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Caroline M.F. Durif, Jan Atle Knutsen, Tore Johannessen and Leif Asbjørn
Vøllestad



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Caroline M.F. Durif¹, Jan Atle Knutsen², Tore Johannessen² and Leif Asbjørn Vøllestad³

³¹CEES Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo,
Norway/Institute of Marine Research-Austevoll, 5392 Storebø, Norway

²Institute of Marine Research, Flødevigen, 4817 His, Norway

³CEES Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo



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Analysis of European eel (*Anguilla anguilla*) time series in Norway**Forfatter(e):**Caroline M.F. Durif, Jan Atle Knutsen, Tore Johannessen,
Leif Asbjørn Vøllestad**Sammendrag (norsk):**

Ålen *Anguilla anguilla* er utbredt over hele Europa – og finnes i både ferskvann og sjø. Noen ål lever hele livet i sjøen, mens mange har sitt oppvekstområde i ferskvann – alle søker imidlertid å vandre tilbake til Sargassohavet for å gyte. I de fleste europeiske land er bestanden av ål i sterk tilbakegang – noe som har vært påpekt av ICES Working Group on Eel siden 1998. Alle data som ligger til grunn for disse vurderingen er fra ål som søker å vandre opp i ferskvann. De fleste negative miljøfaktorer som påvirker ål virker sterkere i ferskvann enn i sjø, og de fleste er menneskeskapte (dammer og andre vandringshindre, forurensning, fiske), og det er derfor uklart om den delen av den europeiske ålebestanden som lever sitt liv i sjøen opplever en tilsvarende tilbakegang. Den eneste tidsserien med data for ål i sjøen er den standardiserte strandnotundersøkelsen som er utført langs Skagerakkysten av Havforsknings-instituttet Flødevigen helt siden 1904. Det er også den lengste tidsserien for ål som finnes som er fiskeriavhengig. Her analyserer vi denne serien, samt at vi analyserer en tidsserie for opp- og nedvandrende ål fra Imsa (data samlet av Norsk Institutt for Naturforskning fra 1975). All seriene viser nedadgående trender. Oppgangen av ålefaringer (vandrende åleunger) i Imsa kollapset rundt 1981. Dette sammenfaller med nedgangen i rekrutteringen til ferskvann som har vært observert i andre europeiske land – f. eks. startet nedgangen i rekrutteringen av glassål i Nederland rundt 1982. Nedgangen i produksjonen av utvandrende blankål i Imsa startet ca 7 år etter nedgangen i rekruttering. Denne forsinkelsen sammenfaller med generasjonstiden til ål i dette vassdraget. Antall ål fanget pr trekk med strandnota startet å synke rundt 1997; i 2007 ble det ikke fanget en eneste ål i nottrekkene. Tidsserien fra Skagerrak var signifikant og negativt korrelert med overflatetemperaturen i Sargassohavet med 7-11 års forsinkelse. Dette indikerer at den observerte økningen i overflatetemperaturen i Sargassohavet – ålens gyteområde – påvirker rekrutteringen av ål, trolig gjennom en reduksjon i primærproduksjonen ved økende temperatur.

Summary (English):

The European eel *Anguilla anguilla* is found all over Europe and in extremely diverse habitats both in freshwater and saltwater systems. Its life strategy also varies, from catadromous to a strictly marine life cycle. Eels are undergoing a severe decline in almost every European country, as concluded by the ICES Working Group on Eel since 1998. However all indicators are based on catadromous eels having spent some part of their life cycle in freshwater. Because most of the factors (mostly anthropogenic) would only affect catadromous eels, it can be questioned whether the subpopulation of eels that remain in marine waters are undergoing a similar decline. The Skagerrak beach seine surveys, initiated and carried out by the Institute of Marine Research in Flødevigen since 1904, constitute the only potential data on such eels. It is also the longest fishery independent time series on *Anguilla anguilla*. Here, we

analyzed these data, as well as other time series for recruitment and escapement of eels in freshwater from the river Imsa in Norway (data collected by the Norwegian Institute for Nature Research. Results showed that trends calculated on all the time series have been decreasing. The collapse in elvers (freshwater recruitment) in the river Imsa began in 1981. This is consistent with declines in other European countries: glass eels in the Netherlands began to decline in 1982. Silver eel escapement from the river Imsa also showed a significant decline 7 years after. This delay corresponds to the mean age of silver eels estimated in previous studies. A collapse in eel numbers was also observed in the Skagerrak time series but beginning later, in 1997. No eels were caught in 2007. This data series was also significantly and negatively correlated with surface sea temperatures in the Sargasso Sea when lags of 7 and 11 years were applied. This suggests that a temperature increase at the eel's spawning ground negatively affects the recruitment of larvae, possibly through a reduction in primary production.

Emneord (norsk):

1. ål
2. tidsserier
3. nedgang

Subject heading (English):

1. eel
2. time series
3. decline

Anne Berit Skiftesvik
prosjektleder

Kathrine Michalsen
faggruppelider

Forord

Den europeiske ålen er en felles ressurs som deles av alle land med kyststripe i Europa og Nord-Afrika. Med bakgrunn i ulike tidsserier av overvåkingsdata har det vist seg at rekrutteringen av ålelarver har blitt redusert dramatisk de senere år. Grunnet denne dramatiske nedgangen i populasjonsstørrelse og rekruttering, ble arten i 2006 ført opp på Norsk Rødliste som kritisk truet (CR).

I Norge har vi et delt forvaltningsansvar for ål. Miljøforvaltningen har ansvar for arten mens den oppholder seg i ferskvann, mens det er fiskeriforvaltningen som har ansvaret mens den er i havet.

I Norge har det vært lite tilgjengelig overvåkingsdata for ål. Det finnes imidlertid et unikt historisk materiale i form av to tidsserier som til nå ikke har vært tilstrekkelig analysert. Det ene er en serie som starter i 1918 over fangster i standardisert strandnottrekk langs Skagerrakkysten, samlet inn av Havforskningsinstituttet, Flødevigen. Den andre er en serie fra fiskefella i Imsa, hvor NINA har registrert oppvandrende og nedvandrende ål fra 1975.

Bestanden av europeisk ål er på et kritisk lavt nivå i hele utbredelsesområdet. Direktoratet for naturforvaltning stilte derfor i 2007 midler til disposisjon for Universitetet i Oslo og Havforskningsinstituttet, slik at de kunne sammenstille informasjon om ål i Norge og få gjennomført statistiske analyser av de to tidsseriene som finnes på ål i henholdsvis ferskvann og saltvann.

Vi takker forfatterne, Caroline M.F. Durif, Jan Atle Knutsen, Tore Johannesen og Leif Asbjørn Vøllestad, for det arbeidet de har utført for å tilgjengeliggjøre den informasjonen som presenteres i denne rapporten.

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Yngve Svarte
Direktør, Artsforvaltningsavdelingen
Direktoratet for naturforvaltning

Table of Content

Sammendrag.....	8
Summary	9
1 Introduction.....	11
2 Methods.....	12
2.1 The Skagerrak beach seine survey.....	12
2.2 Other data	12
2.3 Data analysis.....	14
3 Results and discussion	14
3.1 Time series on fresh water eel – Imsa River	14
3.2 Time series from the Skagerrak coast.....	17
4 Conclusion	19
5 Acknowledgements.....	20
6 Literature cited	20

Sammendrag

Ålen *Anguilla anguilla* er utbredt over hele Europa – og finnes i både ferskvann og sjø. Noen åler lever hele livet i sjøen, mens mange har sitt oppvekstområde i ferskvann. Alle søker imidlertid tilbake til Sargassohavet for å gyte.

I de fleste europeiske land er bestanden av ål i sterk tilbakegang, noe som har vært påpekt av ICES Working Group on Eel siden 1998. Alle data som ligger til grunn for disse vurderingene er fra ål som søker å vandre opp i ferskvann. De fleste negative miljøfaktorer som påvirker ål virker sterkere i ferskvann enn i sjø, og de fleste er menneskeskapte (dammer og andre vandringshindre, forurensning, fiske), og det er derfor uklart om den delen av den europeiske ålebestanden som lever sitt liv i sjøen opplever en tilsvarende tilbakegang.

Den eneste tidsserien med data for ål i sjøen er den standardiserte strandnotundersøkelsen som er utført langs Skagerakkysten av Havforskningsinstituttet Flødevigen helt siden 1904. Det er også den lengste tidsserien for ål som finnes som er fiskeriuavhengig. Her analyserer vi denne serien samt en tidsserie for opp- og nedvandrende ål fra Imsa (data samlet av Norsk Institutt for Naturforskning fra 1975).

All seriene viser nedadgående trender. Oppgangen av ålefaringer (vandrende åleunger) i Imsa kollapset rundt 1981. Dette sammenfaller med nedgangen i rekrutteringen til ferskvann som har vært observert i andre europeiske land, for eksempel startet nedgangen i rekruttering av glassål i Nederland rundt 1982. Nedgangen i produksjon av utvandrende blankål i Imsa startet ca. 7 år etter nedgangen i rekruttering. Denne forsinkelsen sammenfaller med generasjonstiden til ål i dette vassdraget. Antall ål fanget per strandnottrekk startet å synke rundt 1997, og i 2007 ble det ikke fanget en eneste ål i nottrekkene.

Tidsserien fra Skagerrak var signifikant og negativt korrelert med overflatetemperaturen i Sargassohavet med 7-11 års forsinkelse. Dette indikerer at den observerte økningen i overflatetemperaturen i Sargassohavet, ålens gyteområde, påvirker rekrutteringen av ål, trolig gjennom en reduksjon i primærproduksjonen ved økende temperatur.

Summary

The European eel *Anguilla anguilla* is found all over Europe and in extremely diverse habitats both in freshwater and saltwater systems. Its life strategy also varies, from catadromous to a strictly marine life cycle.

Eels are undergoing a severe decline in almost every European country, as concluded by the ICES Working Group on Eel since 1998. However, all indicators are based on catadromous eels having spent some part of their life cycle in freshwater. Because most of the factors (mostly anthropogenic) would only affect catadromous eels, it can be questioned whether the subpopulation of eels that remain in marine waters are undergoing a similar decline.

The Skagerrak beach seine surveys, initiated and carried out by the Institute of Marine Research in Flødevigen since 1904, constitute the only potential data on such eels. It is also the longest fishery independent time series on *Anguilla anguilla*.

Here, we have analyzed these data, as well as other time series for recruitment and escapement of eels in freshwater from the river Imsa in Norway (data collected by the Norwegian Institute for Nature Research.) The results showed that trends calculated on all the time series have been decreasing. The collapse in elvers (freshwater recruitment) in the river Imsa began in 1981. This is consistent with declines in other European countries: glass eels in the Netherlands began to decline in 1982. Silver eel escapement from the river Imsa also showed a significant decline 7 years after. This delay corresponds with the mean age of silver eels estimated in previous studies.

A collapse in eel numbers was also observed in the Skagerrak time series, but beginning later, in 1997. No eels were caught in 2007. This data series was also significantly and negatively correlated with surface sea temperatures in the Sargasso Sea when lags of 7 and 11 years were applied. This suggests that a temperature increase at the eel's spawning ground negatively affects the recruitment of larvae, possibly through a reduction in primary production.

1 Introduction

The life cycle of eels (*Anguilla* sp.) has long been a mystery. Still today part of it remains unknown. From the 1920s and until the 1940s, intensive research was carried out by J. Schmidt to discover the European and North American eels' spawning grounds. The Danish oceanographer found a gradient in the size distribution of leptocephalus larvae in the Atlantic Ocean. From this, he inferred the spawning grounds to be located in the Sargasso Sea area (Schmidt 1922). Leptocephalus larvae are then transported by the Gulf Stream and distributed along the European coast after they metamorphose into glass eels. These colonize brackish and freshwater inland habitats from Iceland and the North Cape in Norway, along the Mediterranean coast, down to north-west Africa. The growth phase lasts an extremely variable amount of time. Morphological and physiological changes that mark the onset of sexual maturation or silvering occur over the summer (Durif et al. 2005, van Ginneken et al. 2007). Typically, eels will start the silver phase between 6-10 years (Tesch 2003), but this can vary, and it is common to find silver eels of 15-20 years. Silver eels migrate downstream during late summer and early fall under the influence of certain environmental factors generally associated with flood conditions (Durif et al. 2003, Vøllestad et al. 1994). They have never been successfully tracked during their spawning migration across the Atlantic Ocean, but they are believed to undergo sexual maturation while they swim approximately 6000 km to the Sargasso Sea. Artificially induced sexual maturation takes a minimum of 18 weeks (Durif et al. 2006), and this may be the duration of migration. Eels probably die after spawning in the spring season.

It is only fairly recently that eels have been redefined as a facultative catadromous species, meaning they do not necessitate a freshwater phase. Some glass eels remain in the marine habitat, where they spend their whole life cycle. In 1998, when the use of microchemistry developed to trace the life history of fish, analyses of otoliths of European (*A. anguilla*) and Japanese (*A. japonica*) eels revealed that some eels never migrated into freshwater (Tsukamoto et al. 1998). Before this, yellow eels found at sea were believed to have been either washed by floods from the rivers or in the process of 'silvering' (*i.e.* maturing) and migrating back to their spawning grounds. Since the work of Tsukamoto et al. (1998), other analyses have been carried out and have shown that eels may present complex life patterns with semi-catadromous behaviors: riverine, estuarine, or strictly marine as well as 'nomadic' behaviors, where eels move from one compartment to another once or more during their growth phase (Daverat et al. 2006, Lamson et al. 2006). Marine residents constituted 85% of the individuals (*A. rostrata*) sampled in saltwater bays in Canada (Lamson et al. 2006). Tsukamoto et al. (1998) mention that 80% of the commercial catch of eels in the North Sea are yellow immature eels with almost certain marine residency. Therefore, marine eels probably contribute significantly to the gene pool as eels constitute a single randomly mating population.

Since the 1980s, a steady decline has been observed in the recruitment of glass eels (ICES 2002, Moriarty and Dekker 1997). In 2006, *Anguilla anguilla* was listed on the Norwegian Red List of species as Critically Endangered. In 2007, information on freshwater recruitment, freshwater stock and fisheries, reviewed by the ICES Working Group on Eel (ICES 2007), confirmed that the stock is outside safe biological limits. However, all indicators are based on data from freshwater: monitoring or commercial catch of glass eel entering freshwater or of silver eel escapement. Many factors suspected in the cause of the decline are only present in freshwater habitats: overfishing (almost entirely practiced on freshwater eels), limited access to upper reaches of the watershed due to dams, entrainment in turbines of hydroelectric power plants, river pollution (PCB's and flame retardants), swim bladder parasite found in

freshwater. Therefore, it is questioned whether the population decline is as steep in marine eels.

The Skagerrak beach seine surveys data from Norway constitute the longest non-fishery dependent set of data. It is also the only potential time series on the subpopulation of marine eels. This unique monitoring program was initiated at the Norwegian Skagerrak coast as a result of a controversy between the founder of the Flødevigen Marine Research Station Gunder Mathiesen Dannevig (1841-1911) and the great pioneer in marine research Johan Hjort (1869-1948) (Solemdal 1997). Every year a series of beach-seine hauls are carried out in some selected fjords of the Norwegian Skagerrak coast. Here we analyze for the first time the time series concerning eels.

The only available time series for eel abundance in freshwater in Norway is the one maintained by the Norwegian Institute for Nature Research at Ims. The observations of upstream migrating elvers and downstream migrating silver eels are regularly reported to the ICES working group on eel (usually meeting every second year). This time series was formally analyzed by Hvidsten (1985a) and by Vøllestad and Jonsson (1988). The later part of the time series has not been analyzed in detail. Further, during the 1980's detailed data on the population dynamic were collected and analyzed (Vøllestad 1990, Vøllestad and Jonsson 1986, 1988). However, Vøllestad did sample more population dynamic data that has not been analyzed in detail – these data include information about age, sex and size of sub-samples of downstream migrating silver eels for a number of years. The downstream migration of the silver eels in Imsa has also been studied in detail (Haraldstad et al. 1985, Hvidsten 1985b, Vøllestad et al. 1986, 1994). In this report, we analyze the complete time series, and include the information contained in the previously unpublished data, to evaluate the recent trends. Information on the methods that are used can be found in the published papers.

2 Methods

2.1 The Skagerrak beach seine survey

The first hauls of the Skagerrak monitoring program were conducted in 1904, and during the following years, new sampling stations were added, and a standard routine for the hauls was developed. Approximately 80 stations are sampled in 20 different areas (Figure 1, Table 1). All hauls are taken at the same season (autumn) and always during daytime. Based on the initial results from these hauls, the monitoring program was established and reached its present form in 1919 (Dahl and Dannevig 1906, Fromentin et al. 1998, Johannessen and Sollie 1994, Solemdal et al. 1984).

2.2 Other data

Eel time series were correlated with two series of environmental data: sea surface temperatures in the Sargasso Sea and the NAO index. Sargasso Sea temperatures were obtained from the Bermuda Atlantic Time Series study and with the help of Dr Rod Johnson (BATS: <http://bats.bios.edu/>). Sea surface temperatures were averaged from per year and over the first 400 m, which corresponded to the mixed layer according to temperature depth profiles. NAO Index Data were provided by the Climate Analysis Section, NCAR, Boulder, USA (Hurrell 1995).

We also analyzed a recruitment time series of glass eels at Den Oever in the Netherlands for comparison. The data were obtained by courtesy of Dr Willem Dekker (Dekker 1998).

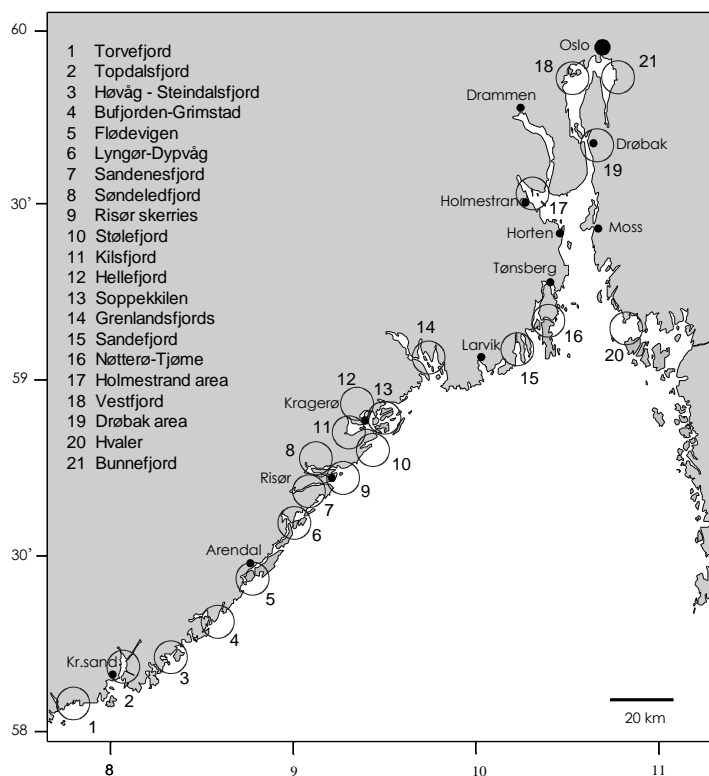


Figure 1. Sampling areas of the Skagerrak beach seine survey.

Table 1. Sampling areas*, sampling periods and number of stations taken during different time spans.

Area no	Area name	Sampling started	Number of stations				Total no of stations	Present no of stations
			>70 yrs	50-69 yrs	30-49 yrs	<30 yrs		
1	Torvefjord	1919 -	2			3	5	5
2	Topdalsfjord	1920 -	3		5	11	19	8
3	Høvåg - Steindalsfjord	1919 -	7	2	6	9	24	9
4	Bufjorden - Grimstad	1919 -	2			3	5	5
5	Flødevigen	1919 -	2	1	1	8	12	2
6	Lyngør - Dybvåg	1962 -			4	4	8	5
7	Sandnesfjord, Risør	1919 -	7		1	1	9	8
8	Sønedeledfjord, Risør	1919 -	5		9	11	25	8
9	Risør skerries	1919 -	2			5	7	4
10	Stølefjord, Kragerø	1919 -	2		1	2	5	2
11	Kilsfjord, Kragerø	1919 -	3		2	2	7	4
12	Hellefjord, Kragerø	1919 -		1	3	5	9	3
13	Soppekilen, Kragerø	1919 -	2	2	1	1	6	3
14	Grenlandsfjords	1953 -			9	11	20	10
15	Sandefjord	1962 -			5	8	13	6
16	Nøtterø - Tjøme	1936 -		5	2	4	11	7
17	Holmestrand area	1936 -		6	2	4	12	7
18	Vestfjord, Inner Oslofjord	1936 -		6	3	14	23	11
19	Drøbakk area	1936 -		4	1	5	10	5
20	Hvaler	1936 -		6	2	7	15	8

*Only areas with a reasonable number of stations and years are included.

2.3 Data analysis

The Skagerrak sampling areas representing at least 4% of the total catch (Figure 2) were analyzed. Data were standardized according to:

$$X_{i,j} = \frac{x_{i,j} - \mu_j}{\sigma_j} \text{ where } i \text{ is the year and } j \text{ is the area.}$$

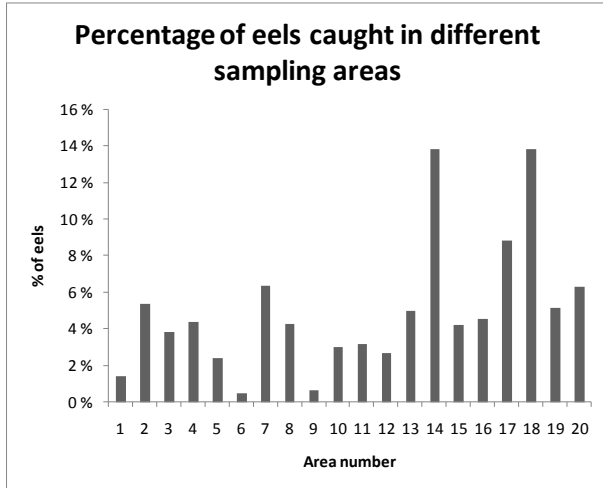


Figure 2. Percentage of eels caught in the different sampling areas of the Skagerrak beach seine survey between 1925 and 2007.

Trends were calculated using the cumulated function - CUSUM (Ibanez et al. 1993). 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 mean per area of the series). After subtracting k from each data point, the residuals are added successively:

$$S_p = \sum_{i=1}^p x_i - pk$$

For successive values equal to k , the curve will be horizontal, and for successive values lower than k , the slope will be negative, and vice versa. The plot allows one to determine exactly the 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 .

Pearson's correlations between the time series and environmental factors were calculated on the original series.

3 Results and discussion

3.1 Time series on fresh water eel – Imsa River

The ascent of elvers has decreased strongly the last years (Figure 3), and on the log scale the trend is clearly linear. Before 1995, the number of elvers entering the elver trap in Imsa has varied between 5 000 and 50 000, with large annual variation. In the last 10 years the number of ascending elvers has been extremely low, and decreasing. Earlier analyses of the data, the first 10–15 years of the time series, did indicate a relationship between temperature and number of ascending elvers (Hvidsten 1985a, Vøllestad and Jonsson 1988). The suggestion was that more elvers ascended fresh water when water temperature during summer was high.

Most elvers ascend Imsa during June – July. To test if the temperature hypothesis could also help explain the long-term trends, we collected data on mean June – July air temperatures from the Meteorological Institute (measured at Sola). Overall mean summer temperature has varied strongly among the years (Figure 4), but there was no relationship between the number of ascending elvers (ln-transformed) and temperature ($r = 0.007$, $P > 0.9$). On the log-scale, 63% of the variation in elver number could be explained by time. Even after removing the temporal trend (de-trending), there was no additional effect of temperature on number of ascending elvers (multiple regression, $P > 0.1$). The complete collapse in eel recruitment in the Imsa thus is very similar to what is happening all over Europe (ICES 2007).

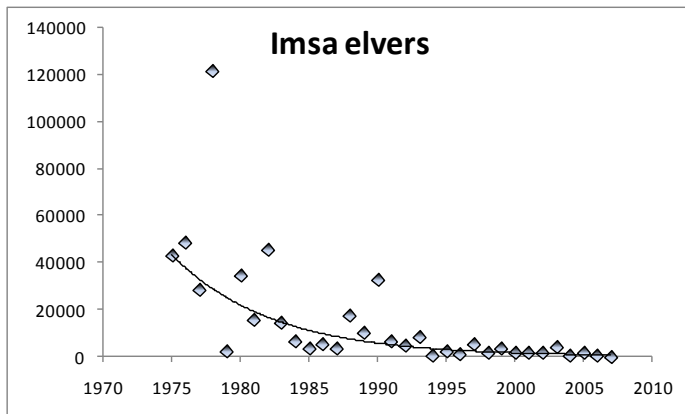


Figure 3. Number of elvers ascending the river Imsa (exponential fit).

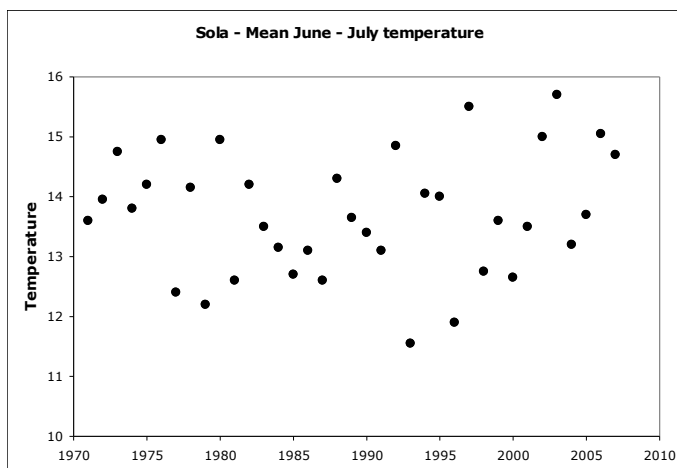


Figure 4. Sola mean June-July temperature (data from the Norwegian Meteorological Institute).

The silver eels are intercepted at downstream migration during autumn. The numbers were high during the early part of the time series, before a reduction starting in the mid 1980's (Figure 5). What is striking, however, is that the silver eel numbers have remained relatively stable (but low) in spite of the recent strong reduction in recruitment. A simple model with log-transformed numbers of silver eels as response and time as predictor, can explain 34.9% of the variation ($P < 0.001$). However, there is large year-to-year variability, a lot of which can be explained by variation in year-class strength (Vøllestad and Jonsson 1988). The recruitment of some year classes was very weak originally (i.e. the 1979 year class and all year classes since 1994), whereas other year classes are very strong (i.e. 1976 and 1983). To add complexity, the 1985 year-class was used in a growth experiment at the research station, and very few elvers were allowed to migrate upstream. In total this should lead to large variability in silver eel production.

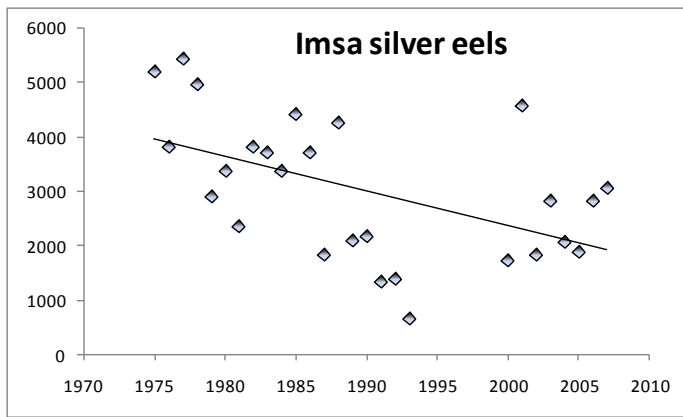


Figure 5. Number of silver eels descending the river Imsa.

In the last ten years, recruitment has been on the same scale as the total annual silver eel production. The time lag between recruitment failure and production collapse may be due to three different factors:

1. Each year, a number of older eels migrate upstream and are not measured as elvers. These eels are 1- 4 years old (Vøllestad and Jonsson 1988). This means that recruitment is somewhat higher than estimated by the elver numbers. However, over the years, the number of older migrants have been less than 1000 in number, thus the influence on population dynamics will be of minor importance.
2. The mean age of downstream migrating silver eel has previously been estimated at about 7-8 years (Vøllestad and Jonsson 1986, 1988). Based on the more extensive sample available and analyzed now, it is evident that this has been stable throughout the period of sampling (1982-1992) (Figure 6). This time lag between recruitment and subsequent migration, will lead to a slow response to recruitment failure, with a response starting to appear 7-8 years after the reduction in the recruitment failure. Since recruitment failure was evident around 1990, a strong reduction in silver eel production should have been evident now. However, population dynamic processes may mask the effect of recruitment failure for some time.

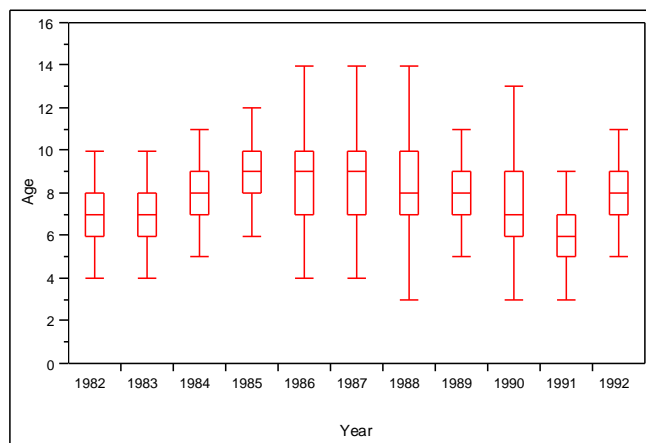


Figure 6. Age structure of eels in the river Imsa. The box plot shows median, 25th and 75th quantile, and the 5th and 95th quantile.

3. In Imsa, strong density dependent mortality has been documented – especially for the stronger year classes (Vøllestad and Jonsson 1988). Such strong density dependent mortality in river-living eel has recently been documented clearly (Lobon-Cervia and Iglesias 2008). To what degree density influences growth is unknown. However, in general, density-dependence will regulate population size, and damp variation at older ages.

Taken together, these three factors may have masked the recruitment failure. But with the recent extremely low recruitment, even very strong density dependent compensatory mechanisms cannot help, and an immediate crash in silver eel numbers is to be expected.

3.2 Time series from the Skagerrak coast

Eel catch during the Skagerrak survey has fluctuated substantially since 1925, but with a substantial decline in catch the last 10 years. The peaks and troughs on the CUSUM trend calculated on the standardized catch, indicate the time of major changes in the local mean (Figure 7). Eel catch was initially low (from 1925 to 1936), after which it increased to reach its highest level in 1996. The period between 1959 and 1979 was relatively stable (Table 2). The collapse in eel catch began in 1997, and last year's catch (in 2007) was null.

Table 2. Periods defined by the CUSUM trend of standardized catch of eel in the Skagerrak beach seine survey.

Period	Local mean (standardized catch)
1925-1936	-0.26
1937-1958	0.29
1959-1979	0.04
1980-1996	0.27
1997-2007	-0.17

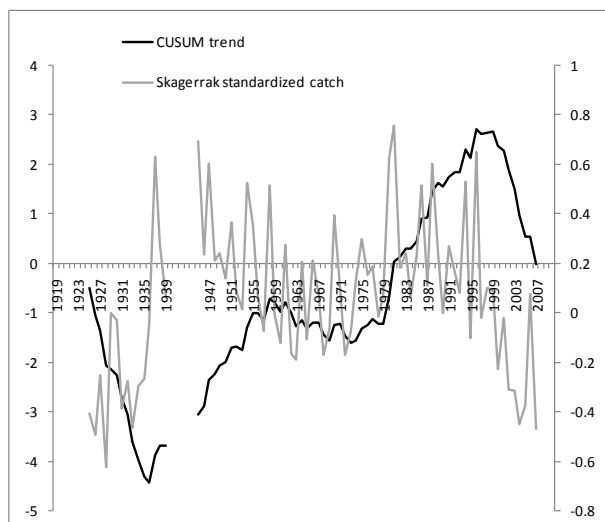


Figure 7. Time series from the Skagerrak coast. CUSUM were calculated on the standardized catch.

The time series from Imsa (freshwater recruitment and escapement) correlated with the Skagerrak data. Significant correlations between the elver and the Skagerrak series were found when lags of either, 0, 1 or 3-6 years were applied (respectively $r = 0.41$; 0.36 ; 0.47 ; 0.40 ; 0.43 and 0.48 ; $P < 0.01$). Significant correlations were also found with the silver eel series at lags 5-6 and 8-11 years (respectively $r = 0.41$; 0.46 ; 0.57 ; 0.45 ; 0.51 and 0.59 , $P < 0.01$). Years when the decline began, can be obtained from the CUSUM trends. Decline in elvers and silver eels on the Imsa began respectively in 1982 and 1988 (Figure 8 and 9). This is consistent with the age structure of silver eels from this river, which are approximately 6-8 years old (Figure 6). The decline in the Skagerrak is first observed in 1997 (Figure 7), 9-15 years later. The fact that the series correlate at several lags is due to the fact that eels from the Skagerrak represent several cohorts (possibly from early yellow stage to silver stage). This is also seen through the body length distribution measured since 1993 (Figure 10). Because the Imsa series are much shorter (only since 1975) than the Skagerrak series, it is improbable that correlations with greater lags would be significant because of too few overlapping data points.

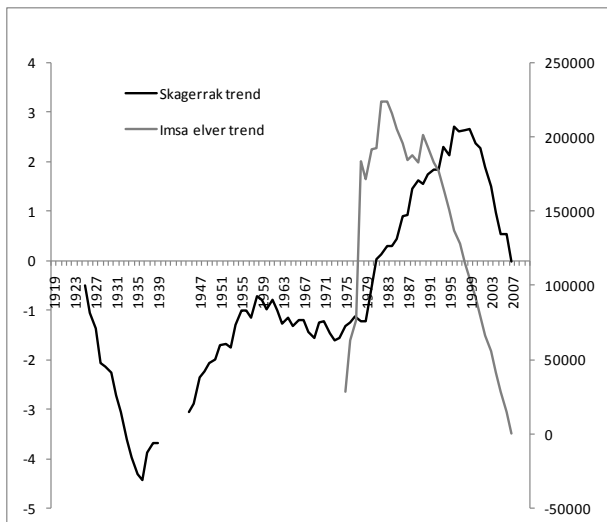


Figure 8. CUSUM trends of the Skagerrak time series and elver monitoring on Imsa.

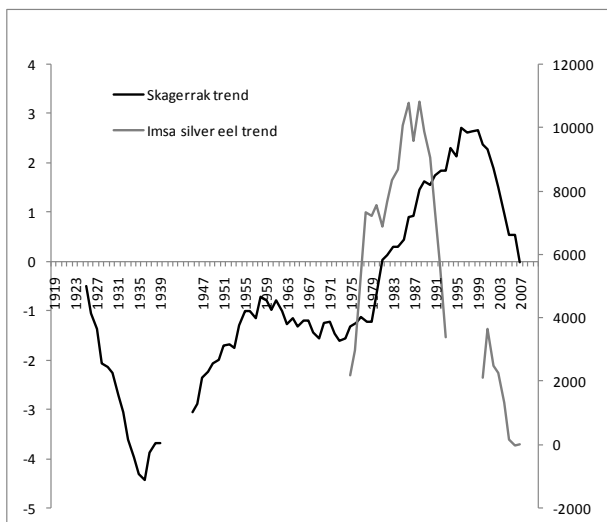


Figure 9. CUSUM trends of the Skagerrak time series and silver eel monitoring on Imsa.

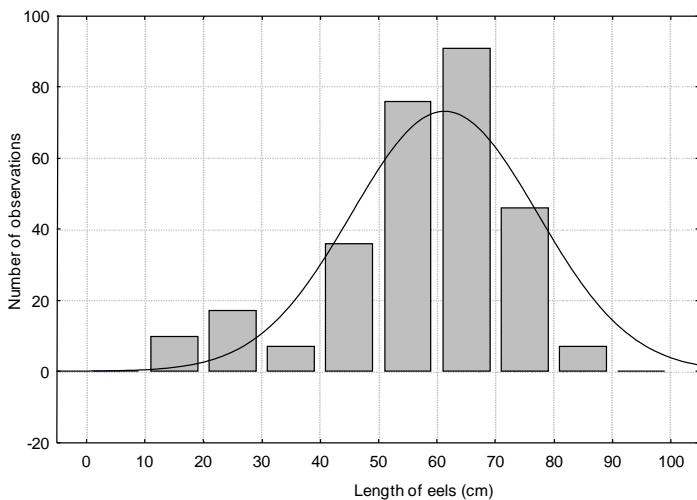


Figure 10. Size distribution of eels measured since 1993 during the Skagerrak beach seine survey.

In order to compare with another longer time series from Europe, a trend was calculated on the recruitment time series (glass eels) at Den Oever, in the Netherlands (Figure 11). A very similar trend was obtained showing an initial low abundance, a period of increase with some period of stabilization, another period of increase, and a complete collapse starting in 1981. A

significant correlation between the two original series was obtained when lags of either 17 or 18 years were applied (respectively $r = 0.28$; $r = 0.34$; $P < 0.01$).

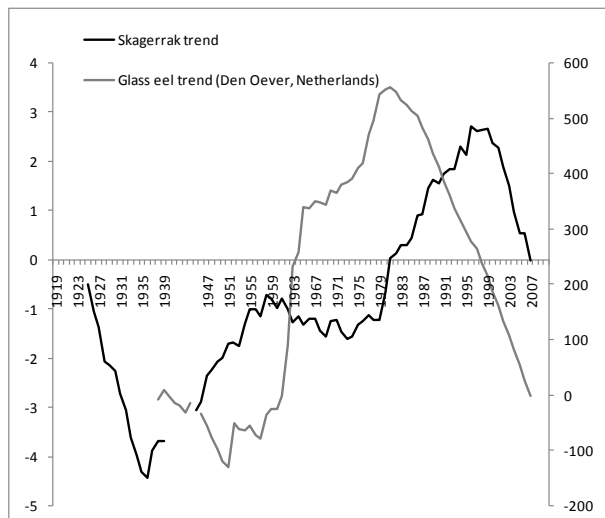


Figure 11. CUSUM trends of the Skagerrak time series and of the Den Oever Index indicator for glass eel recruitment in the Netherlands.

No significant correlations were found between the Skagerrak series and NAO. However, correlations with sea surface temperatures measured in the Sargasso Sea were significant (Figure 12). Standardized eel catch was negatively correlated with temperatures when lags of 7 or 11 years were applied (respectively $r = -0.30$ and -0.32 ; $P < 0.01$). This indicates that eels caught during the Skagerrak survey are probably between 7 and 11 years old. This fits well with the age distribution of yellow eels caught with fyke nets in the Drøbak area of the Oslo fjord (Vøllestad 1985, 1986).

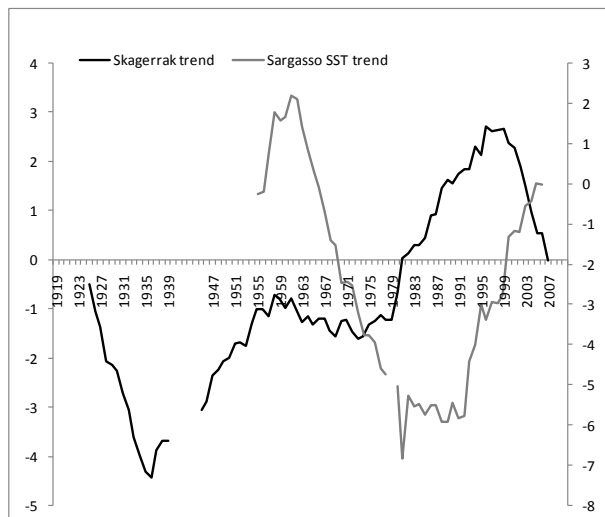


Figure 12. CUSUM trends of the Skagerrak time series and Sargasso Sea surface temperature.

4 Conclusion

Overall, the analyses show a severe decline in European eels (*Anguilla anguilla*) in Norway, both in fresh- and marine water subpopulations. Significant correlations were found between the different time series when lags were introduced. The Skagerrak time series was significantly correlated with temperatures at their spawning grounds (10% of the variance explained by Sargasso Sea temperature). Thus part of the decline can be explained by global temperature changes. An increase in sea surface temperature would result in a reduced mixing

layer and a subsequent decrease in primary and secondary production and less food for the larvae (see also Bonhommeau et al. 2008). Correlations were significant when lags of 7 or 11 years were applied, and thus eels from the Skagerrak can be estimated to be 7 to 11 years old. The decline in the Skagerrak eels occurred later by about 10 years, than the decline of “freshwater” (i.e. catadromous) eels, as seen by comparing with the Imsa (Norway) and Den Oever (Netherlands) series. It may be that this subpopulation of eels has been less affected than catadromous eels, possibly because of the reduced anthropogenic impact and mortality in the marine environment compared to river systems (pollution, habitat loss and turbine entrainment). The absence of certain parasites and pathogens in seawater, such as the swimbladder parasite *Anguillicola crassus*, may also have contributed to delaying the collapse. Nevertheless, we show here that some of the causes of the decline in the eel population also lie in temperature changes at their spawning grounds. Further decreases are to be expected with global warming, reducing possibilities of restoring the eel stock.

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Retur: Havforskningsinstituttet, Postboks 1870 Nordnes, NO-5817 Bergen



HAVFORSKNINGSINSTITUTTET

Institute of Marine Research

Nordnesgaten 50 - Postboks 1870 Nordnes
NO-5817 Bergen
Tel.: 55 23 85 00 – Faks: 55 23 85 31

HAVFORSKNINGSINSTITUTTET

AVDELING TROMSØ

Sykehusveien 23, Postboks 6404
NO-9294 Tromsø
Tlf.: 77 60 97 00 – Faks: 77 60 97 01

HAVFORSKNINGSINSTITUTTET

FORSKNINGSSTASJONEN FLØDEVIGEN

Nye Flødevigveien 20
NO-4817 His
Tlf.: 55 23 85 00 – Faks: 37 05 90 01

HAVFORSKNINGSINSTITUTTET

FORSKNINGSSTASJONEN AUSTEVOLL

NO-5392 Storebø
Tlf.: 55 23 85 00 – Faks: 56 18 22 22

**HAVFORSKNINGSINSTITUTTET,
FORSKNINGSSTASJONEN MATRE**

NO-5984 Matredal
Tlf.: 55 23 85 00 – Faks: 56 36 75 85

**SAMFUNNSKONTAKT OG KOMMUNIKASJON
PUBLIC RELATIONS AND COMMUNICATIONS**

Tlf.: 55 23 85 00 – Faks: 55 23 85 55
E-post: informasjonen@imr.no

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