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Escapement of eel (*Anguilla anguilla*) in coastal areas in Sweden over a 50-year period

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The escapement of eel from coastal areas in Sweden during the last 50 years was assessed using data from voluntary fishery journals and fishery-independent coastal fish monitoring programmes. It was evident that the level of escapement, determined as catch per unit of effort in numbers, from the Baltic Sea decreased over time, with the most rapid decline occurring in the 1960s and early 1970s, but also in recent years. There were, however, differences in the temporal variability in escapement between areas. Escapement from the northernmost studied site did not change significantly during the last 50 years, while there was a rapid decline in the southern areas. Escapement remained relatively stable between the late 1970s and 2000 however, and escapement at the Swedish west coast, inferred from yellow eel catch per unit of effort, generally increased during the same time. The loss in numbers has to some extent been compensated by an increase in mean weight of silver eel. Possible explanations for the retained level of escapement during the last decades despite the continued reduction in recruitment are discussed. Favourable environmental conditions in combination with a lower fishing effort are suggested as the most probable reasons why the escapement decline has not been more dramatic, but stocking and density-dependent effects cannot be ruled out.

Keywords: *Anguilla anguilla*, Baltic Sea, eel, escapement.

Introduction

The global stock size of European eel, *Anguilla anguilla*, is at an all time low. The stock continues to decline and is considered to be outside safe biological limits (EIFAC/ICES, 2010). The species is listed as critically endangered by the IUCN, as a result of the drastic decline in recruitment (Freyhof and Kottelat, 2008). Eel is a catadromic species, spawning in the Sargasso Sea, and the young larvae travel back and transform into unpigmented glass eels when they reach the European continental shelf (Dekker, 2008). Following immigration into coastal waters and rivers and lakes, a prolonged yellow eel stage begins which can last for some 20 years (Dekker, 2008). Upon reaching sexual maturation, the eel transforms to the silver eel stage and starts migrating back from inland and coastal waters towards the Sargasso Sea (Dekker, 2008). Recruitment of glass eels has decreased since the early 1980s, and since 2000 is estimated at just 1–7 % of the pre-1980 levels, and the decline has been especially severe in the North Sea (EIFAC/ICES, 2010). In addition, internationally compiled data show that European yellow eel recruitment, as shown by monitoring of upstream migration in rivers, is currently only 9% of the mean recruitment in 1960–1979 (EIFAC/ICES, 2010). The reasons for the declining recruitment rates are still unclear (Dekker, 2008). Hypotheses include overfishing, an introduced swimbladder parasite (nematode *Anguillicoloides crassus*), blocking of migration routes with dam constructions for hydropower and oceanic factors (Dekker, 2008). Knights (2003) suggests climate effects on larval survival as an additional cause.

Eel has been one of the main target species in the Baltic fishery for centuries. In the 1930s eel was the economically most important fish species in the southern part of Sweden (SCB, 1987). Total fishing effort (measured as the number of gillnets, poundnets, and fykenets) in southern coastal areas in the Baltic Sea and the Sound (ICES Subdivisions 23–25) increased from 1914 to the middle of the 20th century. Eel was one of the main target species in this fishery, and Swedish landings of eels increased to exceed 2000 t in 1950 (SCB, 1987; EIFAC/ICES, 2010). Both effort and landings have decreased since then. Despite this, eel is still a significant target species in the Swedish coastal fishery. In the years 1999–2009, the Swedish commercial coastal eel fishery reported on average 514 t in annual catches (EIFAC/ICES, 2010).

EC regulation (No 1100/2007) required member states to formulate Management Plans for the recovery of the European eel in all habitats by 2008. The objective was to reduce human-caused mortalities, so that the probability of escapement in biomass of silver eel to the sea is at least 40% of the estimated escapement without anthropogenic impacts. Based on this regulation, Sweden presented an eel management plan in 2008, including measures to reduce fishing effort, improve the possibility for downstream migration, increase the stocking of glass eel, and increase the control of the fishery (summarized in EIFAC/ICES, 2009). In order to set appropriate target biomasses and to evaluate the compliance of management actions taken, information on the present and historic (without human impact) levels of escapement is essential.

One of the many problems identified in the management of the European eel stock is the lack of sufficient good quality data. Statistics of landings of yellow and silver eel are notoriously incomplete (EIFAC/ICES, 2010). In addition, time series of yellow eel abundance spanning more than a decade are rare, and the monitoring results are often unpublished (Dekker, 2008). Official fishery data in Sweden are mainly based on fishers reporting catch and effort on a monthly basis. This reporting was not mandatory before 1999 however, and fishing for eel in private waters has only been officially reported since 2005. To describe the temporal change in the escapement of eel in Swedish coastal waters, it is therefore necessary to complement official data with other sources of information. The aim of this study was to utilize two such additional data sources, voluntary fishery journals and fishery-independent coastal fish monitoring, to describe the temporal development in the escapement of eel from the early 1960s to recent years, and also to compare temporal patterns in escapement between areas. Factors possibly influencing temporal variability in escapement are also discussed.

Methods

Background

The Swedish eel fishery is overall a small-scale local enterprise, often combined with fishing for other species or as a complement to a business outside fishing. In the Baltic Sea, the fishery for eel is dominated by poundnets, specially designed for catching migrating silver eel (hereafter called eel poundnets; Bringéus, 1985). Fishing is mainly concentrated in the southern Baltic Proper, ICES Subdivisions 25 and 27 (Figure 1). In Kattegat and Skagerrak (ICES Subdivisions 20 and 21), the fishery is instead dominated by fykenet fishery for yellow eel. The Sound area, ICES Subdivision 23 (Figure 1), is the last part of the eel migration route, before they reach the open sea of the Kattegat and become inaccessible to the coastal fishery. In this area, half of eel landings is made up of silver eels caught by eel poundnets, the rest being yellow eel caught mainly with fykenets.

In the Baltic Sea, the eel fishery has been managed through either private fishing rights or licences distributed by the government to specific sites. In the Sound, the Kattegat, and the Skagerrak areas, the fishery has not been geographically restricted in the same way, but the use of small boats that are fishing for only a day at the time makes the fishery in these areas also relatively local and small scale. As a result of the inherent spatial restriction of the eel fishery, long-term dataseries collected by individual fishers can be used to investigate the temporal development of the eel stock that is not confounded with a spatial variation in catches.

Data were collected from voluntary fishery logbooks from the commercial silver eel fishery, presenting catch per unit of effort from individual poundnets used at exactly the same geographical position during the entire study period. Hence, a basic assumption is made that catch per unit of effort of silver eel in the fishery is a relative estimate of the number of silver eels passing each specific site per unit of time, i.e. a relative estimate of escapement from a specific point along their route of migration. This is considered a valid assumption if the fishery is intense (EIFAC/ICES, 2010), which is the case for the Swedish coastal eel fishery in ICES Sudivisions 20–27. It was also assumed that the efficiency (catchability) of individual poundnets did not change over time. Escapement of silver eel was hence inferred from the catch per unit of effort of silver eel in eel poundnets in the Baltic Sea and in the Sound. On the west coast of Sweden, no information on direct escapement was available for silver eel, so escapement was indirectly inferred from the catch per unit of effort of yellow eel in fishery-independent fykenet surveys, As the yellow eel catch per unit of effort is a function of true abundance and catchability, and as catchability is a function of the locomotive activity of the fish and the efficiency of the gear, and as these factors are assumed to be constant over time, an observed change in catch per unit of effort is interpreted as a change in escapement, assuming a constant relationship between yellow eel stock and escapement over time (EIFAC/ICES, 2010). Apart from the information on catch per unit of effort, these data sources provided information on mean individual weights and total effort in the local fishery. Furthermore, the monitoring surveys provided long-term data on temperature and Secchi depth, two environmental factors that may affect eel production and escapement.

Data on silver eel

Data on silver eel from the eel poundnet fishery were available from voluntary fishery journals in three different areas from the middle to the southern Baltic Proper (Kvädöfjärden, Simpevarp, and Hanöbukten) and one fishery-independent monitoring survey in the Sound (Figure 1, Table 1).

The northernmost area, Kvädöfjärden, is a part of the Swedish coastal fish monitoring programme, and data on water temperature and Secchi depth have been recorded continuously since 1962. In this area, three different eel fishers were contracted to provide data on catch and effort on a daily basis throughout the entire year. Information on individual weights was accessible from eight eel poundnet sites used for 20 years or more in 1972–2001 (Table 1). To avoid differences in catch per unit of effort due to sporadic use of the gear at the start of the season, only the period July–November was included in the analysis.

In the same way, eight different fishers provided voluntary journals on fishing effort and catches in different eel poundnet sites in local fisheries around Simpevarp, as part of the monitoring programme of the nuclear power plant in Oskarshamn from 1962 onwards (Table 1). No effects on silver eel catches from the power plant were recorded (Grimås and Neuman, 1979). In 2005

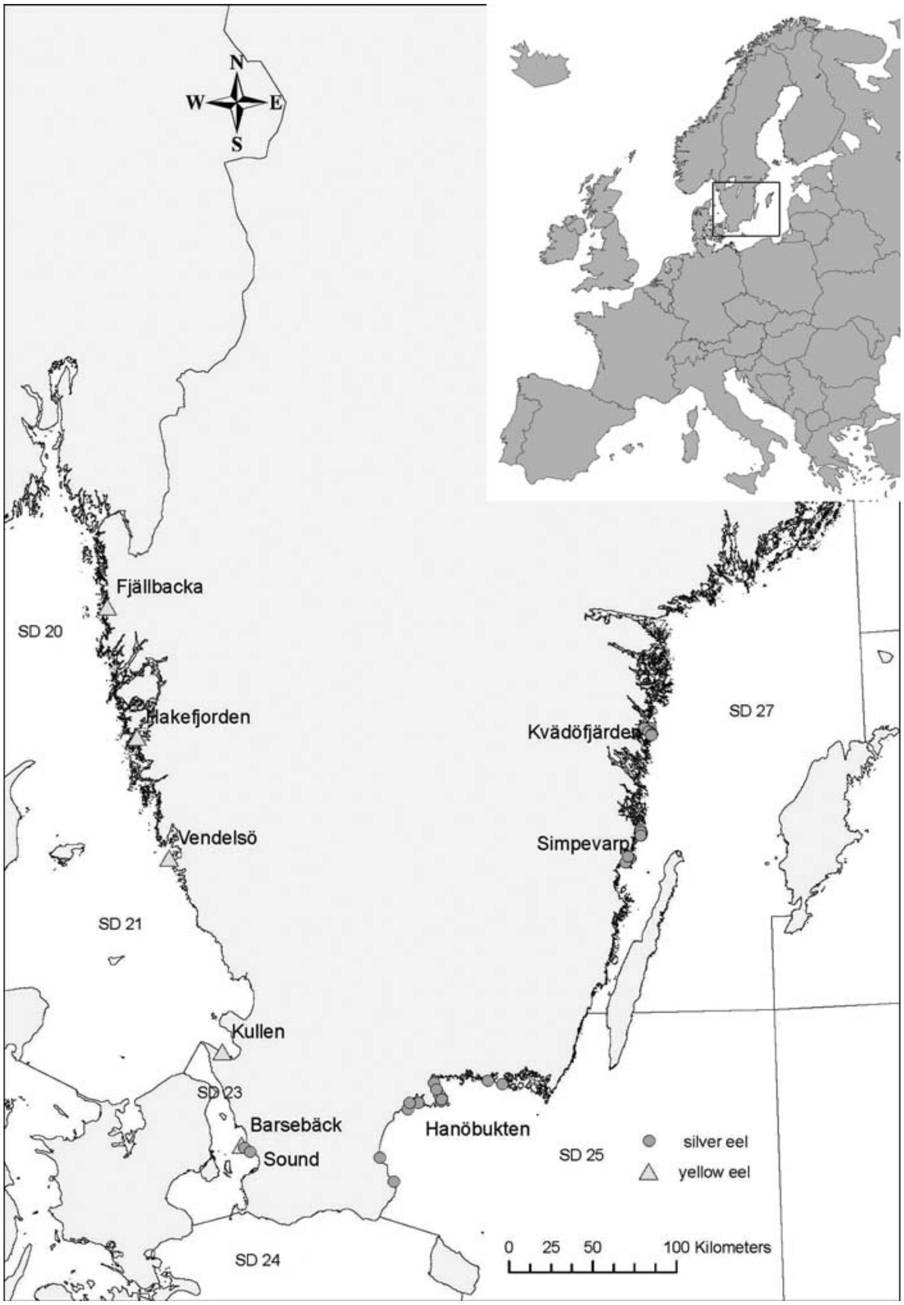

Figure 1. Map of locations of data sources for silver and yellow eel also showing the ICES Subdivisions.

only one fisher remained, fishing in the Marsö area, 5 km north of the power plant. In the area, Dragskär, 10 km south of the power plant, all sites were abandoned in 1999. Individual weights were accessible from 1962 in Dragskär and from 1972 in Marsö. In the data before 1972, no distinction was made between yellow and silver eel. The catch per unit of effort for silver eel was therefore scaled down 23% according to the expected share of yellow eel in the catch after 1972. As for Kvädöfjärden, only data from July–November were used in the analyses.

In the southern Baltic Sea, fishers have provided detailed catch statistics from the eel poundnet fishery for silver eel in Hanöbukten since the late 1950s on a voluntary basis. Catch and effort data from 13 sites, covering different parts of the period, were available (Table 1). As the gear was used more sporadically at the beginning and end of the season, catch per unit of effort was calculated based on data only from the time of the most intense fishing in August and September. No data were available between 1978 and 1980.

In the Sound, fishing with eel poundnets was part of the monitoring programme for the nuclear power plant at Barsebäck between 1971 and 1994. Two different stations were used, one close to the power plant (Barsebäck), the other 2.5 km southeast of the power plant (Vikhög). No effect on silver eel migration by the power plant was observed (Neuman and Thoresson, 1981). Fishing occurred continuously during September–October, and

Table 1. Fishing for silver eel with eel poundnets.

Area	ICES Subdivision	Subarea	Site	Start	End	Period(s)
Hanöbukten	25	Dohlsten	1	1983	2004	Middle
		Hallahålet	1	1994	2008	Late
		Hallasättet	1	1968	1996	Three
		Kongafisket	1	1981	1996	Late
		Kungsören	1	1994	2005	Late
		Oderkärvet	1	1981	2008	Late
		Saxemara	1	1959	1996	Three
		Skaftet	1	1959	1988	Three
		Staggen	1	2000	2005	Late
		Stenören	1	1981	1990	Middle
		Styrsvik	1	1981	2002	Middle
		Utkörningen	1	1959	1965	Early
		Ålahaken	1	1959	1976	Early
Kvädöfjärden	27	–	9	1972	2001	Three
		–	13	1972	2001	Three
		–	19	1972	2001	Three
		–	22	1972	1996	Three
		–	28	1972	1993	Early
		–	36	1972	2001	Three
		–	41	1973	2001	Three
		–	44	1975	2001	Three
Simpevarp	27	Dragskär	1	1962	1976	Early
		Dragskär	2	1962	1976	Early
		Dragskär	3	1962	1981	Early
		Dragskär	4	1964	1980	Early
		Dragskär	6	1962	1988	Early
		Dragskär	7	1962	1985	Early
		Dragskär	8	1972	1998	Three
		Dragskär	10	1973	1998	Three
		Dragskär	13	1972	1998	Three
	27	Marsö	4	1972	2008	Three
		Marsö	6	1972	2008	Three
		Marsö	8	1972	2007	Three
		Marsö	10	1972	2008	Three
		Marsö	13	1972	2005	Three
		Marsö	15	1972	2008	Three
		Marsö	18	1972	2008	Three
		Marsö	26	1972	2008	Three
		Marsö	27	1973	2008	Three
Simpevarp	27	Marsö	36	1972	2008	Three
Sound	23	Barsebäck	7	1971	1989	Early
	23	Vikhög	5	1974	1994	Middle

Data from the Sound are from fishery-independent monitoring surveys, whereas the rest of the data are from voluntary fishery journals. Period(s) refers to the allocated period in the statistical analyses.

the poundnets were emptied three times a week. Catch in numbers and weight per unit of effort were obtained.

Data on yellow eel

Data on yellow eel were available from fishery-independent fykenet surveys in four different areas on the west coast of Sweden (Fjällbacka, Hakefjorden, Vendelsö, and Kullen) and one fishery-independent fykenet survey in the Sound (Barsebäck; Figure 1, Table 2). In all monitoring areas, catch was recorded as the number of individuals per species or life stage in each station. In some areas, the total weight per species and station was recorded. The catch per unit of effort is generally presented as numbers per fykenet and per night.

Table 2. Fishing for yellow eel in monitoring surveys using fykenets.

Area	ICES Subdivision	Start	End	Period(s)
Barsebäck	23	1977	2009	Two
Fjällbacka	20	1998	2009	Late
Hakefjorden	21	2002	2009	Late
Kullen	21	2002	2009	Late
Vendelsö	21	1976	2009	Two

Period(s) refers to the allocated period in the statistical analyses.

In the Sound, fykenets have been used in monitoring the effects of cooling water by the Barsebäck power plant since 1977. Fishing was performed in a standardized way in five stations in a gradient from the area close to the outlet along the coastline to the most distant site 5 km north of the power plant. Initially, three pairs of 60 cm fykenets were used in each site. In 1988–1995, the number was reduced to three single fykenets per site, to be increased again to the original number in 1996. In this year, another three pairs were added on the northernmost site. Fishing was performed annually for 12 nights in August. The power plant at Barsebäck operated in the same way from 1977 until it started closing down in December 1999, and it was totally closed in May 2005. Yellow eel catch per unit of effort did not change as a result of the closing of the power plant (Andersson, 2008). This suggests that any effect of the powerplant on catch per unit of effort of yellow eel was minor, and that changes in yellow eel catch per unit of effort could be used to infer changes in escapement.

Coastal fish monitoring started in Vendelsö on the Kattegat coast in 1976 as a reference site for the nuclear power plant operating in Ringhals, 5 km south of Vendelsö (Figure 1). Six stations were fished annually during nine single nights in August. Each station was made up of two coupled 60 cm fykenets, fished at a depth of 2–5 m close to the shore.

In 1998, monitoring of the coastal fish community with fykenets started in a reference area near Fjällbacka on the Skagerrak coast (Figure 1). In 2002, two new monitoring areas were added to the coastal fish monitoring programme, one in Kattegat (Kullen) and one on the border between Skagerrak and Kattegat (Hakefjorden) (Figure 1). The fishing procedure was the same as in Vendelsö, but with a higher number of stations. In these areas, the surveys were performed annually during six single nights in August.

Data on total effort in silver eel fishery

There is no complete historical record on the total effort in the Swedish silver eel fishery. The analysis of total effort in this report was based primarily on the voluntary journals from the areas Kvädöfjärden and Simpevarp, as the journals provide a total coverage of all poundnets used in these two areas. In the Hanöbukten area, the journals did not offer a complete temporal or spatial coverage of total effort in silver eel fishery. However, previously published effort data for the eastern part of Hanöbukten as well as from the Sound (Neuman and Thoresson, 1981) were included in the analysis. The unit of effort in all cases was one poundnet fished during one night.

Statistics

Trends in catch per unit of effort (number of eels caught per gear and per night) were analysed with both autoregression and quantile regression analyses. Temporal trends in the respective time periods for silver and yellow eels separately were analysed using autoregression (PROC AUTOREG in SAS). Since not all sites were fished over the entire investigated time frame, the sites were divided into three different periods according to when they were fished: early = 1958–1976, middle = 1977–1994, and late = 1995–2009. For silver eels, only sites covering all three periods were used, with the exception of the Sound which was only fished during the middle period. For yellow eels, no data were available for the early period and only sites that covered both the middle and late periods were used in the analyses. In order to reveal eventual general trends in eel catch per unit of effort, the t-values for the slope were used as input in a meta-analysis. In the meta-analysis, the sites were clustered over area and periods, and over periods only. The meta-analysis was done using MetaWin statistical software (Rosenberg *et al.*, 2000). Prior to all analyses, the catch per unit of effort values were log transformed (common logarithms).

The QUANTREG procedure in SAS was used to model the effects of time (e.g. year was the covariate) on the conditional quantiles of catch per unit of effort (response variable) (cf. Koenker and Bassett, 1978). The effects of the covariate were analysed using a non-parametric Multivariate Adaptive Regression Spline (MARSpline). For both the yellow eel and silver eel data, the catch per unit of effort was divided into seven regions. The data were fitted using a non-parametric spline function for the median, and the 10th, 25th, 75th, and 90th percentiles.

Mean weight was calculated by dividing total annual weight by the annual number of eels reported in voluntary journals from the eel poundnet fishery in Kvädöfjärden, Simpevarp, and Hanöbukten. Trends over time were studied by using a non-parametric spline function for the median for each area.

Temperature and Secchi depth were analysed as follows: first the values were fitted to a non-linear regression using the TableCurve® software (2002) with month as the independent variable. The residuals from the equation giving the highest r^2 were used for calculating adjusted values by adding residuals to the total average. This method was chosen for two reasons. First, Secchi depth and temperature were measured irregularly; different months were lacking in different years, making a general linear model unreliable, and just by removing one observation a different result was obtained. Second, the non-linear model returned a higher F-value and a slightly higher r^2 value. Total averages for temperature and Secchi depth were calculated for the entire seasons, but, as measurements were taken with lower frequency during the winter, the average was weighted, using the frequency of each month in the data. Trends in yearly averages were analysed by linear regression. The levels of significance for temperature and Secchi depth were adjusted using the Šidak method (Šidak, 1967), and the mean number of months per year measurements was used as the number of replicates (temperature = 9.39; Secchi depth = 8.20).

Trends in the total yearly effort were analysed with linear regression for each area separately and the correlations were pooled to reflect the average change in effort [i.e. pooled within-class correlations (partial correlations based on the pooled within-class covariances; Harris, 1913)].

Results

Catch per unit of effort

Considering sites where data were available for the entire period, both Hanöbukten and Simpevarp showed a significant decrease in catch per unit of effort of silver eels in the meta-analysis, while no trend was detected in Kvädöfjärden (Figure 2). In the Sound, where data were only available from the middle period, there was also a significant decrease of catch per unit of effort of silver eel over time (Figure 2). The decrease in Simpevarp was lower than the decrease in Hanöbukten and the Sound. Pooling data from all areas showed an overall significant decrease in catch per unit of effort of silver eel over time, while the catch per unit of effort of yellow eel increased (Figure 2).

The quantile regression of silver eel catch per unit of effort shows that catch per unit of effort was at its highest in the middle of the 1960s and then decreased rapidly (Figure 3). In the middle of the 1970s the catch per unit of effort slightly increased again over the next 10-year period, and then slightly decreased until 2000, wherafter it fell more sharply. Compared with the decrease at the beginning and end of the data-series the catch per unit of effort remained relatively stable between the 1970s and 2000. The highest catch per unit of effort (75th and 90th quantile) increased after 2000 to be close to the high values in the 1960s (Figure 3). Median catch per unit of effort, however, decreased in the few last years. Removing the area with no significant trend in the first analysis (Kvädöfjärden) gives a similar picture (results not shown).

The result of the quantile regression of yellow eel catch per unit of effort shows that catch per unit of effort of yellow eel increased during the 1980s to the beginning of the 1990s, remained stable until the late 2000s, and then decreased again (Figure 4).

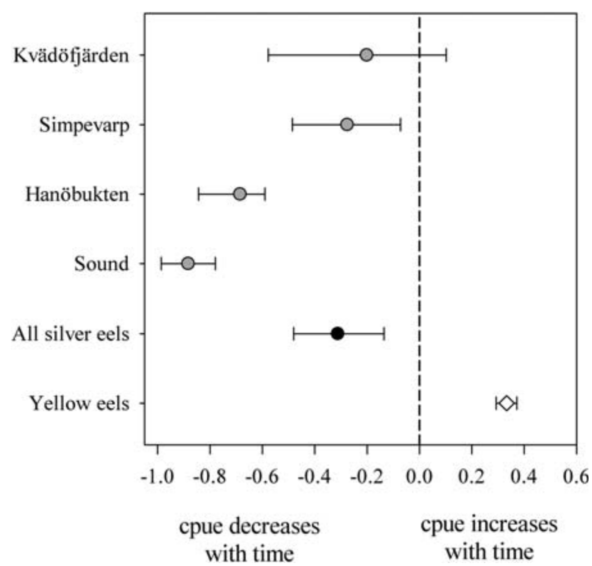

Figure 2. Catches (cpue = numbers per unit of effort) of silver eels from three areas in the Baltic Sea (Kvädöfjärden, Simpevarp, and Hanöbukten) and from the Sound, and yellow eels from the Swedish west coast. Median cpue and 95% confidence intervals are shown, i.e. if the error bars cross the vertical dashed line indicating effect size = 0, the change in cpue over time was not significant. The values for confidence limits were estimated using bootstrapping.

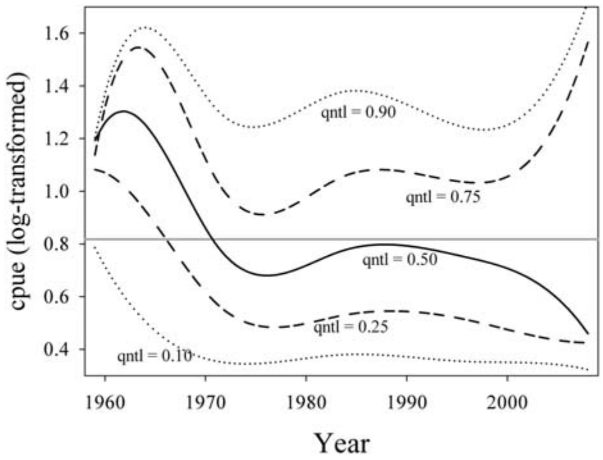

Figure 3. Results of the quantile regression analysis of silver eel catch per unit of effort (cpue). The grey horizontal line indicates the median for all years. All quantiles were significant (Wald χ^2: q10, $\chi^2 = 13.10$, $p = 0.042$; q25, $\chi^2 = 44.65$, $p < 0.001$; q50, $\chi^2 = 142.88$, $p < 0.001$; q75, $\chi^2 = 74.29$, $p < 0.001$; q90, $\chi^2 = 15.73$, $p = 0.015$).

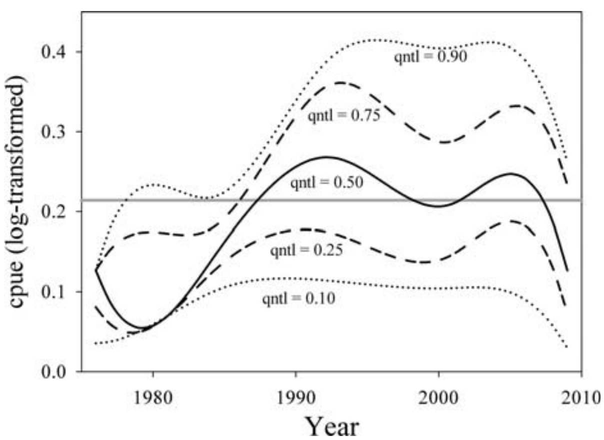

Figure 4. Results of the quantile regression analysis of yellow eel catch per unit of effort (cpue). The grey horizontal line indicates the median for all years. Only the median quantile was significant (Wald χ^2: q10, $\chi^2 = 0.74$, $p = 0.99$; q25, $\chi^2 = 6.28$, $p = 0.39$; q50, $\chi^2 = 15.51$, $p = 0.017$; q75, $\chi^2 = 10.77$, $p = 0.096$; q90, $\chi^2 = 7.63$, $p = 0.266$). Note that Figure 4 has a different *x*-axis timescale from that of Figure 3.

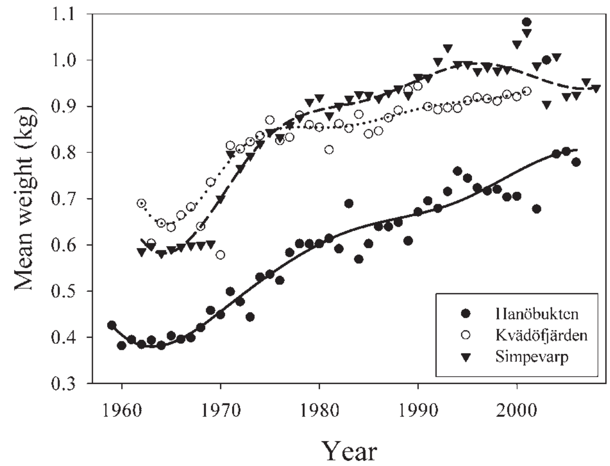

Figure 5. Mean weight of landed eels from three different areas along the east coast of southern Sweden. The data were fitted using a non-parametric spline function for the median for each area [Wald χ^2; Hanöbukten (solid line), $\chi^2 = 546.3$, $p < 0.001$; Kvädöfjärden (dashed line), $\chi^2 = 219.6$, $p < 0.001$; Simpevarp (dotted line), $\chi^2 = 714.5$, $p < 0.001$].

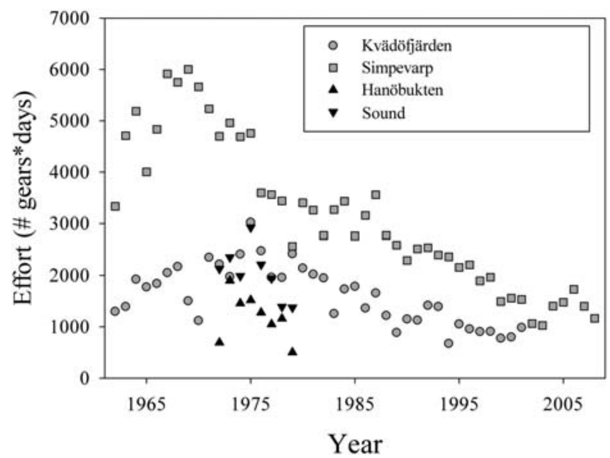

Figure 6. Fishing effort expressed as numbers of poundnets multiplied by numbers of fishing nights in four areas on the Swedish coast (July–November). Pearson correlation coefficients: Kvädöfjärden, $r = -0.64$, $p < 0.001$; Simpevarp, $r = -0.91$, $p < 0.001$; Hanöbukten, $r = -0.42$, $p = 0.30$; the Sound: $r = -0.63$, $p = 0.094$; pooled correlation for all four areas: $r = -0.799$, $p < 0.001$.

Mean weight

The mean weight of silver eel in Kvädöfjärden and Simpevarp increased from 0.6 kg in the 1960s to close to 1 kg in the late 1990s (Figure 5). The mean weight also increased in Hanöbukten from ~0.4 kg in the 1960s to 0.8 kg in the 2000s (Figure 5).

Effort

The effort was substantially reduced since the early 1970s (Figure 6). The magnitude of the decrease is 80% in Simpevarp and in Kvädöfjärden where the major fishery closed down after 2001 (Figure 6). Data from Hanöbukten and the Sound support a decreasing trend in the 1970s (Figure 6).

Environmental factors

Temperature increased significantly during the investigated period (linear regression, $r = 0.253$, $p < 0.001$) while Secchi depth decreased (linear regression, $r = -0.575$, $p < 0.001$).

Discussion

Escapement

This study shows a major decrease in silver eel escapement in the 1960s when the overall median catch per unit of effort decreased by almost 50%. There were, however, differences between areas. Escapement from the northernmost studied site, Kvädöfjärden, did not decrease during the last 50 years, whereas there was a steep decline in catch per unit of effort in the southernmost site.

One reason for these spatial differences could be that the more southern areas are more influenced by eel migrating from the southern and eastern parts of the Baltic basin (ICES, 2010). Another interesting finding is the increased variability in escapement during recent years, inferred by the different trends in high and low quantiles for silver eel catch per unit of effort in the 2000s (Figure 3). This suggests, furthermore, a spatial variation in escapement, with some sites showing a high escapement despite the overall median escapement going down.

The decline of the silver eel stock in the mid 1960s, as shown in this study, corresponds well to the diminishing European landings of eel seen in FAO statistics (Dekker, 2003, 2008). Median catch per unit of effort of silver eel revealed in this report was 3.3 eels per poundnet per day at the beginning of the 1960s, and 1.6 eels per poundnet per day in the late 2000s, which can be compared with 12.6 eels per poundnet and day in the 1930s (Hessle, 1933). Even if this comparison is not entirely valid, due to changes in fishing patterns and gear efficiency, it indicates a change in stock density, which started even before the period included in this study. However, although landings have continued to decline, our results show that catch per unit of effort stabilized at the levels of the 1970s into the 2000s. This is supported by the results of Svedäng (1996) who found no significant changes in silver eel catch per unit of effort from the Baltic Sea in the period 1972–1993. The decrease after 1980, seen in both the pan-European and Swedish indices of recruitment (ICES/EIFAC 2010), is hence not as evidently reflected in silver eel catch per unit of effort in the Baltic Sea as would be expected from a strong recruitment–spawning stock relationship (Svedäng, 1996; this study). The major decrease in recruitment of young yellow eel to the central parts of the Baltic Sea took place in the 1950s and the 1960s, and stayed at a 10–20% level compared with the pre-1970s in the last four decades (EIFAC/ICES, 2010). The lack of correspondence between the general trend observed in the North Sea and all over Europe after the 1980s and the recruitment indices retrieved from upstream migration in the remotest Baltic rivers (Motala Ström and Dalälven) imply that secondary and not well understood processes govern the spreading upstream into these areas. This might in turn partly explain the relative stability of the silver eel catch per unit of effort in the period 1970–2000. The level thoughout this period was higher than expected from the observed decrease in recruitment, which will be discussed further below.

It is not possible to estimate silver eel escapement directly from the part of the yellow eel stock living in coastal habitats on the Swedish west coast. However, a plausible assumption is that escapement is correlated with the size of the regional yellow eel stock and that catch per unit of effort of yellow eel in the fykenet monitoring presented here can be used to analyse relative changes in stock size and escapement over time. If the assumption is valid, silver eel escapement from the Swedish west coast did not decrease during the last three decades. Our results are in contrast to the overall notion that yellow eel abundances have declined in large areas (Moriarty and Dekker, 1997; Dekker, 2008; EIFAC/ICES, 2010), but in agreement with Knights *et al.* (2001) and Svedäng (1999) who see no evident decline in yellow eel abundance in England/Wales and Skagerrak/Kattegat, respectively. The Swedish coastal fishery landed 200–300 t of eel annually most years from 1950 until 2006, the year before landings were reduced due to management actions (EIFAC/ICES, 2010). The lack of trend in landings during such a long period of time supports the conclusion of a relative stability of the stock of yellow eel on the Swedish west coast.

Considering catch per unit of effort as an estimate of escapement, we conclude that escapement of silver eel from the Baltic Sea as well as from Skagerrak/Kattegatt decreased less than would be expected by changes in recruitment alone until the early 2000s. Possible explanations for this seemingly paradox are discussed below.

Stocking?

Stocking is currently part of the Swedish eel management plan, but it is questionable whether stocking in Sweden so far has contributed substantially to the silver eel catches in the Baltic coastal fishery. The national stocking of eel in Sweden has been modest compared with the natural recruitment (Svedäng, 1996). Stocking was practised, however, for decades in other Baltic countries, on a much higher level than in Sweden. Hence stocking cannot be ruled out as a reason for upholding the level of escapement, as silver eel from all over the Baltic basin experience a risk of being caught in the Swedish fishery. It is important to note that stocking has not been undertaken on the Swedish west coast (Svedäng, 1996) and is, therefore, not the explanation for the increase in yellow eel catch per unit of effort during the last 30 years.

Density dependence?

One explanation put forward by Svedäng (1999) for the stabilized stock abundance of eel in Kattegat/Skagerrak, despite continuing diminishing recruitment, may be density-dependent factors at the elver and yellow eel stages moderating variations in glass eel recruitment. Implications of density-dependent effects have also been found in other areas. Investigations during 1974–1989 in Valli di Commachio Lagoon in Italy show that as the density of eel declined, survival increased, and in addition the proportion of females, female body size, as well as age and length of both sexes at sexual maturity increased (De Leo and Gatto, 1996). During the same period, density-dependent mortality of eel has been inferred in a Norwegian river (Vollestad and Jonsson, 1988). Density-dependent changes in sex ratio were also evident in rivers in England and Wales (Bark *et al.*, 2007). In rivers where eel populations were stable, the populations were male biased, while rivers with declining populations were female biased. Furthermore, compensatory mortality effects were also given as the explanation for the same number of eels surviving to the silver stage in both strong and weak cohorts in a Spanish river followed over 21 years (Lobon-Cervia and Iglesias, 2008).

The significant increase in the mean weight of silver eels seen in this study (100% in Hanöbukten and 67% in Simpevarp) may have been caused by density-dependent changes in the size of maturity of silver eels. In addition, a changed sex ratio with an increasing dominance of females during the last century (Svärdson, 1976; EIFAC/ICES, 2010) could have contributed to an increased mean weight, since females mature at a larger size than males (EIFAC/ICES, 2010). An increased female-biased sex ratio, however, cannot explain the increase in mean weight in the Simpevarp area since females have made up 100% of the silver eel catch since 1910 (Svärdson, 1976). Poole *et al.* (1990) observed an increased proportion of females, and increasing size of females, in the silver eel migrating in a west of Ireland River over a similar period.

Decreased effort?

The effort in the eel fishery decreased during the second half of the 20th century. This is evident both in the official records of fishing effort in Sweden (SCB, 1987) and in the records from voluntary logbooks kept by local eel fishers (this study). In addition, assuming that the recapture rate of tagged eel reflects fishing pressure, a review of 100 years of tagging experiments reveals that the mean recapture rate increased from 20% at the beginning of the 20th century to 48% in the mid 1960s, after which it fell to 30% in more recent years (Sjöberg *et al.*, 2008; reviewed in EIFAC/ICES, 2010). Sjöberg *et al.* (2008) and other sources (Bringéus, 1985; Göransson, 1995) indicate that the efficiency in the eel fishery increased after the middle of the last century, due to the introduction of new synthetic gear materials, such as nylon, good prices, and possibly also high eel recruitment in the early 1950s (EIFAC/ICES, 2010). This expansion induced an increasing competition between fishers for the resource, and consequently less profit, starting a long period of reduced effort, as illustrated by local effort data presented in this study. The long period of lower recruitment after the 1960s certainly supported this process. To conclude, a significant reduction in effort has probably strongly contributed to reducing the rate of decline of the silver eel escapement in the last four decades.

Beneficial environmental changes?

The environment has also changed during the investigated period. Mean surface temperature in the central Baltic Sea increased significantly by $\sim 2^\circ C$ in 1962–2007. In the same period, the Secchi depth decreased by 2–3 m, probably reflecting the general eutrophication of the Baltic Sea. Temperature is an important factor influencing both growth and survival of eel (Sadler, 1979; Seymour, 1984), and an increasing temperature may consequently have had a positive effect on silver eel production. Moreover, Bark *et al.* (2007) showed that in rivers at carrying capacity there was a direct positive relationship between the level of nitrate and the biomass of yellow eels. Assuming a positive relationship between yellow eel stock and silver eel production, this may mean that the eutrophication in the Baltic Sea could have a positive influence on the production of silver eel.

Conclusion

The level of escapement from the Swedish Baltic Sea coast inferred from silver eel catch per unit of effort has generally decreased over time, and the most severe decline took place in the 1960s and the early 1970s, and in recent years. Only one of the areas investigated on the east coast showed no temporal trend in escapement. The loss in numbers has to some extent been compensated by an increase in mean weight of silver eel. Escapement remained relatively stable between the late 1970s and 2000, and escapement from the west coast, inferred from the catch per unit of effort of yellow eels, has generally increased over time. Possible explanations for the upheld escapement during the last decades, despite the continued reduction in recruitment, may be favourable environmental conditions, in combination with a decreased fishing effort. Stocking and density-dependent changes in survival and growth, however, cannot be ruled out.

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