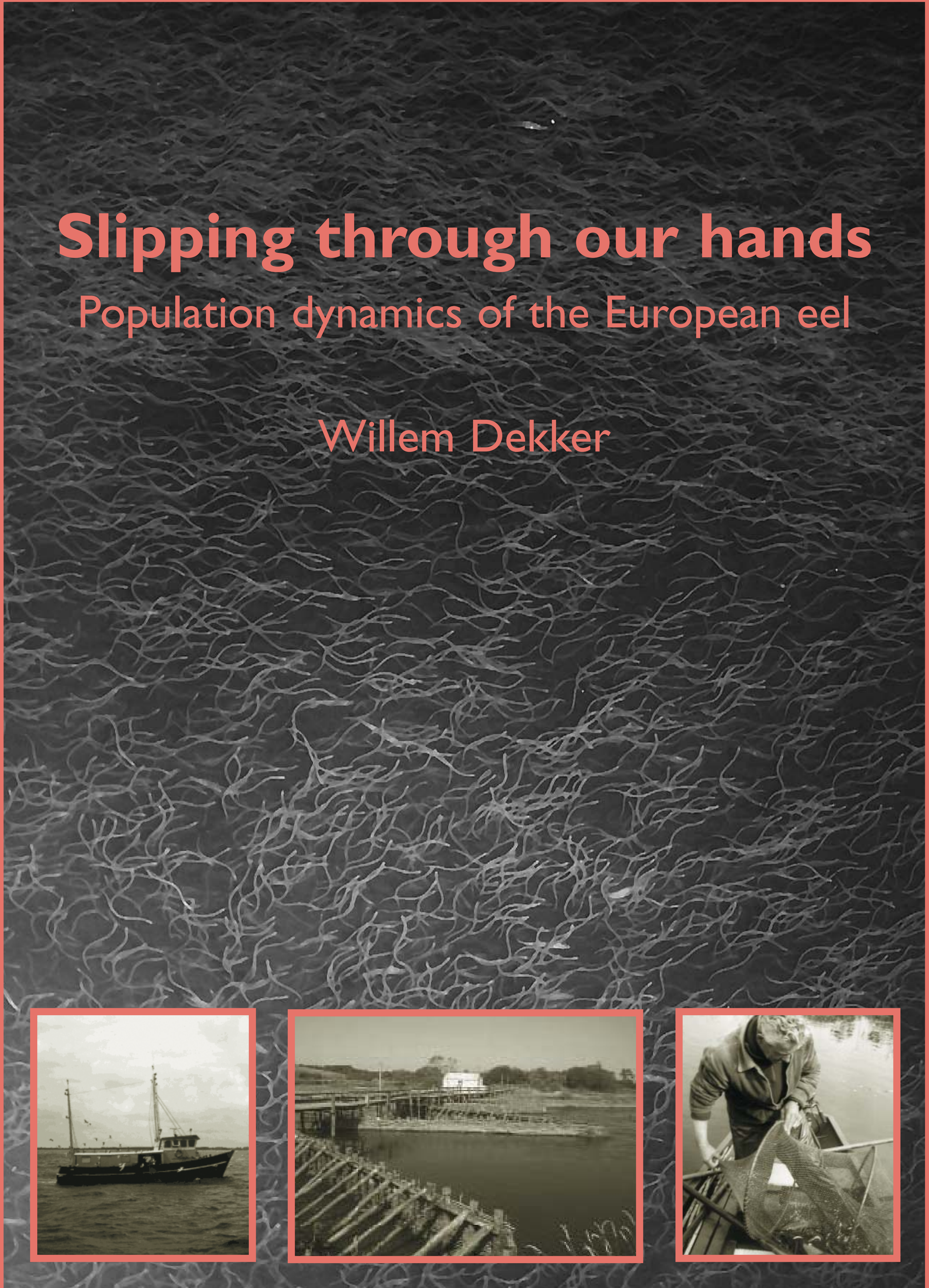
Willem Dekker Slipping through our hands Population dynamics of the European eel



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Samenvatting

De Europese aal of paling *Anguilla anguilla* (L.) komt voor in zoete en brakke wateren en langs de kusten van bijna alle landen in Europa, en langs de Middellandse Zee kusten van Afrika en Azië. De levenscyclus is nog steeds niet geheel bekend, maar bestaande kennis is in overeenstemming met het idee dat jonge aal afkomstig is van een enkele paaistand in de Atlantische Oceaan. In landelijke gebieden in het gehele verspreidingsgebied komt een kleinschalige visserij op de aal voor. De aal draagt daarmee in belangrijke mate bij aan de broodwinning van meer dan 25000 mensen.

In de afgelopen decennia is de stand van de aal drastisch verminderd, met nagenoeg een factor tien per generatie. Een aantal mogelijke verklaringen voor deze achteruitgang is gesuggereerd, waaronder anthropogene en natuurlijke processen, aangrijpend op ofwel de continentale dan wel de oceanische levensfases. Omdat de populatie-dynamica van de aal tot op heden nog vrijwel onbekend is, is de werkelijke oorzaak van de achteruitgang nog onduidelijk. De continentale levensstadia komen zeer verspreid voor, in doorgaans zeer kleinschalige binnenwateren, en bestandschattingen zijn beperkt gebleven tot een zeer klein deel van deze vele wateren.

De doelstelling van dit proefschrift is een analyse te geven van de dynamica van de Europese aal-populatie, met name vanwege de achteruitgang van het bestand in de afgelopen decennia. Tot op heden was onderzoek van de dynamica beperkt gebleven tot kortlopende studies, in begrensde gebieden. De recente ontwikkelingen wijzen echter op een langdurige verandering, die plaats vindt in vrijwel het gehele verspreidingsgebied. De uitdaging is om nu de bestaande ruimtelijke en temporele grenzen van het onderzoek te overstijgen, in meta-analyses (ruimtelijke aspecten) en de analyse van historische gegevens (temporele aspecten).

In de eerste sectie van dit proefschrift (hoofdstukken 2, 3, en 4) wordt de verspreiding van de populatie geanalyseerd, op de continentale schaal. De tweede sectie (hoofdstukken 5, 6, en 7) gaat in op historische ontwikkelingen gedurende de afgelopen decennia: in de intrek van jonge aal, in de abundantie van het continentale bestand en in de opbrengsten van de visserij. De laatste sectie tenslotte (hoofdstukken 9, 10 en 11) geeft een synthese van de informatie over de toestand van de populatie, op een grotere ruimtelijke en temporele schaal, teneinde een analyse te kunnen maken van de processen, die in lokale studies zijn aangetoond of waarvan wordt aangenomen dat ze optreden in de oceaan, welke de opgetreden vermindering van de populatie kunnen verklaren.

Tijdreeksen van de intrek van jonge aal, van de abundantie van het bestand en van de opbrengsten van de visserij tonen, dat de sterfte in de continentale levensfase gedurende de tweede helft van de 20^{e} eeuw is toegenomen. Deze toegenomen sterfte moet ook consequenties hebben gehad voor de omvang van de paaistand. Welke van de geopperde hypotheses deze toegenomen sterfte uiteindelijk verklaart blijft onduidelijk, omdat geen van de genoemde processen in de tijd overeenkomt met de waargenomen achteruitgang, en historische metingen onvoldoende detail (in ruimte en tijd) geven voor een meer gedegen analyse. Een integrale analyse van de veranderingen in het voortplantingssucces in relatie tot enerzijds de omvang van de paaistand, en anderzijds de NAO klimaats-index voor de sterkte van de Warme Golfstroom, toont dat klimaatsverandering onvoldoende verklaring geeft voor de waargenomen afname van de intrek van jonge aal. De relatie tussen enerzijds de waargenomen ontwikkeling in de intrek van jonge aal en anderzijds een (speculatieve) schatting van de omvang van de paaistand, toont dat het voortplantingssucces bij lage paaistand sterk lijkt af te nemen (depensatie). Van andere vissoorten zijn verschillende depensatoire processen bekend. Projectie van die processen op de ontwikkelingen bij de aal, wijst mislukking van sociaal paaigedrag bij geringe paaistand als meest waarschijnlijke verklaring aan. Dit is mogelijk nog versterkt door te grote verschillen in de aankomsttijd van paaiers op de (onbekende) paaiplaats, afkomstig uit het wijde verspreidingsgebied.

De intrek van jonge aal is de meest recente jaren opnieuw verminderd. Een verdere afname van de (paai)-stand in de nabije toekomst is daarom onvermijdelijk. Mogelijkheden voor een succesvol herstel van de aalpopulatie, tot een niveau waarbij geen depensatie meer optreedt, zullen daardoor binnenkort verloren gaan.

Summary

The European eel *Anguilla anguilla* (L.) is found and exploited in fresh, brackish and coastal waters in almost all of Europe and along the Mediterranean coasts of Africa and Asia. The life cycle has still not been completely resolved, but current evidence supports the view that recruiting eel to continental waters originate from a single spawning stock in the Atlantic Ocean. The continental stock supports small-scale fisheries in rural areas all over the continent, and provides main incomes for over 25,000 people.

In the past decades, the eel population has declined by nearly an order of magnitude per generation. A range of hypotheses has been suggested, including anthropogenic and natural causes, operating during either the continental or the oceanic part of the life cycle. Since the dynamics of the population are virtually unknown, the actual causes have not been identified. Within the continental life stages, the population is fragmented over a multitude of small-scaled inland water bodies, and assessments of the local stocks have been accomplished in only a fraction of the overall distribution.

The aim of this thesis is to analyse the dynamics of the population of the European eel, with reference to the decline in abundance observed in the past decades. Nearly all research on population dynamics had been limited to short temporal scales within a spatially restricted area, while the observed decline now points to prolonged processes operating over almost the entire population. The main challenge therefore is to widen the scope of the analysis, by relaxing the temporal and spatial constraints, in meta-analyses (spatial aspects) and analyses of historical data sets (temporal aspects).

The first section of this thesis (chapters 2, 3, and 4) addresses the spatial distribution and the continental scale of the population. The second section (chapters 5, 6, and 7) addresses decadal time-trends in the population, in recruitment, continental stock and fishing yield. Finally, the last section (chapters 9, 10 and 11) synthesises the information on the status of the population on a large spatial and temporal scale, and reviews processes documented in local studies, or hypothesised to occur in the ocean, potentially explaining the dynamics of the population in the past decades.

Time series on recruitment, stock abundance and fishing yield indicate, that mortality during the continental phase increased over the second half of the 20th century, which must have affected spawning stock size. Which of the hypothesized continental processes induced this increase in mortality, remains unclear, since all of them mismatch the observed trends in time, and for none of them detailed information has been collected over an adequate space and time. For the oceanic life stages, comprehensive analysis of the reproductive success in relation to spawning stock size and to the NAO index of ocean climate, refutes potential effects of ocean climate. The relation between the observed recruitment trend and tentative estimates of spawning stock indicates that reproductive success is strongly reduced at low stock size (depensation). Review of depensatory processes known from other species identifies disruption of social mating systems at low stock abundance as the most plausible depensatory mechanism, which may be exacerbated by the temporal subdivision of the stock among spawners originating from different locations on the continent. Because of the continued downward trend in recruitment, a further decline of the stock is anticipated. Therefore, opportunities for restoration of the stock to levels at which depensation is unlikely to occur, will soon fade away.

Résumé

L'anguille européenne *Anguilla anguilla* (L.) est répartie et exploitée en eaux douces, saumâtres et côtières dans presque tous les pays de l'Europe et le long des côtes méditerranéennes de l'Afrique et de l'Asie. Le cycle de vie n'est pas complètement connu, mais les preuves disponibles indiquent que les anguilles pénétrant les eaux continentales sont dérivées de seulement un stock des géniteurs dans l'Océan Atlantique. Le stock continental est exploité par des pêches rurales, distribuées sur tout le continent, qui fournissent les revenus principaux à plus de 25000 personnes.

Dans les décennies passées, la population d'anguille a diminué presque d'un ordre de grandeur par génération. Une gamme d'hypothèses a été suggérée, y compris des causes anthropogènes et naturelles, agissant sur le continent ou dans l'océan. Puisque la dynamique de la population est pratiquement inconnue, les causes réelles n'ont pas été identifiées. Sur le continent, la population est fragmentée en petits plans d'eau, très nombreux, et les évaluations des stocks locaux ont été accomplies dans seulement une petite fraction de la distribution globale.

L'objectif de cette thèse est d'analyser la dynamique de la population de l'anguille, en lien avec le déclin d'abondance observé dans les décennies passées. Presque toute la recherche sur la dynamique de population avait été limitée aux échelles temporelles courtes, et dans un secteur d'espace restreint, alors que le déclin observé suggère maintenant des processus prolongés agissant sur presque toute la population. Le défi principal est donc d'élargir l'échelle d'analyse, en assouplissant les contraintes temporelles et spatiales, dans les méta-analyses (aspects spatiaux) et les analyses des données historiques (aspects temporels).

La première section de cette thèse (chapitres 2, 3, et 4) examine la distribution spatiale et l'échelle continentale de la population. La deuxième section (les chapitres 5, 6, et 7) concerne les tendances décennales de la population, dans le recrutement, le stock continental et le rendement de pêche. En conclusion, la dernière section (chapitres 9, 10 et 11) synthétise l'information sur la population sur une grande échelle spatiale et temporelle, et considère des processus documentés dans des études locales, ou présumés dans l'océan, expliquant potentiellement la dynamique de la population dans les décennies passées.

Les séries chronologiques sur le recrutement, l'abondance du stock et le rendement de pêche indiquent que la mortalité pendant la phase continentale a augmenté en deuxième moitié du 20ième siècle, ce qui doit aussi avoir affecté le stock des géniteurs. Il n'est pas clair quels processus continentaux présumés induisent cette augmentation de la mortalité, puisqu'aucun ne correspond aux tendances temporelles de la population et qu'il manque d'information détaillée dans le temps et l'espace sur ces processus. Pour les étapes océaniques de la vie, l'analyse du succès reproducteur par rapport au stock des géniteurs et par rapport au climat océanique, tel qu'indexé par le NAO, réfute des effets potentiels du climat océanique. La relation entre le recrutement observé et les évaluations expérimentales de stock des géniteurs indique que le succès reproducteur est fortement réduit à faible abondance (dépensation). L'examen des processus dépensatoires connus chez d'autres espèces identifient la rupture des systèmes sociaux à faible abondance comme mécanisme dépensatoire le plus plausible, qui peut être aggravé par la subdivision temporelle des stocks provenant de différents endroits sur le continent. En raison de l'évolution à la baisse continue dans le recrutement, un autre déclin des stocks est prévu. Par conséquent, les occasions pour restaurer le stock à des niveaux où la dépensation est peu probable disparaîtront rapidement.

Introduction

1

Background

The European eel *Anguilla anguilla* (L.) is found and exploited in fresh, brackish and coastal waters in almost all of Europe and along the Mediterranean coasts of Africa and Asia (Moriarty and Dekker 1997). The life cycle has still not been completely resolved, but current evidence supports the view that recruiting eel to continental waters originate from a single spawning stock in the Atlantic Ocean. The continental stock supports small-scale fisheries in rural areas all over the continent, and provides main incomes for over 25,000 people. Additionally, eel often dominates the fish fauna in lower rivers and estuaries, where it represent a considerable component of the aquatic ecosystem, and constitutes a major component in the diet of many other fish and semi-aquatic predators such as otters, cormorants, herons, etc.

In August 1984, when my research in IJmuiden began, I didn't know much about eel: there was some unbelievable story on their reproduction and I had seen annoyingly abundant swarms of glass eel during my nightly light-fishing trips along the Dutch coast. The main question in my research portfolio was to elucidate why the yield of Lake IJsselmeer eel fisheries had gradually declined, and did not recover to expectation after the ban on trawling in spring 1970. In the first years of my research, a decline in recruitment occurred, evidenced by the Den Oever glass eel catches, soon declining to 10% of former levels. Since that time, swarms of glass eel have never cluttered the nightly coast anymore.

In the early 1990s, it became clear that the low recruitment was something real, a lasting and widespread phenomenon. The decline observed in Den Oever occurred in almost the whole population, and the gradual decline of the fishing yield in Lake IJsselmeer was paralleled in many other local studies. The spatial and temporal scale of the IJsselmeer problem appeared to be rather irrelevant for its dynamics, and my attention shifted to the dynamics of the whole population, at the European level. Following my research of Lake IJsselmeer fisheries, this thesis now presents the results of my analyses of the dynamics of the European eel population.

Objective

In the past decades, the eel population has shown a major decline (EIFAC 1985; Moriarty and Dekker 1997; ICES 1976, 1999). Urgent management measures to protect and restore the stock have been advised, and emergency measures are required to reduce exploitation and other anthropogenic mortalities to as close to zero as possible, until a restoration plan is agreed upon and implemented (ICES 2002a). This pragmatic management advice is currently based on the Precautionary Approach (United Nations 1983; FAO 1995), that is: all anthropogenic impacts must be curtailed, which might potentially have contributed to the observed decline. Ultimately, cost-effective restoration measures must focus on the main factors actually causing the current decline. Identification, and quantification, of these factors constitutes a major scientific challenge, given the incomplete knowledge on the biology of the eel, the temporal and spatial scale at which the decline occurred, and the rate at which the eel disappears.

The dynamics of the European eel population are virtually unknown. Within the continental life stages, the population is fragmented over a multitude of small-scaled inland water bodies, and assessments of the local stocks have been accomplished in only a fraction of the overall distribution (Moriarty and Dekker 1997; Moriarty 2003). A range of hypotheses on the causes of the observed decline has been suggested (EIFAC 1993; Castonguay et al. 1994; Moriarty and Dekker 1997; ICES 2002b), the majority of which is derived from local studies showing that specific factors had a considerable impact. These include: exploitation of all continental life stages, habitat loss (land reclamation, migration barriers, increased mortality on emigrating spawners), and increased predation; locally severe pollution and parasite infection have limited effects within the continental life stages, but potentially have a delayed effect on the population dynamics in the oceanic phase. Assessment of the impact of a specific factor on the overall population requires extension of the spatial and temporal scale of the analysis. For the spatial scale, from the local level at which an effect of a specific factor has been established, to the continental scale at which the decline became apparent; and for the temporal scale, from a typical study period of a few years to the decades over which the decline occurred.

The question arises how to analyse the dynamics of a spatially disaggregated population. The small ad-hoc selection of all spatial subunits analysed so far is presumably not representative for the total population. Since neither the size of the overall population and its quantitative distribution, nor the spatial variation within, were known, the objective of the first section of this thesis is to analyse the distribution, size and spatial structure of the population.

The eel is a long-lived animal, with an average age at maturation of 5-15 years for females, and a maximum observed age of 84 years (Vøllestad 1992; Dekker et al. 1998). Dominant trends in the population have occurred at a decadal time scale, whereas most field studies have covered periods of a few years only. Although the decline in the eel population was noted nearly three decades ago (ICES 1976), the declining trends have been documented primarily by circumstantial evidence (Moriarty and Dekker 1997). Evaluation of the processes contributing to the historical decline requires that the trend is adequately quantified. The objective of the second section of this thesis is to provide retrospective analyses of quantitative trends in recruitment, abundance and fishing yield, over the past decades of decline.

The eel stock being in decline, time for in-depth research is running out: more and more data series become discontinued, because of the declining economical interest in eels, and problems in sampling a sparse stock. The hypotheses on the potential causes (EIFAC 1993; Castonguay et al. 1994; Moriarty and Dekker 1997; Feunteun 2002) have been underpinned by evidence on local effects, and by temporal correlations between the assumed effect and the observed decline in glass eel recruitment. Despite major research efforts in the past decade, the aim of a complete analysis of the population dynamics of the eel is still beyond reach. Urgent management advice to protect and restore the population has therefore been based on a precautionary approach: restrict all anthropogenic impacts on the population wherever they exceed sustainable limits (ICES 2002a). The question arises, whether the new information on the status of the stock enables a restriction of the range of hypotheses on the causes of the decline. The objective of the last section of this thesis then is to provide a review on the status of the stock, and to discuss existing hypotheses with reference to current knowledge.

Outline of this thesis

As discussed above, the aim of this thesis is to analyse the dynamics of the population of the European eel, with reference to the decline in abundance observed in the past decades. Nearly all research on population dynamics had been limited to short temporal scales within a spatially restricted area, while the observed decline now points to prolonged processes operating over almost the entire population. The main challenge therefore is to widen the scope of the analysis, by relaxing the temporal and spatial constraints, in meta-analyses (spatial aspects) and analyses of historical data sets (temporal aspects).

The first section of this thesis (chapters 2, 3 and 4) addresses the spatial distribution and the continental scale of the population.

In chapter 2 (*On the distribution of the European eel and its fisheries*), the spatial distribution of the eel population is analysed. Schmidt (1909) described the outer limits of the continental distribution area (North Cape to Canary Islands), but left the quantitative distribution within this large area untouched. A meta-analysis of published records of fishing yields shows that the prime area of glass eel recruitment is the Bay of Biscay, while the highest inland production is achieved in the Western Mediterranean. The relation between the life stages exploited by fisheries and the local stock abundance is shown.

Given our lack of knowledge on the overall population, chapter 3 (*A Procrustean assessment of the European eel stock*) provides an assessment of the stock that is adapted to cope the scarcity of data. Although this pragmatic approach severely limits reliability, it results in an estimate of the overall population size by life stage, which is later used as a benchmark for the overall population assessment in chapter 11.

The wide distribution area, analysed in chapter 2, by no means consists of a coherent stock and a continuous distribution. Chapter 4 (*The fractal geometry of the European eel stock*) analyses the spatial patterns within the continental population, ranging from coherent trends in recruitment over almost the entire continent, to a completely fragmented distribution in inland waters, with major variations between close-by water-bodies. Fisheries in inland waters are as fragmented as the stock. Although the eel is probably one of the fish stocks in Europe yielding highest employment, typical eel fisheries consist of a few fishermen, operating a rural and traditional enterprise.

The second section (chapters 5, 6 and 7) addresses decadal time-trends in the population, in recruitment, abundance and fishing yield. Although declining trends have been noticed decades ago, they have hardly been documented before and an integrated analysis did not exist.

Chapter 5 (*Long-term trends in the glass eels immigrating at Den Oever, the Netherlands*) provides an analysis of four decades of Dutch glass eel monitoring, in order to pick up potential signals of changes in the oceanic life stages. The decline in abundance appeared to be paralleled by a diminishing average length of the glass eel, while the timing of the immigration season only reflects local factors (water temperature). The trend in length hints at altered conditions in the preceding, oceanic life stage.

Information on eel fisheries is often considered scattered, incomplete and unreliable. Chapter 6 (*Did lack of spawners cause the collapse of the European eel,* Anguilla anguilla*?*) provides a statistical analysis of time-trends in published data on yield. Although scattered and incomplete, these data indicate a prolonged decline in fishing yield, starting two or more decades before the drop in glass eel recruitment. Was the recruitment failure in the 1980s the result, rather than the cause of a declining stock?

That raises the question, whether yield dropped owing to diminishing exploitation, or is indicative of a decline in population abundance. For Lake IJsselmeer, data on the commercial exploitation as well as on scientific stock surveys cover more than half a century, and using a complex statistical analysis in chapter 7 (*What caused the decline of the Lake IJsselmeer eel stock after 1960?*) estimates of stock trends by size class were obtained. The decline in abundance started in the 1960s, and was more pronounced in the larger size classes. Since this timing does not coincide with any of the suggested causes, a synergistic or parallel effect of several factors seems most likely.

Chapter 8 (*Impact of yellow eel exploitation on spawner production in Lake IJsselmeer, the Netherlands*) focuses on a specific process, the impact of fisheries and stands somewhat apart from the remainder of this thesis. Based on a length-structured equivalent to the Virtual Population Analysis model, Lake IJsselmeer appears to be extremely over-exploited. Consequently, the local production of silver eel contributing to the spawning stock, is negligible. Sustainable management of eel fisheries requires controls on the exploitation of all life stages, including escapement of silver eels.

The last section (chapters 9, 10 and 11) synthesises the information on the status of the population on a large spatial and temporal scale, and reviews processes documented in local studies, or hypothesised to occur in the ocean, potentially explaining the dynamics of the population in the past decades.

In chapter 9 (*Status of the European eel stock and fisheries*), preceding results are summarised, focusing on the spatial distribution, the time trends, and the structure of exploitation. Potential causes and consequences of the observed decline are reviewed. It is concluded that implementation of a stock recovery plan and extending management and research to appropriate temporal and spatial scales will be a major challenge. Subsequently, chapter 10 (*A conceptual management framework for the restoration of the declining European eel stock*) addresses this challenge on a conceptual level. Although the eel problem constitutes an exceptional case in fish stock management owing to the eel's longevity and widespread but fragmented occurrence, existing nuts and bolts can be selected and linked to constitute an achievable and sustainable management regime.

Despite the clear evidence of a decline in recruitment (chapters 4 and 5), in stock abundance (chapter 7) and fishing yield (chapter 6), the question remains what process caused these trends. Chapter 11 (*Synthesis and discussion: Population dynamics of the European eel*) addresses this question at the population level. Suggested hypotheses are reviewed, and contrasted with available evidence (primarily time trends by life stage), in order to narrow the range of defendable hypotheses on the causes of the decline. The widely adhered view that a change in ocean climate caused recruitment to decline does not match most recent data, and does not explain the preceding decline in abundance and yield. In contrast, if mortality increased during the continental stages, a decreasing abundance and a lower yield would be expected, ultimately resulting in a low spawning stock biomass, restricting subsequent recruitment.

Finally, chapter 12 (*De populatie-dynamica van de Europese aal* [in Dutch]) provides a comprehensive and richly illustrated overview of all information presented in this thesis, for the non-scientific reader. The illustrations presented might assist others not familiar with eel in appreciating the details. Additionally, the context of the Dutch eel fisheries is presented, comparing the eel to other exploited fish stocks in the Netherlands, and discussing the political setting within which the fisheries on Lake IJsselmeer developed.

My research on eel started 20 years ago. I have taken up the challenge to reconsider the analysis of population dynamics of the eel at a spatial and temporal scale matching the natural scale of the population. In the mean time, the decline in the stock has been noted (EIFAC 1985), a warning has been stated that the stock was in a bad state (EIFAC 1993), and an official management advice was issued to compile a stock recovery plan (ICES 1999). Meanwhile, the stock continued its decline, and current monitoring efforts become less effective, more and more often catching no eels at all. The International Eel Symposium 2003 in Quebec therefore raised an urgent alarm that opportunities to protect the eel will fade along with the stock. The epilogue to this thesis (*Worldwide decline of eel resources necessitates immediate action*) reproduces and repeats this insistent alarm.

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On the distribution of the European eel and its fisheries

2

Canadian Journal of Fisheries and Aquatic Sciences 60: 787-799 (2003)

For the distribution of the European eel (*Anguilla anguilla*), only Schmidt (1909) has conducted substantial investigations, yielding a qualitative description (Atlantic and Mediterranean coasts of Europe and Northern Africa). In this article, a meta-analysis of reported fishing yields is presented, showing a major concentration of glasseel yield in the Bay of Biscay (and possibly farther south) and of yellow and (or) silver eel yield in the western Mediterranean. Fisheries target the glasseel stage at highest stock density, and shift to the silver eel stage at low density. Because there is no suitable habitat in the Sahara, the southern limit is, contrary to Schmidt's belief, primarily determined by continental conditions. From the centre of the distribution to the north, a long and slow decline in density occurs. The mismatch between northern temperatures and the species' preference, in combination with the very low abundance, indicates that the European eel is best seen as a warm-water species – like most other eel species (*Anguilla* spp.) – showing a considerable northern diaspora.

The continent-wide distribution of the European eel (*Anguilla anguilla* (L.)) is generally considered a well-established fact. Schmidt (1909) collected information on the distribution area of the different eel species on the continents, and interpreted the distribution in relation to his new insight in the oceanic life stages (Schmidt 1923). To my knowledge, this is the one and only comprehensive study of the distribution area of the European eel (Figure 1). Since 1909, all maps of the distribution area cite Schmidt (1909) as their prime source of information. Schmidt's focus was on the outer limits of the distribution area. Although there is little doubt that eels occur within the outer limits (Tesch 1999), nothing has been published on the variation in density of the stock contained within.

The stock of the European eel is in decline. Recruitment to (Moriarty 1986; Moriarty and Tesch 1996; Dekker 2000a) as well as yield from (Dekker 2003a) the continental stock has been well below average for two or more decades. A stock recovery plan is urgently needed (ICES 1999). Moriarty and Dekker (1997) recommend increasing recruitment by glasseel re-stocking in northern areas, while assuming that recruitment in southern areas is overabundant in relation to the carrying capacity of the inland waters and can be exploited safely. A spatial differentiation in management regime is advocated, but no corresponding management regions have yet been defined.

Eels are notoriously hard to sample. Stock densities vary over short ranges in predictable (Barak and Mason 1992) and unpredictable (Dekker 2000a) ways, and sampling problems make reliable estimation of local stock densities problematic (Knights et al. 1996). In addition, sampling methods have not been standardised or inter-calibrated (Moriarty and Dekker 1997); therefore, comparison of estimates of stock density within and between catchments and countries is not appropriate. Instead, data on commercial landings will be analysed here. Commercial landings are indicative of local stock sizes in as far as fishing takes a constant fraction, i.e. fishing mortality is constant over the distribution area. There is substantial evidence to the contrary (Moriarty and Dekker 1997; Dekker 2000a). However, the number of silver eels escaping to the ocean is negligible in comparison with commercial landings (Dekker 2000b). Variation in fishing intensity will therefore cause the mean age in the catch to vary, but it affects the number of eels caught only marginally. Lower fishing intensity tends to increase the size at catch, but hardly affect the number of eels caught. Therefore, commercial yield provides some index of stock size.

This study seeks to quantify the spatial variation in density of the eel stock. In combination with estimates of the amount of habitat available, this completes the zoo-geography of the eel. Finally, the life stage targeted by the fishery will be related to the stock abundance and density.

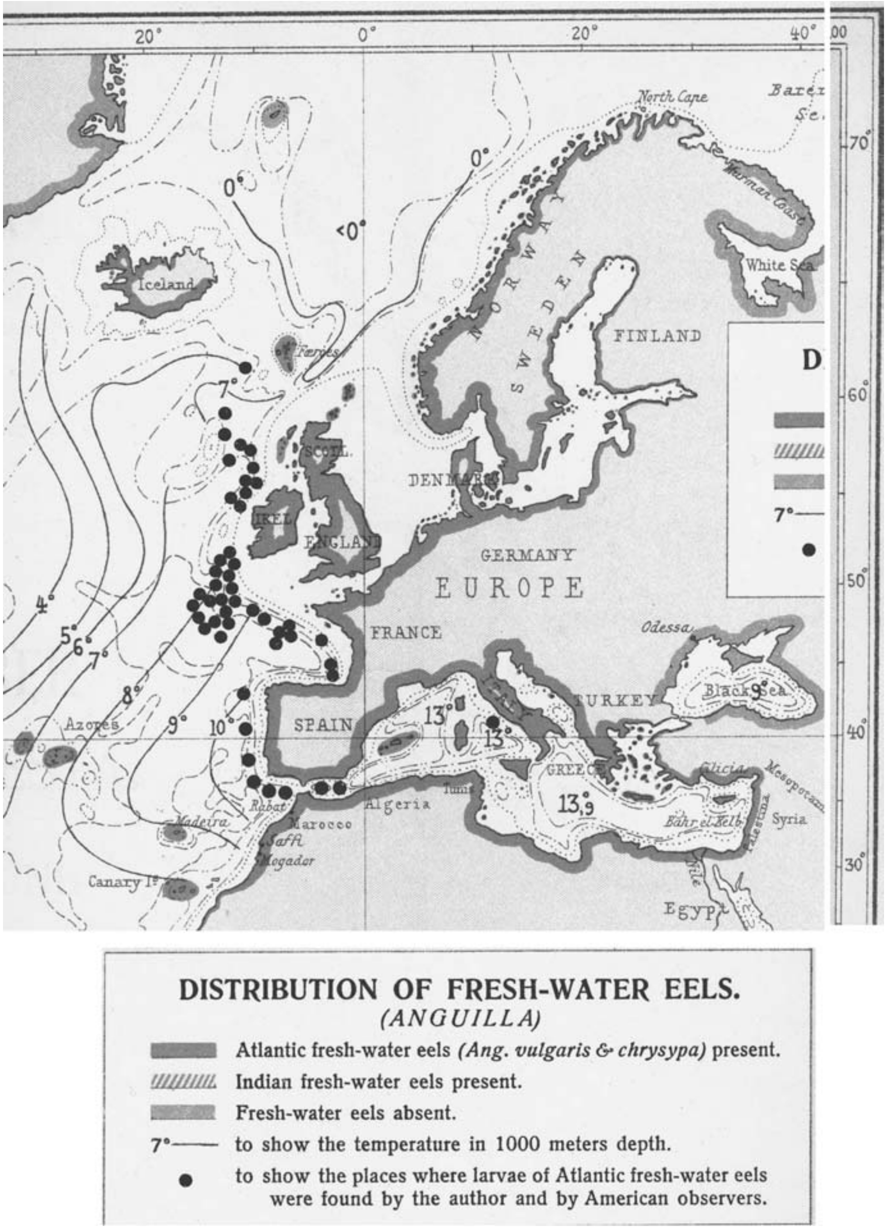

Figure 1 Reproduction of the chart from Schmidt (1909), selecting parts relevant for the distribution of the European eel, 25°N to75°N and 25°W to 40°E.

Material and methods

Data

Data on commercial yields were collected from the literature, starting from three previous reviews of available data (Aubrun 1986, 1987; Moriarty 1997; Moriarty and Dekker 1997). Additionally, the literature listed in Tesch (1999) and in ASFA-1 (FAO 1998) was examined. Data sources were included whenever the following information was specified. (a) *Commercial yield* in weight and whether it concerns either glasseel or yellow/silver eel. (Fisheries on wild eel as well as fisheries on stocked eel were included. Also, semi-commercial fisheries for glasseel for re-stocking purposes in northern countries were included). (b) *Reference year* (in line with Moriarty and Dekker (1997), data for 1993 were preferred, or a year close to that). (c) *Water body* or river system. For (large) river systems, the location of the river mouth was used in the analysis. For lakes, lagoons and reservoirs, a position near the centre was used. Longitude and latitude were rounded to one minute. Data by country (Figure 2) do not

Table 1 Literature sources on commercial yield of eel and the type of surface area measure used. Note that 'accumulated catch' might double-count individual fisheries, when published in two sources and that some publications list both surface area measures.

	Glasseel fisheries		*Yellow/silver eel fisheries*	
	Number of records	Accumulated catch (t)	Number of records	Accumulated catch (t)
(a) Data sources				
Aker and Koops 1974	0	0	1	300
Anwand and Valentin 1981a,b	0	0	4	29
Aubrun 1986, 1987	19	264	9	394
Dekker 2002	5	2	0	0
Elster and Jensen 1960	0	0	1	1
FAO 2000	0	0	1	3
Gagneur & Kara 2001	0	0	1	32
Hahlbeck 1992	0	0	7	34
Kangur 1998	0	0	1	85
Moriarty 1991	0	0	1	50
Moriarty 1997	29	388	67	8027
Müller 1961	0	0	10	429
Navaz y Sanz 1964	1	275	0	0
Paetsch 1983	0	0	2	59
Paulovits and Biro 1986	0	0	1	115
Pedersen 1997	0	0	3	111
Tesch 1967	0	0	6	25
Vallet 1977	0	0	1	<1
Wickström and Hamrin 1997	0	0	11	64
Zaouali 1977	0	0	1	97
Unpublished	0	0	7	1160
Sum	54	929	134	11,002
(b) Surface area measure				
Water surface area	5	5.5	123	10,380
Drainage area	49	924	11	622

refer to natural geographical entities and were only used in the analysis of the life stage targeted by fisheries. (d) *Surface area* of either the water body (wet surface) or the drainage area of the catchment (wet and dry surface combined). If not given, the surface area was derived from any other source available (including searches on Internet) or was roughly estimated from the Times Atlas of the World (Times Books 2001). For countries, land and water surface areas were derived from CIA (2001).

In total, 199 data records were identified, with a cumulative yield of 11,932 tonnes of eel (Table 1, Figure 2).

Surface area measure and exploited life stage

Literature sources list surface area of drainage systems, or surface area of a water body. The relation between the two measures is far from clear. The water surface area of a river system depends not only on the precipitation and evaporation rate, the type of soil, the slope, etc., but also on the magnitude of the system, larger rivers having relatively more water surface. Moreover, for rivers representing fractals (Tarboton et al. 1988), water surface is not easily measured. Consequently, there is no universal way to convert drainage system areas into equivalent water surface areas.

Commercial fisheries in some areas target for glasseel, but elsewhere yellow/silver eel prevail (Dekker 2000b). The glasseel fisheries are negligible in terms of weight but take by far higher numbers (Moriarty 1997). The relation between the number of glasseel entering a river and the corresponding number of (market size) yellow eel available to the fisheries depends on the natural mortality rate and the duration of the stage between. Hence, there is no obvious way of comparing yields from glasseel fisheries with those from yellow/silver eel fisheries.

By cross-tabulating the surface area measure used and the life stage being fished (Table 1), the complexity of the problem appears to be manageable: glasseel fisheries operate in river mouths for which the drainage area is

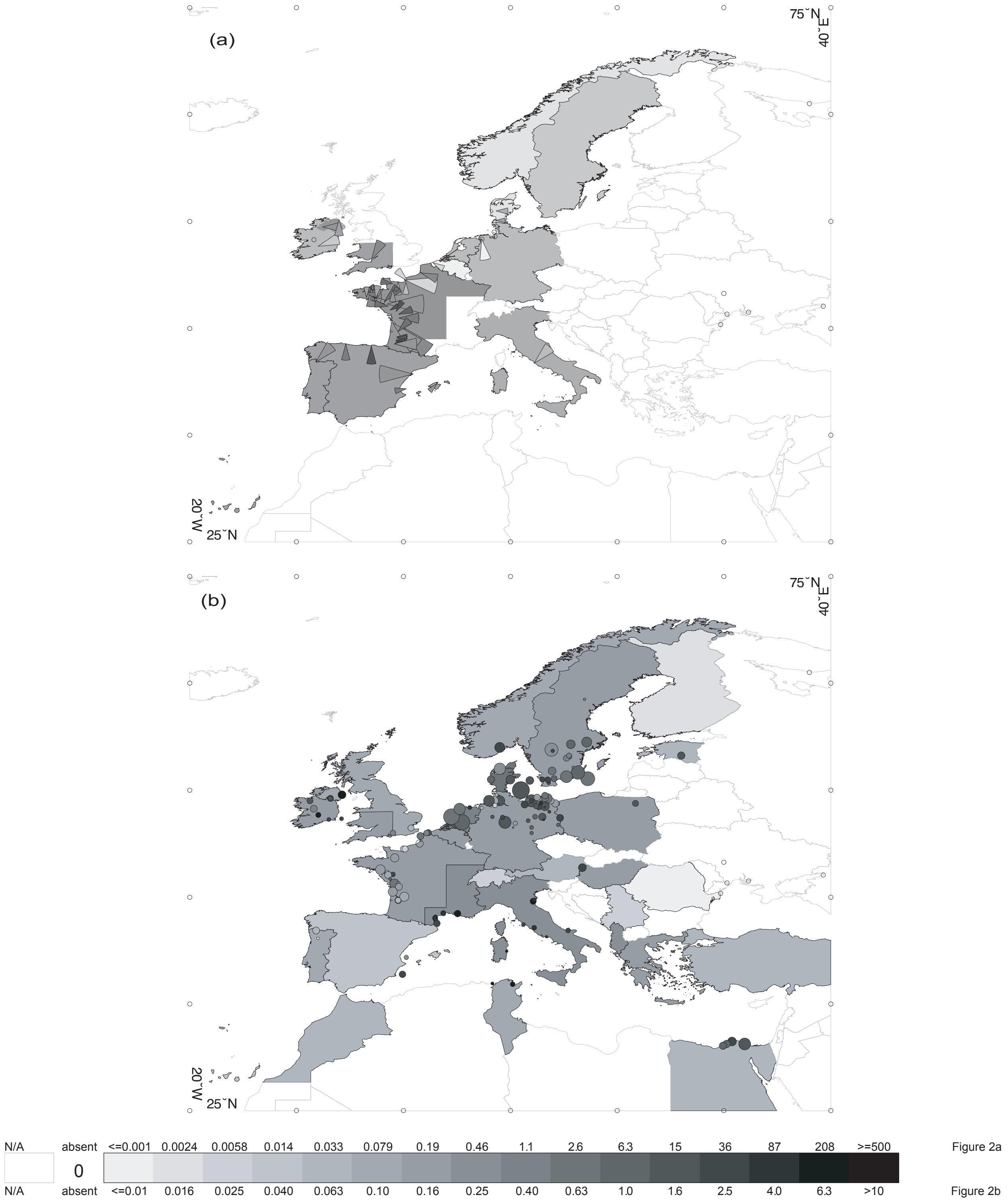

Figure 2 Raw data on yield of eel fisheries, per country (background) and per water system (symbols). Yield per surface area is expressed by the gray-scale of the areas. For individual water systems, the size of the plotted symbols is proportional to the root of the surface area, but water surface areas have not been drawn in proportion to drainage areas. (a) Glasseel yield (kg per km^2 drainage area) in rivers and per country. (b) Yellow/silver eel yield (kg per km^2 water surface) in lakes/lagoons and per country. Legend for Figure 2a, units in kg per km^2, for Figure 2b, units in ton per km2, the scale is logarithmic equidistant.

known, whereas fisheries for yellow/silver eel are largely restricted to lakes and lagoons, for which the water surface is known. A minor quantity of yellow/silver eel data (5%) stems from running waters.

Absence of eel

Few studies report the absence of eel. Schmidt (1909) explicitly reports on absence or presence of eels. Absence (23 records) was interpreted as a zero yield, for both glasseel and for yellow/silver eel, in lakes as well as in rivers. Secondly, some sources (Table 1a) report on one life stage, implicitly or explicitly excluding other life stages (15 records for glasseel, one for yellow/silver eel). Thirdly, Schmidt (1909) argued that *A. anguilla* does not occur outside the outer limits of the distribution in Europe and northern Africa. These implicit zero observations surrounding the distribution in Europe-Africa were implemented as a series of explicit zero records at 10° intervals along the frame 25-75°N, 20°W-40°E, for both life stages and in lakes as well as in rivers (22 records). Finally, Aubrun (1986, 1987) covers all drainage systems along the French coast, including the systems without glasseel fisheries (eight records). Overall, the number of zero records totals 68 for glasseel and 46 for yellow/silver eel.

Analysis of distribution

The logarithm of the yield per surface area (glasseel, drainage system area; yellow/silver eel, lake or lagoon surface area) was analysed using a geostatistical model (Cressie 1993). No fixed effects were included. The spatial component included a Gaussian covariance structure (range and sill) and a nugget effect. Euclidean distances between observations were calculated in degrees, treating degrees longitude and latitude alike. One degree latitude spans 111 km, whereas, one degree longitude spans 101 km at 25°N, 72 km at 50°N and only 29 km at 75°N.

Logarithms of zeroes were avoided by adding a small quantity, equal to the lowest (positive) observation, to all observations: 1.35 g per km^2 (drainage area) for glasseel and 2.7 kg per km^2 (water surface area) for yellow/silver eel.

The model was implemented in SAS (SAS Inc. 1999). The spatial distribution was reconstructed by ordinary kriging (random effects), using 'proc krige2d' with parameters estimated by 'proc mixed'.

Analysis of life stage in fisheries

To analyse the relation between stock density and the life stage targeted by the fishery, data were selected quantifying the yield per life stage. For glasseel, yield density was expressed per drainage area. Comparison of glasseel catch to yellow/silver eel catch therefore restricted the data set to records listing catch of yellow/silver eel per drainage area, i.e., countries and some rivers. Following Dekker (2000b), the French data were partitioned between the Atlantic and the Mediterranean coasts and the British data among the Severn area, Northern Ireland, and the rest of the U.K. For several countries, a small yield of glasseel used for re-stocking was not recorded as commercial catch by Moriarty (1997); using data from Dekker (2002b), these re-stocking catches were added. For the comparison of yellow to silver eel yield, only the records specifying these life stages separately can be used.

The number by life stage in the catch was calculated assuming 3000 glasseels and 5 yellow or silver eels per kg (Moriarty 1997). The fraction of one life stage in the total yield was arcsine transformed ($y = \arcsin \sqrt{\text{fraction}}$) and plotted versus the logarithm of yield density (number per km^2). A regression line was fitted to the transformed data, including observations with a zero yield in one of the life stages. Because the plotted axes were both based on the same observed quantities, they were not independent and no formal statistical tests were applied.

Results

For glasseel fisheries, data were obtained from France, the Iberian Peninsula, the British Isles and several more isolated locations (Figure 2a). Yields ranged from 1.35 (River Ems, Germany) and 6.25 g (River Risle, France) to 75 (Cap Breton, France) and 500 kg (Isle de Ré, France) per km^2 of drainage area. For yellow/silver eel fisheries, data were obtained from all over Europe and northern Africa, with the highest concentration of data in the Netherlands, Germany, Denmark and Sweden (Figure 2b). Yields ranged from 3 kg (Golf du Morbihan, France and several hafs in eastern Germany) to 8 (Vie, France) and 32.4 t (Monaci, Italy) per km^2 of water surface.

The area over which data on the glasseel fisheries were available is much smaller than for the yellow/silver eel fisheries. Consequently, the variogram for the former (Figure 3a) spanned a smaller range of distances than for the latter (Figure 3b). In both data sets, the variation between mutually remote observations was only marginally higher than between nearby observations: for the glasseel fisheries, nearby observations varied by a factor of 10 on average, and remote observation pairs (20° apart) by a factor of 20, whereas for the yellow/silver eel fisheries, these factors are 4 and 10, respectively. For the yellow/silver eel fisheries, maximum differences (up to a factor 10,000) occurred at distances of 10–20°, whereas at greater distances (30–40°) only smaller ratios in yield density (<100–<10) were found. The range of the fitted vari-

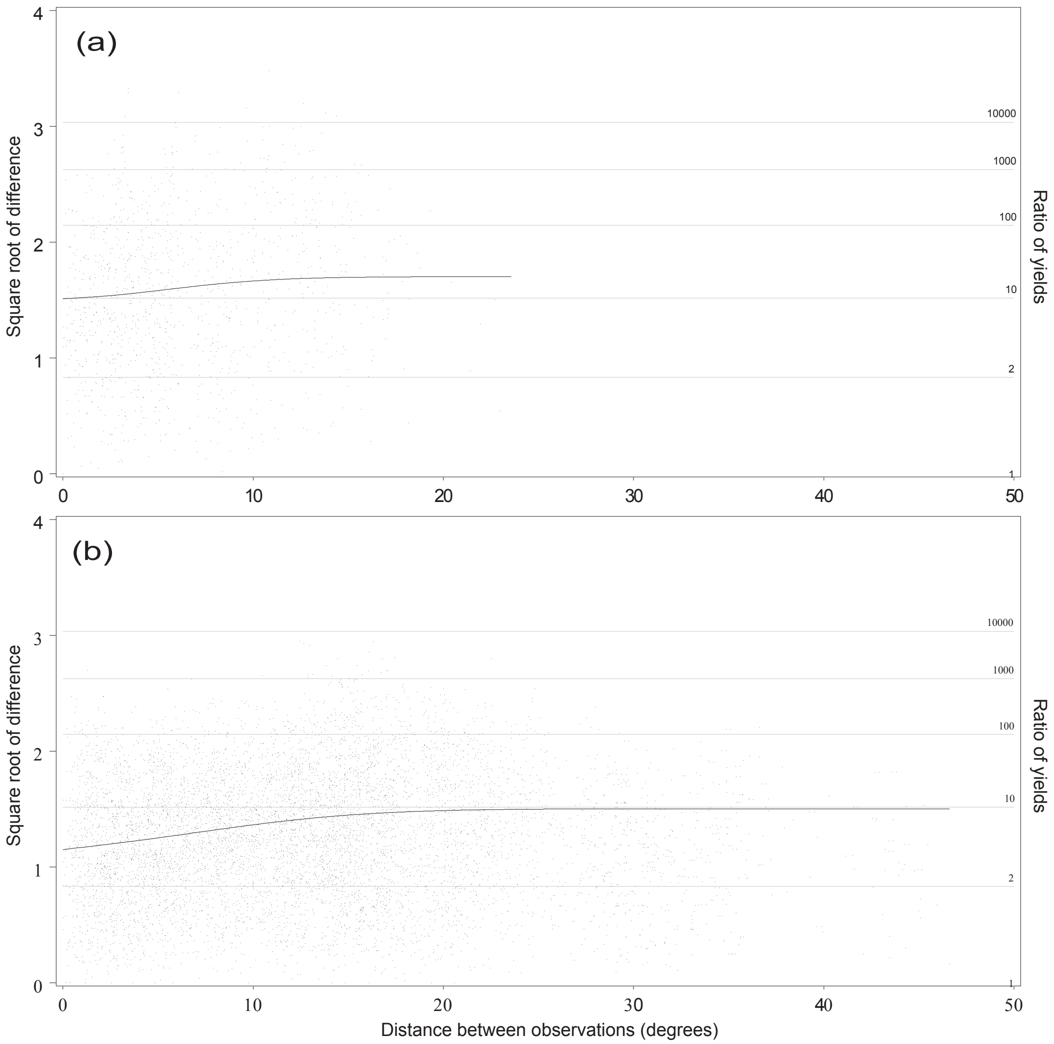

Figure 3 Variogram of the yield of eel fisheries per unit surface area. The left axes refer to the log-transformed data, the right axes to the corresponding un-transformed observations. Points: observations; line: fitted Gaussian variogram. Zero observations have been left out. (a) Glasseel fisheries, yield per drainage system area. (b) Yellow/silver eel fisheries, yield per water surface area.

ogram was 8.1° (latitude or longitude) for the glasseel and 12.5° for the yellow/silver eel data.

Using these estimates, kriging of the primary data (Figure 4) showed highest yield in glasseel fisheries to occur in the south-eastern corner of the Bay of Biscay, and on the eastern Mediterranean coast of Spain. Some isolated high spots were found in central Brittany and just south of Brittany (Isle de Ré, France). The area of highest abundance ended gradually in the Iberian Peninsula, owing to the absence of data. The Iberian glasseel fishery is not well documented; therefore, this analysis may wrongly suggest a southern limit to the distribution of glasseel fisheries. For the yellow/silver eel fisheries, the distribution was much wider, with highest yields around the western Mediterranean. Isolated high and low spots occurred, most notably in eastern Germany, where relatively high and low observations were found close together.

The life stage targeted by fisheries (Figure 5) showed a clear relationship with density of the eel stock. Glasseel fisheries were absent at yield densities of 0.04–50 eels per km^2 (drainage area), and occurred at 15–2300 eels per km^2. With increasing yield, the fraction in the catch (by number) increased from a few percent (in countries with glasseel fisheries for re-stocking) to nearly 100% in the U.K. (Severn area), France (Atlantic), Spain and Portugal. Silver eel catches were inversely related to yield density in lakes (Figure 5b) and were not reported at all in coastal areas. At a density of 1000 eels per km^2 water surface, silver eel made up around 50% of the catch in lakes, declining to almost nil at 50,000 eels per km^2.

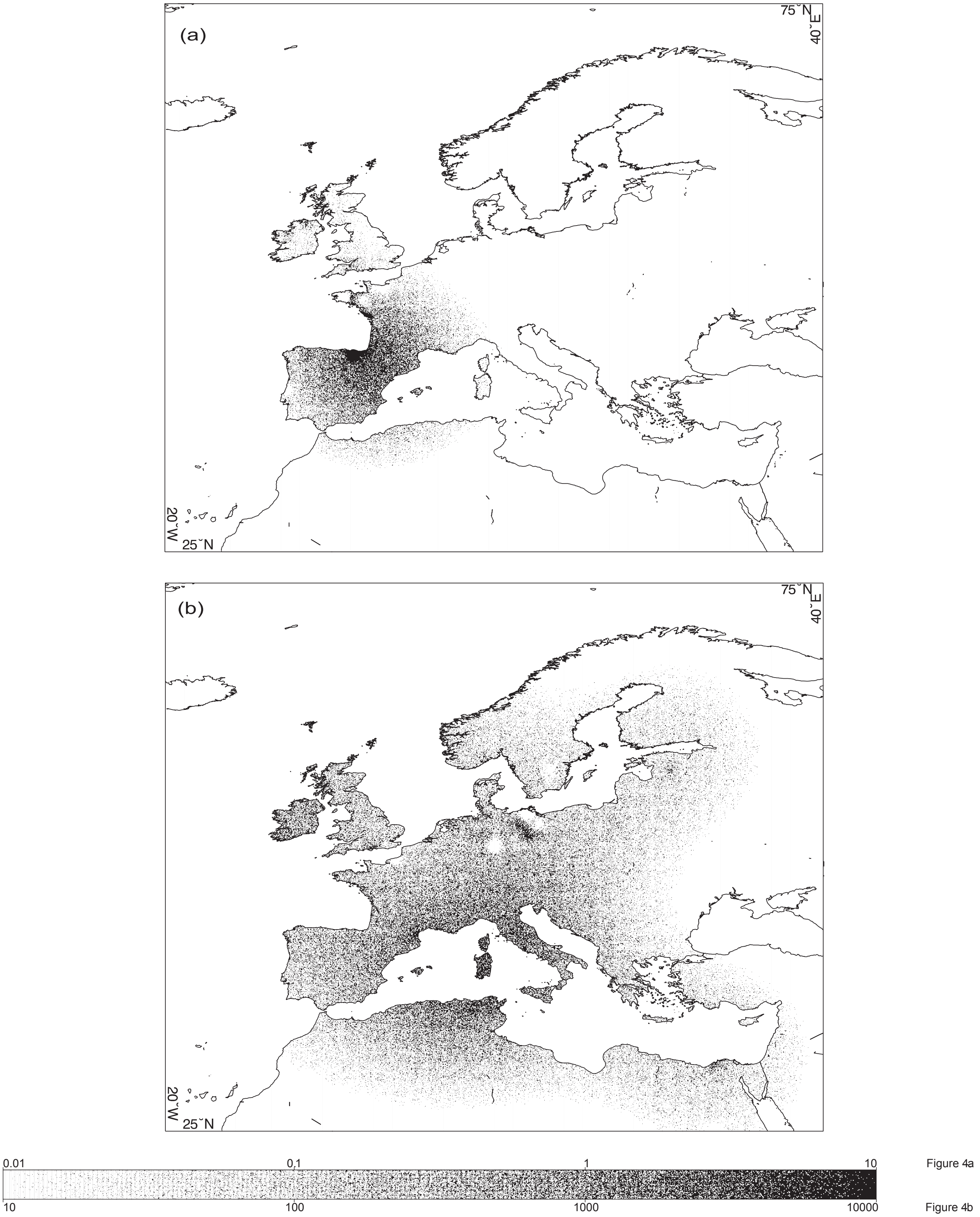

Figure 4 Kriging eel fishing yield per surface area. Spatially predicted values are scaled between minimum and maximum observed values, represented by dithered gray-scales: the higher the density of pixels the higher the yield. Note the logarithmic transformation of the yield. (a) Yield of glasseel per river drainage area. (b) Yield of yellow/silver eel per water surface area. Legend for Figure 4a and b. Units in kg per km^2, the scale is logarithmic.

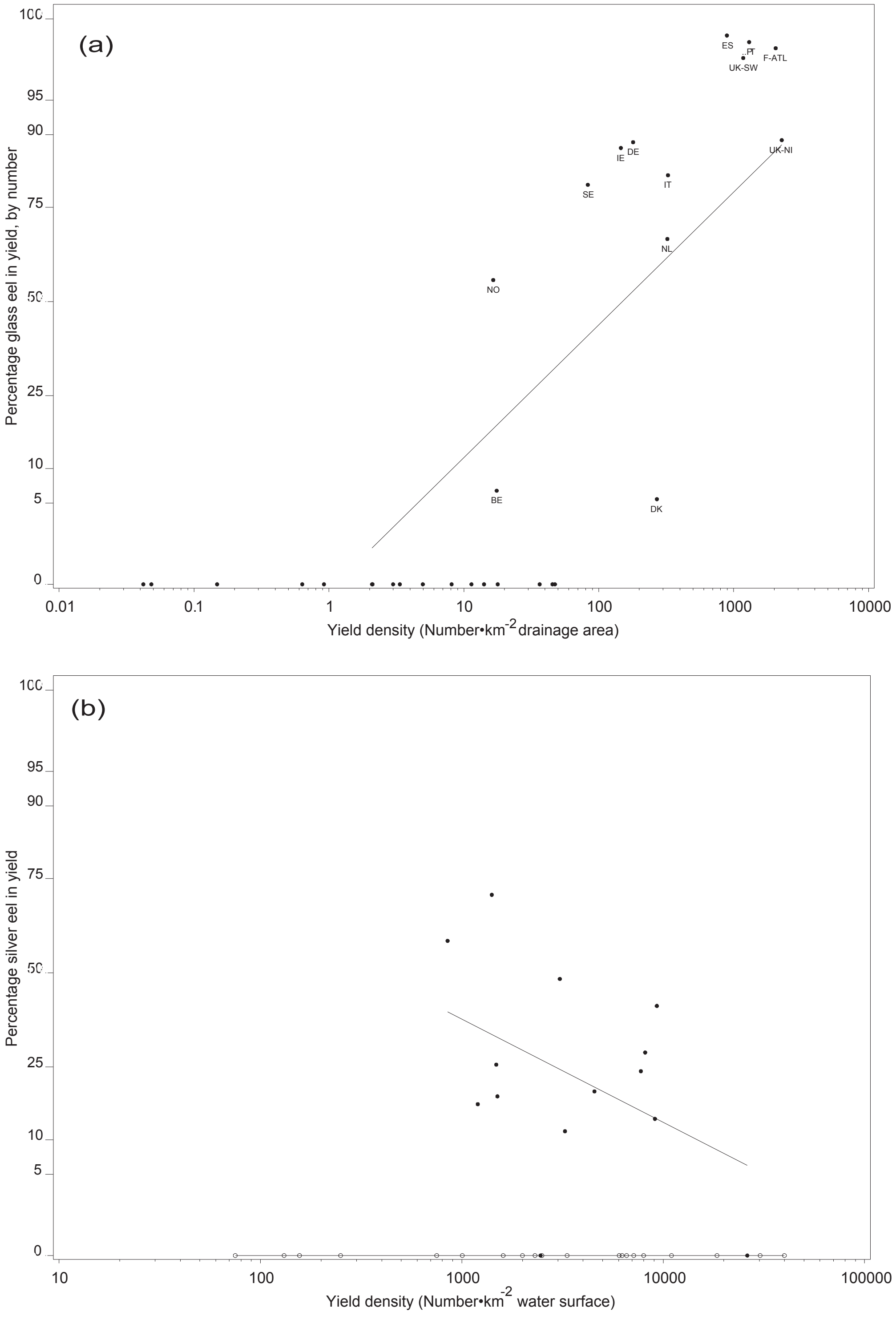

Figure 5 Relationship between the density of the eel harvest and the life stage being exploited. The horizontal axis is on logarithmic scale; the vertical axis lists the fraction a given life stage constitutes of the total catch as a percentage, but values have been arcsine-transformed. (a) Percentage glasseel in the total yield. Individual points represent different countries; non-zero observations have been labelled with a country code. (b) Percentage silver eel in the yield of yellow and/or silver eel. Individual points represent different water bodies; closed symbols for fresh waters, open symbols for coastal areas.

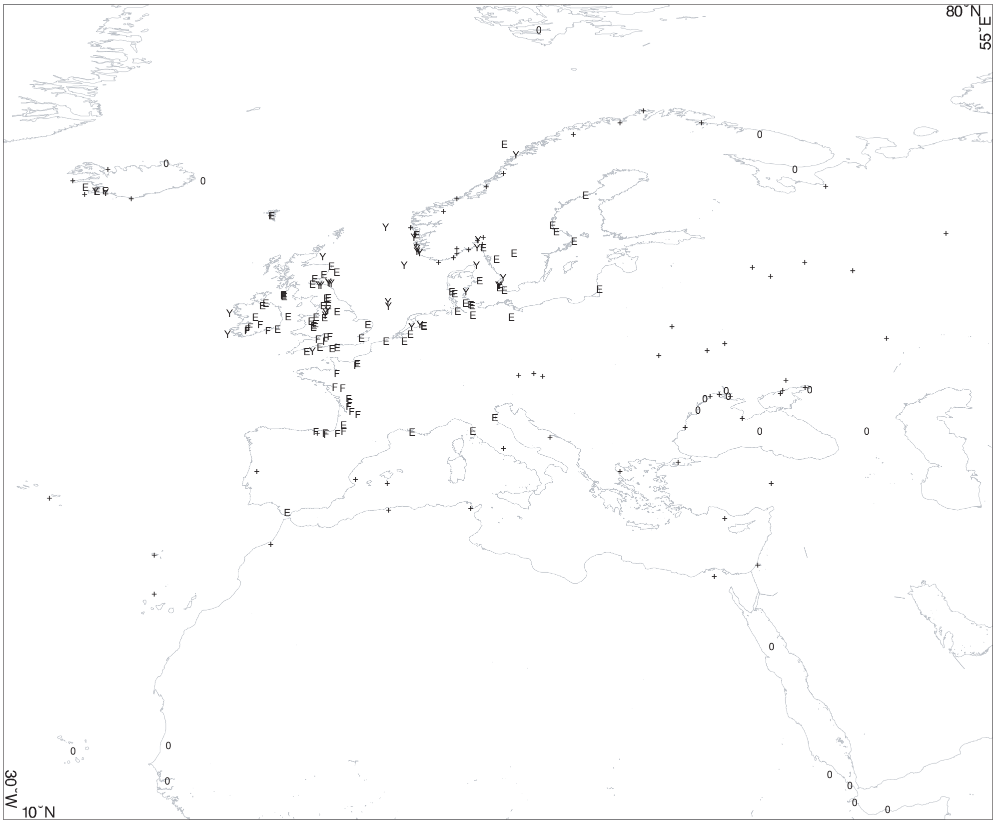

Figure 6 Distribution data provided by Schmidt (1906, 1909, 1925) in the text of his publications. Schmidt lists many place names and rivers, which have been located and displayed in this map. Symbols indicate the descriptions given by Schmidt; his context indicates he used 'elvers' only for glasseel. Legend: 0, absent; +, present; F, elvers as food; Y, young eels in the sea; E, elvers into fresh water.

Discussion

Distribution area

According to Schmidt (1909), the European eel is distributed 'from North Cape in Northern Norway and southwards along the coast of Europe, on all the coasts of the Mediterranean … and on the north-western part of the coast of Africa'. Although this statement may be correct in a qualitative sense, it ignores the quantitative distribution of the stock within the area and as such is an over-simplification. Schmidt used a gradually thinning line to depict a declining density in the northern reaches of the Baltic and in the Propontis (Sea of Marmara), but elsewhere all coasts were marked by a line of constant width. However, major concentrations of glasseel recruiting from the ocean did and do appear in France and Spain, whereas highest productivity of coastal and inland waters occurs in areas bordering the western Mediterranean. Re-analysis (Figure 6) of the information presented in texts by Schmidt (1906, 1909) reveals the concentration of recruitment in the Bay of Biscay. These areas were listed by Schmidt under the heading 'Elvers as food' and in his context, 'elvers' only indicated glasseel. However, his detailed data records were limited to areas north of 43°N, and although this limitation was re-iterated in the text, it is ignored completely in the final distribution map.

Use of fishing yield data

The analysis presented in this article is based on data derived from commercial fisheries, rather than on experimentally assessed data of stock density, as the latter show great spatial and stochastic variation. However, this choice might have biased the analysis, especially for the glasseel fisheries. Observations are largely restricted to a small area with high yield. High yields will be a pre-requisite for commercial exploitation. However, noting the (positive) relation between yield density and the fraction of glasseel in the yield, absence of data on commercial exploitation outside the typical 'glasseel exploitation area' may well be the consequence of low stock densities. In addition, the data on glasseel fisheries for re-stocking do fit in well.

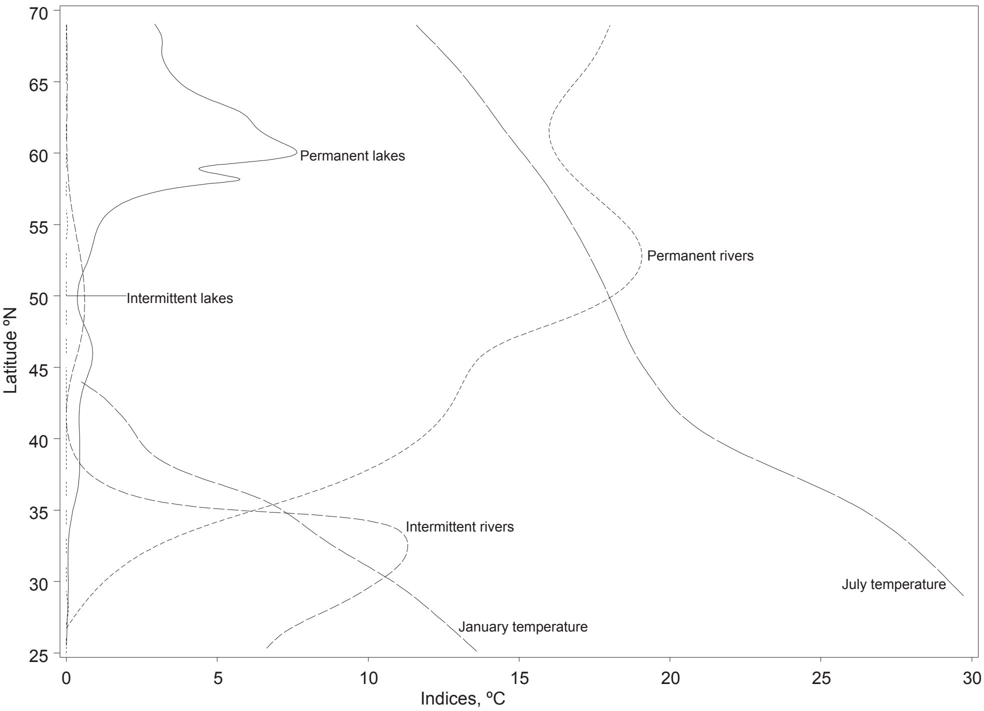

Figure 7 Distribution of fresh water habitats and summer and winter temperature by latitude, averaged over the study area. Note that the axes have been interchanged, to plot (northern) latitude in the vertical.

Shortage of data

The high variability of experimental stock surveys (Barak and Mason 1992; Knights et al. 1996) is also manifested in the commercial yield data in that the broad-scale variation is hardly larger than local variation (nugget effect). Where information is lacking (e.g., for large parts of the Iberian Peninsula), a smooth cline is fitted towards the trivial absence records at the outer limit of the study area. However, such a smooth cline would not adequately describe the local patterns in data-deficient areas. To fill this gap, information on glasseel fisheries in the Iberian Peninsula and north-western Africa and yellow/silver eel fisheries in the Balkan, the eastern Mediterranean, and northern Africa is required, as it has been since Schmidt (1906).

Density and abundance

The analysis of glasseel abundance was based on the yield per km^2 of drainage area. For most of the distribution, this results in an estimate of the absolute yield. In northern Africa, large areas do not have any surface water drainage but are expected to have negligible recruitment. In the Iberian Peninsula, where semi-arid conditions prevail, recruitment is concentrated in few, relatively small streams draining a large area. Such concentrations in smaller rivers should facilitate exploitation and might explain the occurrence of glasseel fisheries down to the southern range of the distribution area (Portugal, Morocco) and their comparatively high share in the yield.

For yellow/silver eel, yield was calculated in relation to water surface area. The estimated density does not correspond to absolute yield, because habitat availability varies greatly from region to region. Quantitative data on habitat availability can be acquired from climatological databases, but these only cover fresh water. Global climatological databases (e.g., Cogley 1994) combine lagoons, estuaries, open ocean, and exposed rocky shores into a single category (saline waters), including habitats that are well suited and unfit for eel. Although this does not allow a detailed analysis, some general trends can be inferred (Figure 7). From north to south, permanent lakes peak at about 60°N (Scandinavia), whereas the number of permanent rivers remains high and rather constant down to 35°N (African north coast). Farther south, rivers as well as lakes dry up completely, which makes it unlikely that any fresh water habitat is permanently available. Consequently, although yield per surface area in the western Mediterranean is high, production in fresh water will be low, total production being dominated by marine catches. For Tunisia, for instance, statistics (FAO 2000) list 55 t per year (averaged over the 1990s) from inland waters and 244 t per year from marine waters. It is noteworthy that scarcity of fresh waters in northern Africa is a relatively recent phenomenon. Reale and Dirmeyer (2000) provided substantial evidence of higher precipitation, more abundant fresh water and richer vegetation during the Roman Classical Period. Anthropogenic degradation of the vegetation might have changed the climate irreversibly to the current desert conditions (Reale and Shukla 2000). Hence, one may wonder whether eel has been as abundant in Roman Africa as in Roman Italy, where many remains of eel culture have been found (Higginbotham 1997).

Northern limit

To the north, Schmidt (1909) took the North Cape as the effective limit of the distribution. The exact location has attracted some discussion (Ege 1939; Sorokin and Konstantinov 1960). The gradual decline towards the north, through Norway, conforms to the Norwegian catches presented by Schmidt (1909): 267 t for areas south of Trondheim (63°N) and only 230 kg for the lengthy coast (>1000 km) farther north. Apparently, the distribution area has no sharp northern limit, but gradually fades out. The stock in Iceland has recently attracted attention because of its peculiar genetic make up, a sympatric occurrence of the European eel and the American eel (*A. rostrata*) and interbreeding of these two species (Avise et al. 1990). However, Iceland has never reported any commercial eel catches. Iceland appears to be at the outer fringe of the distribution.

Southern limit

'In order to understand the distribution of the eels, especially that … they have not been able to penetrate further southwards on the coasts of the Atlantic …', Schmidt (1909) discusses the conditions at the spawning location (i.e. deep and warm water, 'more than 7°C at a depth of 1000 m'). In his view, the conditions 'of the adjacent seas' off the African west coast, from about the Tropic of Cancer southwards, are unsuitable for reproduction. Remarkably, the condition of adjacent warm and deep water does not hold for nearly the entire distribution area. In addition, this requirement does not match with his view on the 'spawning places' in the Sargasso Sea, at a distance of more than 3000 km from West Africa. His inference was based entirely on the presence or absence of eels in continental waters, as deduced from correspondence with Danish Consuls and available literature. Considering the results obtained now and noting the climate conditions in Africa, I propose that absence of continental habitat is a more likely cause. Over a distance of more than 1000 km, there is hardly any suitable habitat. Indeed, where fresh waters are locally abundant (e.g. rivers on the Canaries) a substantial eel stock can be found (H. Encarnaçao, Funchal, Madeira, Portugal, personal communication) and recruitment does not appear to be a bottleneck. That raises the question of whether a fringe of declining numbers of recruits can be found in the ocean farther south. Because the number of observations in this area is low (Boëtius and Harding 1985), this question cannot be answered at present.

Distribution of fisheries

The distribution of fisheries is generally described as glasseel fishing being concentrated in southern areas and silver eel fishing dominating in the north (Moriarty and Dekker 1997). Current results suggest that stock density controls what life stage can be targeted. Glasseel fisheries are found in the centre of the distribution, where stock density is at a maximum, and in more southerly regions, where the incoming recruitment is concentrated in less and smaller rivers. The predominance of silver eel in northern areas has been interpreted as northern areas producing the major portion of the spawner escapement (Castonguay et al. (1994) for the American eel; Svärdson (1976) for the European eel); however, silver eel yield in northern, sparsely populated areas is actually lower than closer to the centre. At a yield of 1000 eels per km^2 of water surface, 370 eels will be silver (37%), whereas at 10,000 eels per km^2, the yield comprises 1300 silver eels (13%). This suggests that the dominance of silver eel in northern catches is probably better understood as an adaptation of the fisheries to low stock densities, that is, as a consequence of the truly low silver eel abundance. Silver eel fisheries attain the maximal yield per recruit (Vøllestad 1990), and the concentration in time (autumn) and space (lake outlets and river mouths) of the silver eel run increases the efficacy of the fisheries. The focus of the northern fisheries on silver eel thus may reflect a retreat from non-profitable yellow eel fisheries.

Cultural patterns in fishing and consumption have been mentioned as factors determining the distribution of fisheries (Moriarty and Dekker 1997), especially for glasseel exploitation, interfering with the relation between stock density and fishing yield. However, comparison of Schmidt's information on glasseel consumption in the early 1900s (Figure 6, 'Elvers as food') with present-day information (Moriarty and Dekker 1997) shows that the tradition of glasseel consumption is lost in England, Wales and Ireland in the course of the 20th century. French glasseel was used for local consumption in the early 1900s, but is now mainly exported to Spain and Eastern Asia (Dekker 2003b). Legal constraints in southern countries (e.g., Spain, Portugal; Moriarty and Dekker 1997) hardly preclude actual fishing. In northern countries, glasseel fisheries for re-stocking replace commercial exploitation. Clearly, so-called traditional fisheries adapt easily to stock abundance and market options, whereas legislation modifies rather than determines exploitation.

Bio-geography

Most *Anguilla* species inhabit tropical waters (Schmidt 1925; Tsukamoto and Aoyama 1998). Large-scale commercial exploitation, however, is largely confined to temperate waters (Dekker 2003b). The temperate species (*A. anguilla, A. rostrata, A. japonica, A. australis* and *A. dieffenbachia*) are described to 'have left the tropical zone to spread out beyond the tropics and as far as the polar circle' (Bertin 1956; 'polar circle' applies only to the European eel). The high yield of the European eel in temperate areas is in strong contrast with the temperature preference of the species, ranging from 10°C (Boëtius and Boëtius 1967) to 38°C, with an optimum of 22-23°C (Sadler 1979). The optimum temperature, routinely applied in aquaculture (Kamstra 1999), only occurs in the southern part (south of 40°N) of the distribution area (Figure 7). Since Schmidt (1909), the absence of eel (of any species) in the southern Atlantic has attracted considerable debate, but discussion has focused on oceanographic conditions exclusively (Schmidt 1925; Bertin 1956; Tsukamoto and Aoyama 1998). The southern limit of the distribution is more likely to be determined by the absence of continental habitat in the Sahara. Penczak and Molinski (1984) describe the most extreme case: a river of 150 m wide, completely drying up in summer, with only one small pool left; afternoon water temperature approaching 40°C, in which they catch an eel alive. An arid zone has been found in north-western Africa throughout the period of speciation of the Atlantic eels (Kutzbach and Ziegler 1993) and therefore may have been of evolutionary significance for the European eel. On the American side of the Atlantic, no desert zone exists and the American eel is indeed found much farther south, down to Guyana, about 5°N (Schmidt 1909), and glasseel has been exploited as far south as 21°N (Fernandez and Vazquez 1978). For the other species, only a smaller desert zone occurs in the north-western Indian Ocean, but the distribution of the species involved, *A. bicolor* and *A. marmorata*, extends on both sides of that zone (Schmidt 1925).

A major portion of the yield of the European eel is produced in the Mediterranean (Table 2), at temperatures in accordance with the species' and genus' preference. However, production in more northern areas, at ambient temperatures far below optimum, is also substantial. Apparently, the distribution area extends beyond the area of optimum conditions. In comparison with other eel species, larval migration from the suspected spawning grounds in the Sargasso Sea to the eastern shores of the Atlantic covers an extremely large distance, over 3000–7000 km (Schmidt 1925). Noting that transport of larvae to the continent is possibly only through passive drifting (McCleave et al. 1998), the northern areas presumably receive only the accidental diaspora of larvae, straying from their long route to more favourable continental areas. If so, recovery of the stock (ICES 2001) crucially depends on the southern European and northern African countries, which so far have only marginally been involved in scientific and management-related initiatives to address the poor state of the stock (Moriarty and Dekker 1997; ICES 2002).

Table 2 Statistics on landings of river eel (FAO 2000), averaged over the 1990s, with minor corrections (see Dekker 2003b), broken down by major drainage basin and fishing area. Countries not bordering the sea have been included under a separate heading 'Inland countries', regardless of their drainage.

Drainage	Inland fisheries	Coastal fisheries	Grand total
Atlantic Ocean	4923	4089	9012
Mediterranean	4520*	1524	6043
Inland countries	493	0	493
Grand Total	9936	5613	15,549

*Includes ca. 2300 t of eel from extensive outdoor aquaculture in Italy, mostly using Italian glasseel.

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A Procrustean assessment of the European eel stock

3

ICES Journal of Marine Science 57: 938-947 (2000)

No assessment of the state of the European eel stock is available due to the absence of adequate data for many areas on the continent. In contrast to past efforts which turned to complete the traditional catch composition data, and which met with little success, we will try to develop a simplified cohort-model (based on life stage, rather than age or size), simple enough for the available data. Under the (incorrect) assumption of stable recruitment and exploitation, the catch-at-life-stage analysis yields a preliminary assessment of the entire European stock, and for the glass eel importing and exporting countries. Recruitment is estimated at about 2000 million eels annually, most of which enter countries around the Bay of Biscay, supporting intensive glasseel fisheries. Elsewhere, the natural recruitment is outnumbered by imported and transported glasseel. The fishing mortality rate accumulated over the total life span is estimated at 5.21 (=99%) for glasseel exporting countries and 3.25 (=96%) for glasseel importing countries. This Procrustean assessment provides a limited view on continent-wide stock. Substantially improved assessments are unlikely at the time scale at which management action is required. However, the development of a co-ordinated system of inter- and intra-national management (i.e., the only effective levels) will benefit the assessment of the European eel stock.

The European eel (*Anguilla anguilla* (L.)) stock is in a bad state: recruitment has steadily decreased since the early 1980s, fisheries have declined and man-made impacts on the habitats of this species have adversely affected production potentials (Moriarty and Dekker 1997). Although the causes of the decline in recruitment are not understood, the longevity of the decline has made radical management action a matter of urgency. The fisheries are no longer within safe biological limits (ICES 1999).

A Symposium on Eel Research and Management in 1976 in Helsinki concluded that 'an assessment of the state of exploitation and of the effect of elver stocking was urgently needed' (Thurow 1979). In the years following, the state of the stock has deteriorated, but the total absence of data from many areas (ICES 1976) has prohibited the intended assessment. Dekker (2000) argued that the absence of sufficient data is inherent to the geometry of the distribution of the continental stock over a myriad of very small local sub-stocks, and that a reliable stock assessment may not be a realistic objective.

But even without a proper assessment, the need for management action in response to the recruitment failure has been communicated several times (FAO 1993; ICES 1997, 1999; Moriarty and Dekker 1997). The precautionary approach (FAO 1995a,b) explicitly states that 'absence of adequate scientific information should not be used as a reason for postponing or failing to take measures'.

Noting the mismatch between management needs and scientific insights, this study tries to reverse the line of thinking followed over the past two decades, when effort was mainly directed towards gathering detailed assessment data (ICES 1976, 1988; Moriarty 1997; Moriarty and Dekker 1997). A first exploration will be made of how far the available data on stock and yield can bring us, accepting that this will provide only a Procrustean* version of the assessment ultimately required.

The eel is a catadromous species, with an incompletely known life cycle. Reproduction takes place somewhere in the Atlantic Ocean, potentially in the Sargasso Sea area (Schmidt 1906). Larvae (Leptocephali) of the latest stage are found on the edge of the continental shelf, where they transform into young, transparent eels, so-called glasseels. At this stage, the young animal proceeds into continental waters, often ending up deep into the fresh water systems. Following immigration to continental waters, a prolonged life stage begins, which lasts for about 5 to 50 years. During this stage, eels grow, but do not mature. At the end of this period, the maturation starts and the eel returns to the

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**Procrustes*: a mythical Grecian who lodged guests coming to his doorstep in an iron bed. Whenever a guest did not fit into the bed, Procrustes stretched or chopped the guest, to make it fit. The guests died in this procedure...

ocean. The non-migratory continental stage is called the yellow eel stage, while the migratory, near-mature eel is known as silver eel.

Few studies have assessed the impact of fisheries on (local) yellow or silver eel stocks. Sparre (1979) applied a cohort analysis model to data on eel fisheries in the German Bight, extending a standard age-structured model to allow for silvering and emigration. Instantaneous fishing mortality rate (*F*) was estimated at 0.2 (=18%) for the most exploited length-groups. ICES (1991) evaluated the potentials of a simple stock production model without much success. Dekker (1993, 1996) developed a length-structured equivalent to age-structured cohort analysis models for the eel fisheries on Lake IJsselmeer, the Netherlands. Instantaneous fishing mortality rate (*F*) for the predominant length classes was estimated at 0.5 per year (=39%). However the estimation procedure is only applicable in heavily exploited stocks, where complicating processes such as silver eel emigration play an insignificant role. Finally, de Leo and Gatto (1995) developed a length- and age-structured simulation model for the eel in the Comacchio lagoons in Italy, which can not be used to assess the impact of fisheries.

Glasseel fisheries in estuaries in the Bay of Biscay have been extensively studied (Elie and Rochard 1994). The effect of these fisheries on abundance has been assessed in the field and simulation models have been applied to understand the dynamics (Gascuel and Fontenelle 1994; Lambert 1994). The effect on subsequent life stages has not yet been considered.

Here, a traditional assessment model will be simplified and generalized, until the limited amount of published data available suffices. Only one sufficiently complete snap shot of landings data is available (Moriarty 1997). There are insufficient data on the composition and distribution of European landings. The resulting model, applied to data given in Moriarty (1997) and Moriarty and Dekker (1997), gives a first assessment of the eel stock at a European scale. The sensitivity of the results to the parameter values will be assessed. Finally, consequences for our view on the stock and fisheries will be discussed.

Materials

Landings

Data on total landings of eel are annually published by FAO (e.g., FAO 1994). These are subdivided by country and region, but not by life stage. However, ICES (1988) and Moriarty (1997) showed official landings comprise only approximately half of the known catches. Moriarty (1997) provides detailed data for 1993 classified by life stage. Here, data were taken from Moriarty (1997) and supplemented by FAO (1994).

Table 1 Parameters of the continental life stages of eel.

Life stage	Duration Δt (years)	Weight (g)	Natural mortality (M) per annum
glasseel			
fisheries	0.25	0.3	0.14
re-stocking	n.a.	0.3	n.a.
yellow eel			
pre-exploited	10 (5-20)	8	0.14
exploited	6 (2-20)	200	0.14
silver eel	0.5	200	0.14
sum of continental life	18 (8-41)		$\Sigma M \times \Delta t = 2.52$

Geographical subdivision of fisheries

The glasseel fisheries in Europe are concentrated at the Atlantic coasts of Portugal, Spain, France and the Bristol Channel area in the United Kingdom (Figure 1). Elsewhere, glasseel fisheries are balanced by re-stocking within the country, often supplemented by imports from the areas mentioned above. The contrast between these areas was the reason for running separate analyses for glasseel producing and for importing countries, following Moriarty (1997, Table 10, on p. 44). This allowed a subdivision of France (Atlantic versus Mediterranean coast) and the UK (Bristol Channel area versus the rest). The eel fisheries in Spain, where only national data are available, were completely attributed to the glasseel producing region. The areas with a net glasseel production were collectively indicated as the *Biscay area*, since they are all adjacent or close to the Bay of Biscay. The rest of the continent was labelled *'Elsewhere'*.

Catch composition

No partitioning of landings between yellow and silver eel was possible. Moriarty and Dekker (1997, Annex 2, Table 1) list total landings concurrently with silver eel landings for selected waters. These total 1591 tonnes (47%) of yellow eel and 1759 tonnes (53%) of silver eel. However, these figures are biased because northern countries are over-represented and the contribution of silver eel is highest in northerly areas: 81% in the Baltic and only 33% in the remaining areas. Since the catch in the Baltic comprises only 7% of total landings, it was decided to use the lower figure (33%) throughout the analysis.

There are only a few eel fisheries for which data on catch composition (length and age distribution) has been routinely acquired: Lake IJsselmeer (The Netherlands), Shannon catchment (Ireland) and the Baltic coast of

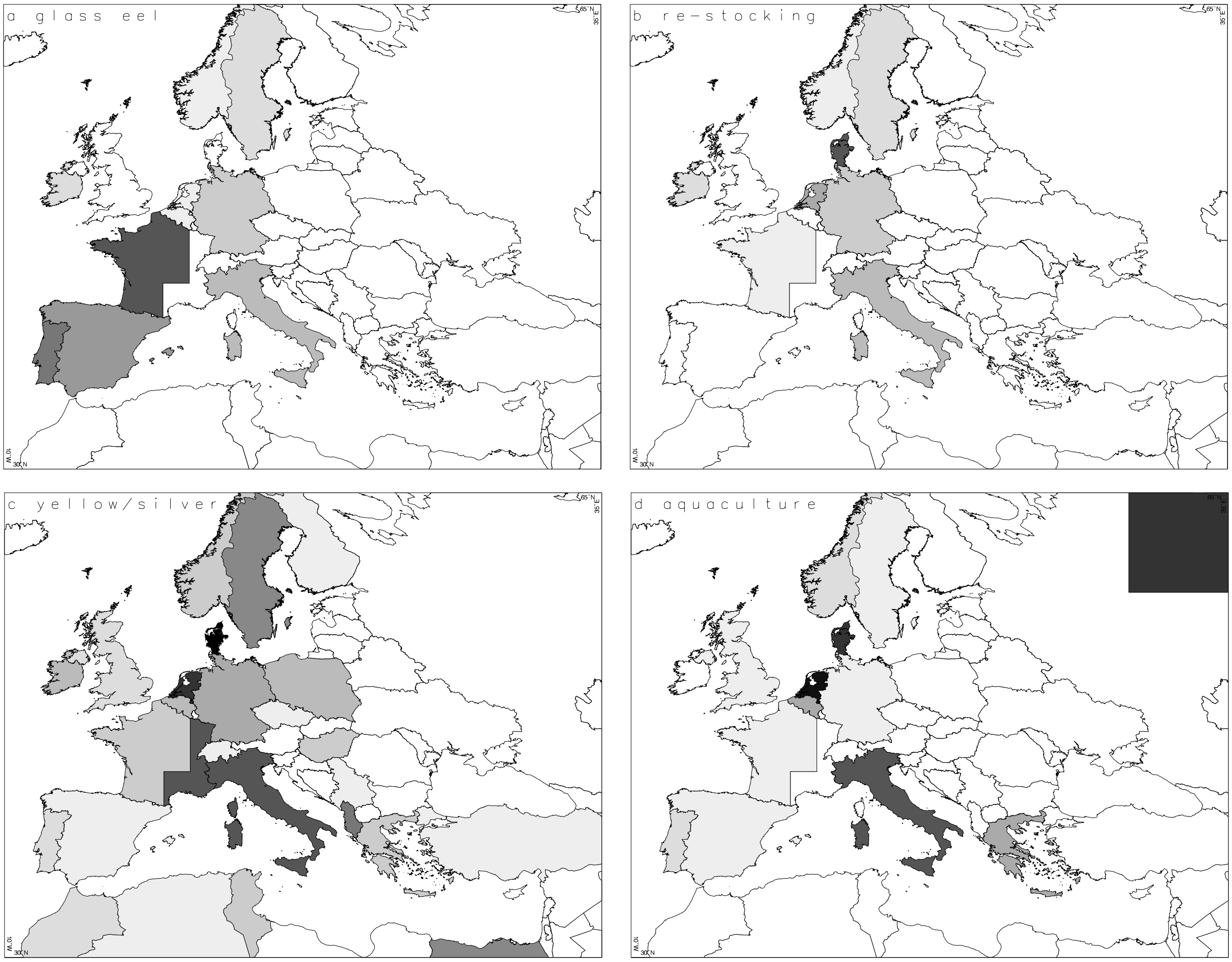

Figure 1 The spatial distribution in Europe of: a) Glass eel fisheries, b) Glass eel re-stocking, c) Yellow/silver eel fisheries and d) Aquaculture. The production of European eel in Asian aquaculture is shown in the top-right corner of panel d, in a square of equal surface area to Japan. Data from Moriarty (1997), adapted.

Legend for glass eel fisheries and re-stocking, g.km^{-2} land surface.

NA	0	>0	25	50	75	100	200	300	400	500	600	700	800	900	1000	
☐	☐	░	░	░	▒	▒	▒	▒	▓	▓	▓	▓	█	█	█	█
NA	0	>0	1	2	3	4	5	6	7	8	9	10	20	30	40	≥50

Legend for yellow and silver eel fisheries, aquaculture, kg.km^{-2} land surface.

Sweden probably being the only substantial ones (Moriarty and Dekker 1997). Moreover, ageing in eel is problematic (Moriarty and Steinmetz 1979; Vøllestad and Næsje 1988; Svedang et al. 1998) and the fraction of correctly aged eel is too low (27%) to provide a realistic basis for stock assessment. Since the ageing procedure does not necessarily contain a systematic bias (Moriarty and Steinmetz 1979), it may be used for determining growth rates. Although growth rates may vary considerably (Dahl 1967; Klein Breteler et al. 1989; Poole and Reynolds 1996), an average growth of 3-4 cm per year seems appropriate for most areas. But Dekker (2000) showed that catch composition data from selected waterbodies are not representative for those in nearby waterbodies, while only a small fraction of all waterbodies have been sampled. Moriarty (1997, p. 47) suggests an average weight for glasseels of 0.33 g. and for yellow and silver eels of 200 g, with an average value of 65 and 6 ECU per kg. The consumer price for glasseel is listed as 95 ECU per kg; restocking material will have been purchased at this price. However, prices of glasseel have fluctuated substantially in recent years, up to 500 ECU per kg (Fontenelle, in Moriarty and Dekker 1997).

The application of a single weight estimate for yellow and silver eel and for male and female eel is evidently a great simplification of reality. Silver eel are undoubtedly bigger than average yellow eel, and females grow to about thrice the weight of males (Vøllestad 1992). However, in the absence of information on mean size of yellow eel and on the ratio of males to females in the catch, there will be no option to differentiate in the current analysis.

Duration of life stages

Moriarty (1997, Table 6) lists minimum legal sizes by country and region. Taking a blunt average of the listed values (35 cm) and assuming these express the true landing minimum size, the average length of the continental stay until recruitment to the yellow eel fisheries should be nearly 10 years. Although this is subjectively judged as a realistic value, the average obscures a wide range from at least 5 to over 20 years (Moriarty 1997, Table 6).

The exploitation of the yellow eel ends when the eel silvers and emigrates. Average time spent in the exploited yellow eel phase can be estimated from the age composition of the catches. Extremes are reported by Dekker (1996) with only two and by Kangur (1993) with more than 10 age classes in the catch. Here, the average of these extremes (6 yr) was accepted as a realistic average value for the duration of the exploited continental phase.

Re-stocking glasseel

Moriarty (1997, Table 6) lists the amount of glass eel used for re-stocking. All known re-stockings combined, including those within river systems, total 125 tonnes. Regarding trap-and-transport within river systems or between systems within single countries, both trapping and re-stocking were interpreted as impacts on the stock, albeit a mutually opposing one (Figure 1).

Natural mortality

Estimates of natural mortality in yellow eel vary considerably, ranging from negligible (Dekker 1989) to close to 100% during incidental pollution accidents (Mueller and Meng 1990) or oxygen depletion in warm summers (Rossi et al. 1987-1988). This suggests that overall natural mortality is composed of a low base level in combination with rare but influential peak mortalities during short incidents.

Moriarty and Dekker (1997, annex 3) conclude that 'stocking studies suggest that natural mortality is in the order of 75% over the total continental life span'. In preliminary runs of the model presented below, such a mortality from glasseel to escaping silver eel leads to incongruous results: the amount of glasseel re-stocked would exceed the population as reconstructed from the catch of yellow and silver eel. Therefore, natural mortality was assumed to average 75% over the pre-exploited life stages only. Natural mortality during older life stages was assumed equal to that in the pre-exploited stages, i.e., 13% per annum (M=0.138).

Escapement of silver eel

The escapement of silver eel from the continent has never been directly assessed. Moriarty and Dekker (1997, annex 2) present a first attempt to quantify the amount of escaping silver eel, assuming a conservative escapement rate of 10% only. Ask and Erichsen (1976) and Sers, Meyer and Enderlein (1993) tagged silver eel in the coastal areas in the Baltic and observed recapture rates of up to 70% in coastal fisheries further down the outward migration route. This implies an escapement rate of 30%, the value which will be used here.

Methods

The approach followed here is based on the dynamic pool model of Beverton and Holt (1957), albeit that data limitations force us to reduce the detail of the analysis considerably in comparison to numerous applications to stocks of other species.

The dynamic pool model is based on a differential equation of the change in number of a cohort of fish:

$$\mathrm{d}N_t \,/\, \mathrm{d}_t = -\,(F_t + M_t) \times N_t$$

where:
N is the number of animals in the cohort at time t [number],
F is a coefficient of mortality due to fisheries [time^{-1}],
M is a coefficient of mortality due to natural causes [time^{-1}],
t is time, in units of a calendar year [time].

Under the assumption that F_t and M_t are constant during an infinitesimal short time interval (t_0, $t_0+\Delta t$), it follows that the catch during that time interval equals:

$$C_{(t_0,\, t_0+\Delta t)} = F_{t_0} \,/\, (F_{t_0} + M_{t_0}) \times (1\text{-}\exp^{-(F_{t_0}+M_{t_0}) \times \Delta t}) \times N_{t_0}$$

The classical model of Beverton and Holt (1957) assumes F_t and M_t are constant during an interval of one calendar year, that is Δt=1, with changes in mortality rates in-between the years. In reality, F_t and M_t are not truly constant during any time interval. The discretised estimate of F_{t_0} thus only represents a kind of time-averaged approximation to the true but volatile value of F_t during the whole time interval.

In the case of the eel fisheries, available data are insufficient to breakdown the catch data over age groups. Instead, only a breakdown by life stage can be achieved, distinguishing glasseel, pre-exploited yellow eel, exploited yellow eel, exploited silver eel and escaping silver eel. Tailoring the model to these data, the time-step must be chosen equal to the duration of a life stage. This implies that the model must be built of time steps of unequal length, varying from about three months for the glasseel stage to 10 years on average for the pre-exploited yellow eel stage. Consequently, the estimated value of F_{t_0} is averaged over short to very long time intervals and thus represents only a first approximation to the true value of F_t, which undoubtedly varies during each life stage.

Having grouped the entire life history into just a few life stages, there still remains the need to assign catches to specific cohorts. Defining the cohorts as individual year classes fails because of the lack of data; therefore a longitudinal analysis will not be pursued. A first approximation can be made by a cross-sectional analysis. This assumes that the fisheries are in a stable state, allowing the analysis of one year's catch as if it represents the catch from a single cohort over their total life span. This assumption is definitely incorrect. Recruitment has been going down and so has the stock. Consequently, results will underestimate the true exploitation rates.

After pooling individual age groups and introducing an unavoidable assumption of stability, a much reduced cohort analysis model remains. Using this simple model, a VPA-like procedure can be built on a matrix of catch-at-life-stage data, yielding estimates of $F \times \Delta t$ and N_{t_0}, following the usual retrospective procedures (Gulland 1965). The number of silver eel escapees in this interpretation conforms to the terminal population number. An assumption that 30% of silver eel escape the fishery, combined with an absolute figure for the silver eel catch, yields an estimate of the number of escapees. The remaining calculations are a straightforward application of VPA-procedures, except that it is now essential to distinguish $F \times \Delta t$ from F, which do not coincide whenever $\Delta t \neq 1$. Since time was discretised into only a few life stages, the convergence property of the traditional VPA (Pope 1972) will hardly apply.

Re-stocking of glasseel creates a specific problem. Since it is positioned between two fisheries in the life cycle, it must be included in the model. One solution is to incorporate re-stockings as a fishery with a negative catch (and consequently with a negative fishing mortality), operating during a time interval of arbitrary short length, at the onset of the continental growing phase.

Finally, the sensitivity to all input data of the fishing mortality at the glasseel stage, the population number at the glasseel stage, and the total mortality throughout continental residence is assessed in a simplified analysis. Relative changes in outcomes as a function of relative changes in inputs are calculated by a finite difference quotient, i.e. $(\Delta y/\Delta x)/(y/x)$. In Figure 2, the absolute value of the estimated sensitivity is plotted. The absolute magnitude of sensitivities indicates to what extent the corresponding input parameter influences the model result, while the sign (coded in the colour) indicates whether a higher input parameter value increases (positive), or decreases (negative) the model result.

Results

The model described above was applied separately to the eel fisheries in the *Biscay area* and *elsewhere*, as well as to the combined data set (Table 2).

The glasseel fisheries in the *Biscay area* constitute 87% of all glasseel catches in Europe and fishing mortality during this phase constitutes 60% of the estimated life time fishing mortality in the *Biscay area*.

Elsewhere, the fisheries for glasseel have a large impact, but these are balanced by re-stocking of the resulting catch. Overall, a net import of re-stocking material occurs here. The number of glasseel re-stocked exceeds all subsequent catches. Consequently, the fisheries outside the *Biscay area*, totalled over all life stages, yields a negative catch by numbers of approximately 77 million eels. The amount of glasseel re-stocked exceeds the estimated natural recruitment, constituting 57% of the subsequent population.

Combining all data over the whole of Europe, the glass eel fisheries exceed the re-stockings by a factor of five.

Estimated fishing mortalities are listed both on a per annum basis (fishing pressure) and for the duration of each life stage (net impact on the stock). High fishing mortalities are estimated on glass eel and silver eel, both in the *Biscay area* and *elsewhere*. On a per annum basis, the fishing mortality on glass eel in the *Biscay area* is estimated at 12.59 (=99.99966%), indicating that virtually all glass eel are caught. The estimates of fishing mortalities on yellow and silver eel are a direct consequence of the geographically undifferentiated assumptions and therefore have not been detailed per area.

The cumulative natural mortality over the continental life stages is assumed to be about 2.5 (=92%). In the *Biscay area*, the cumulative fishing mortality is twice as high. *Elsewhere*, it is estimated at 1.78 (=83%), but this value includes a negative mortality due to re-stockings. The cumulative fishing mortality inflicted upon the natural recruitment is estimated at 3.25 (=96%).

Table 2 Catch data, estimated fishing mortality and estimated stock size of the European eel.

	Catch		Fishery		Stock	
	Weight	Numbers	Mortality		Weight	Numbers
Life stage	(tonnes)	(millions)	F (year^{-1})	$F \times \Delta t$	(tonnes)	(millions)
Biscay area						
glasseel						
fisheries	510	1530	12.59	3.15	538	1616
re-stocking	0	0	n.a.	0	22	67
yellow eel						
pre-exploited	0	0	0	0	547	67
exploited	1090	5	0.10	0.63	3352	17
silver eel	545	3	2.87	1.43	735	4
escapees	0	0	0	0	164	0.8
sum	2145	1538	0.29	5.21	5499	1704
Elsewhere						
glasseel						
fisheries	72	216	4.25	1.06	167	502
re-stocking	-125	-375	n.a.	-1.47	91	272
yellow eel						
pre-exploited	0	0	0	0	5286	648
exploited	10,599	53	0.10	0.63	32,388	162
silver eel	5299	26	2.87	1.43	7146	36
escapees	0	0	0	0	1590	8
sum	15,846	-77	0.09	1.65	48,167	1355
sum excluding re-stockings			0.18	3.25		
Pooled data set						
glasseel						
fisheries	583	1748	7.19	1.80	707	2122
re-stocking	-125	-375	n.a.	-0.74	113	339
yellow eel						
pre-exploited	0	0	0	0	5833	714
exploited	11,689	58	0.10	0.63	35,719	179
silver eel	5844	29	2.87	1.43	7880	39
escapees	0	0	0	0	1753	9
sum	17,991	1461	0.17	3.12	53,647	3063
sum excluding re-stockings			0.21	3.86		

Some model parameters have a large influence on the model output (Figure 2). Increments in the natural mortality of the unexploited growing stage between the glass eel fishery and the yellow eel fishery have a large (six- to sevenfold) effect on the estimated parameters of the glass eel fisheries outside the *Biscay area*. The magnitude and duration of this mortality together determine the overall natural mortality; both have a great effect on the estimates. Larger effects on the assessment result from the magnitude of landings, the natural mortality rate and the average weight of glass eels. Overall, changes in input parameters have less effect on the estimates for the part of the stock in the *Biscay area* than *elsewhere*, with the pooled data set having an intermediate position.

Discussion

Long and slender eels do not fit very well into stout iron beds. The fisheries on the European eel stock constitute a long lasting, multi-levelled, geographically differentiated management problem, for which only a tiny set of consistent data could be compiled. There will be few assessments as poorly detailed as this one. Although the starting point is firmly based in stock assessment methodology, the resulting model does not pass the stage of a back-of-an-envelope-calculation. That is all the available data allow for. However, a stock-wide assessment of the European eel has not been presented before and this simple exercise does provide new insights.

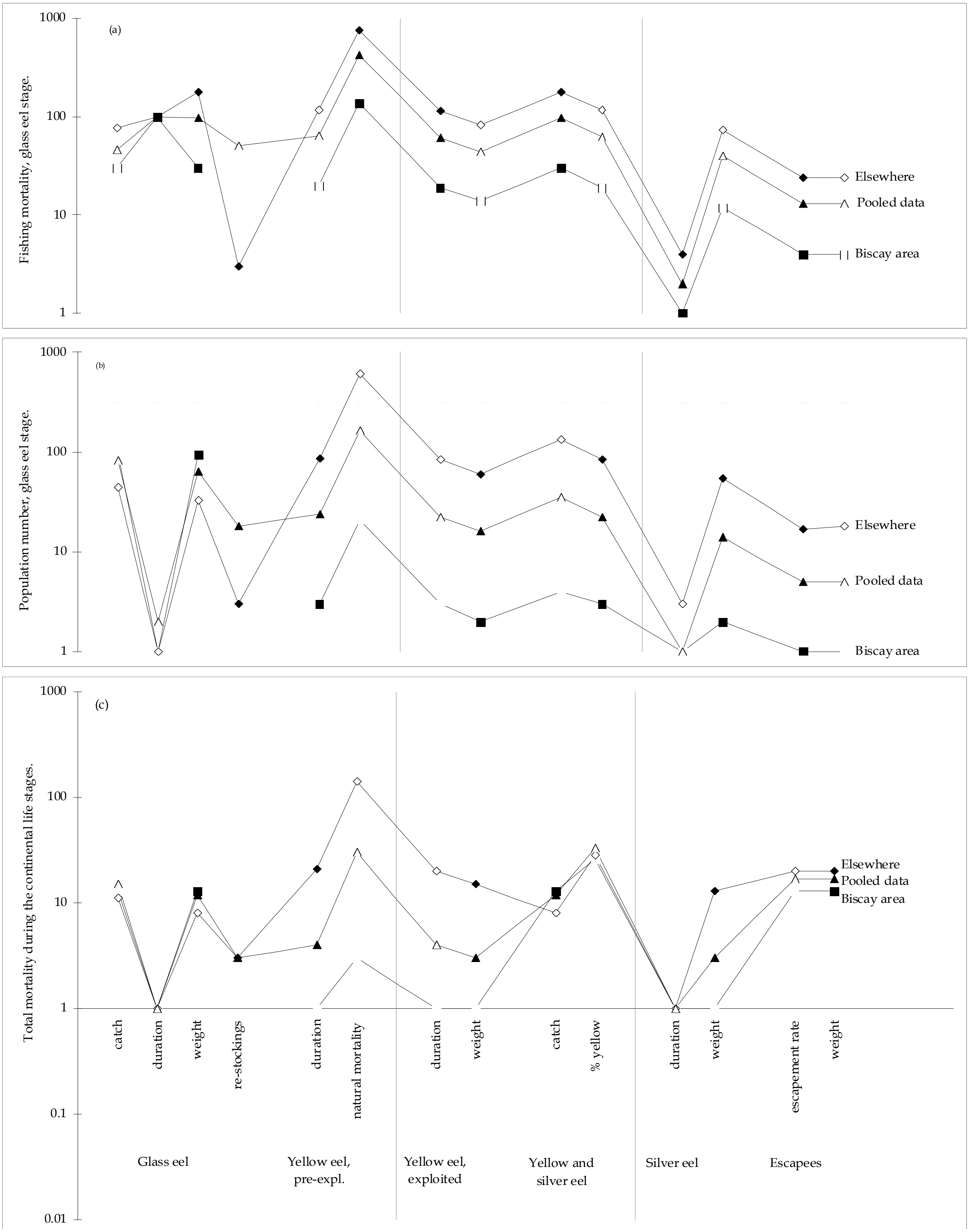

Figure 2 Sensitivity analysis of selected model results to the input parameters. For each of the input parameters, the value of $|(\Delta y/\Delta x)\,/\,(y/x)|$ is plotted, in percentage, on log-scale. Open symbols indicate a positive effect of the input parameter on the model result, black symbols a reverse effect.

For yellow and silver eel, there is a close link between assumptions, model parameters and corresponding results. Results can probably best be viewed as a re-formulation of existing assertions in terms of standard assessment methodology. Results for fisheries on glass eel and recruitment to the continent depend on data and assumptions about the glass eel stage itself, as well as on intermediate yellow and silver eel fishery results of the model. Consequently, results for the glass eel stage are much less sensitive to input parameters than results for the yellow and silver eel stages.

ICES (1988), in a discussion on eel landings, stressed the need to differentiate between glass eel of 0.3 g and yellow and silver eel of 200 g each. Moriarty (1997) made this distinction and revealed the contrast between landings in terms of weight and in terms of numbers. Here, the contrast between the glass eel fisheries and the fisheries on larger eel was explored one step further, by accounting for areas with a net yield of glass eel versus areas where re-stocking is practised. The analysis suggests that 76% of the total recruitment to the continent occurs in the area where intensive glass eel fisheries have developed. These areas constitute only 7% of the distribution area of the European eel, or 6% of the productive water surface (Moriarty and Dekker 1997). Natural recruitment in the *Biscay area* appears to be more than ten times as dense as elsewhere in Europe.

The identity of the biological unit stock of the European eel is not known. The available evidence has not shown any subdivision of the stock (morphological characteristics analysed by Schmidt (1906), genetic markers analysed by Daemen et al. (1997), coherence in recruitment pattern analysed by Dekker (2000)), although a failure to find differences is not a definite proof of panmixia. Noting the geographical concentration of the stock in the *Biscay area*, the evidence for a major contribution to the overall reproduction by eel populating waters elsewhere might be questioned. It might be hypothesised that the stock in the *Biscay area* constitutes a self-sustaining population, with only 24% of its recruitment ultimately scattered over the rest of the continent after their long journey from the spawning grounds to the *Biscay area*.

The exploitation patterns differ between the *Biscay area* and *elsewhere*. The fisheries in the *Biscay area* concentrate on the glass eel newly recruiting to the continent, while *elsewhere* glass eel fisheries serve only to re-stock inland waters. Fisheries for yellow eel and silver eel in the *Biscay area* were assumed to be equally intensive as *elsewhere*, but this was not substantiated by data. Thus, the higher cumulative fishing mortality estimated for the *Biscay area* ($F \times \Delta t = 5.21$, 99.5%) than for *elsewhere* ($F \times \Delta t = 3.25$, 96%) cannot be validated. Therefore, there is insufficient basis to claim that the effects of exploitation in these two areas on the spawner production are significantly different.

Elsewhere, the natural recruitment (estimated at 502 million glass eel), is supplemented by glass eel from the *Biscay area* (159 million). Additionally, 216 million glass eels are trapped and transported, before being returned to outdoor waters. This implies that less than half have completely free access to the continental waters. Westin (1990), in comparing emigration of natural and stocked eels in the Baltic, found silver eel originating from the latter showed aberrant behaviour. The reproductive success of transplanted eel is therefore questionable. Noting that re-stockings exceed natural immigration, one might worry about the effect on the breeding stock.

The stock of the European eel is in a bad state. Recruitment and yield have been declining for two decades or more. ICES (1999) concluded the stock is outside safe biological limits and recommended to set escapement targets on a system-by-system basis. This presupposes a potential stock-recruitment relationship of some kind. Although such a relationship is not known or quantified, the objective of supra-national management will undoubtedly include some restriction of fisheries to levels at which the number of escapees will not limit subsequent recruitment. Noting the unequal distribution of recruitment over the continental areas, the escapement targets must probably be set proportional to the incoming recruitment. This would correspond to setting limits on the cumulative fishing mortality during the continental stages. Although a first estimate is provided of this cumulative fishing mortality averaged over two parts of the continent, the analysis does not give information on target values. Moreover, because of the assumption of stability, the true exploitation levels may be underestimated.

The available information has been used as starting point. In retrospect, the question arises how the analysis could have been improved by acquiring additional information from the field. Several assertions (e.g., the ratio between yellow and silver eel catch, mean weights for each of the life stages, the duration of the pre-exploited and exploited yellow eel stages, the level of natural mortality) were stated for the continental stock as a whole, for both sexes combined. These could easily be replaced when data had been acquired in more detail. However, variation at a scale of a few kilometres appears to be larger than at the continental scale (Dekker 2000). Since data are available for only a few waterbodies scattered over few countries, available data may not constitute a representative sample of all waters in each country, particularly because larger waterbodies tend to be over-represented. Thus, compiling and adding more detail at this stage might easily confound the interpretation of the results, while interfering with the simplicity of the analysis presented. However, when additional and more representative information could be provided by all countries involved, the basis of a continent wide assessment may be improved substantially.

It is acknowledged that the picture of the eel stock presented will not suffice for developing a rational management at the continental level. Substantial improvement of the database underlying the assessment is unlikely, at least at the time scale at which management action is urgently required. However, since effective management of the scattered stock and fisheries must focus on national or lower levels (Dekker 2000), the development of a system of assessment and control at these geographical scales is inevitable. When co-ordinated, this may also accommodate a more comfortable assessment of the European eel stock.

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The fractal geometry of the European eel stock

4

ICES Journal of Marine Science 57: 109-121 (2000)

The European eel *Anguilla anguilla* (L.) is found in most European waters. This widespread species is usually exploited by small-scale companies fishing in localized areas. This implies a contrast of scales. This study analysed data on recruitment, stock and fisheries to determine how they vary geographically. Coherence between 17 data series on glasseel recruitment is analysed by multivariate techniques. It is shown that the majority of these series exhibit a mutually correlated downward trend since 1980; two of the three stations in Ireland, one in the UK and one in Scandinavia show aberrant trends. The geographical distribution of the continental stock is exemplified by a variogram of the length of eel in the Netherlands. It is found that at a distance of only ~10 km a large variance component is found, that can not be explained by mere distance. Apparently, the continental stock is fragmented by the fragmentation of the inland waters themselves. The geographical distribution of the continental fisheries is exemplified in an analysis of the dispersion of Dutch fishing licence holders over the country. It is shown that the licence holders are highly overdispersed, except for the companies fishing on Lake IJsselmeer. It is concluded that the distribution pattern of the European eel is characterised by great uniformity in the recruitment stage over the majority of the continent. In the growing stages, the stock (and fisheries) exist in extremely small, fragmented units. It is argued that this dual distribution characteristic necessitates large scale, continent wide management, while assessment of the fragmented continental stock and centralised management of the scattered fisheries is not practically achievable.

The European eel *Anguilla anguilla* (L.) is found and exploited in most of Europe and in large parts of Africa, in over 90,000 km^2 of continental waters (Moriarty and Dekker 1997). The type of fishery shows a very large regional variation, ranging from hand held dipnet fisheries for (expensive) glasseel in the countries around the Bay of Biscay, to concrete weirs spanning entire rivers, used to take large amounts of silver eel in more northern countries (Moriarty 1997). The annual yield in Europe is at least 20,000 tonnes. More than 25,000 people acquire a substantial income from the eel fisheries (Moriarty and Dekker 1997). The eel is therefore one of the most widespread exploited stocks.

The European eel is a catadromous species, with an incompletely known life cycle. Reproduction takes place somewhere in the Atlantic Ocean. Larvae (Leptocephali) of the latest stage are found on the edge of the continental shelf, where they transform into young, transparent eels, so-called glasseels. At this stage, the young animal proceeds into continental waters, often deep into the fresh water systems. Following the immigration to continental waters, a prolonged life stage begins, lasting for about 5 to 50 years. During this stage, almost all growth takes place, but no maturation. At the end of this period, the maturation starts and the eel returns to the ocean. The non-migratory continental stage is called the yellow eel stage, while the migratory, maturing eel is known as silver eel. Figure 1 shows the traditional representation of the life cycle and presents the names of the life stages.

Throughout the 1980s and 1990s, an intense and prolonged decline in recruitment of glasseel to the continental stock was observed in many parts of Europe (Moriarty 1990, 1997), exacerbating an existing decline of eel fisheries. By 1993, this decline in recruitment had lasted for more than an average eel's life span and eel scientists studying eels became alarmed (Anonymous 1993). The need for international management was been identified (ICES 1997; Moriarty and Dekker 1997; ICES 1999), but has not yet resulted in management actions. This decline in recruitment has now lasted for more than 15 years, without an adequate response from fisheries managers.

Typical eel fisheries consist of small boats making small catches (on average 1 tonne per man per year) in rather small water bodies (Moriarty 1997). Management of the eel fisheries has traditionally operated on this small, local scale. It has taken a considerable time to realise that

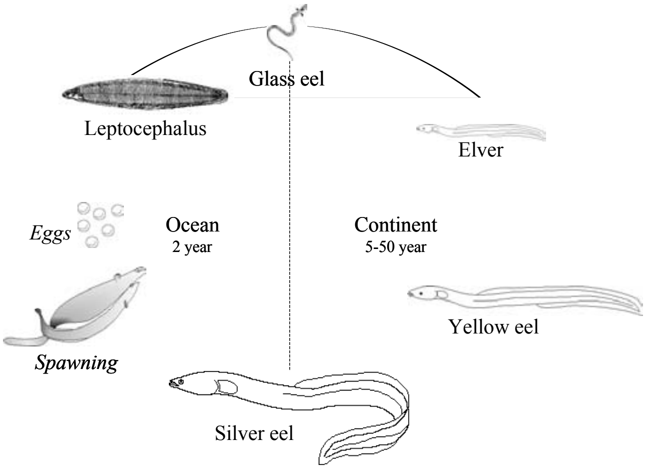

Figure 1 The life cycle of the European eel. The names of the major life stages are indicated; spawning and eggs have never been observed in the wild and are therefore only tentatively included.

the local declines in recruitment observed in many places in Europe were pan-European, and that the stock cannot be conserved by traditional local management.

Thus the European eel stock is characterised on the one hand by a large overall area of distribution and large-scale, long-lasting fluctuations, and on the other hand by partitioning of the stock between small-scale scattered waterbodies, which support small-scale fisheries under local management. It is this contrast of scales, which will be explored here.

Monographs on the European eel have been published throughout the 20th century (Walter 1910; Bertin 1942, 1956; Sinha and Jones 1975; Deelder 1984; Tesch 1977, 1983). All these studies pre-date the present decline in recruitment. These monographs addressed in depth the biology of the eel but remained largely descriptive. With respect to population size and structure of the whole stock, the monographs were based only on extrapolations from particular local stocks. Fragmentary details of local stocks and fisheries throughout Europe were listed, without a major attempt to synthesise or unify.

In an early attempt to address the current decline in recruitment, ICES (1988) compiled a table of total annual catches (of which only half were covered by the official statistics). Moriarty and Dekker (1997) basically repeated the exercise, but included many additional details. The authors of this report were apparently aware of the small size of individual eel fisheries in Europe (causing difficulties in compiling an overview of the stock), but addressed analytically neither the potential coherence between individual fisheries on the continent, nor the assumed uniformity in the recruitment trends between stations. Most data required to make these analyses were indeed made available in Moriarty and Dekker (1997) and are analysed here. However, most of the ideas presented here originate from discussions during the preparation of that report.

In this exploration of problems of scale, the geographical uniformity of trends over the past decades are addressed, by analysing recruitment data for 17 stations over the European continent, and the scattered nature of both the eel stock and the fisheries explored by a geo-statistical analysis of Dutch data. In the discussion, the emerging problems for research and management are contrasted with those in other fish stocks, to highlight the unique situation presented by eel fisheries.

Material and methods

Recruitment

In order to explore the geographical pattern in the recruitment data, three analyses are presented: 1) *Cluster analysis.* Do the observed stations separate into disjunct groups? 2) *Multidimensional scaling.* Do gradual trends in recruitment data occur from area to area? 3) *Factor analysis.* To what extent are the recruitment series at the stations determined by a common background?

Material

Time-series of data on glasseel immigration were taken from the literature (Moriarty 1986, 1990; Desaunay and Guerault 1997). The geographical coverage ranged from Norway (59°N 6°E) and Sweden (58°N 16°E) to Portugal (42°N 9°W) and Italy (42°N 12°E) and the time span ranged from 12 to over 65 years. All data series have been extended up to 1997 (1998) by personal communication with responsible authors or agencies. Some of the series do not pertain to glasseel *sensu strictu*, but to young eel in different stages of pigmentation. This certainly applies to Motala stream data, although Moriarty (1990) questioned other data. Most series represent the quantities of glasseel taken by commercial fisheries, not the absolute magnitude of the recruitment. However, although effort may have varied over the years, it is most likely that variation in total catch volume reflects variation in the amount of glasseel immigrating. At other stations, fishing effort was controlled (research sampling at DenOever) or at least not directly influenced by catch volumes (non-profit fisheries at Ems and Yser).

In Figure 2, all data series have been scaled to 100% over the years 1979 through 1994 for comparisons between stations. The geographical positions can be read from Figure 3.

Methods

All available data series originate from local, uncoordinated studies. Consequently, many sampling characteristics vary between stations and the time periods do not completely coincide. The entire data set is therefore highly unbalanced. In the following, three different approaches will be used: 1) *Selected years*. Data were selected for 1979-1994, i.e. those years during which most stations were reporting. 2) *Selected stations*. Data were selected for the stations Motala, Ems, DenOever, Yser, Loire, Bann, Erne and Nalon, i.e. those stations that reported data for more than three consecutive decades. 3) *Pairwise correlations*. The unbalanced data set was used to calculate correlations between each pair of recruitment series for the period of overlap. The resulting matrix was subsequently used in multivariate analyses, despite the unequal cell frequencies.

To normalise the data sets and to allow for the assumed multiplicative nature of the variation between stations and between years, all primary data were log-transformed prior to the calculation of the correlations. Since none of the entries equated to zero, there was no need to add a positive constant to each observation before taking the logarithm. Because of the sparsity of the data sets, no prior or posterior check on the adequacy of the transformation was undertaken. Data handling, statistical analyses and graphical presentations were implemented in SAS (SAS Institute Inc. 1989, 1990a,b).

Cluster analysis The correlation matrices based on *selected years* and on *pairwise correlations* were used for a cluster analysis (Mardia et al. 1979), analysing the potential existence of a disjunct geographical ordering of the sampling. Distances to a cluster of stations were calculated as the average of the distances to the individual stations in the cluster (averaging method). The results of these analyses were plotted in a dendrogram (Figure 4). The ordering of the stations is only partially determined by the order in which forks are formed during the analysis. The dendrograms could be re-ordered (complete inversion of clusters hinging on their stem) to ensure that the order of the stations in the two analyses are as identical as possible. Only one station could not be matched. In Figure 4, this topological inconvenience happens to apply to the Yser, but alternative solutions may be found, in which one of the other stations is left unmatched.

Multi-Dimensional Scaling The correlation matrices based on *selected years* and on *pairwise correlations* were used in a Multi-Dimensional Scaling analysis MDS (Mardia et al. 1979), analysing the potential existence of gradual trends in the recruitment data from area to area of the continent. Following Mardia et al. (1979, Figure 14.4.1, p. 410), two dimensions were analysed. The co-ordinates of all stations on these two dimensions were subsequently translated, scaled, rotated and flipped to order the stations so that they most closely match the true positions of the stations on the map. The resulting positions were superimposed on a true map (Figure 3). The transformations minimised the (summed) distances between the positions found in the MDS-analysis and the true position on the map. These distances are represented on the map by arrows.

Factor analysis All three correlation matrices of the recruitment data were analysed in a Principal Factor Analysis (Mardia et al. 1979). In preliminary runs using Maximum Likelihood Factor Analysis, it turned out that either only a single factor contributed significantly, or, if more factors could be included, the estimated communality of the first factor was greater than 1 (so-called Heywood cases, Mardia et al. 1979). Apparently, the information contained in the recruitment data does not allow for the estimation of more than one single factor. The unbalanced nature of the data set undoubtedly contributes to this shortage of information content. Below, only results based on a single factor will be presented.

Continental Stock

Data on the continental life stages of the eel are frequently reported in the literature, but these studies rarely report on more than a small geographical area. Meta-studies (Fontenelle 1991; Vøllestad 1990), cover major parts of the continental distribution area, but contain no information on small geographical scales. In the current analysis, the prime interest is in detecting the inherent geographical scales of the continental population. A meta-analysis would exclude part of the potential range of significant geographical scales *a priori*. Wide ranging basic data on the continental population are not yet internationally available and this analysis of scales was therefore restricted to the Netherlands. The selected data set allows for comparison of samples of no more than 250 km apart.

The geographical pattern of the stock in continental waters will be characterised by a basic geo-statistical diagnostic tool: the variogram, applied here to the (sample mean) length of eel in Dutch fyke nets.

The largest consistent cluster (1062 samples) of data in the Dutch data set, covering a whole range of geographical scales, concerns the sampling of commercial fyke net catches. Although the types of fyke net used vary over the country, the legislation is uniform, with a minimum legal size for the eel of 28 cm and a minimum mesh size of 18 mm.

In analysing the Dutch inland eel fisheries, a distinction must be made between Lake IJsselmeer and the rest of the country. Lake IJsselmeer (52°40′N 5°25′E, currently

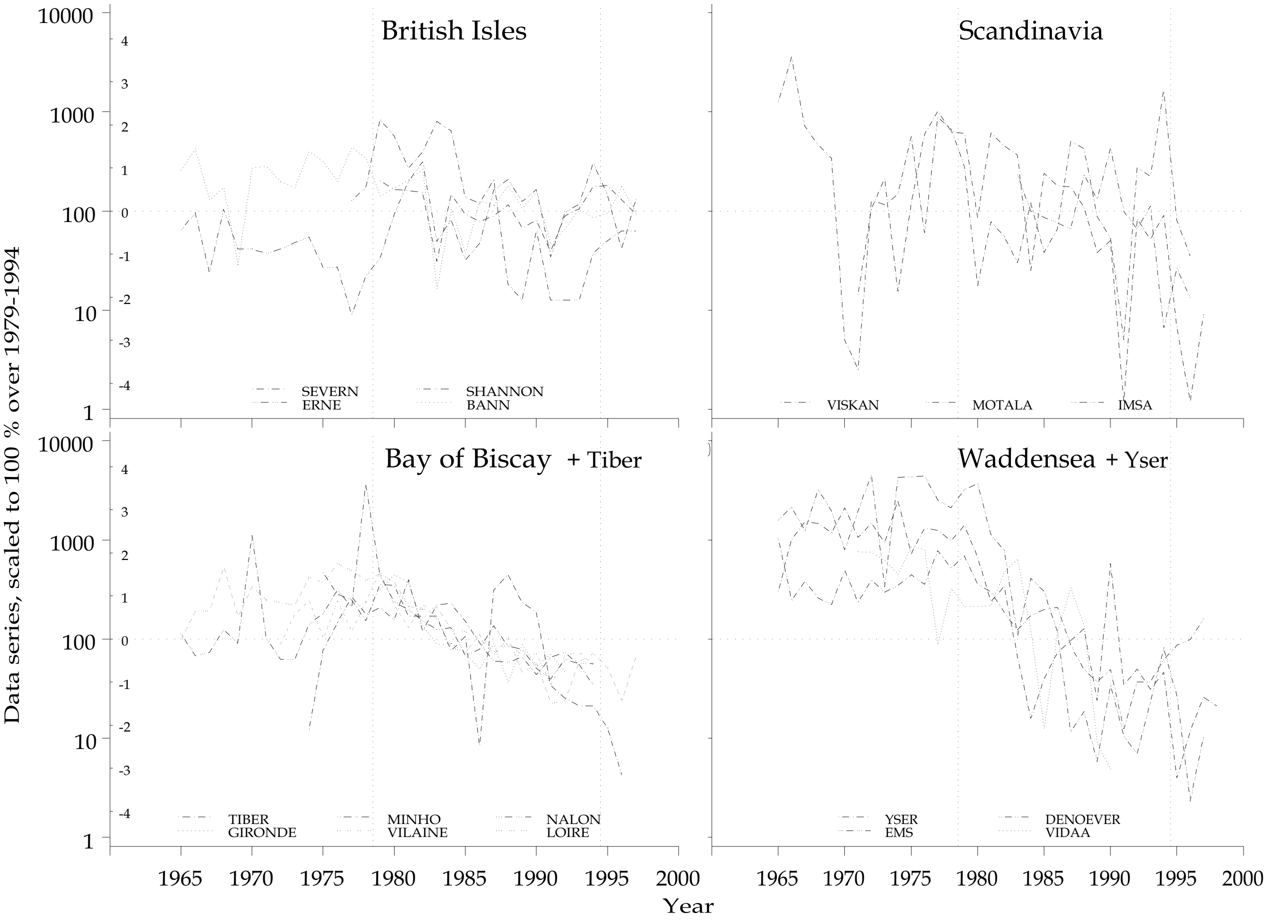

Figure 2 Data series of recruitment of glasseels to the European continent by region, scaled to 100% over the range of years 1979–1994. Dotted reference lines frame this scaling interval.

1820 km^2, average width ± 20 km) is a former estuary of the river Rhine, shut off from the Wadden Sea in 1932. This lake constitutes ~50% of the fresh water area in the Netherlands. An extensive description of the lake and its fisheries is given in van Densen et al. (1988). The commercial fisheries comprise nearly 100 vessels and are under governmental management. In conjunction, there are programmes to monitor fish stocks and fisheries (Dekker 1996). Data from these monitoring programmes dominate the total data set on fyke net catches (56%). The large absolute size of the lake as well as the low fractal dimension of its coastline (D=1.25) qualifies this single water body as atypical of the Dutch inland fisheries. Therefore, data on Lake IJsselmeer were analysed separately. The other waters where commercial eel fisheries are carried out include a wide variety of canals, rivers and lakes, which are generally interconnected in a complex network.

For each sample of commercial fyke net catches, the arithmetic mean total length was calculated. Mean lengths were grouped by decade and variograms compiled, plotting the absolute value of the difference in mean length as a function of the distance between each pair of samples (within one decade). Following Cressie (1993), the individual pairs of samples are plotted, rather than a fitted variogram. No attempt was made to fit a parametric curve through the data cloud.

Fisheries

Government regulation of fisheries in Europe differ greatly between countries (Moriarty and Dekker 1997; Table 2.4), varying from strict control using licences, gear controls and season/area limitations (glasseel fisheries in southern countries, yellow eel fisheries in northern countries) to no governmental control (yellow eel fisheries in southern countries). Consequently, there is no consistent basis for a continent-wide assessment of the geographical pattern in fisheries. The approach taken here will parallel the analysis of the stock structure above. The analysis will

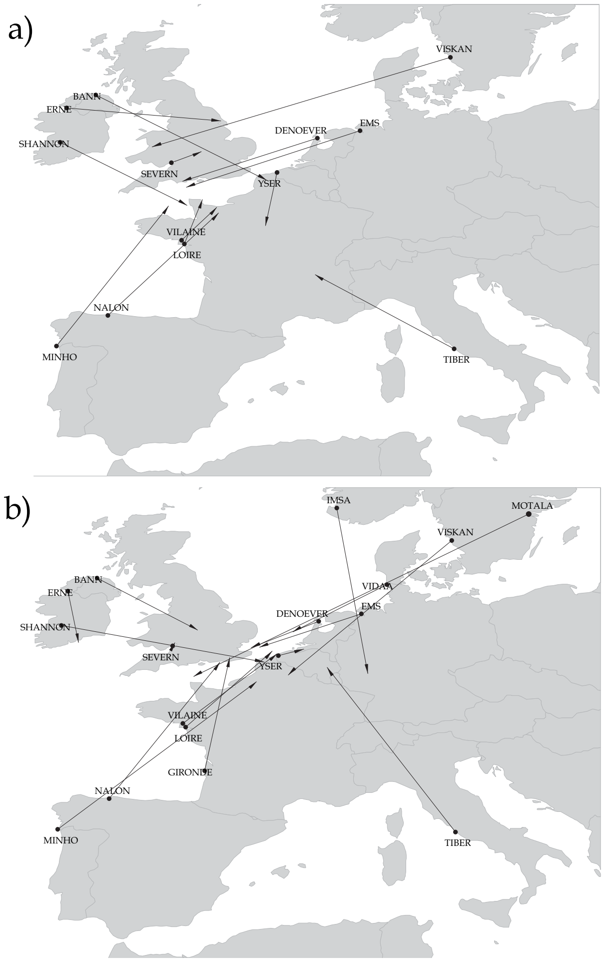

Figure 3 MDS solutions for the glasseel correlation matrices plotted over the true geographical map. The true position of each station is connected to the MDS solution by an arrow. a) Based on selected years. b) Based on pairwise correlations.

be based on a national data set, which restricts the depth of the analysis but has the advantage of being consistent.

The geographical pattern of the fisheries will be characterised by the distribution pattern of the home addresses of fishing licence holders in the Netherlands. In particular, the degree of overdispersion will be analysed, by a simple Poisson-model of the number of licences per local region, to show the degree to which the distribution reflects a random choice of home address, or is influenced by concentrating or dispersing factors.

In the Netherlands, anyone fishing commercially for fresh water fish must acquire a special licence for selling freshwater fish issued by the Fish Board (*Productschap Vis*). The Board keeps a list of addresses of licence holders, and was kind enough to provide a list of zip-codes for the year 1995. On the basis of the zip-codes, the home address of each licence holder could be recovered up to a spatial resolution of approximately 1 km; the total number of zip-code areas in the Netherlands is ~30,000.

Thus, the geographical distribution of the fisheries (Figure 5) could be summarised as a frequency distribution of the number of licences per zip-code, the statistical properties of which were analysed by a Poisson-type model, assuming that the frequency distribution can be characterised by the mean and dispersion parameter only. Data for Lake IJsselmeer (see above) and the rest of the country were again analysed separately. The mean was estimated by maximum likelihood and the dispersion parameter by the deviance divided by the degrees of freedom. In addition, the number of zip codes with no licence at all was estimated in an iterative procedure, in which the assumed number of zip-codes with no licence (input) was matched to the predicted number (output). This procedure conforms to the EM-algorithm given by Dempster et al. (1977).

Results

Recruitment

Cluster analysis

In the cluster analyses based on *selected years* and on *pairwise correlations*, clusters are formed at all distance levels (Figure 4). These levels are almost uniformly distributed between the minimum and maximum distance. Only 3 (*pairwise correlations*) or 4 (*selected years*) of the forks do not join a leaf to a cluster, but amalgamate two clusters. This is indicative of data sets that do not contain disjunct clusters at all. In fact, long chains were found in which individual stations are subsequently added to a cluster. The patterns of cluster forming in the two analyses do not correspond in most cases. Shannon is found to be more related to {Ems, Loire, DenOever} than to Minho and Viskan in *pairwise correlations*, but in *selected years* the opposite holds. The clusters that occur in both analyses sometimes do ({Ems, DenOever, Loire}, {Bann, Severn}), but sometimes do not ({Imsa, Tiber}) form meaningful combinations. In particular the linkage of Imsa (the most northern station) with Tiber (the most southern station), without any of the intermediately positioned stations, must be considered spurious. The set of most aberrant stations {Bann, Severn, Erne, Motala}, however, does correspond in both analyses.

Sampling effort at three stations (DenOever, Ems and Yser) was independent of the quantity of glasseel caught. These stations do cluster together at low distance in *selected years*, but in *pairwise correlations* Yser is only linked at very long distance. In both analyses, the cluster contain-

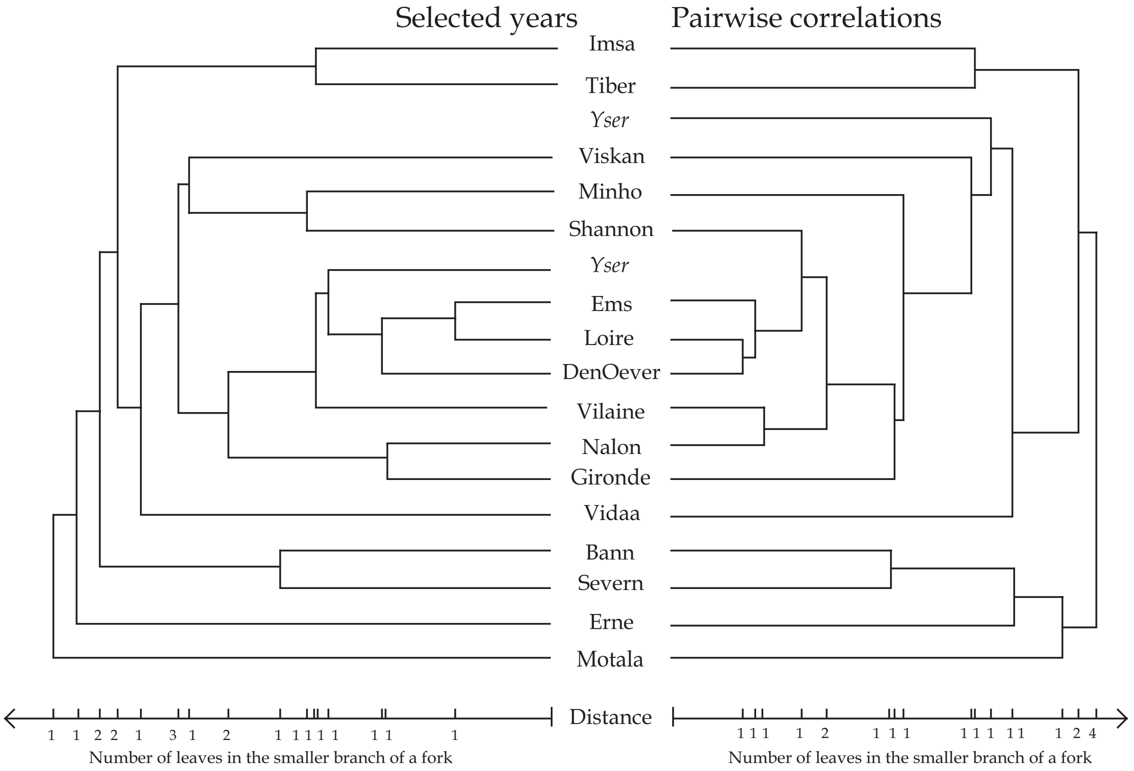

Figure 4 Clustering dendrogram of the stations where eel recruitment is monitored based on *selected years* (left panel) and on *pairwise correlations* (right panel). Note: the position of station Yser in this diagram could not be matched between left and right side and is therefore listed twice.

ing these non-commercial stations also contains the Loire, one of the stations based on commercial catch data.

Multi-Dimensional Scaling

The results of the Multi-Dimensional Scaling analyses are presented in Figure 3, plotted over the true map. Unfortunately, neither map is as self-explanatory as the textbook results presented in Mardia et al. (1979). The relationships between stations as inferred from the recruitment data do not conform to the geographical positions of the stations. In both cases, most stations are arranged in a chaotic area in the centre of the map. The positions within this area do not show any consistent ordering between the analysis based on *selected years* and on *pairwise correlations*. Stations that are in reality distant from the rest (Tiber, Minho, Viskan, Shannon) are projected into this area, while nearby stations (Erne, Bann) are projected to more distant positions. The set of stations further outside these areas (Bann, Severn, Erne, Motala), is, however, identical to the set of aberrant stations in the cluster analyses (Figure 4).

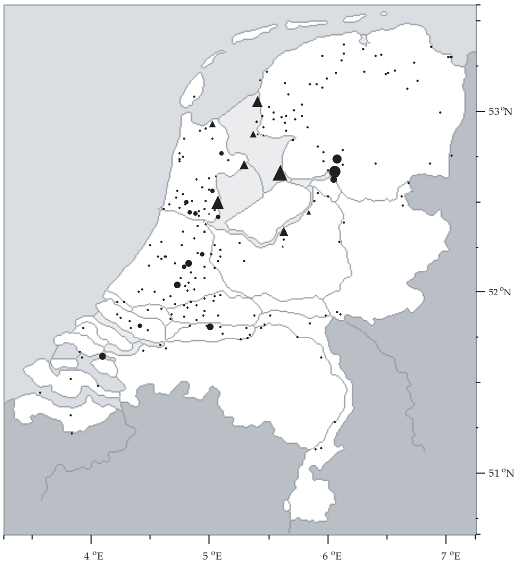

Figure 5 The distribution of holders of a licence to sell fresh water fish in the Netherlands. The number of licence holders per zip code (approx. 1 km) is plotted, distinguishing licence holders fishing on Lake IJsselmeer (triangles) from those fishing elsewhere (dots). Symbols are proportional to the number of licence holders in a particular area.

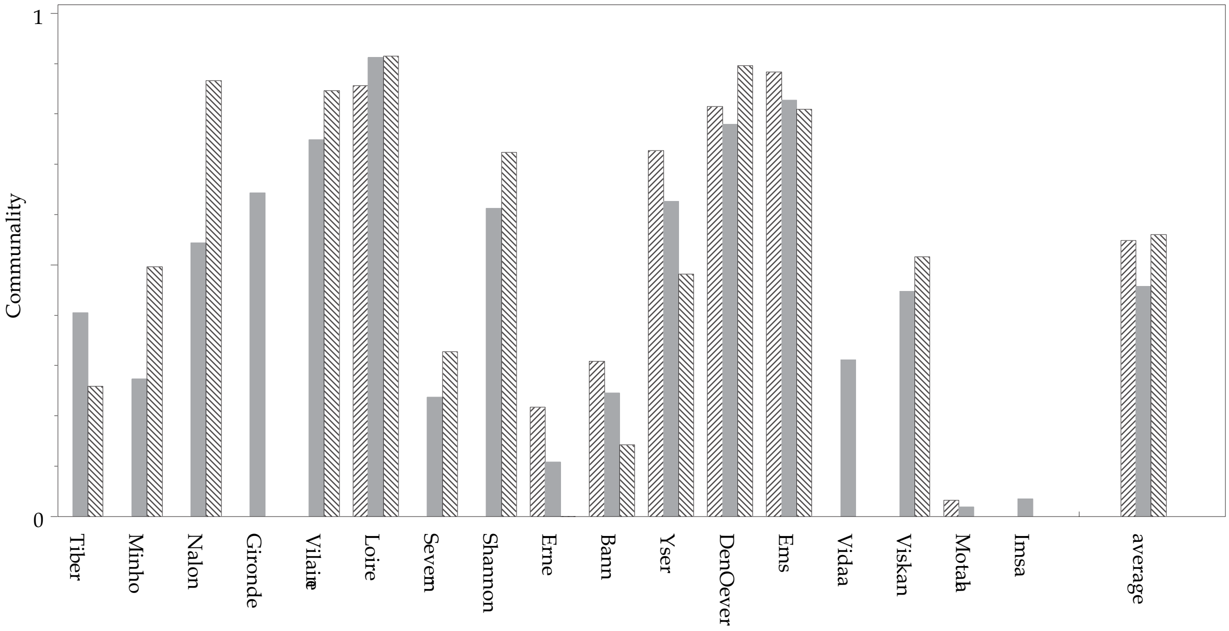

Figure 6 Estimated communalities for each station, based on a single factor fitted to the recruitment data. For each station three estimates are presented, depending on the correlation matrix used: left (upward slanting): selected stations, middle (solid): pairwise correlations, right (downward slanting): selected years.

Factor analysis
Estimated communalities (Figure 6) range from only 1.9% for the Motala, to 91% for the Loire, both using *pairwise correlations*. Average communalities for the three correlation matrices were estimated to be 55% (*selected stations*), 46% (*pairwise correlations*) and 56% (*selected years*). This means that, averaged over the stations, about half of the year-to-year variation in recruitment can be explained by a single factor common to all stations.

Marked differences in communalities among the analyses occur at the following stations: 1) Minho: recruitment figures showed an upward trend in the years prior to the reference years 1979-1994; this trend was not common to all stations and resulted in a marked difference between the analyses based on *pairwise correlations* and on *selected years*. 2) Nalon: recruitment figures showed aberrant high catches in 1970 and 1978. The analysis based on *selected years* excluded these outliers, and therefore estimates a much higher communality.

High communalities in all analyses are estimated for Nalon, Gironde, Vilaine, Loire, Shannon, Yser, DenOever and Ems. This selection of stations matched the results of the cluster analysis and the Multi-Dimensional Scaling analysis. Low communalities occur at Severn, Erne, Bann, Motala and Imsa. This again conforms to the preceding analyses, for the first four of these stations.

The analyses based on *selected years* and on *selected stations* yield, as a side effect, an estimate of the factor scores over the years (Figure 7). The results of the two analyses match rather well. Differences on a linear scale range from 2% (in 1992) to 43% (in 1991), averaging only 19%. The general pattern is a row of high scores in the years prior to 1980, with a slight tendency to increase during the late 1970s. Over the 1980s through to the early 1990s a steep decline occurred, reaching record low levels. During the 1990s, however, the scores level.

Continental Stock

The variogram of eel lengths in Lake IJsselmeer (Figure 8a) shows a stable pattern. Differences in length amount to a few centimetres with a maximum of nearly 10 cm, irrespective of the distance between samples. Outside Lake IJsselmeer, a completely different variogram is found (Figure 8b). For distances between 1 and 10 km, differences in mean length are in the same order of magnitude as for Lake IJsselmeer, but above 10 km the length differences frequently increase to 10-30 cm, with the largest differences occurring at distances over 25 km, levelling thereafter.

Fisheries

The distribution of fishing licence holders in Lake IJsselmeer (Table 1, Figure 9a) differs completely from the distribution elsewhere in the Netherlands (Figure 9b). In the Lake IJsselmeer fisheries, the distribution is highly clustered. Elsewhere, the number of zip codes without

Table 1 Characteristics and estimated parameters of the frequency distribution of the number of fishing licence holders per zip code around Lake IJsselmeer and elsewhere in the Netherlands.

Area	Number of licences	Number of zip-code areas with licences	Estimated number of zip-code areas without licences	Estimated number of licences per zip-code area	Estimated dispersion parameter φ
IJsselmeer	108	24	1.45	4.320	6.2546
Elsewhere	294	201	>50,000	0.005	0.0625

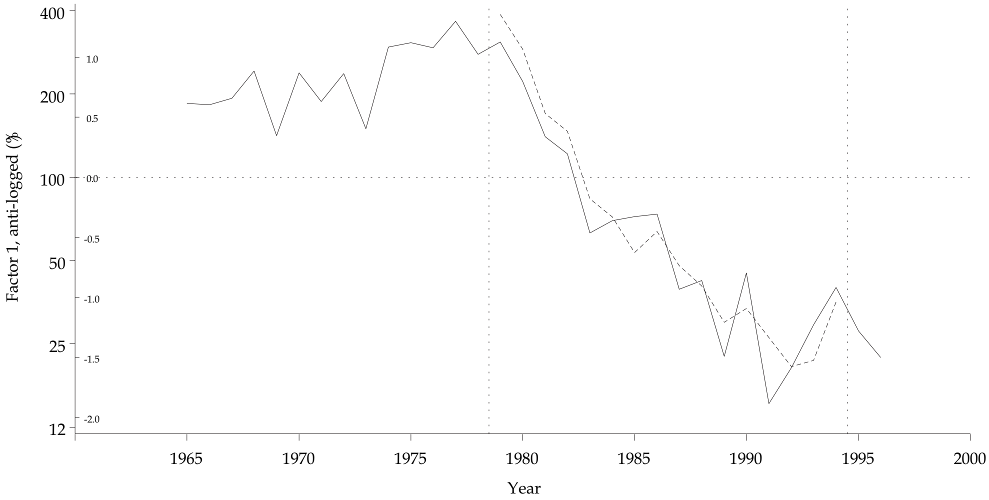

Figure 7 Factor scores over the years, of the single factor in the analysis of *selected years* (dashed) and of *selected stations* (straight line), scaled to 100% over the years 1979 through 1994. Dotted reference lines frame this scaling interval.

licence holders tends to infinity (that is more than the true number of zip codes, which is ca. 30,000), while the distribution is highly scattered. The mean number of licence holders per zip code is much lower, but its value has a strong, negative correlation with the estimated number of zip-code areas without licence holders.

Discussion

The life cycle of the eel is often portrayed as a series of Platonic abstractions, as in Figure 1. Although this diagram orders the life stages and illustrates the amphidromous character of the life cycle, it also suggests a false symmetry between the oceanic and continental stages, which does not occur in the geographical distribution characteristics. This misfit obscures the assessment of the current decline in recruitment and fisheries and clouds the potential for rational management of the stock in the future.

Coherence in recruitment between areas

The stock identity of the European eel is not known. On the basis of vertebrae counts, Schmidt (1906) speculated that the whole European population belongs to a single unit stock. Consequently he assumed there to be only one, panmictic breeding stock. Tucker (1959) even claimed the difference between the European eel (*Anguilla anguilla*) and the American eel (*Anguilla rostrata*) was not evident during his lifetime. Whatever the true unit stock identity, it has been shown here that the downward trend in recruitment since the early 1980s is shared by the majority of monitoring stations on the European continent. Neither disjunct groups of stations (cluster analysis) nor gradual trends from area to area (Multi Dimensional Scaling) could be detected. The degree of communality over such a large geographical area (Minho to Motala >3000 km) is remarkably high (around 50%, factor analysis). Evidently, the recruitment to the continent is primarily a monistic, large scale, slowly developing process, with a common and steep decline since the end of the 1970s.

Castonguay et al. (1994) pointed out that common trends in recruitment may or may not indicate the whole continental population (or in their argument: the populations of *A. anguilla* and *A. rostrata*) is under the dominant influence of a single biological process. Parallel developments in continental waters (such as synchronised pollution events, migration obstructions or area reductions) might induce parallel trends in recruitment, falsely suggesting a common and shared causative mechanism.

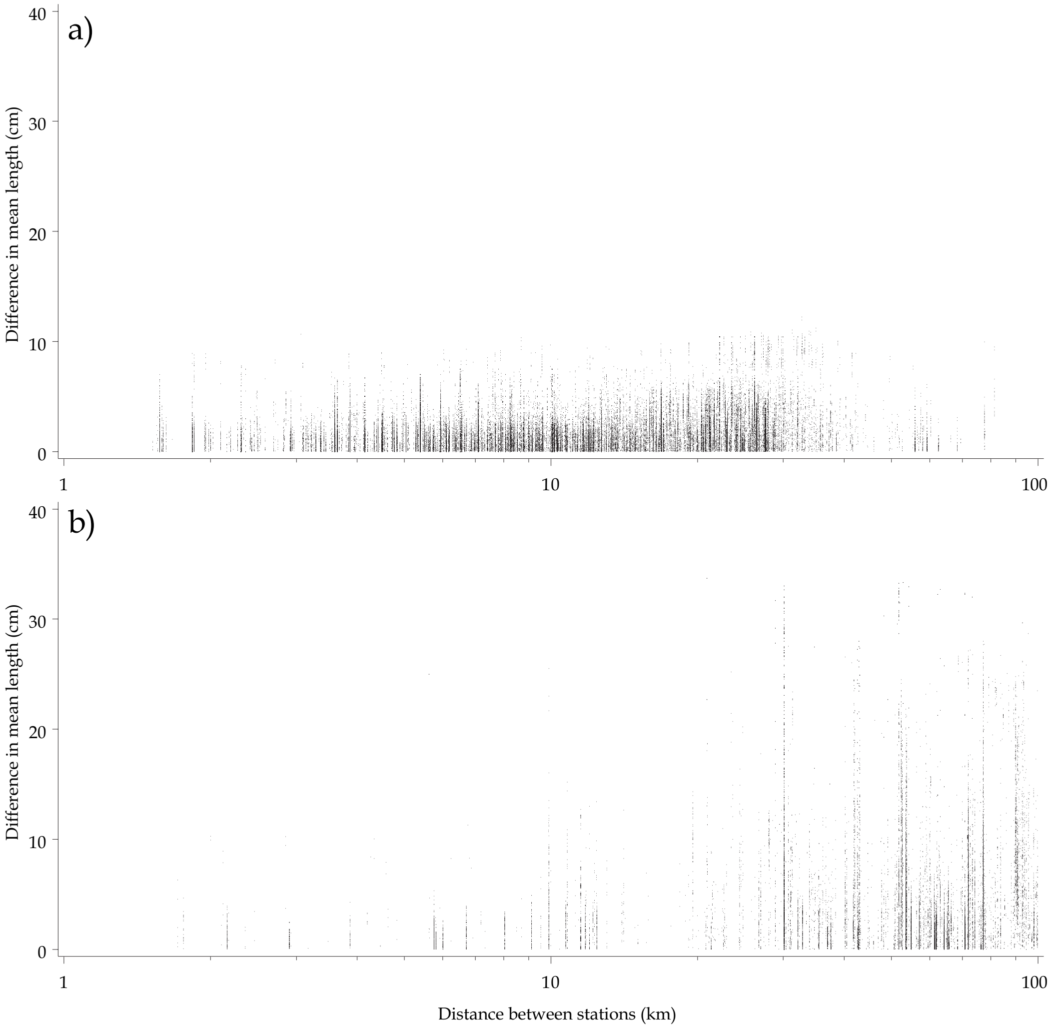

Figure 8 Variogram of (sample means of) the total length of yellow eels caught in fyke-nets in the Netherlands. Observations were grouped into decades before calculation of the variogram. a) Lake IJsselmeer (the Netherlands). (approx. 20 km across). b) Remainder of Dutch inland waters.

Reversing this argument, the aberrant recruitment pattern found at a few stations in Europe (Motala, Erne, Severn, Bann and possibly Imsa) could point towards an independent recruitment process at these stations. However, it might also be the result of local processes, perturbing the otherwise shared recruitment trend. Local climatic and hydrological circumstances, for instance, have been shown to have a substantial effect on monitoring results (e.g. Gandolfi et al. 1984; Dekker 1986, 1998; Desaunay et al. 1987), although this has not been analysed for all stations alike.

Whatever the true causality of the recruitment trend, the decline observed at the majority of the stations during the last two decades poses a serious management problem, common to the entire European population. The archetypical oceanic phases (Figure 1) currently represent a single and common problem. The stock in Europe, however, as well as the human impact on the stock (fisheries and habitat deteriorations) is of a completely different nature.

Fragmentation of stock and fisheries over the continental distribution area

Although the stock and fisheries are found over an extremely large geographical area (>3000 km across), a common and shared stock does not appear to exist. Differences in mean length observed in Lake IJsselmeer were found to be remarkably stable up to distances between sampling locations of 10 km and more, implying homogeneity of the local stock. No corresponding consistency could be found in the variogram of the other, more typically fragmented inland waters. Apparently, differences in stock composition between nearby waterbodies

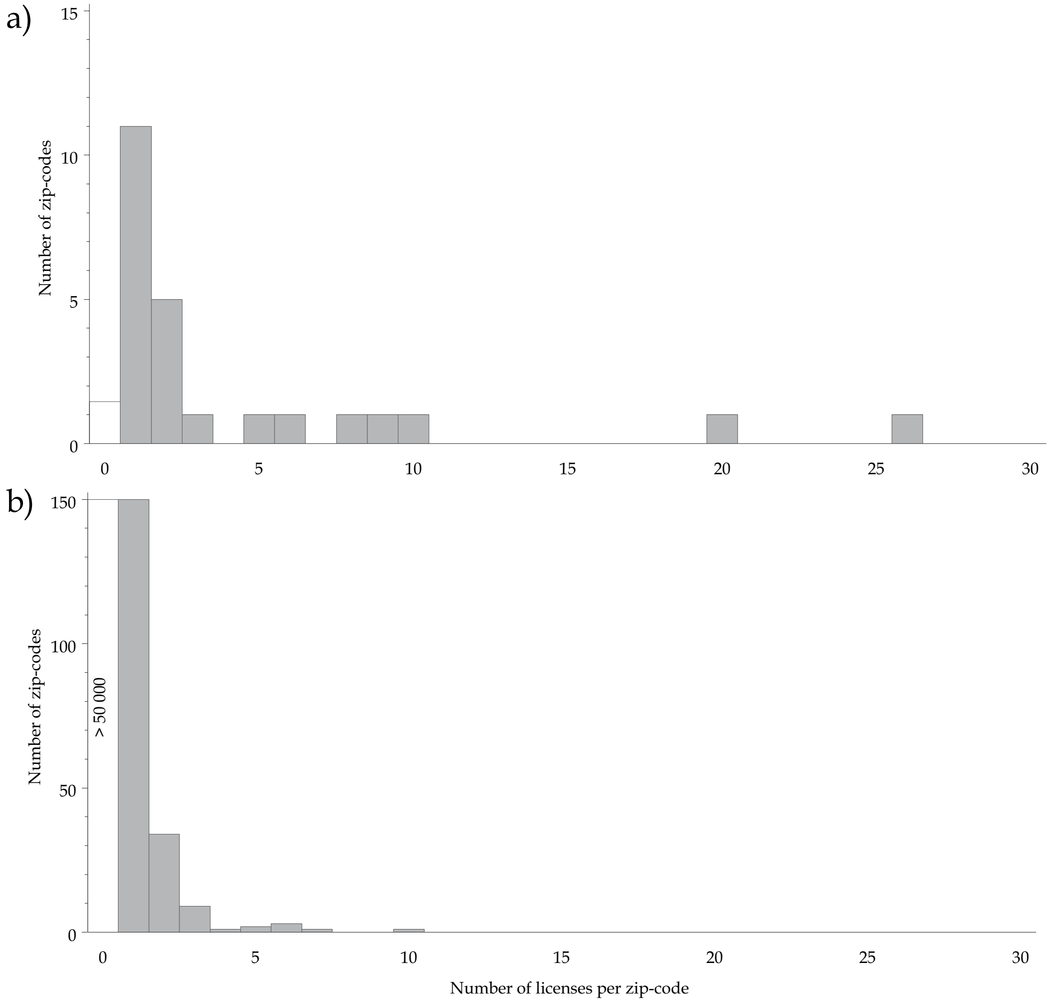

Figure 9 Frequency distribution of the number of fishing licence holders per zip code, for the eel fisheries in the Netherlands. Note that vertical scales in the two panels are different. a) Lake IJsselmeer. b) Remainder of Dutch inland waters.

dominate the variogram here. Whether these differences relate predominantly to the local habitat or to the exploitation pattern in the individual waterbodies remains an open question, although both factors probably contribute to the variation observed.

The distribution of the fisheries matched the distribution of the stock. In the Lake IJsselmeer fisheries, all licence holders exploit a common stock and use the same infrastructure of auctions and wharves. In this case, licence holders aggregate around the common facilities in rather large clusters, located in a few typical fishing villages. Elsewhere, most licence holders fish in privately exploited waters. Although common facilities are available in only a few places in the country, the licence holders are dispersed over the area. Individual fishermen live near to where they fish, taking the distance from their home address to the common facilities for granted. In this case, no typical fishing villages can be identified.

It was shown that in the Dutch context, the size of individual geographical units of the stock is in the order of 10 km across. This is equivalent to 79 km^2 in area, of which ca. 10% is water surface = 7.9 km^2. Assuming this unit surface also applies to the rest of the continental stock, the 90,000 km^2 of continental waters (Moriarty and Dekker 1997) is made of more than 10,000 individual geographical units. Clearly, the fragmentation of the continental waters cannot be fully neglected in the development of a monitoring and management strategy for the whole stock, but so far, only centralised and uniform actions have been proposed (Moriarty and Dekker 1997; ICES 1999).

Life cycle versus fractal tree

It is concluded that portraying the population as a series of archetypical life stages fits the oceanic phases well, but

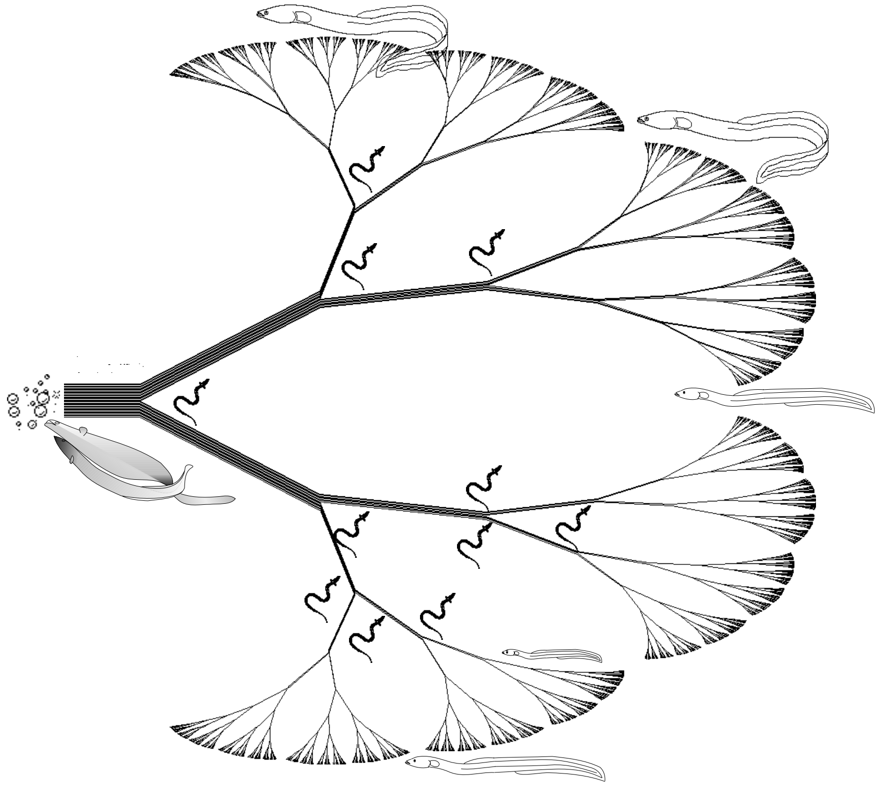

Figure 10 Fractal diagram of the geographical distribution of the eel.

is an abstraction in the life history of the continent, which does not recognise the characteristically fragmented geographical distribution pattern of the continental stock.

Mandelbrot (1977) created and explored an inspiring geometry of objects – *fractals* – that exhibit a meaningful pattern at whatever scale of measurement. The geographical distribution of the eel was shown here to contain both monistic large-scale aspects in its oceanic phases, as well as extreme fragmentation in the continental phases. This corresponds well to a simple fractal derived by Mandelbrot (1977, p. 155), as depicted in Figure 10. Because of the parallel between this fractal and the geometry of the eel stock, the title of Mandelbrot's book has been paraphrased in the title of this article.

Implications for monitoring and research

Around 1970, interest in management of the European eel stock increased, resulting in a Symposium (Thurow 1976), where the conclusion was drawn that 'an assessment of the state of exploitation and of the effect of elver stocking was urgently needed'. The subsequent ICES/EIFAC *Working Group on the Assessment of the European Eel Stock* identified a large gap in eel fisheries statistics, due to the total absence of data from many areas (ICES 1976). The fundamental weakness in stock assessment was the lack of reliable basic data to work with (ICES 1980), although the main objective remained to assess the European eel stock, witness the name of the Working Group. Moriarty (1997, Table 1) listed catch data for countries and/or regions. Although this made a great contribution to our appreciation of the continental stock, it must be noted that this table combined true data (exact figures), estimated orders of magnitudes (rounded figures) and pure guesses (boldly rounded figures).

Lough Neagh (N. Ireland) and Lake IJsselmeer (Netherlands) are the only single waterbodies with a catch exceeding 100 tonnes (Moriarty 1997, Table 1). Data on effort and yield are readily available for these fisheries and monitoring of the local stocks and fisheries can be achieved at relatively low costs. But these larger eel fisheries comprise only 5% of the total continental fisheries. The remaining 95% are made up of small and very small units, which can not be monitored or managed cost-effectively by virtue of their extremely small size. Monitoring representative samples of stocks and fisheries is likely to produce highly divergent results, even at small geographical distances.

The inevitable conclusion is that the fractal distribution pattern renders the acquisition of exact and detailed knowledge of the total continental population simply impossible, and an up-to-date assessment of the European eel fisheries unachievable.

Implications for management

The fractal distribution pattern also has consequences for management and control of eel fisheries. The stock of the European eel is in a deplorable state and the decline in recruitment is a general trend over the entire continent, but management action can only be taken within the scattered continental water bodies. Noting the small size and high number of continental units, the effective implementation and control of centralised management action may be questioned in advance.

In this respect, the eel is in a lonely position. Fisheries on other species operate in international waters where centralised management regulation may effectively steer the human impact on the stock, or operate in very small units (for example fresh water fisheries), where only local management or even no management at all is required. In practice, eel stock and fisheries were in this latter position, until the current recruitment decline began in the 1980s. The decline in recruitment then showed conservation of the eel stock needs both international and national action.

The life cycle of salmon and trout at first sight mirrors the life cycle of the eel. The reproduction of anadromous species in scattered small streams, however, splits the overall population into geographically disjunct stocks. Local management measures will primarily affect the local stock of salmonids, providing managers with feedback from their action. For eel, local management contributes to overall management of the stock, but only the combined effort of many local managers yields a positive feedback. It is therefore concluded that the widespread decline in eel recruitment, in conjunction with the small scale of the continental stock and fisheries, constitutes an unprecedented management problem, due to the fractal geometry of the European eel stock.

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Long-term trends in the glasseels immigrating at Den Oever, the Netherlands

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Bulletin Français de la Pêche et de Pisciculture, Conseil Supérieur de la Pêche, Paris (France) 349: 199-214 (1998)

Immigrating glasseels (*Anguilla anguilla* (L.)) have been sampled in Den Oever, the Netherlands, for numbers per dipnet haul (since 1938) and for length distribution (since 1960). The data from 1960 through 1996 were analysed to detect trends over the years. Special attention is paid to the analysis of potential artefacts caused by the sampling strategy. Mean length and numbers were positively correlated, while the timing showed independent, short-term fluctuations. From 1987 onwards, numbers of glasseels were well below the overall average, and they were significantly smaller. Since the minimum in 1991, numbers and mean lengths are both increasing, although they are still below average. It is tentatively concluded that these long-term changes are related to oceanic conditions, which have caused the prolonged and ocean-wide recruitment failure in eels, with the exclusion of suggested continental causes. Further clarification of the recruitment problem in eel is only to be expected when the reproduction problem is properly addressed, at the international level.

A prolonged recruitment failure of the European eel *Anguilla anguilla* (L.) has been observed since the middle of the eighties all over Europe (Moriarty 1990). At the same time, a parallel downward trend has been found in the few records that are available for the American eel *Anguilla rostrata* (Castongay et al. 1994a). For both species, potential causes have been listed (Castongay et al. 1994b; EIFAC 1993). Since the life cycles are still largely hypothetical (Tucker 1959; Dekker and Welleman 1989), hypotheses on the causes of the recruitment failure are still highly speculative.

The proper identification of the true causes of the historic changes in recruitment levels is hampered by two factors: the oceanic phases are by their very nature far out on the ocean and therefore difficult to study, while the continental phases are found scattered all over Europe, i.e. a continent wide assessment of the state of the stock is practically impossible. Experimental work can easily be implemented locally for the continental phases, but it is almost impossible to study the oceanic conditions far out at sea because of the high costs involved. This asymmetric distribution of costs over land and sea potentially generates a bias towards identifying continental causes as the most likely ones. Although there is a need to explore the oceanic option more extensively, the current paper will analyse a set of continental data for possible information on the oceanic stages.

Eels are long lived, slowly growing animals, with broad overlap in size between cohorts from adjacent years (Moriarty and Steinmetz 1979; Vøllestad and Næsje 1988; Dekker 1996). Escapement to the ocean in any year comprises animals born many years apart and any continental population consists of many cohorts. Essential changes in the total population are not likely to occur in the short run. Noting the longevity and the mixing of cohorts on the continent, it seems more plausible to relate observed year to year changes (Moriarty 1994) to local circumstances or designate them as stochastic variation. This implies that oceanic signals in continental data are likely to be detected only in very long data series.

Glasseels immigrating from the Wadden Sea to Lake IJsselmeer have been sampled at Den Oever for scientific purposes from 1938 onwards (Dekker 1986). Following experimental work on the proximate causes of immigration (Deelder 1958), detailed measurements of the length distributions have started in 1960. Aspects of variation in the annual abundance of glasseels have been analysed before (Dekker 1986, in prep.). In this paper, the data set on length distributions, spanning a period of 37 years now and comprising 65,584 glasseels in 438 samples, is presented and analysed for possible long-term changes; additionally, some new aspects of the data on abundance are presented, relating to 325,104 glasseels in 11,595 dipnet hauls from 1960 onwards.

In particular, the analysis will focus on three aspects: the number of glasseels caught, the timing of their immigration season, and their length distribution. Since no *a priori* relationship between any of these aspects is suspected, each of them is analysed separately. The statistical analyses will focus on factors related to the sampling strategy in order to derive the best estimates. In particular, no effort will be made to relate immigration parameters to local circumstances. Truly oceanic effects might easily be misidentified as local circumstances through spurious correlations. Besides effects of sampling, special attention will be paid to possible confounding of each of the three time series by the two others. *A posteriori*, the resulting time series will be correlated over the years, to detect common, long-term signals that might be attributed to the oceanic phases of the life cycle.

Material

Lake IJsselmeer is a freshwater lake, reclaimed from the Wadden Sea in 1932 by a dike (de Afsluitdijk). The surface of the lake has stepwise declined from an original 3450 km^2 by land reclamation, until in the late sixties only 1820 remained. In 1976, a dike was built separating a 600 km^2 compartment. The discharge of the river IJssel into the lake (average 7 km^3/yr, coming from the river Rhine) is sluiced through the Afsluitdijk into the Wadden Sea at low tide, by passive fall.

Glasseels are attracted by this flow and enter the lake by active swimming, mainly through the sluices and ship locks. In 1938, six years after the closure of the Afsluitdijk, a scientific sampling programme for glasseels was set up at the sluices in Den Oever (52°56′20″N 05°02′70″E), in co-operation between the operators of the sluices (Ministry of Water Management) and the Netherlands Institute for Fisheries Research. This sampling was carried out at night at two-hourly intervals during spring, using a 1 m^2 dipnet with a mesh of 1 mm^2, just in front of one of the closed sluices. The catch of glasseels was counted and returned to the water. The systematic sampling usually starts each year when probing indicates the actual beginning of the immigration, and ends when catches have declined to negligible quantities. The sampling procedure and the results have been described in more detail by Dekker (1986). Additionally, since 1960 the length composition of the glasseels has been sampled. In principle, the samples used for the abundance sampling were used again for length measurements. But when catches were too low, additional dipnet hauls were made or even light devices were used to attract glasseels. In the latter case, sampling was carried out at the ship locks (52°55′90″N 05°02′80″E), not to interfere with the regular dipnet sampling. Sampling usually occurred before midnight, taking 150 animals on average. The following morning, the animals were anaesthetised in a solution of MS222 and measured to the nearest millimetre. Originally, length measurements were taken twice a week, but from 1966 onwards the programme was reduced to only once a week.

In the following analyses, these data sets will be identified as the Catch per Unit of Effort (CPUE) dataset and the Length Frequency distribution (LF) dataset respectively, naming the primary aims of the data collection. The statistical analyses presented in the subsequent paragraphs were carried out using the statistical package SAS© (SAS Institute Inc. 1989), modules Genmod and Catmod. The statistical models will be detailed in the subsequent paragraphs.

Number of glasseels

Statistical model

The CPUE-dataset has been analysed for the numerical strength of the annual immigration by Dekker (1986). Year to year variation, month to month variation, hour to hour variation and variation due to the water temperature were identified as factors of substantial influence. Water temperature was found to be strongly correlated with the month and considered to be a nuisance factor and was therefore dropped. The current analysis takes the same set of explanatory variables. However, the statistical model differs in its stochastic component.

Dekker (1986) fitted a linear model to the log-transform of the number of glasseels (y) caught per haul, taking the log of y+1, i.e. one glasseel was added to the true observation. One glasseel normally is a negligible quantity in comparison with the true observation, but its addition cures the sparse zero observations. The log-transformation was used (1) to normalise the residual error of the statistical model, and (2) to transform multiplicative effects of years, months and hours into additive effects. The analysis of Dekker (1986) was based on the dataset from 1938 through 1985, and did not contain many years in which the average catch was close to 1. However, in the following years, immigration levels dropped to the order of magnitude where one glasseel is no longer a negligible quantity!

Dekker (in prep.) re-analysed the same dataset (extended through 1995) with respect to the proper statistical distribution of the errors, taking a semi-parametric

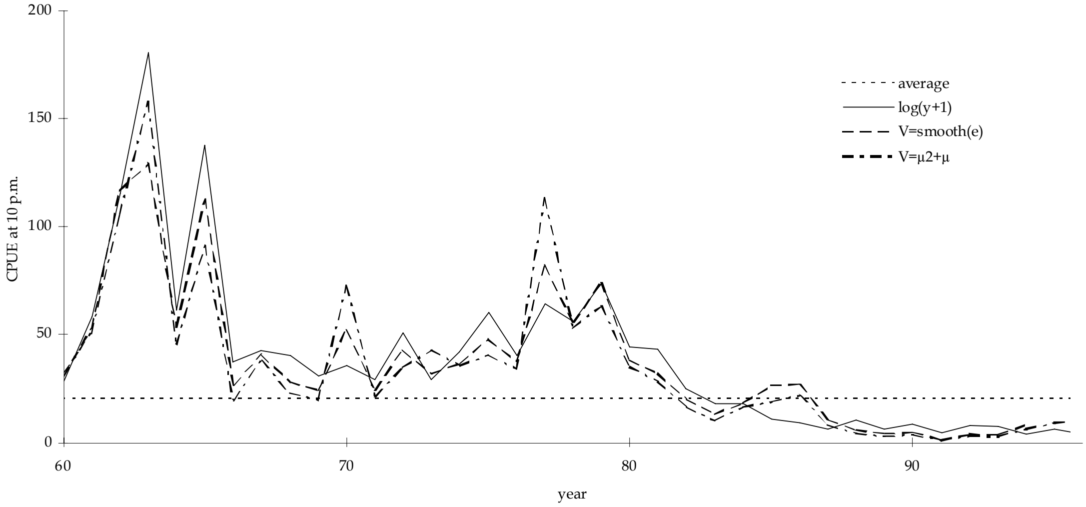


Figure 1 CPUE of glasseels caught at Den Oever (expressed as expected catch in April, at 10 p.m.) as a function of the year of sampling (N/haul): comparison of estimates based on three assumptions about the statistical distribution of the observations (see text).

approach. The analysis showed that the statistical distribution of the residuals is indeed nearly equivalent to a normal distribution of log(y+1). However, Dekker (in prep.) warned against the use of log(y+1) because of the effect that the transformation has on the linearity of the model at low expected values. The use of a parametric quasi-likelihood, with $\varepsilon^2 \infty \mu^2+\mu$ was proposed as an alternative, having an error distribution comparable to log(y+1), but no distortion of the predicted values at low expectations.

Results

This suggestion of a parametric quasi-likelihood was followed in the current analysis, using the module Genmod of SAS® (SAS Institute Inc. 1989), with variance $V=\mu^2+\mu$ and a log link function. Figure 1 presents the estimated year effect conforming to the three models according to Dekker (1986), to Dekker (in prep) and of the current analysis. It shows that the proposed parametric quasi-likelihood ($\varepsilon^2 \infty \mu^2+\mu$) indeed closely resembles the statistically and computationally much more demanding semi-parametric quasi-likelihood. However, it also shows that the transformation log(y+1) does indeed differ substantially from the other two analyses in years with very low expectations due to the corrupting effect of the +1 on the multiplicativity of the model. The log-transform estimates indicate recruitment levels fell steadily from 1981 onwards, while the two others estimate a steeper decline in 1981, followed by a recovery to average values, lasting through 1987. Clearly, the choice of a statistical model is not immaterial to the interpretation of the recruitment failure. In the following, the parametric quasi-likelihood model is used, since it follows the more sophisticated results of the semi-parametric model closely, while keeping computing time and tractability of results at an acceptable level. The number of glasseels at Den Oever is shown as the year term in the log of the expected value, which means that the abundance indices are on a logarithmic scale.

The abundance of glasseels in Den Oever (Figures 1 and 5a) was very high in the mid sixties, high at the end of the seventies, dropped consistently from 1979 to 1983, but did not decline below the overall mean until 1986. Finally, very low values were found from 1987 until 1993, followed by a slight increase in the most recent years. The lowest abundance on record occured in 1991, although the changes in absolute numbers in the years following 1987 are very small indeed. The breakdown of the total variation in the numbers caught over the sources of variation is presented in Table 1.

Confounding by timing of the season

The above analysis of the number of glasseels is based on the assumption that the (log of the) numbers caught can be represented by three, mutually independent effects: year to year variation, month to month variation and hour to hour variation. This assumption is rather restrictive, especially since the estimated numbers of glasseels will be correlated in the following to the timing of the season. Mandel (1959) proposed a test for interaction effects with a low number of degrees of freedom, which is known as «Mandel's bundle of straight lines» (Milliken and Johnson 1989). Instead of the full interaction of two factors, the interaction of one factor with the estimated effects of the

Table 1 Analysis of variance (ANOVA) of the number of glasseels.

source	deviance	%	df	mean deviation	*F*	*p*
year	8597	7	36	238.80	29.14	0.0000
month	1677	1	4	419.21	51.15	0.0000
hour	1290	1	10	128.96	15.73	0.0000
colinearity	895	1				
subtotal	12,458	10	50	249.16	30.40	0.0000
MANDEL(year)*month	84	0	3	27.88	3.40	0.0169
explained	12,541	10	53	236.63	28.87	0.0000
residual	94,583	79	11540	8.20		
total	119,666	100	11593	10.32		

other is modelled. Applying this test to the number of glasseels (Table 1) yields a statistically significant result: strong yearclasses have a higher abundance in May, and a lower in March and April. However, the magnitude of these changes is very small: a yearclass of 10 times the average abundance over the whole season (which is the maximum factor actually observed) will have 6.5 times the average in March, 7.2 times the average in April and 10.6 times the average in May. Less than 1% of the total variance is explained by Mandel's bundle of straight lines test. Thus, the confounding of the estimated number of glasseels by the timing of the immigration season is statistically significant, but in practice negligible.

Confounding by length of the glasseels

The influence of the average length per year cannot be estimated concurrently with the estimation of the number per year, because the one aliases the other. Since confounding of abundance estimates by length distributions seems highly unlikely, it was decided to ignore it, i.e. to assume changes in the average length do not influence the estimation of the number of glasseels in front of the sluices.

Timing of the immigration season

Statistical model

The CPUE dataset can also be used directly to analyse the timing of the immigration. Since the sampling was conducted at (nearly) fixed intervals throughout the season, the total dataset yields a (nearly) unbiased estimate of the date of arrival. In this analysis, the date of sampling is taken as the observation, and the number caught as weighting factor for that observation. Varying sampling intensity at the very start of the season and at the very end does not have a substantial effect on the analysis, since the number of glasseels is very low during these periods.

The main season of immigration usually starts in the beginning of March, peaks at the end of April and ends in the beginning of June, although single glasseels have been observed from December through July. In Figure 2 the earliest (1973) and latest (1963) patterns of immigration are shown, represented by the daily catch, corrected for the hour of sampling. This correction was based on the above analysis of the number of glasseels.

The statistical analysis of the season of immigration was based on cumulative categorical models (Fahrmeir and Tutz 1994). Dates were classified into seven-day periods, starting on January 1st. To avoid weeks without observations, dates before March 10th were pooled (1.1% of catches), as were dates from June 1st onwards (0.6% of catches).

The analysis was carried out using the module Catmod of SAS®, taking each year as a separate population. The cumulative logits of the observed frequencies per week were analysed by weighted least squares. The week number was included as an explanatory variable in the model, i.e. a threshold intercept, to allow for the asymmetric and non-normal distribution of the immigration over the weeks. The changes in immigration season from year to year were modelled as a shift variable.

Results

The breakdown of the variance of the model is shown in Table 2. The total variance is for the larger part attributable to the threshold intercept, i.e. the distribution of the immigrants over the dates does not conform very well to a normal distribution. The statistically expected distribution is shown in Figure 2 (shaded area). Changes from year to year explain about half of the remaining variance. The evolution over the years is shown in Figure 5a (timing). The season of 1963 (shown in detail in Figure 2) turns out to be exceptionally late, although 1962 and 1970 were almost as late. Early seasons occurred in the mid seventies (1973 shown in detail in Figure 2) and early nineties; late seasons in the sixties and eighties. However, the long-

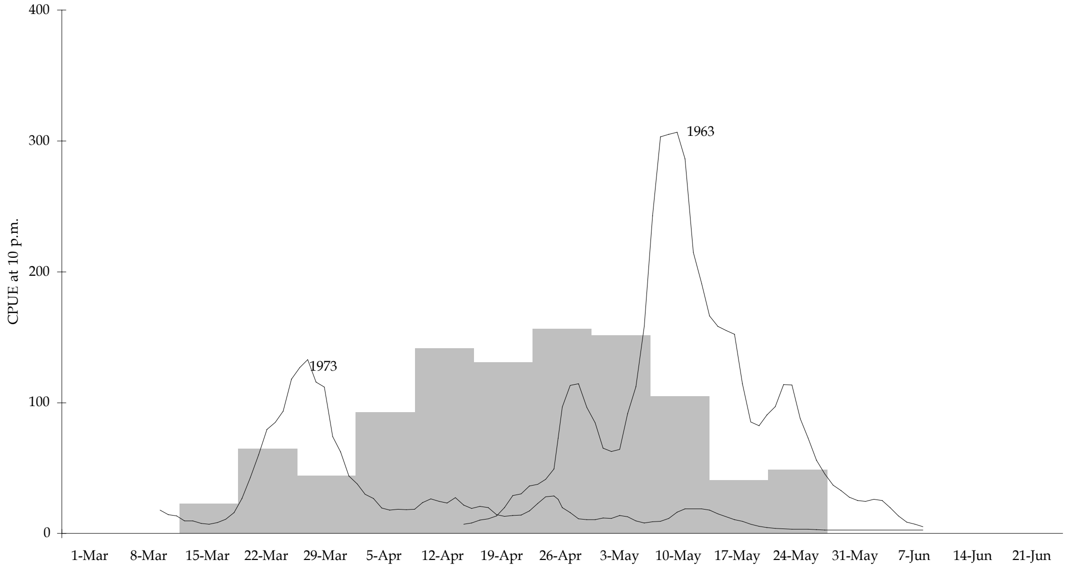


Figure 2 Timing of the glasseel immigration season: earliest (1973) and latest (1963) season, and statistically expected season (shaded).

Table 2 Analysis of variance (ANOVA) of the timing of the season.

source	deviance	%	df	mean deviation	*F*	*p*
threshold intercept	354,431	64	11	32,220.97	121.93	0.0000
year	94,701	17	36	2630.60	9.95	0.0000
MANDEL (number)	155	0	1	154.53	0.58	0.4449
explained	449,287	81	48	9360.14	35.42	0.0000
residual	104,914	19	397	264.27		
total	553,892	100	443	1250.32		

term variation in timing hardly exceeds the short-term variation.

Confounding by the timing of the season and the length of the glasseels

The confounding of these estimates of the timing by the number of glasseels was again tested by Mandel's bundle of straight lines. This test mirrors the test mentioned above on the confounding of the estimated number by the timing of the season. In this case, the parameter estimates of the yearly abundance were entered into the model as a continuous covariate. This explained less than 1% of the total variance (p=0.445). This confirms the conclusion, that the number and timing are not correlated.

As in the case of the numbers, a possible confounding of the analysis of the timing of the immigration season by factors related to the length of the glasseels cannot be tested due to aliasing with the length parameters. However, once again it seems rather unlikely that a change in average length will confound the estimation of the number caught per day, and therefore of the timing of the season.

Length distribution of the glasseels

Statistical model and results

The analysis of the length distribution of the glasseels was based on the LF dataset. Data were pooled per month, and also analysed by a cumulative categorical model. Explanatory variables included a threshold intercept and the year and month of sampling. Glasseels of 60 mm and shorter were pooled (0.1%) as were glasseels of 90 mm and longer (0.0%).

The average length of the glasseels ranged from 67 mm in 1990 to 78 mm in 1963 (Figure 3). The shortest individual glasseel (length 54 mm) was observed in April 1992; the longest one in April 1961 (92 mm). During each immigration season, the average length of the glasseels decreases over the months by 2.5 mm (Figure 3). But the variation from year to year is about fourfold (Table 3, mean deviance of 1,414,867 for year versus 349,279 for month).

The evolution of the length distributions over the years (Figure 5a) shows a gradual decline over the sixties

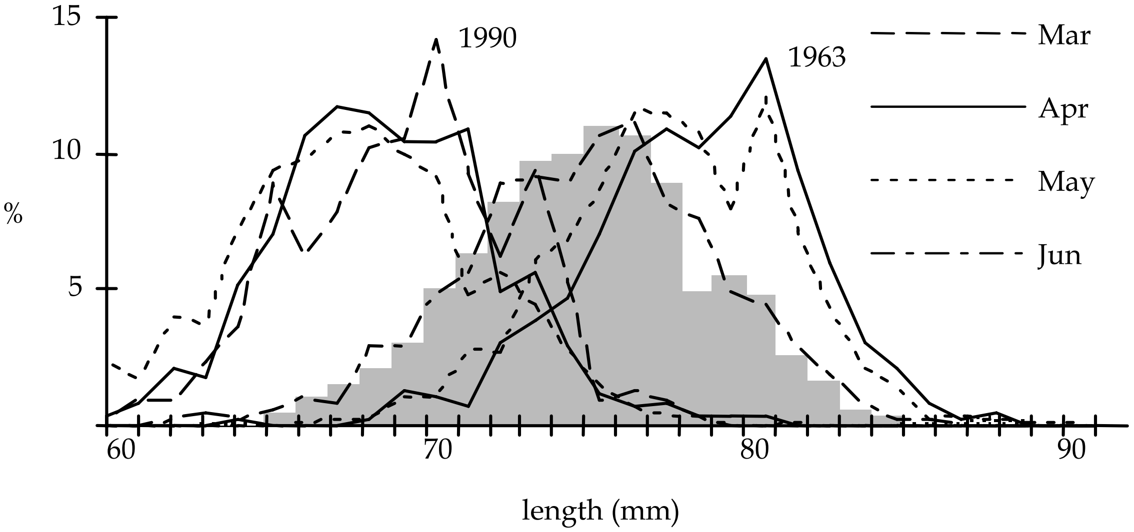


Figure 3 Length distribution of immigrating glasseels: distribution per month in 1990 (shortest observed), 1963 (longest observed) and statistically expected length distribution (shaded).

Table 3 Analysis of variance (ANOVA) of the length of glasseels.

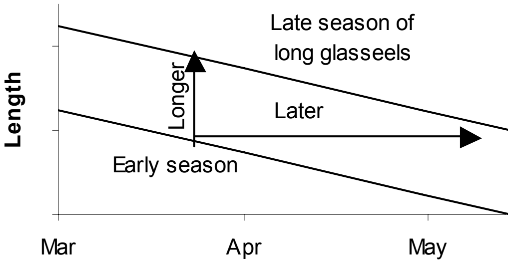
source	deviance	%	df	mean deviation	*F*	*p*
threshold intercept	234,435,884	76	29	8,083,996.00	1189.15	0.0000
month	1,047,836	0	3	349,278.65	51.38	0.0000
year	49,520,336	16	35	1,414,866.75	208.13	0.0000
explained	285,004,056	93	67	4,253,791.88	625.73	0.0000
residual	21,767,653	7	3202	6,798.14		
total	306,771,712	100	3269	93,842.68		

until the mid seventies, followed by a stabilisation until the mid eighties. In the mid eighties, the length of the glasseels drops sharply, with a minimum in 1991. During the last five years the average length recovers, but it is still below former levels.

Confounding by the timing of the season and the abundance of glasseels

Confounding of these estimates on length by the numerical abundance of glasseels is not very plausible. Because of the aliasing with the year effect on length itself, this interaction could not be tested. The case of confounding of the estimation of length by the timing is much more complicated. A simple model without interaction between length and timing results in an estimated year effect of the length that is strongly correlated with the timing of the season (r=0.48, p=0.001), later seasons having longer glasseels. At first sight, this contrasts with the diminishing length of glasseels within each season.

The diagram shows this relationship of timing and length, both in an early and a late season. Because of the relation between month and length, late seasons will apparently have longer glasseels. Again, both aspects (length and timing) cannot be discriminated on statistical grounds. A delay of the immigration by for instance local climatic conditions seems quite plausible. On the other hand, one can hardly imagine what would cause glasseels to be longer than average, even at the start of the season, when the peak of the season still has to come. Therefore, the estimated timing was given precedence over the year to year variation in average length. The diminution of the glasseels over the months was estimated by a model including the timing of the season (Mandel's bundle of



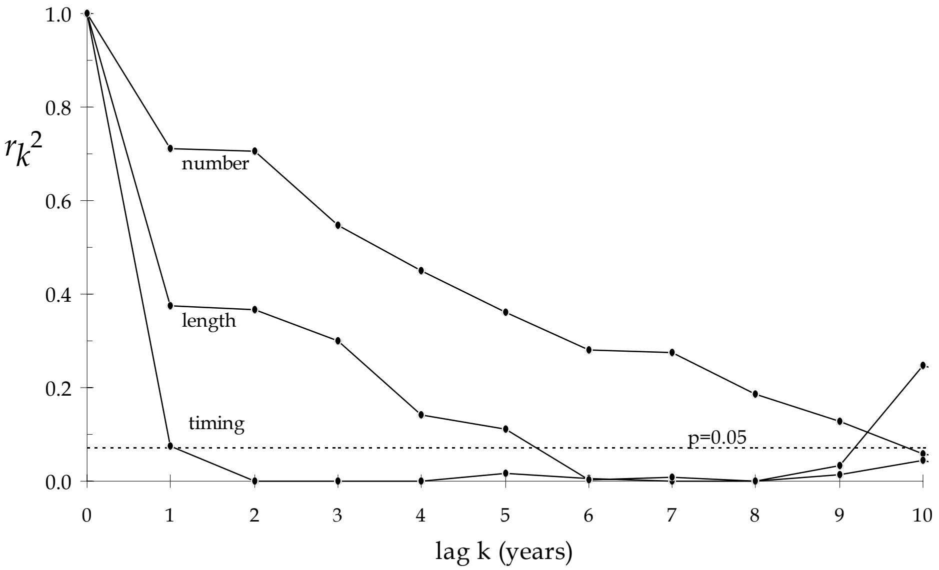


Figure 4 Autocorrelogram of the parameter estimates of the number of glasseels, their length and timing.

straight lines of the parameter estimates of the timing of the season), but without a year effect. Next, the model was rerun, with the parameter of the timing held fixed, but now including a year effect. The remaining correlation of the timing with this (conditional) year effect of the average length is negligible (Figure 5c, r=0.17, p=0.158). The most striking effect of the correction for the timing appears in 1990, an exceptionally early season in the middle of a range of years of small lengths. Without the correction for the timing, the length in 1990 is estimated to be equal to that in 1991; with the correction, 1990 forms the smooth transition from the low 1989 levels to the record low in 1991.

Auto- and crosscorrelations

Autocorrelation

In the above analyses, three aspects of the glasseels immigrating at Den Oever were analysed: numbers, timing and length. Each of the analyses yielded a year effect. The year of sampling was included in the analyses as a class variable. No relationship between adjacent years was enforced by the statistical models. Consequently, the years can be taken as independent realisations of the immigration. The sample autocorrelations of the number, time and length parameters over the years are shown in Figure 4. The cross-relations of the three time series are presented in Figure 5, in a so-called rug-plot (Tufte 1995). Sample correlation coefficients are given in each sub-plot.

The dataset of length measurements now contains 37 years of data, with 10 samples of 150 animals on average per year. For a consistent time series of biological data, the length of the dataset is considerable. But from the statistical standpoint, it is hardly enough to calculate autocorrelations. Consequently, only the first few terms in the autocorrelogram are statistically significant. However, the three time series of parameter estimates behave quite differently. The timing of the immigration season shows no significant autocorrelation at all, the length is positively correlated up to a time lag of 5 years and the numbers show a strong autocorrelation, fading out only very slowly over 10 years.

Given the limited length of the time series, a further formal analysis is not warranted. But the slowly fading out of the autocorrelogram for length and numbers seems to point at a non-stationary process. Long-term behaviour is dominated by trends, not by stationarity. Indeed, inspection of Figure 5a shows prolonged periods of declining or rising numbers and decreasing or increasing lengths.

Crosscorrelations

The timing of the immigration is hardly correlated with the numbers and length. Concerning timing and length, this is at least partially the result of the analysis model: allowance was made for the effect of delays in the immigration season on the perceived mean length per month. This correction reduced the correlation of the timing and length from r=0.48 (p=0.001) to r=0.17 (p=0.158). The long-term variation in the timing hardly exceeds the variation from one year to the next (autocorrelation r_1^2=0.08), while the length has a more gradual development (autocorrelation r_1^2=0.55, or r_1^2=0.38 after correction for timing).

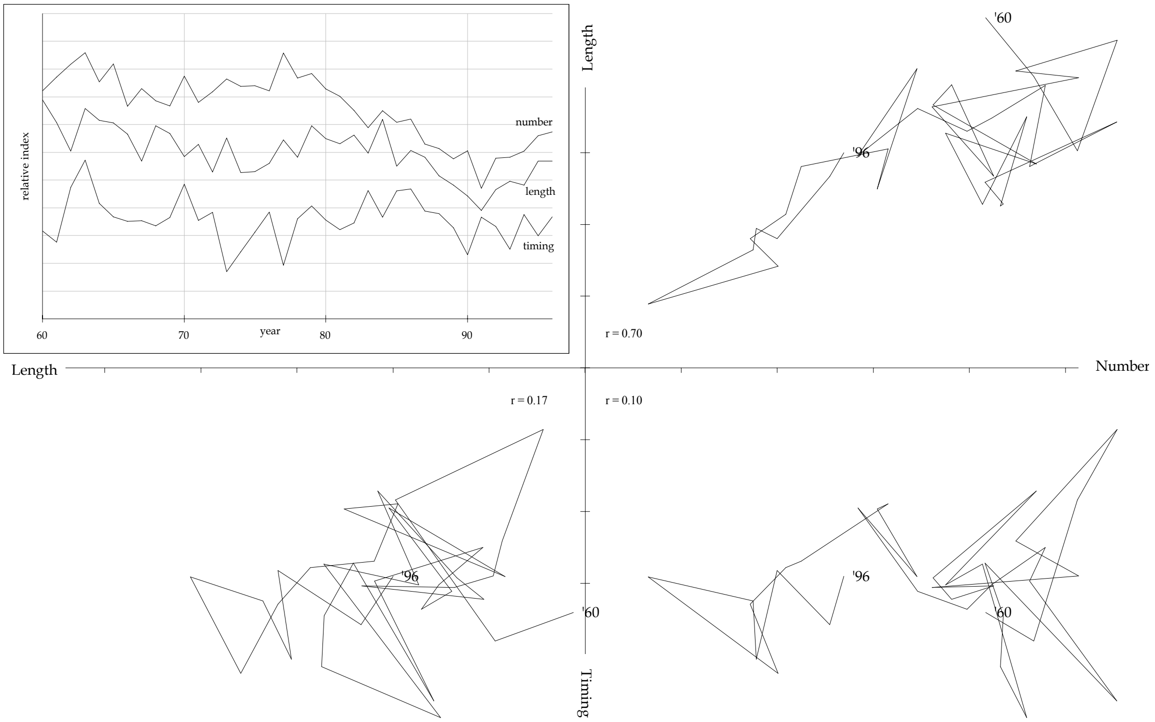


Figure 5 Number, length and timing of glasseels immigrating at Den Oever: correlation of trends in time series. a) Time series. b) Length versus number. c) Timing versus length. d) Timing versus number.

Apparently, the correlation between length and timing is spurious or caused by short-term, probably local circumstances.

The estimated average number caught per year is positively correlated over the years with the length (*r*=0.70, p=0.001). Unfortunately, no way was found to discriminate between possible confounding of one by the other in the sampling or analysis and a true correlation. However, taking in mind that there appears to be no plausible mechanism for the confounding, it is concluded that length and numbers are most likely truly correlated.

Summarising: the length and numbers of glasseels immigrating in Den Oever exhibit long-term and synchronous changes, while the timing of the immigration season fluctuates independently, probably due to local circumstances.

Discussion

Framework of the analysis

The eel is a weird animal. Despite its economical value in many rural areas of Europe (375 M. ECU; Moriarty 1996), there is no stock-wide management of the scattered stock. Local management of eel fisheries in restricted areas of Europe has been effective in actually steering the production, by the grace of plentiful supply of glasseels from the ocean, until the mid eighties, when a prolonged series of poor years of recruitment started. It was only then that attention focused on the collectivity of the resource, first by scientists (EIFAC 1993; Castonguay et al. 1994a,b), later followed by the responsible management bodies at the supranational level (Moriarty 1996; Moriarty and Dekker 1997).

Following the establishment of the recruitment failure of both Atlantic eel species (Moriarty 1990, sources cited in Castonguay et al. 1994a), an inventory of potential causes has been made on both sides of the ocean (Castonguay et al. 1994a; EIFAC 1993; Bruslé 1994), based on the scarce evidence. Furthermore, the coincidence of events on both sides of the ocean was noted (Castonguay et al. 1994b). It is within this framework that the analyses reported in this paper were undertaken, aiming at factual evidence contributing to the process of selection and elimination of proposed hypotheses.

Historical development

The results confirm the reported major event in the European eel population in the eighties and nineties: the number of glasseels changed dramatically over a range of

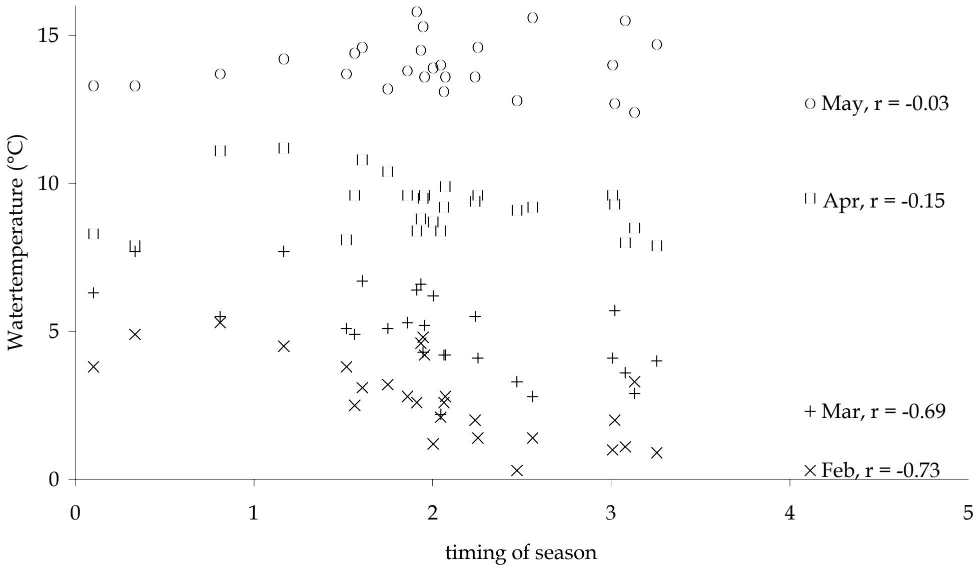


Figure 6 Relation of timing of the glasseel immigration season to the water temperature at the sluices.

years, but so does their length! In 1991, an all time low in numbers was observed in Den Oever, even beating the prolonged recruitment failure observed in the late forties and early fifties. Following 1991, both numbers and lengths show a slight recovery, observations now corresponding to the mid-eighties' level.

The observed variation in mean length of the glasseels is about 11 mm. This exceeds the differences in length reported so far throughout the geographical distribution area of the eel (Tesch 1977, p. 136). Time series of length measurements, except for the Den Oever series analysed here, apparently are lacking, but it seems plausible that Den Oever is not the only site having variation in mean length. Other published data relate to varying ranges of years, or even unspecified periods and are therefore hardly interpretable at the stock-wide level.

During metamorphosis and immigration, the length of leptocephali and glasseels diminishes (Tesch 1977, p. 146), apparently due to the absence of feeding. It seems quite probable to explain the observed variation in length by variation in the duration of the non-feeding phase at sea. In that case, however, one would expect shorter glasseels in the later seasons, which is contrary to the findings. Moreover, the observed changes in length (11 mm) are much larger than the reported shrinkage during metamorphosis (5 mm).

The relationship of (the onset of) the glasseel immigration to local climatic circumstances has been noted before (see Dekker 1986, for the Den Oever data). Indeed, the estimated parameters of the timing correlate well with the water temperature at the sluices in February and March, but much less so with April and May temperatures (Figure 6). In fact, the autocorrelation of the timing of immigration over the years is of the same magnitude as the autocorrelation of the water temperatures.

Cause and effect in the two time series

The analyses showed a 10% reduction in average length of the glasseels. Although no records have been kept of the weight of glasseels, it seems likely that weight will have had a parallel evolution. It has been hypothesised (EIFAC 1993; Castonguay et al. 1994a,b) that the reduction in numbers of recruits is the direct consequence of a strong reduction in the number of adults contributing to the spawning stock. The spawning stock is then thought to have been reduced by overfishing on any of the continental life stages (reducing the numbers directly), or by habitat destruction and migration barriers reducing the profitable dispersion area of the species, or by contamination and parasitism in the adults, hindering the effective spawning migration. If indeed, the decline of the spawning stock is primary to the decline in the number of recruits, it is hard to see why the remaining progeny has attained a smaller body size concurrently with the reduction in their numbers. Density dependent processes would induce larger, not smaller body sizes.

McCleave (1987) proposed a hypothetical mechanism for the settlement of leptocephali on the continental slope, metamorphosing into glasseels. In his view, the physical contact with the ocean bottom might induce the metamorphosis of the Leptocephalus. Castonguay et al. (1994a) summarise this hypothesis, and then state 'The effects of the (...) oceanographic changes (...) on continental invasion of glasseels are also unknown'. Apparently, they hypothesise that oceanographic changes might have induced the recruitment failure by hindering the final settlement of the leptocephali on the continent. This hypothesis, as the ones above, can indeed explain the numerical evolution. But the synchronous evolution of the length of the glasseels makes a bottleneck earlier in the life of the leptocephali more plausible. Wether this occurs in the early larval phases or even in the parental phases is an open question.

Conclusions and speculations

The analyses presented in this paper do not reveal the cause of the observed recruitment failure. But they do narrow the scope for potential explanations. Castonguay et al. (1994a) explicitly list four potential causes: 1) Toxicity from anthropogenic chemical contamination; 2) Anthropogenic habitat modifications; 3) Commercial fishing, and 4) Oceanic changes. Crossing the reported findings with the hypotheses, it soon becomes evident that oceanic changes are the most likely cause. The other hypotheses take the reduction in spawning stock to be primary to the reduction in numbers of recruits. As stated above, this would not explain, or even contradict the observed reductions in length of the recruits. Only the first hypothesis might be reformulated in a sense that toxicity operates through the parental phases on the larval growth and survival, but in the absence of any evidence, this interpretation is rather Procrustean.

However, without actual observations of the reproduction of the eel, it will not be too difficult to find some time series of oceanographic data that correlate exactly with the glasseel observations. The floor is open for speculation. Rather then stepping into this pitfall, it is concluded that the exploitation of the eel stock, and indeed the conservation of the species, is obviously dependent on processes far beyond the current knowledge. Eels still spawn in *terra incognita*. Clarification of this unsolved mystery should be the main and foremost topic on the agenda of the scientists and managers involved in the responsible management of the Atlantic eels.

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Post-scriptum

The article *Long-term trends in the glasseels immigrating at Den Oever, the Netherlands* was first presented at the meeting of the ICES/EIFAC working group on eels in September 1996 in IJmuiden (the Netherlands), and subsequently published in 1998, in *Bulletin Français de la Pêche et de Pisciculture*. The data analysed span the period from 1960 (start of the length measurements at Den Oever) until 1996, the year the analysis was made. Following publication, seven more data years have passed, and insights have grown considerably.

Figure PS.1 presents updated time series. After the minimum in abundance of 1.08 glasseels per haul in 1991 (2.6% of the 1960-1980 level), a slight recovery occurred until 1997, followed by a further decline, to an all time low of 0.55 glasseels per haul in 2001 (1.3% of the 1960-1980 level). Mean length (corrected for the date within the sea-

Figure PS. 1 Trends in abundance and mean length of the glasseel sampled in Den Oever, the Netherlands. Abundance has been corrected for the month and the hour of sampling; mean length for the date within season and the timing of the season itself.

son and the timing of the season), however, showed a slow recovery following the historical minimum of 1991, to a value just above the long-term average in 2003.

The downward trend in recruitment started in the early 1980s. In the early 1990s, there was a growing awareness, that this decline was not just a temporary and passing temporal variation, and potential causes were considered (Castonguay 1994a; EIFAC 1993). The article on long-term trends in Den Oever was the first publication presenting evidence that might have some bearing on the causes of the recruitment decline, and still constitutes one of the few available pieces of factual information. The conclusion of this article, however, that oceanic factors are the most likely cause, is weakened by more recent information presented in Figure PS.1, and follows a *single-cause/single-consequence* line of thought, that conflicts with the precautionary approach taken in providing management advice (ICES 1998; chapter 10). A comprehensive and up-to-date discussion of the processes involved in the decline of the eel stock is presented in chapter 11 of this thesis.

6

Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*?

Fisheries Management and Ecology 10: 365-376 (2003)

Since the 1980s, a 90% decline in recruitment of European eel *Anguilla anguilla* (L.) has occurred across most all of Europe. Whether the continental stock has equally declined is uncertain. This study compiles available landings statistics since the beginning of the 20th century and identifies trends over time and space, using a statistical model that takes varying levels of reporting into account. Landings in the pre-1940s reached over 40,000 tonnes yr^{-1}, declined during World War II, rose to a peak of 40,000 tonnes yr^{-1} in the 1960s (coincident with a peak in re-stockings) and dropped to an all time low of <20,000 tonnes yr^{-1} in the 1990s. The decline in recruitment observed since the early 1980s was preceded by a decline in landings two or more decades earlier, indicating a decline of the continental stock. Considering the continental stock and the spawning stock must have declined in parallel, insufficient spawning stock biomass might have caused the recruitment collapse currently observed.

Since the early 1980s, a steady and almost continent wide decline of 90% has been observed in the recruitment of glasseel (*Anguilla anguilla* (L.)) to the European continent (Moriarty 1986, 1996; Dekker 2000a; ICES 2002). Several hypotheses on the causes of this decline have been proposed (Castonguay et al. 1994; Moriarty and Dekker 1997), including climatic changes in ocean conditions, reductions in (accessible) freshwater habitat, pollution or parasitism, and overexploitation. Although evidence has been presented supporting or contradicting one or other hypothesis (Knights 1996; Desaunay and Guerault 1997; Dekker 1998), no comprehensive approach to unravel the problem has been developed. The decline in recruitment has been presented concurrently with some evidence for a decline of the continental stock (Moriarty and Dekker 1997; ICES 1999). The temporal order in which the continental and juvenile stocks have declined might narrow the range of hypotheses on the causes of the decline.

Recruitment of glasseel towards the continent is monitored at a number of places along the continental coast, and most time series show a parallel trend (Dekker 2000a). For the continental stock, monitoring is much less organised and it is doubtful if data from geographically isolated stations are indicative for the status of the whole continental stock (Dekker 2000a). However, as landings of glasseel are negligible in comparison to yellow and silver eel landings, in terms of weight (Moriarty 1997), trends in total landings will be close to trends in landings of the continental stock, which, presumably, are indicative for trends in the continental stock.

Scientists studying European eel fisheries have a persistent belief that basic landings statistics have been, and always will be, inadequate to monitor stock and fisheries. ‘Because of the secretiveness of eel fishermen it is almost impossible to get reliable catch data; hence one must conclude that statistics are highly untrustworthy’ (Deelder 1984). ‘The gathering together of the available facts serves more than anything to show the inadequacy of the information’ (Moriarty 1997). However, without arguing against the content of these statements, the views expressed have led to severe under-utilisation of major sources of information on the status of the eel stock. Either landings statistics are completely ignored (Bertin 1956; Deelder 1984), or primary focus is on the inadequacy of the data (ICES 1988; Moriarty 1997). In 1976, Thurow (1979) concluded ‘an assessment of the state of exploitation (…) was urgently needed’. In the years following, the state of the stock has deteriorated (Moriarty and Dekker 1997). Clearly, there is an urgent need to present a comprehensive analysis of the available landings data, considering both their validity and the trends observed.

In the current analysis, trends in reported landings will be identified, taking into account the variation in the number of countries reporting. To this end, a succinct statistical model of eel landings during the 20th century is developed, which enables an assessment of the trend in all (reported and non-reported) landings. ICES (1988) and Moriarty and Dekker (1997) showed that official landings statistics for many countries comprised only about half of the true catches in the 1980s and 1990s. This under-reporting (in contrast to non-reporting) will not be taken into account. Finally, causes and consequences for the observed trends in yield will be discussed, specifically focusing on the contrast between oceanic versus continental processes causing the observed recruitment decline.

Material and methods

Data sources

FAO

The Food and Agricultural Organisation FAO (Rome, Italy) of the United Nations maintains a database of worldwide fisheries yields. Statistics are reported on paper (FAO 2000) and data from 1960 onwards are available from Internet (http://www.fao.org). Data for fisheries on 'river eels' were obtained from Internet (October 1st, 2001), selecting all European countries, African and Asian countries bordering the Mediterranean Sea and African countries bordering the Atlantic Ocean north of the Equator. The number of fishing areas listed by FAO was reduced from seven to three (Atlantic, Inland waters and Mediterranean), by merging all inland areas under a single heading and merging the North and Central Atlantic areas. When no fishing area was listed, landings were assumed to represent country totals. In other cases, the dis-aggregated data were used, but no country totals were calculated. This data set was supplemented with information on the years prior to 1960, derived from FAO (1948, 1950, 1961). The earliest records date back to the 1930s, but uninterrupted recordings only exist after 1947. Recent paper sources express landings in 1000 tonnes per year with a single significant digit, that is: data are accurate up to 100 tonnes per year. The FAO database lists tonnes per year, but data prior to 1974 consist of multiples of 100 tonnes per year only. Where multiple data sources were available and conflicts were attributable to rounding off, the most detailed data source was given preference.

ICES

The International Counsel for the Exploration of the Sea ICES (Copenhagen, Denmark) maintains a database of landings of marine, Atlantic fisheries yields. Statistics up to 1988 were reported on paper (ICES 1992). A computerised database with data up to 1998 was made available upon request (by H. Sparholt, ICES, Copenhagen). Landings are reported in tonnes per year, from 1903 onwards. Although data were available by ICES fishing zone, all data were aggregated by country, to match the FAO aggregation level. In general, the ICES database matches the FAO data for the Atlantic, but covers a longer range of years.

Other sources

Both databases contain a few quite surprising data, including landing reports outside the distribution area (Togo and Gambia), erroneous inclusion of aquaculture production in inland landings (Italy since 1984; the Netherlands since 1993; Denmark since 1998) or misclassification of fishing areas (the Netherlands in 1939, while the *Zuiderzee* was converted into freshwater in 1932). Most of these flaws are easily corrected, but, without consolidation of the remaining data, an unbalanced data set could have resulted. Therefore, additional and/or corrected information obtained from various sources, including personal communications, was added to the data set, without replacement. This concerns:

- Italy, landings of inland and marine waters, as previously reported to FAO, but corrected (communicated by Eleonora Ciccotti, Universita Tor Vergata, Rome, Italy).
- Border between Russia (Kaliningrad) and Lithuania: landings from the Curonian lagoon (communicated by Linas Lozys, Institute of Ecology, Vilnius, Lithuania).
- Border between Northern Ireland and Republic of Ireland: landings of yellow and silver eel (separate) from the Erne river and lake fisheries since 1870 (communicated by Milton Matthews, Northern Regional Fisheries Board, Ballyshannon, Ireland).
- Northern Ireland: landings of yellow and silver eel (separate) from Lough Neagh since 1965 (communicated by Robert Rosell, Department for Agriculture of N. Ireland, Dublin, N. Ireland).
- Sweden, landings from east coast, west coast and inland waters separately, since 1925 (communicated by Håkan Wickström, Institute of Freshwater Research, Drottningholm, Sweden).
- the Netherlands, landings of yellow and silver eel from the Zuiderzee area since 1879, irrespective of the reclamation from the sea in 1932 (unpublished data from the author).
- ICES (1975, 1977) list catches for some countries from 1920 through the mid 1970s, derived from national sources. The information clearly duplicates the FAO database, but extends to earlier years (1920).

Table 1 Landings of the European eel in the 20th century: statistics of available data by decade, by latitudinal class, by data source, by fishing area and by country.

	Number of data series	Number of observations	Geometric mean observation		Number of data series	Number of observations	Geometric mean observation
Decade				*Country*			
1900-1909	7	47	193	Albania	2	15	66
1910-1919	7	70	505	Algeria	2	17	25
1920-1929	19	184	474	Belgium	1	15	102
1930-1939	30	267	793	Croatia	1	7	6
1940-1949	36	263	427	Czechoslovakia	1	16	46
1950-1959	44	362	436	Denmark	10	527	1065
1960-1969	69	505	453	Egypt	1	5	616
1970-1979	82	571	264	England & Wales	1	57	17
1980-1989	93	602	162	Estonia	3	23	16
1990-1999	112	714	92	Finland	3	35	8
				France	5	141	613
Latitudinal class				Gambia	1	1	26
10-15	1	1	1	Germany	4	180	449
15-20	1	1	26	Greece	2	31	75
25-30	3	22	52	Hungary	1	13	205
30-35	5	111	51	Ireland	7	246	20
35-40	7	121	65	Italy	6	226	1040
40-45	16	482	332	Latvia	3	35	13
45-50	9	140	208	Lithuania	3	116	26
50-55	29	1147	199	Macedonia	1	6	35
55-60	25	1041	399	Malta	1	2	3
60-65	10	256	143	Morocco	3	70	29
65-70	6	268	895	N. Ireland	3	103	383
				the Netherlands	6	332	704
Data source				Norway	4	164	309
FAO	70	1459	226	Poland	6	209	346
ICES	16	810	282	Portugal	3	58	28
Other sources	26	1321	290	Romania	1	2	1
				Russia, USSR	3	57	94
Fishing area				Spain	5	167	113
Inland waters	42	1102	164	Sweden	9	505	610
Atlantic	44	1826	252	Switzerland	1	15	6
Mediterranean	13	286	225	Togo	1	1	1
Country total	13	376	1356	Tunisia	2	41	130
				Turkey	1	30	365
				UK	3	92	371
				Ukraine	1	1	1
				Yugoslavia, SFR	1	29	20

Data from earlier than 1900 were very scarce and therefore omitted from the analysis. Most paper data sources make a definite distinction between null and non-reported; the FAO database does not consistently do so, but lists zeroes in both cases. It is assumed here, truly zero landings will never have occurred in countries that do have regular reports of landings. Therefore, all listed zeroes are interpreted as missing information. In total, 3590 records are available in 112 data series (Table 1, Figure 1).

Variance stabilising data transformation

First, the relation of the statistical variance to the magnitude of the observations is examined. Commonly, the relation between variance and the mean of genuine replicates is analysed (Taylor 1961). Survey-based data such as landings cover the sampling space completely and therefore do not allow for statistical replication. Instead, the between years variance was taken, treating each data series as an independent, replicated observation. As will

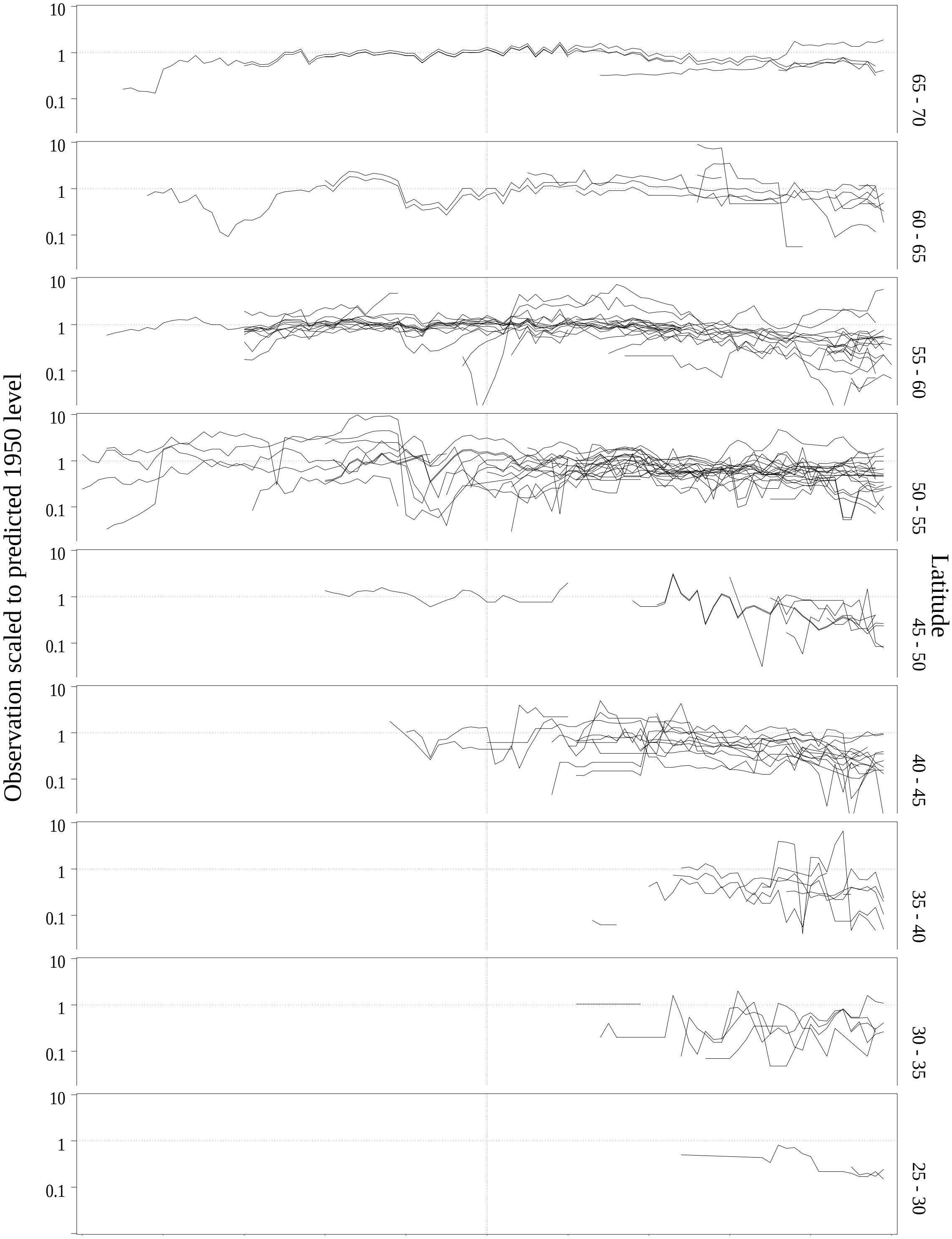

Figure 1 Landings of the European eel in the 20th century, scaled to the estimated value in 1950. For readability, data series are grouped in classes of 5 degrees latitude.

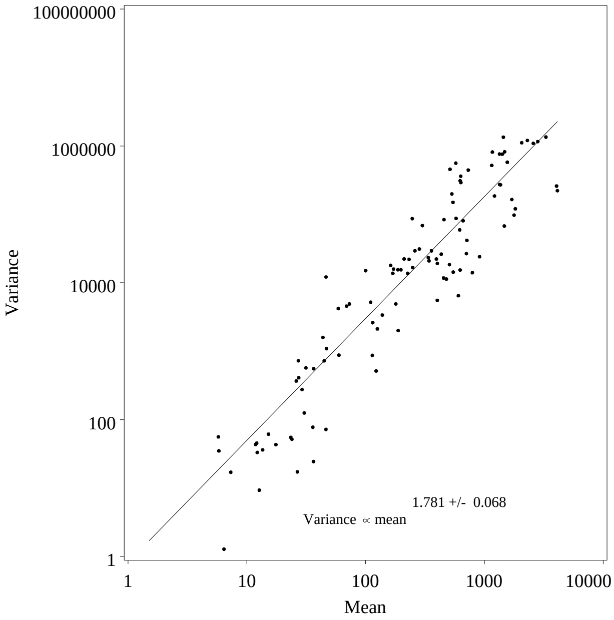

Figure 2 Variance within data series of eel landings as a function of the arithmetic mean per series. Regression function based on log-log regression.

be seen below, the majority of the between years variance is not related to short-term (auto-correlated) variation, nor to long-term trends. Log-log regression of the variance on the mean (weighting by the number of observations in each data series) shows an exponent close to two (Figure 2). Consequently, log-transforming all observations will stabilise their variance. As zero observations were excluded beforehand, this procedure corresponds to the application of the delta-distribution (Pennington 1983). All subsequent analyses are based on log-transformed non-zero data.

Relevant time scale

For each time series, autocorrelations are calculated for time lags from 0 to 30 years. Autocorrelations based on less than 10 observations are discarded. For each time lag, an average autocorrelation (i.e., averaged over the data series) is calculated as the arithmetic average over the data series, weighted by the number of data points on which individual autocorrelations are based. Calculation of autocorrelation at long time lags requires long time series. As the longer time series do not necessarily represent an a-select sample of all available data, average autocorrelations per time lag were also calculated for the selection of longer time series, for which autocorrelations at all time lags were available.

Model construction

To derive a succinct continent-wide view of potential trends in the continental stock, a statistical model of landings must be as parsimonious as possible. This parsimony relates to the number of explanatory factors, and to the level of detail modelled for each explanatory factor. A stepwise inclusion strategy was followed for each explanatory factor, contrasting each step to the common base model. The model was based on linear regression of the logarithm of the reported landings, with additive explanatory variables and a normal distribution of the residuals. This conforms to a multiplicative model of the untransformed landings. Temporal and spatial trends were analysed, first as a series expansion (in year and latitude respectively), and secondly by inclusion of a discrete version of the continuous variate (year as a class variable; assigning each country a separate temporal trend). Latitudinal variation in growth rate (Vøllestad 1992) and in density (Dekker 2000b) of the eel stock have been shown to occur, suggesting the use of latitude as an explanatory variable. The temporal evolution is modelled as a Taylor series expansion of the year, up to degree four. Higher degrees were found not to be estimable. Table 3 lists all models tested.

Between the data series, many interdependencies might exist, related to common data sources, common fishing areas, common temporal trends, common round off levels, etc. Because of the unknown and potentially very complex structure of these interdependencies, no attempt was made to incorporate these into the model structure.

Available data were subdivided by country, i.e. by jurisdictional entities. That is a breakdown, which lacks a clear biological meaning for the eel stock. Countries differ in the area of suitable eel habitat and in stock density and differ in the ratio between inland and coastal fisheries. Thus, the magnitude of landings differs between data series, thus necessitating scaling of the data. This was accomplished by inclusion of a dummy class variable, with a unique value per data series, in each of the models tested.

All other explanatory variables (latitude, fishing area, data source and country) are fully associated with selections from the set of data series. The inclusion of a scaling factor for each data series precluded the analysis of the main effects of these explanatory variables. The interaction of each of these factors with the Taylor series expansion of the year was analysed.

Most data series show aberrant low records in the first years after their initiation (Table 2). Hence, the first records in each data series were assigned a reduced weight in the analyses, linearly increasing from 10 to 100% over the first 10 years.

Table 2 Statistics of eel landings data, in the first years after initiation of data series.

Age of data series (in years)	Recorded landing (% of first record)	Number of series with landing ≥ first record	Number of series with landing < first record
0	100	110	0
1	121	67	43
2	215	66	44
3	231	66	43
4	219	55	51
5	229	51	55
6	254	41	61
7	297	45	56
8	279	49	49
9	326	41	51

Data extrapolation

For most data series, calculation of statistically predicted trends requires considerable extrapolation of results over the whole range of years studied. The geographical coverage was highly correlated with time (Figure 1). For most latitudes, data are available from 1940 onwards, while from 1980 onwards most countries have reported landings. Hence, extrapolations were confined to approximately 1940 and 1980 and later, respectively. In addition, all interpolations and extrapolations were calculated and presented at face value and their validity judged on common sense grounds.

Results

Relevant time scale

The auto-correlogram of the time series of eel landings (Figure 3) showed the typical pattern known as *pink noise*: high autocorrelations only at small time lags, quickly extinguishing with increasing time lags. For lags of ten years and more, average autocorrelations were consistently below 0.15. The longer time series showed a somewhat higher auto-correlation at time lags below 10 years, with a value of 0.75 at lag one, in comparison with 0.50 for the average of all series. Individual autocorrelations fluctuated more and to higher values than the averages, but the reported trend is seen in most data series. The overall pattern was indicative for data series showing random variation in short time periods, while in the long run observations do not err to unbounded high or low values (Nisbet and Gurney 1982).

Model construction

The first model, a scaling constant for each time series, explained more than 80% of the total variance (Table 3). This model is taken as the base line for further analysis.

For a series expansion of *year* (spatially uniform), only the first and second terms contributed substantially to the model. The third was not significant, while the higher order terms failed to contribute to the model completely. This indicates that the data followed on average a very smooth trend over time. Re-defining *year* as a class variable, i.e. allowing the model to fit irregular year to year patterns that are common to all data series, yielded a significant improvement of the model, but at the costs of an unduly large number of parameters (MS=0.79). The series expansion at degree two was used for further analysis of spatial trends. This model (*quadratic trend*) and the model with year as a class variable (*year as classes*) were used for data extrapolation.

For a series expansion of *latitude*, only the first term contributed substantially to the model, in interaction with a linear expansion of year. Higher order terms of latitude and latitude in combination with year squared contributed only marginally, or completely failed to fit. This indicates that the observed temporal trends did not occur uniformly over the continent, but there is no clear sign of more than a general north to south trend, northern areas showing a later and less significant decline. Replacing the latitudinal trend by a separate trend by country yields a significant improvement of the model, but at the costs of a large number of parameters (MS=8.34). The linear latitudinal, quadratic time trend (*latitudinal trend*) and the separate trends by country (*trends by country*) were used for data extrapolations.

Overall, four models were further explored. They were: the spatially uniform *quadratic trend*, the spatially uniform *year as classes*, the linear *latitudinal tren*d of quadratic time series and the quadratic *trends by country*. These models explained, respectively, 9, 14, 10 and 31% of the base line variance. However, explained variance per degree of freedom (MS) amounts to 78.32, 0.79, 8.19 and 8.34. Clearly, the better fit of the more complex models (*year as classes*, *latitudinal trend*, *trends by country*) was not in accordance with their increased complexity.

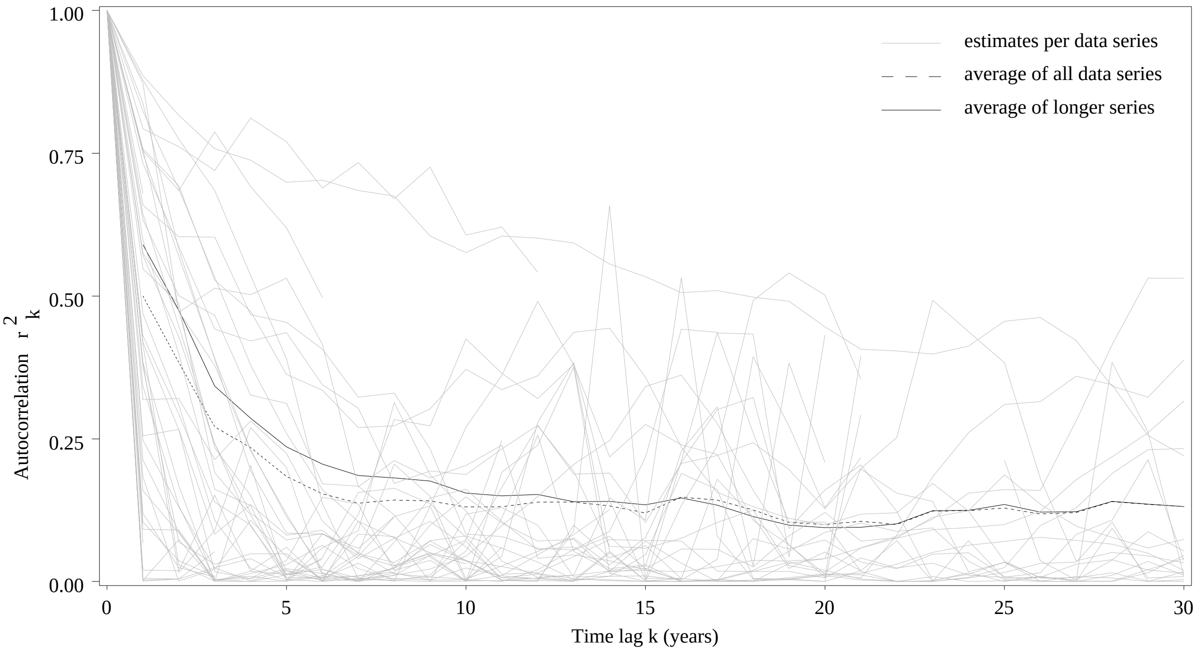

Figure 3 Auto-correlogram of the time series of eel landings in the 20th century.

Table 3 Analyses of variance results of models of increasing complexity. SS=Sum of Squares, df=degrees of freedom, MS=Mean Square, *F*=F-statistic, *p*=probability.

Model		SS	df	MS	*F*	*p*
formal null model		10,475.51	3589	2.92		
scaling each data series		8749.15	111	78.82	158.797	0.000
error		1726.36	3478	0.50		
Stepwise analysis of temporal trend						
year		91.33	1	91.33	206.784	0.000
+year^2	†	65.32	1	65.32	147.901	0.000
+year^3		1.20	1	1.20	2.725	0.099
+year^4		0.00				
year as class variable	†	76.64	97	0.79	2.284	0.000
error		1491.87	3378	0.44		
Stepwise analysis of spatial trend						
+latitude × year		11.99	1	11.99	34.669	0.000
+latitude × year^2	†	4.38	1	4.38	12.669	0.000
+latitude^2 × year		5.52	1	5.52	15.969	0.000
+latitude^2 × year^2		0.00				
+country × year		268.73	32	8.40	24.279	0.000
+country × year^2	†	98.20	12	8.18	23.659	0.000
error		1186.41	3430	0.35		

† These models are selected for further exploration of results.

Data extrapolation

For each of these four models, estimated landings by year and country were calculated. Figure 4 presents the sum of all countries, in parallel with the total of the actual reports to FAO.

The *actually reported landings* showed a slow increase from 12,500 in the 1930s to 17,000 tonnes in the 1990s, with a clear depression during the World War II, a peak in the 1960s and a trough in 1980. For the spatially uniform *quadratic trend* model, estimated landings peaked in 1941 at 41,500 and declined to 18,000 tonnes in the 1990s. For the

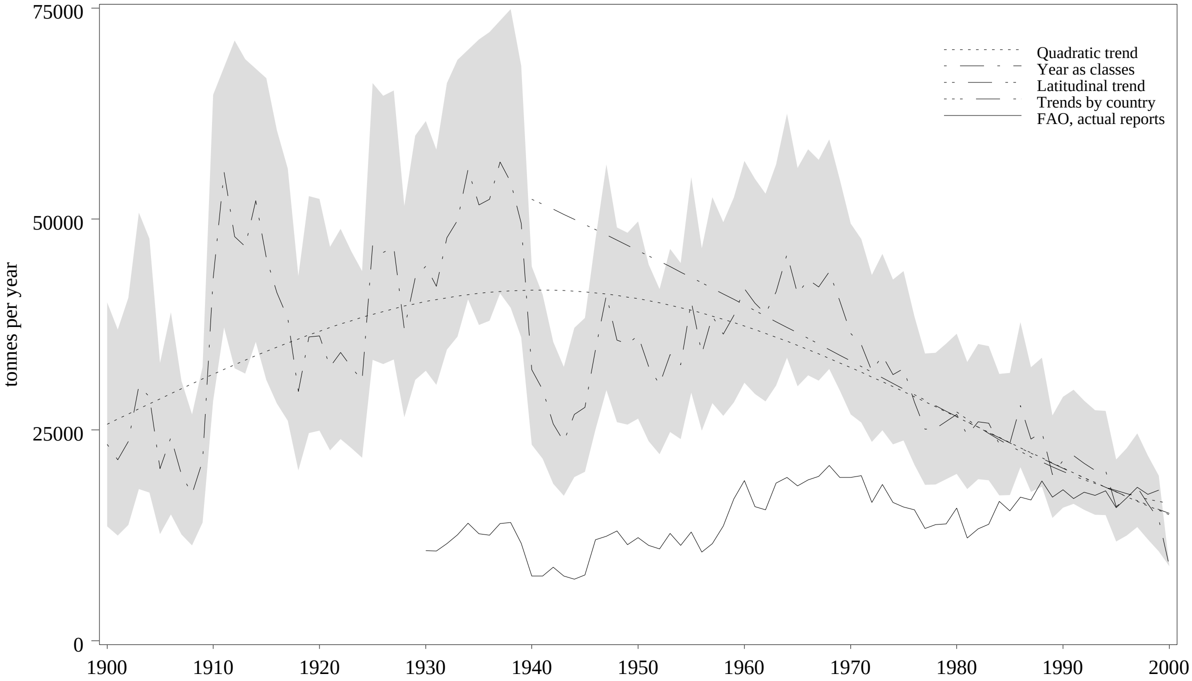

Figure 4 Reported and model-estimated landings in the 20th century, for the whole stock of the European eel. For the year as classes model, standard errors are indicated in grey (±1 s.e.).

spatially uniform *year as classes* model, estimated landings varied considerably in the pre-1940s, with an average of 40,000 tonnes. During World War II, model estimates declined to 27,500 tonnes, followed by a steady increase to 41,750 tonnes in the 1960s. From the mid-1960s onwards, a steady decline was estimated, down to 18,500 tonnes in the 1990s. For the *latitudinal trend* model, the sum of all countries showed a continuously declining trend, from over 50,000 down to 15,000 tonnes, from 1940 to present. The general trend over latitude predicted by this model was for southern vs. northern areas to show a steeper decline, starting earlier. For the *trends by country* model, an even steeper trend was estimated, from over 27,000 tonnes in 1980 down to 18,000 tonnes in the 1990s.

Discussion

The stock of the European eel is in severe decline. For the recruitment of glasseel from the ocean towards the continent, the decline started in the early 1980s (Moriarty 1986) and is observed at most monitoring sites (Moriarty 1986, 1990, 1996; Dekker 2000a). For the continental stock, the decline in the Baltic was recognised quite early (Svärdson 1976), but elsewhere less clear-cut evidence has been presented (ICES 1975). In recent years, the decline in the continental stock is thought to be secondary to the recruitment failure (Moriarty and Dekker 1997; Lobon-Cervia 1999; ICES 2002). The current analysis confirms the decline in the Baltic since the middle of the 20th century, but also suggests a comparable and even steeper decline in the rest of the continental population, lasting much longer than the recruitment decline.

Reliability and variance

Landings statistics of eel have been described as 'highly untrustworthy' (Deelder 1984) and 'inadequate' (Moriarty 1997). In contrast, Kuhlman (1997) claimed that fresh water and marine catches showed miraculously identical trends, but re-analysis of the same FAO source data did not confirm his outcome. The variation in the landing records is high, even between subsequent years (Figure 3). Models allowing for year to year and country to country variation explain less than 30% of the variance (Table 3). Local climatic influences (Tesch 1999) as well as market forces (Fontenelle 1997) will have had substantial influence (process errors), but simple mis-recordings or varying levels of under-reporting (measurement errors) have been identified too. Analyses of trends in stock wide landings data suffer from a high degree of uncertainty, but that does not necessarily imply the data are inadequate.

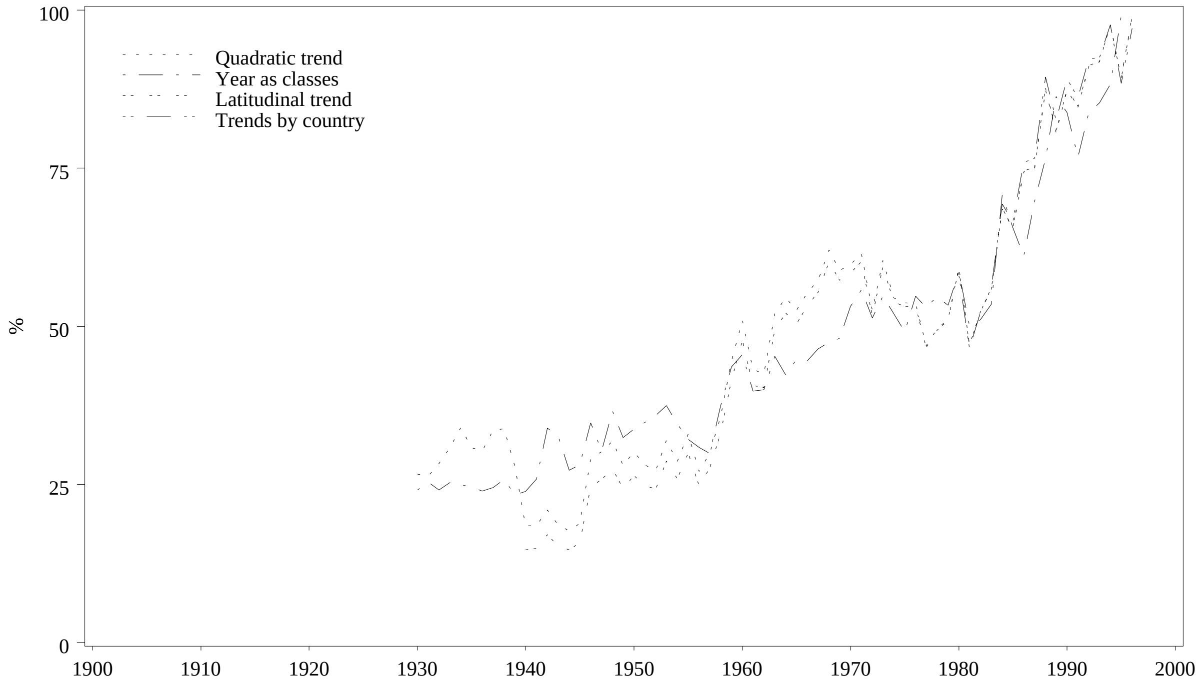

Figure 5 Actually reported landings of the European eel in percentage of the model-estimates, for each of the predictive models.

Model construction

Because of the high variability, rather simple models in the current analysis already exhausted all information in the data, both with respect to temporal and spatial variation (Table 3). The models allowing for geographical differentiation (either as a spatial trend or assuming independent temporal trends between countries) fit reasonably well to the data (Table 3), but yield unreasonably high results upon extrapolation (Figure 4). Within the data range (latitudinal coverage since ±1940, coverage of most countries since 1980s), model predictions from these geographically differentiated models agreed reasonably with geographically uniform models (Figure 4). The overall trend of the undifferentiated models was not contradicted. Apparently, the geographically differentiated models better fit minor details of the data, but do not detect major geographical patterns. Hence the general trend of declining eel landings in the past decades must have occurred consistently all over the distribution area.

The two temporal trend models (*quadratic trend* and *year as classes*) were in reasonable agreement. The *year as classes* model tracked the World War II decline and the peak in the 1960s, but showed large year to year variation in the data-poor period before 1930. Obviously, the reality of the pre-1930 variation is not beyond doubt. The *quadratic trend* model stayed within one standard error of the *year as classes* estimate in almost all years. Thus, the *quadratic trend* model described the general trend as good as the detailed *year as classes* model.

Declining yield

The overall pattern (highest levels in the pre-1940s, severe decline since early 1960s) was not observed in the sum of the actually reported landings (Figure 4). The sum of the actual reports was 25-30% of the model estimates in the 1930s and 75-100% in the 1990s (Figure 5). Realising that the number of data series rose gradually from 30 in the 1930s to 112 in the 1990s (Table 1), the conclusion must be that the increasing number of reports has masked the consistent decline observed in most reports. ICES (1988) and Moriarty and Dekker (1997) estimated that under-reporting of landings was in the same order of magnitude as reported landings. Whether the level of under-reporting has changed over time is hard to determine, but it is not likely to have changed enough to explain the decline detected in the data.

Causes

The analysis suggests that the yield of the European eel has been in decline for 40 years or more, while recruitment has been declining for the last 20 years and below average for only 15 years (Moriarty 1990; Dekker 2000a).

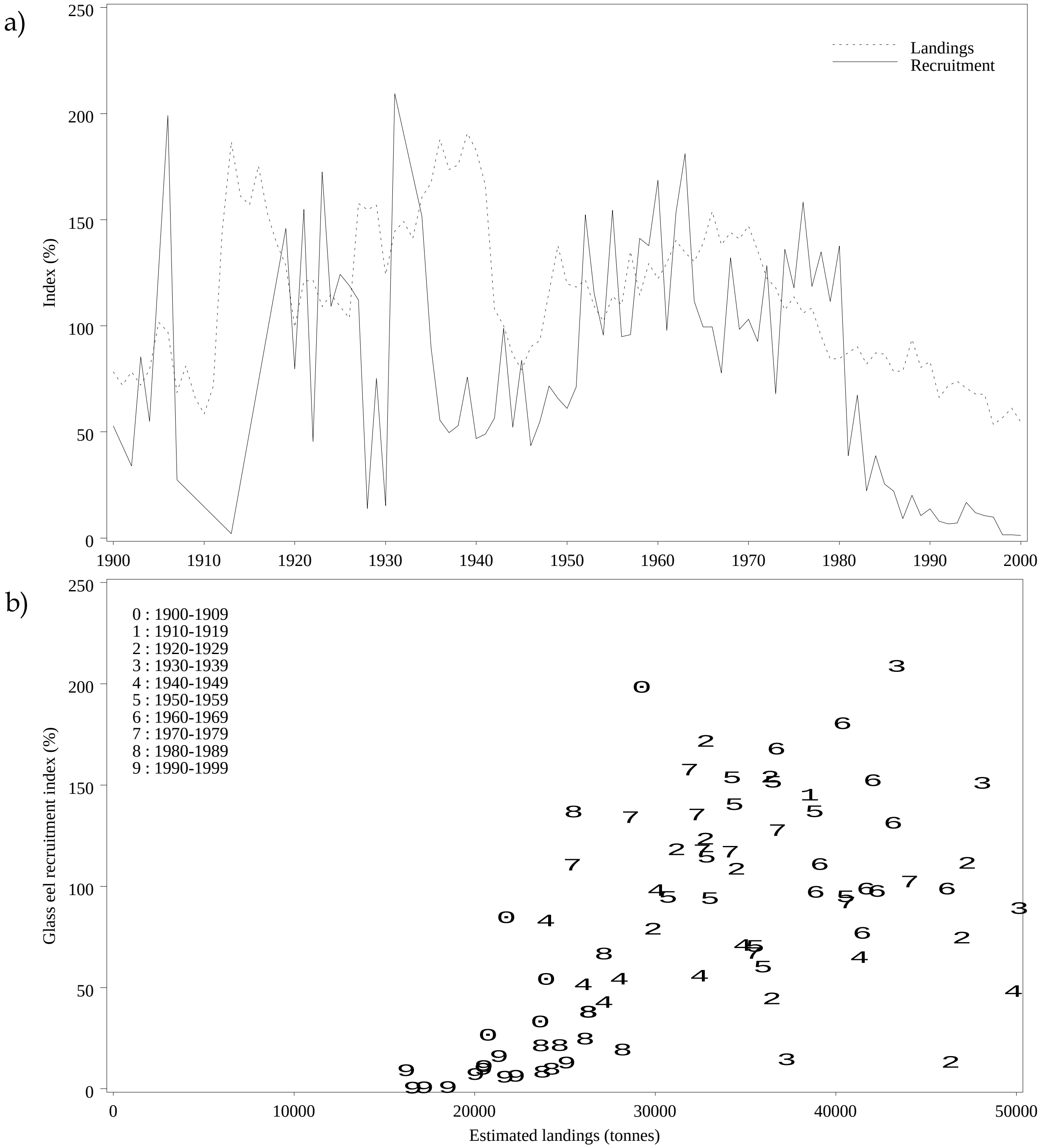

Figure 6 Landings and recruitment of the European eel stock. Recruitment is indexed by the geometric mean of the longest recruitment series, Göta Älv (Sweden), Ems (Germany), Den Oever (the Netherlands) and Loire (France), each scaled to the period 1946-1997. Landings estimates are the result of the year as classes model (current study), scaled to the period 1946-1997. a) Time series of total landings and glasseel recruitment. b) Glasseel recruitment as a function of the total landings two years prior to recruitment to the continent. Digits indicate the decade within the 20th century.

Clearly, the relatively recent recruitment failure cannot be the cause of the long decline in yield. During several decades in which yield declined while recruitment was still high, the yield per recruit must have declined. Moreover, the relative peak in landings in the late 1960s (as actually reported and found in the *year as classes* model) might very well have been produced by artificial restocking of glasseel (Anwand and Valentin 1981; ICES

2002), temporarily mitigating the ongoing decline since the mid-1940s. Indeed, the 1960s peak in landings was predominantly found in northern countries, where glasseel restocking was practised. As restocking has only masked or delayed the ongoing decline, but was not sufficient to halt the downward trend, renewed boosting of recruitment to 1960s-1970s levels by restocking (Moriarty and Dekker 1997) will not suffice to restore the stock to forgone levels.

Current fishing levels are quite high (Dekker 2000b). Therefore, it is likely that the decline in yield signals a decline in the continental stock and is not just a sign of reduced levels of exploitation, as for instance happened during World War II. This is consistent with direct observations on the stock (Wickström and Hamrin 1997). Why the continental stock declined in decades with high glasseel recruitment (1960s and 1970s) remains an open question.

Consequences

Considering the continental stock is in decline at least since the 1960s, the escapement of silver eels to the ocean and hence the spawning stock biomass (SSB) is likely to be depressed too. Interpreting the continental landings as a proportional index of the spawning stock size, a preliminary stock-recruitment relationship can be explored (Figure 6).

Whether or to what extent a depressed SSB limits the production of progeny is a central theme in fisheries biology. For the reduction caused by exploitation, Clark (1991) recommended to keep a minimum SSB of 35% relative to the unexploited state, for demersal species. Mace and Sissenwine (1993) refined this estimate by relating maximum SSB reduction to natural mortality, size at maturity and maximal size, using data on 80 well-studied stocks and estimate spawning stock per recruit (in percentage of the virgin state, %SPR) at replacement level at (weights in units of kg):

$$\log(\mathit{replacement}\ \%SPR) = 2.69 - 0.51 \times \log(WT_{\max}) + 0.38 \times \log(WT_{50\%\mathrm{mature}}) + 3.52 \times M$$

For the female eel, using a maximum weight, $WT_{\max}$ of 0.5 kg (nearly 70 cm length) and median weight at maturation, $WT_{50\%\mathrm{mature}} = WT_{\max}$, a natural mortality rate $M = 0.1$ would result in $\%SPR = 33\%$, while $M = 0.2$ gives $\%SPR = 23\%$. For the eel stock, the unexploited state is unknown and hard to estimate. However, the scale of the decline in yield, as detected, approaches this critical level already. Assuming that the decline of the SSB parallels the decline in yield from over 40,000 in the pre-1940s down to 25,000 in 1980, a relatively minor change in ocean climate (Desaunay and Guerault 1997; Dekker 1998) might have accomplished a total collapse of the stock, as currently observed.

Acknowledgements

Eleonora Ciccotti, Linas Lozys, Milton Matthews, Robert Rosell and Håkan Wickström supplied unpublished landings data. I thank them, and many others who looked in vain for additional information, for the interesting discussions that prompted me to carry out this analysis. Niels Daan and Mous Sabelis critically reviewed an early version of the manuscript.

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What caused the decline of the Lake IJsselmeer eel stock after 1960?

7

ICES Journal of Marine Science 61: 394-404 (2004)

The European eel *Anguilla anguilla* (L.) is in severe decline: landings from and recruitment to the stock have fallen off since the mid 1960s and the early 1980s, respectively. Several hypotheses on the causes of the decline in recruitment have been advanced, some predicting an earlier decline of the adult stock than actually transpired. In order to narrow the range of potential hypotheses, this paper contrasts current ones with trends in abundance and length distribution of the local stock in Lake IJsselmeer (the Netherlands) over the period of the decline. The data set consists of research surveys, market sampling, gear development experiments, etc., since 1904, and is uninterrupted since 1950. A statistical analysis is designed in which sampling characteristics (length selectivity of gears and of mesh sizes, and sample selection procedures) are separated out of trends in the local stock over the years (abundance, length composition). The decline of the stock started in 1960, affected exploited and undersized eels, and was steeper for larger eels. The abundance of the smallest size class in the lake matches the independently recorded recruitment strength, which did not decline before 1980. Excessive exploitation, habitat loss, barriers to migration, introduced parasites, and changes in ocean climate cannot explain the observed trends when taken individually. Therefore, the cause of the decline of the local stock in Lake IJsselmeer is still a mystery and, because the historical information is limited and cannot be added to, is likely to remain so.

During the second half of the 20th century, the yield of European eel (*Anguilla anguilla* (L.)) has declined severely (Figure 1a), and that decline preceded a sharp drop in recruitment (Figure 1b). There are several hypotheses for the decline (e.g. Castonguay et al. 1994; Moriarty and Dekker 1997; ICES 2002; Robinet and Feunteun 2002), but without evidence of the state of the population during the period of decline, speculation is all there is. It is assumed that the decline in fishing yield since about 1965 represents a decrease in spawning stock biomass (Dekker 2003c). Ultimately, the small spawning stock may well have been the cause for recruitment failure, possibly in combination with incidental adverse environmental conditions, but why the yield declined over several decades despite consistently good recruitment in the 1960s and 1970s is still unclear. Data series on eel fisheries are scarce, and only rarely cover more than a few years (Moriarty and Dekker 1997). For Lake IJsselmeer (the Netherlands), data were collected in isolated years before 1950 (Redeke 1907; Havinga 1945), and more or less consistently since 1950. Although spawner production of Lake IJsselmeer is almost absent as a consequence of excessive exploitation (Dekker 2000c), the data set does provide an unique opportunity to analyse the decline of the local stock in detail.

The gradual decline of the eel stock in inland waters was hardly noticed (Dekker 2003b), whereas the later decline in recruitment was noted almost immediately (EIFAC 1985). It contributed to several explanatory hypotheses (Castonguay et al. 1994; Moriarty and Dekker 1997), including pollution, habitat loss as a result of barrages and dams, climate change in the ocean, overexploitation, and man-made transfers of parasites and diseases. Some of these would indeed result in earlier decline of the adult stock while recruitment was still good, but others would not. This work focuses on statistical analysis of the trends in the IJsselmeer stock, and contrasts the results with other proposed hypotheses.

The analysis presented covers half a century of uninterrupted sampling, and spans a full century in total. Characteristics of the estuary/lake changed considerably over the 20th century, as has the eel stock, the fishery, the aim of the sampling, the sampling gears, the selection and recording procedures, etc. Hardly any single experimental set-up has been preserved for more than 10 years, while the trends in recruitment and yield typically run for several decades. In order to assess trends in the local stock over the whole time span, a composite statistical model is developed in which sampling characteristics and trends in the stock are disentangled. Through all sampling set-ups, the length composition of the catch has been recorded almost consistently; though other biological measurements are recorded less frequently. Consequently, the analysis focuses on abundance and length composition of the local stock.

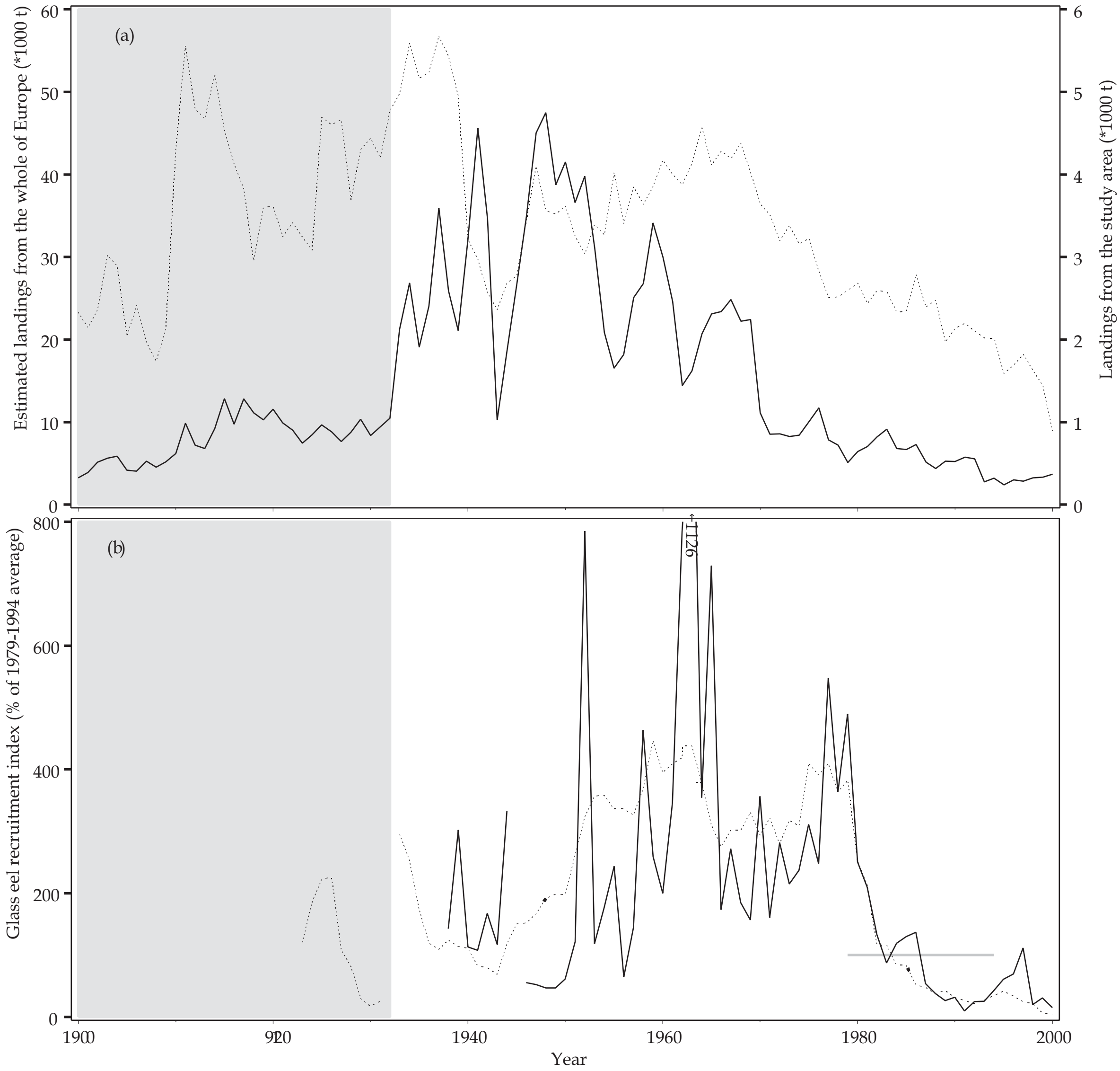

Figure 1 (a) Estimated landings and (b) indices of recruitment of glasseel, for the total population (broken line), and for the study area (solid line), during the 20th century. In 1932, the estuarine study area was transformed into a freshwater lake. Data from Dekker (2002, 2003c) and original.

Material and methods

Study site, eel stock, and fisheries

Lake IJsselmeer (52º40'N 5º25'E) is a shallow, eutrophic freshwater lake, which was reclaimed from the Wadden Sea (53ºN 5ºE) in 1932 by a dike (Afsluitdijk, Figure 2), substituting the estuarine area known as the Zuiderzee. The surface of the lake was stepwise reduced by land reclamation, from an original 3470 km^2 in 1932, to just 1820 km^2 since 1967. In preparation for further land reclamation, a dam was built in 1976, dividing the lake into two compartments of 1200 and 620 km^2, respectively, but no further reclamation has actually taken place. In managing the fisheries, the two lake compartments have been treated as a single management unit. The discharge of the river IJssel into the larger compartment (at 52º35'N 5º50'E, average 7 km^3 per annum, coming from the River Rhine) is sluiced through the Afsluitdijk into the Wadden Sea at low tide, by passive fall.

Freshwater fisheries developed since the closure have been and are still dominated by eel. Glasseels recruit through the sluices in the dike towards the Wadden Sea, at Den Oever (52º56'N 5º03'E), and Kornwerderzand

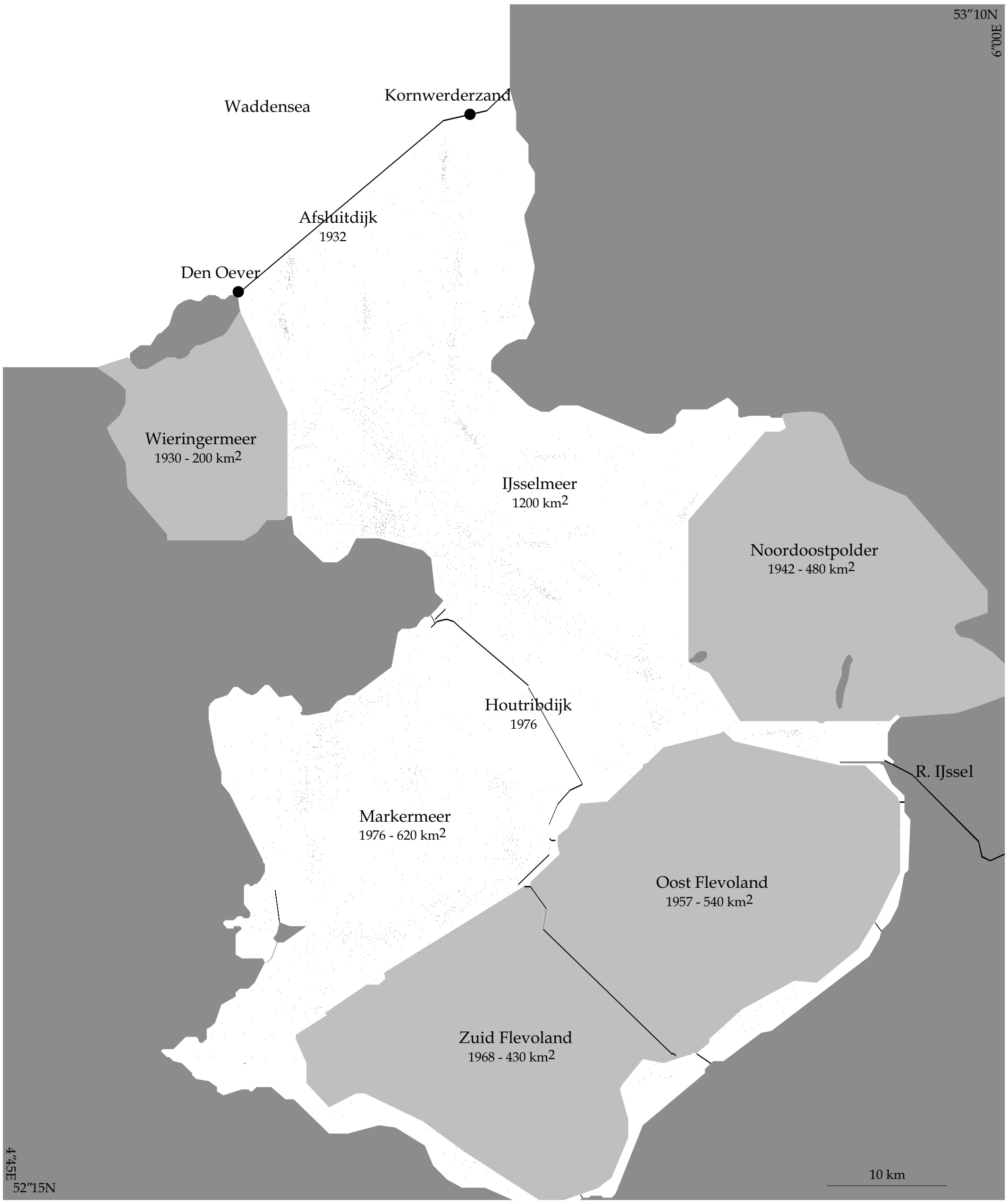

Figure 2 Map of the study area. Major polders and dikes are indicated, with name, year of construction, and surface area. Before 1932, the area constituted an estuary, known as Zuiderzee. Confusingly, since 1976 the name IJsselmeer applies to the northern portion and to the lake as a whole. Data points indicate the position of individual samples. Those located inside polders were taken prior to reclamation.

(53°05'N 5°20'E). The abundance of glasseels in front of the sluices in Den Oever has been monitored since 1938, using a lift net (Dekker 1998, 2002). Recruitment was low in the late 1950s, remained high until 1980, but then declined to an all-time low in 2001 (Figure 1b). Immigration of glasseels is facilitated by slightly opening the sluices during the season. Silver eels migrate through the sluices towards the Wadden Sea. There has been no artificial re-stocking of the lake with glasseels or young yellow eels.

Trawls, fykenets, eel boxes, and longlines have been used to exploit the local stock (Van Densen et al. 1990). Landings of eel were <1000 t before the construction of the Afsluitdijk, rose to a peak of 4750 t in 1948, then declined in several steps to <1000 t from 1970. Since the recruitment failure in the late 1980s, the yield has never exceeded 400 t (Figure 1a). Commercial trawling was the dominant fishing technique until trawling was banned in 1970. Commercial fykenets have been used along the Afsluitdijk, for silver eels mainly. Since the mid 1970s the number of fykenets fishing for both glass and yellow eels has risen sharply (Dekker 1991), 90% being smaller fykenets set in trains, and the balance larger fykenets set on poles near the shore. Eel boxes were developed following the ban on trawling. A minimum legal size limit of 25 cm was established in the 1920s, but on 15 November 1937, it was raised to 28 cm.

Data

Data from various sources have been combined:

- Samples from the commercial fishery, consisting of landings from trawls, fykenets, boxes, and longlines. Often, information on the few eels below the minimum legal size in the catch is completely lost. In most cases, sample size was fixed, and the associated effort data are not available. Before 1989, samples were collected irregularly and did not cover all gear types. Subsequently, all gear types have been sampled consistently and regularly, several times a year. Silver eels are usually distinguished from yellow eels in the catches. Although a large number of samples from the silver eel landings are available, all silver eel samples have been excluded from the current analysis, for the following reasons. First, silver eels may have been caught higher up the River Rhine. Second, the silvering process in itself is highly length-selective, masking information on the stock contained in the samples.
- Samples from the commercial fishery before undersized eels were discarded. In such cases, the associated effort is mostly known. The objective of taking the samples varied, including for stock monitoring for fisheries management, and for collecting information on discards.
- Research vessel survey samples. Until 1980, most research surveys for eels deployed an 8-m beam trawl with 2-mm mesh net, whereas in later years a 3-m beam electrified trawl has been used (Deelder 1974) has been deployed with the same mesh size. In a gear comparison experiment, both nets were fished in parallel during the late 1980s. An 8-m beam trawl with 18-mm mesh used for coarse fish surveys yielded additional information on eels, and research vessels have often collected incidental data. Most data are complete and well documented, but for many samples from the 1950s and 1960s, information is restricted to length classes below the minimal legal size of 28 cm.
- In the 1950s, a series of experiments was made testing different mesh sizes, to adapt the herring and anchovy trawl used in the former Zuiderzee estuary to freshwater eel fisheries.

Recorded information includes gear type, number of nets, duration of fishing operation, mesh size (hook size for longlines), place and date of operation, and the number of eels per length class of either 1 cm or 1 mm. Measurements have been rounded down to 1-cm length classes, but lengths >40 cm have been lumped. Gear types were classified as: 8-m beam trawl (using dan lenoes); 3-m beam trawl (using sledges); electrified 3-m beam trawl (sledges); fykenets of any type; pots and boxes; longlines. Samples were classified in respect of selection procedures as: unrestrained; undersized (after legal-size eels were removed); legal-size eels only; presumably unrestrained; presumably legal-size eels only. The last two categories apply when explicit information is absent, but the length distribution definitely suggests so. Missing information on mesh size or selection procedure could often be restored, based on written notes, background knowledge of the personnel involved in the original sampling, or circumstantial evidence. For instance, while the smallest eels (<15 cm) are only caught in gear with mesh sizes <<10 mm, and trawl mesh sizes are known to equal 2 mm or >10 mm, the presence of many small eels indicates use of a 2-mm mesh.

The abundance of glasseels in front of the sluices in the Afsluitdijk has been monitored annually since 1938 using a small lift-net (Dekker 2002). The (logarithmic) index of such recruitment (Dekker 1998) has been used in the analysis.

All data were computerized and stored in a database. Since 1989, data entry has been completed within a few days following the field trip; older data were computerized recently, from stored paper recordings. An overview of the number, size, and characteristics of the samples is given in Figure 3. In all, 5878 samples have been analysed, a total of 606,210 eels weighing 15.5 t, 0.1‰ of the commercial landings.

Prior to 1950, data are only available for a few short ranges of years (Figure 3); from 1950 onwards, an uninterrupted data series exists, with initially an approximately exponentially rising number of samples per year. Following a brief period in the 1970s and 1980s when large numbers of eels were sampled annually, the total has stabilized at some 10,000 per year. In later years, most data are from research surveys, using an 8-m beam trawl prior to 1980, and an electrified trawl after 1980, both with 2-mm mesh. Market samples (no effort information) involved an approximately constant number of eels since 1950, but recently, many small samples have been collected rather than a few very big ones. Before 1970, it is often not certain whether or not samples were restricted to legal-size eels.

Analytical model

The composite model used reads:

$$C_{\text{year,sample,length}} = E_{\text{year,sample}} \times S_{\text{gear,selection,length}} \times N_{\text{year,length}}$$

where C is the catch in numbers per sample and length class, E the effort applied in obtaining the sample (number of units times the number of hours deployed, S the selectivity of gear type and selection procedure by length class, and N the relative abundance (numbers) by year and length class. The subscripts represent the year of sampling, a trivial sample number (implying gear type and selection procedure), length class, gear type, and selection procedure.

For each factor E, S and N, a separate submodel is developed, selecting from the class of generalized linear models (McCullagh and Nelder 1989). Starting from an initial best guess for all parameters, each submodel is estimated in turn, iterating until the model fit (deviance) changes by <1‰. Depending on initial parameters, this required 5-10 iterations. Because true abundance is unknown, S and N are expressed in relative terms. For S, this relates to the total catch of legal-size eels, for N to the catch of a 2-mm mesh 8-m beam trawl per hour fishing.

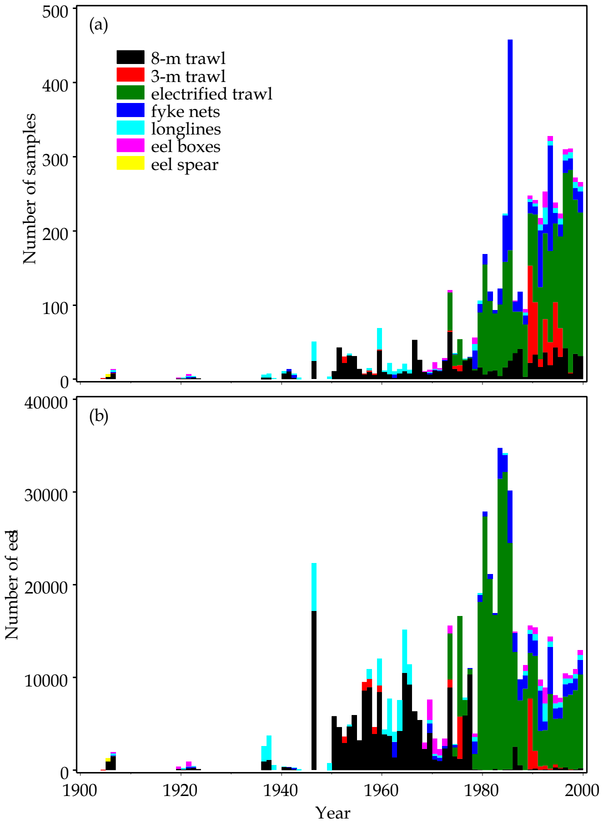

Figure 3 (a) Number of samples, and (b) number of eels analysed by year and gear type.

A generalized linear model was used to model the length class, using a cumulative logit link, and a multinomial error distribution. Observations are weighted by the number observed divided by the relative abundance (see below), i.e.

$$\text{Weight} = C_{\text{year,sample,length}} \,/\, \hat{N}_{\text{year,length}}$$

Explanatory class variables are gear type and selection procedure, whereas square root of mesh size serves as a continuous covariate, assumed proportional to the length of the fish being selected.

Relative selectivity is calculated as

$$\hat{S}_{\text{gear,selection,length}} = \text{Prôb}(\text{length} \le i < \text{length} + 1) \,/\, \text{Prôb}(i \ge 28)$$

where Prôb estimated probability. For samples retaining undersized fish only, relative selection is carried out using an estimate of Prôb($i \ge 28$) under the proviso that all length classes had been retained, i.e. the relative selectivity of undersized eels is assumed to have been unaffected by the posterior discarding of information on legal-size eels.

A generalized linear model of the number per length class in each sample was used to model abundance, using a log link and a Poisson error distribution. An offset is included in the model equal to

$$\text{Offset} = \log(\hat{E}_{\text{year,sample}}) + \log(\hat{S}_{\text{gear,selection,length}})$$

where $\hat{E}$ is known or estimated effort (see below).

Explanatory variables include:

- Gear type as a class variate, carries the relative catchability (ratio of catch rates between gears).
- A series expansion of length and year covers overall trends in abundance. In principle, higher orders in a series expansion can model details in trends, but these are not likely to be easily estimable, and are therefore excluded. The first order of length is not included, because that would alias the selectivity submodel.
- Using a categorical time-series approach (Fahrmeir and Tutz 1994), the abundance in year y-1 is included as an autoregressive variable in year y. The previous year's length class l is matched to the current year's length class l+g, to allow for g cm of growth. For the parameter g, a fixed value of 4 cm per year was assumed (Berg 1990). For each y and l, abundance is

Table 1 Analysis of variance (Type 1) tables for the selectivity and abundance submodels.

source	deviance	df	mean square	*F*	*p*
Selectivity submodel: multinomial model of the length frequency distribution					
gear type	14,141	6	2357	10,810	<0.0001
selection	4140	4	1035	4748	<0.0001
$\sqrt{\text{mesh}}$	3342	1	3342	15,328	<0.0001
residual	41,029	187,495	0.218		
total	62,652	187,506	0.334		
Abundance submodel: log-linear model of the abundance per length class and year					
gear type	4,716,922	6	786,154	153,906	<0.0001
autoregression	150,657	1	150,657	29,494	<0.0001
recruitment index	7401	1	7401	1449	<0.0001
year	8893	1	8893	1741	<0.0001
year^2	43,088	1	43,088	8435	<0.0001
year^3	No fit	0			
year × length	99,726	1	99,726	19,523	<0.0001
year^2 × length	1939	1	1939	380	<0.0001
year × length^2	2878	1	2878	564	<0.0001
residual	979,944	191,844	5.11		
total	6,011,449	191,857	31.33		

calculated as the relative abundance (see below) enlarged by the mean of the residuals observed for y and *l* in the previous model fit. This in itself requires an iterative fitting procedure, which is integrated in the overall iteration. In contrast to the series expansion of length and year, this autoregression easily models trends observed in few length classes, for a small range of consecutive years, if they match the (assumed) growth rate.

- For the smallest length class (7 cm), no autoregressive observations are available, and the recruitment index developed in Dekker (1998, 2002) is substituted. For larger size classes, this explanatory variable is always set to zero.

Relative abundance $\hat{N}$ is calculated as the estimated catch in a standardized gear, a 2-mm mesh 8-m beam trawl per hour fishing:

$$\hat{N}_{\text{year,length}} = \hat{C}_{\text{year,standard gear,no selection,length}}$$

Effort is modelled by a generalized linear model of the number per length class in each sample, using a log link and a Poisson error distribution.

An offset is included in the model equal to

$$\text{Offset} = \log(\hat{S}_{\text{gear,selection,length}}) + \log(\hat{N}_{\text{year,length}})$$

Explanatory variables include only year × sample, representing the effort per sample. In principle, this analysis does not differ from the abundance model above, and could therefore have been integrated there. However, the number of effort parameters to be estimated exceeds 1000. Solving the combined model would require computing times proportional to the square of the number of samples. Because each parameter estimate is determined by the specified offset and the data of one sample only, each parameter is estimated in turn, requiring computing-times proportional to the number of samples. For each sample, estimated effort is calculated, but known effort is not replaced by an estimated value. Each of the submodels was implemented in SAS (SAS Institute Inc. 1999), using 'proc genmod'; macro-code controlled the overall iteration of the model.

Results

Owing to the large number of observations (191,892), even tiny correlations are statistically significant and all model terms contribute significantly to the overall model (Table 1). For the selectivity submodel, major contributions relate to gear type, mesh size, and selection procedure. For the abundance submodel, the prime explanatory variables are gear type, the autoregression, year^2 and year × length. Inclusion of the recruitment index improves the model only marginally, but the regression coefficient is 0.76, indicating a rather strong relationship between the recruitment index and the few length classes directly affected by recruitment. The first and second terms of the series expansion in year are significant, but the third term is not estimable. Year^2 × length and year × length^2 contribute little to the model. Overall, the selectivity submodel explains 25% of the variance, whereas the abundance submodel explains 84%. However, the gear effect in the abundance submodel is related to the units of effort chosen for each gear type. Subtracting the gear effect, only 24% of the remaining variation is explained.

Figure 4 shows the effect of differences in gear type, mesh size, and selection procedure for the selectivity submodel. The three trawl types (3-m beam trawl, 8-m beam trawl, electrified trawl) result in comparable length distributions; fykenets and eel boxes select larger sizes, and longlines select the largest eels. The difference in modal length among gears is never more than 1 cm. Comparison of mesh sizes of 2, 10 and 20 mm (Figure 4b) reveals larger discrepancies. Over the range 28-40 cm, the length distributions are identical. For a 20-mm mesh size, the distribution falls below 28 cm, and for 10-mm mesh size below 24 cm. The distribution of the different selection procedures reveals a close match between known and presumed procedures. Samples selected for legal-size eels (>28 cm) do contain some undersized eels, even as small as 20 cm, and the selection for undersized eels contains a few legal-size eels, up to the top of the size range.

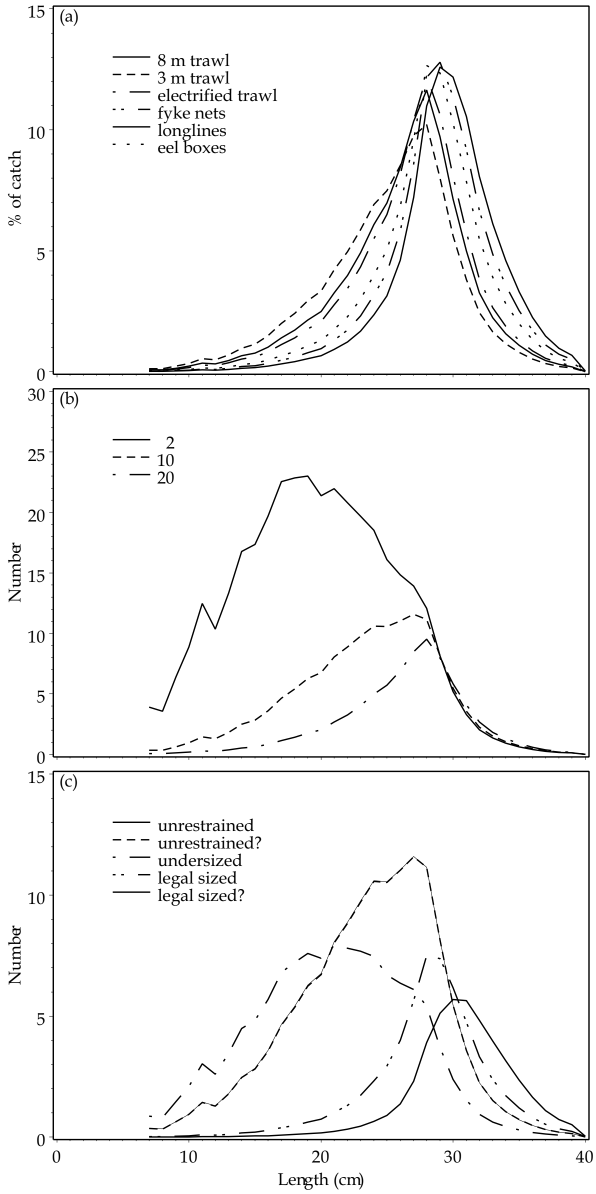

Figure 4 Length frequency distributions estimated by the model for 1980. (a) Unrestrained catch of different gear types. Nets and eel boxes with a mesh size of 20 mm, longlines with hooks of 10-mm gape width. (b) Unrestrained catch of an 8-m beam trawl, with different mesh sizes (mm). (c) Selections of the catch of an 8-m beam trawl with 10-mm mesh.

During the 20th century, the abundance and the length composition of Lake IJsselmeer eels have changed considerably. Until the 1950s (Figure 5), the abundance increased, initially most obviously at lengths ≥10 cm, but following the closure from the Wadden Sea in 1932 also in the smaller length classes. Although there is great variation in the estimated densities in adjacent years, the overall trend indicates a rise in abundance of the smallest length classes (≤10 cm) from 1900 to 1950, followed by a stable period up to 1980, but then a drastic decline in the 1980s and 1990s. Individual years track exceptionally strong (1952 and 1958) and weak (1956, years after 1980) year classes (Figure 1a); i.e. the trend in the smallest length classes largely matches the trend in recruitment. The next length class up (10-15 cm) follows the same trends, often one or two years later. Densities were high from 1950 to the early 1980s. For the 15-20 cm length class, however, densities peaked in 1960, then declined gradually until 1980, when the decline was faster. The 20-25 and 25-30 cm length classes followed similar trends, but the rapid decline in the 1980s was somewhat later for the 25-30 cm length class. For that length class, an isolated peak in abundance is estimated for 1958. The abundance of the 30-35 cm length class increased until 1940, varied at a high level until the mid 1960s, and then declined gradually. Finally, length classes 35+ cm have never been abundant, though they were relatively good through the 1940s and 1950s, before declining gradually and consistently. The lowest value in the record is for 2000.

Discussion

The European eel population is clearly in severe decline. Current results suggest that the Lake IJsselmeer stock began to decline in about 1960, affecting legal-size (≥28 cm) and undersized eels, but also that the smallest size classes remained unaffected until the recruitment failure in the 1980s (Figure 5).

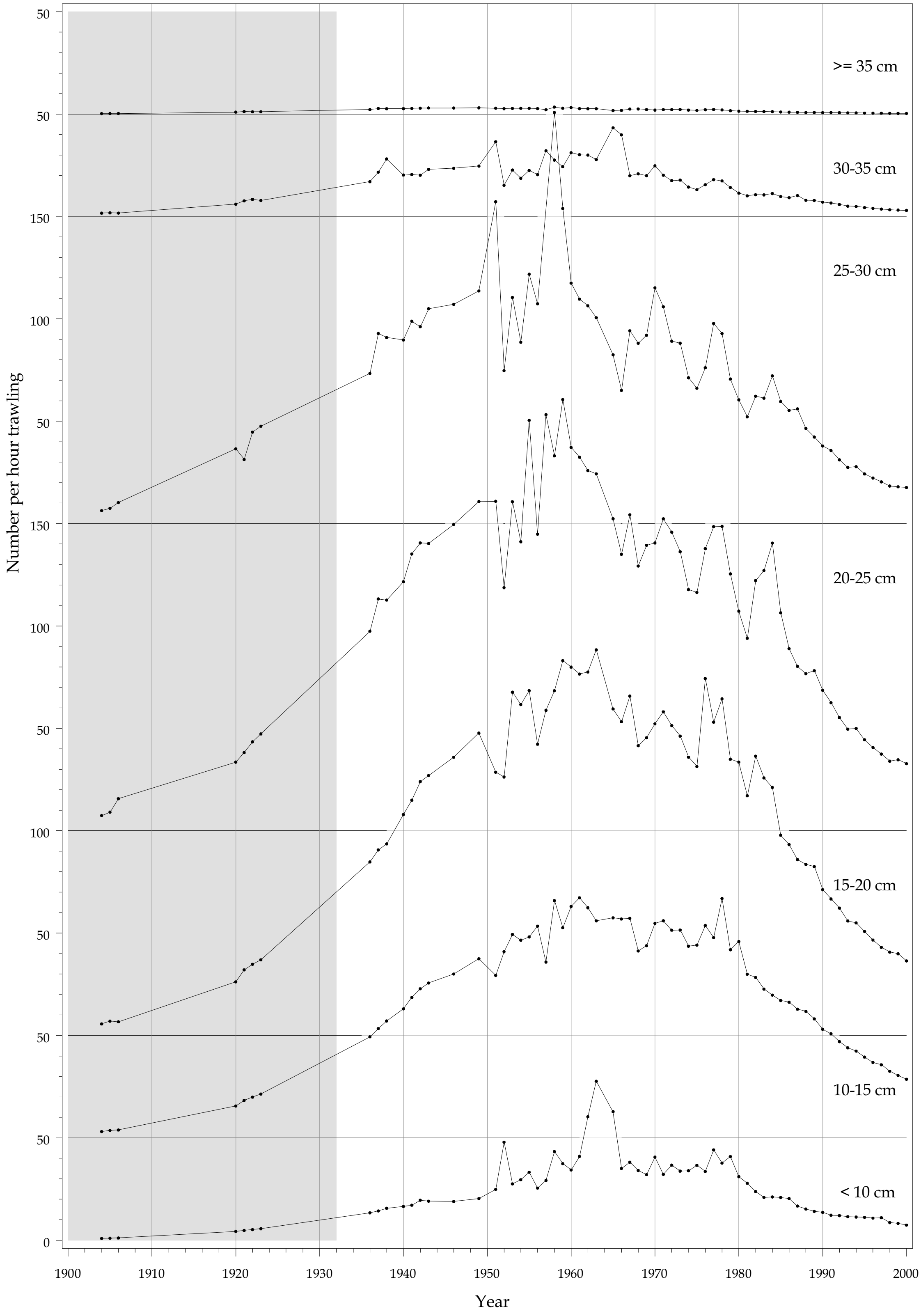

Figure 5 Trends in abundance over the 20^{th} century: estimated catch of an 8-mm beam trawl with 2-mm mesh operated for 1 h, summed over 5-cm length intervals. In 1932, the estuarine area was transformed into a freshwater lake. Since 1937, the minimum legal landing size has been 28 cm.

To my knowledge, no previous studies on long-term trends in yellow eel stocks have been published. For the Baltic, Svärdson (1976) reported a consistent decline in catches of young eels in traps at river mouths after the 1960s, but interpreted this as a drop in recruitment from the open ocean into the Baltic.

The analytical model has largely been driven by the amount of detail available in the historical data. Details of the gear, the time of the day, the exact location being fished, and the speed of towing are simply not available for most samples. However, because eels were the target species for almost all sampling, optimal fishing conditions will have been aimed for consistently throughout the century. As the main fishing trawls have remained virtually unmodified over the decades, modern motor vessels still trawl at speeds comparable with that of old-time sailing ships. Consequently, the observed trends in catch per unit effort likely reflect variation in abundance rather than changing fishing practice. Indeed, the estimated trend for the 25-30 cm length class (Figure 5) is well correlated with the yield (Figure 1a) of the commercial fisheries ($r^2=0.68$ for the period since the last polder construction in 1968; n=33). There are major irregularities in the results for the 1950s and early 1960s, during a period of low sampling intensity. Although uncertainties in the interpretation of historical records might have caused some of the variation in the results (Figure 5), it seems more likely that the number of samples was insufficient for averaging out stochastic variation. High stochastic variation is a recurring theme in the analysis of trends in eel abundance, and explained variance is typically less than 25% of the total variation (Dekker 1998, 2000a, 2003a,c).

Production in continental waters is the net result of recruitment from the ocean, individual growth, fishing mortality, and other causes of death. Each of these processes might have changed over the decades, and could have caused the observed decline in production. Recruitment of glasseels to Lake IJsselmeer has been studied extensively (Deelder 1958; Dekker 1998, 2002), revealing a major drop in recruitment from 1980 onwards only. Growth of eel in Lake IJsselmeer has been analysed (Deelder 1957) through the conventional reading of the age from whole otoliths, but this time-series has been discontinued (Deelder 1976) in favour of an incorrect (Dekker 1986) technique, and has not yet been restarted. Finally, fishing mortality has been estimated for only a few years (Deelder and De Veen 1958; Dekker 2000c). Consequently, the processes determining the production are poorly known, and the current analysis therefore focuses on the state of the local stock, which is assumed to reflect changes in the production processes. In other words, state variables are analysed to derive insight into changes in rate variables. Admittedly this is an indirect approach, but presumably it is the only achievable one covering such a long time span.

What process might have caused the observed decline in recruitment and abundance, reduced growth, or increased mortality? Over the period 1960-1985, the abundance of the eel length class 20-25 cm was reduced by c. 50%. Natural mortality from the glasseel stage to the 20-25 cm length class is unknown, but could be of the order of 50% (Moriarty and Dekker 1997; Dekker 2000b). If a change in growth rate caused the observed decline in abundance, it should have increased to about double the former value and would have led to an increase instead of a decrease in commercial yield. Estimates of the annual growth rate of Lake IJsselmeer eels were 4.5 cm in the 1940s (Havinga 1945), and 4.2 cm in the 1950s (Deelder and De Veen 1958). The rate at which the recruitment failure since 1980 showed up in consecutive 5-cm length classes broadly corresponds to an annual growth rate of 4 cm (Figure 5), so there has been no obvious change. Therefore, although growth variation may not be ruled out completely, it is unlikely to have been the main cause of the decline, and by exclusion, increased mortality seems a more plausible explanation. An increase in annual (non-fisheries) mortality from 10 to 20% could have achieved the observed effect, and both these levels are within the range of confidence limits of most estimates of natural mortality of eels in inland waters (Moriarty and Dekker 1997; Dekker 2000b).

During the study period, nearly half the surface of the original lake was reclaimed (Figure 2), reducing the productive area for the local stock (in 1930, 1942, 1957 and 1968, respectively). According to (retired) fishers, eels inside a polder under construction are easily trapped while moving into open water. Consequently, one would expect a temporary rise in landings (if legally recorded), followed by a period of higher density in the remaining open water, where the escapees and the newly recruiting glasseels are confined to a smaller area. Landings did peak following the 1957 polder construction, but they declined following the 1968 one. However, in neither case was there a corresponding rise in stock density in the remaining area. Density-dependent mechanisms might have limited the abundance in the remaining area, but that density steadily declined either indicates that the carrying capacity was not reached, or that it dropped steadily over the years for some unknown reason. The recruitment failure in the 1980s resulted immediately in a decline in the local stock, which would be highly improbable if the stock was regulated by density-dependent mechanisms. Without density-dependent regulation, habitat loss would have had minor consequences for the dynamics of the stock.

Before the closure of the Zuiderzee from the Wadden Sea in 1932, smaller eels (<15 cm) were relatively scarce. Glasseels arriving at the continental coasts use selective tidal transport to migrate into estuaries and rivers (Creutzberg 1961; McCleave and Wippelhauser 1987; Dekker and Van Willigen 2000). Before the closure of the Zuiderzee, tidal currents could have transported glasseels into the River IJssel, presumably as far up as Deventer (52º15′N 6º10′E), more than 50 km upstream of the river mouth. Most of the few glasseels caught in the Zuiderzee were taken near the mouth of the River IJssel (Plate 29 of Redeke 1907), at a time of year (March, April) indicative of subsequent further migration upriver. The yellow eel stock in the Zuiderzee presumably consisted largely of re-migrants from freshwater, immigration and re-migration being frequent phenomena at the brackish/freshwater interface (Limburg et al. 2002). Closing of the Afsluitdijk will have changed the opportunity for upriver migration completely, the dike and sluices now being the effective tidal limit (Dekker and Van Willigen 2000). Lake IJsselmeer, a large freshwater lake just upstream of the tidal limit, would therefore operate as a trap for incoming recruits, presumably bereaving upstream areas of any substantial recruitment. It is consequently most likely that the sharp rise in eel fisheries in 1932 is a direct result of man-made changes to the habitat and fisheries, not a reflection of changes in the local stock dynamics. The gradual increase before 1932, from 450 to 900 t per year, was attributed to an increase in the market price for eel (Redeke 1907; Havinga 1945).

Following the closure of the Afsluitdijk, the abundance of small eels (<10 cm) in the lake tracks the abundance of glasseels in front of the sluices reasonably well (Figures 1b and 5). Apparently, immigration through the sluices is not a major obstacle.

The bottom line is therefore that the current analysis does not reveal the causes of the decline of the population, but it does narrow the range of hypotheses. The decline in Lake IJsselmeer pre-dates the recruitment failure, is not predominantly caused by loss of habitat, is not a consequence of (altered) barriers in the route of immigrating glasseel, did not phase with eutrophication, peaking in the 1970s, is not related to the excessive but constant exploitation of the local stock, has no relation to apparent changes in ocean climate in the 1980s, began long before the introduction of *Anguillicola* in the mid 1980s (Haenen *et al.* 1994), and bears no relationship to the effects of pollutants on spawner fecundity. None of the individual hypotheses being an obvious explanation, a parallel, successive, or synergistic effect of multiple causes is plausible (Dekker 2003b), but without quantitative analysis of the contributions by the individual causes, the multiple-cause hypothesis is just a replacement for unsolved mysteries. For the crucial decades of the decline, the historical information is limited, so for Lake IJsselmeer and perhaps even more relevantly elsewhere, it is unlikely that we will ever solve the mystery of the decline of the European eel population.

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8

Impact of yellow eel exploitation on spawner production in Lake IJsselmeer, the Netherlands

Dana 12: 25-40 (2000)

Exploitation of eel (*Anguilla anguilla* (L.)) may have contributed to the recruitment decline observed in the past two decades, by depletion of the spawning stock. This study assesses the impact of the relatively well-documented fisheries on Lake IJsselmeer, the Netherlands, on spawner production, using a length-structured cohort analysis model. The yellow eel fisheries in Lake IJsselmeer overexploit the local stock of eel. Current fisheries reduce male spawner escapement to one in seven parts and reduce female spawner escapement to one in seven-hundred parts of the unexploited situation. Eel fisheries on continental life stages may have substantial impact on spawner production in all areas where a local population is dense enough to be fished. Although exploitation has not necessarily caused the currently observed recruitment decline, uncontrolled exploitation levels in major eel fisheries will impede successful recovery of stock and fisheries.

European eel (*Anguilla anguilla* (L.)) are exploited over the entire distribution area. Exploitation reduces the local stock, resulting in reduced production of spawners. The simultaneous decline in eel stocks and recruitment* suggests that exploitation might have contributed to the decline in recruitment, by reducing the spawning stock (ICES 1999). Eel fisheries should be assumed harmful to the spawning stock, unless proven otherwise. The 'burden of proof' clearly rests with current exploitation practices (FAO 1995).

Assessments of the impact of fisheries on local eel stocks are limited in number (Sparre 1979; Dekker 1993, 1996; review in Knights et al. 1996) and do not relate spawner escapement to fishing intensity. Simulation studies (Vøllestad and Jonsson 1988; De Leo and Gatto 1995) have been tuned to field data, but these studies have focused on heavily regulated water bodies, where fishermen concentrate their effort on silver eel using fishing weirs.

Fisheries for glasseel, yellow eel or mixed yellow and silver eel dominate the European eel fisheries, by numbers and by weight (Moriarty and Dekker 1997; Dekker 2000b). Assessment of the impact of these major classes of eel fisheries, especially with regard to the consequences for spawner escapement, is a prerequisite for rational management of the entire stock.

Eel fisheries on Lake IJsselmeer, the Netherlands, constitute 2% of total yield from the European stock (Moriarty 1997). Fisheries and stock are relatively well documented by routine monitoring programmes (Moriarty and Dekker 1997), allowing for an assessment of the impact of yellow eel exploitation on spawner production. This local stock is heavily exploited (Dekker 1996) but may not be representative for other, even nearby, yellow eel fisheries in Europe (Dekker 2000a). Therefore, the current analysis will focus primarily on the processes rather than on the quantification of the impact of yellow eel exploitation on spawner production in Lake IJsselmeer. First, in a retrospective analysis over the years 1989 to 1996, the impact of existing fisheries on Lake IJsselmeer eel stock will be quantified in a length-structured assessment model. Secondly, the relation between exploitation and spawner production will be analysed, by simulation of the effect of reduced levels of exploitation, using the same model in predictive mode.

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*The word *recruitment* sometimes refers to the migration from the nursery area to the adult population, sometimes to the onset of vulnerability to fisheries. In eel, the two processes might not coincide. *Recruit* here refers to the immigrating glasseel.

Table 1 Sample size / number of samples by year, life stage and market category. Measurements include length, weight and (externally determined) maturity. Dissection additionally includes sex and maturity (macroscopic determination of the gonads).

	Yellow eel				Silver eel			
	long-lines	eel-boxes	fykenets		'females' >50 cm		'males' <50 cm	
year	measured	measured	measured	dissected	measured	dissected	measured	dissected
1989	403 / 4	482 / 4	2002 / 15	432 / 9	23 / 1	23 / 1	355 / 5	77 / 5
1990	640 / 4	673 / 4	1540 / 11	146 / 3	22 / 1	22 / 1	336 / 5	60 / 5
1991	540 / 8	661 / 8	1379 / 118	238 / 8	21 / 1	21 / 1	326 / 4	80 / 4
1992	678 / 83	771 / 21	962 / 12	88 / 3	20 / 1	20 / 1	340 / 3	77 / 3
1993	570 / 14	488 / 12	1369 / 167	256 / 9	22 / 1	22 / 1	254 / 3	75 / 3
1994	517 / 12	781 / 12	1187 / 32	206 / 7	20 / 1	20 / 1	315 / 3	76 / 3
1995	565 / 16	500 / 12	1180 / 32	240 / 8	19 / 1	19 / 1	344 / 3	66 / 3
1996	611 / 8	533 / 7	1285 / 17	208 / 8	25 / 1	25 / 1	272 / 4	78 / 4

Materials and methods

Study area

Lake IJsselmeer is a shallow freshwater lake, reclaimed from the Wadden Sea in 1932 by a dike (*Afsluitdijk*). Before reclamation, it was an estuarine area known as *Zuiderzee*. The surface of the lake has stepwise declined by land reclamation, from an original 3450 km^2, until only 1820 km^2 remained since the late sixties. The discharge of the river IJssel into the larger compartment (average 7 km^3 per annum, coming from the river Rhine) is sluiced through the *Afsluitdijk* into the Wadden Sea at low tide, by passive fall. Glasseel immigration is facilitated by slightly opening the sluices during the season. Silver eel migrate through the sluices towards the Wadden Sea.

Fisheries

Fykenets, eel boxes (Deelder 1974) and longlines are used to fish for eel; the former includes both summer fykenets set in trains (90%) and larger fykenets set on poles near the shore (10%). The larger fykenets catch yellow and silver eel; other gears only fish for yellow eel. Fykenets set close to the sluices catch predominantly silver eel. These fykenets are not allowed to span the sluices themselves.

Minimum legal size is 28 cm. Since 1995, a dipnet fishery for glasseel has been allowed to catch 5% of the glasseel immigrating through the sluices in the *Afsluitdijk*, for restocking in inland waters.

Monitoring and sampling

In conjunction with management of these fisheries, the government has kept records of landings at fish auctions. Confidential information acquired from selected fishermen indicates that auction statistics cover a stable fraction of ca. 85% of total landings; data in the current analysis have not been corrected for unrecorded landings. Samples of landings have been acquired at the auctions (Table 1). From 1989 onwards, the market sampling programme has covered all types of fisheries and has been operated consistently. In 1994, co-management by the government and an organisation of fishermen was introduced, and recording of auction statistics was taken over by the Fisheries Board (*Productschap Vis*). This has progressively affected the quality of data in a negative way. Data up until 1996 are almost complete, and will be analysed here.

Eel fisheries have been sampled at least twice each spring (yellow eel) and twice each fall (yellow and silver eel). For each of the major market categories (fisheries for yellow eel by fykenets, eel boxes, long-lines and for silver eel by fykenets), a sample of ca. 10 kg of eel was acquired. Samples were kept for one night within closed plastic bags, killing the eel. Individual length and weight were recorded during the following day. A sub-sample of ca. 25 eel per sample was dissected and sex and maturity were recorded by macroscopic inspection of the gonads. Animals for which a definite sex could not be assigned upon macroscopic examination were marked as 'unknowns' (code: '??').

Catch composition data of the samples were used to breakdown total landings over length classes, sex and life stages. Escapement of silver eel through the sluices in *de Afsluitdijk* has not been quantified. Assuming results of tagging experiments by Ask and Erichsen (1976) and Sers et al. (1993) in the Baltic are applicable in the IJsselmeer fisheries, escapement was assumed to amount to 30% of commercial catches of silver eel.

Assessment model

Dekker (1996) proposed a Markov chain matrix model structured by length as an assessment tool for yellow eel fisheries. The current analysis runs along parallel lines, but is extended to cover the process of silvering and

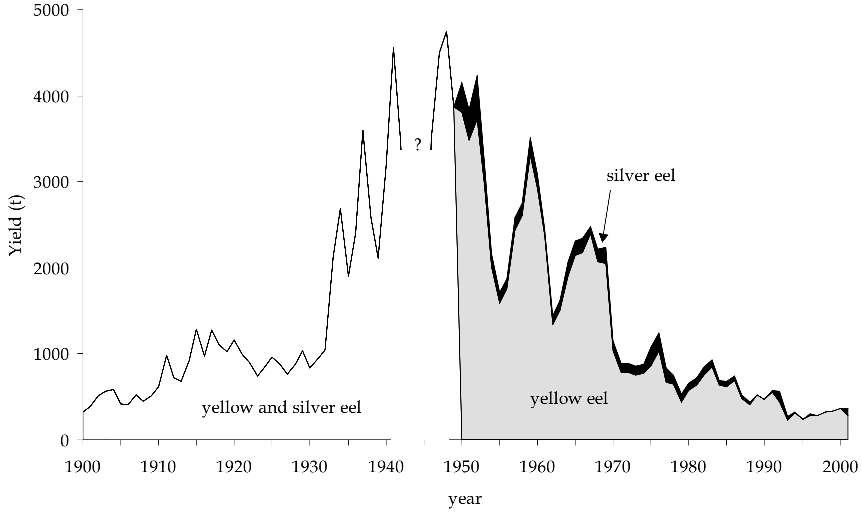

Figure 1 Yield of the Zuiderzee/IJsselmeer eel fisheries by year and life stage.

escapement. The current model is spelled out completely in the Appendix.

Using data on length composition of catches, an assumption of the population in the terminal year and an estimate of the annual growth, the model of Dekker (1996) calculates annual mortality coefficients per length class. Subtracting the natural mortality (assumed constant), an estimate of annual fisheries mortality remains. In the current extension of the model, allowance is made for several fleets fishing for the same stock and for silver eel escapement. The latter is treated as an independent fleet, 'catching' a fixed percentage of the silver eel catch of other fleets.

Following controversies over quantification of eel growth in Lake IJsselmeer (Dekker 1986), no recent estimates of growth are available. It was tentatively assumed that eel growth follows a normal distribution, with a mean growth of 3.5 cm in length per year, and standard error 0.35 cm.

Natural mortality in yellow eel varies considerably, ranging from negligible (Dekker 1989) to close to 100% during incidental pollution accidents (Mueller and Meng 1990) or oxygen depletion in warm summers (Rossi et al. 1987-1988). Moriarty and Dekker (1997, annex 3) suggest natural mortality to be in the order of 75% over the total continental life span, but Dekker (2000b) showed this assumption to lead to incongruous results and used 75% mortality over the pre-exploited yellow eel stage instead, conforming to an instantaneous mortality rate of M=0.138. This latter value will be used here for pre-exploited and exploited yellow eel.

Terminal values for population numbers were derived from catch in numbers in the terminal year 1996 and assumed fisheries mortality

$$F_{term,i} = 0 \qquad i \leq 26$$
$$F_{term,i} = 1-(i-35)^2 / 70 \qquad 26 < i < 35$$
$$F_{term,i} = 1 \qquad 35 \leq i$$

where *term* = terminal year and *i* = length class in cm.

Data for (silver) eel over 40-50 cm in length are sparse, resulting in uncertain estimates of fishing mortalities. Therefore, simulation of alternative management regimes assumed fishery mortality to be stable over lengths over 40 cm and assumed all yellow eel of over 50 cm in length to be female and to silver at a length of 65 cm.

Results

Landings of eel from the *Zuiderzee/IJsselmeer* area at the beginning of this century amounted to 200 to 600 tonnes per annum (0.5 to 1.5 kg/ha/a) and were slowly rising (Figure 1). After the closure of the *Afsluitdijk* in 1932, landings rose to over 2000 tonnes per annum (6 kg/ha/a). Directly following the Second World War, peak landings were recorded of 4750 tonnes per annum (16.4 kg/ha/a). In the following five decades, landings decreased in cycles of richer and poorer years, with peaks every 8 years. Current landings (ca. 300 tonnes per annum; 2 kg/ha/a) are in the same order of magnitude as landings a century ago.

Silver eel catches declined in parallel to yellow eel catches and make up less than 10% of the total catch on average, with peak values in 1975, 1977 and 1992 of 20-25%. Large silver eel (females, of length >50 cm) occurred in all years, but statistics were recorded in a few years only and comprised less than 10% of the silver eel catch in weight, 1-2% in number.

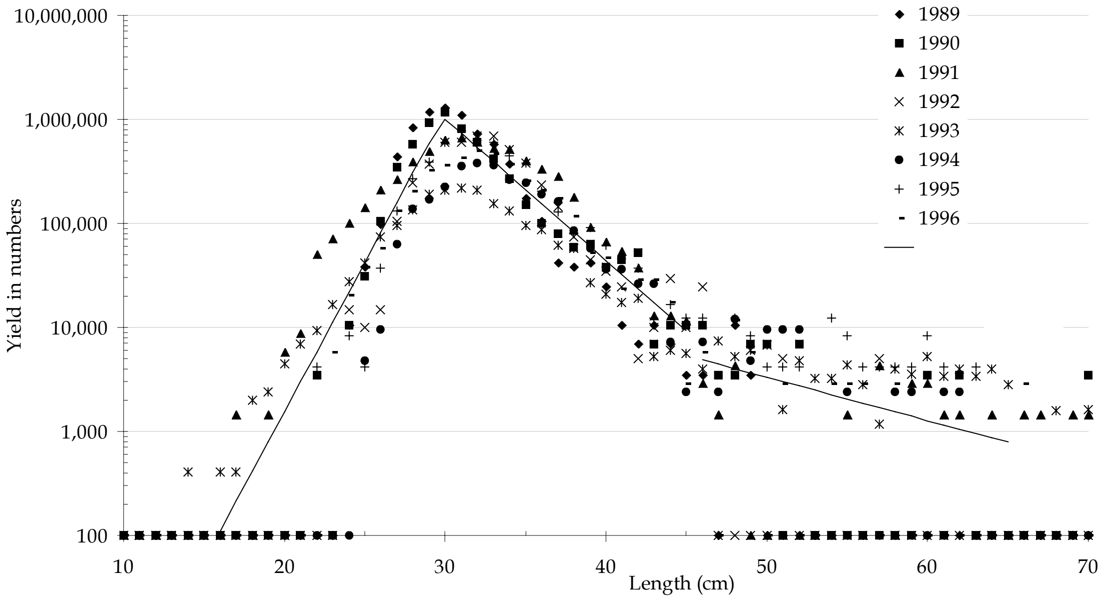

Figure 2 Length composition of the commercial catch by year. Log-linear regression lines have been fit to each of the length ranges 15-29 cm, 30-45 cm and 46-65 cm.

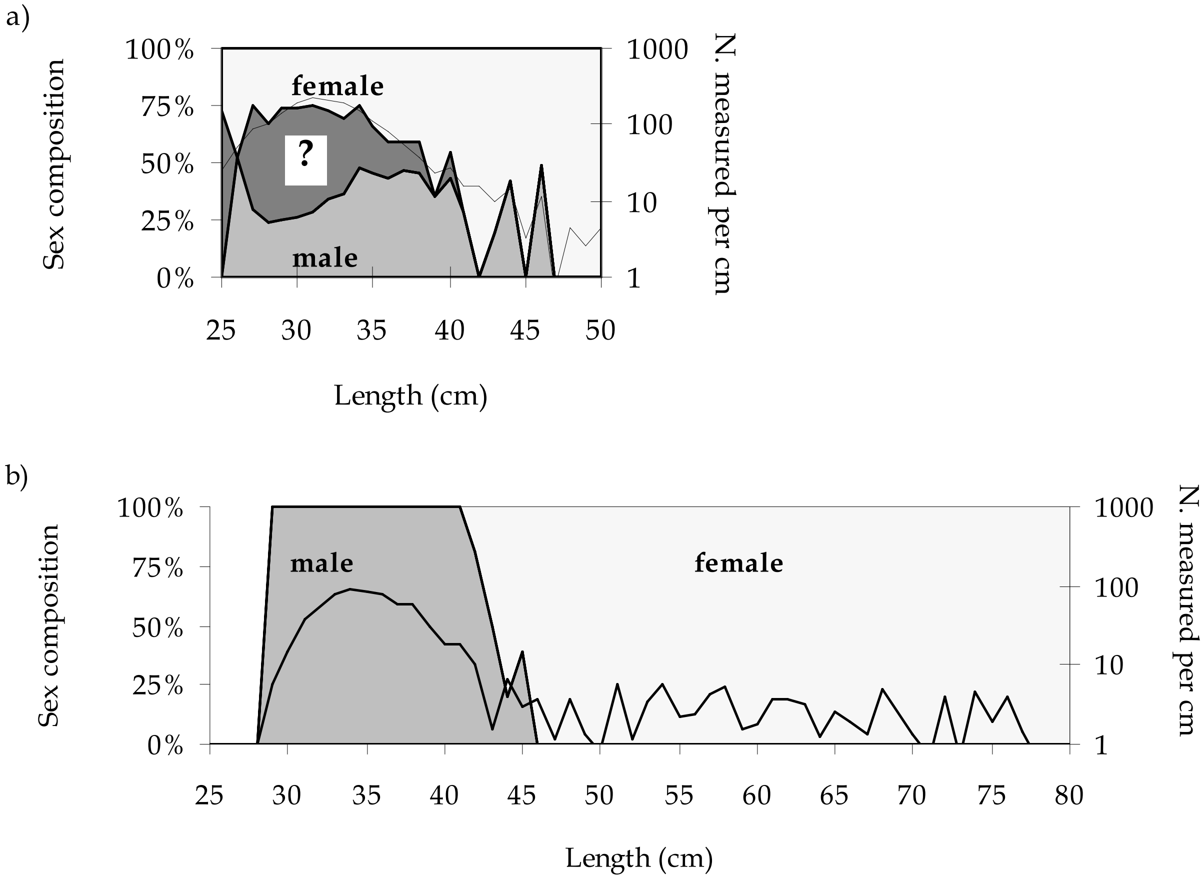

Figure 3 Sex composition of the catch (area) and number of observations (line), summed over the years 1989 through 1996. a) Yellow eel. b) Silver eel. ?=unknown sex.

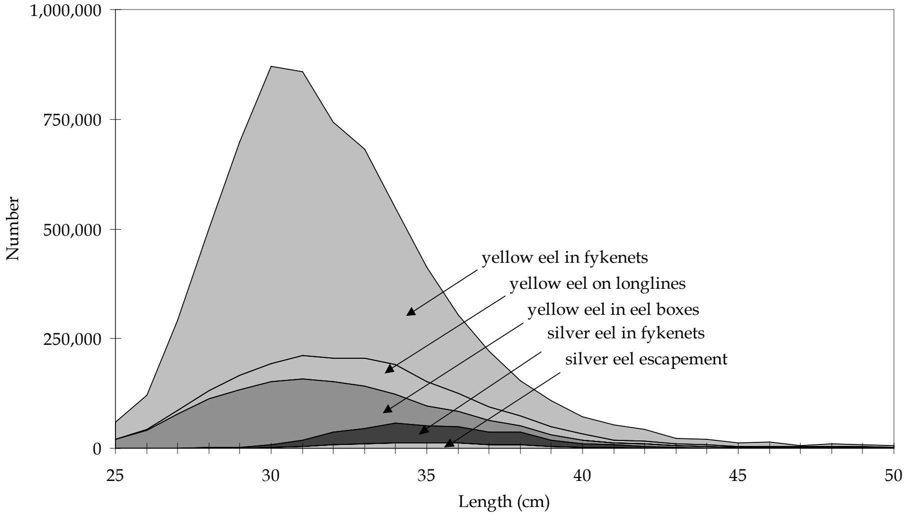

Figure 4 Composition of commercial catch, by length and gear type, averaged over the years 1989 through 1996. The assumed escapement of silver eel is presented additionally.

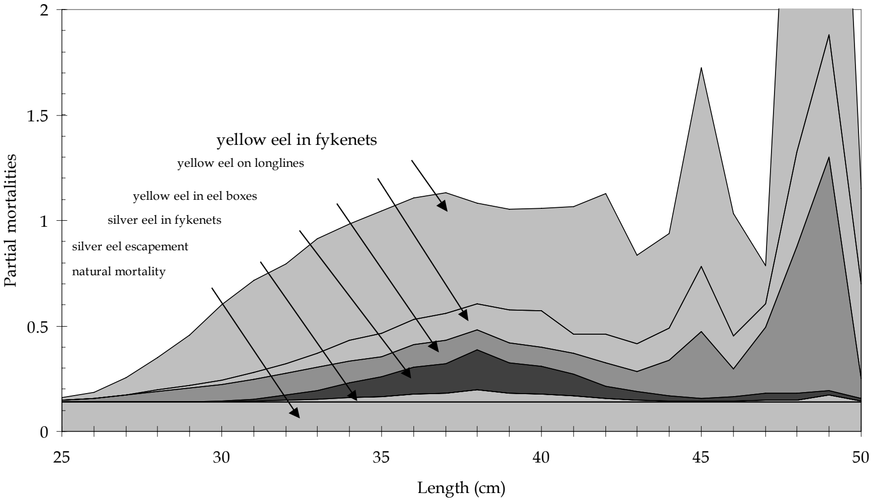

Figure 5 Estimated partial mortalities per year, averaged over the years 1989 through 1996. Silver eel escapement is presented as if it was a true mortality.

Breakdown of catches of yellow eel by length class (Figure 2) leads consistently to three distinct regions: up to 30 cm length, the number caught increases with length; from 30 cm to 45 cm length the number caught decreases with 27% per cm on average; and from 45 cm onwards with 9% per cm on average. Interpreting Figure 2 as a catch curve *sensu* Baranov (1918) and assuming an annual growth of 3.5 cm, annual mortality is estimated equal to 67% (Z=1.09) for length classes from 30 cm to 45 cm and to 29% (Z=0.34) from 45 cm length onward.

Males and females make up about equal shares of landings of yellow eel (Figure 3a), with a similar share for animals of unknown sex. Below 32 cm in length, the unknowns dominate; at 38 cm and above, the majority consists of females. For silver eel (Figure 3b), landings comprise only males up to 42 cm length; only females above 45 cm. In-between, only 21 animals have been observed.

Fykenet catches of yellow eel (averages 1989 through 1996) comprise 70% of total landings (Figure 4; mean length 31.7 cm); eel box catches 15% (mean length 31.1 cm); long-line catches 10% (mean length 33.9 cm) and silver eel catches in fykenets 5% (mean length 35.2 cm). A quarter of yellow eel landings by numbers is smaller than 30 cm in length and 80% is smaller than 35. Less than 1% by number is larger than 45 cm.

Figure 4 presents the breakdown of catches over gears averaged over the years 1989 through 1996. In the

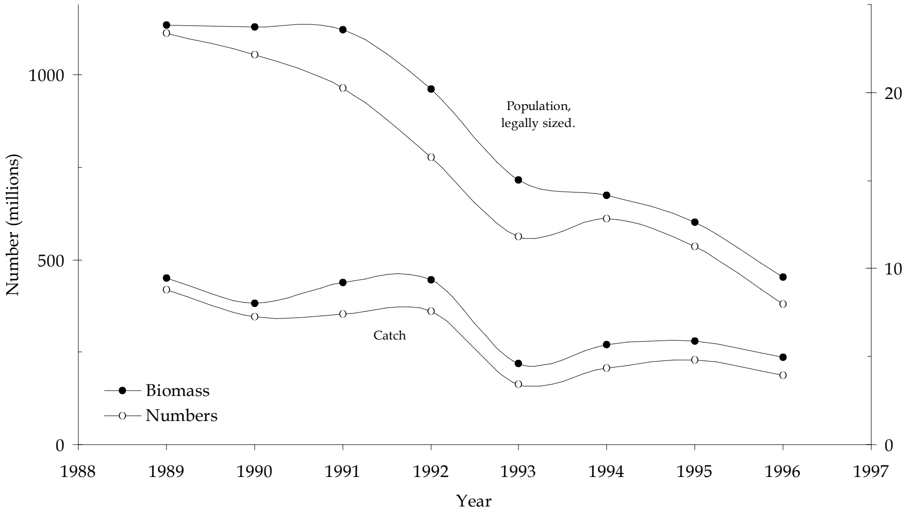

Figure 6 Total yield and estimated population size by year.

Appendix, catches per year are presented, for each of the fishing gears separately.

Fisheries mortalities for all three gears increase slowly from zero at about 25 cm length to a plateau level, remaining stable at greater lengths (Figure 5). For longlines, this plateau is reached at greater length (35 cm) than for the other two (30 cm). Estimated total fisheries mortality at the plateau is 1.0. Silvering occurs over a broad length range, peaking at 38 cm, at 0.25. Above 40 cm length, the rate of silvering declines to virtually zero at 45 cm length.

Population size (Figure 6) is estimated at 23 million (1100 tonnes) in 1989 and has shown a steep decline since 1991, to 8 million (450 tonnes) in 1996. Catches dropped from 9 million (450 tonnes) in 1989 to 4 million (240 tonnes) in 1996. Estimated population number per year class at the minimum legal size in 1989 amounted to 12.5 million, while in 1995 this was reduced to 5 million. Assuming a natural mortality of 75% over the pre-exploited life stage, this conforms to 50-20 million immigrating glasseel per year.

For the current fisheries (Figure 7), commercial yield per recruit was estimated at 15.8 g per immigrating glasseel, including 0.9 g silver eel catch. The annual fisheries mortality is estimated at F~1.0 for the fully recruited length classes. The assumption that silver eel escapement amounts to 30% of silver eel production corresponds to 0.4 g male and 0.02 g female escapement per immigrating glasseel. Reduction of the yellow eel fishery to ±50% of the current level would optimise yield in the yellow eel fishery; reduction to ±33% would optimise the mixed fishery of yellow and male silver eel, which are currently the dominating market categories. Gains in commercial yield would be 2.4 and 4.9 g respectively, but escapement of male silver eel would gain by 0.5 and 1.0 g respectively and escapement of female silver eel would gain by 0.2 and 1.0 g respectively. Cessation of all yellow eel fisheries while keeping silver eel fisheries at current levels would increase catch and escapement of males to 7.0 and 3.0 g respectively per glasseel and catch and escapement of females to 18.3 and 7.9 g per glasseel. The ratio of males to females by numbers would decrease from 225:1 to approximately 2:1.

Discussion

Assessment

Eel does not reproduce in Lake IJsselmeer (Dekker, personal observation) and the local stock does not constitute a closed and self-sustaining population. Bozeman et al. (1985) and Oliveira (1997) report on American eel (*Anguilla rostrata*) having restricted home ranges, but cite Bianchini et al. (1982), who suggest eel might have short-term home ranges in-between long-range movements. Deelder (1984) summarised literature data on migration of (European) yellow eel in the Baltic and in estuaries and rivers in northern Germany and Deelder (unpublished reports) reports massive migrations between IJsselmeer and Wadden Sea. The present assessment assumes that the vast majority of catches on Lake IJsselmeer are constituted of eel from the lake itself; only recruitment of glasseel and escapement of silver eel are accounted for in the model. The local stock of yellow eel appears to contain at least two components (Figure 2): the smaller fish with a (downward) slope of the catch curve >1 and the remainder with a slope of ~0.3, intersecting at 45 cm length. The intersection point at 45 cm suggests the bisection might be

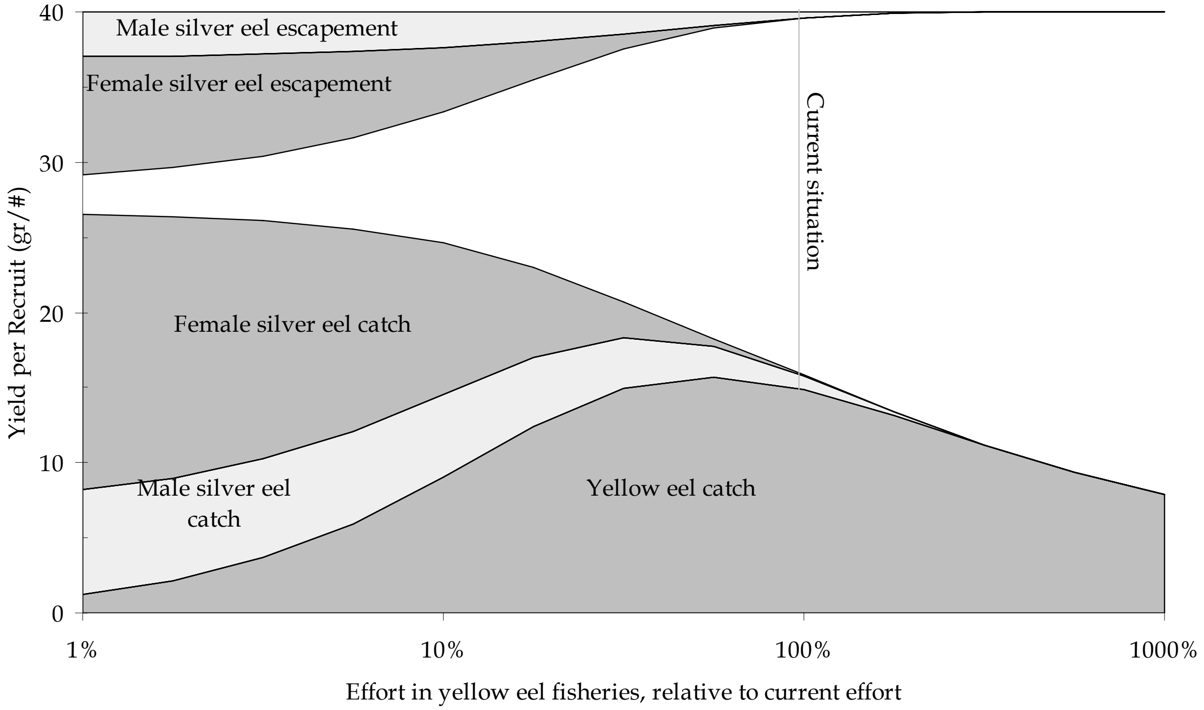

Figure 7 Predicted yield per recruit as function of effort in the fishery for yellow eel. Bottom panel presents yield to the commercial fisheries; top panel presents spawner escapement. Fishing effort is expressed in percentage of current situation, which is F~1.0 per annum for the fully recruited length classes.

related to differential length and rate of silvering of the sexes. However, the absolute scarcity of females over 45 cm (Figure 2) does not match with the abundance of females in smaller length classes (Figure 3a). The steep slope of the major part of the catch tallies with the extreme overexploitation in the decades preceding the period analysed (Dekker 1991). The remainder more likely relates to migrants from stocks in neighbouring areas (up or down streams), which are less heavily exploited. This remainder constitutes less than 1% of catch in numbers. For practical purposes, the IJsselmeer stock of yellow eel up to 45 cm in length can therefore be considered to form a closed population. The close correlation between yellow and silver eel catches over the years indicates, this also holds for the silver eel.

Recruitment has shown a serious decline already before the years included in the analysis (Dekker 1997, 2000a), affecting the stock and yield (Figure 7). Quantitative analysis of the catch curve (Baranov 1918, Figure 2) fails, since the stock is not in a stable state. Instead, data were analysed by a length structured equivalent to the Virtual Population Analysis (Dekker 1996). Estimates of mortality are positively related to the assumed growth rate of 3.5 cm per year (equation 5 in the Appendix gives growth and mortality only as a product) in the retrospective analysis, but possible errors in both should have cancelled out in the predictive simulation of the effect of yellow eel exploitation on silver eel production.

Biological characteristics

Dynamics of silvering have been assessed by analysis of the geographical variation in silver eel (Vøllestad 1992), by guesstimating parameters to conform with field observations (Sparre 1979) and by fitting a sparsely parameterised functional model (De Leo and Gatto 1995). In all studies, an *a priori* distinction between males and females was made. In the current analysis, male and female eel were not distinguished, although *a posteriori* sexes were assigned on the basis of length of silvered eel (Figure 8). When corrected for sex composition, which in itself varies with length (Figure 3a), current results (Figure 8) match very closely with fits of a functional model (De Leo and Gatto 1995). The close match between silvering in Italian and in Dutch waters is in agreement with the finding by Vøllestad (1992), that silver eel shows latitudinal variation in age but not in length. At 40 cm length and above, De Leo and Gatto (1995)'s functional model does not match current findings, but the number of male eel in this length range is extremely low.

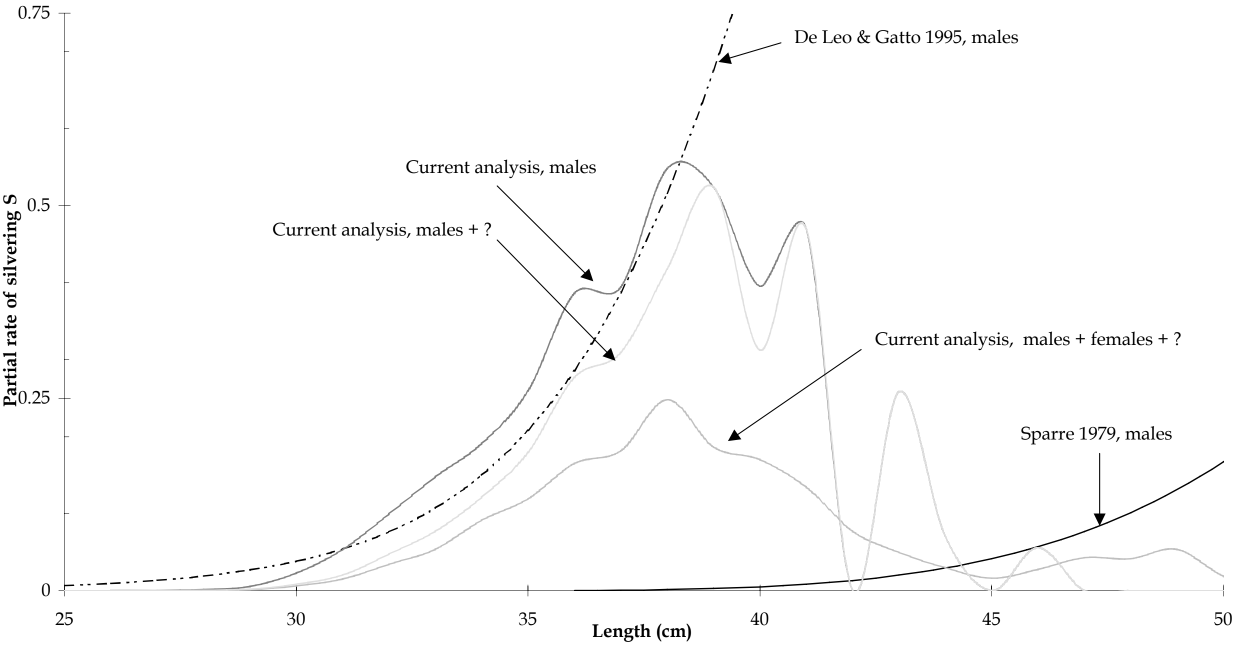

Figure 8 Rate of silvering: current analysis compared to literature data. ?=unknown sex.

Local implications

Yield from Lake IJsselmeer includes 20 tonnes of male silver eels (0.3 million by number) and 2 tonnes of females. Simulation of the impact of yellow eel fisheries on the silver eel production (Figure 7) predicts a potential sevenfold rise in production of male silver eel and a seven hundred fold rise in female silver eel production upon cessation of yellow eel exploitation. This would imply a big increase in yellow eel density, from currently 3-5 kg/ha of eel >28 cm in length, to over 50 kg/ha. Buijse et al. (1993) estimated the production of the main prey species smelt (*Osmerus eperlanus*) in Lake IJsselmeer at 130 kg/ha/a and consumption of smelt at 100 kg/ha/a of which 3.5 kg/ha/a is eaten by piscivorous eel. Consumption by eel seems not the factor limiting smelt density and consumption by eel might very well increase. Whether the predicted increase can be carried in full is questionable.

Dekker (2000b) proposed a tentative assessment of the total European stock, and estimated fishery mortality* $F\times\Delta t=0.63$ in yellow eel fisheries. Sparre (1979) assessed fisheries in the German Bight, estimating $F=0.2$ per year, but his results do not enable calculation of total mortalities over longer time spans. Current results indicate that for an average silvering eel, $F\times\Delta t=3.22$ in the yellow eel fisheries of Lake IJsselmeer, which is well above the European average. The current fishery in Lake IJsselmeer is overexploiting the local stock (Dekker 1996) and a reduction to 30% of current effort would not influence yield negatively in the long run (Figure 7).

The biomass of spawners escaping from European fisheries has been tentatively estimated at 1753 tonnes (Dekker 2000b), of unknown sex composition. According to the analysis presented, the IJsselmeer stock contributed about 10 tonnes of males and 1 tonne of females, but pristine spawner escapement is estimated at 70 and 700 tonnes respectively. Although Lake IJsselmeer fisheries constitute just one of a multitude of local eel fisheries in Europe (Dekker 2000a), its impact on spawner escapement appears to have global dimensions.

Global implications

European eel recruitment is tentatively estimated at two thousand million (Dekker, 2000b). Three quarters takes place in areas surrounding the Bay of Biscay and are fished as glasseel with an estimated mortality of $F\times\Delta t=3.15$ over the glasseel phase. The remaining quarter is scattered over Europe and is fished in the yellow and silver eel stage. Major yellow eel fisheries are found in the British Isles, the Netherlands, Germany and Denmark (Moriarty 1997). Moriarty and Dekker (1997) apparently assumed these fisheries to have a low impact in comparison to glasseel fisheries. However, the current analysis

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*Dekker (2000b) differentiates between annual fishery mortality F and total fishery mortality over a time interval Δt, expressed as $F\times\Delta t$. In this text, the time span Δt always equals the duration of the life stage the estimated mortality applies to.

suggests that yellow eel fisheries in dense (estuarine) yellow eel stocks can indeed be a match for glasseel fisheries. The impact of silver eel fisheries has only been quantified in an outer region of the distribution area (Ask and Erichsen 1976; Sers et al. 1993) and is estimated at $F \times \Delta t=1.43$. The conclusion that continental fisheries (may) substantially affect spawner escapement in all areas where the species is found in any appreciable density is inescapable.

Causes of the observed recruitment decline are unknown and might include natural or anthropogenic factors (Castonguay et al. 1994). Natural changes have been shown to coincide with the observed recruitment trend (Knights et al. 1996) and were indirectly evidenced (Dekker 1997). No trend in anthropogenic factors has been found to match the timing of the recruitment decline (Castonguay et al. 1994). It is unlikely that exploitation is the single cause of the observed decline, but currently uncontrolled exploitation levels in the major eel fisheries will impede successful recovery of stock and fisheries.

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Appendix

This appendix presents an integrated recapitulation of the model of Dekker (1996) and current extensions for multiple fleets and emigration of silver eel.

Representing the number of eels of length *j* in the stock at time *t* by $N_{t,j}$ and the entire stock in number at time t by a vector over length $(N_{t,j})$ growth is modelled as a transition matrix* $[G_{i,j}]$ of dimension length*length, where each cell $G_{i,j}$ quantifies the probability that an animal will grow from length class *j* to length class *i* within a time interval of one year. In the absence of mortalities and migration, the population vector at time *t*+1 is related to the population vector at time *t* by:

$$(N_{t+1,i}) = [G_{t,j}] \times (N_{t,j}) \qquad (1)$$

Following Beverton and Holt (1957), the decline in numbers due to natural mortality, to fisheries and due to silver eel emigration is modelled in a differential equation:

$$\frac{dN_{t,j}}{dt} = -Z_{t,j} \times N_{t,j} \qquad (2)$$

Consequently, the population number at the end of the year relates to that at the beginning as**

$$(N_{t+1,i}) = (\exp^{-Z_{t,j}}) \times (N_{t,j})^T \qquad (3)$$

Each year, new recruits $R_{t,j}$ add to the stock. $(R_{t,j})$ is an almost completely empty vector, except for length class (6)-7-(8), which contains the number of immigrating glasseel. Combining the effects of recruitment, growth and mortality, it follows that:

$$(N_{t+1,i}) = (R_{t,i}) + [G_{i,j}] \times (\exp^{-Z_{t,j}}) \times (N_{t,j})^T \qquad (4)$$

Temporarily dropping indices of time and length,

$$\begin{aligned} Z = {} & M + F_{\text{fykenets}} + F_{\text{eelboxes}} + F_{\text{longlines}} \\ & + F_{\text{silver eel in fykenets}} + S \end{aligned} \qquad (5)$$

where *M* = instantaneous natural mortality (M_0 of Sparre 1979); *F* = instantaneous mortality due to fisheries, including the combined effect of silvering and subsequent capture; *S* = instantaneous rate of decline in population number due to silvering and escapement (M_1 of Sparre 1979).

The decline in numbers*** now equals

$$\begin{aligned} (D_{t,j})^T & = (1 - \exp^{-Z_{t,j}})^T \times (N_{t,j}) \\ & = (\exp^{+Z_{t,j}} - 1) \times [G_{i,j}]^{-1} \times \{(N_{t+1,i}) - (R_{t,i})\} \end{aligned} \qquad (6)$$

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*The notation used mostly adheres to the standard symbols in fish cohort analysis models. Thus capital versus lowercase characters do *not* indicate matrices resp. vectors. Instead, matrices and vectors are given as indexed cells, enclosed in round (vectors) or square [matrices] brackets.

**The superscript *T* indicates the transpose of a matrix, i.e. rows and columns interchanged.

***In traditional fisheries assessments, the decline in numbers due to fisheries is coded as C, for Catch. In the current analysis, decline due to fisheries, due to silvering and due to other (natural) causes are all coded as D, for Decline.

Assuming independence between types of fisheries, and between fisheries and silver eel escapement, each of the components of Z contributes to the decline in numbers D, proportional to its contribution to Z, as

$$\frac{D_{fykenets,t,j}}{D_{t,j}} = \frac{F_{fykenets,t,j}}{Z_{t,j}} \tag{7}$$

Substitutions and rearrangements yield equations for each type of fishery and for silver eel escapement. For example for the fykenet fishery, the catch equals:

$$(D_{fykenets,t,j}) = \left(\frac{F_{fykenets,t,j}}{Z_{t,j}}\right) \times (1 - \exp^{-Z_{t,j}})^T \times (N_{t,j}) \tag{8a}$$

or

$$(D_{fykenets,t,j}) = \left(\frac{F_{fykenets,t,j}}{Z_{t,j}}\right) \times (\exp^{Z_{t,j}} - 1)^T \times [G_{i,j}]^{-1} \times \{(N_{t+1,i}) - (R_{t,i})\} \tag{8b}$$

Given $[G_{i,j}]$, $(N_{t+1,i})$ or $(N_{t,j})$, M and all components of $(D_{t,j})$, equations 4 and 8 can be solved for $(N_{t,j})$ or $(N_{t+1,i})$ and the components of Z. Data for $(D_{t,j})$ are presented in Figures A.1 to A.4; results for $(N_{t,j})$ and Z in Figure A.5 and A.6.

However, Dekker (1996) observed this system of equations to be numerically instable when solved backwards in time, using equation (8b). The population number is adequately assessed, but the distribution over length classes is not: the estimated population is concentrated in a few isolated length classes, with zeroes in-between. Dekker (1996) proposed insertion of a low-pass filter in equation (8b), resulting in

$$(D_{fykenets,t,j}) = \left(\frac{F_{fykenets,t,j}}{Z_{t,j}}\right) \times (\exp^{Z_{t,j}} - 1)^T \times [LP]^a \times [G_{i,j}]^{-1} \times \{(N_{t+1,i}) - (R_{t,i})\} \tag{9}$$

where

$$LP = \frac{1}{3} \times \begin{bmatrix} 1 & 1 & & & & & & \\ 1 & 1 & 1 & & & 0 & & \\ & 1 & 1 & 1 & & & & \\ & & \cdot & \cdot & \cdot & & & \\ & & & \cdot & \cdot & \cdot & & \\ & & & & 1 & 1 & 1 & \\ & 0 & & & & 1 & 1 & 1 \\ & & & & & & 1 & 1 \end{bmatrix} \tag{10}$$

and a=2. Preliminary results of the analysis presented here, indicated a=2 left some of the numerical instability intact. Therefore, a=3 was chosen.

In the current analysis, equation (9) was used in a retrospective analysis of the IJsselmeer fisheries over the period 1989 through 1996, while equation (8a) was used for predictions of alternative management regimes.

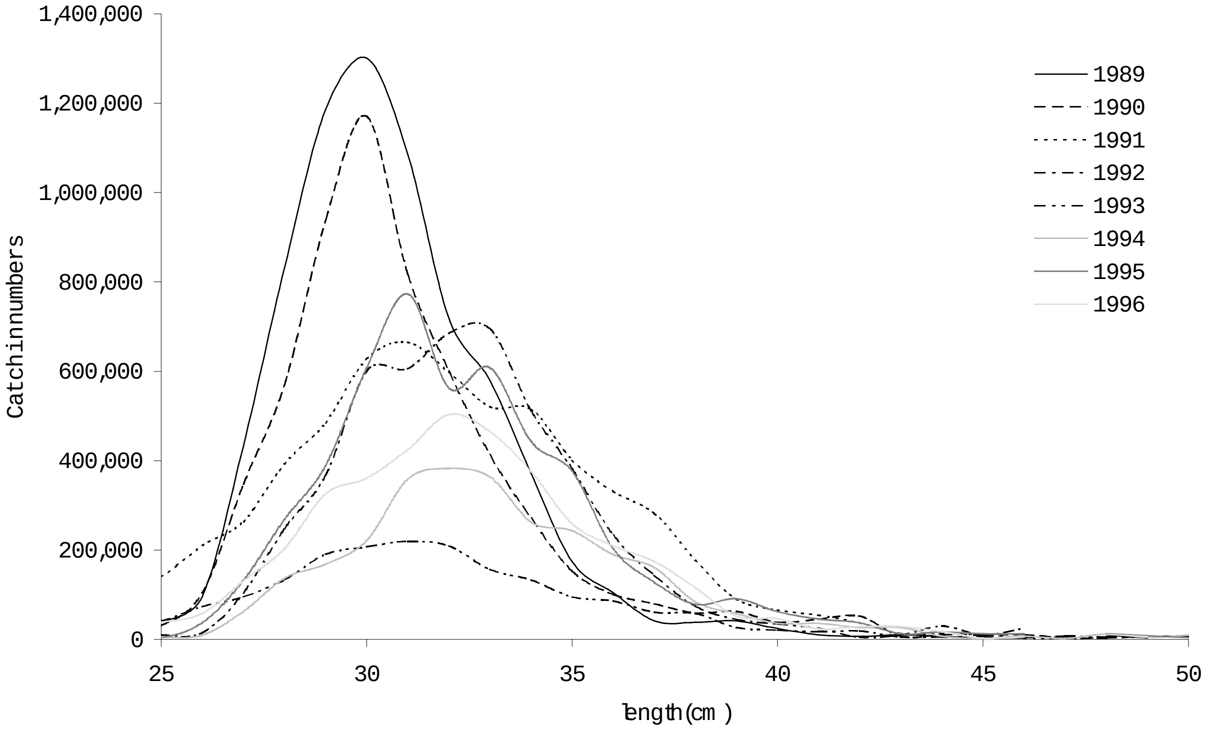

Figure A.1 Catch of yellow eel in fykenets, in numbers per length class and year.

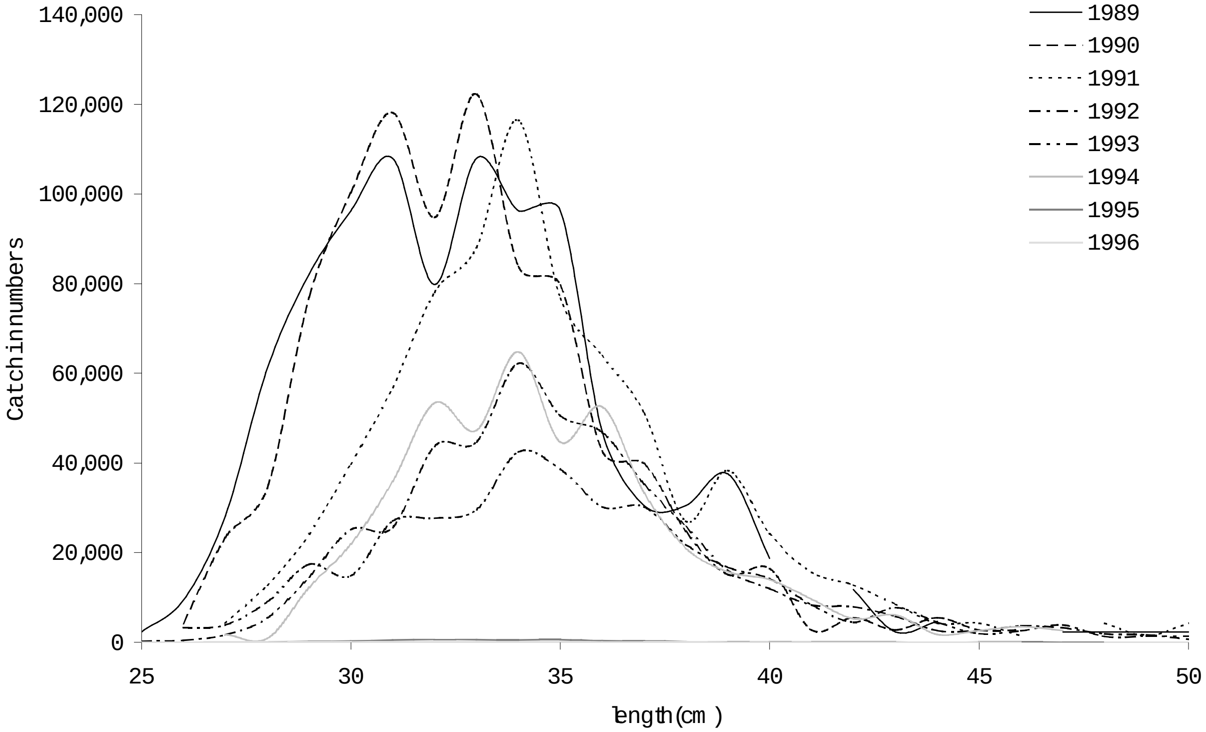

Figure A.2 Catch of yellow eel on long lines, in numbers per length class and year.

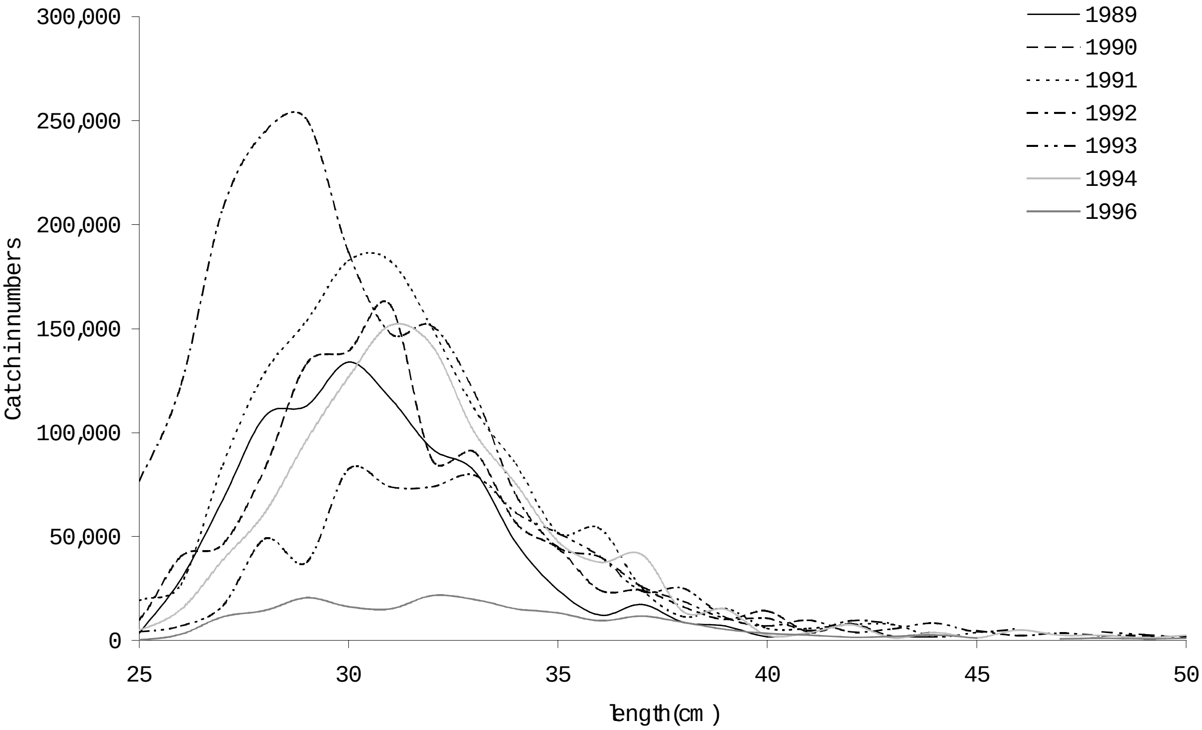

Figure A.3 Catch of yellow eel in eel boxes, in numbers per length class and year.

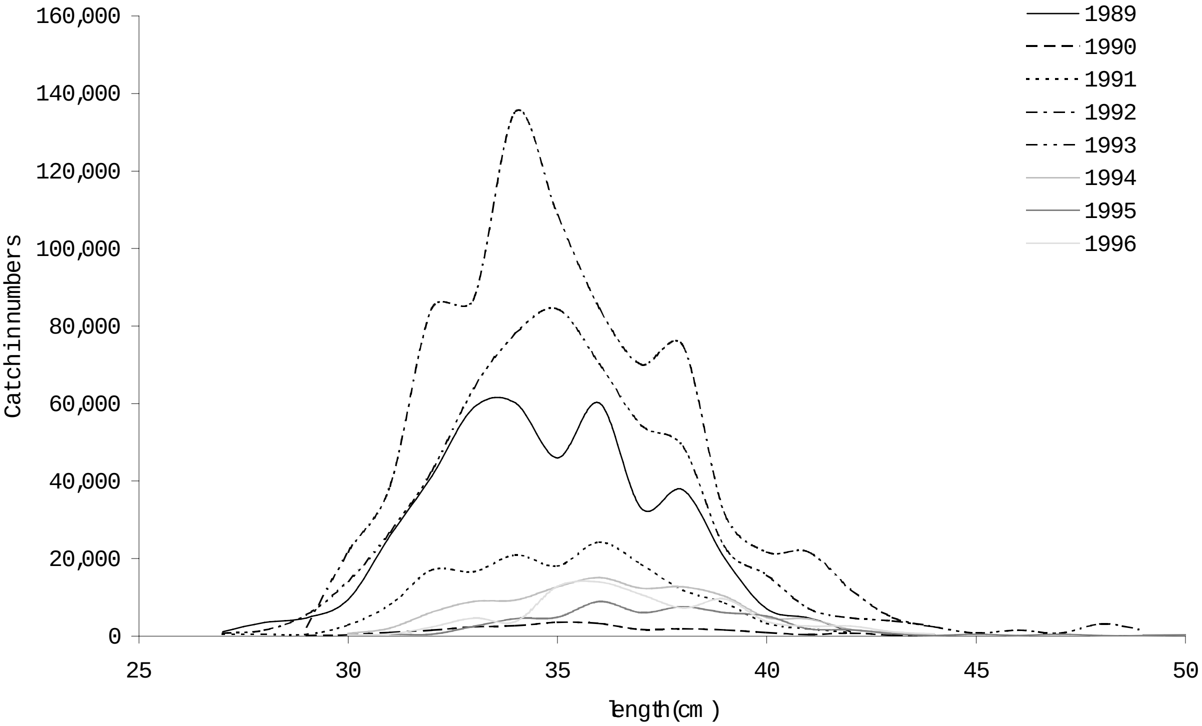

Figure A.4 Catch of silver eel, in numbers per length class and year.

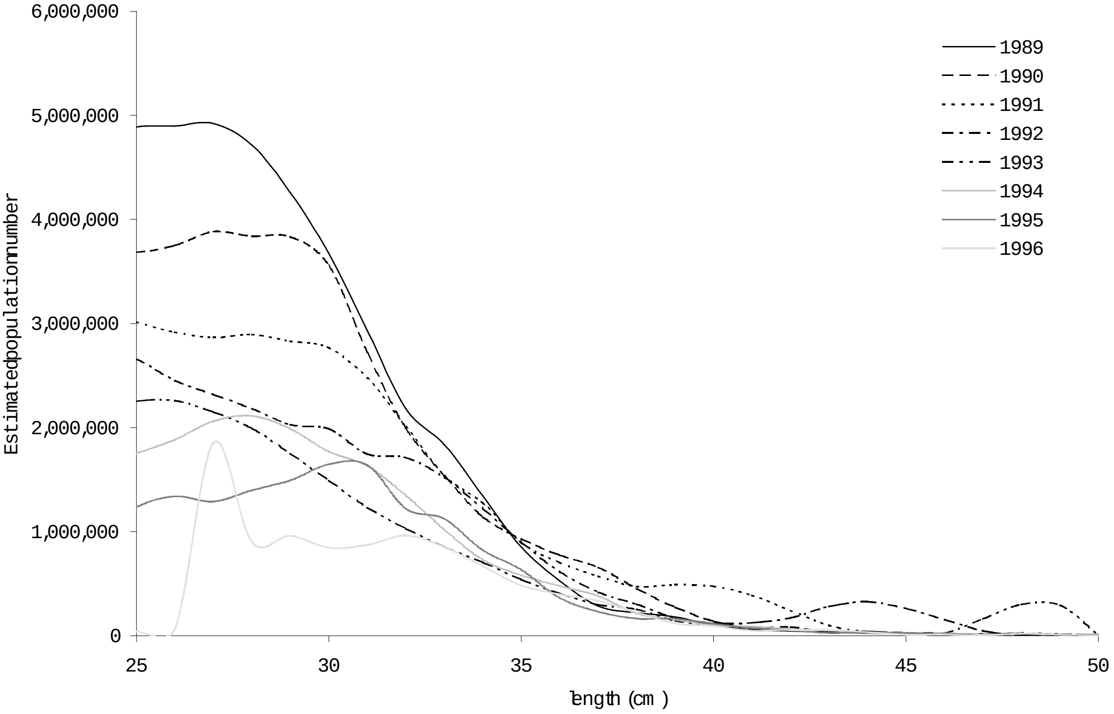

Figure A.5 Estimated population size per length class and year.

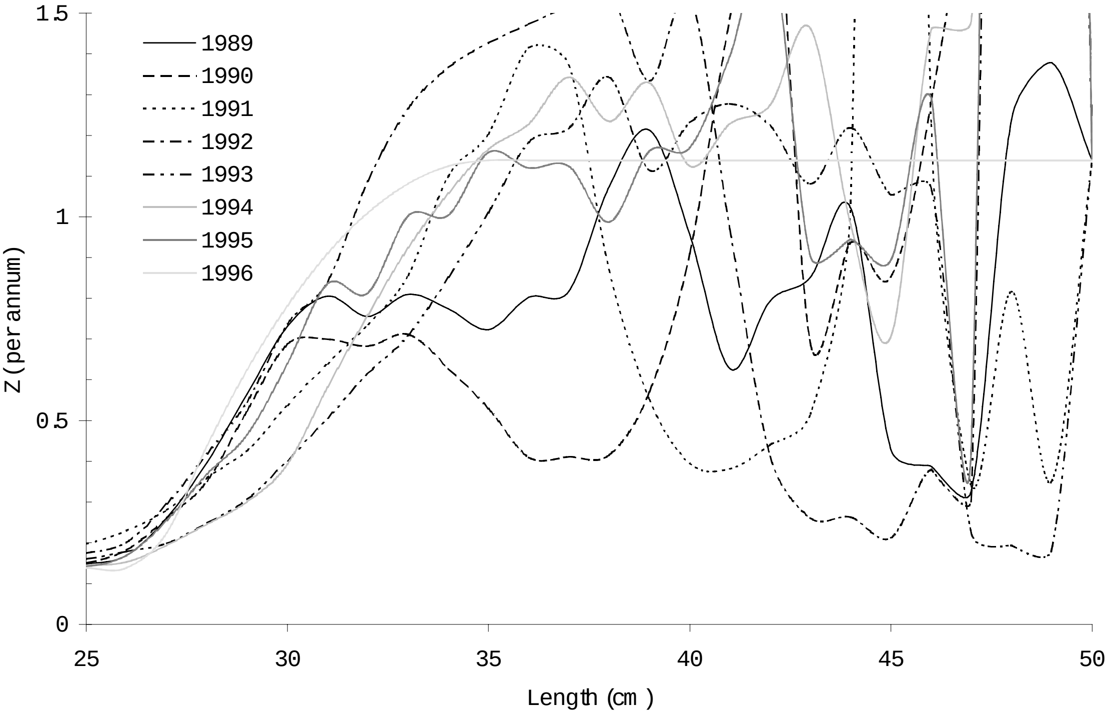

Figure A.6 Estimated rate of decline Z (natural and fishery mortalities, silvering and escapement) per length class and year.

Status of the European eel stock and fisheries

9

In: Aida K., Tsukamoto K. and Yamauchi K. (eds.), Eel Biology. Springer-Verlag, Tokyo, pp. 237-254 (2003)

The European eel (*Anguilla anguilla* (L.)) is the archetypical eel species, and was the monotypic species for the genus (genus described based on a single species). Much of the scientific knowledge about eels has been acquired first for the European eel, starting with Aristotle executing the earliest scientific experiment on fish. Aristotle describes that an isolated pool was scraped out, to find new eels, after the rain had replenished the pool. In his view, this proved spontaneous generation of eels from the mud. The reproductive biology of eels has later been resolved, first for the European eel (Schmidt 1922) and in many aspects of research on eels, the views initiated by Johannes Schmidt has grown to almost mythical proportions. Clearly, the European eel is in a prominent position in the eel world.

The European eel is found in an area spanning the whole of Europe, northern Africa and Mediterranean Asia. Typical eel fisheries are operated by a few fishermen, in waterbodies of typically ca. 8 km^2 (Dekker 2000a). Management so far is run on a local or regional scale only. In contrast to this fragmented distribution and management, the stock has shown a steep decline during the past decades in almost all of its distribution area. Additionally, the market for eels has recently become a world market: freshly caught eels as well as processed end-products are now transported all over the world. Consequently, the status of this resource is no longer the status of some small European fishery, but it is now of global significance. In comparison to other eel species, the fisheries for the European eel are much more abundant (Table 1). The European outdoor production is half the world outdoor production of all eel species. In contrast, the world aquaculture production is completely dominated by the East Asian eel production. The American and Australian/New Zealand fisheries and aquaculture are much smaller. Noting that the distribution area of the Japanese eel is much more confined than that of the European eel, it is likely that the European eel constitutes the largest wild eel stock of the world.

In this article, the status of and trends in the European eel stock and fisheries will be discussed. The geographical distribution, the type of fisheries, the yield and its application will be described and time trends shown. Stock and fisheries are in severe decline. Causes of these declines will be reviewed and consequences for management of the stock and fisheries discussed. Finally, the position of scientific research with respect to this decline will be discussed.

In this article, I will use the word *eel* (without qualification) to indicate the European eel, i.e. *A. anguilla* (L.). Where confusion might arise, I will use *European eel*, but the latter is not meant to restrict the discussion to Europe. In my view, the wording *European eel* is a misconception.

Table 1 The world-wide production (tonnes per year) of anguillid eels in fisheries and aquaculture, averaged over the 1990s. Data from FAO databases.

area	species	fishing yield	aquaculture production
Europe & North Africa	*A. anguilla*	15,262	18,101
America	*A. rostrata*	1480	100
Asia, east	*A. japonica*	1300	187,875
Asia, southeast	mixed	8385	1579
Asia, south	mixed	?	?
Africa, east	mixed	?	?
Australia & New Zealand	*A. dieffenbachii* & *A. australis*	2,241	100
total		>28,668	>207,755

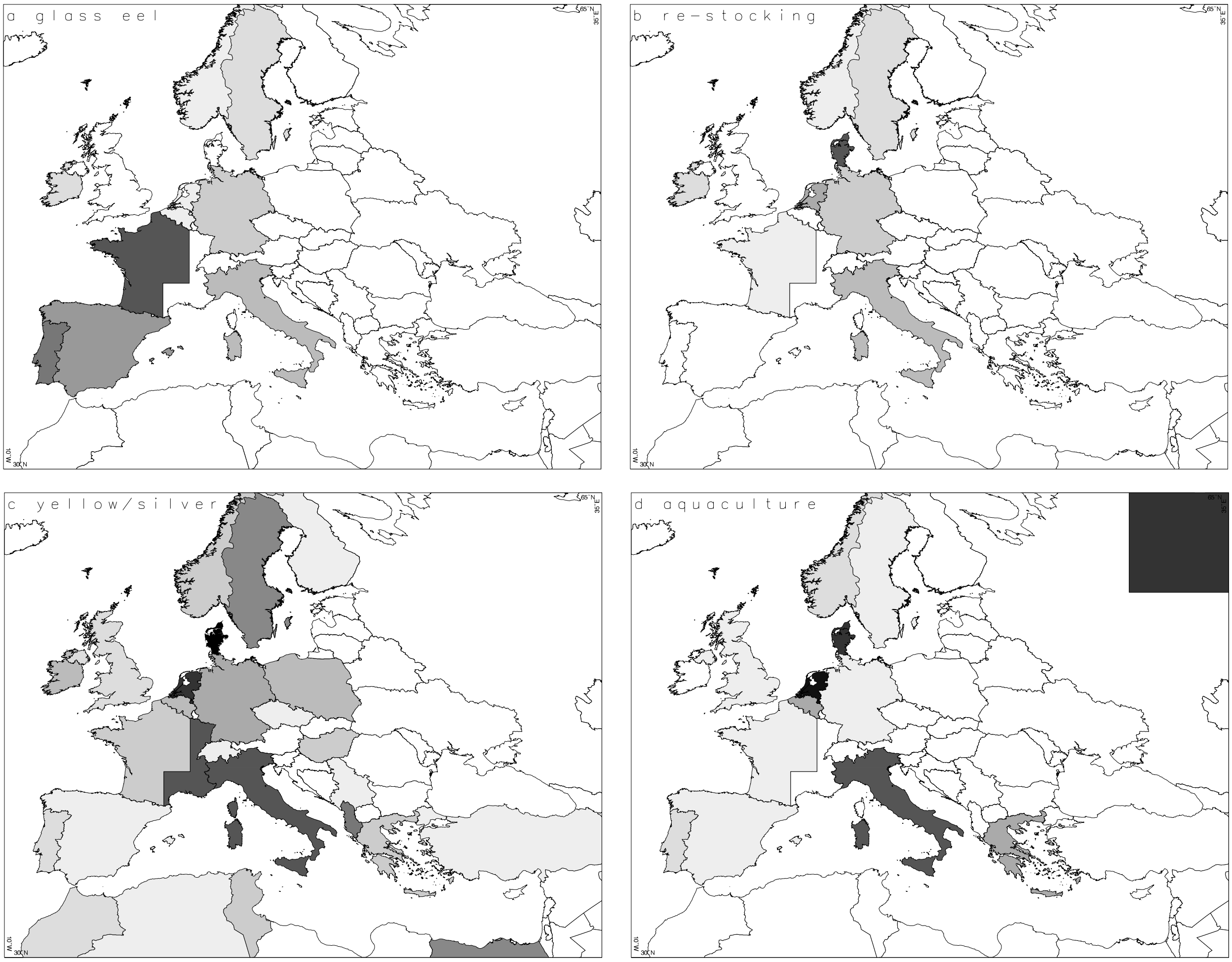

Figure 1 The spatial distribution in Europe of: a) Glass eel fisheries, b) Glass eel re-stocking, c) Yellow/silver eel fisheries and d) Aquaculture. The production of European eel in Asian aquaculture is shown in the top-right corner of panel d, in a square of equal surface area to Japan. Data from Moriarty (1997), adapted.

Legend for glass eel fisheries and re-stocking, g.km-2 land surface.

NA	0	>0	25	50	75	100	200	300	400	500	600	700	800	900	1000	
□	□	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	■
NA	0	>0	1	2	3	4	5	6	7	8	9	10	20	30	40	≥50

Legend for yellow and silver eel fisheries, aquaculture, kg.km-2 land surface.

Glasseel fishery

Following the metamorphosis at the end of the leptocephalus stage at sea, glasseels arrive in the estuaries along the Atlantic Coast in winter (southwestern areas) and spring (eastern Mediterranean, western and northwestern areas). In England (Severn area), France, Spain, Portugal, Italy and Morocco, this stage is exploited commercially (Figure 1a). In more northern areas, glasseel catches are used for re-stocking local waters (Figure 1b).

The glasseel fisheries are executed in the estuaries, in river mouths or in front of dams, exploiting the natural concentration of glasseels in time and space. Glasseels migrate from the ocean into estuaries, using a mechanism known as selective tidal transport (McCleave and Wippelhauser 1987). This transport mechanism uses the natural transports of water masses in estuaries, has a low energy requirement for glasseels and is therefore not very sensitive to low temperatures. To progress upstream, active migration into the river is required, swimming against the river flow. Active migration depends on a minimum water temperature of 10-12ºC (Gascuel 1986). Consequently, under low water temperature regimes, glasseels can easily arrive in the estuary, but can not progress upstream, resulting in large concentrations of glasseels in estuaries in early spring. Most often, this temperature-trap occurs at the upstream limit of the estuary, at the end of the tidal reach, at or near the tidal limit.

Glasseel fisheries are operated using handheld or ship based nets, moving the net, or keeping it fixed in a stream (Dekker 2002a). A wide range of dipnet types is applied, both on foot and using boats (Aubrun 1986), trawls (Aubrun 1987), stow nets (Weber 1986), fykenets (Ciccotti et al. 2000), etc.

The commercial fisheries for glasseels are found from the southwestern end of the distribution area up north to the Severn (England) in the Atlantic and along the Mediterranean coasts of Spain and in Italy (Figure 1a). Along the remaining part of the Atlantic coast, glasseels are caught for re-stocking in inland waters. The latter applies fixed engines, attracting glasseels by an outflow of fresh water into a trap (Rigaud et al. 1988), except for the fishery at the river IJzer (Belgium) using a hand-held dipnet or a small trawl and the fishery at Den Oever (the Netherlands) using lift nets. Several major glasseel fisheries occur in the estuaries of the larger rivers (Loire, Seine and Gironde in France; Nalon and Minho in Spain; Severn in England; etc.), but additionally, many smaller rivers are exploited too. Lara (1994), in describing the glasseel fisheries in Asturias, mentions 15 smaller rivers next to the larger River Nalon; Asturian yield statistics officially relate to the Nalon estuary, but probably include many of the smaller rivers, too. The process of joining smaller estuaries with larger ones is found in many places and might involve transport of fishing effort or of the catch; administrative amalgamation also occurs.

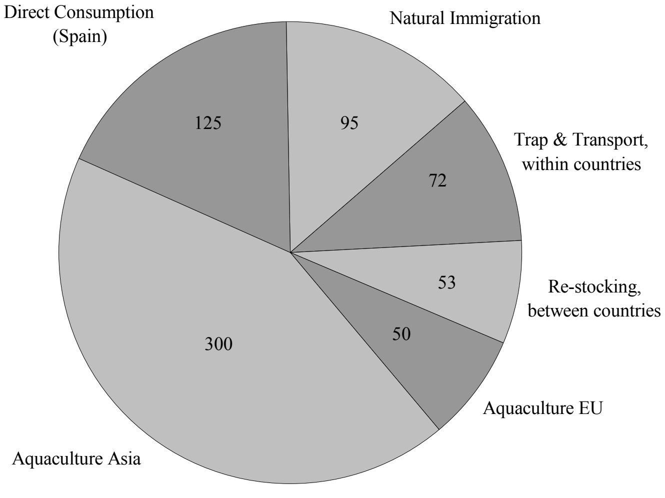

Figure 2 Disposition of glasseel landings. Numbers indicate quantities in tonnes per year. Data for the mid 1990s, from Moriarty and Dekker (1997) and (Dekker 2000b).

The total catch in the glasseel fisheries is estimated at 583 tonnes (Moriarty and Dekker 1997), but this is certainly an underestimate of the true catch in the early 1990s: the landings are often locally processed, illegal or not documented. For instance, Navaz y Sanz (1964) estimated a yield of 275 tonnes from the Basque region (Spain) in 1960, while Moriarty (1997) lists the Basque region for an unknown quantity. There is one earlier estimate of the total glasseel catch (ICES 1988) of 857 tonnes, but this was just a gross estimate not including many undocumented fisheries accounted for in Moriarty and Dekker (1997), especially all Spanish fisheries. However, the apparent decline in production (from ICES 1988 to Moriarty and Dekker 1997) does agree with local trends observed in commercial catches and scientific indices (see below).

There is no international database of glasseel yield and/or trade. Statistics on fishing yield record total catch per country, comprising both glasseel fisheries and fisheries for yellow and/or silver eels (ICES 1988). However, combining data from various sources (Moriarty and Dekker 1997; Dekker 2000b and personal communications), the following picture for the early 1990s emerges (Figure 2). The majority of the annual recruitment is used for aquaculture, mainly in Asia; 20% is consumed as glasseel (mainly in Spain); 20% is trapped and transported to re-stocking areas (within or between countries) and 15% freely immigrates to inland waters.

In many countries throughout Western Europe, the immigration of glasseel is monitored (Moriarty 1990; Dekker 2002a). This concerns statistics from commercial or non-commercial fisheries, from import-export data, from scientific samplings, from trapping stations for young eels, etc. Consequently, this does not only concern the commercial exploitation of the glasseel stage. However, almost all data series exhibit a common trend (Dekker 2000a); there is no systematic distinction between commercial and non-commercial series, nor between northern and southern Europe. Only the glasseel data series from the British Isles and the young yellow eel data from Scandinavia show a somewhat distinctive trend.

Data series range from a few years to over 60 years (France, the Netherlands, Germany and Sweden). Trends can be inferred from 1950 onwards (Figure 3). Directly after World War II, a low catch period lasted a few years. In the 1950s, 1960s and 1970s, the number of glasseels was high, reaching a peak in the late 1970s. Starting in 1980, a decline has been observed that continued to 1990, when a stable but very low level was reached, at about 10% of the former level. In 2001 however, historical low levels occurred of only about 1%; preliminary information suggests this extreme low level recurs in 2002.

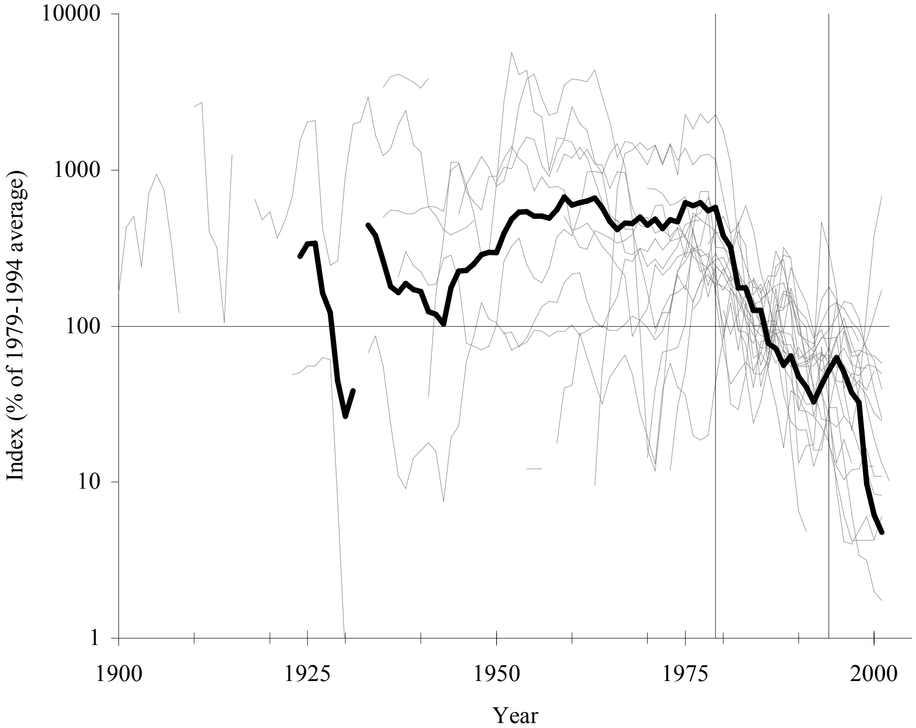

Figure 3 Recruitment of glasseels of the European eel to the continent during the 20th Century. Individual data series given in grey; common trend (average of the four longest data series) in black. Data from Dekker (2002a).

Glasseel re-stocking

Natural populations of eels in rivers are concentrated in the estuary and the lower stretches of the river (Barak and Mason 1992). Upstream, eels have been found at more than 1000 km from the sea, but the average migration of the population amounts to less than 20 km per year. Upstream transport of glasseels and young yellow eels has positively affected the yield, as have transports from the center of the distribution area to the margins. Apparently, upstream population densities in much of the distribution area are far below carrying capacity of the habitat.

In 1908, a German glasseel station was set up in Epney, at the Severn (United Kingdom), dispatching live glasseels to Hamburg, Germany. According to Anwand and Valentin (1981), re-stockings were in the order of 1.3 tonnes per year. After WW-II, the transport of glasseels from southerly countries to central and northern Europe increased considerably (Figure 4). Transports from England and France became a standard practice, with re-stockings taking place in northern and eastern parts of Europe (Figure 1b). In the 1980s, the quantity re-stocked diminished due to the high prices of glasseels on the international market. Recent estimates (early 1990s) amount to 33 tonnes (Moriarty and Dekker 1997). Detailed data series available for some countries (Figure 4) have shown a considerable drop in recent years (ICES 2002).

Re-stocking glasseels or young yellow eels in a particular water body does have a positive effect on the yield, some years later. This has been shown in experimental studies (Klein Breteler et al. 1990), in evaluation studies of large-scale re-stocking programmes in Poland (Moriarty et al. 1990) and is a likely explanation for the upsurge in yield from the whole population following the major re-stocking programmes in the 1950s (Dekker 2002b). Whether re-stocking actually contributes to the spawning stock is unknown. Tagging studies in the Baltic by Westin (1990), using silver eels grown from French glasseels, have provided some evidence that restocked foreign eels may differ from natural immigrants in their ability to find their way back to the breeding grounds and hence their contribution to the spawning stock. Moriarty and Dekker (1997), focusing primarily on the positive effect of re-stocking on fishing yields, have assumed a neutral or hopefully positive effect; ICES (2000), focusing on the protection of the spawning stock, advocated against re-stocking as a stock-rebuilding measure. See also the discussion below, on the causes of the decline of the stock.

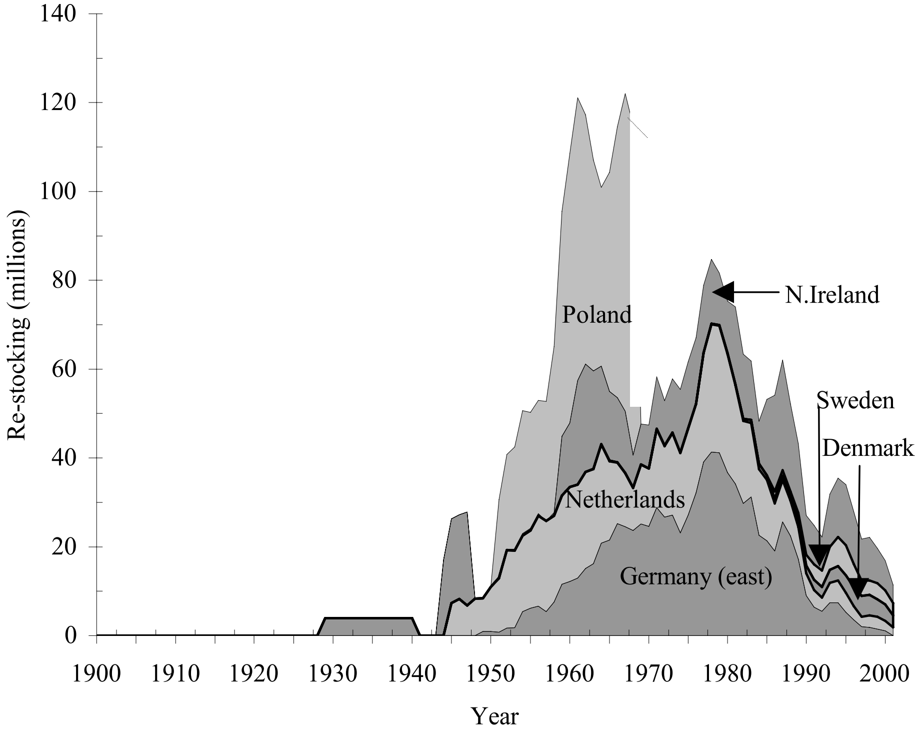

Figure 4 Re-stockings of glasseel during the 20th Century. Data from ICES (2002).

Yellow and silver eel fishery

Fisheries for yellow eels are found throughout the distribution area of the species (Figure 1c). In middle Europe, the yellow and silver eel life stages dominate the landings. In comparison, glasseel catches in southern areas are negligible in terms of weight, but outnumber the yellow eel landings by a factor of 30 (Dekker 2000b). Silver eel fisheries have been operated in historical times in most of Europe using fixed traps in small streams (Mitchel 1965), but directed fisheries for silver eels are nowadays confined to Scandinavia, using pound nets in coastal waters. It seems likely that the focus on silver eels is nowadays an adaptation to low densities of the local eel stock (25 eels per km^2 land surface) in most northern countries. During emigration, the production of the low-density yellow eel stock in inland waters concentrates in time (fall, often during short periods following the new moon) and space (river mouths, often using only small corridors through the river), allowing for a profitable silver eel exploitation of marginally exploitable yellow eel stocks in inland waters. At intermediate densities in middle Europe (400 eels per km^2 land surface) fisheries focus on the yellow eel stage, with a by-catch of silver eels. The density in the typical glasseel fishing area in southwestern Europe amounts approx. 1500 eels per km^2 land surface.

Fisheries for yellow and/or silver eels apply a wide range of gear. Gabriel (1999) provides an extensive overview. Gears include all kinds of nets, spears, pots, hooks, etc. in coastal areas, lagoons, rivers, lakes, streams and still-waters.

The processes contributing to the biological production of the yellow eel stock have been investigated by many authors (reviewed by Tesch 1999), but there are only a few comprehensive studies and hardly any on the interaction between exploitation and spawner production. Tesch (1999) reviews the literature on gross production estimates in order to extract norms for several water types. This holistic approach assumes that trophic characteristics of an ecosystem limit the production; the decline in recruitment since 1980 to 10% (or less) of former levels contradicts this assumption nowadays and disables the application of these norms completely. Analytical studies of growth are numerous, but methodological problems in determining age and growth as well as high local variation in parameters are the recurring theme. However, most studies corroborate a steady and low growth rate, coming to a hold only at very great length (Tesch 1999), usually far beyond the average silvering length (Vøllestad 1992). Therefore, it is reasonable to assume that yellow eels have a nearly constant growth rate over their entire life span. Estimates of natural mortality are much less

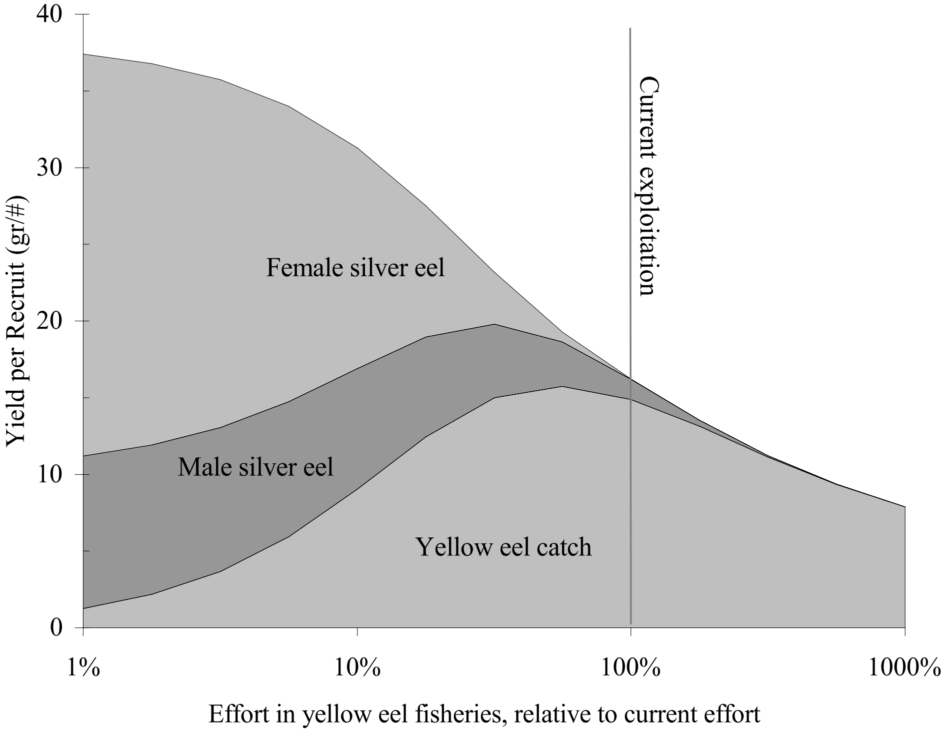

Figure 5 Yield per recruit for a mixed yellow and silver eels fishery as a function of fishing effort. Adapted from Dekker (2000c).

numerous and do not yield length-diversified estimates, but usually a constant natural mortality rate is assumed. The combination of a (nearly) constant growth rate with a constant natural mortality yields an analysis of the dynamics of a yellow eel stock, featuring a constant rate of increase of the stock biomass over the life span of yellow eels. Consequently, stock biomass reaches a maximum at the onset of the silver eel stage, which is in accordance with life history strategy theory for this semelparous species. Full pursuit of optimisation in yield would therefore result in maximisation of silver eel fisheries (Figure 5), and where silver eels escape easily, fishing for larger yellow eels will substitute.

Assessments of the impact of fisheries on local eel stocks are limited in number (Sparre 1979; Dekker 1996; review in Knights et al. 1996) and did not relate spawner escapement to fishing intensity. Simulation studies (Vøllestad and Jonsson 1988; De Leo and Gatto 1995) were tuned to field data, but these studies have focused on heavily regulated water bodies, where fishermen focus exclusively on silver eel fishing at weirs. Dekker (2000c) analysed the heavily documented fishery for yellow eels on Lake IJsselmeer, the Netherlands, using a length-structured cohort assessment model. The yield-per-recruit-curve derived (Figure 5) agrees with the preliminary calculation by Sparre (1979), but additionally yields an estimate of the relative spawner production by the inland stock. Current exploitation (instantaneous fishery mortality F=1.0) is estimated to reduce the production of female spawners to 0.14% of the unexploited state. Optimising the yellow eel fishery (F=0.5) corresponds to a reduction to 2.5%. A reduction to F=0.3 would optimise the combined yield of yellow and male silver eel, at a female spawner escapement of 12.5%, while a female spawner production of 30% would be achieved by a reduction to F=0.2. In the discussion below, a reduction of the female spawner production to 30% of the unexploited state will be seen as a threshold level for sustainable management. It should be noted here, that this threshold can only be achieved by a reduction of fishing effort below the levels maximising catch in the yellow eel exploitation, or in the combined yellow and male silver eel exploitation.

Statistics on the landings of eel are notoriously incomplete. ICES (1988) and Moriarty (1997) have shown 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 (Figure 6) based on all available data series (Dekker 2002b) shows, landings varied in the pre-WW-II period around 47,500 tonnes. Following a clear depression during WW-II, landings gradually increased to 47,000 tonnes in 1964, to decline to an all time low of 22,000 tonnes recently (unre-

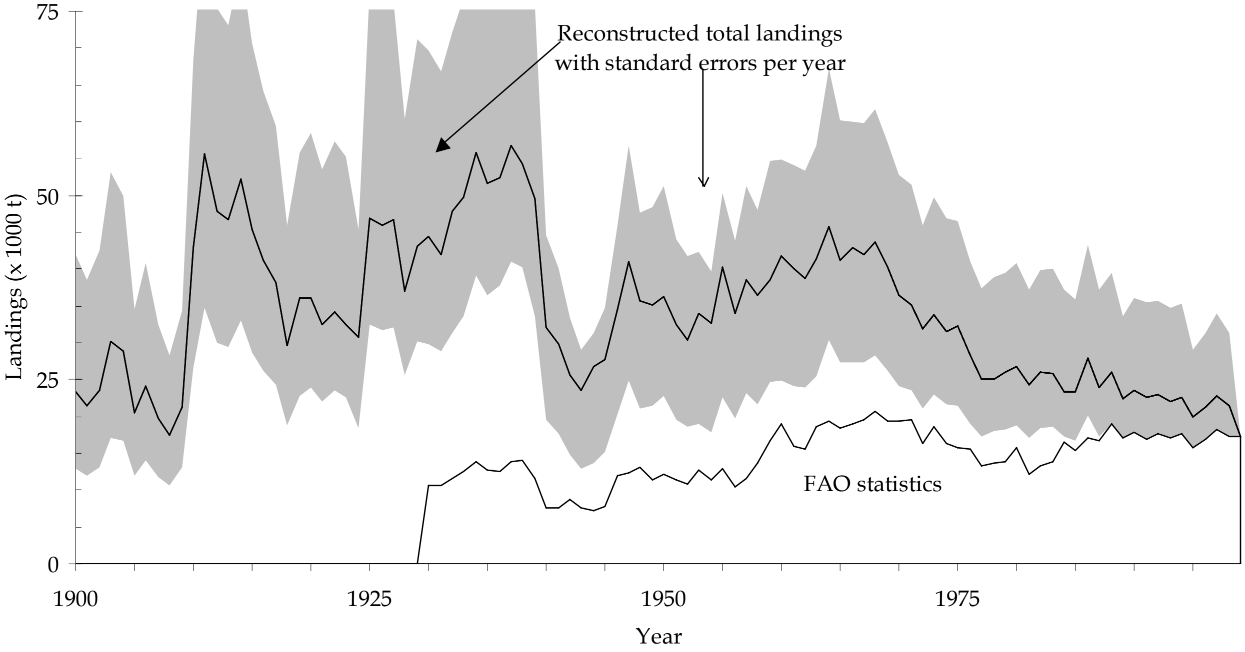

Figure 6 Landings of the European eel in the 20th Century. Data from Dekker (2003).

ported catches not included). The rise in production from 1945 to 1965 coincides with the yield expected from the re-stocking programmes, which started soon after WW-II in Northern and Eastern European countries. Moreover, the increase in yield was largely restricted to the northern countries (Dekker 2002b). This suggests, the peak in production in the mid-1960s might very well be the direct consequence of the re-stocking; that is: without the re-stocking, a consistent decline might have been observed since WW-II. Additionally, the re-stocking programmes have released a rising amount of glasseels, at least until 1980; the decline in production since the mid-1960s took place despite an increasing amount of glasseels being re-stocked, in years of stable or increasing natural recruitment. Clearly, production processes in inland waters must have changed (Dekker 2002b).

Aquaculture of the European eel

Aquaculture of the European eel (Figure 7) started much later than the culture of the Japanese eel. In 1970, the European production was estimated at 3,400 tonnes, while the Japanese culture amounted 17,000 tonnes. In the early 1970s, European eels were cultured in Japan for a small number of years, with little result (Egusa 1979). Since the mid-1980s Asian culture of European eel has risen from 3000 tonnes to 10,000 tonnes nowadays. The European culture of the European eel is now estimated just over 10,000 tonnes (Kamstra 1999).

The Italian aquaculture has a tradition dating back to the Romans (Higginbotham 1997). In past centuries, culture has been concentrated in the valli in northern Italy. In this culture system, the natural productivity of lagoons is augmented by manipulation of water flows, favouring the natural immigration of glasseel and increasing the natural productivity of the ecosystem. Originally, no artificial re-stocking of glasseels was applied, but in recent decades, glasseels have been imported from the Italian West Coast. In addition to this traditional aquaculture, modern intensive systems have developed, in Italy and elsewhere.

The intensive aquaculture is exclusively based upon highly automated indoor facilities equipped with water re-circulation systems. In the (late) 1980s, this type of aquaculture system was introduced in a range of countries all over Europe, but during the 1990s, only the aquaculture in Denmark and the Netherlands has grown. Currently, these countries dominate the market, while the Italian production is somewhat in decline.

The production of the European aquaculture is mostly marketed in Europe. Re-stocking of cultured eels in out-

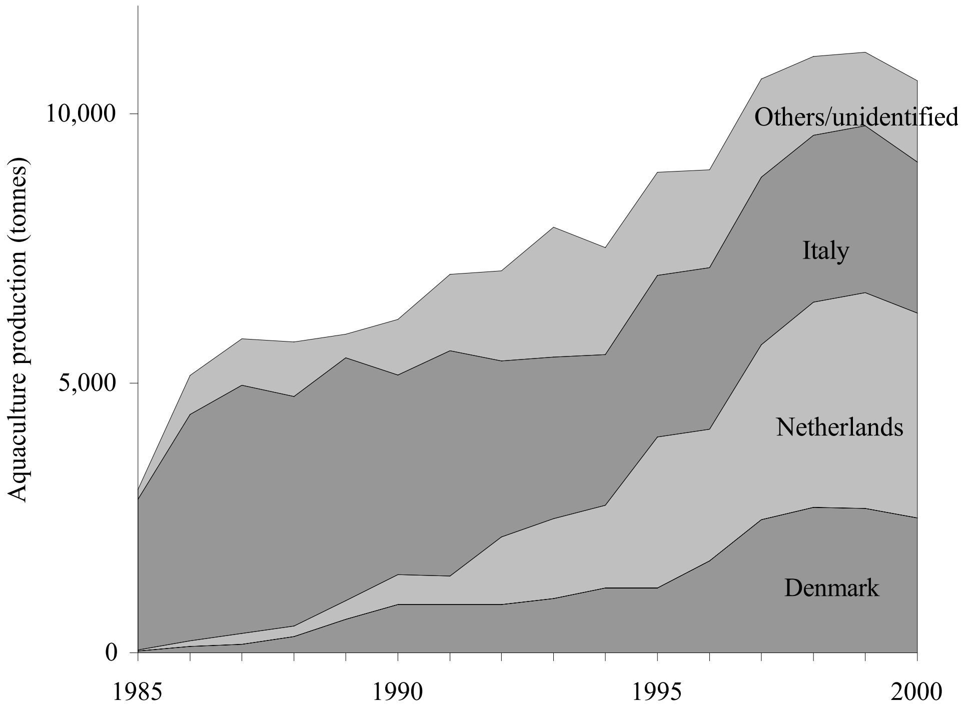

Figure 7 Production of eel aquaculture in Europe. Data from ICES (2002).

door waters is rare and presumably does not contribute to the spawning stock at all.

Causes of the decline of the stock

The stock of the European eel is obviously in decline. Recruitment has declined since 1980, to 10% of former levels and latest observations suggest a much further decline. Landings of the yellow/silver eel fisheries have been in decline for several decades, at least since the mid-1960s, but the stock might have already been in decline since WW-II.

The decline in recruitment was first noted in 1985, but it was only in 1993 (EIFAC 1993), that the effect upon the stock and fisheries was first considered. Several hypotheses for the declining recruitment have been suggested (Castonguay et al. 1994a; Moriarty and Dekker 1997), including pollution, habitat loss due to barrages and dams, climatic changes in the ocean, overexploitation and man-made transfers of parasites and diseases. Comparing time trends in the decline of the eel stock and its hypothesised causes, Castonguay et al. (1994a) concluded that no specific hypothesis can be singled out, but that toxicity and habitat modifications mismatch the decline by several decades.

Knights (1996) has reviewed the state of affairs in contamination of eels by organochlorine pesticides and PCBs. Although contamination levels are often quite high, he concludes that organochlorine contamination has not been a major cause of recent declines in eel recruitment. Further studies on the impacts of organochlorine on the reproductive capacity of eels is required.

Moriarty and Dekker (1997) and ICES (2002) have considered the effect of dams and barrages on the amount of habitat available to eels. The former presented educated guesses of the amount of habitat lost (25% of river habitat lost on average, but over 90% in the Iberian Peninsula, where glasseel densities are highest), while the latter presented a time series of the construction of major dams in Europe. Just after WW-II, the number of new dams built rose about four-fold, coinciding with the decline in the eel stock.

The effect of long term climatic changes on the oceanic phases of the life cycle can not be studied analytically, due to the scarcity of direct observations, both on climate and on eels. Castonguay et al. (1994b) interpreted the parallel development in recruitment data for the American and European eel (data from St. Lawrence river respectively Den Oever, the Netherlands) as evidence for a common cause and speculated that climate changes in the Atlantic Ocean might affect both species. Dekker (1998) analysed Dutch time series of glasseel abundance and biometrics from 1960 to present. The decline in recruitment in the 1980s coincided with a reduction in length of the incoming recruits. In his interpretation, this pointed to some unknown process in the oceanic phase, having an effect on length and number of the larvae. Desaunay and Guerault (1997), analysing some years of French data and adding information over a longer time span from the literature, confirmed the relationship between abundance and biometrics, and proposed a mechanism based on the link between plankton production and larval growth and survival.

Scientists have long studied the eel and its exploitation, but until recently, focus was exclusively on development of the fisheries (gear development, production enhancing factors, etc.). Consequently, the information to quantify the impact of exploitation on the stock is hardly available. Dekker (2000b) compiled a snapshot overview of the impact in the early 1990s, using the available information, summarized in Figure 8. Clearly, exploitation had a considerable impact on the stock in the 1990s. In this article, time series of the major constituents of the stock dynamics have been presented. The state of stock and fisheries has changed considerably over the past decades and a snapshot for the 1990s might have only limited relevance for the decades of decline of the stock. However, theoretical calculations on the impact of exploitation indicate that yield-optimised fisheries reduce the production of spawners to 2.5-12.5% relative to the unexploited state (see above). Typical eel fisheries are small-scaled (Dekker 2000a) and individual fishermen often have the liberty to adjust their fishery to their liking and yield-optimisation is a common situation, resulting in a reduction of the spawner production to 2.5-12.5% (relative to the unexploited state). A reduction of the spawning stock biomass below 30% is generally assumed to introduce a serious risk of stock collapse (Clark 1991). Consequently, the impact of current exploitation is likely to be excessive.

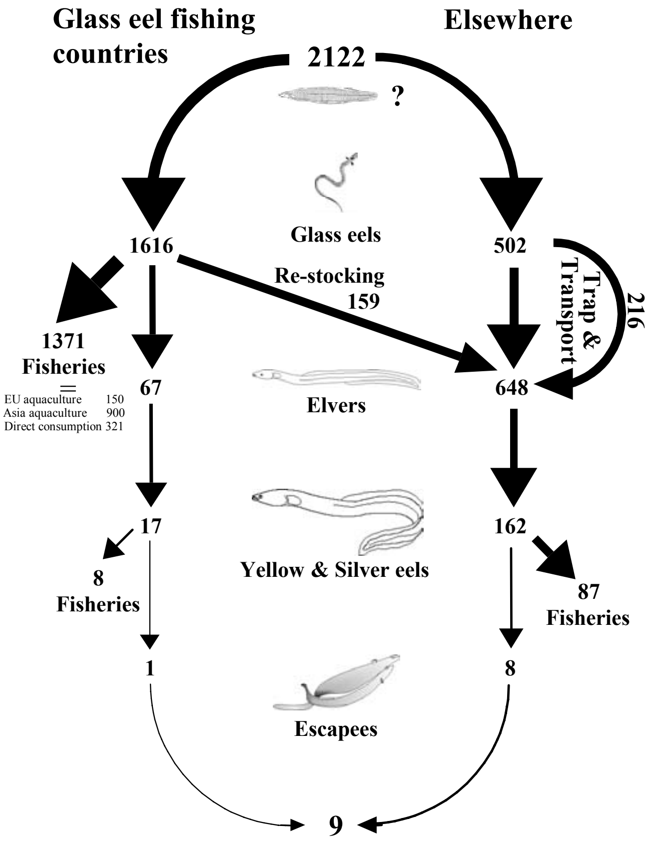

Figure 8 Dynamics of the European eel stock (numbers in millions), in the early 1990s. Estimates based on a cross-section in time, assuming a steady state. Countries with commercial glasseel exploitation to the left, other countries to the right. Data from Dekker (2000b).

Additionally, the impact of exploitation and the loss of habitat discussed above, might have a complicating interaction. Moriarty and Dekker (1997) assume natural recruitment of glasseels to inland waters in southwestern Europe results in densities far beyond the carrying capacity of the ecosystem. Consequently, harvesting the surplus recruitment will not affect the inland production. In this setting, loss of habitat leads to reduced productivity and enables harvesting of an extra surplus recruitment. Deciding on measures to limit exploitation or to restore habitat loss involves a political judgement, beyond the scope of this article. Whatever the prime cause, habitat loss and exploitation, individually or jointly, will negatively affect the population in southwestern Europe.

As a result of world-wide transports of live eels, there has been a great increase in the number of non-native parasites and diseases in the past decades (Køie 1991). It has often been suggested, this might have had negative consequences for the reproductive output of the eel stock. Especially the effect of *Anguillicola crassus*, a parasite of the swimbladder, on the ability of silver eel to perform the oceanic spawning migration has been mentioned. Although direct effects of *Anguillicola* in healthy natural stocks are limited, synergistic effects with bacterial infections or other stress factors might be considerable (Køie 1991).

Summarising the above, it is concluded that several hypotheses for the decline of the stock have been proposed, each of which does have supporting evidence. None of the individual hypotheses explains the observed decline completely. Therefore, a synergetic effect of several of the proposed causative effects is most likely. However, looking more closely at the timing of the decline in recruitment and fisheries (Figure 9), the potential causes of the decline might be sequenced. Factors pri-

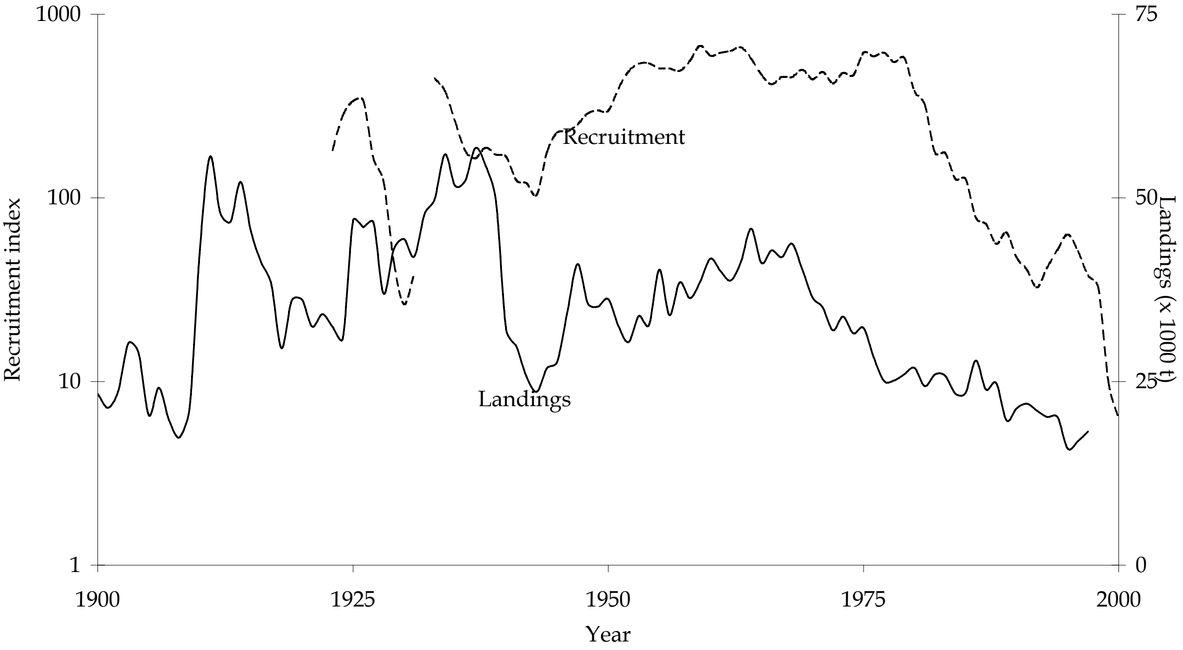

Figure 9 Recruitment to and landings from the European eel stock during the 20th Century.

marily affecting the productivity of inland waters (habitat loss and overexploitation) might have affected the stock negatively over a long time span, while relative minor changes in the factors operating in the oceanic phase (pollution, climate change, parasites) then accomplished a total collapse of the stock, as currently observed.

Consequences of the decline of the stock

The eel stock is outside safe biological limits and the current fishery is not sustainable (ICES 2001). Anthropogenic factors (exploitation, habitat loss, contamination and transfer of diseases) have had negative effects on the stock. All information indicates that the stock is at a historical minimum. Consequently, the compilation of a stock rebuilding plan has urgently been advised (ICES 2001). Although the content of this plan is beyond the scope of this article, some characteristics of the problem will be discussed here.

In recent years, substantial effort has been invested in the formulation of a Precautionary Approach to exploitation of fisheries resources (United Nations 1983; FAO 1995) and the derivation of corresponding scientific and management tools. Implicit in this development is the assumption that there is a relationship between spawning stock and recruitment. The Precautionary Approach dictates that, unless proven otherwise, such a relationship between stock and recruitment should be assumed to exist, also for eel. Existing information on the trend in eel stock and recruitment (Figures 9 and 10) does support this assumption.

The decline in recruitment (Figure 3) was first noted in 1985, but the much longer decline in yield (Figure 6) has gone almost unnoticed (Dekker 2002b). Although the causes of the observed decline are not known, several anthropogenic impacts (exploitation, habitat loss, pollution) have been shown to exceed reasonable limits in many places. The Precautionary Approach implies a need for management actions to reduce all these impacts, even though no full scientific proof is available.

Initial management recommendations have focused on mitigating measures; notably re-stocking of southern glasseels in northern waters (Moriarty and Dekker 1997). Re-stockings peaked in the mid-1970s (Figure 4), during years of stable or rising natural recruitment (Figure 3), while landings were already in severe decline (Figure 6). Therefore, it is rather unlikely that the proposed mitigating measures will be effective. Reductions in exploitation and pollution as well as restoration of (access to) lost habitats will be unavoidable.

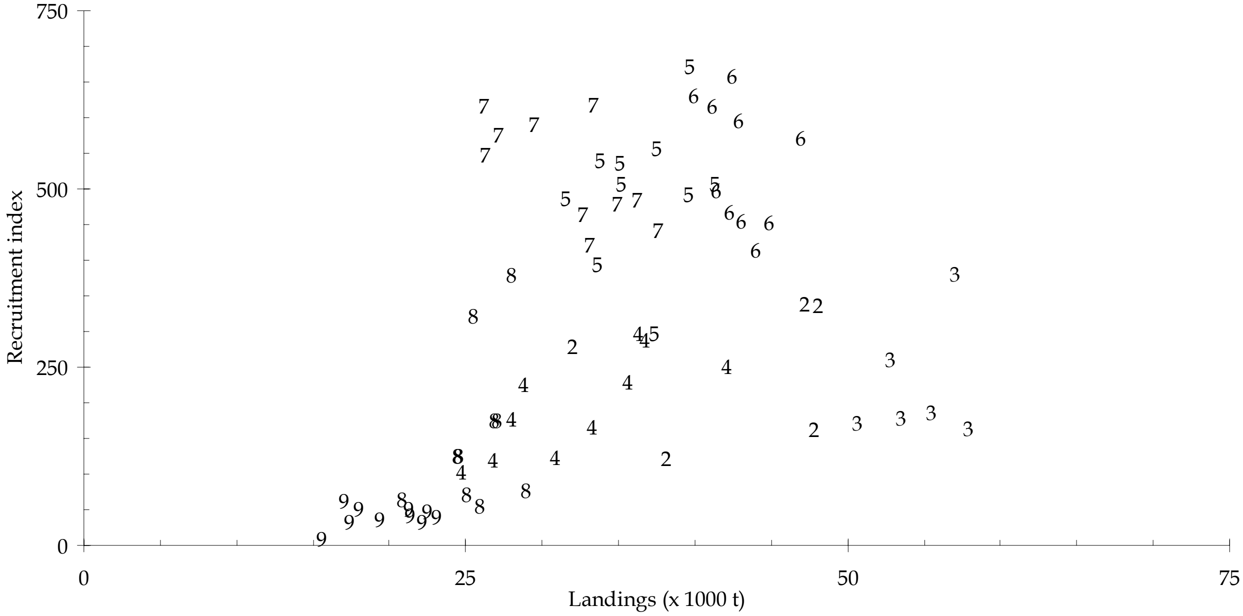

Figure 10 Speculative relationship between recruitment and spawning stock size, the latter being indexed by the landings. Numbers indicate the decade of the 20th Century.

The eel fishery is typically small-scaled and scattered over rural areas. Management of the habitat and fisheries is generally organised at low political levels (nations, regions or local management). Fishermen generally aim at economic optimisation of their enterprise, while no single government has ever enacted any measures aiming at sustainability. In contrast, declining trends in yield and recruitment have been observed (almost) all over the distribution area. Sustainability of the exploitation pattern necessitates reductions in fishing effort below economically optimal levels. This can only be accomplished when local exploitation aims at global objectives and global objectives are effectively enforced by local managers in rural areas. The contrast between the rural scale of stock and fisheries and the global need to protect and sustain the stock constitutes an unprecedented, major challenge to the fishing industry, aquaculture, world-wide trade and management.

Research, stock decline and sustainable management

Current international consideration of the European eel began at the 5th Session of the European Inland Fisheries Commission (EIFAC) held in Rome in 1968. In the 1970s the primary focus was on the assessment of the state of exploitation and of the effect of elver stocking. However, due to the total absence of data from many areas, progress was slow. Neither full coverage of each reporting country, nor full coverage of all countries in the distribution area was achieved. Official statistics comprise not more than half the known catches in reporting countries (ICES 1988; Moriarty 1997); the Mediterranean eel fisheries yield nearly half the stock-wide yield, but have started reporting only quite recently (FAO databases) and have not appropriately been included in international analyses (Moriarty and Dekker 1997). Major geographical differentiation in the stock (Tesch 1999) and fisheries (Gabriel 1999) have not been acknowledged.

The decline in recruitment since 1980 was first noted in 1985, but it was only in 1993 (EIFAC 1993), that the effect upon the stock and fisheries was first considered. The much longer decline in yield (Dekker 2002b) has gone almost unnoticed. Major research efforts have focused on the biology of the species and on development of fisheries and aquaculture. Consequently, the decline of the stock over the decades has only recently been considered.

It might be questioned why the slow but long decline of the stock has gone unnoticed for such a long time. The European eel is a panmictic, long-lived (Svärdson 1949) semelparous species, with a large distribution area. Stock

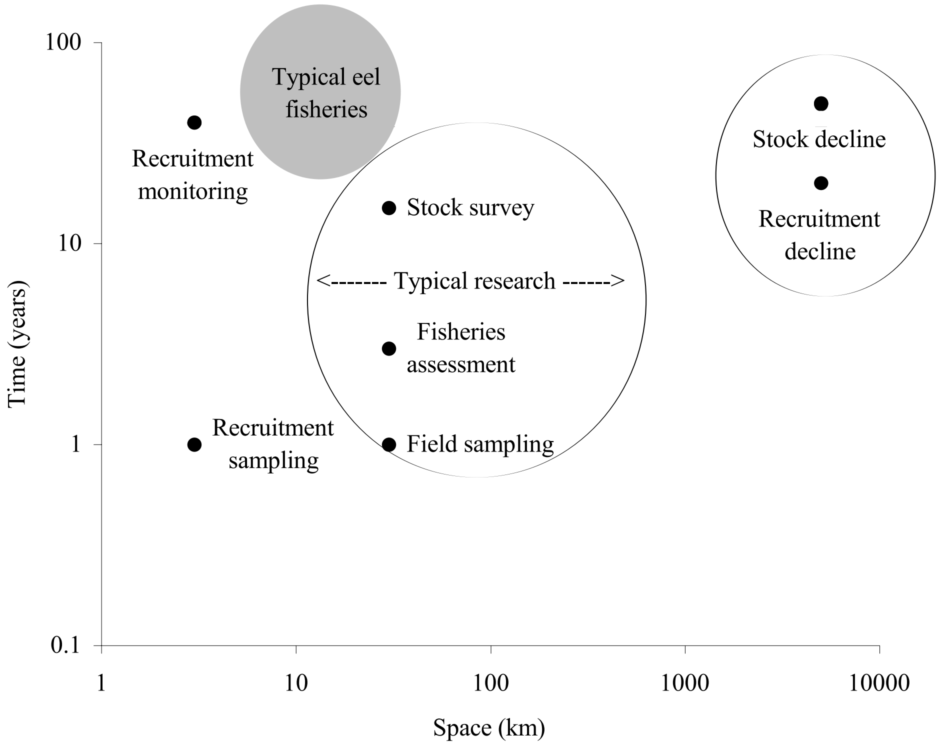

Figure 11 The position of eel monitoring and research in space and time in relation to the observed decline of the stock.

densities vary latitudinally, from over 1500 in southwestern Europe to less than 25 eels per km^2 (land surface) in northern and eastern areas. Growth rate is temperature related and shows a latitudinal cline (Vøllestad 1992). Sex determination is controversial, but is probably related to stock density. On average, females grow about twice as large as males. Almost each of these characteristics might explain the long duration of the decline of the stock under adverse conditions; in combination, the species is foredoomed to a very slow and hardly noticeable decline. Large and old mature females from the periphery of the distribution area might long have sustained an adequate quantity of spawners, masking the collapse of the spawner production in the center. Gradual deterioration of the status of the stock might partially have been compensated for by a change in sex ratio. Due to the long life-span, negative impacts on the stock might have lasted decades, before any secondary effects became perceptible. The ultimate causes of the observed decline might be ubiquitous and operate only gradually. Recovery of the stock, therefore, can probably only be achieved in the long run, if research and management address the problem at an appropriate temporal and spatial scale.

Current research (and management) of the European eel stock and fisheries usually extends over periods of one to ten years, covering individual sampling locations or single river catchments (Figure 11). The decline observed in the stock and fisheries has occurred in the whole distribution area (>3000 km) and has lasted for several decades or more. Extending these scales to larger areas (international co-operation) and longer time-scales (historical analyses) will be a major challenge for the scientific community studying the eel stock and fisheries.

Conclusion

The European eel stock is found in the whole of Europe, Northern Africa and Mediterranean Asia. It is evident from the presented time series that a major decline of the stock and fisheries has occurred since the mid of the 20th Century, first in the yield of the fisheries on yellow and/or silver eels, lateron also in recruitment from the ocean and the yield of the fisheries on glasseels. Several hypotheses on the causes of the decline have been proposed. Although supporting evidence is presented for several of the hypotheses, no final explanation can be identified; a synergistic effect of several causes is more likely. A stock-wide management plan for the scattered stock and fisheries are urgently required. There is a strong mismatch between (past and ongoing) research on one side and the biology of the eel and the decline of the stock on the other, both in time-frame and geographical coverage. Compilation and implementation of a stock recovery plan and extension of research to appropriate temporal and spatial scales will be a major challenge for eel management and research

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A conceptual management framework for the restoration of the declining European eel stock

10

Proceedings of the International Eel Symposium, Quebec, Canada, August 2003 (submitted)

The stock of the European eel (*Anguilla anguilla*) is in a critical state. A prolonged downward trend in landings since 1960 suggests a steady decline of the continental stock, while incoming recruitment fell to record low levels in the 1980s over almost all of Europe. Although the effect of oceanic factors cannot be ruled out, continental processes depleting the spawning stock are the more likely cause. An innovative management scheme preserving adequate spawner production is urgently required. Setting objectives and post-evaluating effects typically constitute the roles for the global level; implementation via specific management measures and monitoring of the stock must be performed locally, coordinated over all management levels. Eels are long-lived animals, and research and management are slow processes. Analysis of the population dynamics indicates the stock has been in slow transition in the past two decades, from a stable and high abundance towards a secondary stable state, near extinction. It has taken considerable time to recognise the decline; it will take further time to develop and implement an appropriate management framework. The longer we wait, the lower the odds for reversing the downward trends. One must act. Now!

The stock of the European eel (*Anguilla anguilla* (L.)) has shown a marked decline over the last decades. Recruitment to (Moriarty 1986; Dekker 2000a) and yield from (Dekker 2003d) the continental stock have been well below average for two or more decades. Several authors have speculated on possible causes of the decline (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002a), but none of the hypotheses so far explains the observed decline adequately (Dekker 2003b). A stock protection and recovery plan is urgently needed (ICES 1999), but no substantial progress in managing the stock has been accomplished (ICES 2004) while the decline continued (ibid.). Scientific advice to restrict fisheries to prevailing levels (ICES 1997a), to re-distribute recruitment of glasseel towards the outskirts of the distribution area (Moriarty and Dekker 1997), or to reduce all human impacts on the stock to as close to zero as possible for some time to come (ICES 2002b), has not yet been followed, despite the intention to secure sustainable development of eel fisheries.

In the past decades, substantial effort has been invested in the formulation of a precautionary approach to exploitation of fish resources (United Nations 1983; FAO 1995) and the derivation of quantitative reference points for fisheries management (Caddy and Mahon 1995; ICES 1997b). This framework is now routinely applied for scientific advice on the exploitation of typical (marine) fish stocks in Europe (ICES 1997b), and has been the basis for the advice on eel (ICES 1999, 2002b). However, despite the alarming state of the eel stock, few actual management measures have been taken (ICES 2004).

In this paper, existing evidence on the decline of the stock will be summarised, potential causes reviewed, and a conceptual framework for management of the stock presented. In this article, I will use the word *eel* (without qualification) to indicate the European eel, although the presented ideas will probably apply to management of other (temperate) eel species too.

Managing the stock: an impossible bargain?

Management strategies readily applied to many other fish stocks might not work as well for eel (Feunteun 2002). Complications arise from the eel's biology, fisheries and management.

The eel stock in Europe, northern Africa and Mediterranean Asia (Dekker 2003a) constitutes an (almost) panmictic population (Wirth and Bernatchez 2001; Avise 2003). Reproduction has not been observed in the wild, but all evidence supports the view of a semelparous reproduction, in or near the Sargasso Sea, at 3000-7000 km from the continent. The fisheries, in contrast, are scattered all over

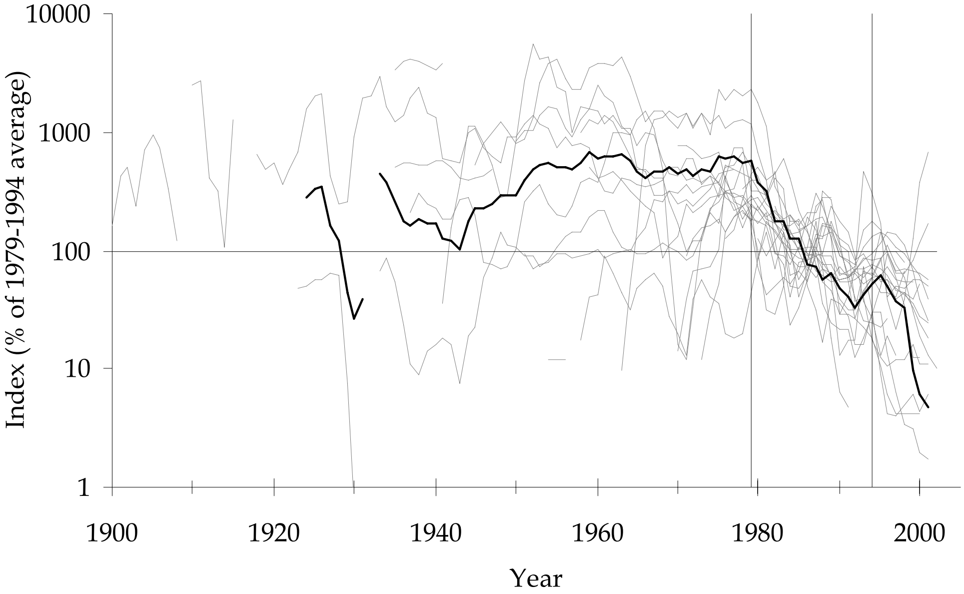

Figure 1 Recruitment of glasseel of the European eel to the continent during the 20th century. Individual data series given in grey; common trend (geometric mean of the four longest data series) in black. Data from Dekker (2002).

the continental distribution area, in an estimated number of >10,000 waters (Dekker 2000a). Managing the stock engages fisheries, scattered over more than 30 countries, of which 10 are regularly involved in international research and management (unpublished data from the author). The commercial fisheries are rarely and only weakly organised, whereas national or regional authorities generally have minimised their involvement. Legislation of fisheries often considers typical marine and fresh water environments, with the possible addition of a separate heading for salmonids, none of which fits the peculiarities of the eel.

The continental life stage lasts for 5 to 15 years. During this phase, the stock is exploited in the migratory life stages (glasseel and silver eel), and the resident life stage (yellow eel). Concentrated in space during migration, or vulnerable to exploitation over many years, the eel is a preferred target for exploitation, yielding more than double the price (FAO 2000) of other fish (except sturgeons, at double the price of eel). The long migration routes require accessible routes from the sea towards inland waters. Additionally, the occurrence in up to the smallest water systems maximises the vulnerability to anthropogenic impacts, such as pollution, habitat loss and poaching. Highest stock densities are found in lowland river stretches, around which human populations reach peak densities. Managing the eel comes down to managing anthropogenic impacts that often affect the eel only indirectly.

Typical fish stock management relies heavily upon scientific information on the status of the stock, and the impact of exploitation, as well as upon opportunities to steer the exploitation pressure. For the eel, neither the knowledge nor the management opportunities satisfy the current needs adequately, while conflicting anthropogenic interests complicate the matter. Rather then giving in to this seemingly impossible bargain, I will analyse the problem below and assemble a suggestion for a solution from existing nuts and bolts of fish stock management.

Status of the stock

The overall status of the eel stock is hardly known (Moriarty and Dekker 1997). Neither the absolute size, nor the overall impact of exploitation and other anthropogenic factors have been assessed with any accuracy (Dekker 2000b). Local monitoring series have been run because of local application, but posterior meta-analyses have shown common downward trends in large parts of the distribution area, in recruitment (Dekker 2000a) and fishing yield (Dekker 2003d).

Recruitment from the ocean

In southwestern parts of the distribution area, commercial fisheries are found in estuaries and river mouths, targeting glasseel freshly recruiting from the sea (Moriarty and Dekker 1997; Dekker 2003a,d). For a number of river systems, landing statistics of the fisheries have been record-

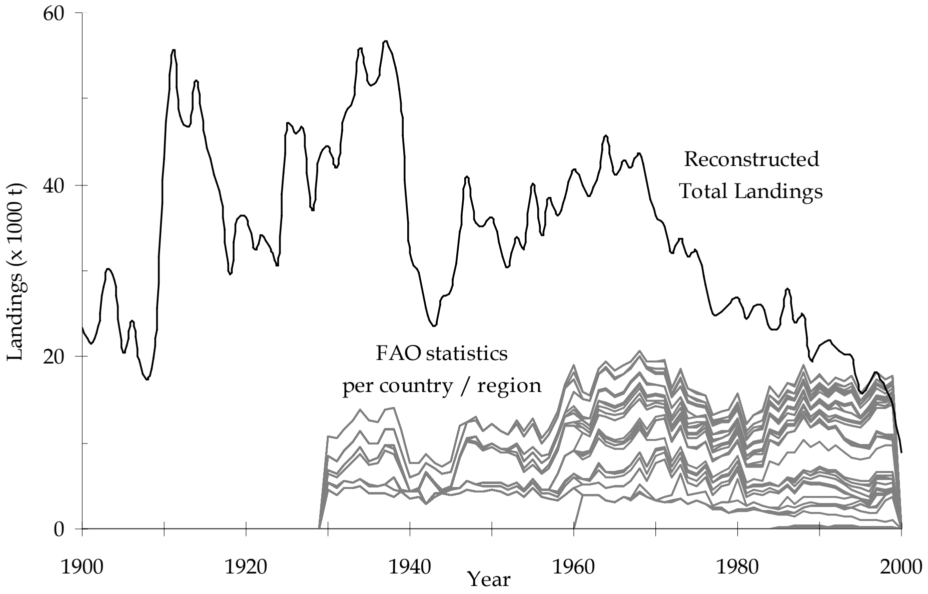

Figure 2 Landings from the European eel stock during the 20th century. Statistics on eel landings have been recorded by a total of 37 countries. Some of these data series run for more than a century, while others show a few recent records only; administrative regions have changed over the years and resulted sometimes in double counting; (indoor) aquaculture production is ultimately derived from the natural stock, and is sometimes erroneously included in (outdoor) fishing yield. Consequently, the raw FAO statistics (FAO 2000) falsely suggests a non-decreasing trend, while reconstruction of the total landings indicates a continuous decline since the mid 1960s (Dekker 2003d).

ed, for periods up to several decades. Although variation in fishing effort might have occurred, the trend in landings will also reflect those of the incoming recruitment. North of 50°N, glasseel fisheries are carried out on a non-commercial basis (major exception on the British West coast, commercial fishery in the Bristol Channel, at 51°36N) for re-stocking inland waters, while north of 55°N, glasseel have transformed into yellow eel before entering fresh waters, and are trapped on their way into a river for re-stocking. Statistics have been recorded for a period of decades up to a century. Finally, scientific glasseel monitoring has been operated in the Netherlands since 1938.

Each of these data series has been recorded because of its relevance for local management. In the mid 1980s it was realised that several of the data series showed a common, downward evolution (Figure 1; EIFAC 1985; Moriarty 1986) and subsequent analysis of data series from all over Europe (Dekker 2000a) indicated high correlations between all stations, with minor exceptions in the Baltic (where the decline might have started earlier) and the British Isles (where the decline was less severe). Apparently, local monitoring programmes were tracking a global development throughout the distribution area.

Yield from continental waters

Fisheries for yellow and/or silver eel are found throughout the distribution area of the species (Dekker 2003a,c). Statistics on total landings are notoriously incomplete. ICES (1988) and Moriarty (1997) have shown that official statistics often comprise only about half the true catches. However, reported data series display a common trend in most of the 20th century (Figure 2; Dekker 2003d), showing a peak in the 1960s, corresponding to a total yield of 47,000 t, to decline slowly to a historic low of less than 15,000 t in 2000.

This trend in yield parallels a seeming trend in the stock, detected in various sources of circumstantial (Moriarty and Dekker 1997) and direct (Dekker 2003b) evidence. Thus, the trend in yield is apparently due to a change in stock abundance, rather than to variation in fishing pressure. For Lake IJsselmeer (the Netherlands), research surveys have directly evidenced a declining trend in the stock since 1960 (Dekker 2003b).

Causes of the decline

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

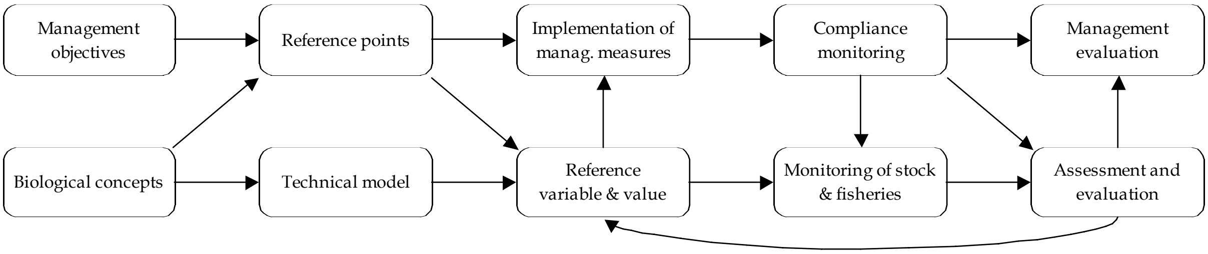

Figure 3 A framework of conceptual and technical steps in the implementation of a management scheme for fisheries (after Caddy and Mahon, 1995; strongly modified). Arrows indicate the flow of concepts, information and data.

considerable less attention than that in recruitment. Several hypotheses for the decline in recruitment have been suggested (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002a), but without proper evidence, no definite causes can be identified, and a parallel effect of several of the proposed causative factors is most plausible (Dekker 2003c).

The suggested hypotheses categorise into two distinct groups. On one side, one has suggested some process in the ocean might have reduced larval survival and/or growth (Castonguay et al. 1994b; Desaunay and Guerault 1997; Dekker 1998), which process might possibly be related to the North Atlantic Oscillation (ICES 2001a; Knights 2003). This process is unlikely to be anthropogenic, and will not be related to the size of the spawning stock. Recovery of the original climate conditions is expected to lead to restoration of the abundant recruitment almost immediately. The observed spatial correlation in the decline in recruitment, as well as the assumed impact on the (nearly) panmictic oceanic life stages indicate, that oceanic processes operate on the stock as a whole.

On the other side, a range of continental factors has been suggested, including pollution, habitat loss due to barrages and dams, overexploitation of either glasseel or yellow and silver eel, and man-made transfers of parasites and diseases (Castonguay et al. 1994a; Moriarty and Dekker 1997; ICES 2002a; Robinet and Feunteun 2002). All of these factors are anthropogenic, operate primarily in the continental life stages and affect the abundance of recruitment only through their effect on the size or quality of the spawning stock. When a fatal reduction in the size or quality of the spawning stock occurs, an abrupt drop in recruitment is expected. This will be hard to reverse, since lower recruitment in turn will reduce the spawning stock. Each of the processes impacts a local substock on the continent, but it is their combined effect on the shared spawning stock that will have caused the recruitment decline, ultimately.

Although tentative analyses indicate, that the latter group of hypotheses (continental factors) fits available data better (Dekker 2003d,e), no evident and ultimately convincing proof exists. A stock restoration plan must be developed in the absence of fully adequate scientific information (FAO 1995). However, excessive anthropogenic impacts on the stock must be curtailed irrespective of the ultimate cause of the decline. Whether these impacts have summed up to cause the global decline of the stock or not, hardly affects the need to take conservation measures.

A framework for the management process

In the past decades, a precautionary approach to exploitation of fisheries resources has been developed (United Nations 1983; FAO 1995). This framework is routinely applied for scientific advice on fisheries (ICES 1997b), including advice on the European eel stock (ICES 1999, 2002b). Caddy and Mahon (1995), in their discussion of quantitative reference points, outline the conceptual steps in the development of quantified reference points for fisheries management. The current discussion will extend their ideas, distinguishing between the management process proper (Figure 3, top row) and the development of scientific advice (bottom row) and elaborating on the special case of eel fisheries in Europe.

Recent scientific advice and the current discussion were triggered by the decline in recruitment observed since 1980. In the preceding decades, management focused on the development of stock and fisheries, as witnessed by the execution of large-scale re-stocking programmes (Dekker 2003c), but this has been replaced recently by a focus on stock protection. The coincidence of the decline in recruitment during the 1980s and 1990s with the upsurge in discussions on stock protection implies, that the current collapse of the stock goes beyond limits acceptable for management. If possible, the stock should be sustained at levels above those currently pertaining.

The biology of the eel has been described as incompletely and poorly known, providing only a weak basis for management and restoration (ICES 1976, 1999; Moriarty and Dekker 1997; Tesch 1999). In its general form, this claim embraces two aspects: qualitatively speaking, processes operating on the stock might be unidentified; on the quantitative side, parameters of the processes and the state of the stock might be inadequately known. In the 1970s and early 1980s, attention was focused on quantification, on the compilation of an international database on stocks and fisheries, but in the 1990s, focus shifted to possible causes of the observed recruitment decline. All suggested hypotheses fit in the general framework of fish population dynamics, that is: if more data had been available, a straightforward selection and elimination procedure could easily have shown which process caused the observed decline. But neither the data, nor a shared analysis exists. Twenty years after the onset of the recruitment decline, the scientific community working on eel still lacks a comprehensive technical model for the dynamics of the population. Analysis of the (potential) processes causing the current stock decline is still in a primordial phase, tracing true and spurious correlations. Thus, the derivation of preliminary reference variables and values for stock management (ICES 2001b) hinges on the assumed parallel to quite unrelated fish species and does not relate to existing management practices.

Management and monitoring of eel stocks have a long tradition, related to regulation of local exploitation, but there is a marked regional variation in approaches, reflecting the widely differing traditions in eel fishing and consumption. Local monitoring activities have been shown to provide reliable information on the overall status of glasseel recruitment (Dekker 2000a, 2002), but assessment of fisheries and escapement has not been tried. Management measures have been listed (Moriarty and Dekker 1997; ICES 2001a, b), but have not been related quantitatively to objectives or stock status. Clearly, there is an intention to protect and restore the declining stock, there is a list of tools available, but the connection between implementation of management measures and fully detailed scientific advice is still lacking completely.

Temporal and spatial scales of stock dynamics

Management, monitoring and fundamental research of eel stock and fisheries have been carried out at the national level, almost without co-ordination between the individual countries. The spatial distribution of the stock exhibits fractal characteristics, showing large-scale as well as small-scale variation (Dekker 2000b); the temporal structure shows comparable fractal patterns. In setting up a management system for the stock and fisheries, these patterns should be considered and an appropriate spatial and temporal scale for management actions must be selected. In this section, the major processes in the dynamics of the stock will be characterised in time and space (Figure 4), setting the scene for a corresponding management scheme, developed later.

The European eel is distributed in almost all continental waters of Europe, along the coast of northern Africa and the Mediterranean parts of Asia. That is probably the most widely distributed exploited single fish stock, but individuals in inland waters are confined to single rivers or lakes, of less than 10 km^2 on average (Dekker 2000a). In comparison to many other exploited fish species, the eel shows an extreme longevity, related to the slow growth and late maturation. Age at maturation for female eel ranges from 5 in the Mediterranean to 15 years in the Baltic (Vøllestad 1992). In contrast to this small-scale and long-duration character of the continental half of the life cycle, the oceanic life phases cross thousands of kilometres (Van Ginneken and Van den Thillart 2000), in a most likely time frame of approximately two years (McCleave et al. 1998). In this life phase, individuals from different continental origin contribute to a common spawning stock (Avise 2003). The ocean phase thus characterises as a short-duration and large-scale phenomenon.

Anthropogenic impacts on the stock, including fisheries, range from instantaneous (e.g. pollution incidents, glass and silver eel fisheries) to long-term effects (e.g. gradual land reclamation, yellow eel fisheries). However, most of the anthropogenic impacts affect only a minor part of the population directly. Spatially significant effects only occur where local impacts are driven by a common force, such as the worldwide demand for glasseel, or the

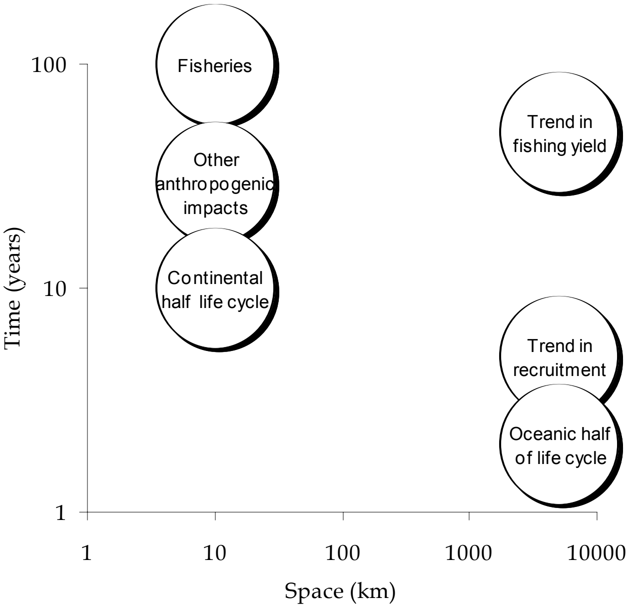

Figure 4 Temporal and spatial scale of observed trends, major processes and anthropogenic impacts on the stock.

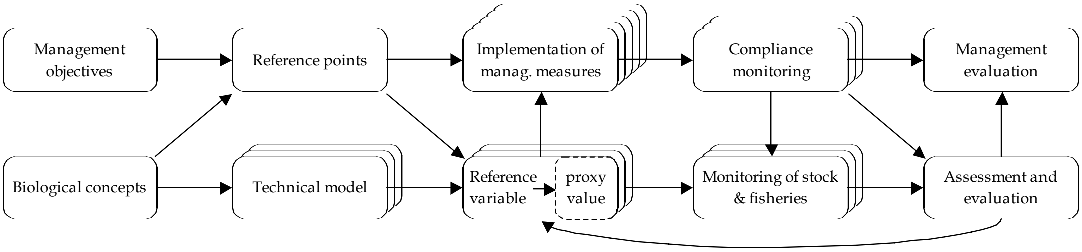

Figure 5 A revised framework for management of eel fisheries, taking into account the spatial differentiation of the eel stock and fisheries. For the sake of readability, items with a limited number of instances are shown in triplicate, while the thousands of waters in which management measures must be implemented is shown as just five.

continent-wide industrialisation. Incidents such as pollution spills seldom cover more than an isolated area, and are hardly of influence on the stock. Significant anthropogenic impacts operate on small spatial, but prolonged temporal scale. Stock-wide effects only occur because of external synchronisation between impacts on isolated and small waters.

The glasseel decline has been described as a prolonged stock-wide recruitment failure (Dekker 2000a). But as early as in 1985 (EIFAC 1985), it was realised that the recruitment of the European eel was in decline in the major part of the distribution area, that is: within five years, a widespread regime shift was noted. The gradual decline in fishing yield, in contrast, began in the mid 1960s and has continued almost consistently, that is: it has an inherently prolonged temporal scale. Like the recruitment failure, it occurred throughout the distribution area.

There is a sharp contrast in temporal and spatial scale between the oceanic (wide-spread, short time frame) and continental life stages (localised, long-lived); anthropogenic impacts predominantly fit the patterns of the continental phase, but the widespread and gradual decline in fishing yields suggests a causatory process of a different temporal and spatial scale: wide-spread and gradually developing.

Cracking the management problem

The contrast in spatial and temporal scale in major processes and anthropogenic impacts, sketched above, poses serious problems for management of the stock. Long-term global objectives must be achieved by small-scale and immediate actions in rural areas all over the continent. Neither central managers without direct influence on rural fisheries all over Europe, nor national or regional managers bereft of opportunities to influence the overall stock, will be able to solve the problem, unless a dedicated framework is developed. In this section, I will propose elements of a management scheme (Figure 5) that might achieve this goal.

Objective and target

Implicit in the development of a precautionary approach is the assumption that there is a relationship between spawning stock and recruitment. The precautionary approach dictates that, unless proven otherwise, such a relationship between stock and recruitment should also be assumed to exist for the eel and available evidence seems to corroborate the relation (Dekker 2003d). Current scientific knowledge is inadequate to derive spawning stock size targets specific for eel. Under data poor conditions, exploitation securing 30% of the virgin spawning stock biomass is generally considered a reasonable provisional reference target. This rule is conventionally labelled as %SPR, for Percentage Spawner Production per Recruit, which presupposes spawner production is proportional to recruitment. In southwestern Europe, with overabundant recruitment (Dekker 2003a), silver eel production is more likely to be proportional to (accessible) habitat, disabling the per recruit basis. However, the notion of a targeted spawning stock size relative to pristine conditions stands as it is. Considering the many uncertainties in eel management and biology and the uniqueness of the eel stock (one single stock, spawning only once in their lifetime), a precautionary reference point for eel must be stricter than the universal reasonable target of 30%. A value of 50% has been suggested (ICES 2001b).

Reference points and proxies

For the eel, the concept of protection of the spawning stock is hypothetical: spawning has never been observed in the wild. The escapement of spawners from the continental stock, however, is thought to be a good indicator of the supposed spawning stock size, for which management targets can be derived (ICES 2001a). The number of case studies actually measuring silver eel escapement is extremely limited (Ask and Erichsen 1976; Westin 1990; Sers *et al*. 1993; Pedersen and Dieperink 2000) and not likely to be extended considerably because of the research effort required. Cascading one step further, an assessment of the continental stock producing silver eels on the continent (Dekker 2000c) suffers from the same high research requirements.

Less demanding approaches, focusing on the yellow eel stock, such as the average size in the catch (Francis and Jellyman 1999), though not adequate for year-to-year management, might be suitable for long-term purposes (Figure 6). In my view, there is considerable scope for development of more low-demanding approximations to escapement targets. Management schemes for local situations can be built upon easy-to-grasp local targets, if these proxy targets correspond to their ultimate counterparts theoretically, and monitoring corroborates the net effect. For the glasseel fisheries, the concepts of stock abundance, habitat availability and carrying capacity still need to be worked out (ICES 2002a), but for this case too, a simplification in proxies will be required for implementation in any practical management situation.

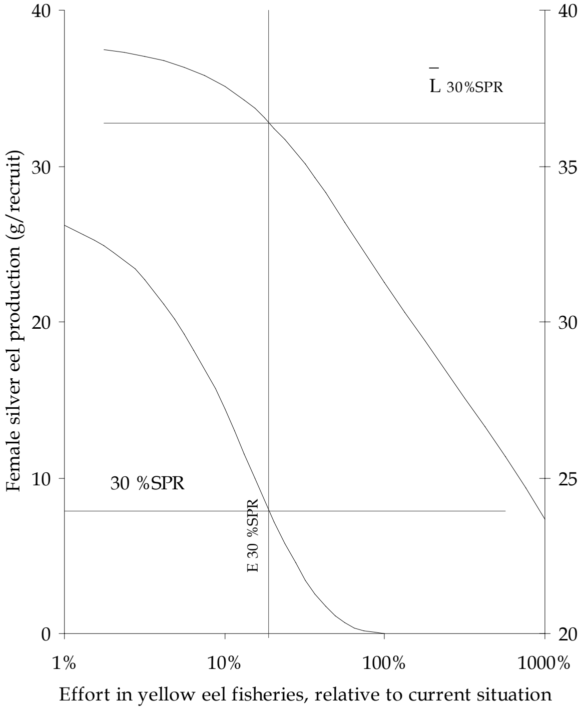

Figure 6 Mean length in yellow eel fishery in Lake IJsselmeer (the Netherlands) provides a proximate indicator for the level of female silver eel production under varying fishing effort. Dashed reference lines indicate 30 %SPR, the corresponding effort and mean length, based on current gear selectivity and the minimum legal size of 28 cm. (Unpublished results from Dekker 2000c).

Subsidiarity and orchestration

Management of local fisheries interacts with the common (oceanic) stock only through the immigration of glasseel and the escapement of silver eel. Intervention of international management in local fisheries need only concern the inputs (glasseel) and outputs (silver eel) of national systems. Global evaluation of local management considers the (relative) impact of local actions on spawner escapement and need not concern local means and local consequences. In particular, there is no basis for a continent-wide ban on either glasseel fisheries or silver eel fisheries, as proposed by opposing stakeholders.

Taking the subsidiarity one step further, the responsibility for management of national fisheries might be shared by governments and fisheries organisations, opening up the whole suite of co-management opportunities and tools (e.g. Pinkerton 1994). In particular, this might avoid the need to monitor and manage a multitude of water bodies, if monitoring samples only a small but representative number of the multitude of waters (random or stratified, but not fixed), and results are used to manage the fishery in the whole population of waters.

While the implementation (and monitoring) can only be executed at the lowest management level, objectives, reference points and evaluation necessarily refer to the whole population, at international level. Local managers hardly have any opportunity to influence the overall status of the stock, and have no natural incentive for implementing sustainable management. International managers, in contrast, cannot reasonably influence the stock directly, but do have an option to enforce a common objective through lower management levels, and to evaluate the global effect on the basis of local and widespread monitoring. Subsidiarity and orchestration of lower management levels constitute the global managers' tools to achieve the overall objectives.

Adaptive management

At the national or regional level, global objectives and targets must be translated into actual management measures, that is: required escapement levels, mortality rates or stock abundances must be matched to a corresponding fishing effort, fishing season, mesh size, closed area etc. The quantitative effect of specific measures is generally unknown, and local experiments do not extrapolate well to other water bodies, because of differences in size, morphology, physical and chemical characteristics, exploitation patterns and ecosystem characteristics between nearby waters. Assuming the net effect of a specific set of measures on the stock and fishery is adequately monitored, an adaptive management scheme might realise the appropriate rigour of the measures. That is: monitoring results can be used to tune management measures, establishing a short-term negative feedback in the management system (Figure 10, leftward pointing arrow).

In its initial definition (Walters and Hilborn 1976), adaptive management was introduced as an active experimenting with alternative (extreme) management regimes, to gain insight into the biological processes. For management of eel stocks in scattered waters all over Europe, only a self-regulating feedback in establishing local management measures is required. Since the overall dynamics of the stock will hardly respond to local actions, local experimenting will not gain any insight in the global processes. Local adaptive management requires, apart from correct implementation and monitoring, that measures are strengthened or weakened at short order when monitoring indicates so, in moderate steps. Big steps might overshoot the target, creating oscillations or jitter, but too small steps or delayed implementation jeopardises a convincing effect. Applying a somewhat stricter rule for weakening of restrictive measures than for strengthening creates a reference zone rather than a reference point, ensuring greater stability in the feedback system, and allowing for somewhat more severe initial measures.

Tit-for-tat

A major advantage of a continuous feedback system is its ability to correct for external perturbations. Adverse conditions (e.g. immigration of cormorants) or favourable improvements (e.g. habitat restoration) automatically translate into an optimal management regime for the prevailing conditions eventually, avoiding the need to assess local conditions for each and every water body. If, in a co-management set-up, the adaptive management considers only one easy to implement and easy to control measure (e.g. season closure), while all other potential measures (e.g. fishing effort, closed areas, etc.) are left to the fishery as voluntary options to improve their business, a conceptually very simple management model results. For the adaptive management scheme, all the voluntary options constitute external perturbations, to which the feedback will respond appropriately. For example, an overexploited state might gradually shorten the open season, while a subsequent (voluntary) reduction in fishing effort results in a longer season, only after the fish stock has restored to a sustainable level. This arrangement between government and fisheries conforms to the set-up known as tit-for-tat in game theory (Axelrod and Hamilton 1981), in which voluntary co-operation has been shown to be an optimal and stable strategy for both players.

Targets and tools

The exploitation of the eel encompasses three well-separated metiers: fishery for glasseel, for yellow eel and for silver eel, operated predominantly at high, medium and low stock densities (Dekker 2003a). Additionally, loss of habitat and installation of hydropower generation plants constitute common phenomena. Rather than developing and establishing a separate management scheme for each river system in all countries (ICES 1997a), a small set of reference situations might be considered, tackling the major processes and concepts in the typical settings. In my opinion, half a dozen model systems will suffice to analyse management approaches for almost all eel fisheries in Europe, while the use of such a small set of common methodologies will greatly enhance the opportunities for monitoring, assessment and evaluation at the global level.

Habitat loss

Habitat loss might have contributed to the decline of the stock significantly, but its restoration is probably not the most urgent issue in major parts of the distribution area. The gradual decline in habitat has impacted the continental population, resulting in steadily decreasing spawner escapement. In the 1980s, recruitment suddenly failed. Although loss of (accessible) habitat might ultimately have caused this collapse (through a stock-recruitment relation), cause and effect are definitely not in proportion: the declining spawning stock has switched recruitment to a much lower state. Recruitment has declined to 1-10% of former levels, which requires only 1-10% of the former habitat, until the stock-recruitment-relation switches back to its abundant state. Re-stocking and (local) trap and transport programmes have been shown to contribute to fishing yield. Where increased recruitment benefits production, available habitat cannot be the limiting factor.

In contrast to the rest of Europe, southwestern France and the Iberian Peninsula receive abundant recruitment (Dekker 2000b, 2003a), and here, the amount of (accessible) habitat is of paramount significance. Since the highest loss of habitat (Moriarty and Dekker 1997) has occurred exactly in the areas of highest recruitment (Dekker 2003a), local restoration projects in the Bay of Biscay and the Iberian Peninsula might have significance for the global stock. However, unlike management of fisheries, in which long-term gains are balanced to short-term profits for a single stakeholder, setting targets for habitat restoration requires Solomonian judgements between stakeholders, between fish conservation and, for instance, agricultural irrigation. In this case, reference points cannot be derived rationally, and agreed targets express the political willingness to invest in sustainable management. A pragmatic ranking of management options on the basis of their feasibility, as ICES (2002a) proposed (i.e. full use of existing habitat; restore habitat where easily done; full use of existing recruitment; restore historical habitat; restore pristine conditions), supports the Solomonian decision process, but does in no way relate to sustainable management targets or stock status.

Glasseel fisheries

For glasseel fisheries, it is generally assumed that fishery exploits surplus recruitment that would have experienced intense density dependent mortality if not harvested (Moriarty and Dekker 1997; ICES 2000). Although not yet explicitly evidenced, this implies a limited carrying capacity of inland habitats. Management targets relate to the abundance of the yellow eel stock, rather than the mortality rates exerted by the fishery on the immigrating glasseel. The 30 or 50 %SPR-rule allows for some reduction of the stock below carrying capacity, but doing so will yield only slightly more. Restricting glasseel exploitation progressively until no further rise in the abundance of the yellow eel stock in the hinterland occurs determines a realistic target for an adaptive management scheme. Management of glasseel fisheries thus requires monitoring of the yellow eel stock. None of the conventional fisheries regulation tools (effort restrictions, closed areas or seasons, gear controls) establishes a constant compliance under time-varying glasseel abundance. Following a substantial decline in catches, a considerably lower fishing effort in the glasseel fishery will be required to keep the yellow eel abundance at target level.

Yellow eel fisheries

Yellow eel fishery in inland waters yields between 1.6 and 80 (max. 400) $kg \bullet yr^{-1} \bullet ha^{-1}$ of water surface (Dekker 2003a). Since re-stocking generally has a positive effect on yield (Wickström 2001), the wide range in stock density and yield is predominantly related to variation in stock abundance, and not to carrying capacity and production potential. Management targets related to potential production (in terms of biomass states) differ considerably from those related to actual abundance (in terms of mortality rates). Because of the very unequal distribution of recruitment amongst countries (Dekker 2003a), the choice between these two options requires political back-up. However, due to its disproportionate protection of the outskirts of the distribution area and its time-varying restrictions on fisheries under temporal recruitment fluctuation, I doubt the approach based on (potential) biomass. Additionally, applying a mortality rate approach brings the major part of eel fisheries management in line with that of most other exploited fish species. Unlike the glasseel fisheries, all conventional fisheries regulation measures apply, including effort restrictions, closed areas or seasons, gear controls including minimal mesh size, and minimal legal sizes. However, setting (proxies for) management targets in terms of the average fish length excludes the use of size restrictions.

Silver eel fisheries and hydropower plants

During the silver eel descent from inland waters to the sea, mortality occurs due to fisheries (directed on silver eel) and hydropower generation plants (unwanted side-effect). Control of their impact on the stock is mandatory to sustain adequate spawner escapement. In both situations, the absolute amount of silver eel affected is relatively easily determined, but the relative impact on the silver eel run is hard to assess, due to the absence of direct information on the escapees. Estimation of the total number of silver eel running, based on yellow eel production estimates or mark-recapture programmes, is generally not accurate enough to warrant adaptive management. Therefore, anthropogenic silver eel mortality is probably best treated as a fixed mortality, not involved in adaptive feedback. Management measures (closed areas, closed season or periods, effort control; for fisheries as well as for hydropower generation) will be required to establish an acceptable mortality level and to keep it fixed.

Temporal and spatial scales of the management process

The stock and fisheries for the European eel have shown a prolonged and wide-spread decline, for which the development of a stock-wide restoration plan has been advised, requiring 5-20 years to become effective due to the longevity of the species. In the foregoing discussion, stock-wide management objectives have been discussed, essential concepts for a management strategy proposed and targets and tools for pertinent implementation in small-scale fisheries have been proposed. The question arises, whether these together constitute a viable management scheme (Figure 7).

Management of eel stocks and fisheries have been carried out for centuries on a local (national or regional) scale, aiming at various local objectives. Following the continent-wide decline in stock and recruitment, most fishermen and managers are painfully aware of the alarming state of the stock. Although views on causes and consequences may vary substantially, the willingness to amalgamate into a population-wide management net-

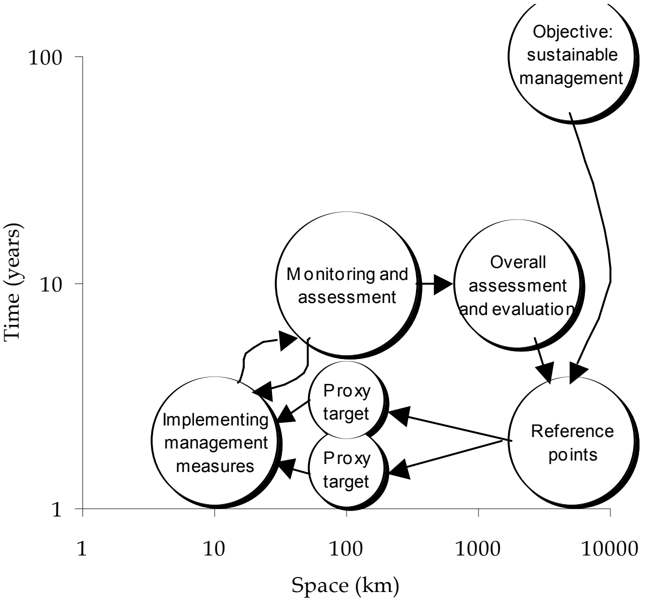

Figure 7 Temporal and spatial scale of the proposed framework for management of the stock and fisheries. Implementation of local management of eel stocks, together with the global development of reference points (and their proxies) related to global evaluation, constitute an overall framework establishing a sustainable management of the stock and fisheries. Arrows indicate the flow of concepts, information and data.

work aiming at restoration of the stock has been expressed by many stakeholders.

To implement the proposed framework, further development is required of proxy targets and of global monitoring and assessment programmes. Following a prolonged period of bottom-up data collection and status and trend assessment (ICES 1988-2004), strengthening the central level and imposing objective-driven, top-down management is first priority. The development of (proxy) targets is a long-term process, requiring strict coordination to acquire spatial consistency, preceding the implementation in local management. As an alternative to provisional stringent emergency measures (closure of fishery), as proposed by ICES (2002b), one might consider initiating local management aiming at the final objective, using provisional (somewhat over-restrictive) proxy targets, that is: initiate the local short-term management process immediately, rather than installing an intermediate regime all over Europe. This would also produce a start for a stock-wide monitoring and assessment programme, based on co-ordinated (but not necessarily standardised) local data series (cf. Dekker 2002).

The objective of sustainable management is a long-term widespread aim, which must be accomplished by short-term local actions. The substitution of proximate targets allows managers to implement a local management scheme, including monitoring and adaptive feedback. Because of the adaptive feedback, it will require several years before any proxy target is set and met. Additionally, the proxy targets might turn out to be rather poor representations of the ultimate goals, which necessitates intensified monitoring and assessment initially. However, due to the longevity and widespread distribution of the eel, local management can be off-target for a considerable period, as long as many local situations sum up to a global pattern meeting the global target at a temporal scale of a lifetime. If systematic bias is avoided, considerable scattering in management achievements will not jeopardise the global management objective.

The decline in yield has lasted for four decades. Subsequently, in the early 1980s, a failure in recruitment developed over a few years, but it was only in 1993 (EIFAC 1993), that the effect upon stock and fisheries was first considered, and only in 1998 (ICES 1999), that adequate management advice was formulated, while no substantial action has been undertaken yet to restore the stock (ICES 2004). In my view (Dekker 2004), the recruitment failure was a secondary consequence of the (spawning) stock decline. In turn, reduced recruitment induces a decline of the stock, and thereby establishes a very much unwanted negative feedback in the dynamics of the stock. Restoration measures will have to compensate for the ultimate causes of the decline, and to escape from the negative feedback. The longer we wait, the smaller the remaining stock size, and the lower the odds for reversing the downward trends. Current yield is about half that of 1980, when the recruitment failure began. Reckoning the trend in spawning stock developed in parallel, any management measure with an effect less than doubling the silver eel escapement will be fully in vain. Establishing an ultimately sustainable management scheme might not do anymore for the current depleted situation. Immediate and widespread restoration measures are required. Now!

Acknowledgements

In this article, I have compiled a coherent framework of concepts, I hope. Most ideas, however, stem from recurrent discussions with many colleagues and fishermen. I am thankful for this stimulating and cooperative working environment. Wim van Densen and Charlotte Deerenberg gave valuable comments on a draft of this text.

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Synthesis and discussion: Population dynamics of the European eel

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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),

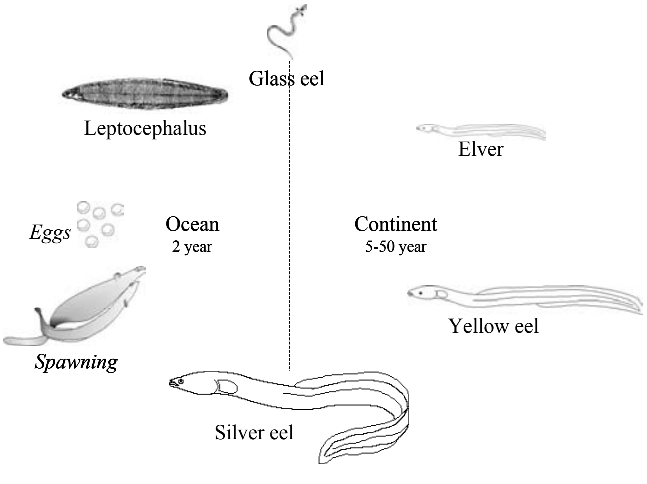

Figure 1 The life cycle of the European eel. The names of the major life stages are indicated; spawning and eggs have never been observed in the wild and are therefore only tentatively included.

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 glasseel, which has the same shape as an adult eel, but is unpigmented. Glasseel arrive in coastal waters in winter in southern Europe to late spring in north-most areas (Tesch 1999), and migrate into coastal waters, estuaries and for the major part further into fresh water, using selective tidal transport (Creutzberg 1961; McCleave and Kleckner 1982). Following pigmentation, the immigrating eel is referred to as an elver, but there is some confusion whether this word refers solely to the pigmented stage (in the first summer following immigration) or also to the unpigmented glasseel. Farther upstream, the eel 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 (Vøllestad 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 40ºN (mid Spain), to 10 and 14 years at 60ºN (central Sweden), with an average of respectively 6 and 9 years (Vøllestad 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 glasseel 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 glasseel 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 km^2, representing over 100,000 km^2 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 km^2; 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

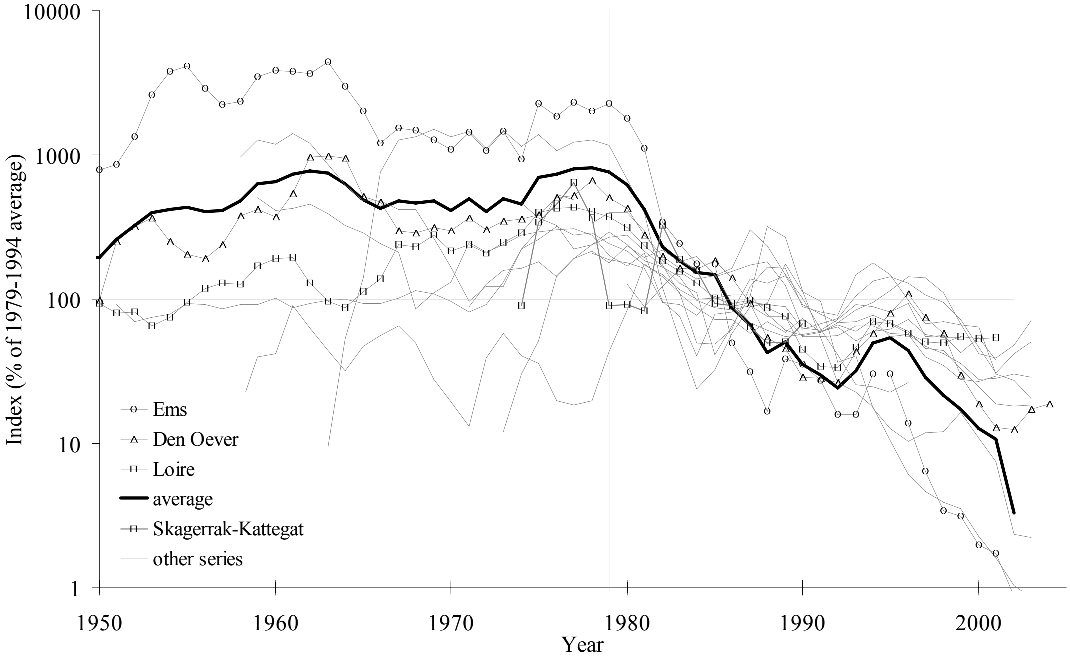

Figure 2 Trends in glasseel recruitment to the continent. Individual dsata series are given in grey; common trend (geometric mean of the three longest data series) in black. Note that recruitment data series concerning yellow eel are presented in Figure 4. Data from ICES (2004) and Hagström and Wickström (1990).

(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 glasseel, 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.

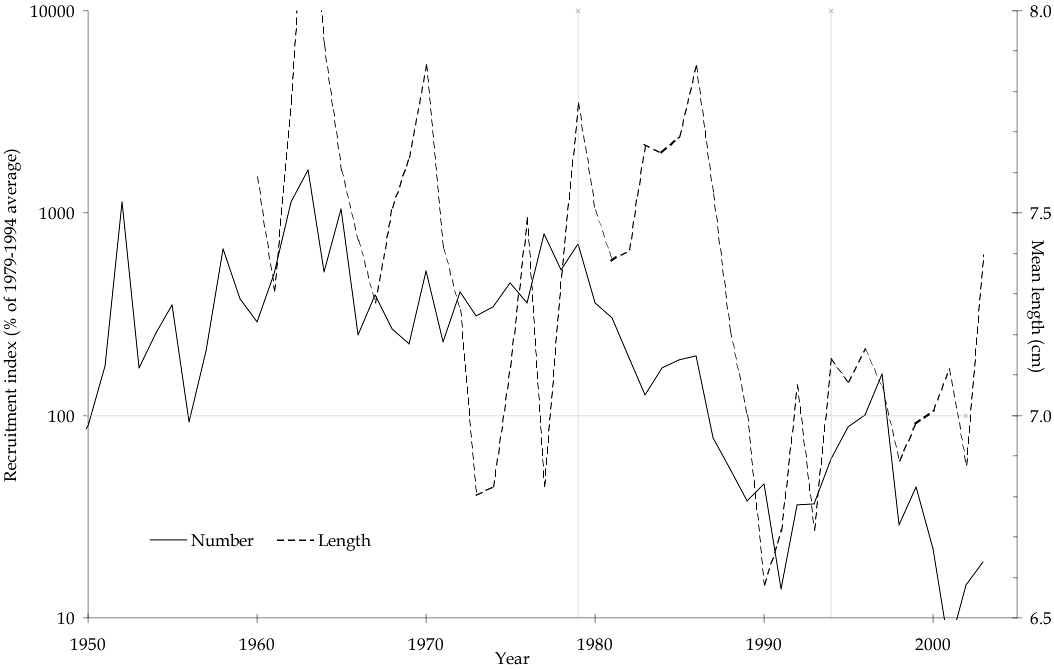

Figure 3 Trends in abundance and mean length of the glasseel sampled in Den Oever, the Netherlands. Abundance has been corrected for month and hour of sampling; mean length for the date within and timing of the season (Dekker 1998; updated until 2003).

Observed trends

Recruitment

In most countries in Western Europe, the abundance of glasseel 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 glasseel 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 (Svärdson 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.

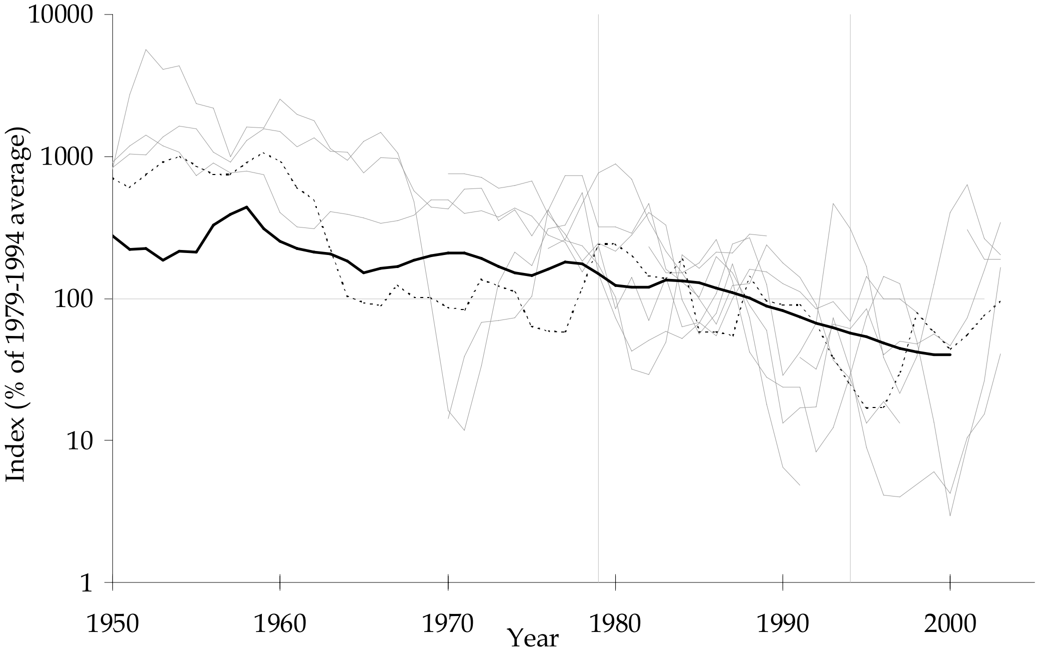

Figure 4 Trends in abundance of yellow eel in inland waters, during the 20th century. Lake IJsselmeer surveys of eel between 20-25 cm length in black; data series on Scandinavian traps catching recruiting yellow eel in grey. Data for River Lagan (Sweden) dashed. Data from ICES (2004) and Dekker (2004a).

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). Svärdson (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 glasseel recruitment had not yet begun. In hindsight, Svärdson's interpretation, although consistent with his observations, would not seem the most obvious one. An increased mortality between the glasseel 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 Svärdson's data (Wickström 2002; ICES 2004), and extension to glasseel 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-

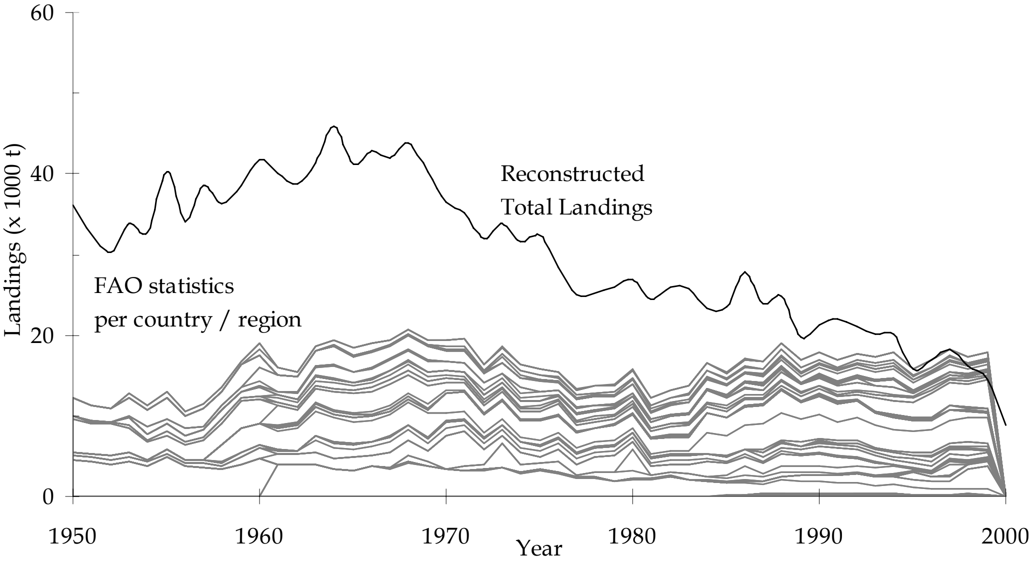

Figure 5 Trends in fishing yield from the whole population. FAO statistics include an increasing number of reporting countries, and therefore give a false suggestion of a stable or increasing yield. Analysis of the trends in individual data series results in a reconstructed trend for the whole population (Dekker 2003c).

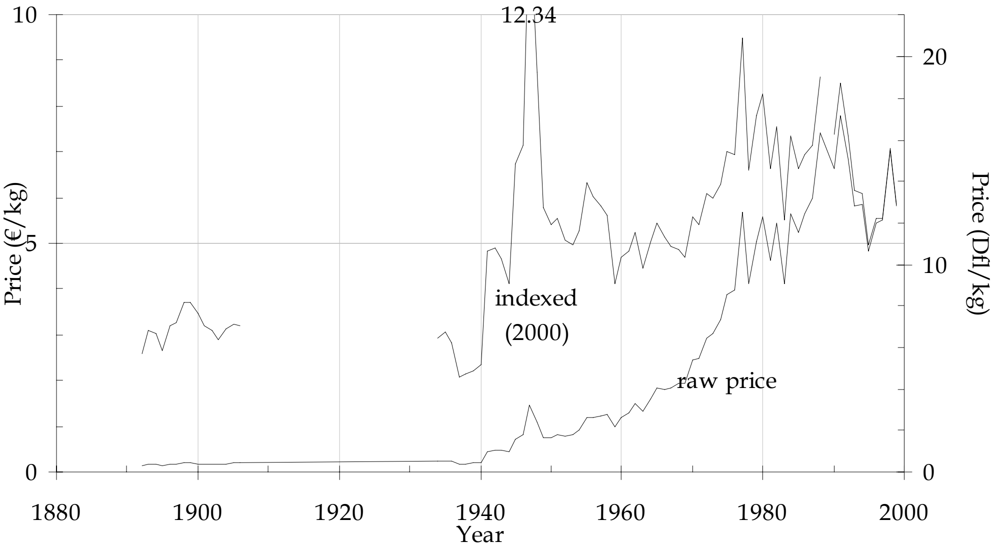

Figure 6 Trend in market price for yellow eel from Lake IJsselmeer during the 20th century, corrected for within-season trends and variation between fishing gear (unpublished data from the author).

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):

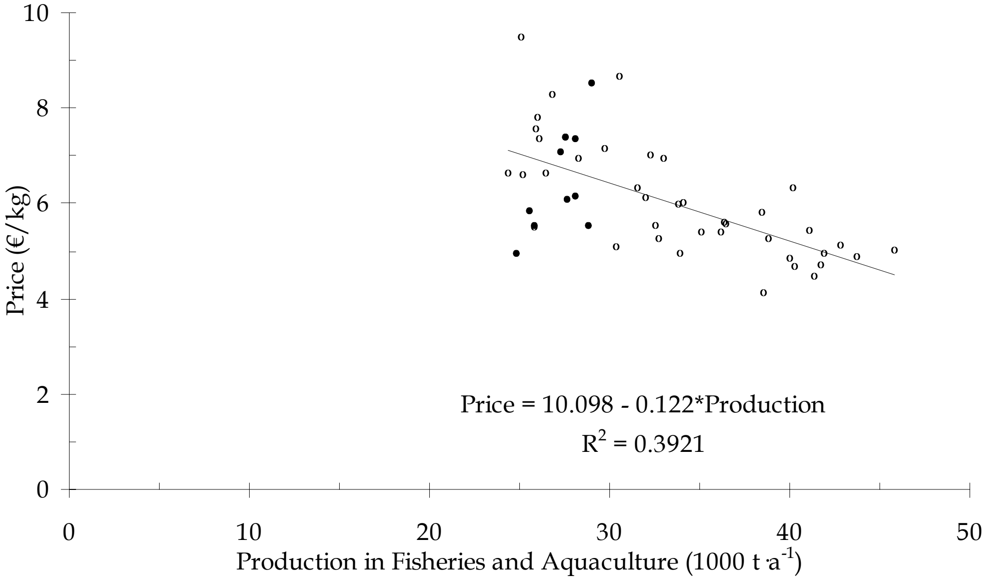

Figure 7 Relation between indexed market price (the Netherlands, year 2000 price level) and the European production (fishing yield and aquaculture combined), before 1990 (open symbols) and after 1990 (closed symbols). Data from Dekker (2003b,c) and Figure 6.

Glasseel 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

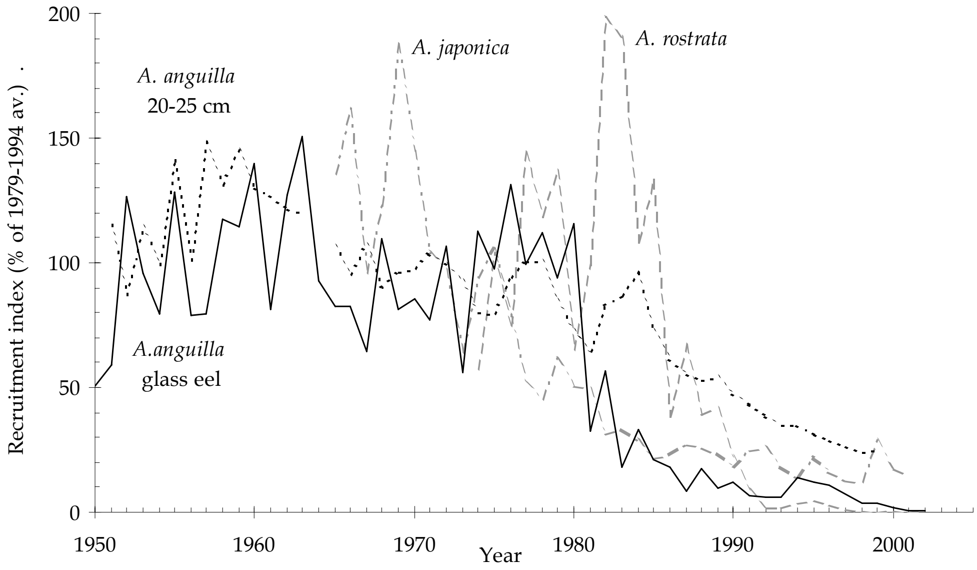

Figure 8 Trend in recruitment of the temperate species, American eel (*A. rostrata*, yellow eel), Japanese eel (*A. japonica*, glasseel), and European eel (*A. anguilla*, glasseel), and the abundance of yellow eel (20-25 cm length) in Lake IJsselmeer. Data from ICES (2001), Tatsukawa (2003) and Dekker (2002, 2004a).

(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 glasseel 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 glasseel 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)

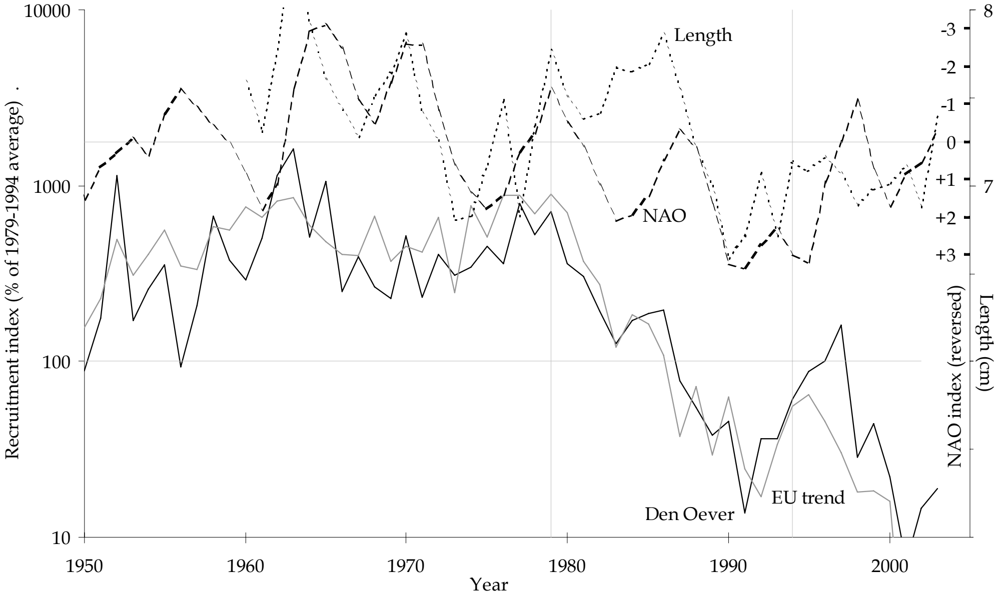

Figure 9 Trend in glasseel recruitment, and mean length (in Den Oever), and the NAO index, averaged over three years. Data from Dekker (1998, updated until 2003), NAO winter indices from Hurrell (1995).

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

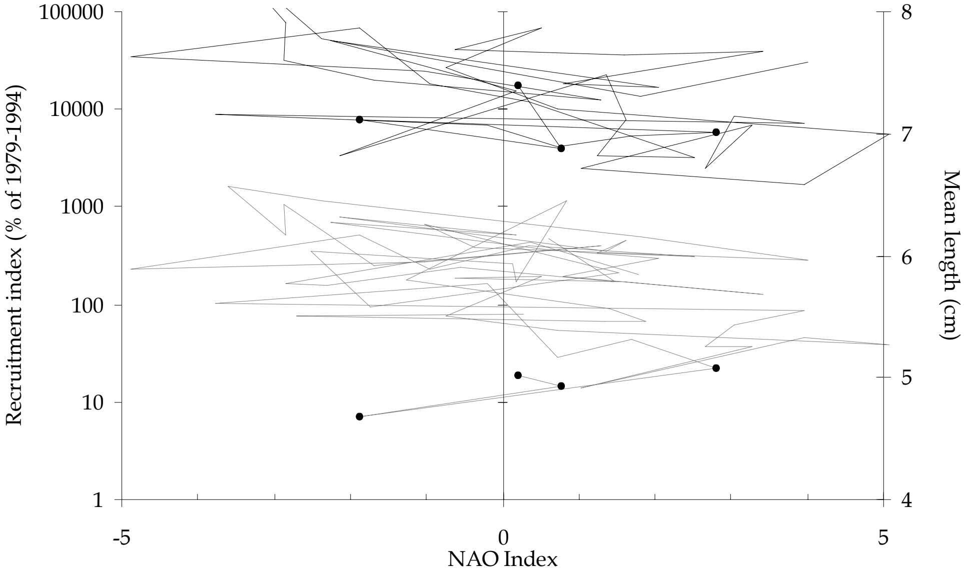

Figure 10 Relationship of mean glasseel length (top; r^2=0.26) respectively glasseel abundance in Den Oever (bottom; r^2=0.13) to the NAO Index. Data points from 2000 and later are marked by a •.

Oever. 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 glasseel 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 glasseel 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 glasseel 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 (Køie 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 (Køie 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 glasseel 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:

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

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…10; NAO_{i-k} is the NAO winter index (derived from http://www.cgd.ucar.edu/~jhurrell/nao.html) in year i-k, time lagged by k=0…3 years; γ_k are parameters of the climate effect, k=0…3, and α 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.

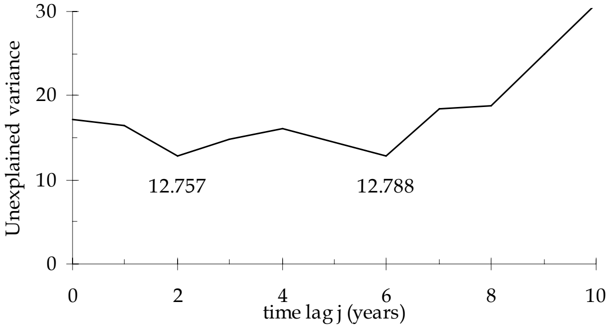

Figure 11 Goodness of fit (sum of squared residuals) as a function of the time lag between the year of catch and year in which the progeny of escaping fellows recruits.

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 silvering of the escaping fellows, the duration of the migration to the spawning place, the reproductive and larval phase, the metamorphosis to glasseel 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 Beverton and Holt (1957) used an asymptotically increasing relationship between recruitment and spawning stock biomass equivalent to:

$$\log\left(\frac{R_i}{SSB_{i-j}}\right) = \log(\alpha) - \log\left(1 + \frac{SSB_{i-j}}{\beta}\right) \tag{2}$$

where α and β 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.

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

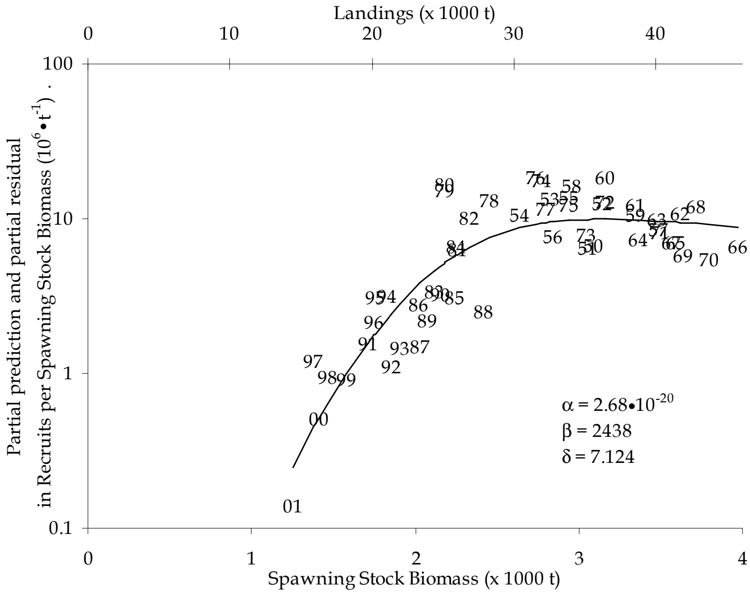

Figure 12 Relation between reproductive success (number of recruits per unit of SSB) and the SSB, corrected for the correlation with NAO (time lags 0-3). SSB is assumed proportional to continental landings, 2 years prior to recruitment. Data labels indicate the years 1950-2001.

sis 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:

$$\log\left(\frac{R_i}{SSB_{i-j}}\right) = \log(\alpha) + (\delta - 1)\times\log(SSB_{i-j}) - \log\left(1 + \frac{(SSB_{i-j})^{\delta}}{\beta}\right) \tag{3}$$

where δ 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:

$$\log\left(\frac{R_i}{SSB_{i-j}}\right) = \log(\alpha) + (\delta - 1)\times\log(SSB_{i-j}) - \log\left(1 + \frac{(SSB_{i-j})^{\delta}}{\beta}\right) + \sum_{k=0}^{3}\gamma_k \times NAO_{i-k} + \varepsilon_i \tag{4}$$

with ε_i representing an independent and normally distributed error term in year *i*.

The structure of this model, encompassing a stock-recruitment component and environmental effects, is comparable to the linear model proposed by Chen and Irvine (2001), although the Beverton and Holt stock-recruitment relationship (including depensation) yields a non-lineair model. Parameters were estimated by standard approximation methods for non-lineair models as implemented in SAS, 'proc nlin' (SAS Inc. 1999). Goodness of fit of both full and reduced models was tested by Analysis of Variance (Table 1). The full model explains 79% of the total variance, of which 59% is linked

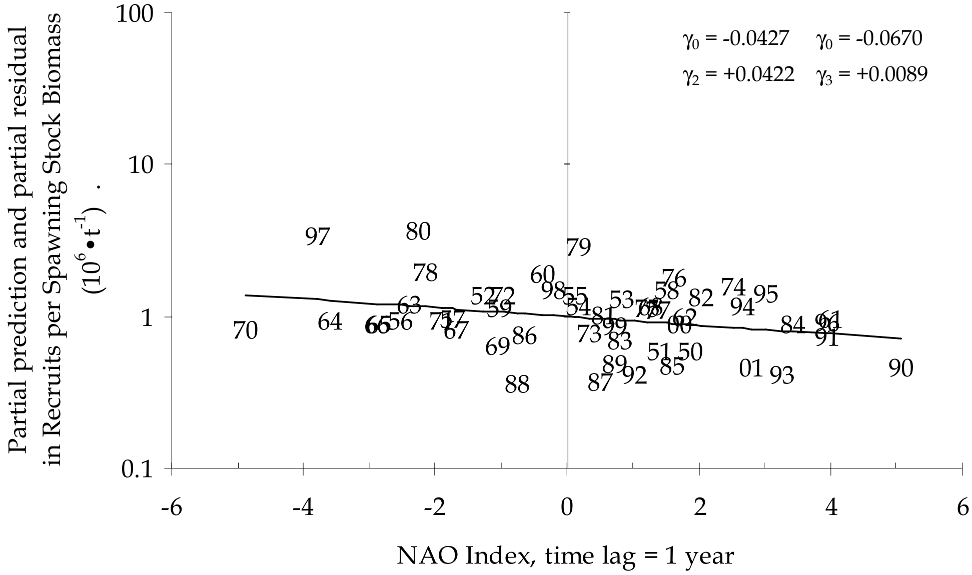

Figure 13 Relation between reproductive success (number of recruits per unit of SSB) and the NAO Index (time lag 1), corrected for the stock-recruitment relation. Data labels indicate the years 1950-2001.

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 (Vøllestad 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 fish populations. Therefore, the above analysis poses the question, whether there is a plausible depensatory mechanism that applies particularly for 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 (*Oncorhynchis* 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 allopatry 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 (Boëtius 1980), hybridisation is apparently restricted to Icelandic waters (Avise 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 (Courchamp 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.

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De populatie-dynamica van de Europese aal

12

Voor u ligt een proefschrift over de populatie-dynamica van de Europese aal. In de voorafgaande hoofdstukken bent u statistische analyses en complexe redeneringen tegenkomen, handelende over de achteruitgang van de aalstand in onze wateren. Taaie kost over een glibberig onderwerp, terwijl de essentie toch makkelijk te vatten is: het gaat steeds slechter met de aalstand, dat is overal in Europa het geval, en dit proces is al jaren lang gaande. Maar waardoor het steeds slechter gaat is uiteindelijk niet echt duidelijk.

In dit laatste hoofdstuk wil ik de resultaten samenvatten voor een niet-wetenschappelijk publiek, een aantal achtergronden over het voetlicht brengen, informatie uit andere bronnen samen vatten, begrippen illustreren, etc. De nadruk ligt hierbij op gegevens, processen en hypotheses. Een poëtischer beschrijving van de aal, de visserij en het onderzoek is kortgeleden door Thomas Fort gepubliceerd*. In vergelijking tot een dergelijke meester-schrijver ben ik maar een povere wetenschapper, die zijn gedachten het gemakkelijkst uitdrukt in grafieken en statistieken.

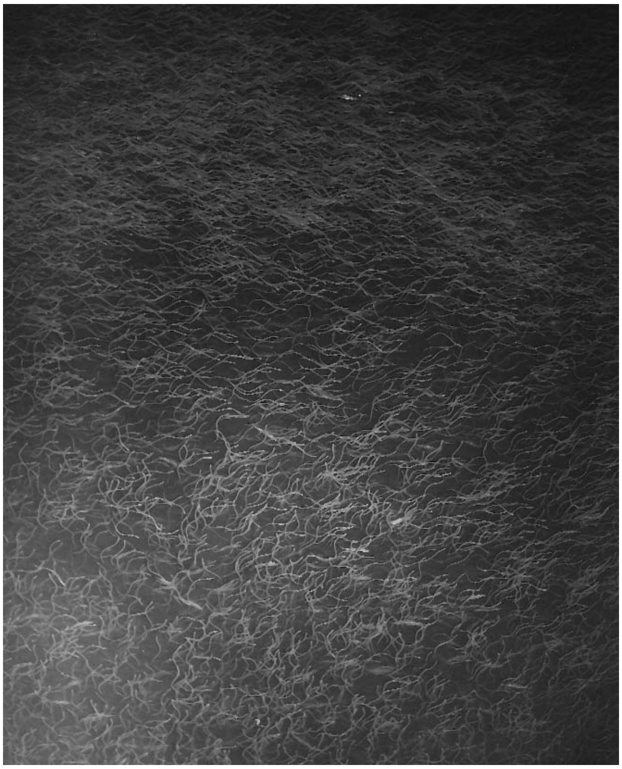
Achtereenvolgens zal ik een korte beschrijving geven van de biologie van de aal, facetten van de visserij documenteren, de ontwikkelingen in de aalpopulatie bespreken en de oorzaken en consequenties van de vastgestelde achteruitgang analyseren en een vergelijking maken met de belangrijkste commerciële vissoorten van de Noordzee. Tenslotte komt de toestand van de IJsselmeervisserij en de aalvisserij in de overige binnenwateren ter sprake, in relatie tot mogelijkheden voor herstel van de aalstand en de duurzame uitoefening van de aalvisserij.

Biologie

De aal is een uitzonderlijke vis. Met zijn slangachtige uiterlijk wordt hij in de volksmond zelfs niet altijd tot de vissen gerekend. ('Handel in haring, aal en vis'). De wetenschappelijke aanduiding is *Anguilla anguilla* (L.), dat zoveel betekent als: het slangetje. Voorts worden veel lokale namen gebruikt: paling, peling, pellik en nog vele anderen, waar zelfs ik dikwijls nog maar zelden van gehoord heb. Slechts de naam zeepaling duidt op een andere soort: de Conger, die uitsluitend in zee voorkomt.

Uit de modder

De voortplanting vindt ver van Europa op de oceaan plaats, op een nog steeds onbekende locatie. Lange tijd is onduidelijk geweest of de aal zich voortplantte; pas veel later verplaatste de vraag zich van òf naar wáár en hóe. Aristoteles (384-322 v. Chr.) was zo gefascineerd door een dier dat zich niet leek te kunnen voortplanten, dat hij de proef op de som nam. Bij mijn weten was dat het eerste wetenschappelijke experiment met een vis. Hij beschrijft hoe een zoetwaterpoel werd leeg geschraapt en alle aal verwijderd. Nadat de regen de poel weer had gevuld, bleken er opnieuw alen in de poel aanwezig te zijn. Aristoteles leidde daaruit af, dat aal in de modder spontaan kan ontstaan, zonder dat er vooraf aal aanwezig is (*generatio spontaneis*). Later zijn nog andere, wildere spe-



Figuur 1 Glasaal voor de sluizen van Den Oever, in 1958. De zee helemaal wit van de glasaal, dat is nu al jaren niet meer gezien. (foto Cees Deelder)
Glasseel in front of the sluices at Den Oever (the Netherlands). Glasseels so abundant that the water surface becomes white; that hasn't been seen in many years now.

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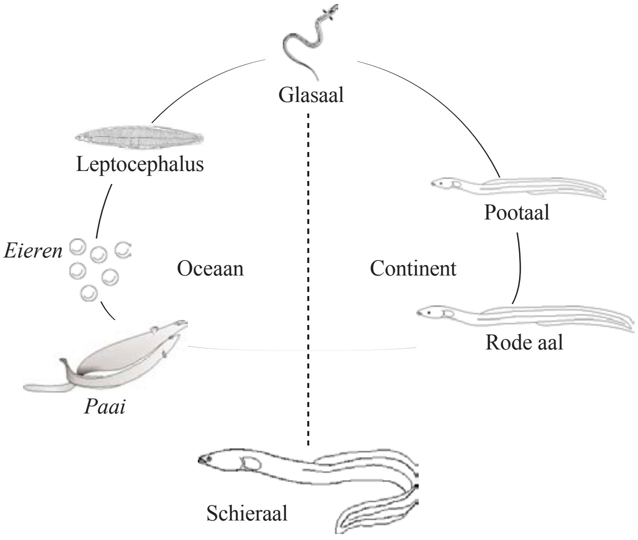
*Thomas Fort, The Book of Eels. Harper Collins Publishers, London. 2002. 287 pp.



Figuur 2 De levenscyclus van de aal. De paai en de eieren zijn in de natuur nooit werkelijk waargenomen.
Life cycle of the eel. Clockwise from the top: glasseel; bootlace; yellow eel; silver eel; spawning; eggs; and the Leptocephalus *larva. Spawning and eggs have never been observed in the wild.*

culaties gevolgd, zonder dat een alleszins bevredigende oplossing gevonden werd.

In de Straat van Messina

In 1896 kweekten de Italianen Grassi en Calandruccio een visje in een aquarium op, die ze in de dieptes van de Straat van Messina (Sicilië) hadden gevangen. Tot hun verrassing bleek dit diertje, dat tot dan toe als *Leptocephalus brevirostris* bekend had gestaan, een gedaanteverwisseling te ondergaan en een jonge aal te worden. De *Leptocephalus* was dus geen aparte diersoort, maar de larve van de aal. En het probleem van de voortplanting van de aal was plotseling ook een stuk kleiner: ergens in de diepte van de (westelijke) Middellandse zee moest een paaiplaats liggen. Maar waar?

In de Sargassozee

Toen de Deense onderzoeker Johannes Schmidt in 1904 ook *Leptocephalus*-larven ten westen van Schotland ving, en uitvond dat verder naar het westen in de Atlantische Oceaan veel kleinere larven te vinden waren, kwam de zaak in een stroomversnelling. Na enkele jaren wist Schmidt te melden, dat de kleinste larven in de Sargassozee voorkwamen, en claimde hij dat de paai dan wel in de diepte van de Sargasso zou plaatsvinden. Een geweldige doorbraak (kleine larven in de Sargasso), maar tegelijkertijd ook een geweldige bluf (paai in de Sargasso). Lang is Schmidt's lezing absoluut aanvaard, tot in 1959 Dennis Tucker (Zoölogisch Museum van Londen) de fundamentele kritiek uitte, dat de paai helemaal niet was waargenomen (en hij met een inmiddels weerlegde, alternatieve verklaring kwam). Tot op de dag van vandaag is het mysterie van de aal blijven voortbestaan, evenals de controverse tussen vele Schmidt-adepten en een klein aantal ongelovige Thomassen; nog steeds is de natuurlijke paai ons onbekend. Ik zal niet ontkennen dat dit mysterie een geweldig verleidelijke uitdaging voor een aal-onderzoeker betekent, maar daar staat tegenover dat – na ruim een eeuw waarin de oplossing niet werkelijk is gevonden – het wellicht verstandiger is niet te licht in deze verzoeking te treden. De kleinste larven zijn gevonden in de Sargassozee; met alleen die kennis zal de wetenschap het voorlopig moeten doen.

De Leptocephalus-larven in de oceaan lijken in het geheel niet op alen, maar hebben de vorm van een wilgenblaadje, die op zijn smalle kant zwemt (Figuur 3). Nabij het Europese continent vormt deze zich om in een jonge, doorzichtige aal: de glasaal, met een lengte van 7 cm. Deze wordt aangetroffen langs bijna alle kusten van Europa en Noord Afrika, waar ze in kust- en binnenwateren opgroeien.

Een kleurrijke vis

Al gauw na de intrek in de binnenwateren begint de glasaal kleur te krijgen. De rugzijde wordt donker, groenbruin, de buik krijgt een licht, geel-groene of geel-witte kleur. In dit stadium staat de aal bekend als *rode aal*; in het engels als *yellow eel*. De kleuraanduiding *rood* lijkt nogal onverklaarbaar, maar kortgeleden vertelde een beroepsvisser me, dat dit afgeleid zou zijn van het werkwoord *rooien*, oogsten. Een *te rooien aal* zou, als gevolg van hypercorrectie van de uitspraak, verbasterd zijn tot *rode aal*. Daar staat tegenover dat er uit 1518 al een tekst bekend is, waarin gesproken wordt van *Anguillae rubiae*, letterlijk: rode aal. Dat betrof overigens een bekeuring van Nederlandse handelaren in Londen, die moesten beloven nooit meer rode aal te komen verkopen; tot op de dag van vandaag domineren Nederlanders de internationale markten voor aal, ook in Londen. Naast de aanduiding *rode aal*, worden er onder vissers nog tal van andere benamingen gebruikt, waaronder groene aal (van het Wad), blauwe aal (magere, veelal vrouwelijke dieren, met een dunne, blauwachtige huid), spijkers, lange dunne, slokkers, etc.

Aan het eind van zijn levensfase in onze binnenwateren verandert de aal van uiterlijk, en wordt dan aangeduid als *schieraal*, vanwege de witte=schiere buik. Een eeuw geleden werd in Nederland meestal over zilverpaling gesproken, een aanduiding die tot op de dag van van-

Figuur 3 Een *Leptocephalus*, de larve van een aal-achtige vis, in dit geval van *Conger oceanicus*. (foto Uwe Kils)
A Leptocephalus*, the larva of anguillid fish. This is the larva of* Conger oceanicus.

Figuur 4 Een glasaal. (foto Claude Belpaire)
A glasseel.

Figuur 5 Een goudaal is een gedeeltelijk albino rode aal, waarbij de bruine en groene pigmenten ontbreken. (foto Derek Evans)
A golden eel is a partially albino yellow eel, missing the brown and green pigments.

daag in Vlaanderen nog gangbaar is. Schieraal wordt soms ook wel *paling* genoemd, maar meestal zijn de woorden *aal* en *paling* synoniem. Het lijkt erop, dat het woord *paling* in Nederland bovenal door stadse mensen wordt gebruikt, en dan nog zelfs speciaal voor het hapklare product; *aal* wordt dan primair gereserveerd voor het gehele, levende dier. Een broodje *paling*-filet veronderstelt toch wat anders dan een gladde *aal* in een emmer snot, terwijl de woorden *stoofaal* en *stoofpaling* ongeveer evenveel voorkomen.

Figuur 6 Een schieraal uit het Kattegat. (foto Uno Andersen)
A silver eel from the Kattegat.

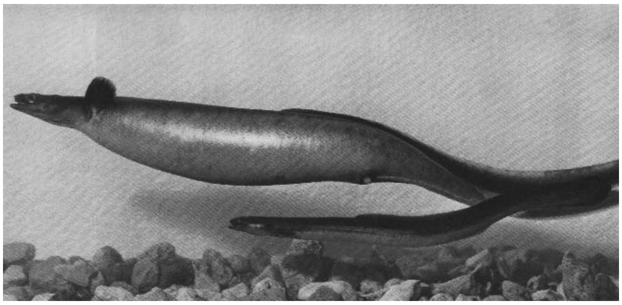
Voedsel

Eenmaal in de kust- en binnenwateren aangekomen, eten de aaltjes allerlei levende prooien, zoals wormen, watervlooien, kreeftjes en insecten. Grotere alen, vanaf ca. 25 cm, eten tevens jonge vis. Dat ook kadavers gegeten zouden worden, is slechts een fabel. Alen houden helemaal niet zo van dood vlees: hoe verser hoe beter. Daarom aast een visser zijn vistuig met pas gevangen spiering. Vroeger waren halve kikkers ook heel gebruikelijk; die kon je makkelijk vers houden, en op het laatste moment nog halveren.

Niet dat alen geen merkwaardige voedingsgewoontes erop nahouden. Bij hoogwater op de rivieren geven de overstroomde uiterwaarden de aal een kans, regenwormen te gaan zoeken op de weilanden. In rietkragen eten ze loopkevers, die boven de waterlijn rondlopen; dit komt zo vaak voor, dat het zeker geen toevalstreffer is: de aal zal ‘s nachts wel boven de waterlijn foerageren. Jonge eendjes zijn ook lekker.

Groei

In vergelijking tot andere vissen, groeit aal bijzonder langzaam: bij ons marktwaardige aal van minimaal 28 cm lang is 6-8 jaar oud. De langzame groei hangt samen met de lage temperaturen in onze buitenwateren. In zuidelijke streken en in kwekerijen kan een groei van 20 cm per jaar of meer worden bereikt, maar in uitzonderlijke gevallen kan zo’n snelle groei ook in koude buitenwateren wel eens optreden. Na de extreem koude winter van 1963 is dat bijvoorbeeld in een aantal polders waargenomen. Ondermaatse aal, in het voorjaar uit het IJsselmeer naar de polder meegenomen, groeide nog dezelfde zomer uit tot prachtig grote schieraal in het najaar. Die laatste heeft een lengte van 35 tot 45 cm (mannetjes) of meer (vrouwtjes) en trekt terug naar zee om daar aan de voortplanting te gaan deelnemen. Bij deze trek wordt zonodig een korte tocht over land niet gemeden, maar erg vaak zal dat niet gebeuren: ik heb het nog nooit gezien. Fysiologisch gezien is de



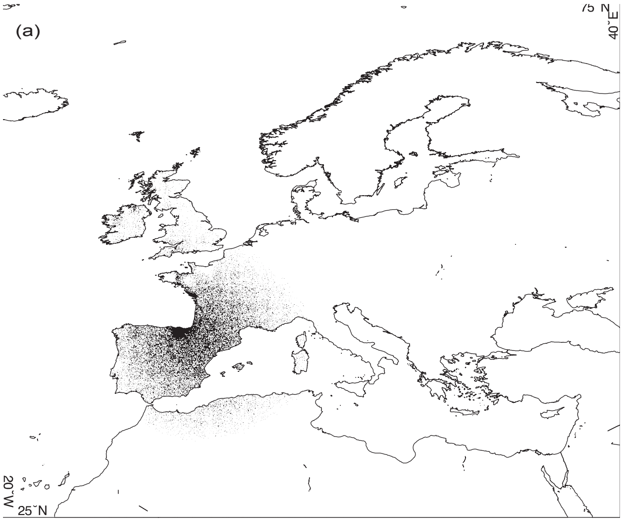
Figuur 7 Paairijpe aal (boven: vrouwtje, onder: mannetje) kunnen worden verkregen m.b.v. experimentele injecties van hormonen. (foto Jan en Inge Boëtius)
Eels in full nuptial dress; produced by hormone injections. Female above and male below.

schieraal nog vèr verwijderd van een werkelijk geslachtsrijp stadium. Een volledig geslachtsrijpe vrouwelijke aal ziet er bepaald anders uit: een zeer dikke buik, heel grote ogen en vrijwel zwarte vinnen en neus.

Een wijd verspreidingsgebied

De Europese aal komt in geheel Europa, in noordelijk Afrika en in het aan de Middellandse Zee grenzende deel van Azië voor. De Canarische eilanden in het zuiden, de Noordkaap in het noorden, de Azoren in het westen en de rivier Asi (Turks) of Orontes (Syrisch) in het oosten vormen de uiterste begrenzingen. Dat geeft de indruk van een heel ruim verspreidingsgebied. In meer detail blijkt dit echter geen juiste voorstelling van zaken te zijn: 90% van de glasaal is te vinden langs de (Franse en Spaanse) kusten van de Golf van Biskaje. Mogelijk dwaalt een klein deel van de *Leptocephalus*-larven op hun lange tocht vanaf de Sargassozee naar de Golf van Biskaje per ongeluk af, en komt in de rest van Europa terecht.

Het bestand van de rode aal op het Europese continent toont weer een heel andere verspreiding. Hoe zuidelijker men komt, des te meer aal men van een gegeven wateroppervlak kan oogsten. Vooral in de westelijke Middellandse zee komen enorm dicht-bezette en productieve wateren voor. Dat houdt waarschijnlijk verband met de hogere temperaturen, die dichter bij het optimum van 25°C liggen. Anderzijds geldt ook dat hoe zuidelijker men komt, des te minder binnenwater er voorkomt. In de Sahara is geheel geen (zoet) oppervlaktewater meer te vinden; alle rivieren drogen hier in de loop van de zomer op. In de Romeinse tijd was dat echter nog bepaald anders, en was Noord-Afrika een vruchtbaar landbouwgebied. Wellicht was daar toen ook meer aal te vinden.



Figuur 8 Verspreiding van de glasaalvisserijen naar hun opbrengst per km^2 stroomgebied van een rivier.
Distribution of glasseel fishing, according to their yield per km^2 of a river's drainage area. (See chapter 2)

Figuur 9 Productie van de rode en schier-aal naar het wateroppervlak. NB In deze figuur is geen rekening gehouden met de beschikbaarheid van (zoet) oppervlakte-water. Het Middellandse Zee-gebied is relatief erg droog en heeft weinig zoet oppervlakte-water; in de Sahara is helemaal geen water.
Production of yellow and silver eel per unit of water surface area. Note that in this figure, the abundance of (fresh) surface waters is not included. In the Mediterranean, fresh surface waters become rare, while in the Sahara, no permanent surface water exists at all. (See chapter 2)

Figuur 10 De zeezijde van de sluizen in Den Oever. Het net op de voorgrond wordt gebruikt voor de glasaalvisserij ten bate van de uitzet in onze binnenwateren. (foto Jan van Willigen)
A sea-side view on the sluices in Den Oever. The foreground net is used for glasseel fishing, re-stocking the catch in inland waters.

Glasaal-visserij

Na de metamorfose aan het eind van het *Leptocephalus*-stadium trekt de jonge glasaal naar de estuaria van de rivieren langs de Atlantische kusten, in de winter (zuidwestelijke streken) en het voorjaar (oostelijke Middellandse Zee, westelijke en noordwestelijke gebieden). In zuidelijke landen wordt de glasaal commercieel bevist, voor consumptie of verdere opkweek. Verder naar het noorden wordt de vangst van glasaal alleen gebruikt voor uitzet in nabijgelegen buitenwater.

Alle riviermondingen van Europa

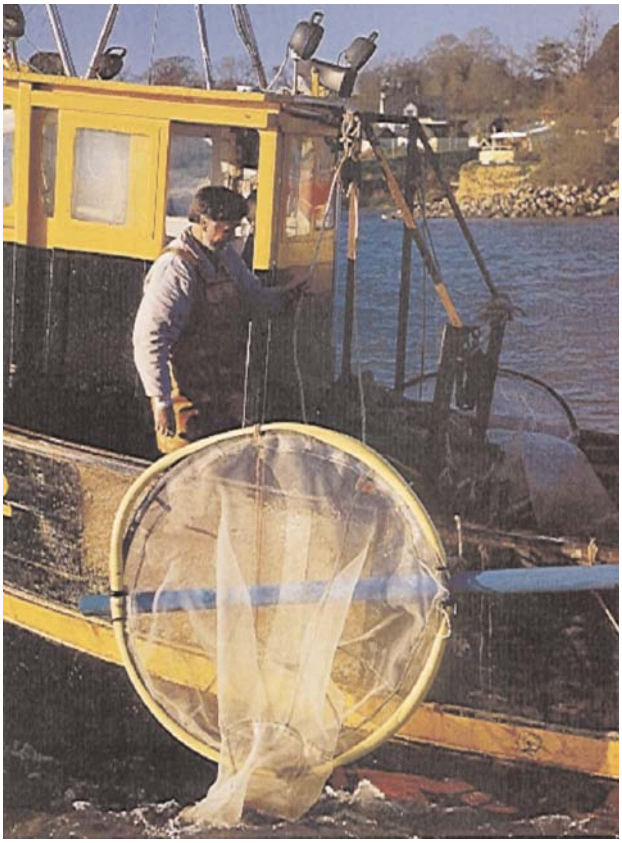
De glasaal-visserij vindt plaats in estuaria, in riviermondingen of voor dammen en barrières. In al deze gevallen is er sprake van een (meestal natuurlijke) concentratie van de glasaal, in tijd en ruimte. De migratie vanuit zee naar binnen maakt gebruik van een mechanisme, bekend als het *selectief getijden transport*. Hierbij maakt de glasaal gebruik van de natuurlijke waterbeweging, het estuarium in tijdens de vloed, terwijl ze zich tijdens de eb schuil houden in of vlakbij de bodem. Dit transport-mechanisme vraagt weinig inspanning en wordt daardoor nauwelijks gehinderd door lage watertemperaturen. Om verder de rivier op te komen moet de glasaal actief gaan zwemmen; dat vraagt een minimale temperatuur van 10-12ºC. In de winter, als het rivierwater nog koud is, kan de glasaal makkelijk het estuarium inkomen met het getij, maar moeilijk doorzwemmen de rivier op. Dientengevolge ontstaat er dan een grote concentratie, die goed te bevissen is. Deze concentratie is meestal te vinden aan de bovenstroomse kant van een estuarium, waar de vloedstroom tot stilstand komt tegen de uitstromende rivier in. Of, in de meeste Nederlandse gevallen, op de plaats waar de vloedstroom door een sluis of dam wordt tegengehouden, zoals voor de sluisdeuren van Den Oever.

Glasaal-vistuig

Glasaal-visserijen maken gebruik van allerlei verschillende vistuigen. Het meest eenvoudige is een schepnet, dat vanaf de walkant door het water wordt getrokken (Figuur 11). Veelal is er aan de onderkant van de stok ook nog een touw bevestigd, en wordt er met twee man gevist. Dezelfde methodes worden ook gebruikt vanaf een klein schip (Figuur 12). In dat geval wordt er meestal met het schip rondgevaren in de riviermonding, om de glasaal zo op te scheppen. Een vergelijkbare methode wordt ook gebruikt door de Franse *pibalours* (Figuur 13), die een rechthoekig frame aan weerskanten van de boeg van hun schip voortduwen, waarachter een lang en zeer fijnmazig net hangt. Hoe sneller men met een dergelijk net rondvaart, hoe groter de vangst; motorvermogens van meer dan de maximaal toegestane 100 pk zijn beslist geen zeldzaamheid. Naast al deze vormen van schepnetten en duwnetten, wordt er ook wel gebruik gemaakt van fuiken, opnieuw met een zeer fijne maaswijdte (Figuur 14). Fuiken zijn in het bijzonder geschikt voor plaatsen met minder grote hoeveelheden glasaal. Slechts éénmaal per dag hoeft de visser zijn fuiken te komen legen.

In noordelijke landen is de dichtheid van de glasaal meestal te gering, om er handmatig op te vissen. Nederland ligt zo ongeveer op de grens. Toen er nog veel glasaal binnentrok (tot 1980) kon er met een eenvoudig netje op gevist worden. Sinds de vermindering van de

Figuur 11 Glasaal-visserij met een in de hand gehouden schepnet. (foto Gerard Castelnaud)
Glasseel fishing, using a hand-held dipnet.



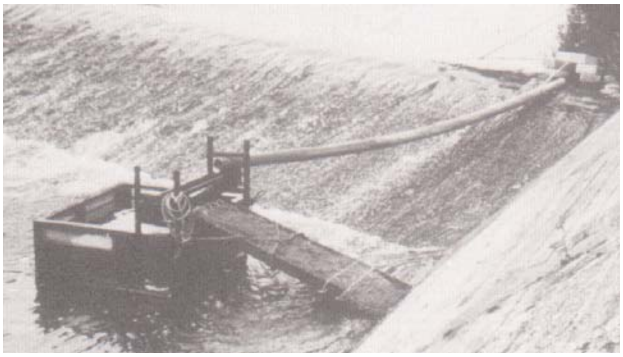
Figuur 12 Glasaal-visserij met een aan een stok aan de boot bevestigd net. (foto Gerard Castelnaud)
Glasseel fishing using a net, fixed to a boat by a pole.

intrek is dat nauwelijks meer lonend. In noordelijker landen wacht men tot de glasaal zelf de rivieren opzwemt. Door een soort val te plaatsen juist waar een rivier door een dam wordt geblokkeerd, kan de intrekkende glasaal of jonge rode aal eenvoudig worden opgevangen. De val bestaat uit een soort opvangtank, waaruit een waterstroompje sijpelt over een kunstmatig watervalletje (Figuur 15). De aal denkt de waterval te kunnen passeren, en kruipt zelf de opvangtank in.

Sinds de Afsluiting van de Zuiderzee is er in Den Oever voor wetenschappelijke doeleinden op de binnentrekkende glasaal gevist. Hierbij is gebruik gemaakt van een simpel kruisnetje, een vierkant net van 1*1 m, met een maaswijdte van 1*1 mm, dat van de bodem naar het oppervlak wordt getrokken (Figuur 16). Ogenschijnlijk is dit een inefficiënte methode. Omdat sinds 1938 altijd dezelfde methode is gebruikt, levert dit echter een heel lange reeks van onderling zeer goed vergelijkbare gegevens op.

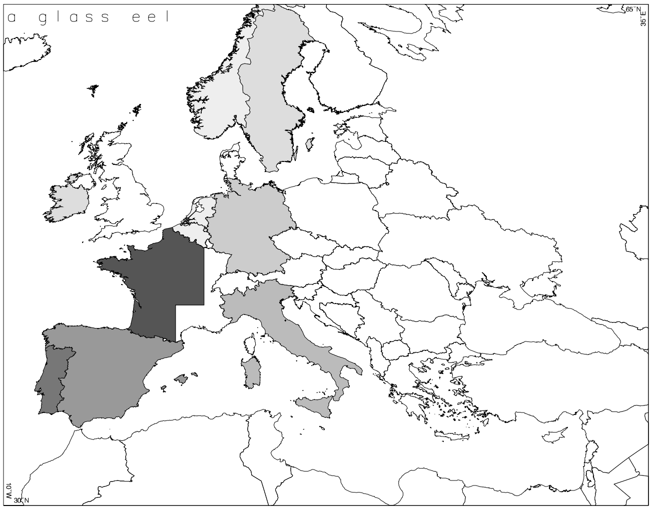
Figuur 13 Een Franse *pibalour*. Het net wordt door de boot voor zich uitgeduwd. Voor deze foto is het net iets boven het water uitgetild. (foto Gerard Castelnaud)
A French pibalour. *The net is pushed in front of the boat, just under the water surface.*

Figuur 14 Een glasaal-fuik in de Tiber, Italië. (foto Eleonora Ciccotti)
Fykenet fishing for glasseel in the River Tiber, Italy.



Figuur 15 Een typische pootaal-val, bij Adara, in de rivier the Maigue (Ierland). Links de opvangtank, van rechtsboven de water-aanvoerleiding, naar rechtsonder een lange platte bak met wilgentenen, waardoorheen water sijpelt.
A typical eel trap at Adara, in the River Maigue (Ireland). The holding tank can be seen on the left, to the right-top the water supply, to the right-bottom the ramp filled with willow twigs, with water seeping through.

Figuur 16 In Nederland wordt voor wetenschappelijke doeleinden met een simpel kruisnetje gevist. Voor deze foto is er overdag gevist, maar normaliter vindt dit ‘s nachts plaats, in het donker. (foto Jan van Willigen)
The Dutch glasseel sampling uses a simple lift net. Although this is a day-time photograph, sampling usually takes place at night time.



Figuur 17 Verspreiding van de glasaalvisserij per land, in de jaren 1990. De vangst in Spanje en Portugal is waarschijnlijk nogal onderschat. Hoe donkerder een land is aangegeven, des te hoger de vangst. In veel landen valt echter niet vast te stellen, welk deel van hun totale vangst uit glasaal bestaat.
The distribution of glasseel yield per country, in the early 1990s. Yield in Spain and Portugal is presumably severely underestimated. Darker colours indicate higher yields. In many countries, the share of glasseel in the total yield is unknown. (See chapter 9)

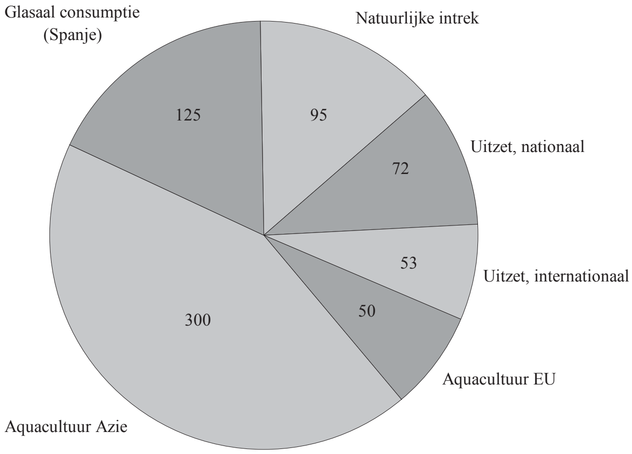
Glasaal-vissende landen

De commerciële glasaal-visserijen zijn te vinden in het zuidwesten van Europa, noordelijk tot in Engeland (Bristol Channel) en langs de Mediterrane kusten van Spanje, Italië en Afrika (Figuur 17). Langs noordelijker Atlantische kusten wordt glasaal alleen gevangen voor uitzet in binnenwateren. De grootste glasaal-visserijen worden beoefend in de grotere rivieren (Loire, Seine en Gironde in Frankrijk; Oria, Nalon en Minho in Spanje; Severn in Engeland; etc.), maar daarnaast worden ook de meeste kleinere riviertjes dikwijls wel bevist. Officiële gegevens over de kleinere visserijen worden soms wel en soms niet gevoegd bij de informatie van de grotere; soms wordt de glasaal van de kleine naar de grote rivier gebracht en daar verhandeld, soms kunnen de vissers kiezen waar ze vissen, soms worden alleen de aanvoerstatistieken achteraf bij elkaar opgeteld. Maar in de meeste gevallen is niet precies bekend of er gevist en hoeveel er gevangen wordt.

De opbrengst van de glasaalvisserij

De totale vangst van de glasaalvisserij in de jaren 1990 wordt geschat op ruim 500 ton, maar dit getal vormt zeker een onderschatting van de werkelijk gevangen hoeveelheid. Vangsten worden dikwijls in kleine vissersplaatsen al verwerkt, zijn illegaal of worden niet gedocumenteerd. In Baskenland, in Noord Spanje, werd rond 1960 een vangst van 275 ton glasaal gemeld, maar tegenwoordig is er geen enkele opgave meer beschikbaar. In de jaren 1980 is al eens eerder geprobeerd de totale vangst te berekenen (857 ton) op basis van schattingen door deskundigen. Het is wel zeker dat toen een groot deel van de vangst gemist is, waaronder geheel Spanje. De lagere vangst-cijfers in de jaren 1990 komen in ieder geval overeen met de daling in onafhankelijke, betrouwbare cijfers over de hoeveelheid glasaal (zie hieronder).

De internationale statistieken van de aal-vangsten maken geen onderscheid tussen glasaal enerzijds en rode en schier-aal anderzijds. Omdat rode en schieraal zoveel zwaarder zijn dan glasaal, zeggen deze cijfers dus eigenlijk niets over de glasaal-vangsten en het gebruik van die vangst. Op basis van de beperkte beschikbare statistieken en met aanvullingen uit gesprekken met vissers en handelaren, kan het volgende beeld voor het eind van de jaren 1990 worden opgebouwd. Het grootste deel van de vangst wordt gebruikt voor aalkweek in Azië; ca. 20% van de glasaal wordt als glasaal geconsumeerd, merendeels in Spanje; ca. 20% wordt gevangen en elders (binnen en bui-



Figuur 18 Gebruik van de glasaal. De cijfers geven de geschatte hoeveelheden (ton per jaar) aan.
Disposition of glasseel landings. Numbers indicate estimated quantities in tonnes per year. (See chapter 9)

ten het land van herkomst) uitgezet in buitenwateren en ca. 15% van de glasaal kan vrijelijk de rivieren opzwemmen.

Sinds 1980 steeds minder glasaal

In vele landen in West Europa wordt de omvang van de glasaal-intrek wetenschappelijk vastgesteld. Hierbij wordt gebruik gemaakt van statistieken van commerciële vangsten, import-export-gegevens, wetenschappelijke bemonsteringen, vangststations voor pootaal etc. Het gaat zowel om de glasaal-visserij, als visserij-onafhankelijke gegevens. In deze cijfers is een opmerkelijke, abijna overal optredende ontwikkeling zichtbaar: een daling sinds 1980, tot op een niveau van ca. 10% ten opzichte van de periode daarvoor. De daling is opgetreden in zowel commerciële als in niet-commerciële gegevens, in Noord- en Zuid-Europa, etc. Slechts de pootaal in Scandinavië en de glasaal van de Britse Eilanden laten een ietwat afwijkend beeld zien, met een eerdere resp. mindere daling.

Sommigen van de reeksen lopen al langer dan 60 jaar (Frankrijk, Nederland, Duitsland en Zweden). In het bijzonder de kruisnet-bemonstering in Den Oever vormt een van de allerlangste en de meest betrouwbare series. Vanaf ca. 1950 kan een duidelijke trend worden vastgesteld (Figuur 20). Direct na de Tweede Wereldoorlog was er een arme periode van een aantal jaren, gevolgd door een zeer rijke periode in de jaren 1950, 1960 en 1970. Maar vanaf 1980 trad een gedurige daling op, die tenminste tot 1990 doorzette. Gedurende de jaren 1990 was er sprake van een redelijk stabiel, maar laag niveau. In 2001 trad echter een zeer scherpe verdere daling op, tot op nog maar 1% van het oorspronkelijke niveau. Daarna is de situatie niet verder verslechterd, maar van herstel is ook geen sprake.

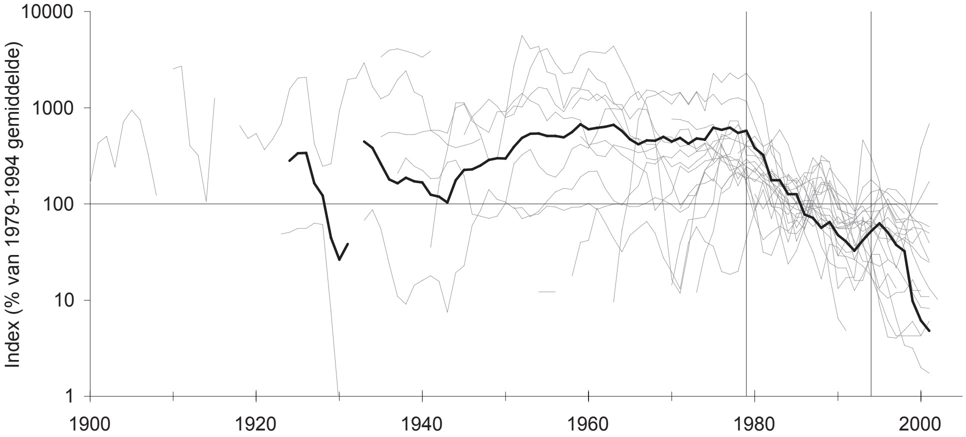
Glasaal-uitzet

Natuurlijke aalpopulaties concentreren zich meestal in estuaria en de benedenloop van rivieren. Bovenstrooms zijn alen aangetroffen tot op meer dan 1000 km van de monding, maar de gemiddelde verplaatsing rivieropwaarts is meestal niet veel sneller dan ca. 20 km per jaar. Een door de mens uitgevoerd transport van glasaal en pootaal van beneden naar boven in de rivier heeft dikwijls een aantoonbaar positief effect op de visserijopbrengst, net als transporten van het centrum van de verspreiding (Frankrijk en Spanje) naar de randen (Nederland, Duitsland, Scandinavië, Midden-Europa). Kennelijk is de dichtheid van de natuurlijke stand in grote delen van het verspreidingsgebied ver beneden de capaciteit van het ecosysteem, terwijl het bestand in Frankrijk en Spanje wel een deel van hun glasaal kan missen.

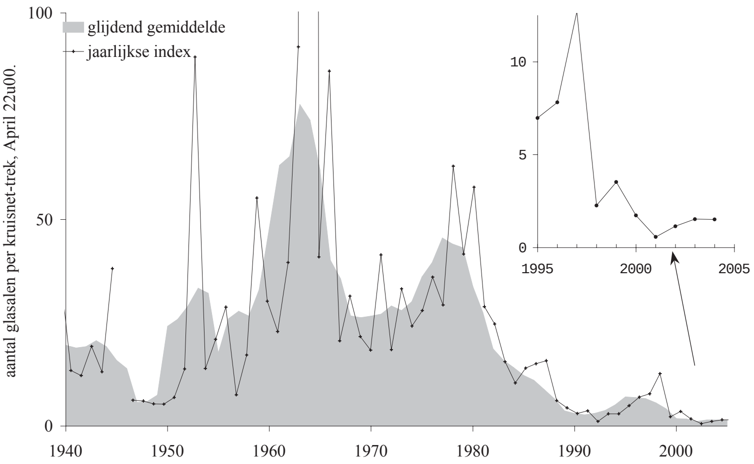
Ontwikkeling in de uitzet van glasaal

In 1908 hebben de Duitsers in Epney, op de oever van de Severn in Engeland, een glasaal-station opgezet, waarvandaan levende glasaal naar Hamburg werd getransporteerd. In de periode voor de Tweede Wereldoorlog betrof dit ruim één ton per jaar. Na de Oorlog nam het transport van glasaal vanuit Zuid-Europa naar Centraal en Noord-Europa een grote vlucht (Figuur 22). Uitzet van Franse en Engelse glasaal werd een van de standaard beheersmaatregelen in Noord- en Oost-Europa (Figuur 23). Na 1980

Figuur 19 Een oude foto van een onderzoeker op bezoek bij het glasaalstation in Epney. Vermoedelijk een opname uit 1955.
An old picture of a scientist visiting the Epney glasseel station. This picture dates from 1955, presumably.



Figuur 20 De ontwikkeling in de aanwas van glasaal over de afgelopen eeuw. Individuele gegevens-reeksen uit alle deelnemende landen in grijs, de gemeenschappelijke trend (gemiddelde van de vier langste series) in zwart.
Trend in glasseel recruitment during the past century. Original data in grey, common trend (average of four longest data series) in black. (See chapters 4, 5 and 9)

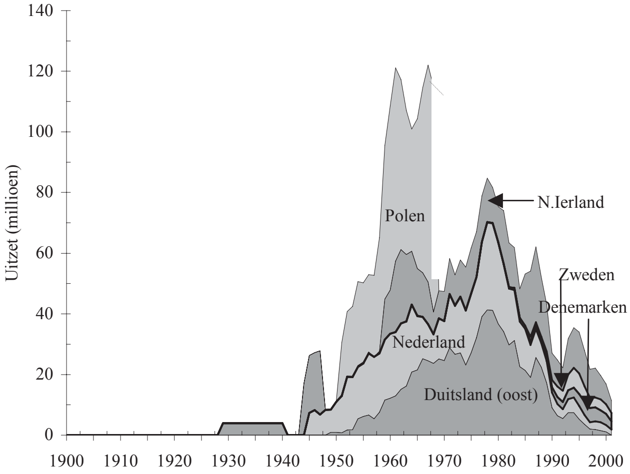


Figuur 21 De ontwikkeling van de glasaal-intrek in Den Oever. De vangsten van de gehele nacht en het gehele voorjaar zijn gemiddeld en worden hier uitgedrukt als een vangst (in april) in de vooravond (22u00).
Trend in glasseel recruitment at Den Oever. Data referring to whole nights, throughout each spring, have been averaged, and are here expressed as an expected catch in April, at 10 p.m. (See chapter 5)

werd de glasaal echter zo schrikbarend duur, dat uitzet niet langer betaalbaar was. De meest recente schatting voor geheel Europa (begin jaren 1990) noemt nog 33 ton, maar sindsdien is de hoeveelheid zeker nog aanmerkelijk gedaald.

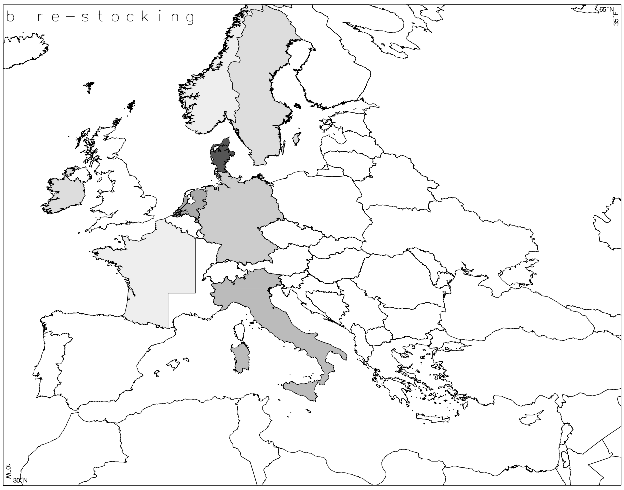
Het effect van uitzet van glasaal

De uitzet van glasaal in afgesloten wateren heeft een positief effect op de opbrengst een paar jaar later. Dit is onder meer gebleken in vijverproeven in Nederland, maar ook in de evaluatie van wetenschappelijke experimenten in Zweden en grootschalige uitzet-programma's in Polen. De omvangrijke uitzet in geheel Europa is de meest waarschijnlijke verklaring voor de toename van de vangsten in de jaren 1960, in het bijzonder in de noordelijke helft van Europa. Of uitgezette glasaal wel leidt tot de productie van volwaardige schieralen is echter nog niet zeker. Merkproeven in de Oostzee met schieraal afkomstig van Franse glasaal toonden, dat deze de uitweg uit de Oostzee niet altijd kon vinden, in tegenstelling tot de natuurlijk ingetrokken glasaal. Het is daarom waarschijnlijk veiliger aan te nemen dat uitgezette glasaal niet bijdraagt aan het behoud van de paaistand.



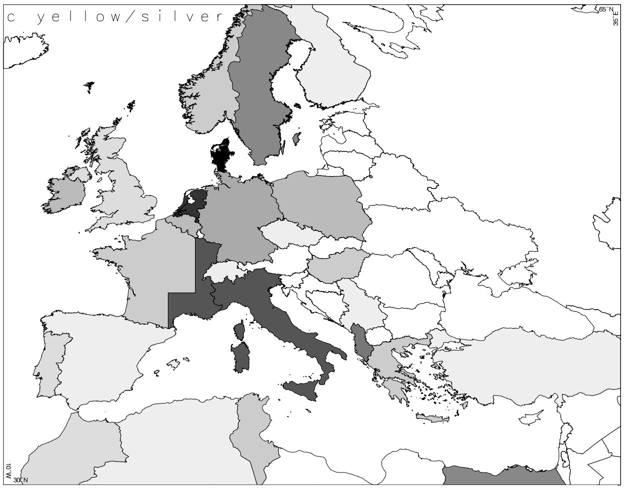
Figuur 22 De ontwikkeling in de uitzet van glasaal gedurende de 20e eeuw. Gegevens over Polen na 1970 zijn niet bekend.

Trend in glasseel re-stocking during the 20th century. Data for Poland after 1970 are unknown. (See chapter 9)



Figuur 23 Verspreiding van de uitzet van glasaal in de jaren 1990. Hoe donkerder een land is aangegeven, des te meer glasaal er uitgezet is.

Distribution of glasseel re-stocking, in the early 1990s. Darker colours indicate higher quantities being re-stocked. (See chapter 9)



Figuur 24 Verspreiding van de rode en schieraalvisserij in de jaren 1990. Hoe donkerder een land is aangegeven, des te hoger de vangst.

Distribution of yellow and silver eel fisheries in the early 1990s. Darker colours indicate higher yield. (See chapter 9)

Rode en schieraalvisserij

In nagenoeg alle kust- en binnenwateren van Europa is de aal te vinden. En waar dat van nature niet zo is, heeft de mens wel glasaal uitgezet. En in al deze wateren wordt er ook op rode aal gevist. Over heel Europa gerekend, levert dat een bonte verzameling van visserijen, met tal van vismethodes.

Verspreiding van de visserij

Visserij op rode en schieraal vindt plaats in het gehele verspreidingsgebied van de aal (Figuur 24). In Midden- en Noord-Europa vormt dit de belangrijkste aalvisserij. In zuidelijke landen komt weliswaar visserij op rode of schieraal voor, maar is de glasaal veel belangrijker (ca. 30 maal meer alen, ruim 3 maal de waarde). Schieraalvisserijen zijn al bekend uit de steentijd, toen met vast opgestelde visweren gevist werd. Nu komt exclusief op schieraal gerichte visserij eigenlijk alleen nog maar in Scandinavië voor, waar in de kustwateren met zeer grote fuiken gevist wordt. Waarschijnlijk is de focus op de schieraal een manier om de lage aalstand in Noord-Europa (25 alen per km^2 stroomgebied) nog te kunnen exploiteren. Gedurende de schieraaltrek concentreert de in de binnenwateren geproduceerde aal zich in tijd (najaar) en ruimte (riviermondingen), waardoor een profijtelijke visserij in zeer dunbevolkte gebieden mogelijk wordt. In Midden-Europa, bij een gemiddelde dichtheid van de aalstand (400 stuks per km^2 stroomgebied) richt de visserij zich grotendeels op de rode aal, met een bijvangst van schieraal. Ter vergelijking: in typische glasaalgebieden bedraagt de dichtheid van het bestand ca. 1500 glasalen per km^2 stroomgebied.

Vistuigen voor rode en schieraal

De visserij op rode en schieraal maakt gebruik van een heel scala aan vistuigen, zoals netten en fuiken, speren, potten en kisten en haken, en wordt uitgeoefend in kustgebieden, in lagunes, in rivieren, meren, beken en alle

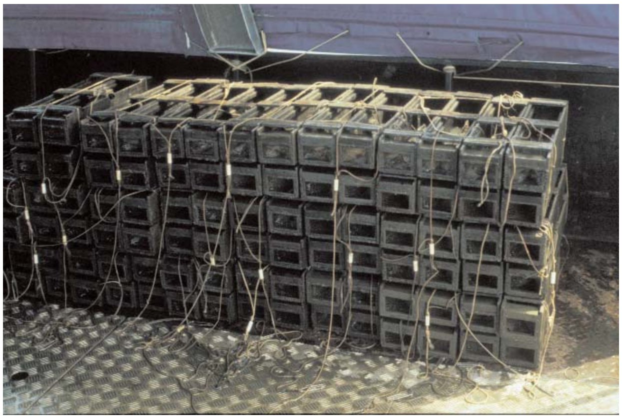
Figuur 25 Fuikenvisserij op rode aal. (foto Jan van Willigen)
Fyke-net fishery for yellow eel.

Figuur 26 Drogende schietfuiken langs de weg bij Makkum. (foto Jan van Willigen)
Summer fyke-nets near Makkum, set along the road side to dry.

Figuur 27 Komfuiken bestaan uit een zeer lang schutwant (waarvan alleen de lange rij drijvers in de verte te zien is), met een komvormige kamer (drijvers op de voorgrond). De bodem van de kamer kan opgetrokken worden, zodat de vis (in de kamer en in de daaraan bevestigde fuiken) makkelijk verzameld kan worden. Komfuiken (*bottengarn* of *bundgarn)* worden in de Oostzee veelvuldig gebruikt voor de schieraalvisserij. (foto Robert Russell)
*Pound nets are very large nets, consisting of an extremely long leader (visible by the long line of floats to the background), with a chamber at the end (floats in the foreground). The bottom of the chamber can be lifted, in order to collect the catch (from the chamber and the attached fyke-nets). Pound nets (*bottengarn *or* bundgarn*) are commonly used in the Baltic, fishing for silver eel.*

mogelijke kleinere wateren. Wellicht het meest gangbare vistuig is tegenwoordig de fuik, in al zijn soorten en maten. Dat varieert van een kleine polderfuik (Figuur 25), tot een grote komfuik in de Oostzee (Figuur 27). Voor de invoering van de moderne kunststofgarens, waren fuiken duur en moeilijk te onderhouden. In die tijd waren kubben veel gangbaarder, maar ook nu wordt er nog met kubben gevist. Het belangrijkste verschil met een fuik is dat een kub van wilgentenen gevlochten is, en dikwijls van wat aas wordt voorzien. De moderne variant daarvan is gemaakt van plastic, maar ziet er nog steeds uit als gevlochten wilgentenen. Een stap verder zijn de aalkistjes van het IJsselmeer (Figuur 28): een (multiplex) houten kistje, waarin altijd wat aas aangebracht wordt. Vrijwel het hele kistje is gesloten; slechts aan de twee uiteinden is een opening, afgesloten met een klein netje, dat de aal maar in één richting doorlaat.

Lijnen met haken vormen een tweede groep van aalvistuigen. Deze komen in een aantal verschillende vormen voor. Dobbers hebben telkens één haak aan een drijvertje, en werden vooral gebruikt in gebieden met overvloedige waterplanten. Het hoekwant (Figuur 29) bestaat uit een lange lijn, die in het water over de grond ligt, en waaraan telkens zijlijntjes met een haakje zitten. Hoekwant is vooral in gebruik op grotere wateren, zoals het IJsselmeer. Alle vistuigen met haken worden van aas voorzien, dat door de aal gegeten moet worden. Meestal wordt hier vis voor gebruikt: spiering, of vroeger ook pos, soms ook halve kikkers of regenwormen. Omdat de aal bijzonder kieskeurig is, moet de visser ervoor zorgen dat het aas zo vers mogelijk is, en niet met vieze handen (vroeger had men petroleumlampen aan boord) is aange-



Figuur 28 Aalkisten staan op het dek gereed. Nadat de kisten zijn ge-aast, kan de deksel erop, en kunnen ze aan een lange lijn te water worden geschoten. (foto Jan van Willigen)

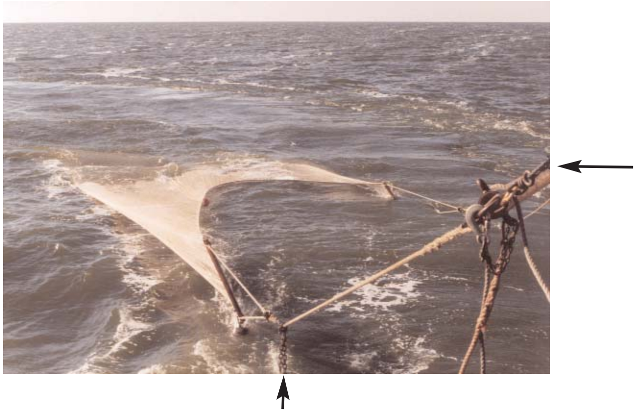
Eel boxes stowed on board, ready to be set. After the bait has been added, the lid is closed, and a string of boxes attached to a long line is released into the water.

Figuur 29 Het hoekwant bestaat uit een lange lijn (de balk), met daaraan dwarslijntjes met haken; op de foto zijn de haken netjes op een staande spleet geregen. Elk haakje wordt met de hand van aas voorzien. (foto Jan van Willigen)

A typical longline fishery consists of a long rope, to which smaller side lines are attached, fitted with hooks; the hooks in the photograph are carefully arranged on a vertical peg. Bait is attached to each hook by hand.

Figuur 30 Een peur bestaat uit een op een wollen draad opgewonden kluwen wurmen, met een loodje erboven. De toehappende aal blijft net lang genoeg hangen, om binnen boord gehaald te kunnen worden.

A sniggle consists of a bunch of worms, coiled around a woollen thread, with a weight on top. When an eel bites, it is left dangling on the sniggle, just long enough to hoist it into your boat.



Figuur 31 Het belangrijkste vistuig op het IJsselmeer was tot 1970 de grote kuil, bestaande uit een 27 m lang net (links), opengehouden door twee stokken van 1 m hoog en een 8 m brede houten boom (rechts nog tegen het schip aan, pijl rechts), dat met gewichten (pijl onder) op de bodem gehouden wordt. Het net wordt achter het schip gesleept. (foto Betty van Os)

*The main fishing gear on Lake IJsselmeer until 1970 was a trawl (*grote kuil*) consisting of a 27 m long net (left), opened by two vertical wooden poles (*dan lenoes*) and a horizontal 8 m beam (right, close to the ship; arrow); weights attached to the beam kept the net to the bottom. The net is towed behind the ship.*

pakt. Omdat alleen grotere aal (>25 cm) geregeld vis eet, vissen hoekwant en dobbers selectief op grotere aal.

De peur is een heel speciaal aalvistuig, waarmee hengelaars goed aal kunnen vangen. Het bestaat uit regenwormen aan een hengel. Anders dan bij de gewone hengel of dobber, zit er niet een haak in, maar een wollen draad. De toehappende aal blijft met de tandjes op zijn kaken hierin hangen, net lang genoeg om snel boven water uitgetild te worden. Juist aanvoelen wanneer er een aal hapt, en snel de aal binnen boord hijsen is nog een hele toer. Is men die kunst machtig, dan kan de peur een flinke hoeveelheid aal opleveren.

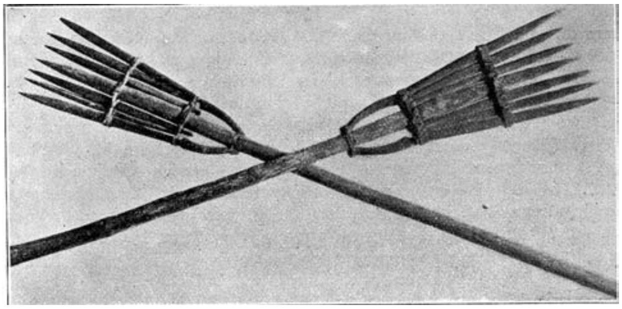
De vroegere Zuiderzee en het huidige IJsselmeer kenmerken zich door uitgestrekte open wateroppervlakken, met een relatief ondiepe en vlakke waterbodem. Deze kenmerken zijn van toepassing op vele kustwateren nabij de monding van rivieren. In deze omstandigheden wordt meestal op een geheel andere wijze gevist, met een gesleept net, zoals een kuil (Figuur 31) of een kor (Figuur 32). Op de Noordzee is de oorspronkelijk gevarieerde Nederlandse visserij inmiddels vrijwel volledig overgegaan op gesleepte netten (veelal aangeduid met de Engelse naam *trawl*; een trawler). Ook de visserij op de Zuiderzee werd gedomineerd door gesleepte netten, hoewel er begin 20^{e} eeuw een zeer felle politieke strijd is gevoerd tussen vissers met gaand en staand want. Na de Afsluiting van de Zuiderzee is deze visserij op het IJsselmeer voortgezet, tot in 1970 het verbod op gesleepte netten, dat in de overige Nederlandse binnenwateren gold, ook tot het IJsselmeer werd uitgebreid. In de jaren 1930-1970 werden proefvisserijen aan boord van onderzoeksschepen opgezet met gesleepte netten (voornamelijk met de grote kuil), en die worden tot op de dag van vandaag nog steeds gebruikt. Nog ieder jaar vist MS *Stern* (Figuur 52) met een type net van een halve eeuw oud, en de snelheid van een zeilschip, op het IJsselmeer. En juist die ogenschijnlijk conservatieve benadering maakt, dat een lange reeks gestandaardiseerde gegevens beschikbaar is, waarmee een goede vergelijking gemaakt kan worden tussen de visstand van toen en nu.

Figuur 32 In midden jaren 1970 is de elektrokor ontwikkeld die, in tegenstelling tot de grote kuil, ook bij helder weer en overdag goed aal kan vangen. Bij deze kor zijn de losse stokken vervangen door vaste sloffen, en tussen de sloffen wordt een elektrische spanning van ca. 300 V aangelegd (gele kabels rond de boom en sloffen), die de aal uit de bodem naar boven jaagt. Dit net-type is nooit in de commerciële visserij toegestaan, maar vormt het belangrijkste vistuig voor het huidige aalonderzoek op het IJsselmeer. (foto Betty van Os)

In the mid 1970s, an electrified trawl was developed. In contrast to the traditional beam trawl, this electrified trawl could also be operated under clear weather conditions, and during the day. The dan lenoes are replaced by fixed sledges, and a 300 V electric power is applied between the sledges (yellow cables around the beam and sledges), chasing the eel out of the mud. This trawl has never been allowed in the commercial fishery, but is the main fishing gear in current eel research surveys on Lake IJsselmeer.

Tenslotte is er nog een groep van vistuigen voor rode aal, waarbij de visser zelf actief de aal moet vangen. Heeft men eenmaal een aal gezien, dan kan deze met een traditionele aalspeer (Figuur 33) worden verschalkt. Elgers (*eel gears*) hebben de vorm van een puntige hark, en worden lukraak door de bodem getrokken. Hoewel in Europa het gebruik van aalsperen en elgers eeuwenlang gangbaar is geweest, zijn ze nu nog maar op enkele plaatsen in gebruik. Arbeidsintensief, en bovenal is mooie grote aal zeldzaam geworden.

Een zeer modern aalvistuig, is het elektro-schepnet (Figuur 34). Tussen een boot en het schepnet wordt een elektrische spanning aangelegd, waar de aal door wordt aangetrokken. Zodra de aal binnen het bereik van de vis-



Figuur 33 Traditionele aalsperen van de Maori (Nieuw Zeeland). In Europa werden vergelijkbare, smeedijzeren aalsperen gebruikt.

Traditional eel spears from the Maori (New Zealand). Comparable spears in Europe were produced from welded iron.

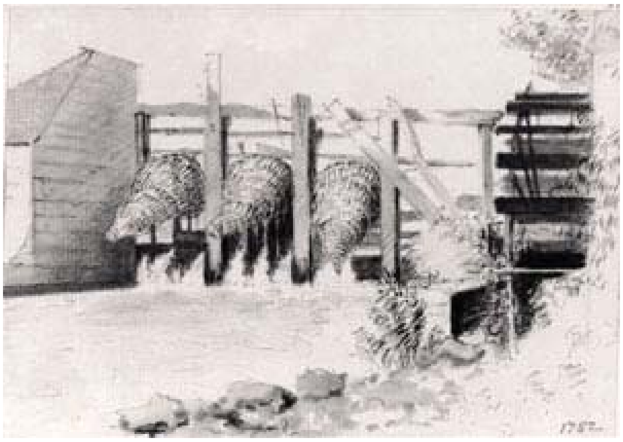
ser is gekomen, kan deze eenvoudig met een tweede schepnet worden opgevist. Het gebruik van elektrische apparatuur stelt natuurlijk eisen, maar het elektro-schepnet is een zeer efficiënt vistuig.

De schieraal trekt in het najaar terug naar zee, veelal 's nachts, bij donkere maan. Tijdens deze reis wordt er niet meer gegeten. De snelste route naar zee is tevens ook de makkelijkste: de aal laat zich simpelweg meevoeren op de waterstroom van de rivier. En op deze manier wordt ook gegarandeerd de weg naar zee gevonden. Dieren in afgesloten of moeilijk bereikbare wateren zullen actief op zoek moeten naar een uitgang. Als die afwezig is, willen ze daarbij zelfs wel eens een korte route over land nemen, maar erg vaak komt dit niet voor.

De visserij op schieraal maakt gebruik van netten die de trekroutes blokkeren (fuiken met lange vleugels, dichtzetten), of het water van de rivier filtreren (Figuur 35). Een goede blokkade van de trekroute kan ook worden verkregen met dammen van stenen en wilgentenen (Figuur 37) met daartussenin een net.

Figuur 34 Het elektroschepnet (voor) lokt de aal uit de rietkraag, een tweede net wordt gebruikt om ze op te scheppen.
The electro-fishing equipment (foreground) lures the eel from the reed fringe; a second net is then used to scoop them out.

Figuur 35 Een drietal schokkers ligt voor anker op een vaste plaats in de rivier, met een ankerkuil terzij. De wegtrekkende schieraal laat zich op de stroom voortdrijven, en zwemt recht de ankerkuil in, die hier aan bakboord (voor de kijker rechts) van het schip nog juist aan het wateroppervlak zichtbaar is. Bij twee schepen hangt het net in de mast te drogen. (foto Jan van Willigen)
Three schokkers, *with their stow nets, anchored at a fixed place. Silver eel, migrating towards the sea, swims with the water current, and gets caught in the net. The beam on top of the net can be seen on port-side (for the viewer right) of the ship. Two of these ships have their net hoisted into the mast, in order to dry.*



Figuur 36 Bij Engelse watermolens werden wilgentenen manden gebruikt voor de schieraalvangst. Hier een tekening van de watermolen bij Iffley.
English watermills were often equipped with willow twig baskets to catch silver eels. This drawing depicts the watermill at Iffley.

Figuur 37 De schieraal-weer bij Portna in de Bann, N. Ierland. (foto Robert Rosell)
The silver eel weir at Portna, River Bann (N. Ireland).

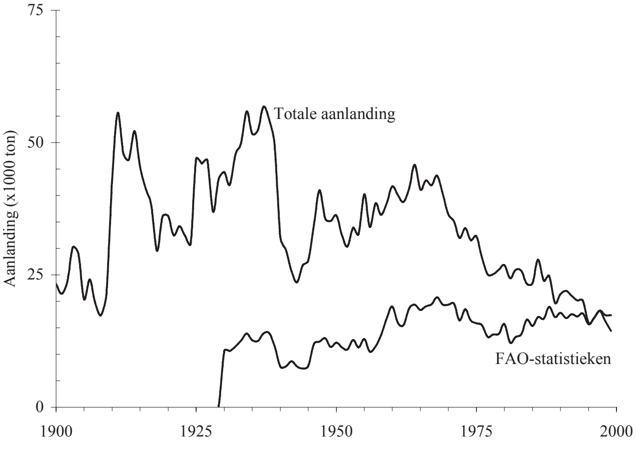
Bij watermolens was de schieraalvisserij vaak ingebouwd in de molen en watergangen, en vormde de visserij een eeuwenoud en belangrijk onderdeel van het inkomen van de molenaar (Figuur 36).

Ontwikkelingen in de vangst

Gegevens over de omvang van de totale aalvisserij zijn gerenommeerd onvolledig. Vergelijking van de officiële cijfers met de best beschikbare schattingen maakt aannemelijk dat de statistieken voor vele landen slechts ongeveer de helft van de werkelijke vangsten omvatten. Dat is ook voor Nederland het geval. Recentelijk gerapporteerde cijfers maken zelfs geen onderscheid meer tussen aalvisserij en aalkweek en zijn daarmee helaas volstrekt onbruikbaar geworden.

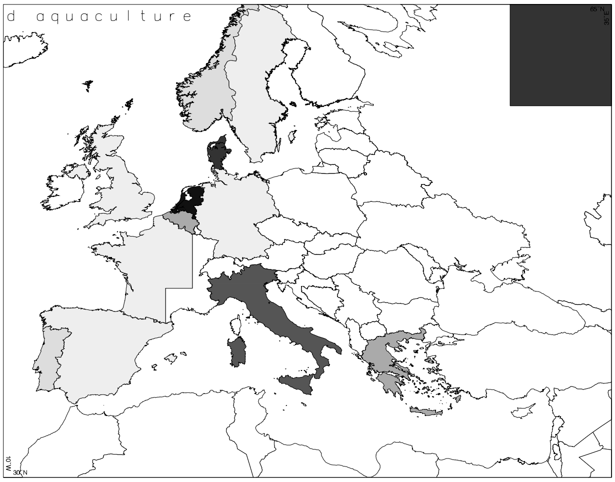
Op basis van alle beschikbare (officiële en onofficiële) cijfers is toch de trend in de internationale vangsten zo goed mogelijk gereconstrueerd (Figuur 38). In de periode voor de Tweede Wereldoorlog zijn weinig gegevens beschikbaar, waardoor niet veel meer gezegd kan worden dan dat de vangsten varieerden rond een gemiddeld niveau van ca. 47000 ton. Gedurende de oorlog is er een duidelijk en begrijpelijk dal te zien, gevolgd door een geleidelijke stijging tot 47000 ton in 1964. Daarna zette een zeer langzame maar gestage daling in, tot op een historisch dieptepunt van 22000 ton in de afgelopen jaren. De getoonde reconstructie compenseert voor het feit dat vele landen pas in de laatste decennia zijn gaan rapporteren, maar houdt geen rekening met omvangrijke vangsten die nog nooit in de statistieken zijn terechtgekomen. Nederland rapporteert sinds 1939 hoeveel er op het IJsselmeer gevangen werd, maar vangsten elders in ons land ontbreken nog immer in de statistieken. Waarschijnlijk hebben die ongedocumenteerde vangsten wel een zelfde trend meegemaakt.

De stijging van de vangsten tussen 1945 en 1964 valt samen met de verwachte opbrengstverhoging ten gevolge van de uitzet van glasaal sinds de Tweede Wereldoorlog. Bovendien vond deze stijging vooral plaats in Noordelijke landen, waar de uitzet juist het meest omvangrijk plaatsvond (Figuur 23). Dit maakt het aannemelijk dat zonder deze uitzet er mogelijk al veel eerder een gestage daling was ingezet. Tegelijkertijd is het ook duidelijk, dat de uitzet van glasaal lang is toegenomen, tenminste tot 1980 (Figuur 22). De achteruitgang in de vangsten sinds 1965 vond dus plaats, ondanks dat er meer en meer glasaal werd uitgezet, en terwijl de natuurlijke intrek ook maximaal was. De dalende vangsten in de jaren 1960, 1970 en 1980 zijn dus niet te wijten aan een tekort aan glasaal, maar moeten samenhangen met een verandering in de binnenwateren.



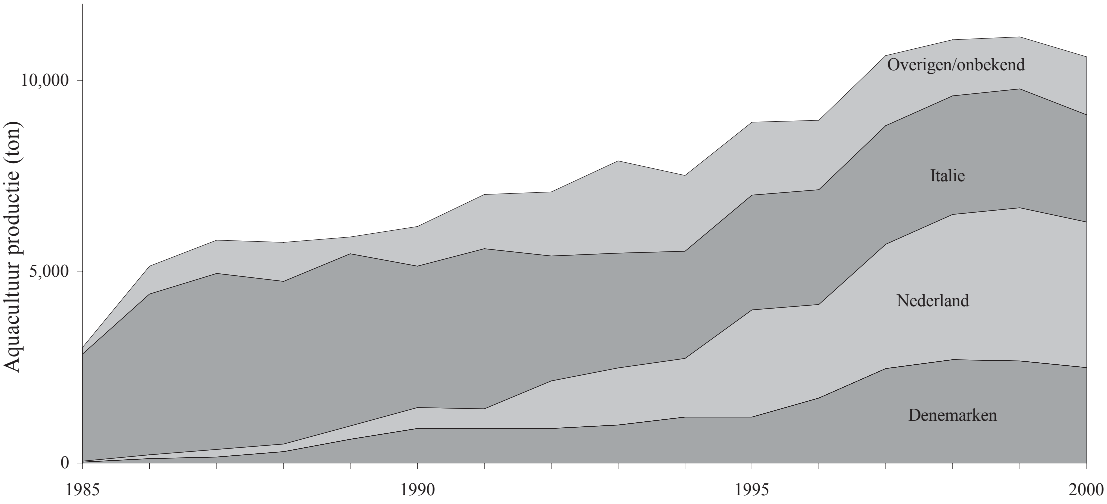
Figuur 38 Aanlanding van aal gedurende de 20^{e} eeuw: reconstructie van de trend op basis van beschikbare gegevens. De som van de FAO-statistieken laat ogenschijnlijk een toename zien, maar dat is vertekend door een toenemend aantal rapporterende landen.

Landings during the 20th century. The raw sum of statistics reported to FAO shows an apparent increase, but a reconstruction of the total does not. Not the yield, but the reporting rate has increased. (See chapter 6)



Figuur 39 Verspreiding van de aalkweek in Europa. De kweek in oost Azië is in een vierkant rechtsboven aangegeven, op een oppervlak gelijk aan dat van Japan. Hoe donkerder een land is aangegeven, des te hoger de opbrengst van de aalkweek.

Distribution of aquaculture in Europe. The production in Eastern Asia has been indicated in the top-right corner, in a square of the same surface area as Japan. Darker colours indicate higher production. (See chapter 9)



Figuur 40 Ontwikkeling van de aquacultuur-productie in Europa.
Trend in aquaculture production in Europe. (See chapter 9)

Kweek van de Europese aal

De kweek (of aquacultuur) van Europese aal is veel later van de grond gekomen dan de kweek van de Japanse aal. In 1970 bedroeg de Europese kweek ca. 3400 ton, terwijl in Japan al 17000 ton werd gekweekt. Rond 1970 hebben de Japanners een aantal jaren geprobeerd Europese aal te kweken, maar dat had toen weinig resultaat. In het midden van de jaren 1980 hebben ze het nogmaals geprobeerd, resulterend in een groei van 3000 ton (1985) naar 10000 ton nu. De kweek in Europa wordt momenteel ook geschat op ca. 10000 ton (Figuur 40). In het Verre Oosten wordt inmiddels meer dan 180000 ton van alle aalsoorten samen gekweekt.

De Italiaanse aquacultuur heeft een lange geschiedenis, tenminste teruggaand tot de Romeinen. In de afgelopen eeuwen heeft de kweek zich geconcentreerd in de *valli* in Noord-Italië. In deze systemen worden natuurlijk ingetrokken glasalen opgekweekt in natuurlijke lagunes, waarin de mens echter ingrijpt in de waterloop

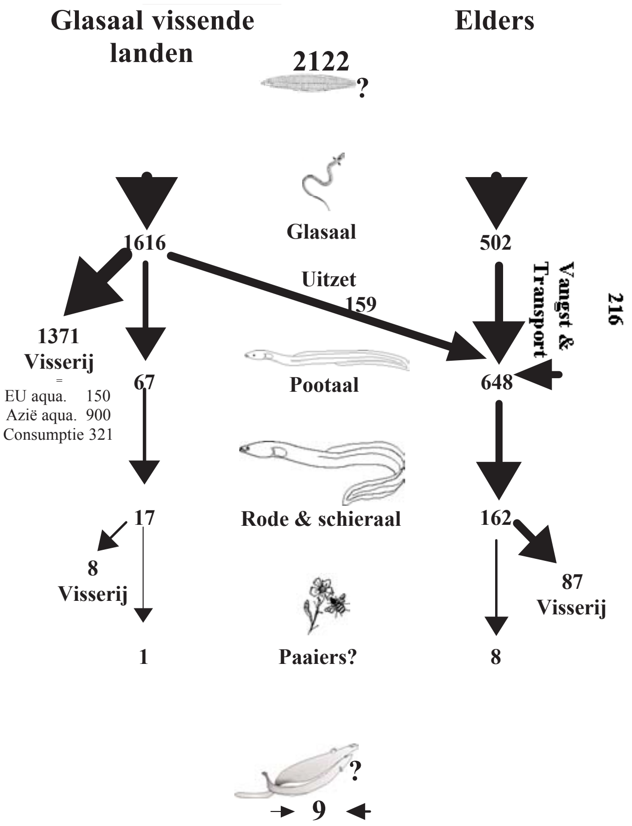
Figuur 41 De vangst van schieraal in de kweekvijvers, de *valli* van Comacchio, Italië.
Harvesting of silver eel in the ponds, the valli *of Commacchio, Italy.*

Figuur 42 Een moderne aalkwekerij, met midden-boven een voederautomaat. (foto Andries Kamstra)
Modern eel aquaculture. An automatic feeder can be seen in top-centre.

(zoet/brak/zout, koud/warm, zuurstofrijk/-arm, etc.) en daardoor de productie tot grote hoogte kan opschroeven. Sinds de achteruitgang van de glasaal (1980) is in toenemende mate gebruik gemaakt van uitgezette glasaal, afkomstig van de Italiaanse west-kust. Daarnaast zijn er een aantal moderne aalkwekerijen ontstaan, vergelijkbaar met moderne bedrijven in noordelijker landen.

De moderne, intensieve kweek van aal is geheel gebaseerd op een hoog-technologische en vèrgaand geautomatiseerde bedrijfsvoering, waarin meestal gebruik gemaakt wordt van waterzuivering en -recirculatie. Aan het eind van de jaren 1980 zijn deze systemen in gebruik genomen in een hele reeks van landen. Gedurende de jaren 1990 is de kweek in Denemarken en Nederland gestaag doorgegroeid, terwijl elders alweer sprake was van een afname. Denemarken en Nederland domineren nu de markt, terwijl de kweek in Italië nog steeds omvangrijk is, maar licht afneemt.

De kweekaal wordt merendeels afgezet binnen Europa. Uitzet van kweekaal in buitenwateren is tegenwoordig zeldzaam en draagt waarschijnlijk niet bij aan de voortplanting.



Figuur 43 Samenvattend overzicht van de omvang van de Europese aalstand per levensfase (aantallen in miljoenen). De aantallen hebben betrekking op de vroege jaren 1990. Telkens is aangegeven hoeveel dieren er aanwezig zijn, hoeveel daarvan door de visserij worden opgevist, etc. De niet-verklaarde afname van de aantallen is het gevolg van natuurlijke sterfte.

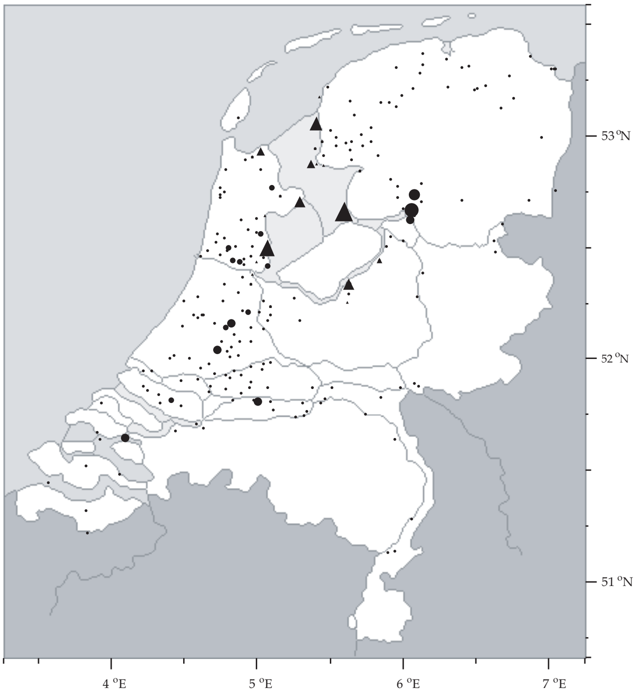
Schematic overview of the population size of the European eel by life stage (numbers in millions). Numbers refer to the early 1990s, and indicate the size of the population, respectively the number of eels harvested. Natural mortality explains the missing numbers in this picture. (See chapters 3 and 9)

Vele kleintjes maken een grote

Hierboven is een overzicht gegeven van de aalstand en aalvisserij in Europa. Voor elk levensstadium op het continent is de verspreiding van de visserij en de ontwikkeling in de tijd besproken. De hele situatie nu samenvattend (Figuur 43), ontstaat een beeld van een intensief door de mens beïnvloede vis. Dat betekent echter geenszins dat er ook sprake is van een grootschalige visserij. Sterker nog: de aalvisserij is in Europa de wijdst verbreide visserij, met een grote werkgelegenheid (>25000 mensen), maar is opgebouwd uit vele kleine bedrijfjes, vissend in kleine binnenwateren (Figuur 44). Slechts een enkel groter water kent een wat omvangrijker visserij; het IJsselmeer (Nederland) en Lough Neagh (Noord Ierland) zijn daarvan de meest bekende, en maken samen maar ca. 5% van de totale visserij uit. Alleen rond deze wateren zijn typische vissersplaatsen te vinden, met een scheepswerf, een visafslag, e.d. Elders is er sprake van een kleinschalig, en dikwijls traditioneel visserijbedrijf, waarin één of enkele vissers samenwerken, en zelfstandig de aalstand in hun water beheren. Bemoeienis door overheid en onderzoek beperkte zich tot visserij-stimulerende maatregelen, zoals de import van buitenlandse glasaal voor uitzet, de ontwikkeling van nieuwe vistechnieken of de verbetering van de handel en afzet. Dat hele systeem van locale visserijen met een zeer beperkte overheidsbemoeienis werkte uitstekend, totdat na 1980 onverwacht de glasaalintrek afnam. Toen werd plotseling pijnlijk duidelijk, dat al die kleine watertjes tezamen het leefgebied van één enkele vispopulatie uitmaken, en dat de achteruitgang van het bestand voor alle vissers gevolgen ging hebben: dat al die kleine snippertjes dus samen een groot probleem hadden.

Oorzaken van de achteruitgang

De stand van de Europese aal gaat duidelijk achteruit. De intrek van glasaal is afgenomen sinds 1980, tot 10 en recentelijk slechts 1% van het oorspronkelijke niveau. De vangst van rode en schieraal daalt al enkele decennia. Als oorzaak van deze achteruitgang zijn een aantal mogelijke verklaringen genoemd, waarvan de belangrijkste zijn: kli-



Figuur 44 De woonplaatsen van alle 402 Nederlandse binnenvissers in 1995. Driehoekjes: IJsselmeervissers; rondjes: overige bedrijven. De grootte van de symbolen komt overeen met het aantal bedrijven per postcodegebied; de kleinste stipjes komen overeen met precies één bedrijf.

Home addresses of all 402 Dutch fishermen in 1995. Triangles: companies fishing on Lake IJsselmeer; circles: other companies. The size of the symbol indicates the number of companies per zip code area; smallest symbols indicate a single company. (See chapter 4)

maatsverandering in de oceaan, verlies van opgroeigebied als gevolg van dammen en stuwen, toegenomen predatie door aalscholvers, overbevissing, door de mens geïntroduceerde ziektes en parasieten en vervuiling. Elk van deze factoren wordt hieronder afzonderlijk besproken.

Klimaat

De glasaal die in het voorjaar in onze rivieren naar binnen trekt, heeft al een flinke wereldreis achter de rug: naar ons beste weten zijn ze afkomstig uit de Sargassozee (een zeegebied groter dan Europa), op een afstand van 3000-7000 km. Daarvandaan brengt de Warme Golfstroom ze naar Europa, wat waarschijnlijk meer dan een jaar in beslag neemt. Een kleine verandering in de Golfstroom zou wellicht een geweldige invloed kunnen hebben op het aantal dieren dat deze lange tocht overleeft. Het probleem is dat de Oceaan groot is, en er eigenlijk maar heel weinig van bekend is. Gedetailleerde metingen van stromingen, temperaturen, voedselbeschikbaarheid, etc. zijn simpelweg niet aanwezig. Wel is er een index van de luchtdrukverdeling boven de Oceaan (Figuur 45), waarvan men aanneemt dat die indicatief is voor de sterkte van de Golfstroom. In deze index wordt de luchtdruk boven de Azoren vergeleken met die boven IJsland. In de jaren 1980 nam de luchtdruk bij IJsland relatief af, min of meer gelijk opgaand met de afname van de glasaal. Begin jaren 1990 werd voor beiden een minimum bereikt, waarna midden jaren 1990 een licht herstel intrad. Daarna is de hoeveelheid glasaal echter nog dramatisch gedaald, terwijl de luchtdrukverdeling juist op normale waarden terugkwam.

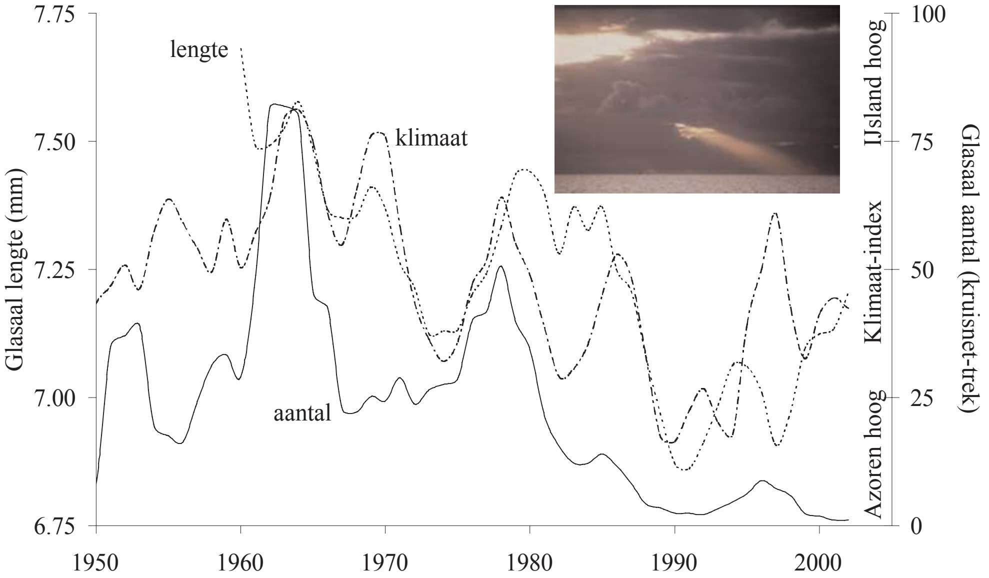
Er is nog een tweede aanwijzing voor een effect van het Oceaan-klimaat: de glasaal die bij ons binnentrekt, brengt in zijn lijf als het ware een verslag van zijn reis op de oceaan met zich mee. Juist in de jaren dat er het minste glasaal binnentrok (1991), bleek de gemiddelde lengte (gemeten in Den Oever) ook aanzienlijk kleiner geworden dan in de voorafgaande decennia (Figuur 45). Het lijkt aannemelijk dat de glasaal klein bleef, omdat ze onvoldoende voedsel vonden in de Oceaan. En dat zou dan goed overeenkomen met een verandering in de stroming en de klimaatindex. Midden jaren 1990 is de luchtdrukverdeling weer naar gemiddelde waarden teruggekeerd en nam tegelijkertijd ook het aantal en de lengte van de glasaal weer toe. Maar rond 2000 wordt dat verband verbroken: de lijn van het klimaat en van de glasaallengte gaan samen verder omhoog, maar het aantal glasalen daalt naar een absoluut dieptepunt. Hoewel de relatie tussen glasaallengte en klimaat lijkt te blijven bestaan, levert het opgetreden herstel van het klimaat nu niet meer glasaal op.

Polders en dammen

Half Nederland ligt beneden de waterspiegel. Grote delen van de laaggelegen gebieden hebben oorspronkelijk deel uitgemaakt van het leefgebied. Afdammen, inpolderen en droogmalen hebben dus allemaal invloed gehad op de aalstand en zullen de opgroeimogelijkheden verkleind hebben. De vraag rijst, of de afname van de aalstand soms het gevolg kan zijn van onze waterbouwkundige werken. Voor het IJsselmeer zijn er vrij nauwkeurige gegevens bekend (Figuur 45). Was de Zuiderzee nog ca. 3600 km^2 groot, het IJsselmeer is geleidelijk verkleind tot ca. 1850 km^2. Hoewel deze cijfers een onjuiste indruk kunnen geven dat het effect van inpolderingen exact kan worden ingeschat, wordt toch wel duidelijk dat de achteruitgang van de aalvangst (voor het IJsselmeer: van 4000 naar 400 ton in 50 jaar) wezenlijk groter is geweest dan verklaard kan worden uit de halvering van het oppervlak. Onduidelijk is, hoe groot de invloed van de Afsluitdijk, en later de Houtribdijk, op het achterliggende water is, en welke rol het bovengelegen stroomgebied van de IJssel (en kleinere rivieren) kan hebben gespeeld.

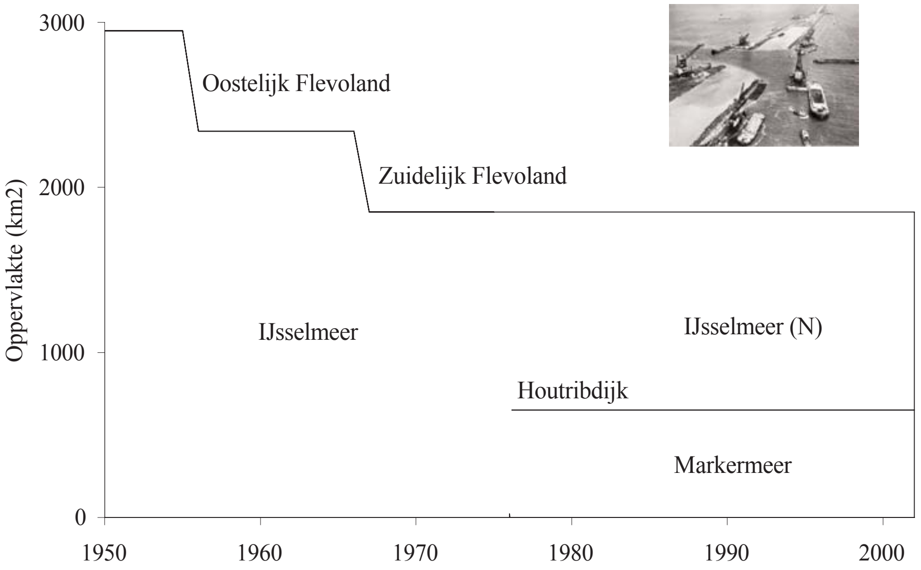
Aalscholvers

Aalscholvers hebben de naam bovenal aal te eten. Voor het IJsselmeer is dat niet het geval. Analyse van hun dieet toont aan dat minder dan 1% van hun voedsel uit aal bestaat, hetgeen maar ca. 18 ton per jaar zou zijn. Dat kan daarom nauwelijks de oorzaak zijn van de grote achteruitgang. Buiten het IJsselmeer eten aalscholvers waarschijnlijk veel meer aal. Vergelijking van de toename van het aantal aalscholvers (Figuur 47) met de daling in de aal (Figuur 38) maakt echter duidelijk, dat de aalscholverpopulatie pas echt van betekenis werd, toen het grootste deel van de aal al was verdwenen.



Figuur 45 De ontwikkeling in het klimaat op de noordelijke Atlantische Oceaan, het aantal glasalen en hun lengte, gemeten in Den Oever sinds 1950.

Trend in climate indices for the Northern Atlantic, the number of glasseels and their length, in Den Oever, since 1950. (See chapter 11)



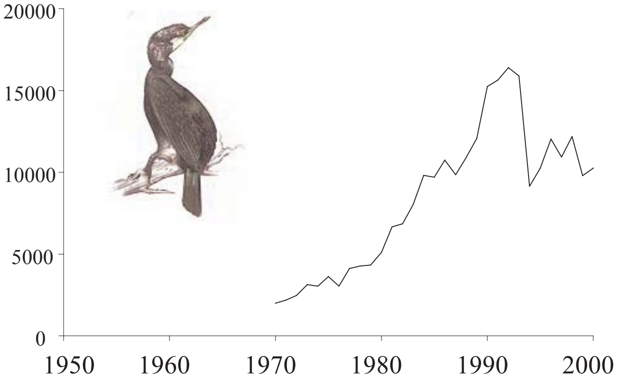
Figuur 46 De afname van het oppervlak van het IJsselmeer sinds 1950.

The decline of the surface area of Lake IJsselmeer since 1950. (See chapter 7)

Visserij

De vraag of de visserij mede oorzaak van de achteruitgang kan zijn is niet eenvoudig te beantwoorden. Hierboven is een hoge aalvangst in 1950 beschouwd als een teken dat er veel aal aanwezig was. Tegelijkertijd kan een hoge vangst juist ook een oorzaak zijn van een sterke achteruitgang in het bestand. Hoewel de achteruitgang van de vangsten gepaard is gegaan met een afname van het aantal bedrijven op het IJsselmeer, heeft de visserijinspanning daarmee geenszins gelijke tred gehouden. In de periode 1970-1985, met afnemende vangsten en een afnemend aantal schepen, nam het aantal fuiken juist zeer snel toe.

Verderop zal nog uitgebreid op de invloed van de visserij worden ingegaan.



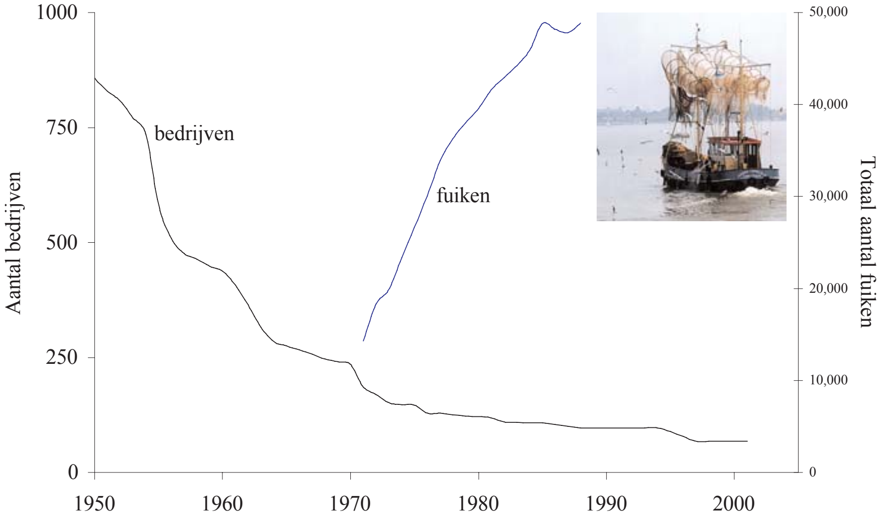
Figuur 47 De ontwikkeling van het aantal aalscholvers rond het IJsselmeer sinds 1950. (Gegevens: M. van Eerden, RWS-RIZA)
Trend in the number of cormorant breeding pairs visiting Lake IJsselmeer since 1950.

Parasieten

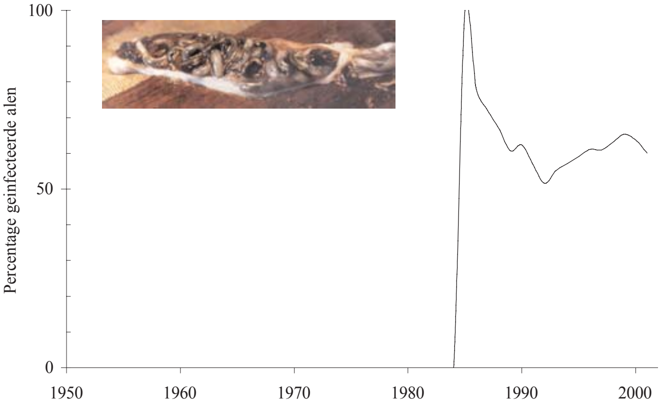
In 1985 werd een buitenlandse zwemblaasparasiet in Nederland ingevoerd in een transport van levende aal. Nog hetzelfde jaar was nagenoeg alle aal geïnfecteerd en werden ook dode of sterk verzwakte exemplaren aangetroffen. Nederland was een van de eerst geïnfecteerde landen. In de daarop volgende jaren is de infectie bij ons weer wat afgezakt en was er ook geen uitwendige schade meer waarneembaar. Daarmee is overigens niet gezegd dat een schieraal met een verziekte zwemblaas de lange weg terug door de Oceaan kan volbrengen. Wel is duidelijk dat de daling van de glasaalintrek al begonnen was voor de parasiet goed en wel door heel Europa verspreid was.

Vervuiling

Net als voor de zwemblaasparasieten, geldt ook voor de vervuiling met PCB's (een belangrijke groep afvalstoffen), dat mogelijke effecten waarschijnlijk optreden in een levensstadium waarover weinig bekend is: tijdens de schieraaltrek in de Oceaan en bij de rijping van de geslachtsorganen. Een bijkomend probleem is dat metingen van cruciale componenten van de vervuiling pas op

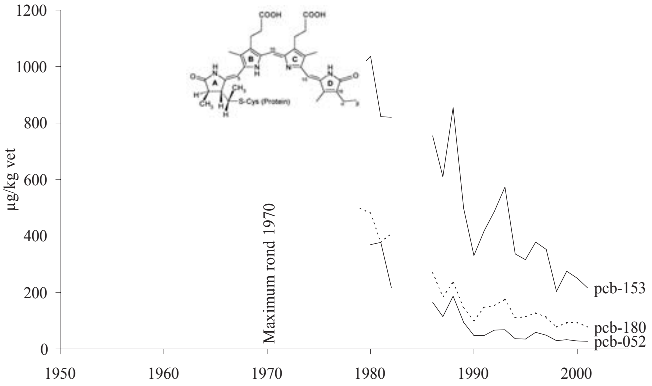


Figuur 48 De ontwikkeling van het aantal visserijbedrijven op het IJsselmeer sinds 1950 en het aantal fuiken in de periode 1970-1988.
Trend in the number of companies fishing on Lake IJsselmeer since 1950, and the rise of the number of fyke nets used, in the period 1970-1988.



Figuur 49 De ontwikkeling van de zwemblaasparasiet in de aalstand van het IJsselmeer. In 1985 werd de parasiet voor het eerst waargenomen en werd meteen een vrijwel volledige besmetting bereikt.

Trend in the abundance of the swimbladder parasites in Lake IJsselmeer eel. Following the first observation in 1985, maximum infection levels were observed almost immediately.



Figuur 50 De ontwikkeling in PCB-gehaltes van aal van het IJsselmeer. De metingen zijn in 1978 begonnen, d.w.z. pas na de top van de vervuiling. Gegevens: RIVO database prioritaire stoffen 1978-2002.

Trend in PCB contamination of Lake IJsselmeer eel. Observations began in 1978, only after the peak occurring around 1970.

gang zijn gekomen (1978), toen de ergste vervuiling (rond 1970) eigenlijk al voorbij was (Figuur 50). Het lijkt waarschijnlijk dat de concentratie PCB's geleidelijk is opgebouwd in de periode 1950-1970. In deze periode was de glasaal nog talrijk aanwezig, maar nam de vangst van rode aal al af. Het voor vervuiling gevoelige levensstadium (de voortplanting) was nog succesvol, terwijl het minder gevoelige stadium (groei) juist achteruitging; dat lijkt niet op een sterke invloed van de vervuiling te wijzen.

Samenloop van verschillende oorzaken

Wat de uiteindelijke oorzaak is geweest, zal mogelijk nooit duidelijk worden. Voor elk van de geopperde hypotheses is wel wat te zeggen, maar geen enkele simpele verklaring past precies. Omgekeerd kan ook geen van de hypotheses echt uitgesloten worden. Het meest waarschijnlijke scenario is daarom dat de samenloop van omstandigheden geleid heeft tot de achteruitgang in de aalstand. Inpoldering, visserij en vervuiling en vervolgens ook aalscholvers, parasieten en een ongunstig oceaan-klimaat hebben allemaal bijgedragen aan de daling van de aalpopulatie tot het huidige, zorgwekkende niveau.

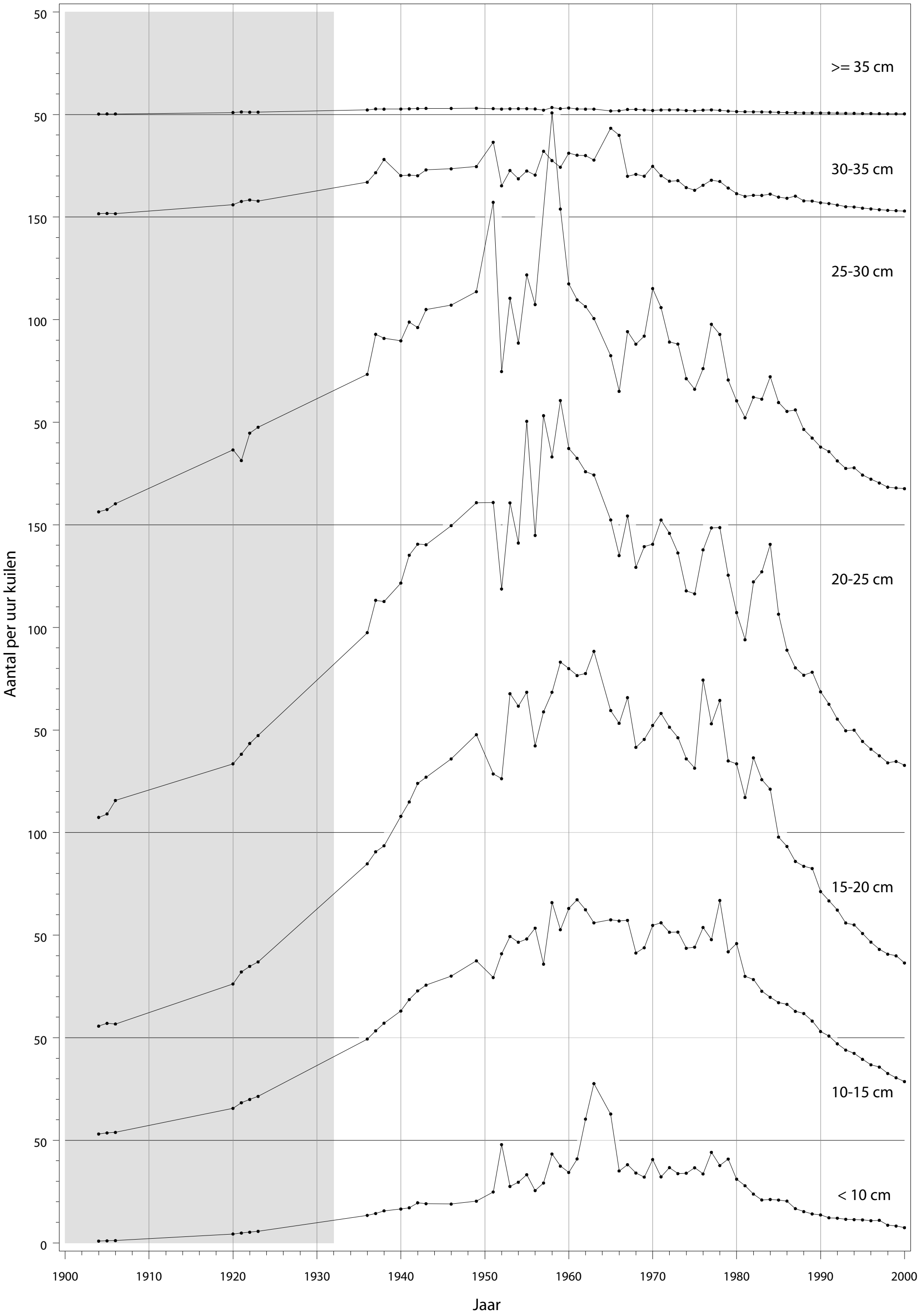
Nauwkeuriger beschouwing van de trends in glasaal (Figuur 19) en rode aal (Figuur 38) geeft nog een aantal belangrijke aanwijzingen: gedurende de jaren 1960-1980 kwam er wel veel glasaal binnen, maar die leverde steeds minder rode aal op. Tegelijkertijd nam de schieraaluittrek ook geleidelijk af, maar niettemin leverde de paaistand onverminderd veel nieuwe glasaal op. Pas in de jaren 1980 ging het met de glasaal mis. Kennelijk is er sprake van een langzaam en langdurig proces, dat plaatsvond tussen het glasaal- en het schieraalstadium, in onze binnenwateren, waarbovenop een veel sneller en heftiger proces kwam in de jaren 1980, tussen het schieraal- en glasaalstadium (in de Oceaan).

Een gedetailleerde analyse van Zuiderzee- en IJsselmeergegevens over de afgelopen eeuw toont dat de achteruitgang ook daar rond 1960 begonnen is, zoals ook al uit de opbrengst van de visserij gebleken was. Interessanter is, dat het aantal kleinste (en jongste) alen pas in 1980 begon te verminderen, toen ook de glasaalintrek minder werd. De wat grotere alen namen al eerder af, de nog grotere nog eerder, terwijl de grootsten tezelfdertijd en even snel als de opbrengst van de visserij afnamen in aantal. Gedurende de tweede helft van de 20^{e} eeuw werd de situatie steeds slechter, en naarmate elke aal in het IJsselmeer verder opgroeide, trad een steeds sterkere daling op. Dat beeld lijkt verdacht veel op de accumulatie, de ophoping van een of andere toxische stof, maar dan is de gelijktijdige achteruitgang in geheel Europa (binnenwateren, kustwateren, noord en zuid, oost en west) wel een heel wonderlijke coïncidentie.

Zal er ooit duidelijkheid komen?

Ruim veertig jaar geleden is een onbekend proces begonnen, dat tot een gestage daling van de aalstand heeft geleid. Al in de jaren 1970 is de daling opgemerkt, maar die is toen niet begrepen en vervolgens ook niet verder onderzocht. De daling ging daarna onverminderd voort. Nu alsnog uitzoeken wat er gebeurd is, wordt gehinderd door een gebrek aan feitelijke informatie. In de geschreven teksten van die tijd is de situatie niet goed onderkend. Visserijgegevens over die periode tonen ons de achteruitgang (Figuur 38), maar geven geen inzicht in de oorzaak.

Onderzoeksgegevens zijn dun gezaaid. Voor het IJsselmeer kan, op basis van vergelijking van heel verschillende vistuigen, en van heel verschillende onderzoe-



Figuur 51 Ontwikkeling gedurende de 20^{e} eeuw in de aalstand in Zuiderzee en IJsselmeer, naar lengte-groep.
Trends in the abundance of eel in the Zuiderzee respectively Lake IJsselmeer, by length group. (See chapter 7)

Figuur 52 Het onderzoeksschip *Stern* levert sinds 1983 het merendeel van de onderzoeksgegevens van het IJsselmeer. Midscheeps is langs de railing nog net de 8-m lange boom van de grote kuil (Figuur 31) te zien; midden op het dek een vis-sorteer-tafel. (foto Marcel de Vries)
Research vessel Stern *has been the main source for data on Lake IJsselmeer, since 1983. Amidships, the 8-m beam of the traditional trawl (Figuur 31) can be seen alongside the railing; a fish-sorting table stands in the middle.*

Figuur 53 De langste aal van Europa (133 cm) werd gevangen op de dijk voor Almere. Ze moet aanzienlijk ouder dan de dijk zijn geweest.
The longest eel in Europe (133 cm) was caught on the dyke of a polder in Lake IJsselmeer. She must have been considerably older than the dyke.

kingen, een analyse van een lange periode worden gemaakt (Figuur 51), maar elders zijn eigenlijk nergens lange gegevensreeksen beschikbaar. Voor het IJsselmeer zijn er verder gedurende 60 jaar gehoorsteentjes van de aal verzameld en bewaard, waaruit nog hun ouderdom en groeisnelheid kunnen worden afgeleid. Misschien kunnen die ook nog gebruikt worden voor een analyse van genetische veranderingen. Maar daarmee zijn de mogelijkheden om alsnog historische ontwikkelingen te achterhalen dan wel uitgeput. Dit proefschrift presenteert diverse historische reeksen, die bij nadere beschouwing toch nog waardevolle informatie bleken te bevatten. Maar de kans dat er hierna nog veel meer aan het licht gebracht kan worden, wordt snel kleiner. Daarna rest alleen nog, de daling te nemen voor wat hij is, en er de consequenties uit te trekken.

Consequenties

De aalstand gaat zienderogen achteruit. Het wetenschappelijke advies van de Internationale Raad voor het Zeeonderzoek (ICES) aan de Europese Unie stelt dat de stand zich niet meer binnen biologisch veilige grenzen bevindt, en dat de visserij onder de huidige omstandigheden niet duurzaam zal kunnen worden bedreven. Op een aantal verschillende manieren (visserij, habitat verlies, vervuiling en introductie van parasieten) heeft de mens een negatieve invloed gehad op de stand. Alle informatie wijst erop dat de aalstand op een dieptepunt is aangekomen, waaruit hij zich wellicht niet langs natuurlijke weg kan herstellen. Daarom luidt het wetenschappelijk advies om zo spoedig mogelijk een herstelplan voor de aal op te stellen. Dat zal een complex proces worden, waarbij heel Europa betrokken zal moeten worden. Bovendien gaat het om kleinschalige visserijen, met grote regionale verschillen en belangentegenstellingen en bovenal grote wetenschappelijke onzekerheden. Hieronder volgt een nadere beschouwing van een aantal uitgangspunten, dat in deze discussie een rol speelt.

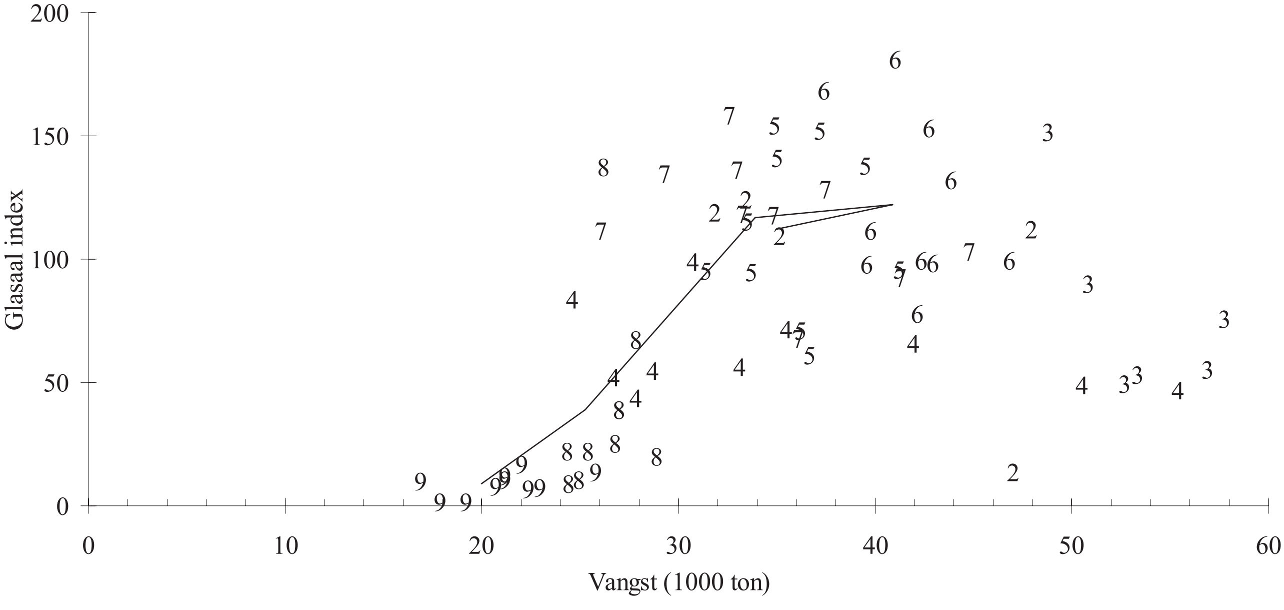
Voorzorgsbeginsel

In de afgelopen jaren is internationaal hard gewerkt aan een samenhangend stelsel van politieke doelstellingen en richtlijnen voor de benutting van natuurlijke hulpbronnen, die bekend zijn geworden onder de noemer: toepassing van het Voorzorgsbeginsel. Deze benadering is enerzijds gebaseerd op het Verdrag over het Zeerecht (1983), anderzijds op de Milieu Conferentie in Rio de Janeiro in 1993. De kern hiervan is dat er verantwoord omgesprongen dient te worden met natuurlijke hulpbronnen, dat exploitatie slechts toelaatbaar is als duidelijk is dat er geen (blijvende) schade wordt toegebracht. Deze politieke uitgangspunten zijn vervolgens in technische zin uitgewerkt tot praktische regels, die nu standaard door de ICES worden toegepast bij de opstelling van beheersadviezen.

Aangenomen wordt, dat er (voor alle vissoorten) een verband bestaat tussen de grootte van de paaistand en de hoeveelheid nakomelingen, in die zin dat er een minimale paaistand nodig is om voldoende nageslacht te kunnen produceren. Boven dat niveau resulteert een grotere paaistand niet in meer jongen, maar een kleinere leidt wel tot een daling. De kunst is dan vast te stellen bij welke paaistand dat minimum ligt, bij welke kritische waarde een verdere vermindering gevolgen gaat krijgen voor het nageslacht. Als dat minimum bekend is (of een voorlopige schatting ervan politiek overeengekomen), kunnen vervolgens beheersmaatregelen gekozen worden, die ervoor zorgen dat de paaistand boven dat minimum blijft. Het Voorzorgsbeginsel stelt nu, dat ook voor de aal een dergelijk verband tussen paaistand en nakomelingen moet worden aangenomen. Daaruit volgt, dat een herstelplan er in ieder geval ook op gericht moet zijn, een voldoende grote paaistand te behouden.

De zorg om de paaistand

Maar de aal zou de aal niet zijn, als alles hiermee opgelost kon worden. Paaistand en nakroost moeten alle twee gezocht worden op een onbekende verre plaats in de Oceaan, waar praktisch gezien niets te meten valt. Voor beide grootheden kan wel een benaderende maat gevonden worden. Het geproduceerde nageslacht komt tenslotte als glasaal aan onze kust. In heel Europa is een zelfde daling in de glasaalintrek vastgesteld. Kennelijk zijn de waarnemingen maatgevend voor een gemeenschappelijk proces ver weg op de Oceaan, wellicht op de paaiplaats. De paaistand is veel moeilijker vast te stellen. Van ontsnappende schieraal is onbekend hoeveel het er zijn, en er zijn ook geen historische metingen die als index gebruikt kunnen worden. Maar misschien valt er wel wat te zeggen over de trend in de hoeveelheid schieraal die door het aalbestand in de continentale wateren is geproduceerd. In de afgelopen halve eeuw is er in heel Europa een sterke afname in de aalvangsten te zien geweest (Figuur 38), welke waarschijnlijk het gevolg is geweest van een afname in het bestand (Figuur 51). Die afname van het bestand zal onvermijdelijk ook gevolgen hebben gehad voor de productie van schieraal, en daarmee voor de paaistand.



Figuur 54 Het verband tussen het aantal paaiende dieren en de hoeveelheid nakomelingen van de aal is niet bekend, maar het zal waarschijnlijk lijken op het verband tussen de vangst van grote alen (rode en schier) en de hoeveelheid intrekkende glasaal, zoals in deze grafiek. De cijfers duiden decennia in de 20e eeuw aan (2=1920-1929, 3=1930-1939, etc); de lijn verbindt het gemiddelde per decennium, vanaf 1950.

For eel, the relation between spawning stock size and recruitment is unknown, but is possibly approximated by the relation between the yield of yellow and silver eel on one side, and the recruitment of glasseel on the other. The numbers in this graph indicate the decade (2=1920-1929, 3=1930-1939, etc.), while the line connects decadal averages since the 1950s. (See chapters 6 and 11)

Hoewel niet ideaal, zal het verband tussen paaistand en nakomelingen daarom wel enigszins lijken op het verband tussen aalvangst en glasaalintrek (Figuur 54). En dat verband suggereert, dat er ook bij de aal wel degelijk sprake is van een relatie: de geleidelijke afname van het (paai)-bestand in de jaren 1920-1960 had weinig effect op de glasaal, maar toen vervolgens in de periode 1960-1990 de afname steeds verder ging, werd rond 1980 het minimum gepasseerd, en stortte de glasaal plotseling in. In deze optiek was het effect van bijvoorbeeld de klimaatsverandering op de oceaan (Figuur 45) de druppel die de emmer deed overlopen, maar niet de oorzaak van de achteruitgang. De instorting van de glasaal was onvermijdelijk, omdat de stand in de continentale opgroeigebieden gestaag terugliep.

De teruggang in de glasaal is hier geschetst als het gevolg, en niet de oorzaak van de afname van het aalbestand in continentale wateren. Dit idee is afkomstig uit het hier beschreven onderzoek, maar is nog geen vaststaand feit. De vraag is, of er al consequenties getrokken moeten worden. Moet het beheer van de aal zich richten op het herstel van de paaistand, en daarmee op het herstel van de hoeveelheid schieraal? Moet het roer om, vanwege een nog onbewezen stelling? Het Voorzorgsbeginsel maakt een onverbiddelijke keuze: het zekere moet voor het onzekere genomen worden, de paaistand moet gespaard worden. Zorg ervoor dat de visserij niet meer dan een redelijk deel van het bestand vangt; zorg ervoor dat dammen en sluizen geen onoverkomelijke barrière vormen voor de migratie.

Wat is redelijk? Waar moet naar gestreefd worden? Gegevens ontbreken of geven slechts een indicatie (Figuur 54). Daarom is het wetenschappelijke advies opnieuw gebaseerd op het Voorzorgsbeginsel. Voor vele andere vissoorten kan de paaistand verkleind worden tot op ca. 30% van de oorspronkelijk onbeviste situatie, zonder dat dat nadelige gevolgen heeft voor de aanwas van jonge vis. Voor de aal ontbreekt de kennis om een specifieke keuze te maken. Dezelfde norm van 30% zou gekozen kunnen worden, maar gezien de grote onzekerheden wordt een hoger getal (van bijvoorbeeld 50%) aanbevolen.

Remedies

De aalstand gaat hard achteruit. Dit zou mede veroorzaakt kunnen worden door een te kleine paaistand, onder meer als gevolg van menselijk handelen. Maatregelen gericht op het herstel van de paaistand zijn aanbevolen; in de praktijk zal ernaar gestreefd moeten worden de vrije uittrek van schieraal op tenminste 30% van de natuurlijke toestand te verzekeren. Voor de verschillende sectoren werkt dat verschillend uit.

Figuur 55 In Spanje en Portugal komt een zeer kleinschalige glasaalvisserij voor. (foto Isabel Domingos)
In Spain and Portugal, the glasseel fishery is often organised at very small scale.

Glasaalvisserij en aquacultuur

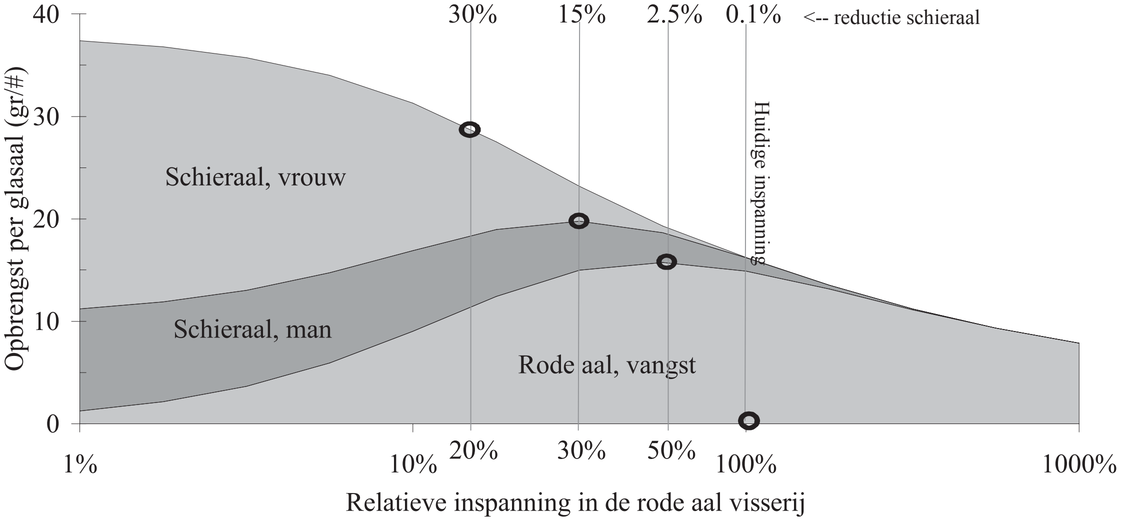
De kweek van aal maakt, net als de visserij, gebruik van het natuurlijke bestand. De Nederlandse visserij vist op Nederlandse aal, maar de Nederlandse kweek maakt gebruik van glasaal uit Zuid-Europese wateren. Naar beste weten, behoren die tot dezelfde aalpopulatie, maar de beheersproblemen daar zijn toch anders dan in onze wateren. De hoeveelheid glasaal die in zuidelijke wateren binnentrekt, is bijzonder groot. Voor de Vilaine (de grootste rivier van Bretagne) is berekend, dat in de jaren 1970 meer dan 15 kg glasaal per hectare wateroppervlak de rivier binnenkwam. Ter vergelijking: in noordelijk Europa wordt meestal 0.1 kg/ha uitgezet, of in uitzonderlijke gevallen maximaal 0.5 kg/ha. Die 15 kg glasalen in de Vilaine zullen dus zeker niet allemaal hebben kunnen overleven, maar een groot gedeelte moet kort na de intrek door voedsel- en ruimtegebrek zijn overleden. Daarom kon de glasaalvisserij ongestraft een deel van de intrek oogsten. Kon, want op een gegeven moment komt er zo weinig glasaal binnen, dat alles wel een plaatsje in de rivier kan vinden (in 2001 trok nog 0.58 kg/ha binnen). De natuurlijke productie van schieraal in deze wateren wordt veel meer bepaald door de beschikbaarheid van binnenwater, dan door de intrek van de glasaal. Hoe groter de (bereikbare) rivier, hoe meer glasaal zich kan vestigen. Beheer moet er daarom op gericht zijn een deel van de glasaal te laten ontsnappen aan de visserij (dat was tot voor kort in de Vilaine niet zo), en de opgroeigebieden te herstellen en bereikbaar te maken (dat was in de Vilaine ook niet het geval). De vraag is of dat een verantwoordelijkheid van de zuidelijke landen is, of ook van de noordelijke landen die de glasaal gebruiken voor aquacultuur.

Figuur 56 De resultaten in dit proefschrift zijn gebaseerd op noeste metingen van vele alen. Op de foto worden alen opengesneden, om geslacht, maaginhoud, parasieten etc. te bepalen, en om gehoorsteentjes te verzamelen, waarvan de leeftijd kan worden afgelezen.
The results in this thesis are essentially derived from laborious field work, sampling many eels. The picture shows how eels are dissected, to measure their sex, stomach contents, parasite burden, etc. Otoliths are collected, from which the age of the fish can be determined.

Rode aal en visserij

Van de visserij op rode aal in ons land is het meest bekend van het IJsselmeer, omdat de overheid hier mede verantwoordelijk is voor het beheer. Bekend is ook dat het IJsselmeer extreem overbevist is, terwijl dat in andere binnenwateren veel minder het geval lijkt te zijn. Maar de resultaten betreffende de IJsselmeervisserij blijken heel goed in lijn te liggen met de weinige analyses die in het buitenland van de rode aalvisserij zijn gemaakt.

In Figuur 57 is het verband geschetst tussen de visserijintensiteit (horizontaal, in procenten van de huidige IJsselmeervisserij) en de opbrengst van rode en schieraal (in gram per binnengetrokken glasaal). Voor de duidelijkheid is hierbij in het midden gelaten of de schieraal alsnog gevangen wordt of naar de paaiplaats kan doortrekken. Het zal niemand verwonderen dat de hoogste productie van schieraal bereikt wordt, als de rode aalvisserij zo veel mogelijk beperkt wordt. Inmiddels staat echter de bescherming van de paaistand voorop. Behoud van 30% van de schieraal vereist een beperking van de IJsselmeervisserij tot 20% van de huidige rode aalvisserij. Maar een ferme beperking van de IJsselmeervisserij zal niet alleen de paaistand ten goede komen, maar ook leiden tot hogere vangsten tegen minder kosten voor de IJsselmeervissers zelf.



Figuur 57 Het berekende verband tussen de intensiteit van de rode aal visserij op het IJsselmeer en de productie van paairijpe schieraal. De invloed van de gerichte *visserij* op schieraal is buiten beschouwing gelaten. De positie van een aantal kenmerkende scenario's (huidige situatie; maximalisering van rode aal vangst; idem van rode aal en mannetjes schieraal; behoud van 30% van de vrouwelijke schieraal) is met een verticale lijn aangegeven.
Relation between fishing intensity for yellow eel in Lake IJsselmeer, and the production of silver eel. The effect of fisheries *targeting the silver eel is not included here. Typical scenarios are indicated by vertical lines: status quo, maximising yellow eel yield, idem yellow eel and male silver eel, protection of 30% of female silver eel. (See chapter 8)*

Paling van Urk. 4 Juli 1905.

	Centimeters																				totaal	Kg
	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
Stuks	1	19	33	54	60	67	41	54	46	28	24	22	25	18	14	10	10	2	2	1	531.	25

Gemiddelde lengte 21.9 c/m.

Figuur 58 Op een oude meetlijst van 1905 maken potloodstrepen duidelijk, dat men op zoek was naar een verstandige minimum-maat: 20, 25 of 30 cm? Op 26 juni 1911 is tenslotte een maat van 25 cm ingevoerd, die op 23 oktober 1937 naar 28 cm is verhoogd.

This old form from 1905 shows pencil marks at 20 cm, 25 cm and 30 cm. What would be the best minimum legal size? On June 26, 1911, a minimum legal size of 25 cm was established, later on raised to 28 cm, on October 23, 1937.

Een maximale vangst wordt verkregen bij een visserijintensiteit overeenkomend met 30-50% van de huidige, maar dat heeft wel een reductie van de schieraal tot gevolg tot 2,5-15%. Dat is beneden de minimum norm van 30%. Behoud van een minimum paaistand en optimalisering van individuele visserijbedrijven gaan daarom niet automatisch hand in hand. Een deel van de potentiële oogst zal voor het behoud op lange termijn gereserveerd moeten worden.

Schieraal en visserij

Nog niet zo heel erg lang geleden gold ontsnappende schieraal als puur verlies. Gepoogd werd het beheer van spuisluizen aan te passen, zodat wegtrekkende schieraal voor de visserij behouden bleef. Sinds 23 Oktober 1937 bedraagt de wettelijke minimummaat op aal in Nederland 28 cm. Binnen Europa is dit uitzonderlijk laag. De redenering was echter, dat een hogere maat zou betekenen dat de mannetjes schier zouden worden (vanaf ca. 32 cm lengte), en naar zee zouden kunnen ontsnappen. Alles liever dan dat, dus werden ze een jaar tevoren gevangen, vanaf 28 cm lengte. Maar de tijden veranderen en behoud van voldoende paaistand is nu prioriteit nummer één.

Ogenschijnlijk staan schieraalvisserij en behoud van de paaistand lijnrecht tegenover elkaar. Elke gevangen schieraal is er eentje minder voor de paaistand. Daar staat tegenover, dat de schieraalvisserij een hogere opbrengst geeft dan de visserij op rode aal. Visserijbeperkingen zouden daarom beter op bescherming van de rode aal gericht kunnen zijn. Met een ongelimiteerde visserij op rode aal (zoals op het IJsselmeer) kan de schieraalvisserij gesloten worden zonder dat dat een noemenswaardig effect op de schieraaltrek zou hebben. Anderzijds kan een efficiënte schieraalvisserij het effect van andere beheersmaatregelen wel volledig ongedaan maken.

Hoe efficiënt is de schieraalvisserij? Voor Nederland zijn er momenteel nog te weinig cijfers bekend, om nu al een schatting voor het hele land te kunnen maken. Uit het buitenland komen tegenstrijdige resultaten. In de Oostzee is uit merkproeven gebleken dat 50-70% van de schieraal gevangen wordt. In Ierland zijn in de rivier de Bann twee onder elkaar gelegen dichtzetten aanwezig (netten die de gehele rivier afsluiten), waarvan de onderste dikwijls hogere vangsten maakt dan de bovenste. Dan moet de bovenste kennelijk heel wat schieraal hebben doorgelaten.

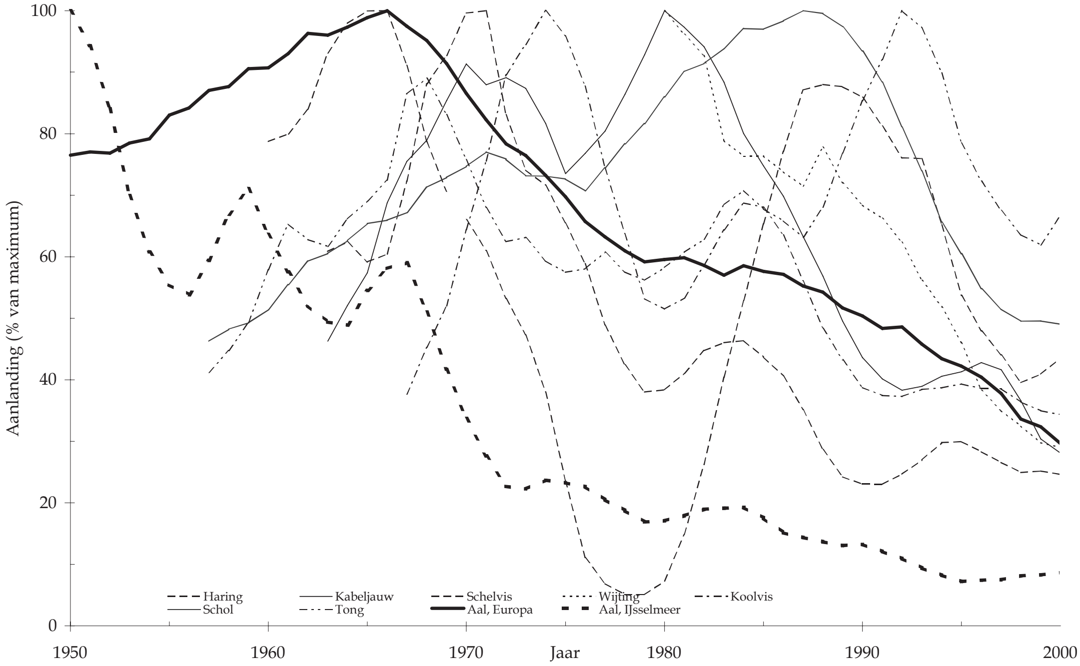
Herstel van leefgebied

Volledig herstel van de oorspronkelijke situatie, waarbij half Nederland onder water stond, is niet erg realistisch. Anderzijds is er in Nederland vrijwel geen enkel water meer zondermeer toegankelijk voor de aal, en zonder verdere maatregelen ziet de toekomst er in ons land bijzonder slecht uit. Er zal een balans gevonden moeten worden tussen wensen en mogelijkheden. In het meest recente wetenschappelijke advies wordt voorgesteld een stapsgewijze benadering te kiezen. Het beginpunt is makkelijk te realiseren, maar wellicht niet genoeg; het eindpunt is ideaal, maar niet erg realistisch. De eerste stap behelst verbetering van het beheer in de bestaande wateren; de tweede de installatie van vistrappen of aalgoten, of desgewenst de uitzet van glasaal boven stuwen of gemalen; in de derde stap wordt een zodanig herstel van leefgebied nagestreefd, dat alle binnentrekkende glasaal een plaatsje kan vinden; de vierde stap richt zich op herstel van een nog betrekkelijk kort geleden verloren gegane, historische situatie; terwijl uiteindelijk in stap vijf een volledig natuurlijke situatie wordt nagestreefd. Tot welke stap dit pad gevolgd moet worden, is een kwestie van overleg. Maar elke stap voorwaarts brengt het herstel van de leefgebieden weer verder in de goede richting.

Haring, aal en vis

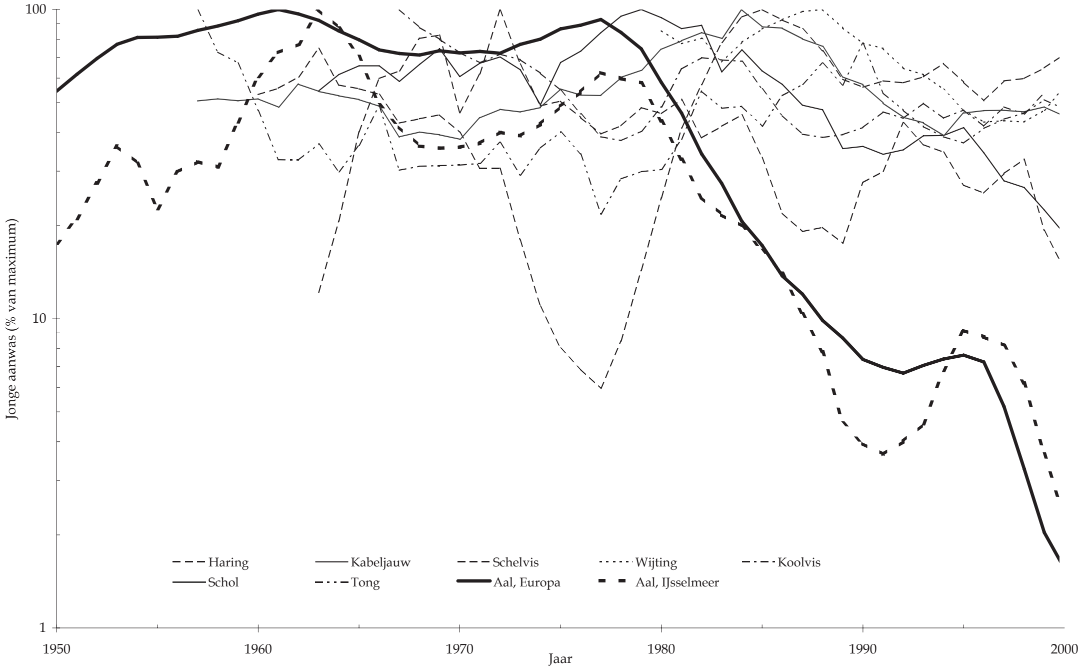
De achteruitgang van de aal staat niet alleen. Ook voor andere vissoorten zijn vergelijkbare trends beschreven. De problemen in de Noordzeevisserij krijgen dikwijls ruim aandacht in politiek en pers. Hoe verhoudt zich de aal tot de Noordzeevis?

De kabeljauwstand in de Noordzee verkeert in zorgelijke toestand. In de afgelopen 20 jaar is de aanvoer met ca. 75% gedaald, vergelijkbaar met de Europese aal, zij het dat het voor de kabeljauw wel twee maal zo snel ging. Als



Figuur 59 De ontwikkeling in de aanlanding van de belangrijkste commerciële soorten van de Noordzee, en voor de aal, op het IJsselmeer, en in heel Europa.

Trends in the landings of the main North Sea fish species, in comparison to eel from Lake IJsselmeer and from the whole of Europe. (The fish species listed are from left to right: [top row] herring, cod, haddock, whiting, saithe; [bottom row] plaice, sole, eel in Europe, eel in Lake IJsselmeer).



Figuur 60 De ontwikkeling in de aanwas van jonge vis, voor de belangrijkste commerciële soorten van de Noordzee, en voor de aal van het IJsselmeer en van heel Europa.

Trends in recruitment of the main commercial species from the North Sea, in comparison to the glasseel at Den Oever, and averaged over the whole of Europe. (The fish species listed are from left to right: [top row] herring, cod, haddock, whiting, saithe; [bottom row] plaice, sole, eel in Europe, eel in Lake IJsselmeer).

echter bedacht wordt, dat een aal gemiddeld ongeveer tweemaal zo oud wordt als een kabeljauw, dan zijn de dalingen heel erg vergelijkbaar.

Geheel anders wordt de vergelijking als de aanwas van jonge vis erbij betrokken wordt (Figuur 60). Waar andere soorten hoogstens zijn teruggezakt naar een aanwas van 10% vergeleken bij weleer, is bij de aal sprake van een daling naar 1%. Slechts de haring is in het midden van de jaren 1970 kortstondig even onder de 10% gezakt; de sluiting van de haringvisserij heeft toen ongetwijfeld bijgedragen aan het herstel van de volwassen stand, en daarmee waarschijnlijk ook van de aanwas. De neergang van de glasaal lijkt ongeveer even lang geduurd te hebben als die van de kabeljauw, maar omdat aal zo oud wordt, zijn er sinds 1980 voor aal net twee generaties verstreken, terwijl dat er voor de kabeljauw al zes zijn. Toch is er nog geen begin gemaakt met daadwerkelijke bescherming van de aal, nationaal noch internationaal.

Een razend snelle achteruitgang

De vraag rijst, of er sprake is van een herstelbare achteruitgang. Dat hangt er natuurlijk van af of de oorzaak verdwijnt, of niet. Hierbij moet men denken aan een mogelijk herstel van het oceanische klimaat, maar ook aan herstelmaatregelen, gericht op de visserij, de vervuiling en herstel van leefgebieden. Daar komt echter mogelijk nog een geheel ander probleem bij, dat samenhangt met de biologie van de aal.

Figuur 61 De lengte van een vis wordt bepaald met behulp van een maatlat. Deze V-vormige meetbak moet ervoor zorgen dat een aal lang genoeg stil ligt om gemeten te kunnen worden. In de loop van de 20e eeuw hebben 606 210 alen deze behandeling ondergaan op het IJsselmeer.

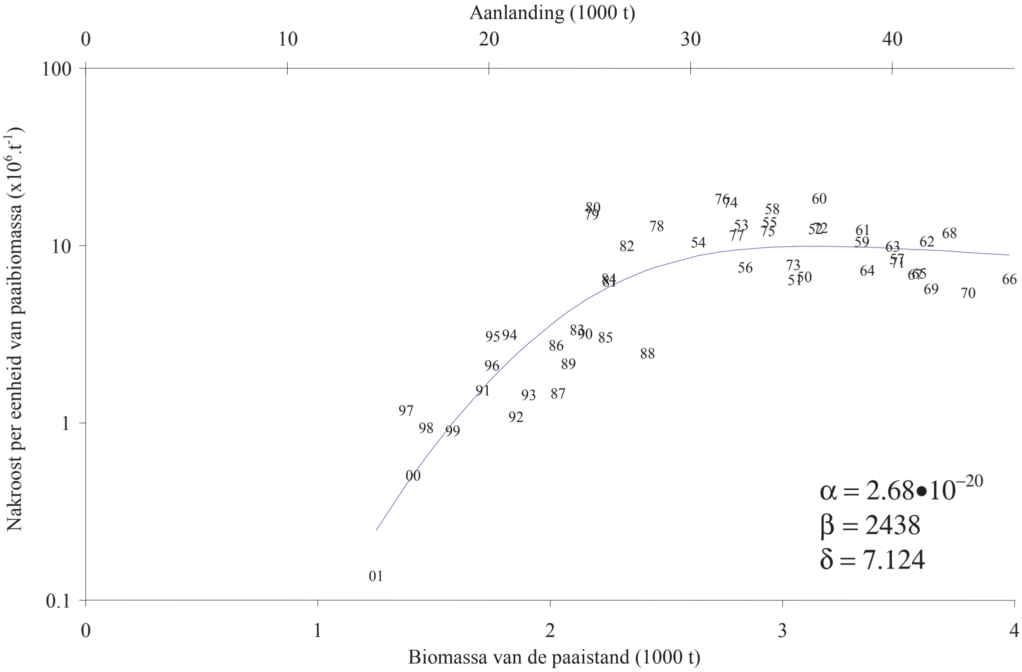
The length of a fish is determined using a standard ruler. This special V-shaped ruler keeps the eel in a fixed position long enough to be measured. During the 20th century, 606 210 eels have undergone this treatment in Lake IJsselmeer.

Het succes van de voortplanting wordt mede bepaald door de omvang van de paaistand. Hoe meer volwassen alen er zijn, des te meer kunnen ze elkaar beconcurreren om de ruimte op de (ons onbekende) paaiplaats; hoe meer larven er geproduceerd worden, hoe minder er van het spaarzame voedsel voor elk beschikbaar is. Hoe groot de paaistand is, is onbekend. Wel is duidelijk, dat de aalstand, en de aanlanding door de visserij, de afgelopen decennia is afgenomen. Het ligt voor de hand aan te nemen, dat ook de paaistand evenredig is afgenomen. Het verband tussen de vangst en het voortplantingssucces (Figuur 62) toont inderdaad een kleine toename, naarmate de paaistand afnam van 4000 naar 2500 ton; maar bij een nog lagere paaistand lijkt het tegenovergestelde het geval te zijn: het succes neemt af bij afnemende paaistand. Dit verschijnsel staat bekend als het Allee-effect, en komt bijvoorbeeld voor, als individuen elkaar opzoeken, om gezamenlijk aan de voortplanting deel te nemen; groepsseks dus. Zijn er te weinig dieren, dan zullen groepen van voldoende grootte zeldzaam worden, en vele dieren moederziel alleen rondzwemmen, op zoek naar soortgenoten. Een afnemend voortplantingssucces bij lage aantallen wordt op theoretische gronden algemeen voorspeld, maar is in de praktijk moeilijk bij commerciële vissoorten aan te tonen. Kennelijk moeten er wel erg weinig dieren zijn, wil dit effect ook zichtbaar worden. Dat het hier al bij een paaistand van 2250 ton zou optreden, d.w.z. al vanaf ca. 4 miljoen wegtrekkende vrouwelijke schieralen, is dan ook wonderbaarlijk. Natuurlijk zal een groot deel van de dieren op hun reis naar de paaiplaats dood gaan, en ook is de omvang van de mogelijke paaiplaats bepaald groot: de Sargassozee meet 2 miljoen km^2. Maar dan toch blijft het verbazen.

Als dit Allee-effect inderdaad optreedt, kan een mogelijk herstel van de aalstand buitengewoon moeilijk worden. Voorlopig is er een geringe paaistand, met dientengevolge een zeer gering succes van de voortplanting. En dat geringe succes zal op zijn beurt weer niet bijdragen aan het herstel van de paaistand. Het Allee-effect leidt er dan ook toe dat de populatie makkelijk terecht kan komen in een negatieve spiraal, met een slechte afloop voor de soort.

Van Zuiderzee- naar IJsselmeervisserij

Een deel van dit proefschrift heeft betrekking op de aalvisserij van het IJsselmeer. De aal is, sinds de Afsluiting van de Zuiderzee, de belangrijkste vissoort voor de IJsselmeervisserij geweest. De neerwaartse ontwikkeling in de aalstand is tegelijk ook de teloorgang van de



Figuur 62 Het verband tussen het gemiddelde individuele voortplantingssucces en de omvang van de paaistand, hier geïndexeerd door de omvang van de aalvangsten.
The relation between individual reproductive success and the size of the spawning stock; the latter is represented by the size of the commercial yield. (See chapter 11)

IJsselmeervisserij, maar daarmee is het drama van de Zuiderzeevisserij bepaald niet volledig beschreven.

Eens ging de zee hier tekeer
Maar die tijd komt niet weer
Zuiderzee heet nu IJsselmeer
[de Zuiderzeeballade van Willy van Hemert]

De Zuiderzee – wat had ik die graag eens gezien. Een hele grote ondiepe binnenzee (3650 km^2), met een open verbinding naar de Noordzee. Met vissersplaatsen langs een dijk, die in onze moderne ogen nauwelijks een dijk zou mogen heten. Waar ieder voorjaar de ansjovis en de haring uit de Noordzee kwamen binnentrekken. En elke boer met een praam die maar een beetje kon varen, vrij was een tijdje visserman te worden en te delen in de overvloed aan vis (12 miljoen kilogram, 1.4 miljoen gulden). Althans, als de vis kwam, want in sommige jaren…

Maar die tijd ging voorbij. In 1932 werd de Zuiderzee afgesloten en ontwikkelde zich een visserij op zoetwatervis. De eerste jaren na de Afsluiting zullen een turbulente periode zijn geweest: ander water, nieuwe vissoorten, veranderend vistuig. Na de oorlog brak een betere periode aan: grote aal-vangsten in rustiger vaarwater, en met aanzienlijk hogere prijzen dan ooit tevoren (Figuur 64).

Dat was een periode waarin de overheid ervoor koos de visserij te saneren. Enerzijds om ruimte te krijgen voor inpolderingen, maar anderzijds om het gemiddelde inkomen van een visser te verbeteren. Want wel lagen de totale vangsten hoog, maar er waren ook wel erg veel vissers (>1000 bedrijven). De gewenste sanering kreeg de vorm van een uitstervingsbeleid: opvolging van oudere vissers werd in vele gevallen niet toegestaan. En herhaaldelijk werden aanvullende maatregelen genomen, zoals de verboden op de typische Zuiderzee-vistuigen. De laatste in die reeks is in 1970 het verbod op de kuilvisserij geweest. Nota bene het gevolg van een invloedrijke hengelsportlobby.

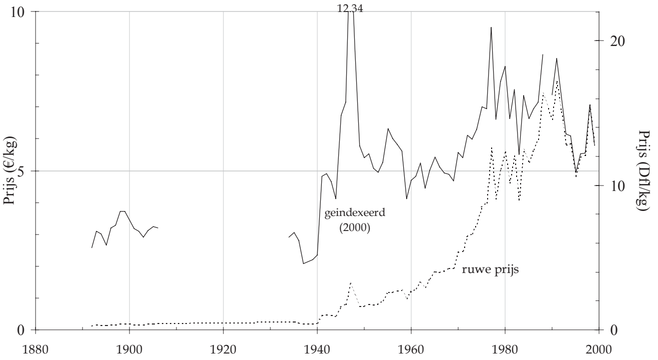
Nu rijzen vragen als: is het uitstervingsbeleid voor de IJsselmeervissers geslaagd, is de visserij tenslotte gezond geworden? Achteraf is het antwoord nogal simpel te geven: het aantal visserijbedrijven is nog steeds sterk aan het dalen (<70), maar de visstand blijft extreem overbevist, de economische positie van de bedrijven is doorgaans zwak en de visserij heeft ongewenste neven-effecten op de natuurwaarde van het IJsselmeer: een grote bijvangst van onverkoopbare – en gedeeltelijk zelfs beschermde – vis en de verdrinking van tienduizenden duikeenden in de netten. De overheid had zich ten doel gesteld het aantal schepen te beperken om al deze problemen te voorkomen, maar is links ingehaald door de inten-

Figuur 63 De VD357 '*Moed en Vertrouwen*' vist met het hoekwant op de Zuiderzee, ca. 1900. Schipper was P. Sier Lz.

VD357 'Moed en Vertrouwen' *[Courage and Confidence] fishing with long lines in the Zuiderzee (now: Lake IJsselmeer), in around 1900. P. Sier Lz. was the skipper.*

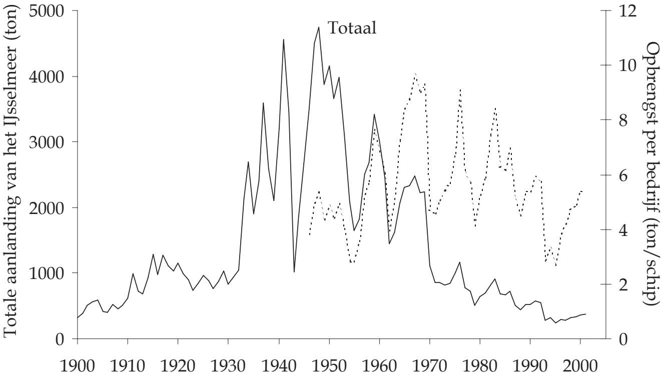
sivering en modernisering van elk van de overblijvende schepen. In de jaren vijftig was er de overgang van zeilschepen naar motorvaartuigen, in de jaren zestig de opkomst van kunstvezels voor de netten, in de jaren zeventig de geweldige groei van de fuikenvisserij en in de jaren tachtig de vergroting van de fuiken. In de jaren negentig de liberalisering van de regelgeving – door de overheid zelf in gang gezet – waardoor de visserij nu veel efficiënter van de visrechten gebruik kan maken. Niet zozeer een stringent beleid heeft het lot van de IJsselmeervisserij bepaald, maar de autonome technische vooruitgang en het gelijktijdig afsterven van de zwakste bedrijven. Daarmee is het einde van de ontwikkelingen nog niet bereikt. Er zijn nog steeds technische verbeteringen mogelijk, de liberalisering is nog lang niet ten volle benut, de beoogde saneringen verlopen nog steeds buitengewoon traag.

Te late en te lakse saneringsmaatregelen, een nauwelijks rendabele visserij, een extreem overbeviste visstand, met ongewenste neveneffecten voor de natuur. Willen we deze situatie laten voortbestaan, en zo nee, waar willen we dan naar toe? In mijn ogen moeten er expliciete keuzes gemaakt worden tussen een aantal mogelijke scenario's. Zonder een expliciete breuk met het beleid in het verleden (te laat, te laks) blijven er zonder twijfel een zeer klein aantal (ca. 5) grote visserijbedrijven over, die in onderling overleg de overbevissing kunnen beperken tot een voor henzelf wenselijk niveau. Willen we dat niet, dan kunnen we ook kiezen voor realisering van het alom bekende – maar momenteel onterechte – imago van de IJsselmeervisserij als een kleinschalige, duurzame visserij, vanuit authentieke havenplaatsen, met ambachtelijke vis-



Figuur 64 De prijs van verse aal van het IJsselmeer is halverwege de 20^{e} eeuw fors gestegen, tot vanaf ca. 1980 de aalkweek de wildvangst verre overtrof, hetgeen een geleidelijke daling veroorzaakte. De enkele hoge piek in 1948 hangt samen met prijsmaatregelen direct na de oorlog.

In the middle of the 20th century, the price for fresh eel from Lake IJsselmeer rose suddenly. Development of aquaculture since 1980 depressed the price gradually. The single peak in 1948 is related to food price policies, directly following World War II. (See chapter 11)



Figuur 65 De totale opbrengst van de aalvisserij op het IJsselmeer is, sinds de bloeiperiode kort na de Afsluiting van 1932, periodiek gedaald, en ligt nu weer beneden het oorspronkelijke niveau. Sanering van de vloot na de Tweede Wereldoorlog heeft de opbrengst per schip aanvankelijk doen stijgen, maar die is sindsdien weer gedaald tot ongeveer het oude niveau.

Following the creation of Lake IJsselmeer in 1932, eel fishing yield increased considerably, but lateron declined down to the original low level. After World War II, the governmental policy to reduce the number of ships effectively increased the average catch per ship. In later decades, however, a gradual fall back to the original value has occurred. (See also chapters 7 and 8)

Figuur 66 Een moderne IJsselmeer-kotter, ca. 1990.
A modern-day fishing vessel on Lake IJsselmeer, ca. 1990.

Figuur 67 Tijdens de Tweede Wereldoorlog zag de tekenaar van deze prent, dat de vroegere ansjovis-visserij van de Zuiderzee wel wat te intensief was geweest. Na de oorlog moest de visserij beter verlopen; maar zestig jaar later is dat nog steeds niet gebeurd.
A war-time picture of the former anchovy fisheries on the Zuiderzee. The designer knew that this was not a sustainable exploitation pattern. After the War, a better time would begin; now sixty years later, that still hasn't happened.

rokerijen, in een gezond ecosysteem. Kiezen we voor deze trendbreuk, dan zal er wat moeten gebeuren.

In 1988 is door het Visserijschap (later opgegaan in het Produktschap) – in eendrachtige samenwerking met visserijorganisaties, de hengelsport en het onderzoek – een plan opgesteld voor een gezonde IJsselmeervisserij, onder de titel 'Beheren door Beheersing'. Doel van het plan was het inkomen van de visserij te verhogen, met behoud van het aantal bedrijven (toen nog 104) en de toestand van de visstand aanmerkelijk te verbeteren, als randvoorwaarde voor een rendabele visserij en leidend tot een natuurlijker visstand. Dat zou stevige ingrepen vergen (een vermindering met 75% van het aantal gebruikte fuiken en netten) en een absoluut halt aan onwenselijke technische 'verbeteringen'. Ik heb destijds met hart en ziel aan dat plan bijgedragen. Daarop terugkijkend, moet ik erkennen dat de benadering soms wat naïef was. Maar de kern, de keuze voor een gezonde en natuurvriendelijke visserij, is vervolgens helemaal niet gemaakt: 'Beheren door Beheersing' heeft opnieuw te laat tot een aantal halve ingrepen geleid, opnieuw zonder wezenlijk resultaat.

De structuur van de IJsselmeervisserij, de keuze van de vistuigen, de lage opbrengsten, de wijze van beheer, de gestelde doelen, de ondoelmatige middelen, en de voortdurende ongewenste neveneffecten, vormen tezamen een erfenis van de toentertijd ongecontroleerde visserij op de Zuiderzee, die zich onbeperkt kon moderniseren, maar nooit een typische kleinschalige binnenvisserij is geworden. De huidige malaise duurt nu al meer dan een eeuw, en maakt ons gezamenlijk onvermogen zichtbaar om er iets beters van te maken.

Een grafschrift voor de aal?

Het gaat slecht met de aal, en het is niet duidelijk wat de oorzaak daarvan precies is. Toch is het van belang om nu maatregelen te nemen, ongeacht het gebrek aan inzicht. Het risico van onnodige maatregelen moet daarbij worden ingecalculeerd; geen maatregelen nemen leidt immers tot een nog groter risico. Bij het opstellen van wetenschappelijke adviezen is er daarom voor gekozen maatregelen voor te stellen voor al die factoren, waarvan redelijkerwijs mag worden aangenomen dat ze een probleem kunnen vormen. Als (en waar) de visserij overbevist, moeten er beperkende maatregelen volgen; als waterkrachtcentrales en stuwen een grote invloed op het bestand hebben, moet er naar een oplossing gezocht worden. Niet omdat iets de enige oorzaak van de achteruitgang is, maar omdat het er mogelijk ook toe bijgedragen heeft.

Een sterk verbreide en kleinschalige visserij, waterwerken, vervuiling, aalscholvers; goed beheer en goede bescherming zullen geen gemakkelijke klus worden. Geredeneerd vanuit de noodzaak de aal in heel Europa te beschermen, zal de gewenste aanpak internationaal moeten worden aangestuurd. Daar staat tegenover dat de aal juist voorkomt in alle kleine binnenwateren, en beïnvloed wordt door allerlei locale factoren, die een locale aanpak noodzakelijk maken. Een systeem van centrale coördinatie en locale uitvoering, met creatieve oplossingen voor de typische problemen, zal moeten worden ingevoerd. De contouren van een dergelijke aanpak zijn vrij makkelijk te schetsen. Maar het grote probleem is, dat de uitwerking en invoering ervan veel tijd zullen vragen, jaren tijd. De snelle achteruitgang van de aal, zeker als daarin een Allee-effect meespeelt, maakt dat er mogelijk nog maar heel weinig tijd over is. Er moet daarom snel wat gebeuren.

Figuur 68 Een IJsselmeervisser op het water bij zijn grote fuiken. (foto Jan van Willigen)
A fisherman on Lake IJsselmeer, attending to his fyke nets.

Epilogue:
Worldwide decline of eel resources necessitates immediate action

Fisheries 28: 28-30 (2003)

The steep decline in populations of eels (*Anguilla* spp.) endangers the immediate future of these legendary fish. With less than 1% of major juvenile resources remaining, precautionary action must be taken immediately, to sustain the stocks.

Eels are curious animals. Despite decades of scientific research, crucial aspects of their biology remain a mystery. In recent decades, juvenile abundance has declined dramatically (Figure 1): by 99% for the European eel (*A. anguilla*) and by 80% for the Japanese eel (*A. japonica*). Recruitment of American eel (*A. rostrata*) to Lake Ontario, near the species' northern limit, has virtually ceased. Other eel species also show indications of decline. The causes of the downward trends are yet unclear, in part due to the catadromous life history of these fishes, which has so far made it impossible to observe their spawning adults in the open ocean. Because of this, the annual spawning stocks of eels that successfully complete the long migration to their spawning areas have never been assessed. The lack of access to basic life history information about the oceanic phase of eels makes it especially difficult to monitor and identify the cause of their population declines. This is in distinct contrast with other declining fishes such as anadromous salmon, whose spawning adults can be relatively easily surveyed when they return to freshwater to spawn, and Atlantic cod, which spawn relatively close to continental margins and can be surveyed by standard fishery techniques. In the case of eels, which depend on freshwater and estuarine habitats for their juvenile growth phase, but anthropogenic impacts (e.g., pollution, habitat loss and migration barriers, fisheries) are considerable and may well have been instrumental in prompting these declines. Loss of eel resources will represent a loss of biodiversity but will also have considerable impact on socio-economics of rural areas, where eel fishing still constitutes a cultural tradition. Research is underway to develop a comprehensive and effective restoration plan. This, however, will require time. The urgent concern is that the rate of decline necessitates swifter protective measures. As scientists in eel biology from 18 countries assembled at the International Eel Symposium 2003 organised in conjunction with the American Fisheries Society Annual Meeting in Quebec (Canada), we unanimously agree that we must raise an urgent alarm now. With less than 1% of juvenile resources remaining for major populations, time is running out. Precautionary action (e.g., curtailing exploitation, safeguarding migration routes and wetlands, improving access to lost habitats) can and must be taken immediately by all parties involved and, if necessary, independently of each other. Otherwise, opportunities to protect these species and study their decline will fade along with the stocks.

Quebec (Canada),
August 14, 2003 and thereafter

For researchers of European eel:
Willem Dekker
For researchers of American eel:
John M. Casselman and David K. Cairns
For researchers of Japanese eel:
Katsumi Tsukamoto
For researchers of southern-temperate eels:
Don Jellyman
For Aboriginal Nations involved with eel:
Henri Lickers

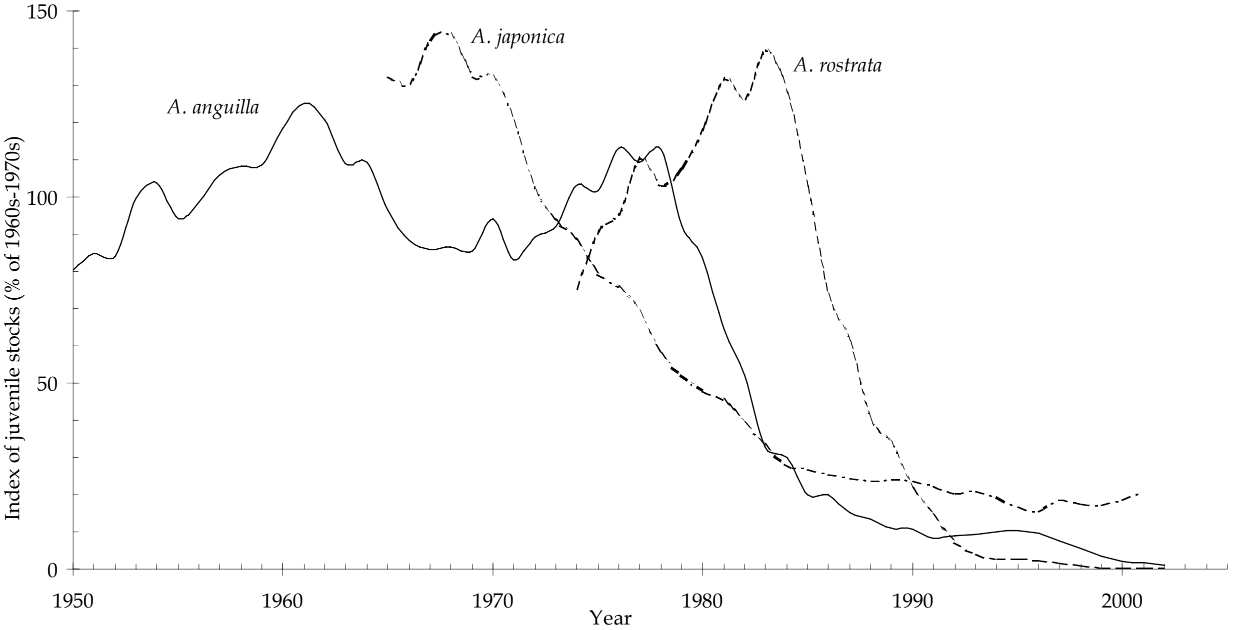


Figure 1 Time trends in juvenile abundance of the major eel stocks of the world. For *Anguilla anguilla*, the average trend of the four longest data series is shown, which trend appears to occur almost continent-wide; for *A. rostrata*, data represent recruitment to Lake Ontario; for *A. japonica*, data represent landings of glasseel in Japan.

Background to this letter

This letter was prepared as a result of the plenary discussion at the end of the International Eel Symposium. Following a suggestion by Prof. Giulio A. De Leo (University of Parma, Italy), we unanimously agreed to bring this immediate concern to light. Signatories to this letter have been selected to represent the scientific communities working on each of the *Anguilla* species, listed in order of magnitude of the resource, with representation by Aboriginal Nations because of their longstanding association with eel. Participants in this discussion were, in alphabetical order by country (affiliation) and name: ABORIGINAL NATIONS: H. Lickers; BELGIUM: C.G.J. Belpaire, G.E. Maes; CANADA: D.K. Cairns, J.M. Casselman, M. Castonguay, B. Jessop, L.A. Marcogliese, K.B. Reid, V. Tremblay; DENMARK: M.I. Pedersen; FRANCE: C. Briand, G. Castelnaud, C. Durif, E.P. Feunteun, P. Lambert, C. Sechet; GERMANY: U. Dumont; INTERNATIONAL (Great Lakes Fishery Commission): C.I. Goddard, R. Stein; IRELAND: T.K. McCarthy; ITALY: G.A. De Leo; JAPAN: J. Aoyama, M.J. Miller, K. Tatsukawa, K. Tsukamoto; KOREA: T.W. Lee; NETHERLANDS: W. Dekker; NEW ZEALAND: J. Boubee, D.J. Jellyman; SWEDEN: H. Wickström; TAIWAN ROC: Y.S. Han, Sin-Che Lee, Mei-Chen Tseng, W.N. Tzeng; UNITED KINGDOM: A.W. Bark, B. Knights, B. Williams; UNITED STATES OF AMERICA: L.S. Brown, S.D. Hammond, A. Haro, L.M. Lee, J.D. McCleave, V.J. Vecchio, J.A. Weeder, S.A. Welsh.

Acknowledgements

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The preparation of this thesis has lasted for twenty years in the end, and brought me all around Europe. In widening the temporal and spatial constraints of research on eel, I have visited a wide area over a long time span, and broadened my own field of view. Over all those years and places, I have met friendly people, who supported me, provided the material I asked for, improved my foreign tongue, suggested lines of thought, corrected me where I went astray, encouraged me when I lost hope, and most often just helped me out and made me feel welcome. Although this is my own thesis, in the end, I realise how much and how many people have contributed, in so many ways.

Reading my own publications, it strikes me that I forgot to add a courteous acknowledgement to several manuscripts; courtesy and decorum are not my forte. Now that I have finally managed to get it all together, I will try to put that right. Can I list all, who provided support or help? More and more names and occasions spring to mind; older memories are now somewhat fainter, but often as dear as new experiences; and nearby home was sometimes as exotic as the furthest outpost. While my list of names lengthens, completion seems to escape endlessly. Trained as a quantitative scientist, I recognise a skewed frequency distribution: an innumerable group of colleagues, fishermen and passers-by who helped me at some occasion, enclosing a smaller circle of (national and international) colleagues and friends, who contributed substantially and recurrently, and knew the lines of thought I developed. Rather than drawing a line between those to be named and those to be left out, where there is no clear distinction in-between (and the risk of accidentally forgetting someone), I choose to express my gratitude to all of you. Reading this thesis, you will recognise where you were involved, and hopefully realise how much I owe to all the helping hands. Finally, in the tail of the distribution, the few odd cases that do not nicely fit in with the rest, dominating the overall picture. Rather than treating them as rare but accidental extreme outliers, I will name them and identify their role.

Niels Daan has been one of the few constant factors during the two decades of my work. Each time I returned to true science, fed up with privatisation foolishness and political intrigues, I found a listening ear and a helping hand. Conscientious in your analyses, strict for yourself and your companions, compassionate with fish and fishermen, what better teacher could I have?

Having spent so many years before actually compiling this thesis, I was aiming for an academic promotion, but eventually without an officially supervising promotor: Niels Daan's professorship had ended years before. Maus Sabelis' willingness to take over the official responsibility from Niels, at a point in time when most of the contents of this thesis were already outlined, is greatly appreciated. His comments were not always easy, but have certainly improved the quality of my work.

Ups and Downs are part of life. One dark day I found out, that my research job was my employment, but not my research. Up 'til today, I am surprised by Adriaan Rijnsdorp's immediate recognition, that I was at a point of no return, and by his swift and unconditional support. A couple of years' research completed my thesis, saved my career as a scientist, and prevented a lifelong cynicism about broken dreams. That day started as a nervous Down and ended as a yet unconfident Up.

During the first international meeting I visited following my appointment as eel biologist 20 years ago, a mathematician pitied me: 'eels are weird things'. For twenty years, I have tried not to believe this, but to follow a rational line of thought. The permanent discussions with Jan van Willigen, experienced technician as he is, were coloured by an intense personal friendship, in which we could afford ourselves viewpoints often as opposing as there are weird things and rational analyses. And weird they are!

Eel fishermen throughout Europe vary in culture and character, but they share the traditional way of life, living amidst their natural resources. Across the professional, cultural and language barrier that separated me from them, it has not always been easy to communicate, but I did and do appreciate the friendly contacts. I enjoy the rural life style, and the close association between fish and fisher still puzzles my mind. Sipke Bootsma, fisherman in Hindeloopen, has been the *primus inter pares* of the fishermen for me. Historical and current day eel fisheries alike, our discussions brought my abstract results alive.

Finally, the people much closer to me than to my work. My mother, Moei, always being there, and always supporting, but in the end always leaving it up to me. Following my childhood's faithful strictness – confidence and patience have been the main maternal contributions

to this thesis; and at this day, still being there. And last but not least, my children Rozemarijn and Fokke, and above all my wife Nienke. As usual, a major commitment from the home front is essential for writing one's thesis. In my case, completion has lasted a long time; the many interesting trips abroad must have been much less interesting when staying behind, at home. But home it always was and is!

This thesis has been supported financially by the Netherlands Institute for Fisheries Research RIVO in IJmuiden (*Strategische Expertise Ontwikkeling*, and a contribution to the printing costs), and the Ministry of Agriculture, Nature and Fisheries LNV in The Hague (a century of routine research programmes related to legal obligations of the government, and a contribution to chapter 7, in 2002 and 2003). Invitations to participate in the 2001 International Eel Symposium in Tokyo (Japan), and the 2003 International Eel Symposium in Quebec (Canada) sparked off chapters 9 and 10, respectively. The University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, took care of the layout of the thesis.

Curriculum Vitae

CV

Willem Dekker was born on Saturday February 11, 1956 in Doorn (Utrecht), the Netherlands. Following elementary school in Driebergen and Almelo, he got his secondary education (Gymnasium β) at the Erasmus Lyceum in Almelo. Since 1974, he studied at Groningen University, and in 1983 he received his MSc in Animal Ecology (subsidiaries in Population Genetics and Fisheries Biology) with the qualification *cum laude*. A major part of his MSc training concerned the mathematical analysis of the multispecies models of the North Sea fisheries, and the statistical analysis of prey size preference of North Sea cod. This work took place at the Netherlands Institute for Fisheries Research RIVO in IJmuiden.

Since 1984, he has been permanently employed at RIVO in IJmuiden – initially as computer programmer, but soon as fisheries biologist, focusing on the inland eel fisheries. From 1989 onwards, he has been Head of the Inland Fisheries Department for some years. As time passed by, political priorities altered, necessitating shifts in his research portfolio: around 1990, research on the typical inland fisheries (outside Lake IJsselmeer) was discontinued and further staff reductions diluted the eel research completely. Finally, from 2000 to 2002, when he received a RIVO-specific part-time grant (*Strategische Expertise Ontwikkeling*, Strategic Development of Expertise), he decided to return to his initial research theme: the population dynamics of the eel. This grant has enabled (completion of) most of the research presented in this thesis.

Willem Dekker has been a member of the Eel Working Party of the European Inland Fisheries Advisory Committee EIFAC, and of the Eel Working Group of the International Council for the Exploration of the Sea ICES, both since 1985. He has participated in international research projects on eel, and initiated and coordinated the international project on glasseel monitoring (Dekker (ed.) 2002), covering 19 countries in Europe and the Mediterranean area. He has chaired the ICES Working Group from 1988 to 1991, whereafter this Group was merged with the EIFAC Eel Working Party. Since 1997, he has hold the chair of this combined Working Group.

A. Paul Weber 1974: Tote Fische - denn sie wissen nicht, was sie tun!

Uitnodiging

Op maandag 11 oktober 2004
om 13u00 verdedigt
Willem Dekker het proefschrift

Slipping through our hands

Population dynamics of the European eel

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