latitudinal pattern. Also, FAO landings from Norway showed positive correlations with NAO, which is contradictory with our results.

The drift of larvae to the Skagerrak coast depends on changes in ocean circulation [44]. Of all the NORWECOM sections covering the North Sea, only three fluxes showed significant correlations. Results were consistent with an arrival of glass eels during the winter and early spring season (Q1–Q2), which was favoured by increased currents through the Orkney–Shetland section (CR1) versus the Feie–Shetland section (CR2), and reduced westward transport along the Skagerrak coast (CR3). During those conditions, glass eels will tend to settle along the Norwegian Skagerrak coast rather than continuing their journey towards the Swedish Skagerrak coast and the Baltic.

Our data indicate that the arrival of glass eels occurred in January–March; this is consistent with the presence of glass eels in the Skagerrak Kattegat (Sweden) area, caught during the International Bottom Trawl Surveys (IBTS) during the month of February (H. Wickström, Swedish Board of Fisheries, Institute of Freshwater Research, Sweden, 2009, personal communication). Autumn currents showed inverse relationships with SSC compared with the other seasons. A westward transport across the Skagerrak was associated with higher abundance 2 and 8 years later. Lags were shorter than those calculated for the winter means. This may reflect eels migrating out of the Baltic at that time of year [45], which stop along the Skagerrak coast before resuming their migration the following year. Indeed, close to half of the eels sampled presented silver eel characteristics. Silver eels that are interrupted by cold water during autumn migration often postpone the migration for 1 year [46,47]. The lags of 2 to 8 years may indicate that eels actually postpone their migration for much more than 1 year. Eels do show high variability in age and length at migration (reviewed in [48]). This is probably linked to their incredibly long-distance migration and the necessity to build up energy while they are still in coastal areas. Brackish and coastal waters offer high productivity at these latitudes [45] and many maturing eels may delay their migration to increase their fat stores.

(c) Influence of local factors

Other factors influence eel abundance along the Skagerrak coast. Several eel fisheries are located along the coast, most being in the Risør area (figure 1a). Registered fishing gear (since 1971) has increased over the years and peaked in the

1980s, but was not correlated with SSC (analysis not shown). The sea grass coverage (where eels are usually found) has varied within the last century [19,49]. Coverage in the 1930s was very low owing to a disease affecting *Zostera marina*. Influence on eel abundance was probably limited as the number of eels was high during 1937–1958. Since 1945, the bottom flora has increased regularly and was especially high when eel abundance was low in the middle of the century. Finally, movements of eels in and out of freshwater systems may regulate the density in the different compartments [50]; however, the density along the Skagerrak coast has probably never been so high as to induce density-dependent mortality.

All of these factors may have affected the local abundance, but their influence over the years (between recruitment and the time of capture) was not substantial enough to remove the underlying cycle linked to oceanic factors.

(d) *Comparison between time series*

Abundance in the Skagerrak was significantly correlated with the glass eel index from the Netherlands, with a lag of 18 years. When superimposing the two CUSUM trends, one can see similarities (figure 3). In both time series, we identified five major periods. The lag of 18 years is partly explained by the life stage: glass eel for the DOI, and several cohorts (up to 12 years) for the SSC. Although change points are not easily identifiable on the DOI series, they are very clear on the SSC trend (figure 3). In the Skagerrak series, these change points are clearly related to changes in oceanic factors. The effect of oceanic factors is much more visible on the Skagerrak series because of its geographical location, being in first position on the trajectory of larvae migrating from the North Atlantic into the North Sea. Thus, we can assume that the equivalent change points in the DOI are also due to the same regime shifts, but modulated by factors encountered during the remaining transport to The Netherlands. These factors can be linked to local circulation, additional mortality and settlement of eels in saltwater versus entry into freshwater.

5. CONCLUSION

Efficient management of eels and perhaps restoration will only be possible once we understand the relationships between stock fluctuations and climatic regime shifts. The recruitment and stocks of European (and the North American and Japanese) eels are clearly cyclic and affected by oceanic factors (this study; see also [7–11,51]). Thus, eel abundance will depend on climate-driven changes encountered by the larvae at the time of spawning and during their oceanic migration. In this study, we hypothesized that the NAO affects the larvae during their trans-Atlantic migration, possibly through a faster transport in the Gulf Stream, which would affect their distribution along a latitudinal gradient. During high-positive NAO index years, increased currents towards the North Atlantic may send larvae into the sub-polar gyre before they are ready to metamorphose and settle, resulting in low recruitment in Norway for these years. Would this benefit more southern parts of Europe? It does not seem to be the case as subpopulations from all over Europe appear to decline, although there is a

lack of analyses of wide ranges of robust fishery-independent evidence, especially in the Mediterranean/North Africa ([2]; W. Dekker 2010, personal communication). The recent decline of eels in the Skagerrak (1996; this study) was also affected by the documented regime shifts that occurred in the North Sea in 1988–1989 and 1996 [44,52]. Changes in inflow affected several biotic and abiotic variables, among which were landings of several commercial sea fishes, surface temperature and surface oxygen [44]. The cyclic nature of eel recruitment driven by changes in environmental conditions leaves hope for some natural recovery. Recent estimates of larval mortality indicate that eels are extremely well adapted compared with other teleosts [53], and we should hope that with the eel's extraordinary ability to adapt to diverse environments, as well as a wide flexibility in life tactics, recovery of the stock is possible.

Several people have contributed to this manuscript by making data available and by commenting on the manuscript. Our appreciation goes to Tore Johannessen for carrying out the sampling of the Skagerrak data. We thank Rod Johnson for the Sargasso Sea temperature data, as well as comments on preliminary results, and Hein Rune Skjoldal and Morten Skogen for fruitful discussions, very constructive comments on the manuscript and help with the NORWECOM data. Thanks also to Eva Thorstad and Howard Browman for comments on the manuscript. We also acknowledge Willem Dekker for the DOI data and his contribution, which greatly improved this manuscript. C.M.F.D. was supported by the Norwegian Institute of Marine Research (Sensory Biology and Behaviour Project).

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