Slipping through our hands. Population of the European Eel
Dekker, W.

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
The population of the European eel *Anguilla anguilla* (L.) is in rapid decline. Recruitment of juveniles to the continent dropped since 1980 by nearly an order of magnitude per generation (Moriarty 1986; Dekker 2000a). Continental stocks and fishing yield have declined more gradually over several decades (Moriarty and Dekker 1997; Dekker 2003c, 2004a), and a further drop is expected, given the continued decline in recruitment (ICES 2004). A parallel decline in recruitment has been observed for the American eel *Anguilla rostrata* (LeSueur) in the St Lawrence River system (Castonguay et al. 1994a). A range of potential causes has been suggested (Castonguay et al. 1994b; EIFAC 1993; Moriarty and Dekker 1997; ICES 2002) including habitat loss, overfishing, pollution and climate change. Temporal correlations with the observed trends have been discussed, but the potential mechanisms involved have hardly been analysed, prohibiting problem-oriented restoration measures. Based on a precautionary approach, urgent protective measures have been advised: anthropogenic impacts must be curtailed, where they exceed sustainable limits (ICES 2002). In the past decade, new information on the spatial structure of the population (Wirth and Bernatchez 2001; Dekker 2000a, 2003a) and on trends in characteristics of the population during the period of decline (Dekker 1998, 2000a, 2003c, 2004a; Desaunay and Guerault 1997) has been published. Existing knowledge is still too fragmented to allow a full analysis of the dynamics of the population, but the likelihood that enough information may be collected in time is fading out rapidly with the collapse of the stock (Anonymous 2003). Cutting the coat to the cloth, I will review the available information, to narrow the range of defendable hypotheses for the observed declines. First, the spatial delineation of the stock is discussed, followed by a discussion of the dynamics during the continental and oceanic life stages. Observed trends in the stock during the past five decades are then used to estimate a comprehensive model of stock dynamics and climate effects. Finally, prospects for the dynamics of the stock in the near future are explored.

**Life cycle**

This section introduces the life cycle and some biological characteristics of the eel, and specifically names the various life stages (Figure 1). A full review of the biology of the eel, but not the population dynamics, is given in Tesch (1999).

Although the life cycle is incompletely known, the eel is undoubtedly a catadromous species. Reproduction must take place somewhere in the Atlantic Ocean, presumably in the Sargasso Sea area, where the smallest larvae have been found (Schmidt 1906). Neither adults in the process of spawning nor eggs have ever been observed in the wild. Larvae (Leptocephali) of progressively larger size have been found from the Sargasso Sea up to European continental shelf waters. Transport to the continental shelf is presumably just by passive drift on the Gulf Stream (McCleave et al. 1998), which may take from late spring to winter/spring nearly two years later. However, our knowledge of the larval phase is extremely limited, and length of the larval phase (Lecomte-Finiger 1992),

![Life cycle of the European eel](image)

**Figure 1** The life cycle of the European eel. The names of the major life stages are indicated; spawning and eggs have never been observed in the wild and are therefore only tentatively included.
their food sources (Mochioka 2003), and dispersion mechanisms (McCleave et al. 1998) are still in dispute. At the shelf edge, the laterally flattened *Leptocephalus* transforms into a rounded glasseeel, which has the same shape as an adult eel, but is unpigmented. Glasseeel arrive in coastal waters in winter in southern Europe to late spring in northern Europe to swim actively against the river flow, often in very dense formations performing group locomotion, known as *cordon* in French. Following immigration into continental waters, the prolonged yellow eel stage begins, which lasts for about 2 to 20 years. During this stage, the main growth occurs, but no maturation. At the end of this period, the maturation starts and the eel return to the ocean; this stage is known as silver eel. Average length of silver eel is 40.5 cm for males, and 62.3 cm for females (Vølstad 1992). Growth rate varies with temperature and latitude; mean age of silver eel ranges from 3 years for males and 5 years for females at 40°N (mid Spain), to 10 and 14 years at 60°N (central Sweden), with an average of respectively 6 and 9 years (Vølstad 1992). Sex differentiation mechanisms are not fully understood, and may depend on local stock density. In densely populated, downstream areas males dominate, while a sparser female-dominated stock is found upstream.

The biology of the returning silver eel in ocean waters is completely unknown. The migration back to the Sargasso is assumed to take up to half a year (fall to spring). The total generation time then will be in the order of 8.5 years for males and 11.5 years for females.

**Spatial population structure**

The spatial structure of the population will be considered for the ocean and continental life stages separately.

**Ocean phase**

For the ocean phase, in the absence of information on distribution of the eggs, larvae and silver eel, spatial aspects of the structure of the population remain obscure. Thus, the structure in the ocean stock has been deduced from information referring to the next following life stage, the glasseeel recruiting from the ocean to the continent. Schmidt (1906) found that vertebral counts of eel were remarkable uniform over the entire distribution range, and concluded that the population must be panmictic. This conclusion was later corroborated by studies of allozymes (Comparini and Rodino 1980), and of mitochondrial DNA (Avise et al. 1986; Lintas et al. 1998). Recently, the panmixia hypothesis has been challenged based on micro-satellite DNA analyses, claiming genetic differentiation by distance; Icelandic and Moroccan substocks would differ substantially from the main Atlantic stock (Avise et al. 1990; Wirth and Bernatchez 2001; Daemen et al. 2001). However, there seems no debate on the panmictic status of the major part of the population, in mainland Europe, Scandinavia and the British Isles (Dekker 2003a). To what extent the panmixia has been influenced by long-distance transport of young eel by man, is not clear. The quantities of glasseeel transported from southern and south-western Europe to central and northern Europe for re-stocking (Moriarty and Dekker 1997), has declined considerably over the past decades (Dekker 2003b), but was still of the same order of magnitude as natural recruitment to those areas in the early 1990s (Dekker 2000b). Long-distance transport of live yellow eel has been practised for centuries (Ypma 1962) and is still common practice (Moriarty 1997), though deliberate mixing of full-grown eel into local stocks has become rare.

**Continental phase**

During its continental life stages, the eel is distributed over Europe, northern Africa and Mediterranean Asia (Schmidt 1909; Dekker 2003a), over a geographic range of more than 10 million km², representing over 100,000 km² of water surface. The continental habitat is scattered over lakes, rivers, estuaries and lagoons (with an average individual water surface area in the order of 10 km²; Dekker 2000a) and effectively forces the population to split into numerous local sub-stocks of, on average, considerably less than a million individuals (Dekker 2000b), without natural interactions in-between. Abundance and growth characteristics of these stocks vary considerably over a short (10 km) spatial range (Dekker 2000a, 2003a). The overall pattern is one of high recruitment in the area surrounding the Bay of Biscay, rapidly thinning out with distance, while productivity (as measured by fishing yield per unit of water surface area) is highest in the western Mediterranean, and falls off gradually, towards the Eastern Mediterranean and Northern Europe (Dekker 2003a). The Biscay area (<10% of the distribution area), receives three-quarters of the recruitment, while producing only 10% of the silver eel biomass (Dekker 2000b). Size at maturation hardly varies over the distribution area.
Synthesis and discussion: Population dynamics of the European eel

![Graph showing trends in glasseeel recruitment to the continent. Individual data series are given in grey; common trend (geometric mean of the three longest data series) in black. Note that recruitment data series concerning yellow eel are presented in Figure 4. Data from ICES (2004) and Hagström and Wickström (1990).](image)

Figure 2

(Vøllestad 1992), implying a much higher life-time mortality in the Biscay area than elsewhere.

The oceanic and continental life stages together determine the population dynamics of the eel. In the continental phase, gradual trends in population characteristics are observed, as well as sharp contrasts between neighbouring waters. Although local processes dominate in local dynamics, their effect on the total population may only become effective at the continental scale, at which there is little evidence of any spatial structure in the major part of the population. The density of the few potential sub-populations that might exist is too low to contribute significantly to the overall population dynamics. The European eel population is effectively dominated by one panmictic stock.

**Continental stock dynamics**

**Analytical studies**

During the continental life stages, growth, sexual differentiation, mortality and migration determine the local stock dynamics. A considerable corpus of publications exists for each of these processes separately (see for an extensive review Tesch 1999). At the bottom line, all these aspects and their mutual interactions are still being debated, and commonly accepted views are virtually absent. Methodological problems in measuring each process, large individual and geographic variation, and complex relations to other, seemingly unrelated processes, are still common themes.

Comprehensive studies of local stock dynamics are limited. Vøllestad and Jonsson (1988) evaluated exploitation scenarios for the fishery in the River Imsa (Norway), using a simulation based on the Beverton and Holt (1957) model. Sparre (1979) assessed the impact of the eel fishery in the German Bight, using a steady-state, length-structured model. De Leo and Gatto (1995) simulated the dynamics of the stock in the Comacchio lagoons (Italy), using a functional model tuned to a limited set of field data. Dekker (2000c) developed a length-based virtual population assessment model of the eel fishery on Lake IJsselmeer (the Netherlands). All these studies assumed that the recruitment of glasseeel, and the run of silver eel in their local study area is either constant, or irrelevant for local stock dynamics; that is: none of these studies covered a temporal (decadal) or spatial scale (continental) relevant for the dynamics of the total population, while each of these local stocks is now dominated by common downward trends in the population.
Figure 3 Trends in abundance and mean length of the glasseye sampled in Den Oever, the Netherlands. Abundance has been corrected for month and hour of sampling; mean length for the date within and timing of the season (Dekker 1998; updated until 2003).

**Observed trends**

**Recruitment**

In most countries in Western Europe, the abundance of glasseye recruitment is monitored using statistics from scientific sampling, commercial or non-commercial fisheries, import-export data, etc. (Moriarty 1986; Dekker 2002). Nearly all these data series exhibit a common downward trend (Dekker 2000a). General trends can be inferred from 1950 onwards (Figure 2). After a brief period of relatively low recruitment shortly after World War II, numbers of glasseye were high in the 1950s, 1960s and 1970s, reaching a peak in the late 1970s. Starting in 1980, a steady decline has been observed, until a low level was reached around 1990, one order of magnitude below former levels. In the late 1990s, a further decline occurred, leading to an all-time low in 2001, again an order of magnitude below the level observed only 10 years before. In most recent years, no substantial recovery in recruitment levels was found. Most data series from the British Isles showed a less severe decline than those of mainland Europe, but recruitment to the river Erne did not show any significant trend.

**Fishing yield**

Statistics on fishing yield of eel are notoriously incomplete. ICES (1988) and Moriarty (1997) showed that official landings statistics for many countries comprised only about half the true catches in the 1980s and 1990s. A reconstruction of the trend in reported landings (Dekker 2003c) shows, that landings during the pre-WW-II period varied around 47,500 tonnes (Figure 5). Following a clear depression during the war, landings gradually increased to 47,000 tonnes in 1964, to decline to an all-time low of 22,000 tonnes recently (correction for under-reporting was not included in this reconstruction).

**Stock abundance**

Time series on yellow eel abundance spanning more than a decade are few, and results are rarely published. Analysis of trends in stock abundance is based on incidentally collected information (Moriarty and Dekker 1997), on re-execution of discontinued historical surveys (Knights et al. 2001), on records of yellow eel immigration into rivers (Svärdsön 1976; Wickström 2002), or on the analysis of commercial fishing yields (ICES 2004). The research surveys on Lake Ijsselmeer (the Netherlands) are presumably the only long-time, fishery-independent data source (Dekker 2004a). Results indicate a gradual decline in abundance since 1960 (Figure 4), with a sharper decline for the larger size classes. The other sources of information largely support the notion that the yellow eel abundance has declined over wide areas, with the exception of the English re-surveys, that did not indicate a general decline over the last 20-25 years.
Synthesis and discussion: Population dynamics of the European eel

The question arises, whether the decline of the IJsselmeer stock is representative of the continental population, or is an exceptional case. There are three arguments in support of the former view.

Firstly, the trend observed in Lake IJsselmeer parallels the decline in yellow eel recruiting to Swedish rivers (Figure 4). Svårdson (1976) interpreted the Swedish data as indicating a decline in recruitment from the ocean to the Baltic. At the time of his publication, the IJsselmeer stock had already declined considerable, but this had not been published, while the continent-wide drop in glassseel recruitment had not yet begun. In hindsight, Svårdson’s interpretation, although consistent with his observations, would not seem the most obvious one. An increased mortality between the glassseel stage recruiting from the ocean and the yellow eel stage monitored would have explained the observations equally well, and by a mechanism shared with Lake IJsselmeer. Updates of Svårdson’s data (Wickström 2002; ICES 2004), and extension to glassseel in the (marine) Skagerrak-Kattegat area (Hagström and Wickström 1990) do not contradict the view that mortality in the yellow eel stage has increased, except for the data on small yellow eel (average 12 cm length) recruiting to the River Lagan (Figure 4), which showed a steep decline during the 1960s and no general trend afterwards, rather than a gradually decline over the decades.

Secondly, if fishing yields declined since the mid-1960s throughout the continent (Dekker 2003c) despite high yellow eel abundance, fishermen progressively must have underexploited their resources. According to Knights et al. (2001), market demands in England have collapsed since the late 1960s, which could explain the reduction in fishing yield. However, between the 1960s and 1980s, the average price for live eel in the Netherlands rose gradually, from 4.90 to 7.20 €/kg (corrected for inflation to 2000 price level; Figure 6), while the estimated annual international yield declined from 40,000 to below 25,000 tonnes. The rise in price suggests, that the international market was driven by limited supply, rather than by decreasing demand. Since 1980, an aquaculture industry for eel developed in Europe (Dekker 2003b), finding insatiated markets. Aquaculture production increased to 10,000 tonnes, and prices fell to 5.80 €/kg in the late 1990s. Increased prices and declining supply more likely reflect a decline of the stock, than reduced demand. The reason why the English market showed an aberrant development (Knights et al. 2001) is yet unclear.

Thirdly and finally, there is circumstantial evidence, summarised in Moriarty and Dekker (1997), indicating higher yellow eel abundance in the past. Overall, it appears that the decline observed in Lake IJsselmeer eel stock does not stand by itself, but is indicative for a wide-
Figure 5 Trends in fishing yield from the whole population. FAO statistics include an increasing number of reporting countries, and therefore give a false suggestion of a stable or increasing yield. Analysis of the trends in individual data series results in a reconstructed trend for the whole population (Dekker 2003c).

Figure 6 Trend in market price for yellow eel from Lake IJsselmeer during the 20th century, corrected for within-season trends and variation between fishing gear (unpublished data from the author).

spread trend in stock abundance over a large part of Europe.

Processes involved in the decline of the continental stock

The decline in recruitment was first noticed in 1985 (EIFAC 1985). The prolonged decline in yield has been mentioned as early as 1975 (ICES 1976), but has received considerable less attention than that in recruitment (Dekker 2004b). Consequently, the causes of the decline of the continental stock remain an open question. However, several hypotheses for the decline in recruitment have been suggested (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002), which imply an earlier decline of the continental stock. The following processes have been hypothesised (listed in the order of the life stages affected):
Synthesis and discussion: Population dynamics of the European eel

**Glaasell fisheries.** The exploitation of glasseel in estuaries reduces the number migrating upstream. In exceptional cases (Briand et al. 2003a), virtually all glasseel can be removed, but the average percentage caught amounts to 80-95% (Dekker 2000b).

**Barriers to upstream migration.** Dams in rivers (for hydropower generation, or reservoirs) impede the upriver migration of glasseel and elvers. Many of the (larger) dams in Europe constitute a complete blockade, if they are not equipped with fish passes or eel ladders. It is generally assumed, that this results in a loss of silver eel production, since natural mortality is higher in the downstream areas (Briand et al. 2003b). However, the net effect of all barriers on the total population is unknown.

**Habitat loss.** Physical loss of habitats, owing to land reclamation, swamp drainage or water course development, effectively has the same effect as migration barriers: concentration of the local stock in smaller and more downstream areas, resulting in increased (density-dependent) mortality.

**Increased predation.** Eel serve as prey for a variety of predators, including cormorants, herons, otters, whales and seals (ICES 2002). The number of cormorant breeding pairs has increased from less than 5000 to over 300,000 since 1970 (Van Eerden and Gregersen 1995) and estimates of their food demands indicates a considerable consumption of eel (ICES 2003). To what extent predation is counteracted by density-dependent compensatory processes is unknown (Dekker and De Leeuw 2003).

**Yellow and/or silver eel fisheries.** Exploitation of yellow eel reduces the local stock and ultimately the production of silver eel, if no strong density-dependent regulation occurs. Fisheries targeting silver eel reduce the run of silver eel from the continent, irrespective of potential density dependence. In exceptional cases (Dekker 2000c), yellow eel fisheries may reduce the production of female silver eel to 0.1% of the unexploited situation, but overall the reduction is estimated at some 47% (Dekker 2000b).

**Impeded downstream migration.** In many rivers, hydropower stations block the migration route of silver eel. Passage through the turbines of these stations poses risks of immediate death, serious injuries, or damages with delayed effects. Up to 100% of the eel entering the headrace of a turbine may be injured (average 30-70%; Larinier and Dartiguelongue 1989, Larinier and Travade 1999), but the effect of hydropower stations on the overall stock remains unknown.

At the bottom line, potential causes for a decline of the continental stock have been proposed. Some of these have been shown to occur and to have a considerable impact locally, but the net effect for the total population has not been quantified, except for fisheries (Dekker 2000b). For Lake IJsselmeer, an increase in mortality, rather than altered growth rate, presumably has caused the decline in abundance, but the underlying causes are not known.

![Graph](image_url)

**Figure 7** Relation between indexed market price (the Netherlands, year 2000 price level) and the European production (fishing yield and aquaculture combined), before 1990 (open symbols) and after 1990 (closed symbols). Data from Dekker (2003b,c) and Figure 6.

Price = 10.098 - 0.122 * Production

$R^2 = 0.3921$
(Dekker 2004a). The timing did not coincide with major changes in any of the factors implied by existing hypotheses (Castonguay et al. 1994a; EIFAC 1993), including habitat loss, migration barriers, eutrophication and the introduction of parasites (Dekker 2004a). Consequently, a parallel or synergistic effect of several factors seems most likely (Dekker 2003b). However, there is no procedure to estimate the relative contribution of each factor in the past, since only total mortality can be deduced from observed changes in historical abundance, and explaining the observed decline by increased mortality due to an unknown combination of factors therefore results in circular reasoning.

Oceanic stock dynamics

The oceanic phases of the life cycle cover the long spawning migration, the mating and spawning process, the development of the eggs into young Leptocephali, and the crossing of the Atlantic by the Leptocephalus. In the absence of adequate information on each of these phases, the dynamics during the oceanic life phase can only be reconstructed from trends in the adjoining life stages, notably the run of silver eel to, and the recruitment of glassseel from the ocean. This prohibits an analytical assessment of the processes involved and necessitates the adoption of a heuristic approach.

As discussed above (Continental stock dynamics – Observed trends), recruitment of glassseel from the ocean to the continent is in decline since 1980, and is now approximately two orders of magnitude below former levels, while the run of silver eel towards the ocean has not been quantified, but circumstantial evidence (overall fishing yield and local abundance estimates) indicates a gradual decline since the mid 1960s, to less than ca. 50% of the former level.

The hypotheses put forward to explain the decline in recruitment (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002), can be categorised into two distinct groups. First, some oceanic factors might have reduced larval survival and/or growth (Castonguay et al. 1994b; Desaunay and Guerault 1997; Dekker 1998), possibly related to the North Atlantic Oscillation (ICES 2001; Knights 2003). Secondly, continental factors might have reduced growth, survival or fecundity. This includes continental factors such as pollution, habitat loss, overexploitation of one or another life stage, and anthropogenic transfers of parasites and diseases (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002; Robinet and Feunteun 2002). All continental factors may affect the recruitment only through their effect on the size and/or quality of the spawning stock.

Oceanic hypothesis

Climate index

Long-term climate variation in the North Atlantic has been shown to correlate with observed trends in aquatic and terrestrial ecosystems throughout Europe (Ottersen et al. 2001). The widely used NAO index (Hurrell 1995)
Synthesis and discussion: Population dynamics of the European eel

**Figure 9** Trend in glasseel recruitment, and mean length (in Den Oever), and the NAO index, averaged over three years. Data from Dekker (1998, updated until 2003), NAO winter indices from Hurrell (1995).

quantifies alterations in atmospheric pressure between the subtropical Atlantic (Azores) and the Arctic (Iceland). An increased Azores High induces more and stronger winter storms crossing the Atlantic in a more northerly track, and shifts the Gulf Stream to a more northerly position. A number of alternative indices have been defined, varying in the number of months included, the analysis procedure and the exact locations measured. The NAO winter index (Hurrell 1995) is the most frequently used, because it provides the most pronounced signal. From the early 1940s until the early 1970s, this index exhibited a downward trend, followed by a gradual increase until the mid 1990s. The most recent data indicate a return to average values (Figure 9).

Processes involved in the decline of the oceanic stock

After leaving the continent, silver eel possibly swim actively against the Gulf Stream, to the presumed spawning place in the Sargasso. Leptocephali drift with the Gulf Stream (McCleave et al. 1998), towards the European continent. The migratory phase of adults and larvae as well as the egg and larvae production might have been influenced by climate variation. The following processes have been hypothesized:

**Adult migration.** Adult silver eel can reach the Sargasso by active swimming (Van Ginneken and Van den Thillart 2000), but an increased strength of the Gulf Stream might have slowed down and hampered the migration (Castonguay et al. 1994b; Knights 2001);

**Adult congregation.** To spawn effectively, adults presumably congregate somewhere in the North Atlantic, possibly triggered by the existence of thermal fronts. Altered climate might have changed the strength or position of these fronts (Castonguay et al. 1994b), and thereby have affected mating success;

**Nutrient availability.** Spawning might be synchronized with spring mixing of surface and deeper water in the ocean, leading to increased nutrient availability and plankton blooms (Knights 2001), which could link larval productivity to climate (Castonguay et al. 1994b; Feunteun 2002);

**Larval growth and survival.** Growth, survival and development of Leptocephali might have been impaired by climate change (Dekker 1998; Desaunay and Guerault 1997) through a prolonged migratory phase (Feunteun 2002; Knights 2001), or a mismatch to the temporal or spatial window for successful metamorphosis to the glasseel stage (Castonguay et al. 1994b), resulting in poor recruitment or an aberrant distribution.

Observed trends

The most pressing argument in favour of an oceanic hypothesis has been the striking similarity in trends observed for the European and American eel recruitment (Castonguay et al. 1994b; Figure 8). The American data refer to the ascent of young yellow eel at the Moses Saunders Dam, near Ontario in the St Lawrence River, while the European recruitment refers to glasseel in Den
The eel at the Moses Saunders Dam have an average age of 4 fresh-water years, which might explain the observed time lag behind the Den Oever data. However, the trend in abundance of 20-25 cm yellow eel in Lake IJsselmeer (corresponding to an estimated age of approximately 4 fresh-water years) does not match nearly so closely (Figure 8). The correlation between these even-aged data series is similar to that between European and Japanese eel recruitment, while the latter can hardly be believed to be governed by the same type of oceanic process, because the Atlantic (NAO) and Pacific (El Niño Southern Oscillation) climate indices do not correlate (Stenseth et al. 2003).

In the late 1980s, the glassseel arriving in estuaries were smaller than before (Figure 3; Dekker 1998; Desaunay and Guerault 1997). Following a trough in 1991, average length in the Netherlands recovered to a value (in 2003) just above the long-term average. The observed minimum length in 1991 (when the NAO index reached a maximum; Figure 9) may have indicated bad feeding conditions for the Leptocephali, which in turn might have caused low survival (Dekker 1998; Desaunay and Guerault 1997). However, both the NAO index and average glassseel length recovered to average values since 1991, while abundance dropped further, to a new all-time minimum in 2001. The link between feeding conditions and ocean climate apparently continued, but not that for ocean climate and the abundance of recruitment (Figure 10).

In summary, the oceanic hypotheses have triggered considerable speculation, but the support given recently vanished, because the latest recruitment information did not fit the earlier established pattern, and the cross-Atlantic correlation fails when the same life stage is considered.

Continental hypothesis

While oceanic hypotheses essentially assume that the production of new recruits depends primarily on environmental factors, and is therefore largely independent of the number of spawners, a declining spawning stock must at some stage start to affect future recruitment. Implicit in many of the suggested continental hypotheses (as explicitly raised by Dekker 2003c), is the assumption that the current size of the spawning stock already affects the number of progeny.

During the continental life stages, the weight of individual eel increases (from 0.3 to 100 and 400 g for males and females, respectively), while the number of eel in an early 1990s year class declines from by two orders of magnitude from >2000 million glassseel down to less than 10 million silver eel (Dekker 2000b). While growth rate may vary geographically, spatial variation in the average size at silvering is small (Vøllestad 1992); information on temporal variation in size at silvering is lacking. This suggests, that if the biomass of the spawning stock has been reduced, this has more likely been caused by a reduction
in the number of spawners, than by a reduction in individual weight.

As discussed above (Continental stock dynamics – Observed trends), a prolonged decline has been observed in fishing yield throughout Europe, and in stock abundance locally. Potential processes contributing to this decline have been hypothesised (Continental stock dynamics – Processes involved in the decline of the continental stock), but the ultimate causes have not been determined. All hypotheses infer that total mortality in the continental phase has increased over the past decades (either directly, or through reduced growth, leading to a prolonged continental phase), which is consistent with the observed decline in abundance of the stock in Lake IJsselmeer and in Swedish recruitment series (Figure 4), as well as with the trend in total fishing yield (Figure 5). Increased mortality in the continental phase should have led to a lower production of spawners, which in turn might have limited subsequent recruitment.

In addition to the hypotheses focusing on increased continental mortality, two hypotheses have been raised, in which the quality rather than the quantity of silver eel has been affected. These are: Parasites, affecting swimming potential negatively. The increasing number of non-native parasites and diseases, recorded during the past decades (Keie 1991), might have had negative consequences for the population. In particular, Anguillicola crassus, a parasite of the swimbladder, might have negatively affected the swimming ability of silver eel on their way back to the spawning grounds. Although the direct effects of Anguillicola in healthy natural stocks appear to be limited, synergistic effects with bacterial infections or other stress factors might be considerable (Keie 1991). Contamination, affecting fecundity negatively. Owing to their high fat content, eel easily accumulate high concentrations of organochlorine pesticides and PCBs. Although contamination is high in many waters, direct effects are limited, since these substances remain stored in the body fat (Knights 1996). However, delayed effects during spawning migration and on fecundity may be envisaged once the fat reserves are being used and substances released in the blood (Robinet and Feunteun 2002).

These two hypotheses assume that continental processes have a delayed effect on the reproduction through the quality of the silver eel running from the continent. Information on the continental processes is available locally, but the average effect on the overall silver eel run is unknown.

Putting the hypotheses to the test

To quantify the potential role of the main factors in the overall population dynamics, a comprehensive model will be developed, for which parameters can be estimated from the data series presented above (Continental stock dynamics – Observed trends and Oceanic stock dynamics – Observed trends).

There are three main processes to consider, potentially explaining the observed decline in recruitment:

- Quality of silver eel escaping to the ocean;
- Effect of ocean climate on reproductive success; and
- Relation between recruitment and spawning stock biomass.

Because there is no quantitative evidence on population-average contamination levels or parasite burden and their potential effect during the un-observed ocean migration, there is no way to test the spawner-quality hypothesis. Consequently, this hypothesis has to be ignored here.

Ocean climate

The assumption is made that the NAO index is linearly related to larval survival. Since there may be an unknown time lag between the impact of ocean climate on a particular life stage and the glass eel recruitment, and because climate may have a cumulative effect over several years, the NAO index was lagged by 0 to 3 years in the analysis, each time lag being concurrently evaluated:

\[ \log \left( \frac{R_i}{SSB_{i-1}} \right) = \log(\alpha) + \sum_{k=0}^{3} \gamma_k \times NAO_{i-k} \]  

where \( R_i \) is the number of recruits in year \( i \), geometric mean of the recruitment trends of Ems, Loire and Den Oever (ICES 2004), scaled to the absolute value for 1993 (Dekker 2000b); \( SSB_{i,j} \) is the spawning stock biomass* in year \( i-j \); time trend (Dekker 2003c), scaled to the absolute value for 1993 (Dekker 2000b), time lagged by \( j \) years, \( j = 0 \ldots 10 \); \( NAO_{i-k} \) is the NAO winter index (derived from http://www.cgd.ucar.edu/~jhurrel/nao.html) in year \( i-k \), time lagged by \( k = 0 \ldots 3 \) years; \( \gamma_k \) are parameters of the climate effect, \( k = 0 \ldots 3 \), and \( \alpha \) is a constant, scaling recruitment and spawning stock biomass.

*Terminology: Spawning Stock Biomass usually refers to the biomass of females taking part in the spawning process. Here, the run of silver eels from the continent is assumed proportional to landings from fisheries in continental waters, while an assessment of the whole continental stock is used to scale this trend. Thus, the figures on SSB presented refer to the mixed-sexes stock running from the continent, rather than females-only biomass on the spawning grounds. These two estimates change proportionally, if sex ratios in the silver eel run and sex-related mortality during spawning migration have not changed over the years.
The spawning stock biomass $SSB_{i-j}$ is assumed proportional to the time-lagged continental yield. The lag period should cover the variable time interval between commercial harvest and silverying of the escaping fellows, the duration of the migration to the spawning place, the reproductive and larval phase, the metamorphosis to glassieel and the migration into the estuaries; this takes an unknown period in the continental phase, and presumably two years in the ocean. The goodness-of-fit of the final model (paragraph Oceanic stock dynamics - Comprehensive analysis) as a function of SSB time lag shows two nearly equal minima, at 2 and 6 years (Figure 11). The remainder of the analysis uses a time lag of 2 years only, because trial runs with time lags between 2 and 6 years did not show substantially different results.

**Stock-recruitment relation**

Ricker (1975) assumed a lineair relationship between reproductive success (quantified by the logarithm of the number of recruits divided by spawning stock biomass) and the size of the spawning stock, resulting in a decline in recruitment at very high spawning biomass, while Bevorton and Holt (1957) used an asymptotically increasing relationship between recruitment and spawning stock biomass equivalent to:

$$\log \left( \frac{R_i}{SSB_{i-j}} \right) = \log(\alpha) - \log \left( 1 + \frac{SSB_{i-j}}{\beta} \right)$$

where $\alpha$ and $\beta$ are constants to be estimated, scaling recruitment and SSB respectively.

Recently, interest has been raised in the behaviour of stock-recruitment relationships at low spawning stock biomasses (Myers et al. 1995). Once a low spawning stock biomasses has been reached, this might result in an unavoidable extinction of the stock, if the reproductive success falls down at low spawning stock size. At the individual level, such a decline in reproductive success at low density is known as the Allee effect (Allee 1931), while the term depensation is used for comparable declines at the population level. The existence of depensation has serious effects on the likelihood of stock collapse (Stephens and Sutherland 1999), but is difficult to prove. In a meta-analy-

**Table 1** Analysis of variance in reproductive success [log(Recruits per unit of SSB)]. Stock/Recruitment relations are developed as a Type 1 analysis (sequential inclusion of depensation), NAO indices as a Type 3 analysis (marginal contributions of each index), while the combined analysis is a Type 3 analysis.

<table>
<thead>
<tr>
<th>Model</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stock/Recruitment relation</td>
<td>11.049</td>
<td>1</td>
<td>11.05</td>
<td>38.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Stock/Recruitment relation with depensation</td>
<td>24.909</td>
<td>1</td>
<td>24.91</td>
<td>87.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Sub-total</td>
<td>35.957</td>
<td>2</td>
<td>17.98</td>
<td>63.42</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NAO, time lag: none</td>
<td>0.353</td>
<td>1</td>
<td>0.35</td>
<td>1.25</td>
<td>0.270</td>
</tr>
<tr>
<td>NAO, time lag: 1 year</td>
<td>0.754</td>
<td>1</td>
<td>0.75</td>
<td>2.66</td>
<td>0.110</td>
</tr>
<tr>
<td>NAO, time lag: 2 years</td>
<td>0.303</td>
<td>1</td>
<td>0.30</td>
<td>1.07</td>
<td>0.307</td>
</tr>
<tr>
<td>NAO, time lag: 3 years</td>
<td>0.015</td>
<td>1</td>
<td>0.02</td>
<td>0.05</td>
<td>0.818</td>
</tr>
<tr>
<td>Colinearity between NAO-indices</td>
<td>0.366</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sub-total</td>
<td>1.776</td>
<td>4</td>
<td>0.44</td>
<td>1.57</td>
<td>0.200</td>
</tr>
<tr>
<td>Colinearity of NAO and Stock/Recruitment</td>
<td>10.294</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Explained</td>
<td>48.027</td>
<td>6</td>
<td>8.00</td>
<td>28.24</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Unexplained</td>
<td>12.757</td>
<td>45</td>
<td>0.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>60.784</td>
<td>51</td>
<td>1.19</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Synthesis and discussion: Population dynamics of the European eel

Figure 12 Relation between reproductive success (number of recruits per unit of SSB) and the SSB, corrected for the correlation with NAO (time lags 0-3). SSB is assumed proportional to continental landings, 2 years prior to recruitment. Data labels indicate the years 1950-2001.

ysis of 128 stocks, Myers et al. (1995) showed that three showed signs of depensation.

Depensatory variants of the Ricker stock-recruitment curve (e.g. Chen et al. 2002) include an offset for the spawning stock biomass, below which the function is undefined. This model discontinuity poses serious problems for parameter estimation, and therefore the (continuous) depensatory variant of the Beverton and Holt stock-recruitment relation is preferred here:

\[
\log \left( \frac{R_i}{SSB_{i-j}} \right) = \log(\alpha) + (\delta - 1) \times \log(SSB_{i-j}) - \log \left( 1 + \frac{(SSB_{i-j})^\delta}{\beta} \right) + \sum_{k=0}^{3} \gamma_k \times NAO_{i-k} + \epsilon_i
\]

where \(\delta\) is the depensation parameter to be estimated.

Comprehensive analysis

Combining the models for climate variation and a (depensatory) stock-recruitment relationship, and adding an error-term, the final model reads:

\[
\log \left( \frac{R_i}{SSB_{i-j}} \right) = \log(\alpha) + (\delta - 1) \times \log(SSB_{i-j}) - \log \left( 1 + \frac{(SSB_{i-j})^\delta}{\beta} \right) + \sum_{k=0}^{3} \gamma_k \times NAO_{i-k} + \epsilon_i
\]
Chapter 11

Figure 13 Relation between reproductive success (number of recruits per unit of SSB) and the NAO Index (time lag 1), corrected for the stock-recruitment relation. Data labels indicate the years 1950-2001.

to the depensatory stock-recruitment relation. Without the depensatory effect, the stock-recruitment relation explained only 18% of the variance, fitting an upward sloping straight line through what appears to be a curved relationship (Figure 12). Only 3% of the total variance can be attributed to the NAO index variation directly, which is statistically insignificant, but 17% is shared among climate indices and the stock-recruitment relations.

The variation in the NAO index from -5 in 1969 to +5 in 1989 corresponded to a decrease in reproductive success, by a factor 2 in the full model (Figure 13), and by a factor 8 in a reduced model excluding the stock-recruitment relation. The estimated SSB varied from 4000 t in 1966 to 1250 t in 2001. Reduction from the maximum to 3100 t increased predicted reproductive success marginally, while the further reduction to 1250 t lowered predicted reproductive success by a factor 40. NAO index and stock-recruitment-relation together predicted a 100-fold variation in reproductive success, somewhat less than the 300-fold variation in the observations.

In conclusion, recruitment has fallen since 1980, by nearly an order of magnitude per generation. The observed variation in ocean climate as represented by the NAO index, is not significantly correlated to this observed trend. If the low spawning stock size is largely responsible (i.e. a stock-recruitment relation), strong depensation effects must have occurred in the years after 1980, below an estimated spawning stock biomass of 2250 t. Other factors affecting quality of spawners (e.g. parasites or contamination) might be involved as well, but those hypotheses cannot explain the discontinuity in reproductive success since 1980, the absence of adequate data for a formal test prevents judgement of their relevance.

Potential depensatory mechanisms

Eel in contrast to other fish

The relation between individual reproductive success and population abundance has been investigated, at a theoretical level (reviewed by Courchamp et al. 1999) as well as in field studies for a range of taxa. In fish, several mechanisms inducing Allee-effects have been suggested: chance extinction of sub-stocks (Routledge and Irvine 1999); depensatory predation (Shelton and Healey 1999); spawners predating juvenile competitors (Walters and Kitchell 2001); size dependent predation (De Roos and Persson 2002); and social mating behaviour (Rowe and Hutchings 2003). However, the evidence for depensation in exploited populations is bleak (Myers et al. 1995; Myers 2001). Current results suggest that strong depensation occurs in eel at a spawning stock biomass below 2250 t, which is only half the historical maximum. Assuming an equal sex ratio initially, an annual mortality of 0.24 (Dekker 2000b) experienced by females for about 3 years more than by males, and a 4 times higher weight for females than for males at silvering (Vollestad 1992), 70% of this biomass will consist of females, amounting to circa 4 millions individuals. Strong and discernable depensation at this population level would single out the eel amongst exploited
Synthesis and discussion: Population dynamics of the European eel

Spatial and temporal isolation
Spatial isolation of sub-stocks might give rise to depensation, because this increases the risk of local extinction even at moderate total population size, as shown for coho salmon (Oncorhynchus spp.) by Routledge and Irvine (1999). For eel, evidence for a life-long spatial subdivision of the population is scant, and current discussions focus on potential clinal variation (Wirth and Bernatchez 2001; Daemen et al. 2001). However, the wide continental distribution and variable-length migration routes may result in temporal isolation of sub-stocks on the spawning grounds. Silver eel from different parts of the distribution area have to travel at least a great circle distance to the Sargasso Sea (26°N, 55°W) ranging from 4600 km on the Portuguese west coast and 4900 km in south-western Ireland, to 7000 km in Finland and 8200 km from the River Nile. The typical migration season lasts from September to December in most of the distribution area (Lobón-Cerviá and Carrascal (1992) report a longer season in northern Spain, lasting from September through March; many other literature sources touch upon the typical season in passing, but I have not found explicit information). Under a reasonable assumption for the trans-Atlantic swimming speed of half a body length per second (cf. Van Ginneken and Van den Thillart 2000), the variation in distance would correspond to an estimated duration of the journey of 106 to 190 days. In combination with a typical migration season of at least 3 months, silver eel may be expected to arrive in the Sargasso Sea during more than six months of the year. After arrival and following a straining migration across the Atlantic, individual eels may not be in a condition to wait for indefinite periods before finding a mate. Thus, the instantaneous size of the spawning stock present at any point in time may vary, depending on the number of eel that have arrived during the preceding period. A temporal analogy to the analysis of spatially isolated coho sub-stocks by Routledge and Irvine (1999) then predicts that the instantaneous spawning stock might be below the minimum threshold for successful spawning during parts of the season, even at a moderate total spawning stock biomass. Reductions in total spawning stock might result in progressively more isolated and shorter intervals of successful spawning, and increased genetic differences between spawning peaks. The suggested spatial mechanism for creating temporal sub-stocks closely resembles temporal allopatry, a possible explanation for observed clinal variation in genetics in European eel (Wirth and Bernatchez 2001), and in Japanese eel (Chan et al. 1997). However, temporal alloptry additionally presumes non-random recruitment, maintaining a cross-generation link with the parental origin on the continent, for which there is no evidence (McCleave et al. 1998). But even without this link, the mechanism of a widespread distribution creating a temporal structure in the spawning stock may have contributed to the observed strong depensation.

Genetics
The level of inbreeding, genetic drift and hybridisation are related to population size. Effective population size for the European eel may be estimated at \(10^4\) (Wirth and Bernatchez 2003). Inbreeding is present, but at a level typical for fish (Daemen et al. 2001). Although American eel occur in low numbers in mainland Europe (Boëttius 1980), hybridisation is apparently restricted to Icelandic waters (Avice et al. 1990), a far-out corner of the distribution area (Dekker 2003a). Moreover, the risk of hybridisation for the European eel not only depends on its own abundance, but also on the abundance of related species with crossbreeding potential. In the Atlantic, the only candidate, American eel, declined at about the same time and the same rate (Castonguay et al. 1994b) and therefore has posed little risk for increased hybridisation in the past decades.

Predation
Predation mortality may induce Allee effects (Walters 1986; Shelton and Healey 1999), if predators increase their search efforts when prey are scarce, and relax when they are easily satiated by abundant prey, i.e. when predator-prey encounters are not just random events. Sources of eel mortality during the ocean life stages are unknown, although Tesch (1986) tentatively listed dolphins, whales and deep-sea fish as potential predators. The spawning aggregation of eel is presumably taking place in a well-defined area (Tsukamoto et al. 2003), in a well-defined period of the year (March into June), effectively creating a predictable feeding opportunity for any suitable predator. However, if predation induced the apparent depensation, it is not clear why the unknown predator has gradually increased its impact over the past two decades of consistently low spawner abundance, and did not shift its attention to other prey or decline itself.

Social behaviour
Finally, several aspects of social behaviour have been suggested to induce depensatory processes, such as successful mate finding, complex mating systems, social facilitation by non-reproducing helpers and common brood care (Couchamp et al. 1999; Rowe and Hutchinson 2003). In eel, both eggs and youngest larvae are assumed pelagic; brood care for the free-floating offspring, either by parents...
or helpers, is hard to envisage. Although Deelder (1984) assumed promiscuous mass spawning in the wild stock, mating and spawning behaviour is only known from experimentally matured eel (Boëtius and Boëtius 1980), in which social spawning has been observed indeed (Van Ginneken et al. subm.). However, in all continental life stages, eel exhibit social, cooperative or mass behaviour: the bands of glasseel (cordon in French) migrating upriver (Bertin 1942, 1956); territorial behaviour and mass aggregations of yellow eel (Seymour 1984; Knights 1987); and mass aggregations of silver eel in open water (Nilsson 1860) and in front of migration barriers. Since group behaviour is observed in all life stages except in free-floating larva, it could well be an important feature of the mating and spawning behaviour too, determining reproductive success.

In conclusion, strong depensation clearly explains the collapse in recruitment observed in the European eel after a prolonged period of gradually declining abundance in continental waters. The most likely proximate cause of the depensation mechanism is disruption of a social mating system below a minimum threshold spawner density, during an increasing part of the spawning season.

**Prospects**

The abundance of the European eel in continental waters has been declining at a rate of ca. 4% per year for several decades, as has fishing yield, at ca. 3% per year. Analytical studies have documented local stock dynamics, but none has covered a period long enough to detect this gradual decline, or achieved a precision adequate to detect a slowly rising trend in mortality. These trends are easily detected in long-term retrospective data, but the detail available is insufficient to identify the processes involved. The recruitment failure since 1980 is probably secondary to the gradual decline of the continental stock, by means of Allee-effects (depensation) in the dynamics of the oceanic life stages, causing a 40-fold decline in reproductive success. Since 1980, recruitment of glasseel to continental waters has declined by 15% per year, or 85% per generation. In combination, gradually declining survival in the continental phases and dramatically declining reproductive success in the ocean constitute an inevitable extinction vortex. In the long run, management of the stock and fisheries may achieve a sustainable regime (Dekker 2004b), but in short term, any beneficial effect will be eclipsed by extremely low reproductive success. The most urgent management priority, therefore, is to restore the spawner run from continental waters to a level at which no depensation is likely to occur. Current low spawner production is linked to recruitment levels nearly one generation-time ago, in the mid-1990s. Since subsequent recruitment has been much lower than before, an even lower spawner production is expected in the near future. Opportunities for restoration will therefore soon fade away.

**Literature**


Synthesis and discussion: Population dynamics of the European eel


Chapter 11

Hydrobiologie: 707-716.


 Robinet T. and Feunteun E. 2002. Sublethal effects of expo-
Synthesis and discussion: Population dynamics of the European eel
