Interactions between fisheries and birds in IJsselmeer, The Netherlands

Promotor:	Dr. E.A. Huisman Hoogleraar in de Visteelt en Visserij
Co-promotoren:	Dr. ir. M.A.M. Machiels Universitair docent bij de leerstoelgroep Visteelt en Visserij
	Dr. A.D. Rijnsdorp Hoofd afdeling Biologie en Ecologie van het RIVO, IJmuiden (Rijksinstituut voor Visserij Onderzoek)

Interactions between fisheries and birds in IJsselmeer, The Netherlands

P.J. Mous

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Abstract

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IJsselmeer, a eutrophic, shallow lake (mean depth 4 m) of 180,000 ha, is heavily exploited by a fishery that catches dfl 11 million worth of eel *Anguilla anguilla*, perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca* and of the small zooplanktivorous smelt *Osmerus eperlanus,* the main prey for perch and pikeperch and for the piscivorous birds of IJsselmeer. The population of cormorant *Phalacrocorax carbo* affects the fisheries through its predation on perch and pikeperch, whereas black tern *Chlidonias niger* and black-headed gull *Larus ridibundus* are affected by the availability of smelt in IJsselmeer. The spatial distribution of prey fish and piscivorous birds was described in relation to spatial scale, water transparency and water depth. The carrying capacity of IJsselmeer for the production of prey fish was assessed, and a dynamic simulation model was constructed to predict consequences of fishery management measures on the fisheries and on the food availability for piscivorous birds.

PhD Thesis, Fish Culture and Fisheries Group, Wageningen University, P.O.Box 338, 6700 AH Wageningen, The Netherlands

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Voorwoord

Als een van de weinige studenten die een afstudeervak deden aan de Leerstoelgroep Visteelt en Visserij aan het eind van de tachtiger jaren was ik slechts zijdelings betrokken bij het promotieonderzoek van Tom Buijse over het IJsselmeer. In plaats daarvan deed ik een afstudeervak in Tanzania, aan de Nijlbaars van het Victoriameer. Ook mijn eerste werkervaring na mijn afstuderen had betrekking op de tropen. Dat ik uiteindelijk toch ben begonnen aan het vervolg-promotieonderzoek over het IJsselmeer, waarvan het resultaat nu voor U ligt, had met name te maken met het vertrouwen dat ik had in Wim van Densen als begeleider en inspirator. Bovendien bood het onderzoek mij de gelegenheid om kennis te maken met het Rijksinstituut voor Visserijonderzoek (RIVO-DLO) in IJmuiden, waar ik de eerste drie jaar van mijn promotieonderzoek gestationeerd zou zijn.

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Summary

The objective of this study was to quantify interactions between the fishery and fish-eating birds as governed by biomass flows and by spatial distribution patterns of predators and prey in IJsselmeer, so to contribute to the rational management of the IJsselmeer lake ecosystem. IJsselmeer is a large (180,000 ha), shallow (mean depth 4m) eutrophic lake in The Netherlands, with water transparency varying between monthly averages of 0.3 m and 0.8 m. The catches of the highly intensive lake fishery, now exerted by ca. 75 fishing units catching about dfl 11 million worth of fish, declined dramatically over the years. The 180 fishermen with a total annual income of only dfl 6 million blame the management authorities for not controlling the population of fish-eating comorant *Phalacrocorax carbo*, which they believe affects the fisheries resource base and which increased monotonously from 4,000 breeding pairs in 1978, to 15,000 breeding pairs in the early 1990s. IJsselmeer is an important foraging, resting, and moulting area for aquatic birds, making it a wetland of international importance.

The fishery targets for eel *Anguilla anguilla* and for piscivorous pikeperch *Stizostedion lucioperca* and perch *Perca fluviatilis*, the total catch of which decreased from ca. 15 kg.ha^{-1}.yr^{-1} in the 1970s to ca. 5 kg.ha^{-1}.yr^{-1} in the 1990s, now supplemented with catches of small smelt, *Osmerus eperlanus* (20 kg.ha^{-1}.yr^{-1}). Smelt is the main prey for pikeperch and perch (90% of diet) and for fish-eating birds (40% of the diet) and now contributes 15% in value and 75% in weight in the fishery. The decrease in eel catches is caused by both over-exploitation and by less glass eel immigrating into the lake. In case of pikeperch and perch, both over-exploitation and cormorant predation (7 kg.ha^{-1}.yr^{-1}), also on pikeperch and perch, may affect the fishery (top-down effect). Bottom-up effects of changes in the fish stocks on bird populations might operate as well. Although black-headed gull *Larus ridibundus* consume most smelt (8.1 kg.ha^{-1}.yr^{-1}), they are not fully dependent on smelt as are small, migratory black tern, *Chlidonias niger*, which almost complete northwestern European population uses IJsselmeer as their feeding ground in August.

Spatial distribution of prey fish affects its availability for piscivorous birds and prey density averaged over the entire lake may have little direct meaning, when fish is highly aggregated. So factors affecting the distribution of both predators and prey fish, mainly smelt, young-of-the-year perch and ruffe, *Gymnocephalus cernua*, were studied at various spatial scales, using hydroacoustics, trawl surveys and aerial surveys. Comparison of fish density estimates based on hydroacoustic observations and on trawl surveys proved that lower trawl catches at sites with a higher light intensity at the bottom are due to lower fish abundance, and not to a stronger escapement of the fish from the trawl at these sites. So numbers caught per trawl haul (*CpUE*) can directly be used to study the environmental characteristics, governing distribution patterns of prey fish. Hydroacoustic observations further showed that aggregations of fish at a spatial scale between 0.01 and ca. 1 km do not exist, and so predator-prey relationships are not affected by such aggregations. At the larger scale of 1 – 50 km, the horizontal distribution of prey fish species

is affected by both water depth and by water transparency, but in different ways depending on the time of the year. During summer, 0-group perch concentrate in the shallow and ruffe in the deep areas of the lake, but during winter smelt, 0-group perch and ruffe all concentrate in the deeper areas. During both summer and winter smelt, much affected by water transparency, are about 200 times more abundant at the most turbid site than at the clearest site in the lake. After having corrected trawl catches for water depth and transparency, spatial autocorrelation in prey fish density was absent on a spatial scale of 1 – 50 km, so no other distribution patterns exist. Between areas of 3000 m^2 of constant water depth and transparency, 67% of the prey fish densities as experienced by avian and fish piscivores varied randomly within a factor $3.2^{\pm 1}$ of the geometric mean density over these areas.

The availability of smelt for surface-feeding birds such as black tern, is also much affected by variations in water transparency, as water transparency influences the vertical distribution of 0-group smelt. During daytime smelt concentrate near the surface at turbid sites (0.5 m Secchi depth), and near the bottom at clear sites (1.2 m Secchi depth). Both piscivorous black tern and omnivorous black-headed gull, as recorded during an aerial survey, show spatial association with their prey, surface-dwelling smelt, as observed by trawling, at a spatial scale between 5 and 20 km. The abundance of these birds and of smelt was higher in more turbid areas. Overall, a 1.5-fold increase in gull abundance corresponded with a 10-fold increase in smelt abundance. At the larger spatial scale of ca. 30 km, spatial association between piscivorous birds and surface-dwelling smelt was absent. For black terns, one area with a high prey fish density was too far away from their main roosting site, whereas the large-scale distribution of black-headed gulls was determined by the local availability of alternative food resources.

Production and utilization estimates showed that in the 1980s and 1990s the biological production of smelt was almost fully utilized by piscivorous fish and birds and by the fishery on spawning aggregations of smelt. Perch and pikeperch consumed 40 $kg.ha^{-1}.yr^{-1}$ of smelt, and the fish-eating birds and the fishery took equal shares of ca. 20-25 $kg.ha^{-1}.yr^{-1}$. In the period 1970-1994 67% of the fairly stable annual production estimates for 0-group smelt varied within a factor 2 around the inter-annual geometric mean. Growth of both zooplanktivorous smelt and benthivorous ruffe were strongly density-dependent. The balance in smelt production and utilization, and the density-dependency in production suggest that the carrying capacity of IJsselmeer for producing prey fish is reached. Hence, a fishery management strategy that aims for more piscivorous fish is only effective if the smelt fishery is reduced, or if one allows less fish-eating birds around the lake. The simulation model build for evaluating effects of fishery management measures confirmed this finding. A simulated 50% reduction of the gillnet fishery and of the fykenet fishery for eel, known for its bycatch of juvenile perch and pikeperch, resulted in a 5% increase of perch catches and a 35% increase of pikeperch catches. But if the smelt fishery would also be reduced by 50%, catches of perch anyway would increase stronger (35%). The influence of cormorant predation on the outcome of the fishery was inferred from leaving out the cormorants from the model, resulting in a 16% increase in the value of the total catch, being the combined effect of gains in perch catches, but losses in smelt catches. The effect of effort and mesh size regulations in the fishery on availability of prey fish for cormorants is moderate, varying between -23% and +76%. The simulation made also clear that stochastic recruitment and cyclic trends in predator and prey abundance will always strongly obscure the effectiveness of the moderate management measures evaluated here.

The history of the IJsselmeer fishery since 1946 can be summarized in three successive stages: I. 1946-1969. High catches of eel (ca. 11 kg. $ha^{-1}.yr^{-1}$, 90% of total value) with pikeperch as the other species of importance (1970 ban on trawling), II. 1970-1981: Lower catches of eel (ca. 4.6 $kg.ha^{-1}.yr^{-1}$, 60% of total value) and pikeperch (25%) and perch (15%) contributed more, III. 1982-1998. Further decrease in eel catches (2.8 $kg.ha^{-1}.yr^{-1}$). Based on auction statistics the catch of eel, pikeperch and perch combined averaged only 4 $kg.ha^{-1}.yr^{-1}$ in the period 1990-1998. Perch is now second in importance both in volume and value and the new smelt fishery contributes 75% in volume and 15% in value of the fishery. There is no significant recruitment overfishing of the stock of smelt. Yet, in years with incidental low densities of 1-group smelt combined with high water transparency as in early 1993, cormorants and their young especially, will become much dependent on the few resources still left. This requires a precautionary approach both on behalf of the fishery and of nature conservation.

Samenvatting

Het doel van deze studie was een bijdrage te leveren aan een rationeel beheer van het ecosysteem IJsselmeer, door de interacties tussen de visserij en visetende vogels te kwantificeren. Deze interacties worden bepaald door biomassastromen in het voedselweb en door ruimtelijke verspreidingspatronen van prooivis en predatoren. Het IJsselmeer is groot (180.000 ha), ondiep (gemiddelde diepte 4 m), en eutroof, met een zichtdiepte die varieert tussen maandelijkse gemiddelden van 0.3 en 0.8 m. Anno 1998 vertegenwoordigt de vangst van de zeer intensieve visserij door circa 75 schepen, een waarde van 11 miljoen gulden. De vangst aan commercieel belangrijke soorten is sinds de jaren 50 dramatisch afgenomen. De 180 vissers die, na aftrek van operationele kosten, samen slechts 6 miljoen gulden verdienen, verwijten de overheid dat er niets wordt ondernomen tegen de toename in het aantal aalscholvers *Phalacrocorax carbo*, een visetende vogelsoort. In het IJsselmeer nam het aantal broedparen van de aalscholver toe van 4.000 in 1978 tot 15.000 in de vroege jaren 90.

De visserij is primair gericht op aal *Anguilla anguilla*, en op de visetende snoekbaars *Stizostedion lucioperca* en baars *Perca fluviatilis*, waarvan de totale vangst daalde van ca. 15 kg. ha^{-1}.jaar^{-1} in de jaren 70, tot ca. 4 kg.ha^{-1}.jaar^{-1} in de jaren 90. Sinds 1982 wordt er ook op spiering *Osmerus eperlanus* gevist (20 kg.ha^{-1}.jaar^{-1}), een kleine zooplanktivore prooisoort. In het IJsselmeer is deze spiering de belangrijkste prooivis voor snoekbaars en baars (90% van het totale dieet) en voor de visetende vogels (40% van het totale dieet). De spieringvangst vertegenwoordigt nu 15% van de waarde, en 75% van het gewicht van de totale aanvoer. De afname in de aalvangst wordt veroorzaakt door zowel over-exploitatie als door een afnemende immigratie van glasaal in het IJsselmeer. Voor snoekbaars en baars zouden zowel over-exploitatie, als predatie door aalscholver op snoekbaars en baars (7 kg. ha^{-1}.jaar^{-1}) de visserij kunnen beïnvloeden (*top-down* effect). Effecten van veranderingen in het visbestand kunnen doorwerken op de populaties van visetende vogels (*bottum-up* effect). Hoewel de kokmeeuw *Larus ridibundus* populatie het meeste spiering eet van alle vogelsoorten die op het IJsselmeer voorkomen, zijn ze niet zo afhankelijk van spiering als de veel kleinere zwarte stern *Chlidonias niger*, waarvan bijna de gehele noordwest Europese populatie het IJsselmeer in de maand augustus gebruikt als rust- en foerageergebied.

De ruimtelijke verspreiding van prooivis beïnvloedt de voedselbeschikbaarheid voor visetende vogels, en de gemiddelde visdichtheid over het gehele meer is van geringe betekenis als de verspreiding van vis zeer geaggregeerd zou zijn. Daarom werden de factoren die de ruimtelijke verspreiding beïnvloeden van twee visetende vogelsoorten en van prooivis, voornamelijk spiering, 1-zomerige baars en pos *Gymnocephalus cernua*, bestudeerd op verschillende ruimtelijke schalen, gebruikmakend van hydroacoustiek, van sleepnetsurveys, en van vogelsurveys vanuit een vliegtuig. Vergelijking tussen visdichtheidschattingen gebaseerd op simultaan uitgevoerde hydroacoustische waarnemingen en sleepnetvangsten bewees dat de lagere sleepnetvangsten op plekken waar de lichtintensiteit aan de bodem hoger was, werden veroorzaakt door een lagere visdichtheid ter plekke, en niet door een hogere ontsnappingskans vanwege de grotere hoeveelheid licht. Daarom kan het aantal vissen gevangen per sleepnettrek (*CpUE*) direct gebruikt worden om het effect van omgevingkarakteristieken op de ruimtelijke verspreiding van prooivis te bestuderen. Verder lieten de hydroacoustische waarnemingen zien dat aggregaties van vis op een ruimtelijke schaal van 0.1 tot ca. 1 km in het IJsselmeer niet voorkomen, en dat daarom predator-prooi relaties niet beïnvloed worden door zulke aggregaties. Op een grotere ruimtelijke schaal van 1 - 50 km wordt de ruimtelijke verspreiding van prooivissoorten beïnvloed door de diepte en door de helderheid van het water, maar de wijze waarop wordt bepaald door de periode van het jaar. In de zomer concentreert 1-zomerige baars zich in de ondiepe gedeeltes en pos in de diepe gedeeltes, maar in de winter concentreren spiering, 1-zomerige baars en pos zich alledrie in de diepe gedeeltes van het IJsselmeer. In zowel zomer als winter was de dichtheid van spiering ca. 200 maal hoger op de meest troebele plek dan op de meest heldere plek. Na correctie voor de effecten van diepte en helderheid, bleek ruimtelijke autocorrelatie op een ruimtelijke schaal van 1 – 50 km tussen sleepnetvangsten afwezig. Het is daarom waarschijnlijk dat andere factoren dan diepte en helderheid geen invloed hadden op het verspreidingspatroon van prooivis in het open water van het IJsselmeer. Tussen gebieden met ieder een oppervlakte van 3000 m^2 en met een constante diepte en helderheid, varieerden 67% van de prooivisdichtheden *random* binnen een factor $3.2^{\pm 1}$ van het geometrisch gemiddelde over deze gebieden.

De voedselbeschikbaarheid voor vogels die op spiering jagen, die vlak onder het wateroppervlak zit, varieert met de helderheid van het water, omdat deze helderheid het verticale verspreidingspatroon van de 1-zomerige spiering sterk beïnvloedt. Overdag concentreert spiering zich onder het wateroppervlak als de helderheid laag is (0.5 m Secchi diepte), en bij de bodem als de helderheid hoog is (1.2 m Secchi diepte). Zowel de piscivore zwarte stern als de omnivore kokmeeuw zijn ruimtelijk geassocieerd met hun prooi, de aan het oppervlak zwemmende spiering, op een ruimtelijke schaal tussen 5 en 20 km. De dichtheid van zowel deze vogels als van spiering was hoger in gebieden met troebeler water. Een 1.5 maal hogere dichtheid van kokmeeuwen correspondeerde met een 10 maal hogere dichtheid aan spiering. Op een grotere ruimtelijke schaal van ca. 30 km was er geen ruimtelijke associatie tussen visetende vogels en spiering meer aan te tonen. Bij zwarte sterns werd dit vermoedelijk veroorzaakt doordat een van de onderzochte gebieden met een hoge spieringdichtheid ver weg lag van de slaapplaats van de sterns. De ruimtelijke verspreiding van meeuwen op een dergelijk grote ruimtelijke schaal werd bepaald door de lokale aanwezigheid van alternatieve voedselbronnen.

Schattingen van de productie en de benutting van spiering lieten zien dat in de jaren 80 en de vroege jaren 90, de biologische productie van spiering bijna geheel werd benut door visetende vis, door visetende vogels en door de visserij op paai-concentraties van spiering. Baars en snoekbaars consumeerden 40 kg spiering $ha^{-1}.jaar^{-1}$, en visetende vogels en de visserij onttrokken ieder 20 – 25 kg spiering $ha^{-1}.jaar^{-1}$. In de periode 1970 – 1994, varieerden 67% van de vrij stabiele jaarlijkse productie aan 1-zomerige spiering *random* binnen een factor $2^{\pm 1}$ van het tussen-jaarlijkse geometrisch gemiddelde. De groei van zowel zooplanktivore spiering als benthivore pos was sterk dichtheidsafhankelijk. De balans tussen productie en benutting van spiering, en de dichtheidsafhankelijke productie suggereren dat de draagkracht van het IJsselmeer voor de productie van prooivis bereikt is. Daarom kan een beheerstrategie die tot doel heeft om een hogere productie aan piscivore vis ten behoeve van de visserij in het IJsselmeer te bewerkstelligen, alleen effectief zijn indien de visserij op spiering ingeperkt wordt, of indien toegestaan wordt dat de voedselbeschikbaarheid voor visetende vogels op het IJsselmeer afneemt. De uitkomsten van het simulatiemodel dat geconstrueerd werd om de effecten van visserijbeheer te evalueren bevestigde deze conclusie. Een gesimuleerde 50% reductie in de kiewnetvisserij en in de fuikenvisserij voor aal, die gepaard gaat met bijvangsten aan juveniele baars en snoekbaars, resulteerde in een toename van 5% in de baarsvangst, en een toename van 35% in de snoekbaarsvangst. Als ook de spieringvisserij met 50% ingeperkt zou worden zou de toename in de snoekbaarsvangst ongeveer gelijk blijven, maar de baarsvangst zou veel sterker toenemen, namelijk met 35%. De invloed van aalscholverpredatie op het resultaat van de visserij werd gereconstrueerd door de aalscholvers uit het model te laten, hetgeen resulteerde in een 16% toename in de totale waarde van de vangst, voornamelijk het gevolg van een toename in de baarsvangst gecombineerd met een afname in de spieringvangst. Het effect van de gesimuleerde beheersmaatregelen met betrekking tot visserij-inspanning en maaswijdte op de voedselbeschikbaarheid voor aalscholvers varieerde tussen -23% en +75%. De simulatie maakte verder duidelijk dat de stochastische variatie in jaarklassterkte en de cyclische trends in predator- en prooidichtheid de effectiviteit van gematigde beheersmaatregelen sterk zal maskeren.

De geschiedenis van de IJsselmeervisserij sinds 1946 kan worden samengevat in drie opeenvolgende stadia: I. 1946 – 1969. Hoge aalvangsten (ca. 11 kg. $ha^{-1}.jaar^{-1}$, 90% van de totale besomming van de IJsselmeervisserij), waarbij snoekbaars de andere belangrijke vissoort voor de visserij is. In 1970 werd de sleepnetvisserij op aal verboden. II. 1970 – 1981: Lagere aalvangsten (ca. 4.6 kg. $ha^{-1}.jaar^{-1}$, 60% van de totale besomming), en snoekbaars (25%) en baars (15%) dragen meer bij aan de totale besomming. III. 1982 – 1998. Verdere afname in de aalvangsten (2.8 kg. $ha^{-1}.jaar^{-1}$). De veilingstatiststieken laten zien dat de gecombineerde vangst van aal, snoekbaars en baars slechts 4 kg. $ha^{-1}.jaar^{-1}$ bedraagt in de periode 1990 – 1998. Baars is nu belangrijker dan snoekbaars in zowel volume als waarde. De spieringvisserij is nu 75% in volume en 15% in waarde. Er zijn tot nog toe geen aanwijzingen voor overbevissing van het paaibestand van de spiering. Maar na jaren waarin de dichtheid van de spiering laag is, zoals 1992, zijn aalscholvers en vooral hun jongen sterk afhankelijk van de hoeveelheid spiering die na de spieringvisserij in het daaropvolgend voorjaar nog overblijft. Dit betekent dat men ten aanzien van deze visserij het 'voorzorgbeginsel', zowel ten behoeve van de visserij als de natuurbescherming, zou moeten hanteren.

Chapter 1

Introduction

Functions of the IJsselmeer ecosystem

IJsselmeer, named the 'Wet Heart of The Netherlands', is a large (180,000 ha) man-made eutrophic lake that fulfills a number of functions, which can be broadly categorized in four groups (De Groot 1992): production, regulation, carrier and information functions (Table 1.1). Also the fish stocks of IJsselmeer are valued because of the functions they have. Firstly, the fish stocks of IJsselmeer fulfil a *production* function, as they are exploited by a commercial fishery that generates about dfl 11 million worth of fish annually. Secondly, fish stocks have *regulation* functions. Fish stocks affect both the higher trophic levels (bottom-up effect) and the lower trophic levels (top-down effect) in the ecosystem through predator-prey relationships. In lakes, the regulatory capability of fish stocks has been used to enhance water quality through biomanipulation (Meijer *et al.* 1994; Reynolds 1994; Dettmers, Devries & Stein 1996; Phillips, Perrow & Stansfield 1996). Thirdly, fish stocks provide a substrate or medium for the higher trophic levels of the ecosystem (e.g. by providing a forage base for piscivorous birds), and for recreation (sport fishing). De Groot (1992) characterises these functions as *carrier functions*. Finally, fish stocks provide *information functions*, which are defined by Hein & De Kruijf (1997) as 'a variety of functions that do not involve a measurable effect or output, but contribute to human well-being'. Examples of these functions of fish stocks in general are the haplochromine fish stocks of Lake Victoria (East Africa), and the *Barbus* species flock of Lake Tana (Ethiopia), which are valued because of their information content on evolutionary history (Witte *et al.* 1992; Nagelkerke 1997). In IJsselmeer, the fishery of IJsselmeer is sometimes mentioned as having an information function worth preserving, because of its history dating back to the period when IJsselmeer was still a tidal area (Zuiderzee).

Problems arise if one function impedes another, especially if different users groups have an interest in the various functions. The total of all benefits derived from the fish stocks is rarely maximal if the system is unmanaged. This holds for various integration levels. The fishing units of IJsselmeer share the same resource. Thus, the function of the fish stocks to provide an income for an individual fishing unit conflicts with the function to provide an income for the other units. Unmanaged, the fishery will over-capitalize and the total benefits (i.e. catch) derived from the system will be sub-optimal ('tragedy of the commons' cf. Ostrom 1990). At a higher integration level, the fishing community may interfere with users of the fish stocks that represent other functions.

The production function of a fish stock interferes with its carrier functions when the fishery competes with other users for the same resource. Probably the most common conflict over fish stocks is the conflict between the fishery and nature conservationists, who act as representatives for natural predators. There are examples abound of conflicts of this type: e.g. the conflict between the cockle fishery and eider *Somateria mollissima* in the Dutch Waddensea (Dankers & De Vlas 1992), the conflict between the commercial fishery and harbour seal *Phoca vitulina* in the waters near Scotland (des Clers & Prime 1996; Thompson *et al.* 1996), and the conflict between fisheries (both culture and catch) and grey heron *Ardea cinerea* in Loire-Atlantique, France (Feunteun & Marion 1994). In IJsselmeer, a conflict developed in the 1980s and 1990s between the fishermen and nature conservationsts because of the increasing population of the piscivorous cormorants *Phalacrocorax carbo*. This conflict was one of the incentives for this study.

Functions based on the utilization of the fish stocks of IJsselmeer

The commercial fishery of IJsselmeer, presently employing about 180 fishermen who operate ca. 75 ships, heavily over-exploits the lake, yielding each of the fishermen an annual income of only ca. dfl 35,000 (Taal & De Wilde 1997). Since the 1970s, catches of the most important commercial fish species, eel *Anguilla anguilla*, pikeperch *Stizostedion lucioperca* and perch *Perca fluviatilis* have been decreasing, and in 1982 the fishermen started to exploit the abundant, but low-priced smelt *Osmerus eperlanus*, a small zooplanktivorous species. While catches decreased, the population of the cormorants increased nearly 4-fold from ca. 4,000 breeding pairs in 1978 to ca. 15,000 breeding pairs in the early 1990s (Fig. 1.1). The fishermen, seeing the numbers of foraging cormorants in IJsselmeer steadily increasing, became concerned that their decreasing catches were to be attributed to cormorant predation on the commercial fish species. At the same time, the increase in cormorants was heralded as a significant achievement of the species protection measures that were implemented in Europe since the 1960s (cf. Van Eerden, Koffijberg & Platteeuw 1995). Presently, cormorant is the most important piscivorous bird species in IJsselmeer (Buijse *et al.* 1993).

In 1995, a first attempt was made to describe and quantify the competitive relationship between cormorants and the commercial fishery in IJsselmeer (Van Dam *et al.* 1995). It was concluded that consumption of eel by cormorants (0.06 kg.ha^{-1} in 1992) was negligible compared to the total catch of eel by the commercial fishery (3.1.kg.ha^{-1} in 1992). Hence the direct impact of cormorant predation on the fishery for eel, which contributed ca. 60% in value to the total catch of the IJsselmeer fishery (1994-1996, Taal & De Wilde 1997), was marginal. However, the interaction between cormorants and the fishery for pikeperch and perch, together contributing ca. 23% to the value of the total catch of the IJsselmeer fishery (1994-1996, Taal & De Wilde 1997), was stronger. Predation by cormorants on these species was high, ca. 7 kg ha^{-1}.yr^{-1} (mainly consisting of perch), compared to the 3.5 kg.ha^{-1}.yr^{-1} of perch and 1.0 kg.ha^{-1}.yr^{-1} of pikeperch caught by the fishery

(Buijse *et al.* 1993). The fishery for perch and pikeperch is not only affected by cormorants, but also by the fishery itself, as with each kg of eel caught, ca. 10 kg of other fish, including juvenile perch and pikeperch are caught and discarded (Dekker, Schaap & Van Willigen 1993). Most of this discarded fish dies (Willemsen 1985). In the report of Van Dam *et al.* (1995), it was concluded that the negative consequences of predation by cormorants and of discarding by the fykenet fishery on the catches of perch and pikeperch were probably in the same order of magnitude. However, they noted that for a more precise assessment on the interactions between fish-eating birds and the fishery, compensatory mechanisms, such as cannibalism in piscivorous fish, and second-order interactions, such as competition for food between these piscivorous fish and cormorants, should also be considered.

The interactions between fish stocks, fisheries and fish-eating birds in IJsselmeer are governed by predation mortality, which, as in most ecosystems, is affected by spatial distribution patterns of predators and prey. Smelt, which in IJsselmeer rarely exceeds 10 cm body length (Willemsen 1977) plays a key role in the functions of the IJsselmeer ecosystem as the most important prey species, contributing ca. 70% to the total amount of fish consumed by piscivorous fish and birds (Buijse *et al.* 1993). As the most important avian piscivore, cormorant exerts a top-down effect on the fish stocks, and, reversely, fluctuations in the availability of prey fish affect the population dynamics of cormorants (cf. Van Eerden & Gregersen 1995). The much smaller black terns *Chlidonias niger* consume only ca. 1.1 $kg.ha^{-1}.yr^{-1}$ of smelt in IJsselmeer, so it is unlikely that these birds affect their own forage base. But in reverse would variations in the availability of smelt surely affect the population of black terns, because they exclusively depend on smelt, when they use IJsselmeer as their foraging area in August on the way from their breeding areas in northern and eastern Europe to their wintering areas in West Africa. As the number of terns counted at the roosting site in IJsselmeer in August is at least 45% of the total European black tern population (ca. 200,000 individuals, Rose & Scott 1994), smelt is of crucial importance for this population (Schouten 1983; Karman, Winters & Schobben 1995). A third fish-eating bird, black-headed gull *Larus ridibundus*, the most abundant gull species in the IJsselmeer area (Winter 1994), is omnivorous. They prey on surface-dwelling smelt, they scavenge from discards of fishing vessels, and they forage in the agricultural areas and garbage lots near IJsselmeer (Voslamber 1991). Of the fish-eating birds, black-headed gulls rank first in terms of quantity of smelt consumed (Buijse *et al.* 1993), and consumption of smelt by black-headed gulls is ca. 7 times higher than the consumption by black terns. However, being an omnivore, they are not as dependent on smelt as are black terns. Both black terns and black-headed gulls show peak abundance in IJsselmeer in August. Black tern are present during a period of ca. 2 months only, whereas black-headed gulls are present throughout the year. The abundance of cormorants, including chicks, in the IJsselmeer area peaks earlier in the season around June (Fig. 1.2).

The consumption rate of foraging animals is not only affected by the density, but also by the spatial distribution of prey items (Begon, Harper & Townsend 1990). If prey fish are highly aggregated, the density averaged over a large area is a poor indicator of food availability for piscivorous fish or birds. In such situations, prey availability is more related to the chance of finding prey aggregations and to prey handling time (Brandt & Kirsch 1993). Also in fisheries, especially those fisheries for schooling, small pelagic fish, the catch per trip is only weakly related to the average density in the area, if fish concentrate in particular areas and if fishermen can locate these areas easily (Csirke 1988).

Characterizing spatial distributions is a matter of scale. Piscivores, either fish or birds, operate at various spatial scales, where aggregations of prey fish determines their feeding modes: from searching for schools of highly aggregated prey fish, to searching for individual prey fish within large-scale aggregations. The scale of spatial aggregations of prey fish also affects the extent of spatial association between predators and their prey (Schneider 1989, 1994). For example, foraging cod *Gadus morhua* aggregates with its prey capelin *Mallotus villosus* on a spatial scale as small as 3.5 m, but outside the feeding period, spatial association of cod and capelin becomes only manifest at a much larger spatial scale (> 4 - 10 km) (Rose & Leggett 1990).

The spatial distribution of fish in IJsselmeer has never been studied in detail. Buijse, Schaap & Bult (1992) demonstrate that in IJsselmeer during daytime, the catch per haul of a bottom trawl (*CpUE*) used for surveying fish stocks is higher where the light intensity at the bottom is lower. Light intensity at the bottom in IJsselmeer varies between $4.6.10^{-7}$ and $0.9.10^{-1}$ lx (clear midday at 52°45′ on November 1), because of differences in water depth and variations in water transparency (Buijse, Schaap & Bult 1992). However, this relationship between *CpUE* and light intensity at the bottom could not be used for an accurate description of the spatial distribution of fish, because it was not known whether the higher *CpUE* at deeper or at more turbid sites was related to a higher local abundance of fish, or to an increased catchability of these fish by the trawl, caused by a decreased ability of fish to detect the approaching trawl before being caught. Secondly, even if it could be demonstrated that variation in local abundance caused variation in *CpUE*, then still the effect of depth relative to that of water transparency on the local fish density would remain unknown. Therefore, it became clear that to assess the spatial distribution pattern of prey fish in IJsselmeer, either the variability in the catchability of the fish by the trawl needed to be quantified in relation to water depth and water transparency, or another sampling instrument needed to be deployed. So the study started with exploring the possibilities for combining density estimates of fish by trawling and by hydroacoustics.

Outline of this thesis

The overall objective of this thesis was to give a dynamic description of the major factors governing the interaction between the fish stocks, the fish-eating birds, and the fishery of IJsselmeer, under various management regimes. Firstly, the spatial distribution of stocks of prey fish, and the spatial association with avian piscivores were assessed. Questions to be answered were: Which factors govern spatial distribution in prey fish, and to what extent are prey fish aggregated? Does the spatial distribution of prey fish have consequences for the spatial distribution of fish-eating birds and at what spatial scale? The answers were needed to assess the implications of changes in average prey fish density for the food availability of fish-eating birds. Secondly, the carrying capacity of the lake ecosystem for the production of prey fish, and its utilization by piscivorous fish and birds and by the fishery was estimated. The consequences of various fishery management measures for the fish stocks and for fish-eating birds were quantified by constructing a dynamic simulation model. The chapters in this thesis are grouped in three sections, dealing with sampling methodology, with spatial distribution of prey fish and fish-eating birds, and with interactions between the fishery and fish-eating birds.

Section I. Sampling methodology

To study spatial distribution of fish, hydroacoustics is a potentially effective tool, because the volume sampled per unit time is large compared to other sampling methods (e.g. trawling and gill netting), and because it is possible to record fish abundance data with a high spatial resolution. Hydroacoustics is particularly effective for the assessment of small, shoaling fish stocks. As such, it has been used to study the spatial distribution of *Osmerus eperlanus* and *O. mordax* in deep lakes (> ca. 10 m depth) (Northcote & Rundberg 1970; Burczynski, Michaletz & Marrone 1987; Bjerkeng, *et al.* 1991; Brandt et al. 1991; Argyle 1992), and also to study spatial distribution of fish on a small scale of ca. 0.1 - 5 km in IJsselmeer (Piersma, Lindeboom & Van Eerden 1988). Nearly all hydroacoustic studies are done in deeper waters (> 10 m), using a vertically directed acoustic beam where the transducer is positioned just below the water surface. In shallow waters, such as IJsselmeer, a vertical beam is not efficient for surveying larger areas. The insonified volume can be considerably increased by using a horizontal beam, with the transducer facing in horizontal direction. This was challenging, since so far only few has been published on acoustic fish abundance estimation in shallow waters using a horizontal beam (e.g. Kubecka, Duncan & Butterworth 1992; Kubecka *et al.* 1994). To use this technique in IJsselmeer, a towed body was designed (Chapter 2) for mobile surveying with a horizontally directed acoustic beam.

Although it was possible to detect fish with this set-up, it had to be concluded that sampling conditions are usually not good enough for hydroacoustic detection of small fish in a large, windswept lake like IJsselmeer (Chapter 3). Because of the low signal-to-noise ratio of insonified fish, even the largest smelt (9 cm *TL*) could not be detected when fish were insonified in tail aspect, whereas the smallest smelt (3 cm *TL*) were not detected even when they where insonified in side aspect, the position where their target strength is highest. Because of wind-induced variation in noise levels, significantly less fish were detected with increasing windforce (1-5 Beaufort). Even so, the preliminary survey indicated that dense aggregations of fish, which would have showed up on the echogram, were not present in the traject of 70 km length covered during the survey.

So, concluding that hydroacoustics could not be used for lake-wide surveys on IJsselmeer, it was decided to conduct the surveys with a trawl, and to use hydroacoustics for calibration of trawl efficiency. Therefore, first the size selectivity of the survey trawls was studied (Chapter 4). It was concluded that small-meshed trawls are selective towards larger fish, probably due to stowing of the net. If this effect is not accounted for, this may lead to a 20 – 50% over-estimation of L_{50}, the length where 50% of the fish entering the trawl escape through the meshes of the cod-end. It was inferred from this study that the survey trawl used during this research, a beam trawl with a stretched mesh of 2 mm in the cod-end, was not size-selective towards fish smaller than ca. 10 cm *TL*.

To study the effect of light intensity on the catchability of fish to the survey trawl, hydroacoustic observations were made simultaneously with trawling (Chapter 5). For this purpose, the transducer was mounted on the beam trawl. Hydroacoustic estimates of individual fish size corresponded with the mean length of fish in the trawl, and both sampling methods detected more fish in deeper water, where light intensity at the bottom was lower. Weak avoidance behavior of fish from the sampling gear was observed with hydroacoustics, but the strength of avoidance behavior was not affected by light intensity. From this study, it was concluded that variation in trawl *CpUE*, as explained by variation in light intensity at the lake bottom (Buijse, Schaap & Bult 1992), was caused by variation in local fish density, rather than by variation in catchability.

Section II. Spatial distribution of small fish and of fish-eating birds

Spatial distribution patterns of the most abundant small fish species, being smelt, ruffe and young-of-the-year perch, and the association of fish-eating birds with these prey fish, was studied at a spatial scale ranging from 1 to ca. 50 km (lakewide). Both the vertical distribution and the horizontal distribution of prey fish in the lake were found to be governed by water transparency, and the horizontal distribution pattern was affected by water depth also. Association of two bird species, black tern and black-headed gull, with their prey, surface dwelling smelt, varied with spatial scale.

The vertical distribution of young-of-the-year (0-group) smelt and 0-group perch was studied with a pair trawl that was operated at three depths: near the bottom, in the middle of the water column, and in the surface layer (Chapter 6). Hydroacoustic observations were made to study spatial distribution on a finer spatial scale than would have been possible with the trawl. The survey was conducted both during daytime and nighttime at two sites in the lake, in the period June - August 1992. During daytime, the vertical distribution of young-of-the-year smelt was strongly affected by water transparency. Smelt concentrated near the surface if the water was turbid (0.5 m Secchi depth), and near the bottom if the water was clear (1.2 m Secchi depth). Hence, for surface-feeding birds such as black tern, a higher water transparency causes lower food availability. As Secchi depth in August varies around a mean value of ca. 0.6 m (Lammens 1999), spatial differences in water transparency are critical for the food availability of black tern and other surface-feeding piscivorous birds that rely on smelt also. Over the period June - August, the 0-group perch gradually moved to the bottom, but this was probably caused by an ontogenetic shift from a more pelagic behavior as during the larval phase, to a more demersal behavior as during the juvenile and adult phase. The hydroacoustic observations showed that during sunset, 0-group smelt and perch dispersed over the water column, and at sunrise reverted back to their daytime vertical distribution pattern. This dispersal behavior increases the feeding opportunities for the piscivorous bird, great crested grebe *Podiceps cristatus*, and consequently these grebes concentrate their feeding activity in IJsselmeer in the periods around sunset and sunrise (Piersma, Lindeboom & Van Eerden 1988).

The horizontal distribution of prey fish, being smelt, 0-group perch, and ruffe, was studied with a bottom trawl, fitted with a cod-end of 2 mm stretched mesh (Chapter 7). Two surveys were conducted that differed in spatial resolution (mean distance between hauls ca. 5 km vs. ca. 15 km) and sampling area (35 km^2 vs. lakewide). The first survey was conducted in two 35 km^2 areas of IJsselmeer. In each of these areas, between 5 and 7 sampling sites were selected where at each site 3 hauls were made with the bottom trawl. This small-scale survey was repeated 4 times in the period July 1992 – April 1993 to cover possible seasonal effects. The second survey covered the whole northern and the southern basin of IJsselmeer, wherein sampling sites were selected randomly. Now, at each site a single haul was made. This large-scale survey was conducted in early September 1994 and early December 1994. During both surveys, the effects of water depth and water transparency on *CpUE* were studied, and an assessment was made whether, within a homogeneous lake habitat, variability in *CpUE* increased with increasing distance between sampling locations. This spatial autocorrelation was assessed by constructing variograms (Armstrong *et al.* 1992).

For each species, either water depth, water transparency, or both affected the *CpUE* of the beam trawl. All species concentrated in deeper areas during winter, and ruffe preferred deeper areas during summer as well, although to a lesser degree than during winter. During summer, perch preferred shallower areas, whereas the spatial distribution of smelt was not affected by water depth as such. Both smelt and ruffe concentrated in areas with lower water transparency in both summer and winter, but water transparency did not affect the spatial distribution of perch. For smelt, the most important prey fish species in IJsselmeer, the effect of water transparency was most pronounced: both in summer and in winter, smelt were about 200 times as abundant at the most turbid site (0.5 m Secchi depth during summer, 0.7 m Secchi depth during winter) than at the clearest site (1.7 m Secchi depth during summer, 3.0 m Secchi depth during winter).

During most surveys and for most species, spatial autocorrelation (on a scale between 1 and 50 km) was weak or lacking after densities were corrected for effects of water depth and water transparency. The hydroacoustic observations that were made during the vertical distribution survey, suggested that also at a much smaller scale of 10s of m, small fish in IJsselmeer do not aggregate. This implies that aggregations of prey fish at the spatial scale of large schools (> 10 m diameter) were lacking. In an area of constant water depth and water transparency, the standard deviation in log-transformed catch number per trawl haul of each prey fish species was ca. 1.15. This means that 67% of the observations on abundance in an area of 3000 m^2, randomly varied within a factor 3.2 around the geometric mean. It was inferred that this factor corresponds to the maximal random variation in prey fish density that piscivorous birds and fish experienced. The absence of spatial patterns possibly underlying those in the corrected densities of prey fish was confirmed by the spatial distribution of foraging cormorants in the southern basin of IJsselmeer. Here, variation in water depth was small, so spatial distribution patterns of prey fish are supposed to be determined by variation in water transparency only. Apart from wind force and wind direction affecting flight conditions, the spatial distribution pattern of foraging cormorants was indeed exclusively determined by spatial variation in water transparency (Van Eerden & Voslamber 1995).

Because the spatial distribution of fish seems to be determined largely by water depth and water transparency, there is scope to further optimize the annual young fish survey in IJsselmeer. *CpUE* observations at particular sampling sites can be adjusted, using a map showing depth contours and spatial patterns in water transparency (e.g. using Landsat satellite imagery, cf. Lammens 1999, and Fig. 7.2). In this way, the bias in density estimates in the present survey program for small fish IJsselmeer can be removed. For the northern basin, this bias is considerable. For example, the actual mean depth of the northern basin is 4.5 m, whereas the depth at sampling locations in the northern basin was on average 5.5 m (cf. Table A.3 in Chapter 9). In winter, when the survey is conducted, such an increase in depth of 1 m corresponds with an increase in ruffe density of ca. 2 natural log units (see parameter estimates in Table 7.4). The geometric mean of *CpUE* observations thus overestimates the true geometric mean density of ruffe in the lake with a factor 7.4.

Because water transparency affects the local density of smelt and ruffe, any consistency in spatial patterns in water transparency dictates, to some extent, consistency in the spatial distribution of these prey fish. Spatial patterns in water transparency vary with wind force and direction (Pearson correlation coefficients for windforce with Secchi depth are -0.16 for the northern, and -0.67 for the southern basin, $n_{northern}$ = 308 and $n_{southern}$ = 125, $P < 0.01$ for both basins; see also Van Eerden & Voslamber 1995). However, the southeastern part of the northern basin seems to be relatively clear throughout the year (cf. Fig. 7.2, Lammens 1999). Also during the large scale survey of September 1994, the highest water transparency (1.7 m Secchi depth) was measured there. However, conditions could largely vary, and in November 1994, the northeastern part of the southern basin was clearest (3 m Secchi depth). Therefore, for removing bias in *CpUE* observations, a water transparency map should be used that represents the spatial pattern in water transparency at the moment of sampling.

To assess the spatial association of the obligate piscivorous black tern, and the omnivorous black-headed gull with their prey, being surface-dwelling smelt, the spatial distribution of smelt was studied by surface trawling, and that of birds by an aerial survey. The survey was conducted in two sampling areas, one in the northern and one in the southern part of IJsselmeer, which two areas were subdivided into strata. The northern sampling area was situated at ca. 20 km distance from the main roosting site of black terns, and the southern area at ca. 50 km distance. Birds were also counted from the research vessel during trawling, allowing for a closer spatial and temporal match between estimates of bird and of smelt abundance. In the northern sampling area, variation in water transparency determined the spatial distribution of surface-dwelling smelt. The stratum with the highest water transparency (0.7 m Secchi depth), featured the lowest abundance of surface-dwelling smelt. In the strata with the highest water transparency, the number of foraging black terns and black-headed gulls were lower than in the more turbid strata (0.5 m Secchi depth). From the dimensions of the strata in the sampling areas it was inferred that spatial association between these birds and surface-dwelling scale was manifest at a scale between 5 and 20 km. At this scale, a 10-fold increase in smelt abundance was associated with a 1.5-fold increase in abundance of gulls. This corroborated the conclusion of Kennedy & Gray (1993), that the spatial distribution of foraging animals is consistently less extreme than the distribution of their resources.

Furthermore, association between piscivorous birds and their prey mediated by water transparency may disappear totally at water transparencies < 0.4 m Secchi depth. When water becomes that turbid, piscivorous birds are unable to forage any longer. So they avoid very turbid areas, which may still contain high densities of fish (Van Eerden, Piersma & Lindeboom 1993; Van Eerden & Voslamber 1995).

At a smaller spatial scale (0 - 5 km), spatial autocorrelation in the abundance of both gulls and smelt was absent, indicating that at this scale only random variation in abundance was present. This holds for fish abundance in the surface area covered by a trawl haul (0.3 ha), and for bird abundance in a standard counting area during aerial surveys of 4.6 ha. At a larger spatial scale (ca. 30 km), spatial association between birds and surface-dwelling smelt was absent. This was due to the low numbers of birds in the southern sampling area, despite the high abundance of surface-dwelling smelt in one of the strata within this area. Probably, for black terns this food-rich patch was too far away from the roosting site, where they rest during the night. For black-headed gulls, the availability of an alternative food resource, namely the garbage lot that is situated near the northern sampling area, may have caused gulls not to search for other areas with higher prey abundance.

Section III. Interactions between the fishery and fish-eating birds

Biological production of small fish (< 10 cm *TL*), which in IJsselmeer consists mainly of 0-group smelt, but also of ruffe and small perch, is the forage base that sustains the fishery and the functioning of IJsselmeer as a foraging area for piscivorous birds. Hence, it is important to assess the carrying capacity of IJsselmeer as its potential biological production of such small fish. Begon, Harper & Townsend (1990) define carrying capacity as follows: The population density where production is balanced by mortality, in populations where production or mortality is density-dependent. Hence, production, mortality including utilization, and density-dependency are essential issues to be addressed in carrying capacity studies. Individual growth, mortality, and biomass production of small fish in IJsselmeer, and dependencies therein are described in Chapter 9.

Over the period 1970-1994, the fall abundance of young-of-the-year (0-group) smelt, varied maximally a factor 10, but usually much less, around an inter-annual mean of ca. 10,000 ha^{-1} in both the northern and the southern basin. This variation in the absence of a time trend was small indeed compared to the variation in the abundance of 0-group perch of ca. a factor 1000. Also, the abundance of older smelt, almost exclusively 1-group, did not show a time trend, but its abundance as measured in fall was frequently low after the introduction in 1982 of a fishery on spawning aggregations of smelt. The 0-group smelt reached a mean length of 6-8 cm and ≥1-group smelt a length of 8-11 cm. Since the building of the dike in 1975 that separates the northern basin from the southern basin, 0-group smelt in the northern basin was on average 10% (0.7 cm) longer than 0-group smelt from the southern basin. The difference for ≥1-group smelt was 1.7 cm. This difference in mean length was probably caused by a difference in nutrient loading, since the southern basin was separated from the inflow of nutrient-rich water of River IJssel, a tributary of the River Rhine. Consequently, the average residence time of water became more than 4 times as short in the northern basin than in the southern basin (Prins *et al.* 1995). A similar effect with larger sizes in the northern basin was also observed for ruffe, but not for 0-group perch, which length attained at the end of the growing season seemed to vary exclusively with water temperature.

Over the period 1976 - 1994, smelt consumption by piscivorous fish averaged 40 $kg.ha^{-1}.yr^{-1}$, whereas in the period 1982 - 1994, the fishery for spawning smelt during spring extracted ca. 20 $kg.ha^{-1}.yr^{-1}$. Birds extracted ca. 20 $kg.ha^{-1}.yr^{-1}$ of smelt per year in the period 1983-1987 (Buijse *et al.* 1993). Production estimates of smelt were less certain, because 0-group mortality is always hard to estimate. The production estimates suggest that biological production of smelt was in the same order of magnitude as its utilization, which was also found by Buijse *et al.* (1993). Growth of smelt and ruffe was density-dependent, and faster growth of smelt was associated with a larger mean length of its preferred food, *Daphnia spp.* This suggests that the capacity of IJsselmeer to sustain small fish production for utilization by piscivorous fish, piscivorous birds and the fishery was probably reached. Therefore, management scenarios that aim for a higher biological production and so yield of piscivorous fish should either include a restriction of the commercial fishery on smelt, or allow that food availability for piscivorous birds decreases.

To evaluate the effect of fishery management measures on the fish stocks, on the fishery and on the food availability for fish-eating birds, a dynamic simulation model was developed (Chapter 10). The model was confined to the fishery, to piscivorous fish (perch and pikeperch), to prey fish (smelt, ruffe, and juvenile perch and pikeperch), and to the most likely avian piscivore exerting a top-down effect on the fish stocks, cormorant. The three types of fishery in the model were: the gillnet fishery for perch and pikeperch, the fykenet fishery for spawning smelt, and the fykenet fishery for eel with its high proportion of discarded non-target fish. The model was also used to assess the effect of cormorant predation on the fish stocks, by simulation of a theoretical removal of all cormorants, under the condition of an unaltered fishing regime.

The management measures evaluated were reductions of fishing effort in the three types of fishery and enlargement of the legal minimum mesh size in the gillnet fishery. The effects of these measures were compared with a reference situation representative for a management situation and ecosystem conditions as in the 1980s and early 1990s. The model suggested that the exploitation of smelt limits the production of perch and pikeperch. A simulated reduction in effort of both the gillnet fishery and the fykenet fishery for eel with 50%, resulted in only 5% higher catches of perch. If also the fishing effort in the fykenet fishery for smelt was reduced by 50%, the perch catch increased much stronger, namely by 36%. After a simulated, complete removal of cormorants, the value of the total catch in the fishery increases only moderately by 16%, because gains in the catch of perch were reduced by losses in the catch of smelt. The effect of fishery management measures (effort and mesh size regulations) on food availability for cormorants was only moderate, varying between -23% and +76%. A 75% reduction in the number of eel fykenets has the strongest positive effect on the total money value of the catch of commercial fish (+16%). Year-class strength variation, simulated with stochastic recruitment, strongly obscured the effects of selected management measures on the fish stocks, the outcome of the fishery and on the prey availability for cormorants, which finding is most relevant for the fisheries management.

In Lammens (1999), a model (PISCATOR) for the IJsselmeer ecosystem is presented that includes more elements than the model presented here. It includes additional bird species, and interactions between zooplanktivorous fish and benthivorous fish with their prey. Therefore, it allowed for density-dependency in the production of prey fish. Also, the model structure differs: where in the model presented here, dispersion in length of growing fish is simulated by an adaptation of the fractional boxcar train method (Goudriaan & Roermund 1993), PISCATOR uses classes of fish ('superindividuals', Scheffer *et al.* 1995).

There are two simulated management regimes which consequences can be compared between the two models: a theoretical removal of cormorants, and an increase in mesh size of gill nets (cf. Lammens 1999). Both models predicted that removal of cormorants hardly affected the total fish biomass in the lake. PISCATOR predicted that the catch of perch would increase with ca. 100%. The model presented here predicted a slight decrease (3%) in the gillnet catch of perch, and an increase by 68% of perch above minimum legal size that are caught in the fykenets for eel. The effects on the catch of perch in the gillnets and as bycatch in the eel fykenets combined, amounted to an increase of 35%. This difference in model outcome was probably caused by a difference in the assumptions on size selectivity of cormorant feeding behavior. In PISCATOR, it is assumed that cormorant prefers relatively large prey (> ca. 20 cm *TL*, Lammens & Hosper 1998, Lammens pers. comm.), whereas in the model presented here it is assumed that smaller prey fish (12.5 cm *TL*) are preferred. Thus, in PISCATOR, the prey size preferred by cormorant is closer to the size of perch in the commercial catch, and removal of cormorants thus has a more direct effect on the catch of the commercial fishery. In the model presented here, a smaller prey selection size was assumed based on the study of Van Eerden & Voslamber (1995), which demonstrates that the foraging behavior of cormorants (social fishing) typical for IJsselmeer results in a low prey size compared to other water bodies in The Netherlands. Van Eerden & Voslamber (1995) suggest that this foraging behavior is an adaptation to foraging in a turbid environment with relatively small fish.

In the simulation run with PISCATOR, the gillnet mesh size was increased from 100 mm to 150 mm (stretched mesh), whereas in the model presented here an increase from 100 mm to 140 mm was simulated. Both models predicted the same effect: an increase in the catch of pikeperch, and a decrease in the catch of perch. The difference in the magnitude of the change in mesh size between the models was also reflected by the difference in the effect of the catch: PISCATOR predicted that the perch catch would decrease to nearly nil, and that the pikeperch catch would double. In the model presented here, the perch catch decreased less (-77%), and the increase in the catch of pikeperch was only small (10%).

Study area

Morphology, hydrology, chemistry and public works

The creation of IJsselmeer (Fig. 1.3) was part of the Zuiderzee works, a comprehensive land reclamation project that started in 1920. The dike (Afsluitdijk) that separates IJsselmeer from the Waddensea was completed on May 28 1932, after which salinity decreased from 5.9 g $Cl^{-}L^{-1}$ to 0.17 g $Cl^{-}L^{-1}$ in 1937 (de Beaufort 1954). Through successive land reclamation projects, its surface area decreased from 370,000 ha in 1926, when the construction of the dike was started, to its present area of 180,000 ha. In 1975, IJsselmeer was divided in a northern (110,000 ha) and a southern basin (70,000 ha) by the completion of a dike (Houtribdijk), connecting the western and eastern shore of the lake. Through the River IJssel, IJsselmeer receives ca. 9600 million m^3 of water per year from the River Rhine. The influx from the River Rhine represents 71% of the influx from all sources in both basins (Duin & Kaste 1987). By completion of the Houtribdijk, the southern basin became separated from the River IJssel. Consequently, average residence time is shorter in the northern basin (120 days) than in the southern basin (550 days) (Prins *et al.* 1995). The average depth of the northern basin is 4.5 m, the maximum natural depth is 9 m at former tidal channels. The southern basin has an average natural depth of 3.9 m, and variation in natural depth is low. In both basins, sand was extracted, which caused pits with maximum depth of 25 m. The surface area of the sand pits is less than 1% of the total surface area of the lake.

Over the period 1960-1993, water temperature in the northern and southern basin varied between 16 and 19 °C in the 3rd quarter of the year, and between 1 and 6 °C in the 1st quarter of the year (means over daily temperature measurements, data from Rijkswaterstaat, The Netherlands Ministry of Transport, Water Management and Public Works). Water transparency is higher in the northern basin (ca. 0.7 m Secchi depth) than in the southern basin (ca. 0.4 Secchi depth) (Lammens 1999). The lower water transparency in the southern basin is caused by a higher concentration of inorganic suspended particles (Lammens 1999). Already in 1934, two years after the creation of the lake, water transparency in the northern and southern part of the lake differed (de Beaufort 1954). There was no trend in water transparency over the period 1970-1995 (Lammens 1999), although nutrient concentrations markedly changed during this 25 years period (Fig. 1.4). After 1975, total phosphate (total-P) and nitrate concentrations were always higher in the northern than in the southern basin. After 1980, total-P in both basins decreased, but more so in the northern than in the southern basin. In 1994, total-P concentration in both lakes was ca. 0.15 mg $P.l^{-1}$. The decreasing trend in total-P resembled the trend in the River Rhine, whereof River IJssel is a tributary. The nitrate concentration in the southern basin dropped sharply to ca. 0.5 $mg.l^{-1}$ after the closing of the Houtribdijk in 1975. In the northern basin, the nitrate concentration was most stable at ca. 0.2 mg $N.l^{-1}$. Over the period 1970-1995, the average chlorophyll-α concentration varied between 60 and 90 $\mu g.l^{-1}$ in the northern basin, and between 32 and 40 $\mu g.l^{-1}$ in the southern basin. In the northern basin, the chlorophyll-α concentration was ca. twice as high during summer than during winter. In the southern basin, seasonal variation in chlorofyll-α is less pronounced than in the northern basin. There was no trend in chlorofyll-α over the period 1970-1995, just as there was no trend in water transparency (Lammens 1999).

Fish

The most abundant fish species in IJsselmeer are smelt, ruffe, perch, pikeperch, roach *Rutilus rutilus* and bream *Abramis brama*. The biomass-size distributions based on routine trawl surveys in the northern and the southern basin (Fig. 1.5) show that, from small to large individual size, the fish population is dominated by smelt (0.56 – 5.6 g), young-of-the-year perch (1.8 – 5.6 g), ruffe (1.8 - 32 g), perch and roach (18 – 320 g), and bream (320 – 1800 g). The least abundant fish, pikeperch, weighed between 180 and 560 g. Both smelt and ruffe were smaller in the southern basin than in the northern basin. The proportion of ruffe in the total fish biomass is higher in the southern basin than in the northern basin, whereas in the proportion of cyprinids (roach and bream) is higher in the northern basin. Differences between basins in catch weight per haul during the trawl surveys are not meaningful, because the surveys of the northern basin were biased to deeper water, where fish abundance is higher (cf. Chapter 7). In both basins, the amount of larger fish is probably underestimated since larger fish are less vulnerable to the trawl (Gunderson 1993).

Fishery

The present day IJsselmeer fishery targets for eel, perch, pikeperch and smelt. Eel is mainly caught with fykenets during summer and fall. Other gears used for fishing eel are longlines and eel pots. Perch and pikeperch are caught by gillnets during fall and winter. The smelt fishery targets for spawning smelt during a fishing season of ca. 6 weeks in March and April using fykenets.

The fishery is managed by permits, gear regulations, closed seasons and a legal minimum size for eel (28 cm), perch (22 cm) and pikeperch (42 cm). Hitherto, the most drastic intervention in the IJsselmeer fishery was the ban on eel trawling, installed on December 31, 1969. The ban was imposed to end the trawl bycatch mortality of juvenile perch and pikeperch. The fishermen responded to this ban with an intensified effort in fishing with passive gear, such as fykenets, gillnets, longlines and eel pots. Of the 235 fishing companies that were in operation in 1970, ca. 80 decided to make use of the government's buy-out program for reorganizing the IJsselmeer fishing fleet (Nagtegaal & Snel 1984). It is not known at which rate fishing effort with these passive gears increased after 1970. However, during a young fish survey in August 1970, Steinmetz & Oudelaar (1971) observed substantially more passive gear in the lake than in previous years, so probably fishing effort was already high directly after the ban. From 1970 to 1988, the number of deployed gillnets and eel fykenets increased 4-fold (Van Dam *et al.* 1995). In the 1980s, several restrictive measures were implemented. But since actual effort employed was still less than the volume of effort for which permits were granted, fishing effort could still increase (Hamelynck 1992). By 1991, no more fishing gear was allowed to enter the fishery, except for large-meshed gill nets (stretched mesh size > 14 cm) (Hamelynck 1992).

In 1996, the Netherlands Ministry of Agriculture, Nature and Fisheries transferred management responsibilities to the fishermen. For this purpose, a producers organisation (PO) was founded, which is responsible for the economic profitability and day-to-day management of the fishery, whereas the Ministry only takes a responsibility for the sustained viability of the fish stocks. The Ministry required the PO to draw up a fishery management plan, which was to be submitted to the Ministry for approval. A reduction of the fishing effort with 50% by the year 2000 became a condition for the approval of the management plan proposed by the PO, but the PO could decide for themselves how the 50% reduction in effort was to be realized. The fishermen agreed to the new management strategy on the condition that benefits originating from the effort reduction would not be nullified by cormorant predation. Thus, fishery management became more closely associated with the management of piscivorous birds.

Fish auction statistics were collected by the Netherlands Ministry of Agriculture, Nature and Fisheries since the end of the 19th century. In the period 1943-1945, collection of statistics and probably also the fishery itself was not effective because of WW II. Until 1975, sale of fish from IJsselmeer through the fish auctions bordering the lake was compulsory, but it is said that a substantial amount of fish was traded outside the auction. After 1975, probably about 10% of the fish caught were sold legally without using the services of the auctions (Nagtegaal & Snel 1984). For smelt, this proportion is higher: statistics of the amount of smelt auctioned and sold directly to wholesale traders over the period 1990-1993 and 1995 indicated that only between 47 and 62% (mean 54%) of the total amount of smelt caught were auctioned.

Total landings per ha (eel, perch and pikeperch combined) decreased over the period 1950-1994 (Fig. 1.6). The ban on trawling can clearly be traced in the catch statistics of eel, perch and pikeperch: it caused the eel landings to decrease by ca. 50% in 1970, after which the total catch never recovered to former levels. The rise in perch and pikeperch landings was at least partly caused by a rise in gillnet effort exerted by the fishermen. The increased survival of juvenile perch and pikeperch probably contributed to the higher catches in the 1970s as well. The recent decrease in eel catches is mainly caused by a lower glass eel migration into IJsselmeer (Dekker & van Willigen 1993) in the period 1980-1992 (Fig. 1.7).

The bycatch of the trawl fishery for eel before 1970 was landed and sold at the auctions as fodder for the poultry industry. Catch statistics were available for the period 1946-1969 (Fig. 1.8a). In terms of weight, the total bycatch landings exceeded the landings of eel, perch and pikeperch combined by a factor 2. According to routine surveys conducted in the periods 1946-1951 (de Beaufort 1954) and 1966-1969 (Steinmetz & Oudelaar 1971) with trawls similar to the ones used in the fishery, the bycatch consisted of smelt and ruffe mainly. The size of the present day bycatch in fykenets, which is discarded at sea, was estimated with experimental fykenets and a creel survey among the fishermen in 1983, 1987 and 1993 (Fig. 1.8b; Dekker, Schaap & van Willigen 1993). This bycatch is low, and its species composition differs notably from the trawl bycatch, now catching less smelt and more perch, and in 1993 a substantial amount of flounder (ca. 5 $kg.ha^{-1}$, or 36% of the total bycatch). The substantial flounder bycatch was probably caused by an increased immigration of flounder from the Waddensea into IJsselmeer, which was the result of an adjustment in management of the sluices to facilitate migration of fish in 1991.

Since 1900, a fishery for large-sized smelt existed, to satisfy a domestic market, but only since 1982, a large-scale smelt fishery developed for the export market (Fig. 1.9). In contrast to the period before 1982, the present day fishery for smelt targets all size classes, including the young-of-the-year (ca. 7 cm body length). This fishery operates at spawning sites close to the shores of IJsselmeer, notably at the eastern shore of the southern basin and at the southern part of the northern basin.

In conclusion, the history of the IJsselmeer fishery since 1946 can be divided into three periods, wherein the relative contribution of the most valuable species, eel, pikeperch and perch decreases:

1946-1969. High catches of the catadromous eel (ca. 11 kg. $ha^{-1}.yr^{-1}$), contributing 90% to the total value of the catch, with pikeperch (ca. half the price per unit weight of eel) as second most important species.

1970-1981: Lower catches of eel (ca. 4.6 kg. $ha^{-1}.yr^{-1}$), contributing ca. 60% to the total value of the catch, and the second most important fish, pikeperch, contributing ca. 25% to the value of the total catch. The remaining part of the total value of the catch is contributed by perch, which is slightly less expensive than pikeperch.

1982-1998. Even lower catches of eel (ca. 2.8 $kg.ha^{-1}.yr^{-1}$), especially in the 1990s. Perch has become more important than pikeperch in value but also in volume. A significant contribution to the value of the total catch has now to come from smelt, actually the forage base of the simultaneously exploited perch and pikeperch. This low-price, high-volume fishery now contributes ca. 15% to the total value and 75% to the total volume of the catch. The total volume of valuable species (eel, pikeperch and perch), as estimated by auction statistics, averages only 4 kg. $ha^{-1}.yr^{-1}$ in the period 1990-1998.

The present day catch volume of valuable species in eutrophic IJsselmeer is low compared to other lakes in Europe. For example, the total catch of brown trout *Salmo trutta* in an oligotrophic Norwegian lake was on average 5.2 $kg.ha^{-1}.yr^{-1}$ over the period 1958-1972 (Jensen 1977). The total catch of whitefish *Coregonus lavaretus* and perch *Perca fluviatilis* in 20 Swiss lakes of varying trophic status (oligotrophic-eutrophic) over the period 1981-1986 averaged 15 $kg.ha^{-1}.yr^{-1}$ (Müller 1990). The present low yield of perch and pikeperch in IJsselmeer can only be explained by over-exploitation of these piscivores (cf. Van Densen *et al.* 1990; Van Dam *et al.* 1995).

The commercial exploitation of smelt does probably not yet endanger the stock of smelt itself, as there is no indication of recruitment overfishing (cf. Chapter 9). However, the smelt that survive the spawning season are the main prey for piscivorous fish and birds in spring and early summer, until the 0-group smelt have grown to a consumable size. As was demonstrated with the simulation experiment (Chapter 10), the exploitation of smelt thus reduces the scope to optimize the fishery for piscivorous perch and pikeperch. Also, in years with incidental low smelt densities combined with high water transparency, cormorants for the raising of their chicks become much dependent on the resources still left (cf. Fig. 1.1, Chapter 9). This requires a precautionary approach both on behalf of the fishery and the conservation of birds.

Piscivorous birds

The seven most important piscivorous bird species in terms of fish consumption are listed in Table 1.2. Together, these seven species consume 94% of all fish eaten by birds in IJsselmeer. Cormorant consumes ca. 42% of the total amount of fish eaten by birds in IJsselmeer, and it is the only fish-eating bird species that showed a clear increase in numbers in the 1980s and 1990s (cf. Fig. 1.1). According to the criteria formulated in the Ramsar Convention (1971), the IJsselmeer area is a wetland of international importance for each of the bird species in Table 1.2.

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***Table 1.1**. Functions of IJsselmeer, categorized according to De Groot (1992). Source: Rijkswaterstaat, Directie IJsselmeergebied*

production functions
• fishery • drinking water for 1.2 milion people • wind energy (on the dykes surrounding the lake, and on artificial islands in the lake) • cooling water for power plants and industry • sand mining
regulation functions
• water level management in the area surrounding IJsselmeer, notably drainage (winter) and irrigation (summer) of agricultural areas • control of water salinity and protection from flooding (these functions actually relate to the dike that separates IJsselmeer from the Waddensea)
carrier functions
• shipping (mainly to and from Amsterdam) • water sports, amongst others windsurfing and yachting (ca. 70,000 yachts pass through the busiest sluice of IJsselmeer annually) • testing area for artillery • nature conservation (especially the important wetland 'Oostvaarders plassen', bordering the southeastern shore of the southern basin of IJsselmeer, but the lake itself also functions as a resting, foraging, moulting and courtship area for aquatic birds) (cf. Van Eerden & Bij De Vaate 1984). IJsselmeer is a wetland of international importance according to the criteria formulated in the Ramsar Convention (1971) • migration route for anadromous and catadromous fish
information functions
• preserving historical values from the period before the construction of the dike that changed the tidal area 'Zuiderzee' into the freshwater reservoir IJsselmeer

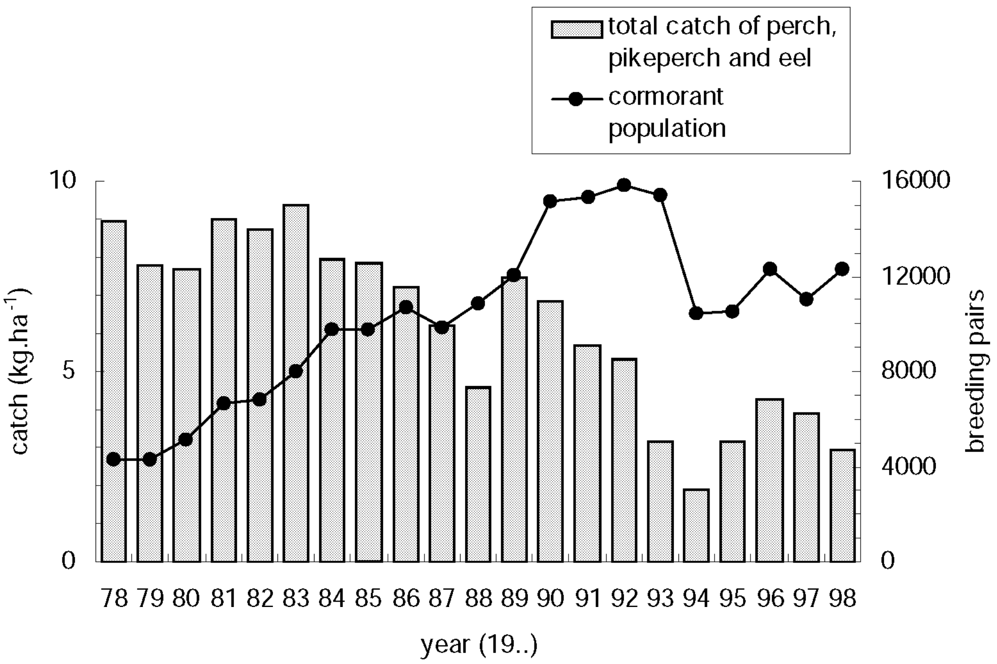

Figure 1.1. *Trends in the commercial catch of eel, pikeperch and perch combined (auction statistics, kg.ha*$^{-1}$*), and in the number of breeding pairs of cormorants in the IJsselmeer area in 1978-1998 (Van Eerden & Gregersen 1995; SOVON).*

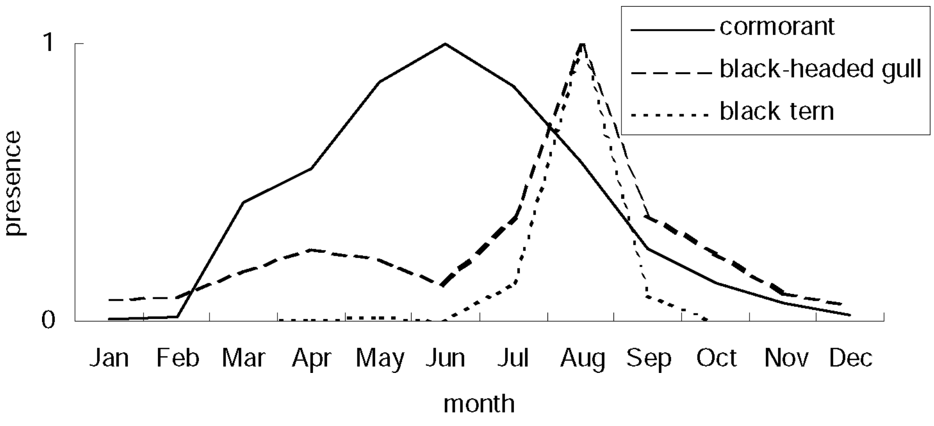

***Figure 1.2**. Seasonal variation in the numbers of cormorant (including chicks), black-headed gull and black tern present in IJsselmeer, expressed as the fraction of the month wherein the numbers of birds in IJsselmeer is highest. After: Winter (1994), Van Dam et al. (1995)*

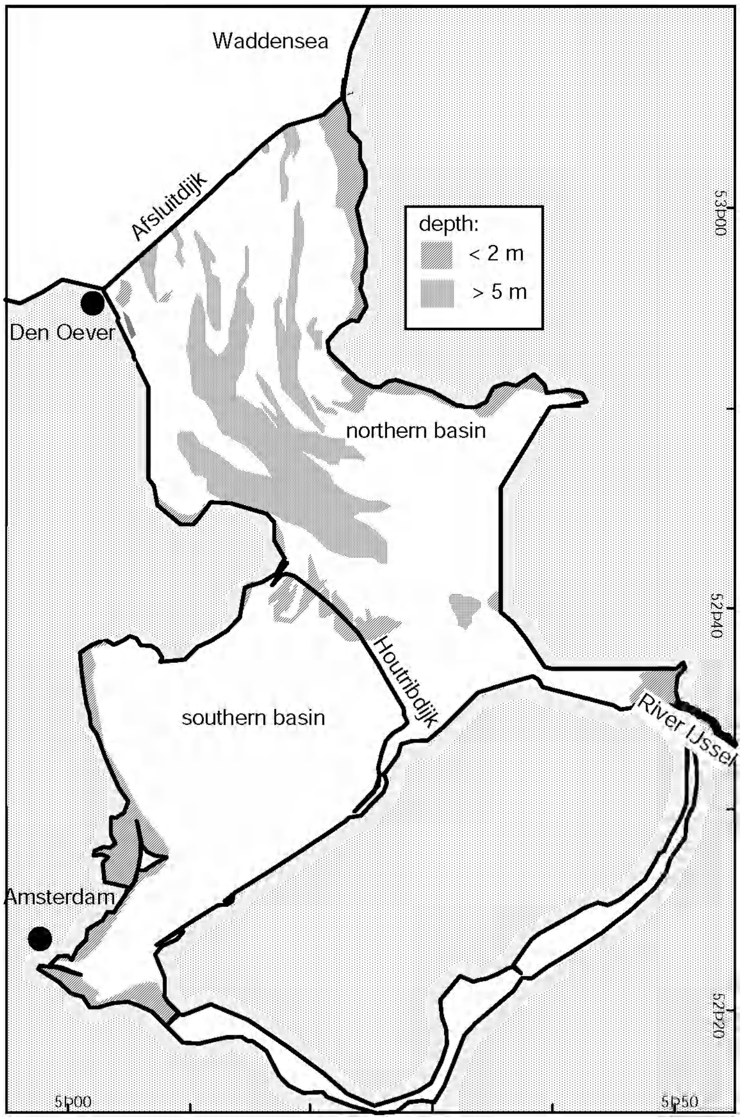

***Figure 1.3**. Map of IJsselmeer, with depth contours.*

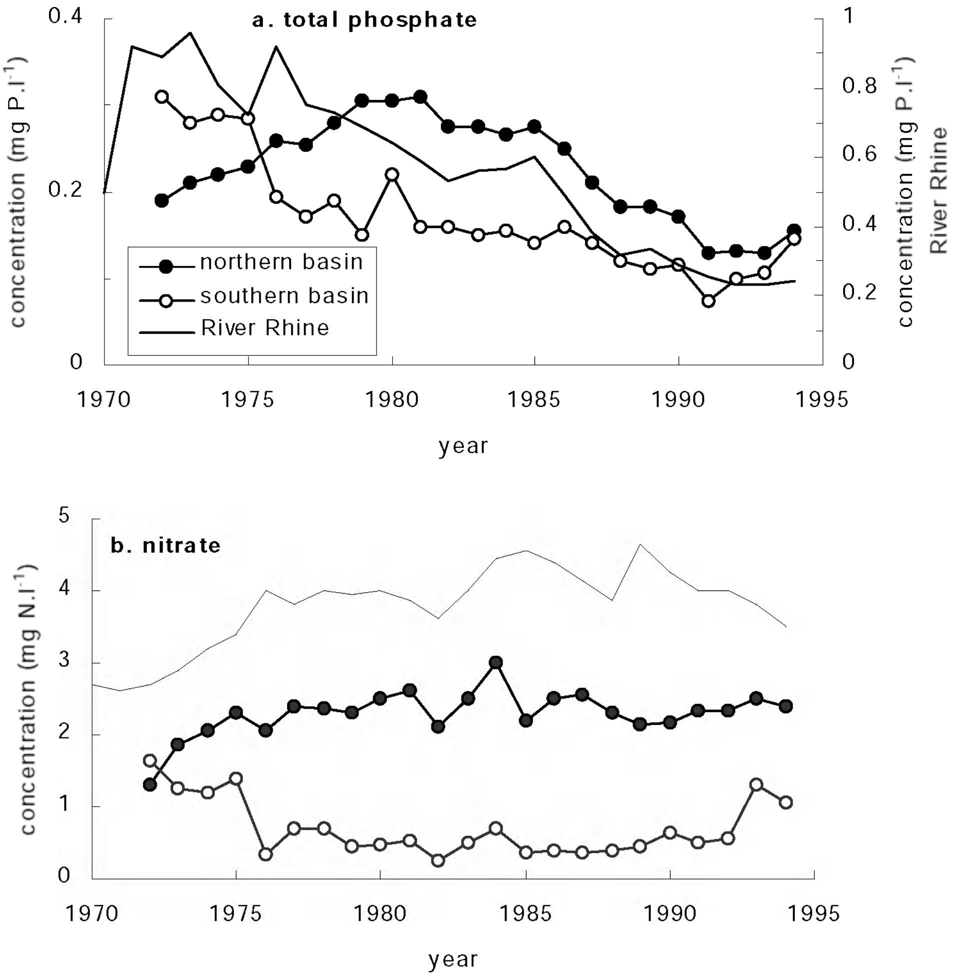

***Figure 1.4**. Total phosphate (a) and nitrate (b) concentration in IJsselmeer and in River Rhine. Source: Lammens & Hosper (1998), Netherlands Ministry of Transport, Public Works and Water Management.*

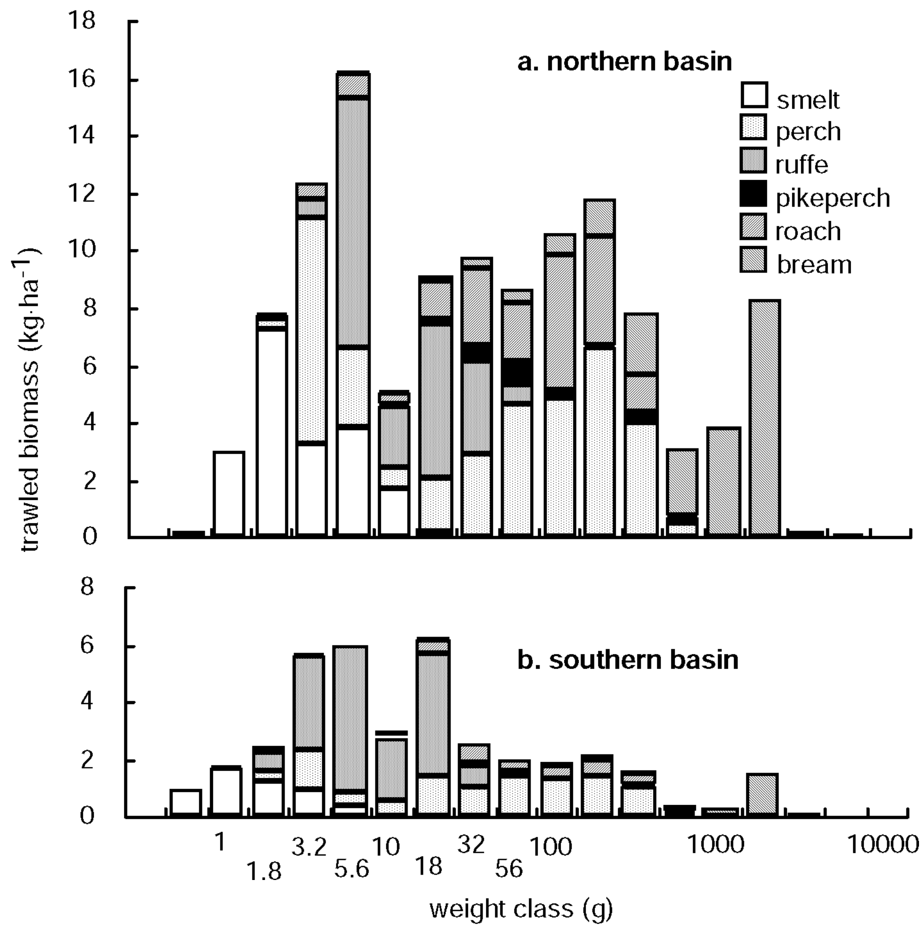

***Figure 1.5**. Biomass-size distribution of the northern and the southern basin of IJsselmeer, averaged over the years 1987-1994, based on fall trawl surveys. The mean length of size classes increases with a factor 1.8 ($10^{0.25}$) to preserve resolution in the smaller size classes, and to group larger fish in more meaningful, wider size classes.*

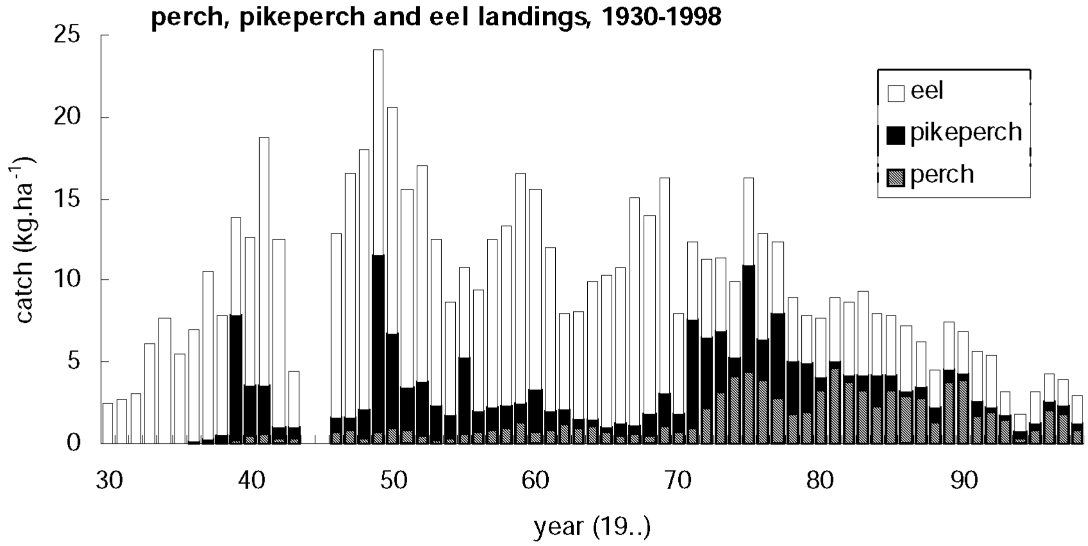

***Figure 1.6**. Annual catch (kg.ha^{-1}) of perch, pikeperch and eel in the period 1930-1998*

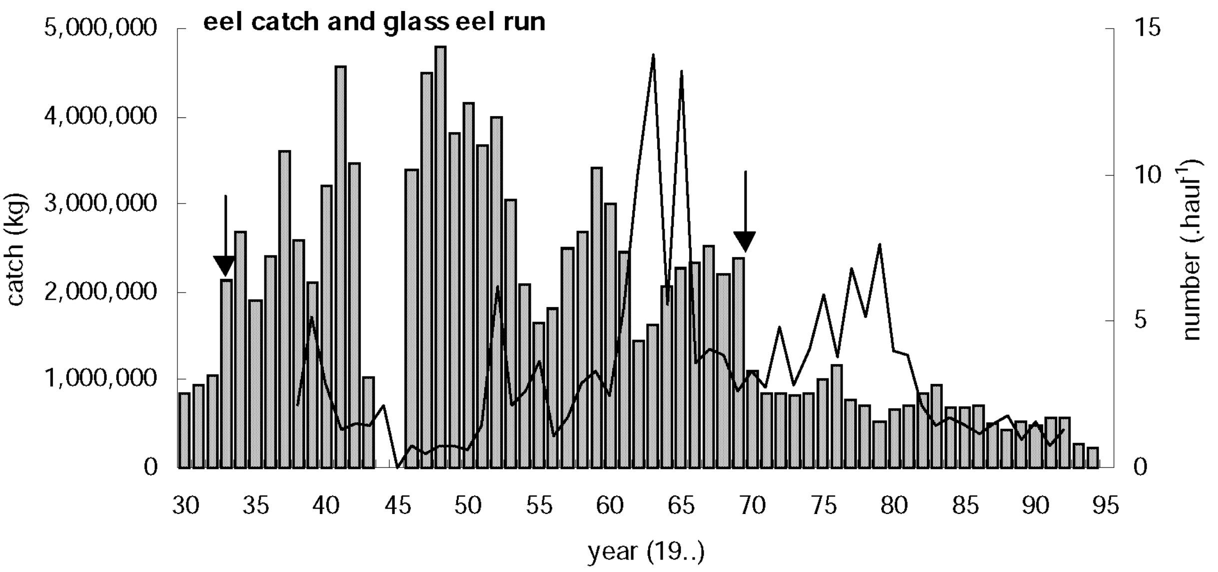

Figure 1.7. *Total eel catch (bars), and glass eel migration into IJsselmeer during the migration period (line). The glass eel run was indexed as number caught per liftnet haul at the sluices near Den Oever, in the northwestern part of the lake. Arrows indicate the year when the dike between the Waddensea and IJsselmeer was closed (1932), and the year when the trawl ban was implemented (1970).*

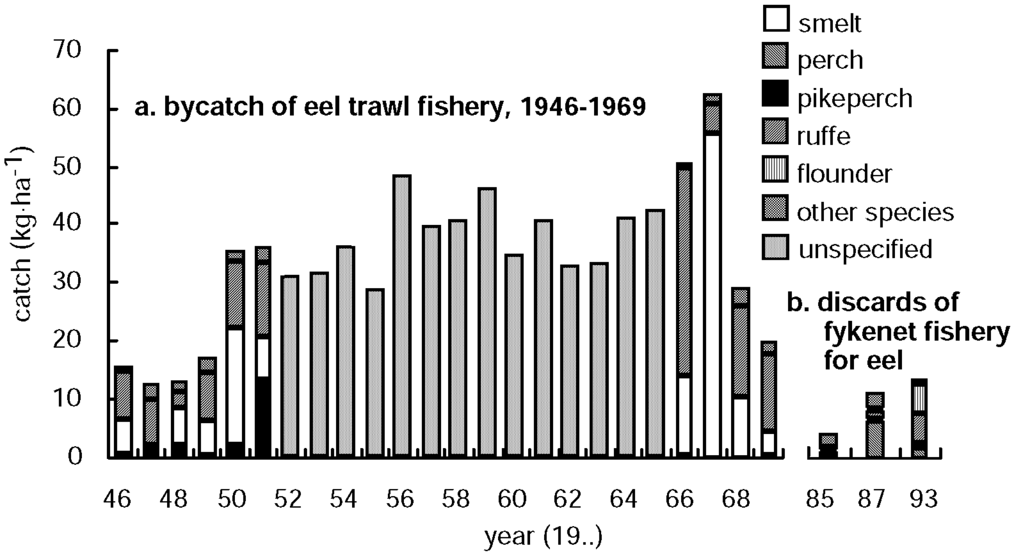

Figure 1.8. *Annual bycatch (kg.ha^{-1}) of the trawl fishery (a) and the fykenet fishery for eel (b).*

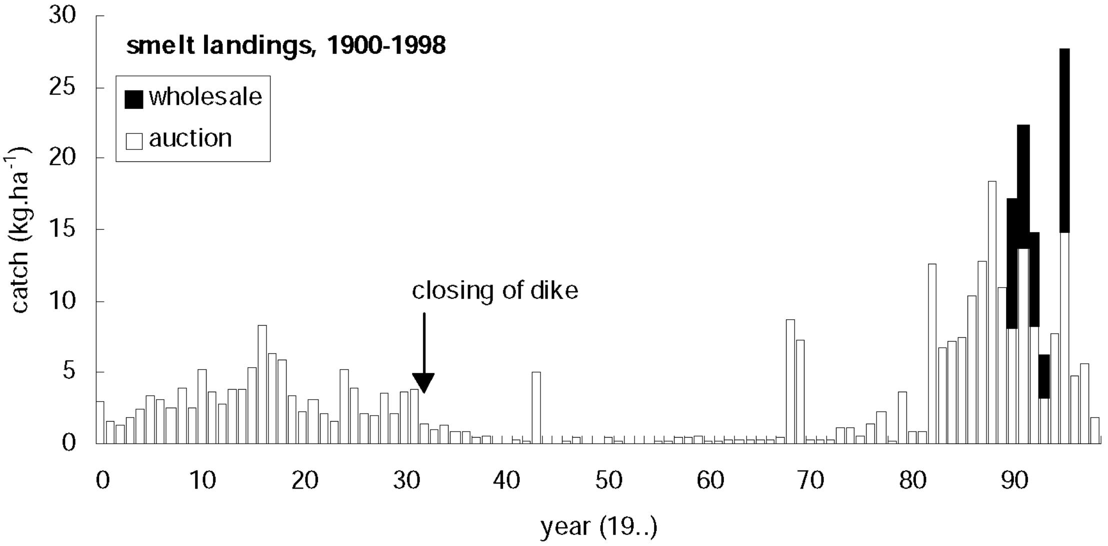

***Figure 1.9**. Annual catch of smelt (kg.ha^{-1}) over the period 1900-1995. Only in 1990-1993 and 1995, statistics on the amount of smelt sold directly to wholesale traders were collected. For these years, between 47 and 62% (mean 54%) of the total amount of smelt caught were auctioned, the rest was traded outside the auction. The year when the dike that separated IJsselmeer from the Waddensea was completed (1932) is indicated).*

Table 1.2*. Fish consumption by birds (kg.ha*$^{-1}$*.yr*$^{-1}$*) (Buijse et al. 1993), importance of the IJsselmeer area for the NW European populations, and seasonal variation in presence in IJsselmeer (Winter 1994). Consumption data are representative for the 1990s (cormorants) and the late 1980s. Importance is rated from + (important) to +++++ (crucial for the viability of the population) (cf ; Van Eerden & Bij De Vaate 1984; RIZA 1993; Beekman & Platteeuw 1994; Winter 1994; Van Eerden & Gregersen 1995;).*

predator	prey								importance	presence
	smelt	ruffe	roach	bream	eel	perch	pike-perch	*total*		
cormorant, *P. carbo*	1.7	8.4	3.1	0.0	0.2	7.3	0.0	*20.7*	+++	Mar-Nov (cf. Fig. 1.2)
black-headed gull, *Larus ridibundus*	8.1	1.0	0.0	0.0	0.0	1.0	0.0	*10.1*	+	all year (cf. Fig. 1.2)
grebe, *Podiceps cristatus*	4.6	0.6	0.1	0.1	0.0	0.4	0.0	*5.7*	++++	all year
goosander, *Mergus merganser*	2.7	0.6	1.5	0.0	0.0	0.8	0.0	*5.6*	++	Nov-Mar
red-breasted merganser, *Mergus serrator*	0.3	0.0	0.0		0.8	0.0		*1.1*	++	Dec-Mar
black tern, *Chlidonias niger*	1.1	0.0				0.0		*1.1*	+++++	Jul-Sep (cf. Fig. 1.2)
smew, *Mergus albellus*	0.9	0.1						*1.0*	+++++	Nov-Mar
other	0.9	0.4	0.7	0.5	0.0	0.5	0.0	*3.0*		
total	*20.3*	*11.1*	*5.4*	*0.6*	*0.9*	*10.0*	*0.0*	*48.3*		

Section I

Sampling methodology

Chapter 2

A towed body designed for side-scanning hydroacoustic surveying of fish stocks in shallow waters

P.J. Mous, J. Kemper and A. Schelvis

ABSTRACT

An aluminum towed body was designed for use in hydroacoustic surveying of fish stocks in shallow (2-10 m depth) inland waters. The design allows application in deep (> 10 m) water bodies as well. Test results showed that towed body was a stable platform for the hydroacoustic transducer. The towed body features adjustable beam direction, allowing a side-looking as well as a vertical-looking mode. As the design of the towed body is simple, it can be easily constructed by any skilled craftsman.

INTRODUCTION

Recently, hydroacoustic methods for studies on fish distribution and fish abundance have been developed for shallow inland waters (< 5 m deep) (Kubecka *et al.*. 1992; Kubecka *et al.* 1994). For hydroacoustic surveys in shallow waters, the axis of the acoustic beam is placed in the horizontal plane, so that a sufficiently large water volume can be insonified. We developed a towed body in which the axis of the acoustic beam could be tilted at any angle, so that the towed body could be used in shallow waters. Criteria for the design of the towed body were: stability (i.e. the towed body should provide a stable platform for the transducer), ease of handling, and an adjustable beam tilt angle.

MATERIALS AND METHODS

The towed body (Fig. 2.1) was made of aluminum. It was constructed in approximately 25 hours by a skilled craftsman. The acoustic axis can be directed in any tilt angle perpendicular to the course of the ship. We used a 25 kg weight as depressor. A winch facilitated setting and retrieving the towed body. The weight of the towed body is 8.5 kg, excluding depressor and transducer.

We mounted a Biosonics® elliptical dual beam transducer with a 5.5°*17.5° wide beam and a 2.2°*7.5° narrow beam in the towed body. The transducer was connected with a Biosonics® ES2000 echo-sounder. The hydroacoustic system was employed from a research vessel of 20 m length. We used this set-up for acoustic surveys in the IJsselmeer, a large (180,000 ha), shallow (average depth ca. 4 m), wind-exposed lake in the Netherlands. The fish community of IJsselmeer consists mainly of smelt, *Osmerus eperlanus*, perch *Perca fluviatilis*, ruffe *Gymnocephalus cernua* and cyprinids of 5-40 cm *TL*.

RESULTS AND DISCUSSION

After launching, the towed body moved to a stable position at the side of the ship within less than a minute. During most recordings, we positioned the towed body ca 1 m below the water surface, the transducer facing slightly downwards (ca 5° from water surface). A towing speed of ca. 6 km.hr^{-1} gave the best results. The fish detection range is limited by the back scattering properties of the water surface and the bottom. In our situation, fish could be detected at a range up to 40 m from the transducer surface. Wind-induced waves caused reverberation by air bubbles and decreased the fish detection range.

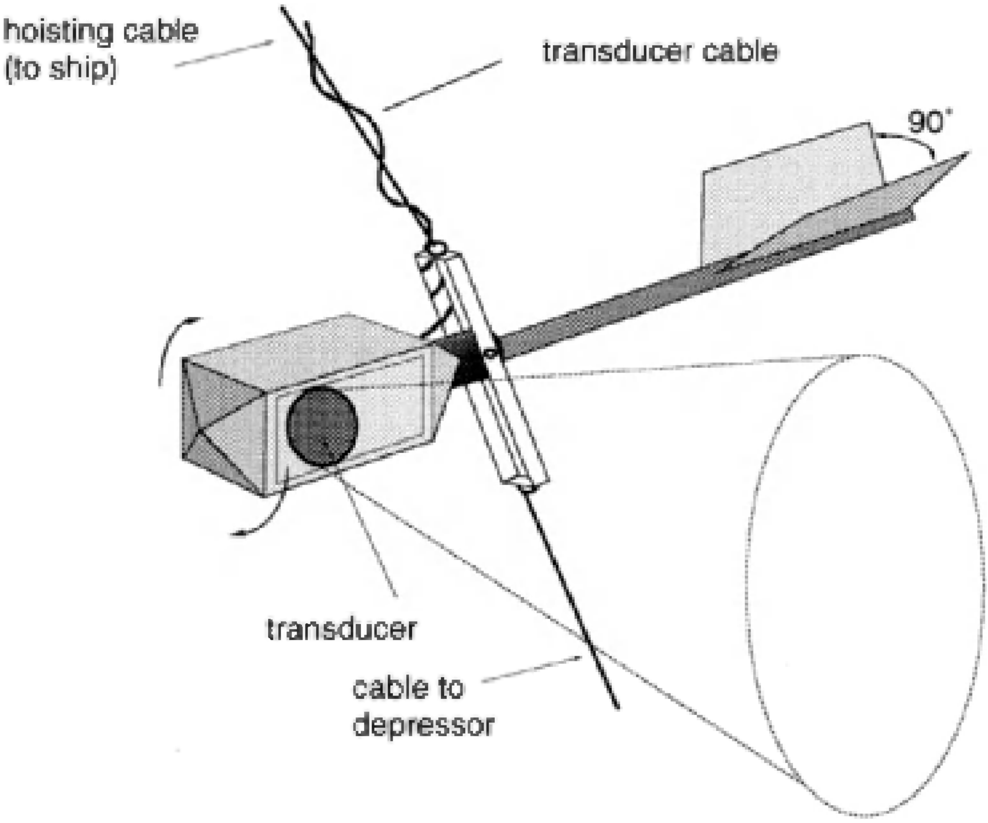

***Figure 2.1**. In situ view of the towed body. The overall length of the towed body is 1.35 m. The transducer is mounted in the head of the towed body. The head of the towed body can rotate around the axis, resulting in an adjustable beam tilt angle. The transducer cable is attached to the hoisting cable. The hoisting cable is fixed to the top ring of the brace; the depressor is fixed to the lower ring. The axis of the towed body can rotate freely around the pin in the brace. The fins stabilize the towed body. An extra cable (not drawn here) attached to the depressor facilitates handling of the towed body. A detailed description of the towed body can be obtained from the authors.*

The towed body can also be used in deep waters, where it can be positioned anywhere in the water column by varying the length of the towing cable, the towing speed and the weight of the depressor. The acoustic beam can be tilted at any angle, which makes it a flexible platform for fish distribution studies. Even a vertical up-looking beam can be used if, instead of a weight to stabilize the towed body, a depressor with adjustable side deflection is used. The side deflection action positions the towed body away from the wake of the ship and ensures that no fish are scared away by the towing cable. This set-up is similar to a dual paravane vehicle (Biosonics, 1987). The availability of the side-looking mode and the simplicity of the design are the unique and novel properties of this towed body as compared to other designs.

The advantage of a towed body compared to a set-up where the transducer is fixed to the research vessel is that the towed body buffers the movements of the ship, resulting in a stable transducer platform. This especially holds for surveys in deeper waters, when more towing cable can be used. Furthermore, a portable hydroacoustic system in combination with a towed body can be easily installed on any vessel with hoisting facilities; we needed one hour only to install the complete system onboard the research vessel. A disadvantage of this towed body compared to a fixed set-up with pan and tilt facilities (Kubecka *et al.* 1994) is the impossibility of adjusting the direction of the beam during recording.

ACKNOWLEDGEMENTS

The field work was made possible by the RV 'Stern', her crew, and by technical assistants from the Netherlands Institute of Fisheries Research. The manuscript benefited of the comments of two anonymous referees from *Fisheries Research*. This research was supported by grants from the Netherlands Ministry of Agriculture, Nature and Fisheries, Directorate Fisheries, from the Netherlands Ministry of Transport, Public Works and Water Management, Rijkswaterstaat, Directorate IJsselmeergebied, from the International Reference Centre for Nature Management, and from the EU project 'Lachs 2000'.

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Chapter 3

Application of a hydroacoustic sampling technique in a large wind-exposed shallow lake

P.J. Mous & J. Kemper

ABSTRACT

A pilot survey was carried out to asses whether hydroacoustics is a suitable sampling tool to estimate the spatial distribution, size distribution and stock abundance of small pelagic fish in a large (180,000 ha), shallow (ca. 4 m), wind-exposed lake. The targeted fish were perch *Perca fluviatilis* and smelt *Osmerus eperlanus* of 3-9 cm body length. A scientific echo-sounder (Biosonics® 2000ES) with a horizontally directed acoustic beam was used. The transducer was mounted in a towed body. Backscattered acoustic signals were identified as fish (*AIF*) by the echo signal processing software of Biosonics. Target strength estimation was facilitated by the dual beam technology of Biosonics. The swimming direction of *AIF* relative to the transducer could be estimated from the change in distance from the transducer of targets in consecutive pings. Detection of targeted fish was hampered by high noise levels and was dependent on the orientation of the fish in the beam. Most *AIF* avoided the research vessel. Backscattering properties of *AIF* avoiding the vessel differed from *AIF* not avoiding the vessel. This was caused by size-specific avoidance behavior or by a difference in orientation between fish avoiding the vessel and fish not avoiding the vessel. Sampling conditions influenced the output of the hydroacoustic system: significantly less fish were detected with increasing windforce (1-5 Beaufort). Hydroacoustics are not recommended for estimating spatial distribution, size distribution and fish abundance on large, shallow lakes. Variable fish behavior and sampling conditions are major sources of bias in the estimates.

INTRODUCTION

IJsselmeer, a eutrophic lake in the Netherlands with an average depth of 4 m, is divided by a dike into a northern basin of 112,000 ha and a southern basin of 68,000 ha. It supports commercial fisheries for eel (*Anguilla anguilla*), perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and smelt (*Osmerus eperlanus*), and it is an important foraging and breeding area of several species of fish-eating birds (Van Eerden & bij de Vaate 1984). The overall objective of the study was to describe the interaction between 3 groups that utilize the smelt stock of IJsselmeer: predatory fish (pikeperch, perch and eel), commercial fisheries and fish-eating birds. To estimate whether the shared resource was scarce, the size and spatial distribution of the smelt stock needed to be determined. Hydroacoustics is potentially an effective tool to estimate stock size and spatial variation in abundance for 3 reasons. First, the sampled volume per unit time is high compared to other sampling methods (e.g. trawling and gill netting), which is an advantage in a large lake. Second, with hydroacoustics it is possible to obtain data on fish abundance with a high spatial resolution, even at a level where the distribution of individual fish can be studied. Third, with hydroacoustic equipment it is possible to study the swimming behaviour of insonified fish, a feature we used in this study to validate our results.

The use of hydroacoustics for the study of fish and other aquatic organisms is well established. Hydroacoustics are used for studies on vessel avoidance by fish (e.g. Gerlotto & Fréon 1992; Fréon, Soria, Mullon & Gerlotto 1993; Misund & Aglen 1992), on diel vertical migration of fish (e.g. Eckmann 1991, Piersma, Lindeboom & Van Eerden 1988; Hartmann, Knöpfler, Löffler & Quoss 1991), on large and small scale spatial distribution of fish and other aquatic organisms in relation to survey design or biological and physicochemical characteristics (e.g. Jolly & Hampton 1990; Kalikhman, Walline & Gophen 1992; Baroudy & Elliott 1993; Williamson 1982; Crawford, Hudon & Parsons 1992; Baussant, Ibanez & Etienne 1993) on feeding ecology of fish (e.g. Janssen & Brandt 1980; Levy 1990) on fish migration in rivers (e.g. Mesiar, Eggers & Gaudet 1990; Johnston & Hopelain 1990; Gaudet 1990), and for studies on bioenergetics (Brandt & Kirsch 1993; Goyke & Brandt 1993). Both moving and stationary transducer platforms were used in these studies. Nearly all hydroacoustic studies deal with deeper waters (> 10 m) using a vertically directed acoustic beam. The transducer is positioned just below the water surface, facing downward. In shallow waters like IJsselmeer, a vertical beam is not efficient because the maximum distance from the transducer where fish can be detected (R_{max}) is limited to the distance from transducer surface to bottom. R_{max} can be increased by using a horizontal beam. In this case, the transducer is positioned in the water column, facing in horizontal direction.

Little is published on acoustic fish abundance estimation in shallow waters using a horizontal beam (e.g. Kubecka, Duncan & Butterworth 1992; Kubecka *et al.* 1994). This new technique seemed to be applicable to our situation, but the technique so far has only been used in small water bodies under 'favorable sampling conditions', meaning no wind or rain (Kubecka *et al.* 1994). Unfavorable sampling conditions generally result in high noise levels. In IJsselmeer, favorable sampling conditions are rare, and because of practical and logistic reasons we had to apply the technique under the prevailing conditions during the sampling period. The hydroacoustic estimate of the fish biomass is biased if the backscattered sound energy of the targeted fish is low compared to the noise level. The backscattered sound energy of fish is related to its size, so it is important to know the size range of the targeted fish by some other sampling method to interpret the hydroacoustic data. In this study, the size range of the pelagic fish community was estimated with a pelagic beam trawl. A check was made to determine whether acoustically identified fish (*AIF*) showed vessel avoidance behavior. Avoidance behavior has consequences for the orientation of the fish in the acoustic beam, which has consequences for the detection and sizing of fish. The influence of varying wind speed on the output of the hydroacoustic system was studied.

MATERIALS AND METHODS

Study area, survey design

Two study areas, one in the northern basin of IJsselmeer (area *A*), and one in the southern basin of the lake (area *B*), were selected. The depth varied between 3.5 and 5.5 m. Sampling took place between 14 and 18 June 1993. A partially randomized stratified sampling design was employed for acoustic transect and the trawl haul locations, as recommended by Jolly & Hampton (1990).

Transects were positioned in east-west direction. Areas *A* and *B* were allocated a number of transects proportional to their surface areas, i.e. three to area *A* and seven to area *B*. The shortest route between the end and the beginning of two adjacent transects was also sampled (Fig. 3.1). The pelagic fish community was sampled with a pelagic beam trawl. In area *A*, four pelagic beam trawl hauls were made and in area *B* 12 hauls were made. Haul duration was 10 min., during which about 0.26 ha were covered. The width of the pelagic beam trawl was 3 m, the cod-end has a stretched mesh size of 2 mm. The length-frequency distribution per species was established for each trawl catch. The length-frequency distributions from the pelagic beam trawl catches were averaged per area and per species.

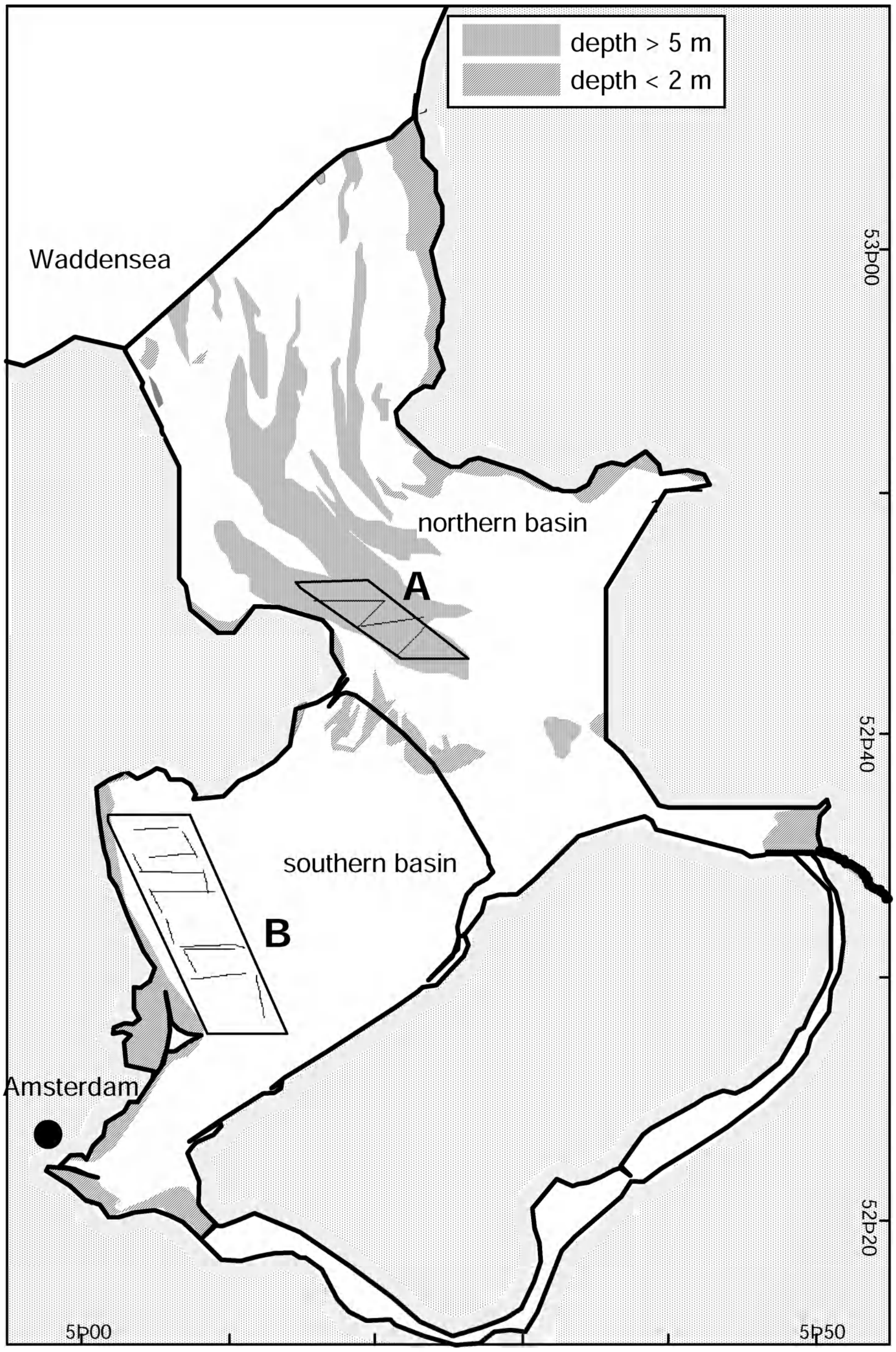

Figure 3.1. *Map of IJsselmeer with sampling areas. Parallelograms indicate sampling areas A and B. Lines in the sampling areas represent acoustic transects.*

Hydroacoustic equipment and data collection

A Biosonics ES2000 echo-sounder, with an operating frequency of 420 kHz, in combination with an elliptical dual beam transducer with a 5.5°*17.5° wide beam and a 2.2°*7.5° narrow beam was

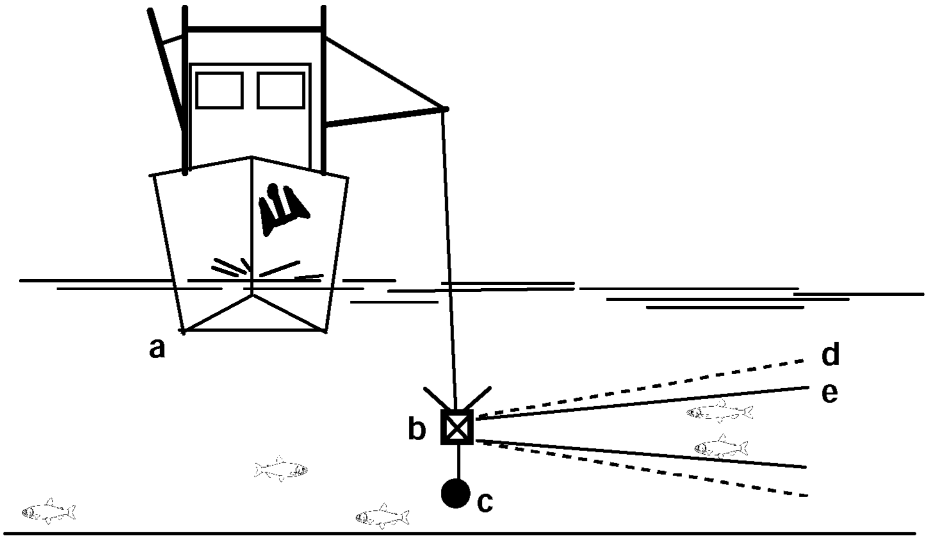

***Figure 3.2**. Front view of research vessel with towed body as used in this study. a = research vessel, b = towed body with transducer, c = depressor (to stabilize towed body), d = wide beam, e = narrow beam.*

used. The equipment generated a pulse width of 0.2 10^{-3}s and a ping rate of $20.s^{-1}$. The system was calibrated by measurements on a tungsten carbide standard target. An oscillograph of received signal voltage against distance from transducer was echoed on the screen of the computer. The equipment was used onboard a 20 m research vessel, powered by a 200 HP engine. The transducer was mounted in a towed body that was pulled alongside the vessel at a speed of 1.8 $m.s^{-1}$. The beam was directed perpendicular on towing direction (Fig. 3.2). Recordings were made at 2-20 m distance from the transducer. At 0-2 m from the transducer no recordings were made because of near field effects (MacLennan & Simmonds 1992). No recordings were made at distances > 20 m, because of permanently high noise levels.

Signal processing was performed by the ESP Model 281 Dual-Beam Processor using 40 log R time varied gain (echo counting). Dual beam technology is described in MacLennan & Simmonds (1992). The advantage of echo counting over echo integration is that it is possible to filter out backscattered signals of unwanted targets. Futhermore, echo counting makes it possible to study fish behaviour at the individual level. Processing took place during recording. The received signal was also recorded on a DAT recorder. Processing consisted of identification of single targets, target strength (*TS*) measurements and combination of consecutively recorded targets into acoustically identified fish (*AIF*). Single targets and *AIF* were identified according to pre-set criteria. For each *AIF* the following variables were measured (Fig. 3.3):

- number of single targets which make up the *AIF*;
- *TS*, estimated as the mean of the *TS* of *n* single targets which make up the *AIF* (dB)
- slope, the change in distance from the transducer in *n* single targets which make up an *AIF* ($m.ping^{-1}$)
- midrange, the mean of the distance from the transducer of the single targets which make up an *AIF* (m).

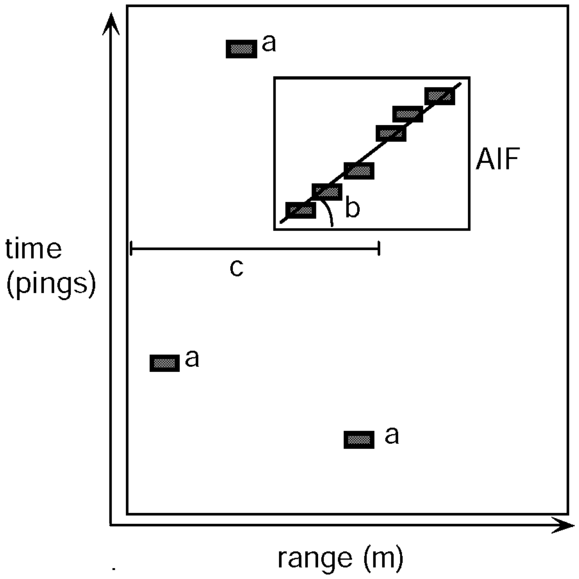

***Figure 3.3**. Schematic representation of an echogram. a = single targets (not interpreted as fish), AIF = acoustically identified fish, b = slope, c = midrange. The AIF in this example is made up of 6 echoes.*

Each *AIF* was written as a record to a file. Data were exported to the SAS® software package for statistical processing.

Target strength measurements

The *TS* of a fish is related to the size of the swimming bladder, to the shape of the swimming bladder and to the orientation of the swimming bladder in the acoustic beam. The other backscattering body tissues have minor influence on the *TS*. Love (1977) developed *TS*-length relations for 14 families of fish, insonified from every aspect. For each aspect, defined as an area on an imaginary spherical surface centered about the fish, he established a function that relates the backscattering cross section to fish length, operating frequency of the echo-sounder and sound speed:

$$\sigma = a\left(L\frac{f}{c}\right)^{b}\left(\frac{c}{f}\right)^{2} \quad \text{[formula 3.1]}$$

where σ is backscattering cross-section (m^2), *f* operating frequency of the echo-sounder (420,000 Hz), *c* sound speed in water (1500 m.s^{-1}), *L* the total length of the fish, *a* and *b* are constants specific for the aspect under study. The *TS* is related to σ as

$$TS = 10\log\left(\frac{\sigma}{4\pi}\right) \quad \text{[formula 3.2]}$$

where *TS* is target strength (in dB), σ the backscattering cross-section (m^2).·

When using a horizontally directed acoustic beam, variation in the orientation in the horizontal plane (yaw) is the main source of variation in *TS* of a fish of given length. We assumed that the caudo-cranial axis of all insonified fish was horizontally oriented and that the ventral-dorsal axis was vertically oriented.

To make sure that no noise is interpreted as fish, it is recommended to set the noise threshold at three times the observed noise level on the oscilloscope (J. Kubecka, pers. comm.). During this survey, the threshold was set at approximately 1.5 - 2 times the observed noise level because there was a need to include small fish in the measurements. However, it was recognized that some noise would be interpreted as fish. The noise threshold of the acoustic equipment was set at the voltage corresponding to a *TS* of -56 dB. This value can be related to a range of fish lengths at several aspects according to the formulas of Love (1977). It was assumed that the acoustic equipment and the pelagic beam trawl sampled the same depth stratum and that the length-frequency distributions of the trawl catches reflected the size range and species composition of the targeted fish. The length-frequency distributions of the pelagic beam trawl and the *TS*-length relations of Love (1977) to evaluate roughly which part of the population could be detected by the hydroacoustic equipment.

Avoidance reaction

Avoidance reaction of fish was studied by analysis of the slope of an identified fish. A positive slope indicated a fish swimming away from the transducer, a negative slope indicated a fish swimming towards the transducer. If insonified fish did not react to the presence of the research vessel, the average slope was expected to equal zero. Since the slopes were not normally distributed, the null-hypothesis 'mean slope equals zero' was tested by calculating the signed rank statistic (*SRS*). In this analysis identified fish from all transects were pooled.

Fish that show an avoidance reaction (*FA*) when the research vessel approached were expected to orientate themselves differently to the acoustical axis from fish that do not avoid the research vessel (*FNA*). Consequently, *TS* of *FA* should differ from *FNA*. First, a parametric model (ANOVA) was used to test whether *TS* of *FA* was different from *FNA*, but residual analysis showed that the conditions of ANOVA were not met. Consequently, differences in shape of the *TS*-frequency distributions of *FA* and of *FNA* were tested with a non-parametric test (Kolmogorov-Smirnov).

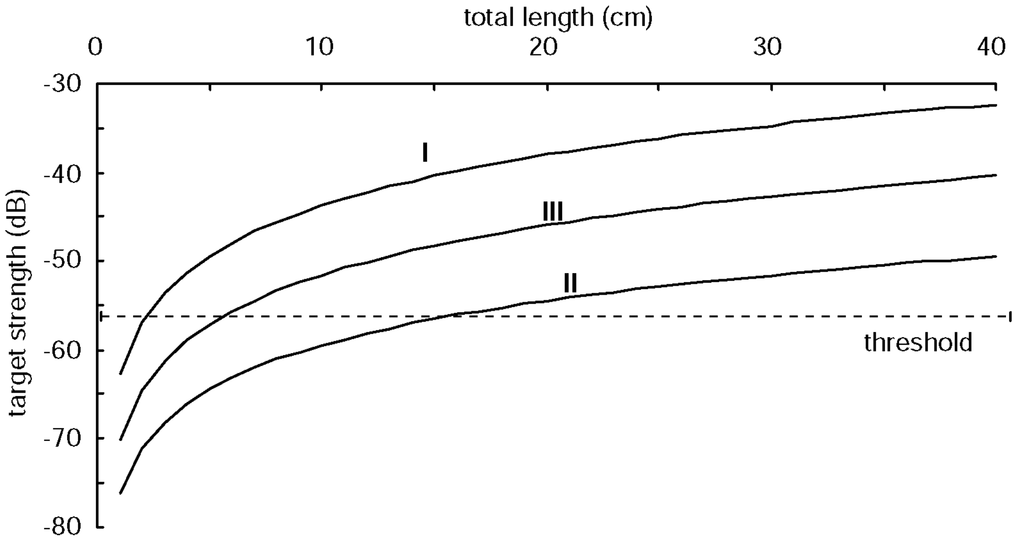

***Figure 3.4**. Target Strength-length (TS-L) relations for fish oriented with varying yaw angle in the acoustic beam. Curve I represents the TS-L relation for fish insonified in side aspect (the maximal TS for a fish of a given length), curve II represents the TS-L relation for fish insonified in tail-head aspect (the minimal TS for a fish of a given length). Curve III represents the average TS-L relation for fish insonified in all aspects between head-tail and tail-head aspect. Relations are calculated from formula 3.1 and 3.2 (see text) with $a = 74 \cdot 10^3$ and $b = 1.90$ for curve I, $a = 4.4 \cdot 10^3$ and $b = 1.66$ for curve II, $a = 14 \cdot 10^3$ and $b = 1.86$ for curve III. The threshold value (- 56 dB) as used during this study is indicated by the dashed line.*

Influence of wind on fish abundance estimates

During the survey, noise was predominantly caused by the backscattering properties of air bubbles in the water column and by backscattering of sound energy by the surface and bottom. Wind caused noise by increasing the number of air bubbles in the water column. The influence of wind increased from bottom to surface, resulting in higher noise levels near the surface. Because targets were more difficult to detect at high noise levels, wind force had an effect on the number of detected targets. This effect was especially noticeable at higher distance from the transducer, because there the sampled volume extended to the surface layer of the water column. Consequently the number of detected fish was related to wind speed and to distance from the transducer. This source of bias was studied by relating the median of the midrange of *AIF* of each transect to the wind speed. It was assumed that the influence of wind speed on noise level within a transect was constant.

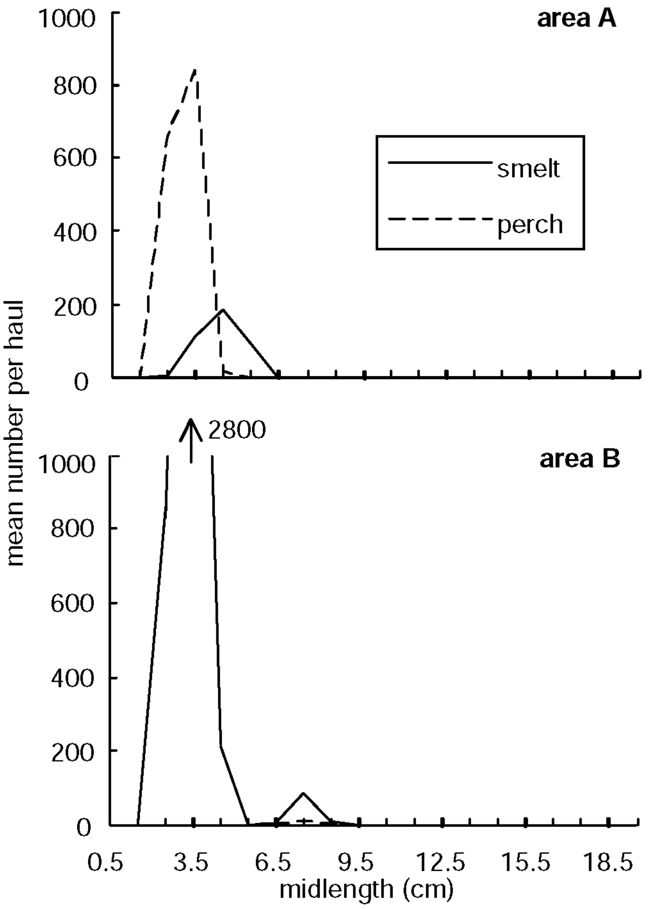

***Figure 3.5**. Average length-frequency distributions of pelagic beam trawl catches in areas A and B. In area A,* mainly *age 0 perch (78.4% of the average catch in numbers) and age 0 smelt (20.5% of the average catch in numbers) were caught. Other species categories, including older perch and smelt, contributed 1.1% in numbers to the average catch. In area B, age 0 smelt contributed 96.8% and age ≥1* smelt *contributed 2.7% to the average catch in numbers.*

RESULTS

Target strength of insonified fish

Hydroacoustic data were processed using a noise threshold corresponding to a *TS* of -56 dB. According to Love's *TS*-length relations a *TS* of -56 dB corresponds to fish in the length range 3 cm (side aspect) to 16 cm (tail aspect) (Fig. 3.4). Most fish caught with the pelagic beam trawl ranged from 2 to 9 cm total length (Fig. 3.5). It is obvious that the signal-to-noise ratio was

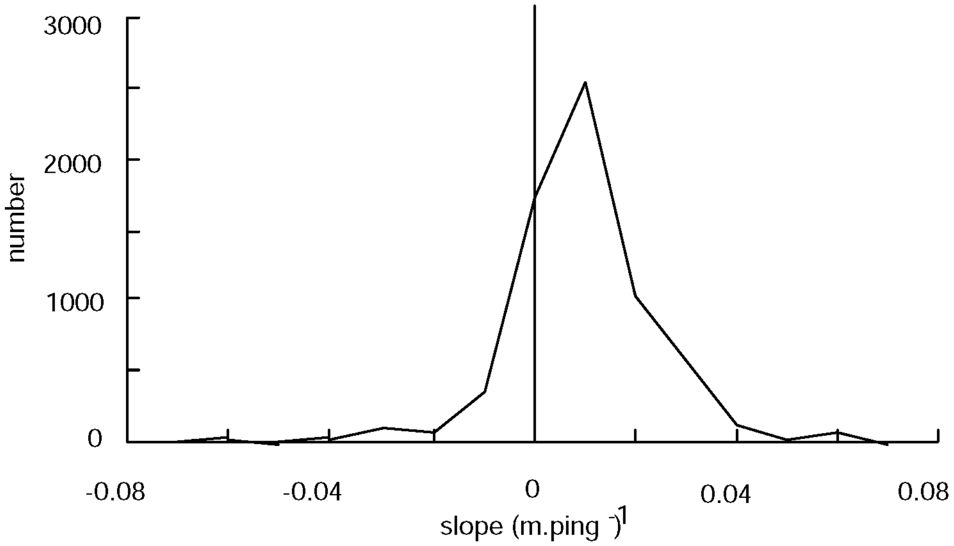

***Figure 3.6**. Slope-frequency distribution of all AIF. Positive slopes indicate fish that move away from the transducer. Values smaller than -0.08 and larger than 0.08 represent 0.6 % of the total observations.*

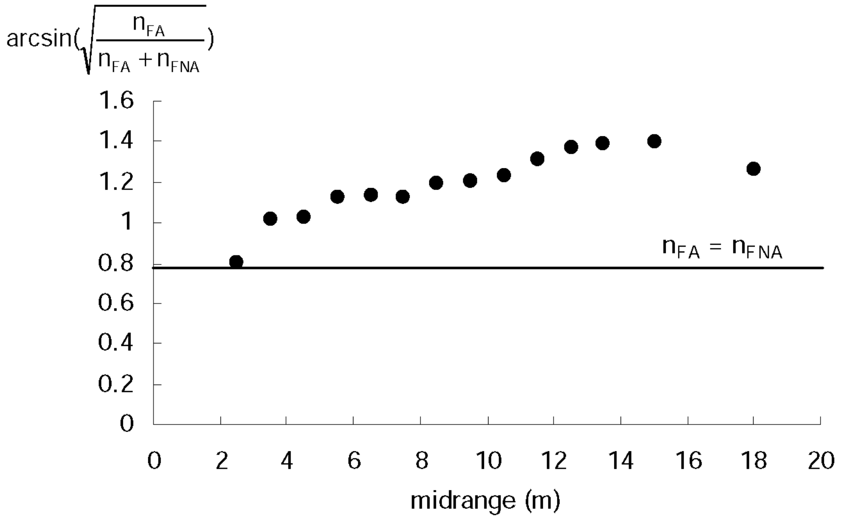

***Figure 3.7**. Scatter plot of the proportion FA of all AIF against the distance from the transducer (midrange). The number of observations per class was at least 20. The width of the midrange classes is 1 m between 2 and 13 m. Midrange classes 14-15 and 16-19 were combined. The proportion was arcsine transformed as recommended by Sokal & Rohlf (1981). The reference line represents the level were the FA equals FNA.*

extremely unfavorable. The smallest fish were recorded only if they were insonified in side aspect. Even the largest fish (9 cm *TL*) were not detected if they were insonified in tail aspect. Of all *AIF*, 95% had a *TS* of less than -45 dB; this corresponded to a fish with a total length of 9 cm, insonified in side aspect. This was in agreement with the length-frequency distribution of the fish caught with the pelagic beam trawl.

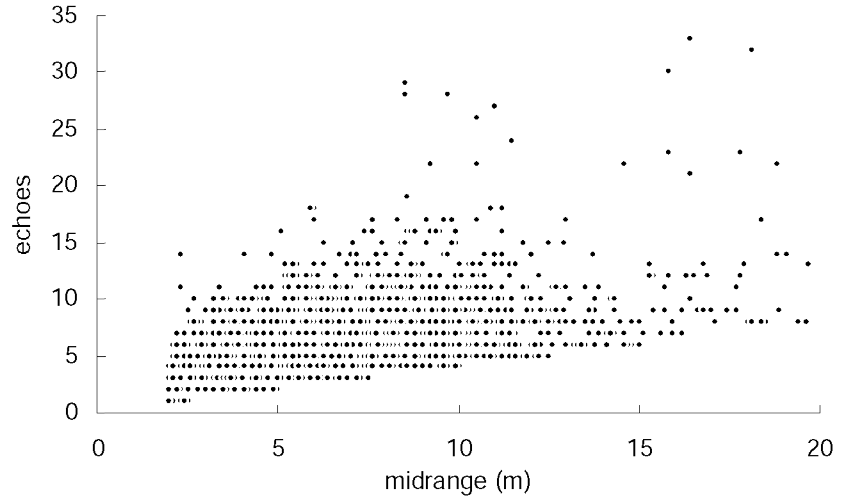

***Figure 3.8**. Scatter plot of the number of echoes that make up an AIF against the distance from the transducer (midrange).*

Avoidance behaviour

Most *AIF* had a slope larger than zero (Fig. 3.6) (*SRS* = 6708402; *P* = 0.001). Thus, most *AIF* moved away from the vessel. At least part of the *AIF* that we recorded must have been fish since the behavior of *AIF* was consistent with vessel avoidance behavior. Assuming that all *FNA* and an equal number of *FA* was noise, 31% of all *AIF* was fish and 69% was noise. Near the transducer, the proportion *FA* of all *AIF* increased with increasing midrange. The data suggest that at a midrange of more than 12.5 m the proportion *FA* was relatively constant (Fig. 3.7). The increase over the full range (2-20 m from the transducer) was significant (linear regression analysis, R^2 = 0.75, $P < 0.01$). The increase of the proportion of *FA* was not consistent with vessel avoidance behavior. Fish closer to the research vessel should have been more likely to show avoidance behavior than fish that were further away. However, at a higher midrange *AIF* consisted of more echoes (Fig. 3.8), and consequently the swimming direction was more accurately estimated. Thus, the low proportion of *FA* near the transducer could have been a sampling artefact. Avoidance behavior seemed to be present at distances of at least 20 m from the research vessel in our situation.

The *TS*-frequency distribution of *FA* was different from the *TS*-frequency of *FNA* (Kolmogorov-Smirnov, $P < 0.01$) (Fig. 3.9). The difference in *TS*-frequency distributions could be explained by bigger fish avoiding the vessel to a larger extent than smaller fish, by the difference in orientation in the beam between *FA* and *FNA* or by a combination of both effects.

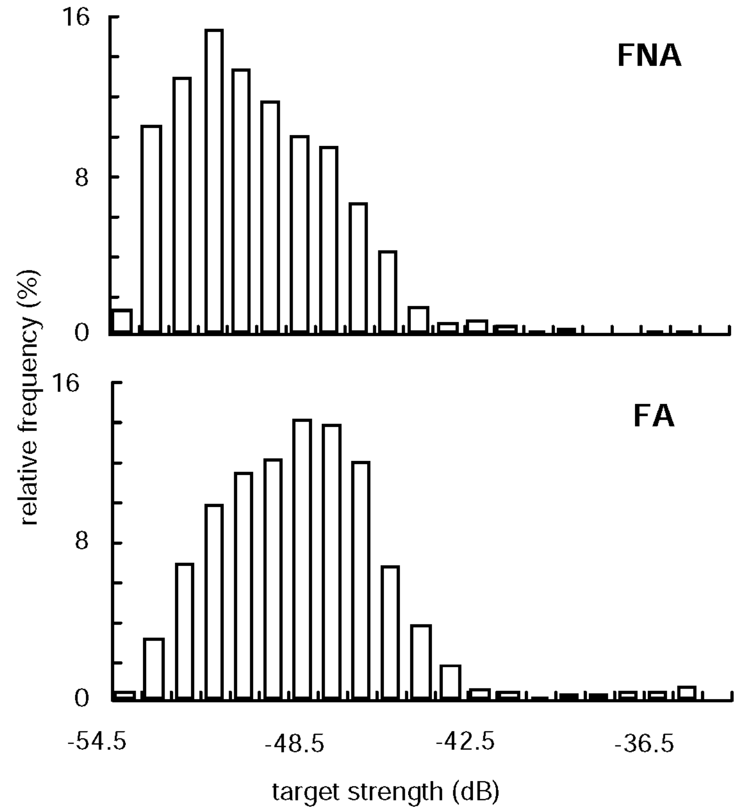

Figure 3.9. *TS-relative frequency distribution of AIF with slope <= 0 (FNA) and AIF with slope > 0 (FA). FA had higher TS.*

Effect of wind on fish abundance estimates

At higher distance from the transducer less fish is detected than closer to the transducer (Fig. 3.10). Apparently, this was caused by the high noise levels at the end of the detection range, where the acoustic beam approaches the water surface and the bottom. The median value of the midrange of AIF over all transects was 4.9 m. The areas with high noise levels at the end of the detection range fluctuated between about 10 and 20 m distance from the transducer. When there were higher wind-induced waves, the noise area became larger and consequently, less fish were detected. This was demonstrated by the relation between median value of midrange of *AIF* and the prevailing wind condition of each transect (Fig. 3.11). During the study period, sampling was performed at wind speeds varying between 1 and 5 Beaufort. At higher wind speed, the median value of the midrange of *AIF* was lower (linear regression analysis, adjusted $R^2 = 0.52$, $P < 0.01$). This indicated that a smaller proportion of the fish present in the population were detected.

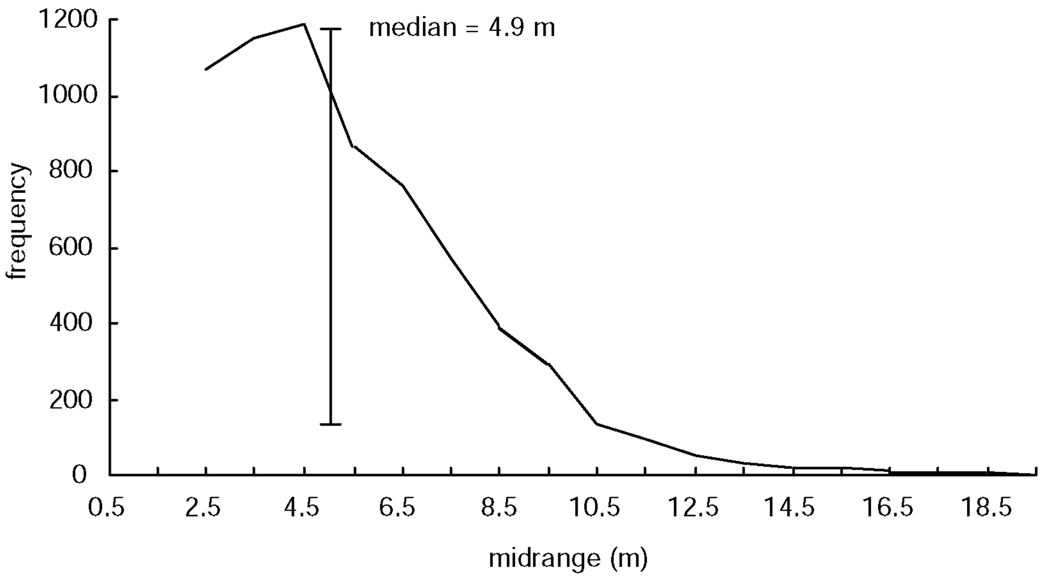

Figure 3.10. *Midrange-frequency distribution of AIF from all transects. The vertical line at midrange = 4.9 m represents the median value of the midrange of all AIF.*

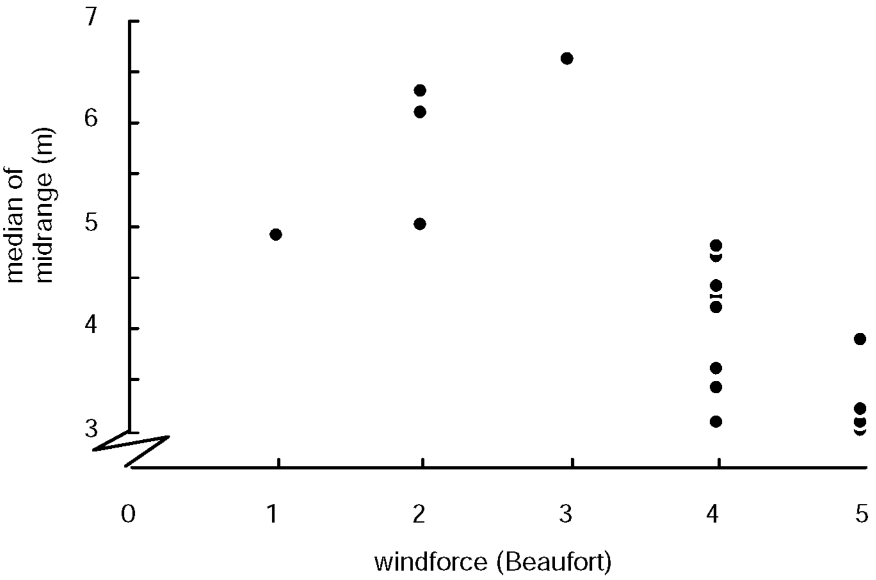

Figure 3.11. *Relation between wind force (Beaufort) and median of midrange (m). Each data point represents AIF from one transect. At high wind speed, the median value of midrange is lower than at low wind speed.*

DISCUSSION

It was possible to detect fish using dual-beam hydroacoustics with a horizontal beam employed in a mobile survey in large shallow water bodies. However, results from the survey should be interpreted with care because of:

- the relatively high noise levels compared to the *TS* of the targeted fish;
- avoidance behavior of insonified fish and possible consequences of avoidance behavior for the *TS*-length relation; and
- variable sampling conditions (wind speed).

The use of a *TS*-length relation without taking into account the orientation of the fish (e.g. Braband 1991; Brandt, Mason, Patrick, Argyle, Wells, Unger & Stewart 1991; Brandt & Kirsch 1993; Burczynski & Johnson 1986; Burczynski, Michaletz & Marrone 1987; Hansson 1993; Jurvelius 1991; Luecke & Wurtsbaugh 1993) was inappropriate for IJsselmeer. The orientation of the fish in the beam is a major source of variance in *TS* (Fig. 3.4). During this survey, the orientation not only affected the estimate of the size distribution of the insonified fish, but also the abundance estimate. Even the largest pelagic fish, smelt of 9 cm *TL*, could not be distinguished from noise if they were insonified in tail aspect.

Furthermore, because of avoidance behaviour of the insonified fish, it could not be assumed that the yaw angle was randomly distributed over 360°. Avoidance behavior of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) is demonstrated at a distance of up to ca 400 m from sea going research vessels (Misund & Aglen 1992). *Sardinella aurita* avoide the research vessel at a distance up to 20 m (Gerlotto & Fréon 1992) and Ona & Godø (1990) notice strong avoidance reactions to a trawling vessel in haddock (*Melanogrammus aeglefinus*) up to depths of 100 m. In this study, avoidance behavior was observed in the total detection range (2-20 m from the research vessel), and it was probable that avoidance behavior influenced the *TS*-length relation (Fig. 3.9). Other vessel induced factors may also influence *TS* measurements: e.g. ships' lights can cause a geometric reorientation of zooplankton which is responsible for a drop of 20 dB in backscattering strength in the area 60 m below the transducer (Sameoto, Cochrane & Herman 1985). The importance of fish behavior in relation to *TS* measurements has also been stressed by other authors (MacLennan *et al.* 1990; Blaxter & Batty 1990; Dawson & Karp 1990; Olsen 1990).

The comparison of length-frequency distributions of the trawl catches and the *TS*-frequency distribution can be made by either peak identification (Bjerkeng *et al.* 1991; Guillard & Gerdeaux 1993) or maximum likelihood procedures (Bjerkeng *et al.* 1991). In this study, peak identification and maximum likelihood analysis were hampered by the absence of more than one peak in the *TS*-frequency distribution and in the length-frequency distributions of the trawl catches. Furthermore, the fraction of *AIF* which was actually noise is unknown. However, the length range of the fish caught with the trawl (3-9 cm total length) was approximately in agreement with the *TS*-frequency distribution.

Wind force had a major effect on the number of fish detected (Fig. 3.11). The effect of wind was reflected by a decrease in the median value of the distance from the transducer of insonified fish. Assuming that fish were distributed symmetrically above and below the acoustic axis it was possible to correct for the effect of wind speed. The median of the midrange of *AIF* could have been used as a correction factor. However, correction for wind speed was not possible for fish that were concentrated near the bottom or the surface. Furthermore, interaction between wind speed and vertical distribution of fish could have lead to erroneous extrapolation of results from favorable to less favorable survey conditions. Another method to account for wind conditions is abortion of the sampling program at high wind speed (Pedersen & Boettner 1992). This method has the disadvantage that if the weather situation remains unfavorable for hydroacoustic sampling during a longer period, not enough time may remain to complete the sampling program.

Factors other than vessel induced behavior of fish or sampling conditions may influence hydroacoustic stock estimates. Diel changes in schooling behavior and spatial distribution are responsible for decreased stock size estimates during periods of higher light intensity (daylight, full moon) (Luecke & Wurtsbaugh 1993, Bethke 1993, Northcote & Rundberg 1970). This may be caused by acoustic shadowing (Appenzeller & Leggett 1992) or by problems with detecting schools closer to the bottom (Burczynski et. al 1987). During this survey, which was conducted during daytime, no schools were detected. This might have been caused by absence of schooling behavior or by the vertical distribution of schools. Schools located near the bottom are difficult to detect by horizontal beam hydroacoustics. Day and night recordings with single beam hydroacoustic equipment in the summer of 1992 suggest that smelt and age 0 perch were more evenly distributed over the water column at night than at daytime (Chapter 6), so problems in detecting fish aggregations may have had some influence on our results. Changes in fish behavior and resulting changes in hydroacoustic detection characteristics may also be seasonal as shown by Goldspink (1990) for perch *Perca fluviatilis* in UK, by Eckman (1991) for whitefish *Coregonus lavaretus* in Lake Constance in Germany and by Northcote & Rundberg (1970) for cisco *Coregonus albula* and smelt *Osmerus eperlanus* in Sweden. A complex of sources of bias in hydroacoustic estimates of fish biomass may lead to considerable discrepancies when results from hydroacoustic surveys and results from other sampling methods are compared. For example, Godø & Wespestad (1993) found a weak correlation between estimates of gadoid abundance by trawl surveys and hydroacoustic surveys. They conclude that relying on either of the two sampling methods may lead to severe bias in the abundance estimate.

The use hydroacoustics as a sampling tool for studying fish abundance, size distribution and spatial distribution on a large shallow lake is not recommended. Variable sampling conditions, high noise levels and avoidance behaviour of fish were the main factors constraining hydroacoustic sampling. Irrespective, the possibility to study avoidance behavior with hydroacoustics can be used to validate the abundance estimates from trawl surveys. Net avoidance behavior in relation to water clarity (Buijse, Schaap & Bult 1992) can be studied in more detail in a simultaneous trawling and hydroacoustic surveying program. Thus, in combination with other sampling methods like trawling or gillnetting, hydroacoustic sampling will increase the accuracy of abundance estimates (c.f. Dahm *et al.* 1992; Kubecka *et al.* 1994). Furthermore, the high spatial resolution makes hydroacoustics a valuable tool to study the distribution of pelagic fish in more detail than is possible with trawling.

ACKNOWLEDGEMENTS

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Chapter 4

The effect of smaller mesh sizes on catching larger fish with trawls

P.J. Mous, W.L.T. van Densen & M.A.M. Machiels

ABSTRACT

Selection curves of small mesh trawls were assessed with one alternate haul and two trouser trawl experiments. The effect of fish length on the ratio (p_i) of the number of fish of length i caught in the large mesh cod-end to the number of fish of length i caught in both cod-ends was estimated with generalized linear modeling. The alternate haul experiment was conducted with beam trawls equipped with 2 mm and 18 mm stretched mesh cod-ends to assess size selectivity for perch *Perca fluviatilis*. None of the perch that entered the cod-end could escape through the mesh of the small mesh cod-end. For small perch (< ca. 10 cm total length), p_i reflected the ratio in areas swept by the large and small mesh nets, but for larger perch, p_i increased. Water flow through the small mesh net must have been lower than through the large mesh net, enabling relatively more larger perch (> ca. 10 cm total length) to out-swim the small mesh net. The trouser trawl experiments were conducted to study selectivity for smelt *Osmerus eperlanus*, using 12 and 22 mm stretched mesh cod-ends, and for American plaice *Hippoglossoides platessoides*, using 39 and 155 mm stretched mesh cod-ends (published data). During both trouser trawl experiments, smaller fish that entered the cod-end could escape through the large mesh cod-ends, so p_i increased with increasing fish size. However, also beyond the size where fish could escape through the large mesh cod-end, p_i continued to increase. This implied that the small mesh cod-end was less selective to larger fish. We demonstrated that the lower selectivity to larger fish in the cod-end with the smaller mesh could result in 20-50% overestimation of the length (L_{50}) at which 50% of the fish entering the cod-end escape through the mesh.

INTRODUCTION

Due to size selectivity, the size frequency distribution of a trawl catch does usually not reflect the size frequency distribution of the fish population. The catch per unit effort in length class *i* ($CpUE_i$) is related to the number in the population of size class *i* (N_i) as $CpUE_i=q_i.N_i$, where q_i is the catchability coefficient for size class *i* (Gulland 1983). The catchability coefficient can be looked upon as the product of an efficiency coefficient, which is not dependent on fish size, and a selectivity coefficient, which depends on fish size and ranges between 0 and 1. The relationship between the selection coefficient and fish size and is characterized with a selection curve. Gunderson (1993) presents a dome-shaped trawl selection curve, where the ascending limb represents the increased retention of larger fish that are engulfed by the trawl net, and the descending limb represents the increased capability of larger fish to out-swim the trawl net before they become engulfed. The existence of the descending limb of the selection curve is usually not recognized in fisheries surveys (Gunderson 1993).

Trawl selection curves are often estimated by comparing catches from a large mesh and a small mesh trawl net (alternate haul method) or by using a special trawl net equipped with a large mesh and a small mesh cod-end (trouser trawls). It is often observed that larger fish are under-represented in the small mesh cod-end (Pope *et al.* 1975, Cadigan & Millar 1992, Millar & Walsh 1992). The under-representation of larger fish is assumed to be caused by a lower efficiency of the small mesh cod-end. To correct for the alleged difference in efficiency, the fractional difference in the number of larger fish is used as a correction factor. This correction factor is applied to the full size range of the catch in the small mesh net, and next the ascending limb of the selection curve is estimated though logistic regression (Pope *et al.* 1975). This procedure, however, leads to over-estimation of L_{50}, the length where 50% of the fish is retained by the net, if the lower number of larger fish in the small mesh cod-end is caused not by a difference in efficiency, but by a difference in selection characteristics for larger fish (i.e., the descending limb of the selection curve). It is likely that a difference between the descending limbs of selection curves occurs when trawling speed is slower for the small mesh cod-end to avoid stowing, or simply because of stowing. In both cases, larger fish may be better able to out-swim the net (He 1993), thus positioning the descending limb of the selection curve of the small mesh net at a smaller size range.

In this study, it is attempted to demonstrate a difference in the descending limbs of selection curves of large mesh and small mesh cod-ends in an alternate haul experiment for perch *Perca fluviatilis* and in trouser trawl experiments for smelt *Osmerus eperlanus* and for American plaice *Hippoglossoides platessoides*. The consequences for the estimation of L_{50} as a function of mesh size are discussed.

MATERIALS AND METHODS

Alternate haul experiment

Perch *Perca fluviatilis* catches from two beam trawl surveys (Table 4.1), conducted in the southern basin of IJsselmeer (70,000 ha; N 52°.35′, E 5°.15′), were used to mimic an alternate haul experiment. During each survey, a different net was used with a stretched mesh size in the cod-end of 2 mm and of 18 mm. Sampling conditions were similar during the two surveys. Haul duration was kept constant at 10 minutes, and the length of the trawl lane was measured using the ships Doppler log. Length-frequency distributions (*LFDs*) of perch were established for each haul. Preliminary analysis revealed no spatial heterogeneity in the trawl catches of each survey, therefore we pooled *LFDs* into one *LFD* for each net. To evaluate whether mesh penetration was likely to occur, we calculated the mesh perimeter to maximal girth ratio (*MP:MG*). We assumed that if *MP:MG* < 1, mesh penetration was physically not possible. The length-girth relationship was established by measuring the length and the girth of 23 perch of 3.8 - 8.1 cm *TL*. Girth was measured with a thin, non-elastic thread, laid close around the body of the fish, at the position where the circumference of the fish body was maximal.

***Table 4.1**. Characteristics of the alternate haul experiment.*

	2 mm cod-end	18 mm cod-end
Net specification		
- width mouth opening	3.0 m	8.0 m
- height mouth opening	0.6 m	1.0 m
- total length	28 m	30 m
- length of cod-end	15 m	10 m
- mesh sizes of net in front of the cod-end (back to front)	19, 36 mm	20, 22, 24, 26, 28, 30, 32, 36, 40, 44, 48, 52 mm
Number of hauls	25	10
Haul duration	10 min.	10 min.
Average trawling speed	1.47 $m.s^{-1}$	1.71 $m.s^{-1}$
Total swept area[a]	66150 m^2	82240 m^2
Sampling period	November 1-16, 1994	December 12-14, 1994
Mean water temperature	8.4°C	9.7°C
Mean Secchi depth	0.30 m	0.30 m
Mean depth	3.8 m	3.8 m

Note

a. Summation of trawl lane length as measured by Doppler log, multiplied with trawl mouth width.

The difference between *LFDs* was analyzed using a generalized linear model and maximum likelihood parameter estimation (McCullagh & Nelder 1989). The response variable p_i was defined as:

$$p_i = \frac{n_{i,LM}}{n_{i,LM} + n_{i,SM}} \quad \text{[formula 4.1]}$$

where $n_{i,LM}$ = the number of fish of length class *i* caught in the large mesh net, and $n_{i,SM}$ = the number of fish caught in the small mesh net. Consequently, p_i has a binomial distribution (cf. Reeves *et al.* 1992; Galbraith, Fryer & Maitland 1994). A logit function g(μ) was used to link the expected value of the response variable (μ) to the linear predictor:

$$g(\mu) = \log(\frac{\mu}{1-\mu}) \quad \text{[formula 4.2]}$$

The linear predictor was defined as a third-order polynomial function of fish length (l):

$$g(\mu) = \beta_0 + \beta_1.l + \beta_2.l^2 + \beta_3.l^3 \quad \text{[formula 4.3]}$$

with parameters β_i. The model was implemented using PROC GENMOD of the SAS® Software Package (SAS® Institute Inc. 1993). Approximate confidence limits of the fitted values were calculated as described in the GENMOD procedure manual (SAS® Institute Inc. 1993). *F*-statistics and associated *P*-values were calculated, and if a term in formula [4.3] did not reduce deviance significantly ($P < 0.1$), it was removed from the model. If both the second-order term and the third order term are removed, formula [4.3] represents the logistic curve. Deviance residuals were plotted against the length of perch to detect systematic differences between the fitted model and the data.

If there is no difference in selection curves between the two nets, none of the terms in formula [4.3] should reduce the deviance significantly. Under the assumption that gear efficiency and selectivity was the same for both nets, the expected value of p_i should theoretically equal the proportional difference in swept area (0.55, cf. Table 4.1) for all size classes.

Trouser trawl experiments

The length frequency distributions of smelt caught in 12 and 20 mm stretched mesh cod-ends of a trouser trawl were used to estimate the selection curve for smelt. Four hauls were made on September 15 1989 in an area of ca. 100 ha. Trawling speed was 1.5 ± 0.1 $m.s^{-1}$, each haul lasted 15 minutes. The length frequency distributions of smelt from each haul were combined into a single length frequency distribution for each cod-end. We used length classes with a width of 1 mm. Data processing was analogous to the alternate haul experiment, except that in [4.1] n_i refers

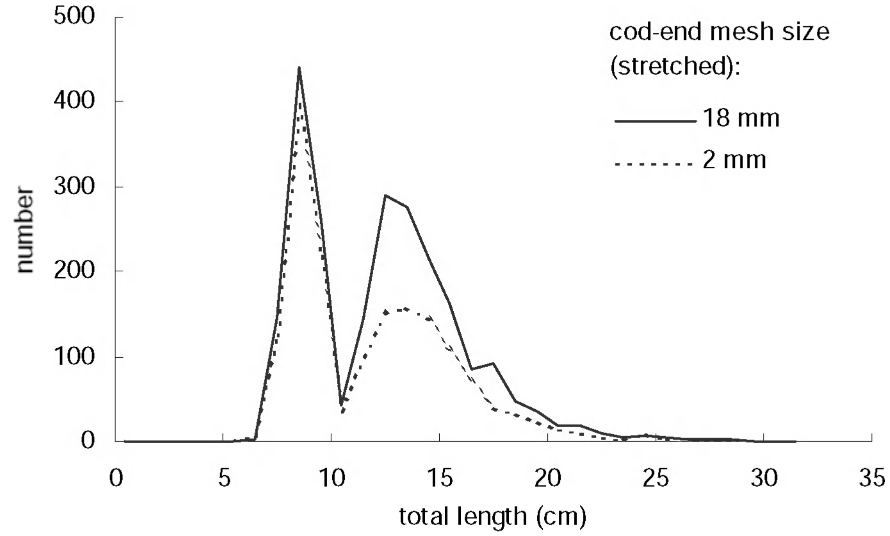

***Figure 4.1**. Length-frequency distributions of perch caught during the alternate haul experiment in the 18 mm (solid line) and the 2 mm cod-end (dashed line).*

to the catch in a cod-end instead of in a net. The length-girth relationship was established by measuring the length and the girth of 19 smelt of 4.2 - 9.4 cm *TL* (see alternate haul experiment).

To evaluate whether the postulated effect of mesh size on the right-hand side of the trawl selectivity curves would also hold for a range of larger mesh sizes, we used published data from Millar & Walsh (1992), who studied selectivity to American plaice *Hippoglossoides platessoides* with a trouser trawl equipped with a 155 mm diamond mesh cod-end and a 39 mm cod-end. In this study, the length-frequency data of Millar & Walsh (1992) were analyzed with the generalized linear model presented above (formula [4.3]).

***Table 4.2**. Statistics of the generalized linear models of data from trawl selectivity experiments. est = parameter estimate, sd_{est} = standard error of estimate; dev = deviance left after including the effect; df = degrees of freedom; F = F-statistic for the significance of the effect; P = significance; n = the number of length classes in which fish were caught; r^2 = percentage of total deviance explained by the model.*

experiment/ parameter	est	sd_{est}	dev	df	F	P
alternate haul, perch (n=25, r^2=36%)						
b_0	0.084	0.14	61.8	0		
b_1	0.040	0.011	39.4	1	13.13	<0.01
trouser trawl, smelt (n = 66, r^2 = 28%)						
b_0	-2.60	0.45	454.9	0		
b_1	0.27	0.054	326.4	1	25.2	<0.01
trouser trawl, plaice (n = 31, r^2 = 90%)						
b_0	-23.7	4.9	175.2	0		
b_1	1.34	0.33	46.9	1	188.9	<0.01
b_2	-0.0252	0.0073	26.3	1	30.4	<0.01
b_3	0.0002	0.0001	18.3	1	11.7	<0.01

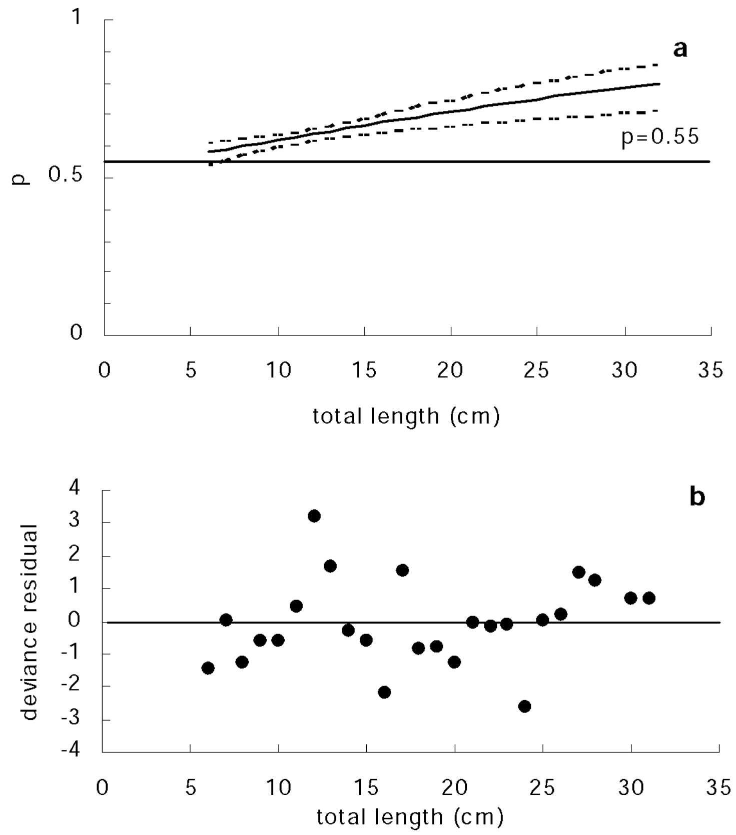

***Figure 4.2**. Fitted model (solid line) with 95% confidence limits (broken lines) (a) and deviance residual plot (b) of alternate haul data for perch. The expected value of p assuming equal gear efficiency, p = 0.55, is indicated as well.*

RESULTS

Alternate haul experiment

In total, 4526 perch were caught, of which 63% in the large mesh trawl (Fig. 4.1). The smallest perch in the catch measured 6.5 cm *TL*, having a maximal girth of 3.9 cm (max. girth = -0.30 + 0.646 *TL*; $P < 0.01$, $R^2 = 0.98$). Hence, the girth of the smallest perch in the catch was larger than the mesh perimeter of the large mesh net.

The first order term of formula [4.3] reduced deviance significantly (Table 4.2). The proportion of perch caught in the large mesh net increased with increasing length, and the estimated *p* for the smallest perch (ca. 6 cm *TL*) was near the fractional difference in swept area (0.55) (Fig. 4.2).

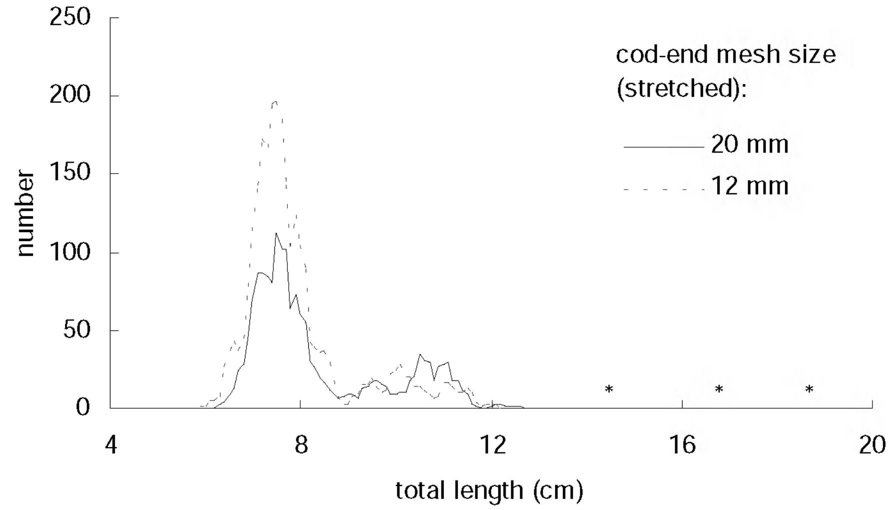

***Figure 4.3**. Length-frequency distributions of smelt caught during the trouser trawl experiment. At total length < 13 cm the 3 point moving average was plotted. Asterisks each indicate 3 smelt caught in the large mesh cod-end.*

Trouser trawl experiment

The length range of smelt caught in the trouser trawl was 6.0-18.7 cm. In the 20 mm cod-end 1696 smelt, and in the 12 mm cod-end 2619 smelt were caught (Fig. 4.3). For the 12 mm mesh, smelt reached *MP:MG* = 1 at a total length of 6.0 cm *TL* (max. girth = -0.27 + 0.445 *TL*; $P < 0.01$, $R^2 = 0.96$). For the 20 mm mesh, smelt reached *MP:MG* = 1 at a total length of 9.6 cm, so smelt < 9.6 cm *TL* were probably able to penetrate the large mesh cod-end.

The first-order term in formula [4.3] reduced deviance significantly (Table 4.2). The fitted model (Fig. 4.4a) showed that at a length of 9.8 cm, smelt were caught in equal number in the 12 mm cod-end and in the 20 mm cod-end. According to the model, smelt larger than 9.8 cm *TL* were caught in increasingly higher numbers in the 20 mm cod-end. The residual plot (Fig. 4.4b) showed that there were no large systematic deviations between the fitted curve and the data.

There was no evidence for *p* leveling off with increasing size to a value between 0.5 and 1, implying that there was no evidence for a difference in efficiency between the two cod-ends. Even if only the length range > 9.6 cm *TL* was included in the analysis, the first order term still seemed to reduce deviance, though not significantly ($P = 0.15$).

In the model of the trouser trawl data (Fig. 4.5) of American plaice (Millar & Walsh 1992), deviance was significantly reduced by first, second and third order terms of length (Table 4.2, Fig. 4.6a). The fourth order term was added as well to the model, but since it did not reduce deviance significantly, it was excluded again. The deviance residuals showed no apparent correlation with total length of plaice (Fig. 4.6b), therefore the model seemed to represent the data satisfactorily.

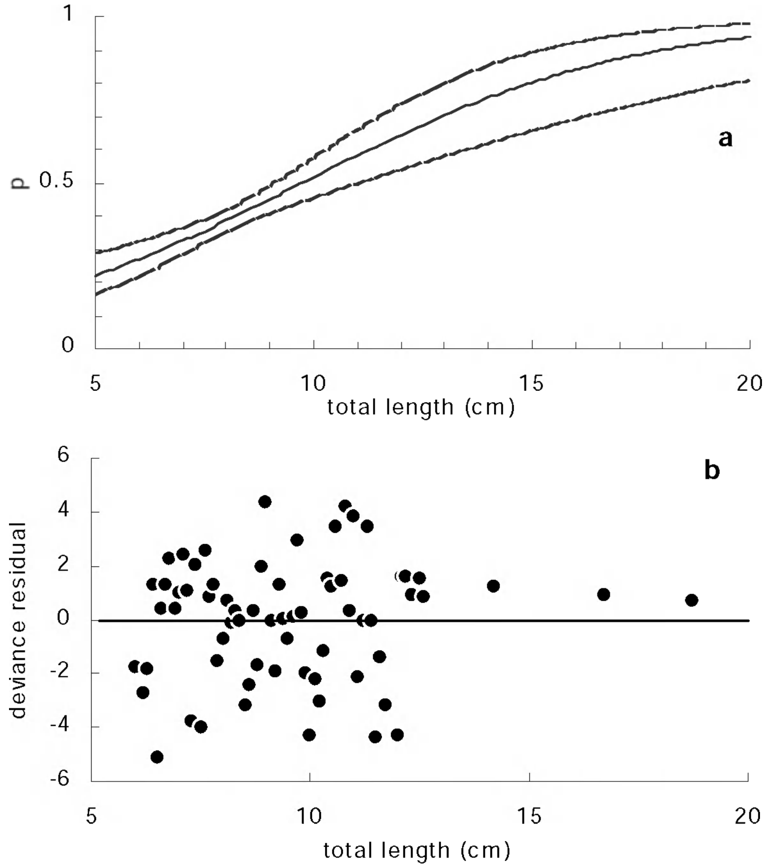

***Figure 4.4**. Fitted model (solid line) with 95% confidence limits (broken lines) (a), and deviance residual plot (b) of trouser trawl data for smelt.*

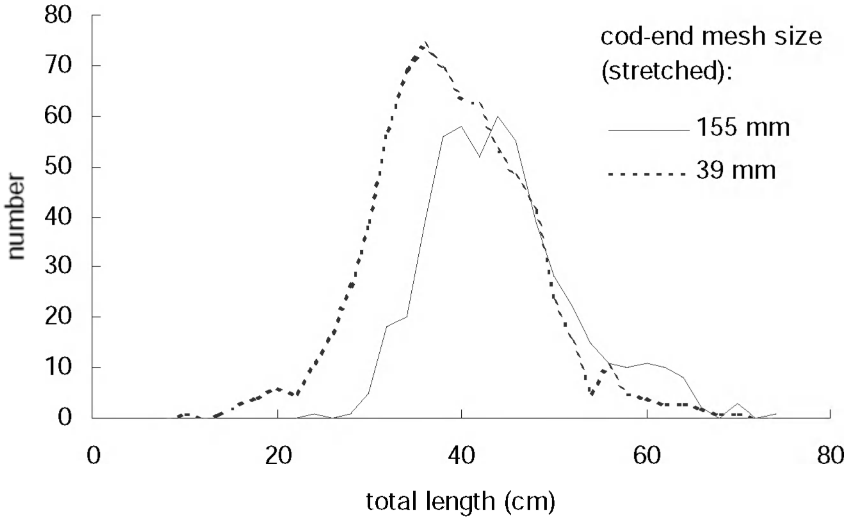

***Figure 4.5**. Length-frequency distributions of American plaice caught during the trouser trawl experiment of Millar & Walsh (1992).*

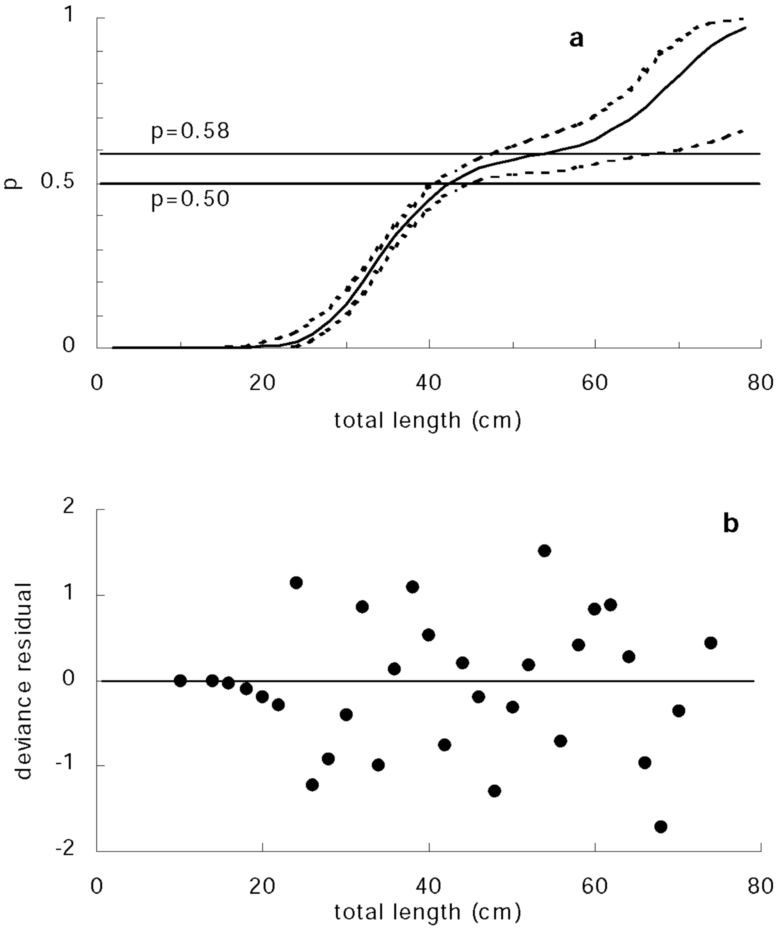

***Figure 4.6**. Fitted model (solid line) with 95% confidence limits (broken lines) (a), and deviance residual plot (b) of trouser trawl data for American plaice from Millar & Walsh (1992).*

Millar & Walsh (1992) fitted a model assuming equal efficiency of both cod-ends (equal split model) and a model assuming unequal efficiency between the two cod-ends (estimated split model) to the data. The unequal split model estimated that 58% of engulfed fish were caught in the large mesh cod-end. Indeed, $p = 0.58$ coincided with a region where the slope of the fitted curve is less steep, but the data do not suggest that the curve leveled off at $p = 0.58$. Actually, even if only data from length classes of 50 cm and above were included in the model, the first order term of length still seemed to reduce deviance ($P = 0.1$). Therefore, the hypothesis that larger fish were more able to escape from the small mesh cod-end was plausible.

DISCUSSION

In the three trawl selectivity experiments that were analyzed, spanning a large range of mesh sizes and of fish caught, the fraction of fish that were caught in the large mesh net seemed to increase continuously, even beyond the fish size where mesh penetration through the large mesh net was likely. We hypothesize that this was caused by the higher capacity of larger fish to out-swim the trawl net (cf. He 1993), coupled with lower trawl speed or reduced water flow in the small mesh cod-end.

Swimming capacity plays a significant role during the catching process. Fish that are encountered by the net tend to keep a constant position relative to the net, even if the net is trawled at a speed lower than its maximal swimming speed. Fish that get exhausted end up in the cod-end (Wardle 1993). As the maximal swimming speed of most fish species varies between 10 and 20 body lengths s^{-1} (He 1993), the trawling speed divided by 15 is a rough indicator for the minimum body length of fish that can escape through out-swimming the net. Perch and smelt of ca. 10 cm body length and above must have had a chance to escape from the net during the alternate haul experiment and the trouser trawl experiment. A slower trawling speed or a reduced water flow in the small mesh cod-end could have increased this chance compared to the large mesh net. The size range where fish had a chance to escape from the net by out-swimming it roughly coincided with the size range where we observed a size-dependent increase in the proportion of fish in the large mesh net.

Our method for analyzing the selectivity experiment data resembled Millar's SELECT (Share Each LEngthclass's Catch Total) method (Cadigan & Millar 1992, Millar & Walsh 1992). In contrast to our method, SELECT assumes, that with increasing fish size, the proportion of fish caught in the large mesh net levels off to a certain value, reflecting a size-independent difference in gear efficiency. Because of this difference, estimates of L_{50}, the length at which 50% of the fish entering the cod-end escape through the mesh, differ as well. Millar & Walsh (1992) estimated L_{50} for American plaice at 38 cm total length, whereas with the method described in this paper, L_{50} was estimated at 32 cm (cf. Fig. 4.5a, at total length where $p = 0.25$). With the trouser trawl experiment for smelt, L_{50} was estimated here at 5.6 cm (cf. Fig. 4.4a, at total length where $p = 0.25$). Analyzing the same data using logistic regression ($R^2 = 0.26$, $P < 0.01$) and using the fractional difference in catch numbers of smelt > 9.6 cm as a correction factor for the alleged higher efficiency of the large mesh cod-end, L_{50} was estimated at 8.5 cm. The overestimation of L_{50} may have serious implications for fishery management through its effect on the estimation of one of the key parameters of yield-per-recruit models, the age-at-capture (Ricker 1975).

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LITERATURE

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Chapter 5

Correspondence between hydroacoustic and bottom trawl observations on fish density at varying light intensities in a shallow, turbid lake

P.J. Mous, W.L.T. van Densen & M.A.M. Machiels

ABSTRACT

Correspondence between hydroacoustic and bottom trawl estimates of fish density and size was assessed to disentangle the effects of local fish abundance and catchability on bottom trawl catches. The study area was a large (182,000 ha), shallow (mean depth 4.5 m), eutrophic lake, and observations were made during daytime. With a beam trawl fitted with two dual beam transducers, observations were made at varying light intensity, where variation in light intensity was caused by variation in water depth. We found a significant correlation between the number of fish caught per haul and the number of insonified fish over a range of light intensities. At a relatively high light intensity (ca. $3.6 \cdot 10^{-2}$ lx), in a shallow area, both sampling methods detected less fish than at a relatively low light intensity (ca. $1.2 \cdot 10^{-6}$ lx) in a deeper area. Weak avoidance behavior was observed, but there was no significant effect of light intensity on avoidance behavior. We concluded that there was no evidence for previously postulated effects of light intensity on catchability.

INTRODUCTION

Understanding ecological processes is the cornerstone of fishery sciences, and 'population estimates or indices are required before any real quantitative understanding of ecological processes is possible' (Gunderson 1993). So the assessment of possible sources of bias in estimates of population density should be of interest in any ecological study. We intended to use a bottom trawl as a sampling instrument for a population dynamics study on the fish community of IJsselmeer, a large (182,000 ha) eutrophic lake in the Netherlands with a mean depth of 4.5 m. To assess whether variation in catch-per-haul (*CpUE*) observations on fish density and size reflected spatial distribution patterns or spatial differences in catchability, the *CpUE* observations were compared to hydroacoustic observations that were made simultaneously the haul (cf. Dahm 1992).

Bottom trawling is a widely used method to obtain estimates of fish density and size distribution. The *CpUE* is related to population density (*N*) as $CpUE=N{\cdot}q$ where *q* is the catchability coefficient (Gulland 1983). The value of *q* ranges between zero and one, if the unit effort is a haul and *N* is the number of fish present in the swept volume. It is generally acknowledged that *q* is dependent on the size of the fish present in the swept volume (cf. Chapter 4), and it is often assumed that the size-dependent function of *q* is constant between the hauls realized during the sampling program. However, *q* of towed gear has been shown to depend on varying fish behavior (Fréon, Gerlotto & Misund 1993), on bottom type (Connolly 1994), on contrast of the net material to the water background (Glass, Wardle & Gosden 1993) and on light intensity (Glass & Wardle 1989).

In IJsselmeer, light intensity has a negative effect on *CpUE* of a bottom trawl employed during daytime, where variation in light intensity is caused by variation in depth (3.6 - 6.5 m) and variation in water transparency (0.25 - 1.10 m Secchi depth) (Buijse, Schaap & Bult 1992). The authors hypothesize that low *CpUE* at high light intensity is caused by the increased ability of fish to escape from the trawl through early detection. Indeed, light intensity affects the behavior of fish towards an approaching trawl (Glass & Wardle 1989), and reactive distance of fish decreases with decreasing water transparency (Barrett, Grossman & Rosenfeld 1992; Gregory & Northcote 1993; Benfield & Minello 1996). However, the phenomenon observed by Buijse, Schaap & Bult (1992) may also be attributed to a decrease in local fish density, caused by avoidance of areas where light intensity is high. Avoidance of high light intensity has been demonstrated in vertical migration studies of fish (Fernö et al 1995; Rudstam & Magnuson 1985), and some species avoid areas with a high water transparency (walleye *Stizostedion vitreum* - Ryder 1977; creek chub *Semotilus atromaculatus* - Gradall & Swenson 1982).

The combined effect of light intensity on density of fish and on their catchability hamper the estimation of fish density from bottom trawl *CpUE*. To disentangle this combined effect, beam trawl catches that were made at varying water depths and light intensities were compared to hydroacoustic measurements on fish density and size distribution. Furthermore, hydroacoustics was used to test whether light intensity affected trawl avoidance behavior of fish (cf. Chapter 3). Hydroacoustics have successfully been used to study gear and vessel avoidance of fish in marine

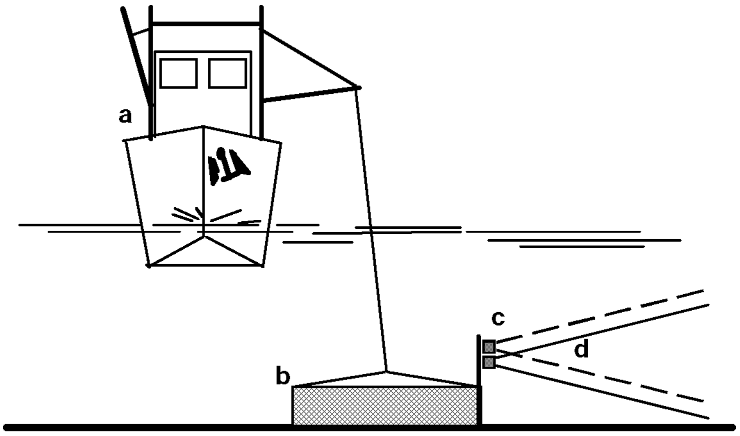

Figure 5.1. *Front view of research vessel (a), towing the beam trawl (b). Transducers (c) were mounted on the beam trawl. The acoustic axis of each beam (d) was directed horizontally, perpendicular to the towing direction.*

situations (Ona & Godø 1990; Gerlotto & Fréon 1992). In this *in situ* study, the use of hydroacoustics provided a new challenge, because hydroacoustics has only recently been used as a sampling instrument in shallow freshwater bodies (Kubecka *et al.* 1994; Kubecka 1996; Chapter 3).

MATERIALS AND METHODS

A beam trawl with mouth width 3 m, mouth height 0.6 m, and a stretched mesh size in the cod-end of 2 mm was used from R.V. 'Stern' (length 20 m, 200 HP). To make a direct comparison of hydroacoustic observations and trawl observations, transducers were mounted on the trawl. The acoustic axis of each transducer was directed horizontally, perpendicular on the course of the research vessel (Fig. 5.1). With this set-up, 14 hauls were made during daytime on March 28-29, 1995. Bottom depth varied between 3.6 and 6.5 m, but Secchi depth was constant (0.45 m). Each haul lasted 10 min, trawling speed was ca. 1.5 $m.s^{-1}$. Acoustic recordings started ca. 0.5 min after setting the beam trawl and ended shortly before the beam trawl was retrieved. Weather conditions, which may seriously affect hydroacoustic measurements in shallow lakes (Chapter 3), were constant during the survey period. Sometimes during surveying, high noise levels caused by wind-induced waves were observed at a distance > 15 m from the transducer. To eliminate this source of bias, the outer boundary of the sampled volume used for further analysis was restricted to a distance of 10 m from the transducer.

For hydroacoustic observations, we used a dual beam Biosonics ES2000 echo-sounder, with an operating frequency of 420 kHz. Dual beam technology is described in MacLennan & Simmonds (1992). Pulse width was set at $0.2 \cdot 10^{-3}$s, and ping rate at $20.s^{-1}$. Two dual beam

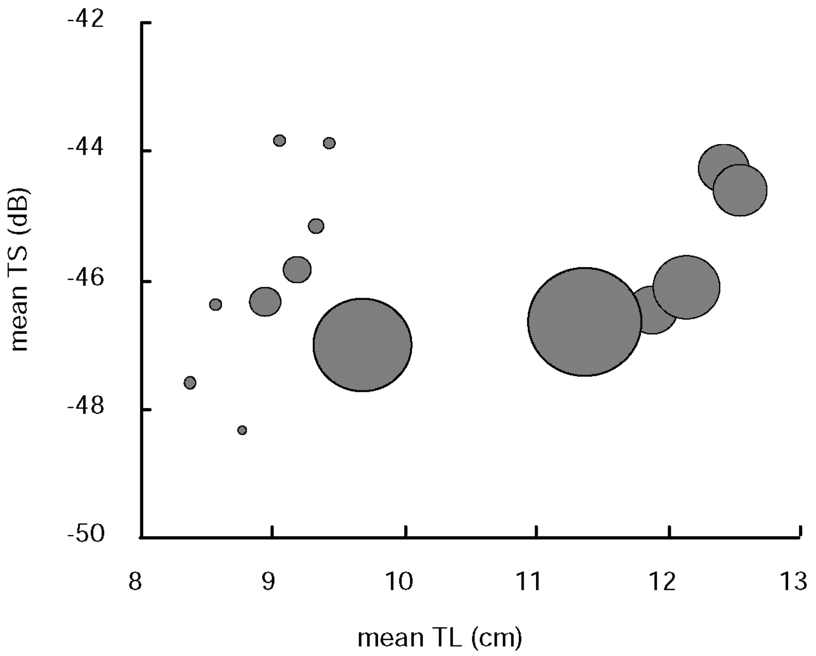

***Figure 5.2**. Relationship between mean TS (dB) and TL (cm). The surface area of plotting symbols is proportional to the value of the weighting variable (CpUE·ApUE).*

transducers, each with a 15° wide beam and a 6° narrow beam, were used. Signal processing was performed by the ESP Model 281 Dual-Beam Processor using a 40 log *R* time varied gain function (*R* is target range). The system was calibrated by measurements on a tungsten carbide standard target.

Of each single target in the acoustic beam, target strength (*TS*) and the distance from the transducer were measured. A threshold was applied on the narrow beam signal, resulting in exclusion from the sample of all on-axis targets with *TS* < -55 dB, and in exclusion of larger targets that were located at higher distance from the acoustic axis. Consecutively recorded targets were combined into acoustically identified fish (*AIF*) according to pre-specified criteria that were kept constant throughout the study period. Of each *AIF*, *TS* (dB) and the distance from the transducer (*MIDRANGE*, in m) were calculated as the mean target strength and the mean range of the single targets that make up the *AIF*. The swimming direction of the *AIF* relative to the transducer (*SLOPE*, in m.ping^{-1}) was derived from the change in range in consecutively recorded targets (cf. Chapter 3). By comparing the distributions of *SLOPE* for hauls made at varying bottom depth, the effect of light intensity on gear avoidance could be studied. The species of *AIF* could not be determined. Correlation between the catch per haul (*CpUE*, in numbers), the *AIF* per haul (*ApUE*, in numbers) and water depth, was studied by calculating Pearson correlation coefficients.

To check the consistency in size distribution estimates of the trawl and hydroacoustics, the *TS*-frequency distribution of *AIF* were compared with the length-frequency distribution of the trawl catch (all species pooled). For this purpose, the length-frequency distribution of the catch was converted to a *TS*-frequency distribution according to *TS*-*TL* relationships of Love (1977). In Love (1977), *TS*-*TL* relationships are given for fish insonified from aspects corresponding to

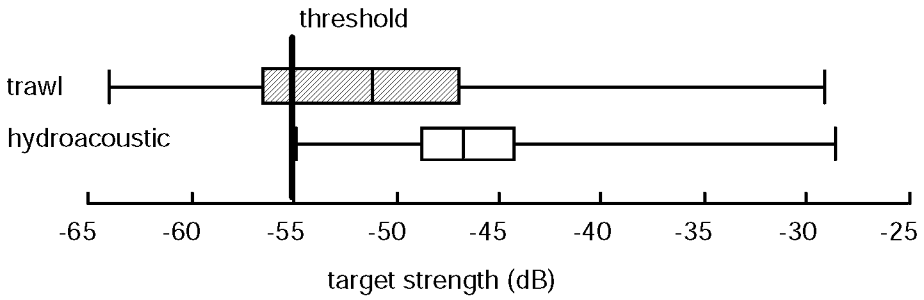

***Figure 5.3**. Boxplots with 25% quartiles of the hypothetical TS-frequency distribution of the trawl catch (shaded box) and the TS-frequency distribution of AIF (white box). The threshold value (-55 dB) is indicated as well.*

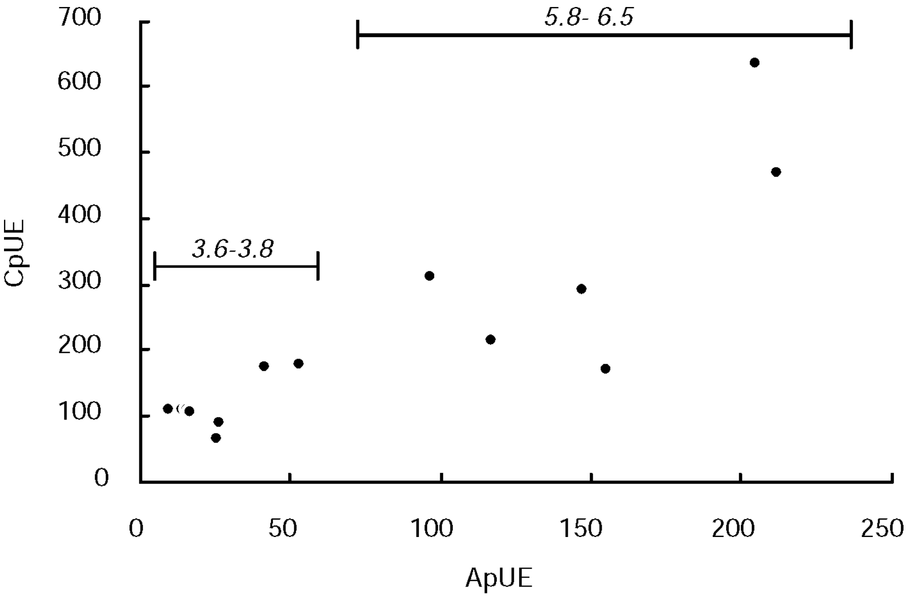

***Figure 5.4**. Relationship between CpUE and ApUE. The range in bottom depth (m) of sampling locations is indicated in italics.*

sections in an imaginary sphere centered around the insonified fish. *TS-TL* relationships are given for 7 aspects from one side of the fish; tail and head aspects cover 15° sections, the other 5 sections cover 30°. Hence, for each length class, 7 *TS* values are defined. Fish in a single length class of the length-frequency distribution were divided over the 7 *TS* values proportionally to the size of the sections. This resulted in a hypothetical *TS*-frequency distribution for each length class of the length-frequency distribution in the catch. Next, the hypothetical *TS*-frequency distributions for each length class were pooled into a *TS*-frequency distribution that represented all length classes in the trawl catch.

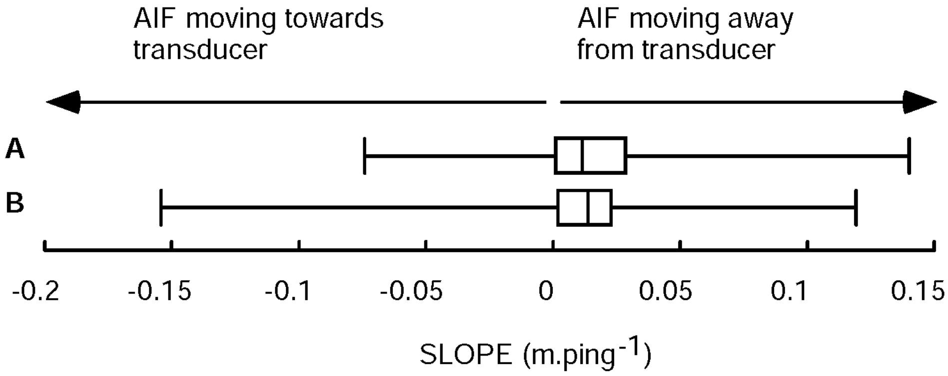

***Figure 5.5**. Boxplots with 25% quartiles of SLOPE values of AIF insonified at a bottom depth between 3.6 and 3.8 m (A) and at a bottom depth between 5.8 and 6.5 m (B).*

RESULTS

The trawl catch consisted of perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca*, ruffe *Gymnocephalus cernua*, smelt *Osmerus eperlanus*, roach *Rutilus rutilus,* bream *Abramis brama* and flounder *Platichtys flesus*. For comparison with hydroacoustic output, smelt and benthic species (ruffe and flounder) were excluded from the trawl dataset, because *TS* of smelt was to low to exceed the threshold value (cf. Chapter 3) and because the benthic ruffe and flounder cannot be detected by a horizontally directed acoustic beam. In total, 1,740 roach, 12,000 perch, 61 bream and 25 pikeperch were caught, and 1138 fish were insonified.

The *TS* of all insonified fish ranged between -55 dB (the threshold value) and -28 dB. The mean *TS* was -46.1 dB, which corresponds to a length of 20 cm according to the overall side aspect *TS*-*TL* relationship of Love (1977). The total length of all fish in the catch ranged between 5 cm and 57 cm, and the mean length of the fish per haul varied between 8.4 and 12.6 cm. Both *TL* of fish in the catch and *TS* of *AIF* differed significantly between hauls (Kruskal-Wallis test, P = 0.0001). The weighted correlation between mean *TS* and mean *TL* of each haul was positive and significant (weight variable *ApUE·CpUE*, Pearson correlation coefficient = 0.58, P = 0.030, Fig. 5.2). Despite this correspondence between hydroacoustic and trawl estimates of the mean size of fish in the population, the *TS*-frequency distribution differed strongly from the hypothetical *TS*-frequency distribution of the catch (Fig. 5.3). This difference was mainly caused by the threshold value for *TS* applied during hydroacoustic sampling.

***Table 5.1**. Pearson correlation coefficients for correlations between CpUE, ApUE and bottom depth. Values between brackets indicate P values for the significance of the correlation coefficients. n = 14.*

	CpUE	*ApUE*	water depth
CpUE	1	0.86639 (0.0001)	0.73041 (0.0030)
ApUE		1	0.87997 (0.0001)

The relationships between water depth and *CpUE,* and between water depth and *ApUE* were positive and significant (Table 5.1). Also, the relationship between *ApUE* and *CpUE* was positive and significant (Fig. 5.4, Table 5.1). However, *CpUE* was generally higher than *ApUE*, probably because of the difference between the swept volume of the trawl and the insonified volume of the hydroacoustics. Furthermore, a large part of the fish in the catch had a hypothetical *TS* below the threshold of the hydroacoustics (cf. Fig. 5.3), so that only part of the fish in the insonified volume were actually detected.

The mean value of *SLOPE* for all *AIF* was 0.01 m.ping^{-1}, corresponding to a mean swimming speed of 0.2 m.s^{-1} away from the transducer. The value of *SLOPE* was significantly different from 0 (signed rank statistic = 148113, $P = 0.0001$). There was no significant difference in *SLOPE* between hauls (Kruskal-Wallis test, $P = 0.41$). After grouping of observations made in shallow locations (water depth 3.6-3.8 m) and deep locations (water depth 5.8-6.5 m), still no significant difference was found (Fig. 5.5; Wilcoxon's signed-ranks test, $P = 0.55$). Therefore, a difference in trawl avoidance behavior of insonified fish between the deeper, darker area and the shallower, lighter area could not be demonstrated.

DISCUSSION

Observations with hydroacoustics and a bottom trawl on fish density and size at sampling locations with a bottom depth varying between 3.5 and 6.8 m were consistent. Therefore, we concluded that daytime *CpUE* of a beam trawl deployed in shallow (< 10 m depth) turbid (< 2 m Secchi depth) water bodies yields an estimate of the abundance of bottom-dwelling small fish (< 10 cm *TL*, cf. Chapter 4) that is not biased by variation in light intensity.

There was a positive and significant correlation between mean size of the fish in the trawl catch and the mean *TS* of *AIF*. However, the *TS*-frequency distribution as observed by the hydroacoustics and the hypothetical *TS*-frequency distribution as derived from the length-frequency distribution of the trawl catch differed. Apparently, thresholding caused under-representation of small fish in the hydroacoustic recordings. As there is some debate on the validity of Love's *TS*-*TL* relationships (MacLennan & Simmonds 1992), the discrepancy might also be attributed to the method used to convert the catch length-frequency distribution to the hypothetical *TS*-frequency distribution. However, we think that the *TS*-length relations we used were valid because *TS* estimates predicted by Love's relationships (Love 1977) correspond reasonably well with *TS* measurements of Kubecka (1994) of fish insonified from different side aspects.

In Chapter 3, the use of hydroacoustics as a stock assessment tool in large shallow lakes was advised against, because of the low signal-to-noise ratio. In the present study, it became apparent that under-estimation of small-sized fish is substantial indeed. Even in situations where the signal-to-noise ratio is high, the correlation between the *TS*-frequency distribution from a horizontal scanning acoustic survey and the length-frequency distribution as estimated by gillnets is weak (Kubecka et al. 1994). The weak correlation is probably caused by the variation in the aspect in which the fish is insonified. In *in situ* studies, the variation in aspect is far larger if a horizontal beam is used than if a vertical beam is used. Therefore, in horizontal beam hydroacoustic studies, the variance in *TS* is larger than in vertical beam studies. In studies where a vertical beam is applied, there usually is a good correlation between *TS*- and length-frequency distributions (Burczynski & Johnson 1986; Burczynski, Michaletz & Marrone 1987; Guillard & Gerdeaux 1993; Barange *et al.* 1994; Parkinson, Rieman & Rudstam 1994). Despite of the shortcomings of the horizontal beam technique, it was encouraging that the relatively small variation in length-frequency distributions (mean length between 8.4 and 12.6 cm *TL*) was reflected by the mean *TS* of *AIF*.

There was a positive, significant correlation between trawl and hydroacoustic estimates of fish density over a bottom depth range of 3.5 - 6.5 m. At an ambient Secchi depth of 0.45 m, the range in bottom depth corresponds to a range in light intensity of $1.2 \cdot 10^{-6}$ - $3.6 \cdot 10^{-2}$ lx (cf. Buijse, Schaap & Bult 1992). Behavioral studies using direct observation methods indicate that fish cease to react in an ordered pattern to an approaching net if light intensity is below 10^{-6} lx. At high light intensity ($>10^{-3}$ lx), fish usually swim ahead of the ground rope of the trawl at sub-maximum speed until exhaustion (Glass & Wardle 1989, Wardle 1993). Considering the range in light intensity in the present study, a difference in fish behavior towards the approaching net between the shallower, lighter areas and the deeper, darker areas was likely. However, the consistency between trawl and hydroacoustic observations suggested that the higher *CpUE* in deeper, darker areas was caused by a higher fish density. It is unlikely that the consistency between trawl and hydroacoustic observations was caused by fish avoiding both the trawl and the acoustic beam, because it was unlikely that fish evaded the beam trawl at a distance higher than covered by the acoustic beam. This behavior has been observed in very clear water only, at a light intensity of > 1 lx (Glass & Wardle 1989).

Hydroacoustic measurement of fish swimming direction did not show a difference in avoidance behavior between shallower, lighter and deeper, darker areas. Fish on average moved away from the transducer with a speed of 0.2 $m.s^{-1}$. This is almost equal to the speed found during earlier horizontal beam acoustic surveys, where the transducer was mounted in a towed body (Chapter 3). Probably, avoidance behavior was caused by the research vessel's noise (cf. Ona & Godø 1990). However, avoidance behavior was only weak, given the 'burst' swimming speed of ca. 1-2 $m.s^{-1}$ for fish of 10 cm *TL* (He 1993).

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Section II

Spatial distribution of small fish and fish-eating birds

Chapter 6

Vertical distribution patterns of zooplanktivorous fish in a shallow, eutrophic lake, mediated by water transparency

P.J. Mous, W.L.T. van Densen & M.A.M. Machiels

ABSTRACT

We examined the hypothesis that the vertical distribution pattern of fish at shallow (5 m depth) sites in a eutrophic lake (IJsselmeer, The Netherlands) was affected by water transparency. The spatial distribution pattern of the fish population was assessed during daytime and nighttime by pair trawling and by hydroacoustics during summer. The pair trawl was operated near the bottom, in the middle of the water column and at the surface. Water transparency was estimated by light intensity measurements in the water column and by Secchi depth measurements. Hydroacoustic observations showed that fish were more dispersed during nighttime than during daytime. Smelt and young-of-the-year perch comprised 97% of the fish population in numbers. The daytime vertical distribution pattern of young-of-the-year smelt was strongly affected by water transparency. Smelt concentrated near the surface, exposing itself to a light intensity of > 200 $\mu W.cm^{-2}$ if the water was turbid (Secchi depth = 0.5 m), and near the bottom if the water was clear (Secchi depth = 1.2 m). It has been reported that smelt avoid a light intensity > 0.1 $\mu W.cm^{-2}$ (Appenzeller & Leggett 1992). We assume that, in IJsselmeer, low water transparency overruled the light-sensitivity of smelt, and made smelt to stay higher up in the water column at a high light intensity. Implications of the vertical distribution pattern of smelt for its availability to piscivorous birds and for depth selective sampling methods are discussed.

INTRODUCTION

In IJsselmeer, zooplanktivorous smelt *Osmerus eperlanus* is the most important prey fish for perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca* and eel *Anguilla anguilla* (Buijse & Houthuijzen 1992; Buijse & Van Densen 1992; Willemsen 1977), as well as for avian piscivores (black-headed gull *Larus ridibundus*, black tern *Chlidonias niger*, grebe *Podiceps cristatus*, smew *Mergus albellus*; Buijse *et al.* 1993). Foraging efficiency of both zooplanktivorous prey fish and their predators are positively affected by water transparency and light intensity (Benfield & Minello 1996; Barrett, Grossman & Rosenfeld 1992). Hence, prey fish must trade off foraging efficiency against predation risk (Gregory & Northcote 1993). Turbid lakes such as IJsselmeer (Secchi depth 0.15 – 3 m) have a steep vertical gradient in light intensity, giving prey fish the opportunity to optimize the trade off by adjusting its vertical distribution pattern. We assessed if and how water transparency affected the vertical distribution pattern (*VDP*) of smelt and other zooplanktivorous fish in IJsselmeer.

The *VDP* of fish has been a major focus in ecological studies in deeper waters (depth > 10 m), where temperature, dissolved oxygen concentration and light intensity shape the *VDP* and its diurnal variation (Bevelhimer & Adams 1993; Rowe 1994; Rudstam & Magnuson 1985). In deeper waters, the trade-off between predation risk and foraging efficiency causes diurnal vertical migration patterns (antipredation window model; Clark & Levy 1988) (Appenzeller & Leggett 1992, Loose & Dawidowiscz 1994). Also in shallow waters, low-amplitude vertical migration patterns may evolve, as has been demonstrated for the carnivorous zooplankter *Leptodora kindtii* (Vijverberg 1991) and smelt *Osmerus eperlanus* (Piersma, Lindeboom & van Eerden 1988) in shallow (depth 1.5-4.5 m) and turbid (Secchi depth 0.3-0.8 m) lakes in The Netherlands. This diurnal variation in the *VDP* of prey fish causes variation in food availability for piscivorous birds, which is reflected by the spatial and temporal patterns in their foraging behavior (Wanink & Goudswaard 1994; Piersma, Lindeboom & van Eerden 1988). It has been suggested that the reduced nutrient loading of IJsselmeer since the 1970s will increase water transparency, thereby eventually changing the *VDP* of prey fish and the food availability for piscivorous birds (Platteeuw 1994). Knowledge of the *VDP* is also necessary to interpret catch-per-unit-effort (*CpUE*) observations of bottom trawls (cf. Crawford, Hudon & Parsons 1992), the most commonly used sampling instrument for fish stock surveying in IJsselmeer since the late 1960s.

In the present study, the diurnal variation in *VDP* of zooplanktivorous fish at shallow sites (5 m depth) is quantitatively described, so that consequences on prey availability for piscivorous birds and effects on abundance estimates from a bottom trawl survey program can be evaluated. We studied the *VDP* by sampling with a pair trawl at the bottom, in the middle of the water column, and at the surface. Hydroacoustic observations were made to validate our trawl data and to study vertical distribution with a finer resolution than was possible with the pair trawl. We showed that a higher water transparency increased the depth where the most abundant prey fish, 0-group (young-of-the-year smelt) *Osmerus eperlanus*, was concentrated during daytime. The *VDP* of another abundant prey fish, 0-group perch *Perca fluviatilis*, was less affected by water transparency.

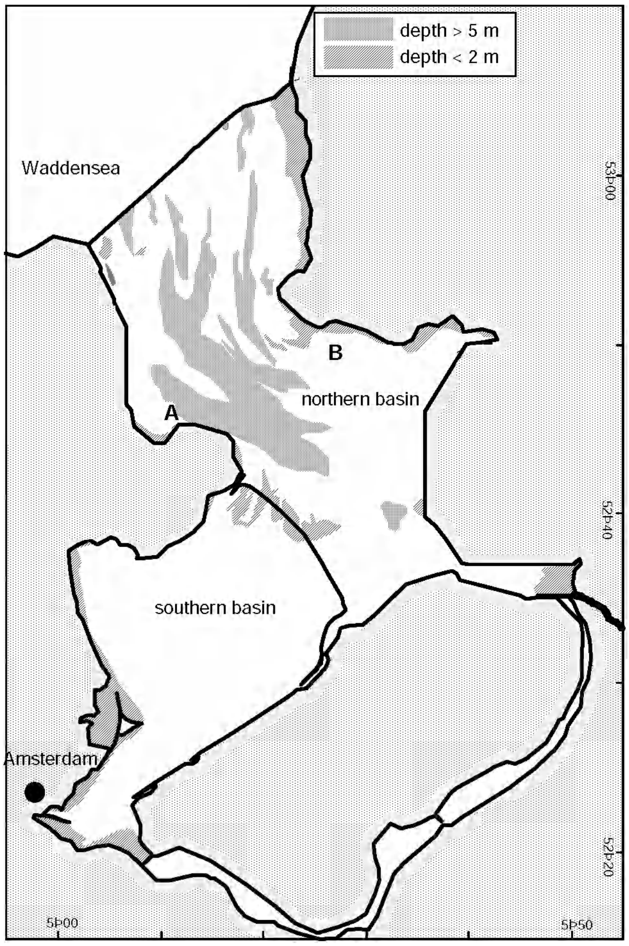

Figure 6.1. *Map of IJsselmeer. Sampling sites are indicated by A and B.*

MATERIALS AND METHODS

Study area and survey design

The study is conducted at two sites in the northern basin of IJsselmeer, a eutrophic lake of 180,000 ha surface area in The Netherlands (Fig. 6.1). The mean depth of the northern basin is 4.5 m, with depressions up to 10 m at former tidal channels. Water transparency as measured during surveys of the R.V. 'Stern' varied between 0.15 m and 3.0 m Secchi depth in the northern basin, and between 0.15 m and 1.3 m Secchi depth in the southern basin during the years 1985-1994.

In IJsselmeer, water transparency decreases with increasing wind speed: over the period 1985-1994, Secchi depth and wind force were negatively correlated ($n_{\text{northern basin}} = 308$ and

$n_{\text{southern basin}}$ = 125, Pearson correlation coefficients -0.16 for the northern basin, and -0.67 for the southern basin, $P < 0.01$). Differences in bottom and surface temperature during summer are small (2°C) and, with few exceptions, persist during the day only (Berger & Sweers 1988). During this study, incidental measurements of temperature and dissolved oxygen concentration at the surface and at 1 and 2 m below the surface showed no gradient.

Sampling took place at two sites of ca. 5 m depth in the northern basin of IJsselmeer (Fig. 6.1) on June 23, June 29, July 6, August 11, and August 18 1992. On July 6 and August 11, part of the sampling program was skipped because of rough weather. The choice of the sampling site was dictated by the roughness of the water at the moment of sampling, which depended mainly the wind direction and force. Observations comprised water transparency measurements, trawling and hydroacoustic observations. Water transparency was measured three times during the 27-hour sampling day: once between 11 AM and 4 PM on each calendar day, and in the evening at around 8 PM. We assumed that the evening measurement was representative for the water transparency during the night. Bottom, mid-water and surface hauls and hydroacoustic observations were repeated during the sampling day (Table 6.1).

***Table 6.1**. Site (cf Fig. 6.1), number of trawl sessions (TRAWL), hydroacoustic observations (HR), light attenuation coefficient (EXT, m^{-1}) and Secchi depth (m) during each period. A trawl session consists of a bottom, a mid-water and a surface haul. Nighttime observations were made in the period between ca. 1 hour after sunset and 1 hour before sunrise.*

PERIOD	site	*TRAWL*	*HR*	*EXT*	Secchi
June 23, day	B	4	3	-1.57	1.00
June 23-24, night	B	2	2	-1.56	1.00
June 24, day	B	3	3	-1.98	0.90
				-1.96	0.90
June 29, day	A	3	4	-1.82	1.00
June 29-30, night	A	2	2	-1.45	1.20
June 30, day	A	3	3	-2.52	0.70
July 6-7, night	B	2	2	-2.49	0.70
July 7, day	B	3	2	-1.98	0.85
August 11, day	A	1	0	-3.23[a]	0.55
August 18, day	A	3	3	-2.70[a]	0.65
August 18-19, night	A	3	3	-2.70[a]	0.65
August 19, day	A	2	1	-2.70[a]	0.65

Notes

a: estimates through light attenuation – Secchi depth relationship

Water transparency

A light profile was established by measuring light intensity in the water column at 10-25 cm depth intervals using a Licor Model LI-185A radiometer. To estimate light attenuation coefficients (*EXT*, in m^{-1}; cf. Golterman, Clymo & Ohnstad 1978), and to test for differences in attenuation coefficients between periods, an ANCOVA model of the light intensity measurements was fitted:

$$\ln(I)=\text{Constant}+ PERIOD + DEPTH + (PERIOD \cdot DEPTH) \quad \text{[formula 6.1]}$$

where *I* is the light intensity at a certain depth, *PERIOD* (class variable) is the effect of the sampling period (cf. Tabel 6.1), and *DEPTH* (covariate) is the depth where the light intensity measurement was made. It follows that an estimate of the attenuation coefficient for each period can be obtained by adding the parameter estimates of *DEPTH* and (*PERIOD.DEPTH*). The model explained 99.7% of the variance in light intensity and was highly significant ($F_{17,143}$ = 2636, P = 0.0001). The interaction term (*PERIOD.DEPTH*) reduced variance significantly (sequential SS = 17.8, $F_{8,143}$ = 134, $P < 0.0001$), indicating that the light attenuation coefficient differed between periods. The distribution of the residuals was normal (Wilk-Shapiro statistic = 0.99, P = 0.95). On August 11 and August 18 the radiometer was not available. Therefore, the attenuation coefficient was estimated from the Secchi depth, using an attenuation coefficient-Secchi depth relationship from the measurements during the other sampling days (R^2 = 0.9, $F_{1,8}$ = 63.2, $P < 0.0001$):

$$EXT = 2.31 \cdot \text{Secchi depth} - 4.04 \quad \text{[formula 6.2]}$$

with Secchi depth in m.

Pair trawling

A pair trawl with a mouth opening of 3.3*0.85 m and a stretched mesh size in the cod-end of 1 cm was used. The net was operated from two open boats, powered by 15 HP outboard engines. Trawl hauls were made at the bottom, at mid-water (2.4 m above the bottom), and at the surface. The location of the net in the water column was controlled by weights. Haul duration was 10 min., and an area of about 0.3 ha was covered with each haul. The catch was sorted by species, and fish were measured to the nearest cm below.

Separate ANCOVA models for daytime and nighttime observations were fitted to explain variation in ln-transformed catch numbers (*LNCpUE*) with the light attenuation coefficient (*EXT*) and the location of the trawl in the water column, expressed as the fractional distance from the bottom (*FDB*, 0 = bottom, 1 = surface). The model reads:

$$LNCpUE = \text{Constant} + PERIOD + FDB + FDB \cdot EXT \quad \text{[formula 6.3]}$$

where *PERIOD* is a class variable (cf. Table 6.1), *EXT* and *FDB* are covariates. The variable *PERIOD* aliases for the effect of the light attenuation coefficient on trawl catch numbers irrespective of *FDB*, for sampling site and for mortality over the period June 23 - August 18. We assumed that aliased effects did not affect the *VDP*. For hypothesis testing, sequential sums of squares were used (SAS® Institute Inc. 1989).

Hydroacoustics

Hydroacoustic recordings were made using a Lowrance X15MA unit in combination with an Eagle XD-2 transducer with a beam angle of 20°. The operating frequency of the sounder was 192 kHz. Recordings were made with a downward-looking transducer, mounted on a small open boat ca. 30 cm below the water surface. With a speed of ca 1 $m.s^{-1}$, recordings of 10 min were made. Noise reduction systems of the Lowrance unit ('discrimination' and 'suppressor' system) were deactivated, and pulse duration *P* was set at 30 µs. Greyline, sensitivity, and paper speed were, on a scale of 0 to 1, set at 0.5, 0.5, and 0.25 respectively. Resolution (*R*, the distance at which targets must be separated to produce individual echoes) was 2.3 cm, given the sound speed in water ($V = 1500\ m \cdot s^{-1}$) and the pulse duration ($R = (P \cdot V)/2$; MacLennan & Simmonds 1992). Because of wave-induced movements of the transducer, fish signals on the echogram could be distinguished from the bottom signal only, if fish were located at least ca. 10 cm above the bottom. The echograms were scanned and converted to bitmap graphics files. The graphics files were imported to an image analysis program (NIH Image 1.52). With this program, grey values of pixels in a selected area of an image can be averaged, and a mean grey value (*MGREY*) of each 0.6 m depth stratum in the scanned echogram was obtained. *MGREY* is a measure for the amount of fish in a particular depth stratum. We tested whether *MGREY* was correlated with trawl *CpUE*. Statistical analyses were done with SAS® software (SAS® Institute Inc. 1989).

Table 6.2. *Mean length (ML, cm), coefficient of variation in length (CV_L, %) and total numbers caught with the pair trawl.*

	0-group smelt			≥1-group smelt			0-group perch		
starting of sampling on day:	*ML*	CV_L	total catch	*ML*	CV_L	total catch	*ML*	CV_L	total catch
June 23	4.5	9.2	14022	9.2	8.5	11	3.7	11.8	9125
June 29	4.6	10.4	37027	9.5	6.8	503	4.1	13.2	3373
July 7	4.9	10.8	10947	9.3	8.1	108	4.7	10.3	5075
Aug. 11	5.4	7.8	976	9.1	5.5	117	5.6	7.8	562
Aug. 18	5.5	7.2	11212	9.4	8.7	649	5.8	8.0	34972

RESULTS

In total 131,000 fish were caught, of which 57% were smelt and 40% were 0-group perch (< 7 cm *TL*) (Table 6.2). Other categories were large perch, roach, pikeperch, ruffe, eel, bream and flounder. Age classes (0-group and ≥1-group) were clearly distinguishable by the distinctive modes in the length frequency distributions. In the research period (June 23 - August 18), mean length of 0-group smelt increased by only 20% from 4.5 to 5.5 cm *TL*, and that of 0-group perch by 60% from 3.7 to 5.8 cm. Growth of ≥1-group smelt was negligible.

The fitted models showed that during daytime, 0-group smelt (Fig. 6.2a) were concentrated near the surface if the water was turbid (*EXT* = -2.8, Secchi depth = 0.5 m), and near the bottom if the water was clear (*EXT* = -1.4, Secchi depth = 1.1m) (*P* = 0.0001, Table 6.3). During nighttime, 0-group smelt (Fig. 6.2b) concentrated near the bottom, but perhaps (*P* = 0.3, Table 6.3) less so under turbid than under clear conditions. Nighttime *VDP* of ≥1-group smelt (Fig.

Table 6.3. *ANOVA on daytime and nighttime ln-transformed catch numbers. MS = mean squares, df = degrees of freedom. See text for further explanation.*

species/	daytime				nighttime			
source	*df*	*MS*	*F*	*P*	*df*	*MS*	*F*	*P*
0-group smelt								
model	9	6.61	4.24	0.0003	5	8.33	5.05	0.0034
error	56	1.56			21	1.65		
effects								
PERIOD	7	3.95	2.53	0.024	3	10.21	6.19	0.0035
FDB	1	4.71	3.02	0.088	1	9.12	5.53	0.029
*EXT*FDB*	1	27.15	17.41	0.0001	1	1.88	1.14	0.3
1-group smelt[a]								
model	-	-	-	-	4	5.54	8.54	0.0002
error	-	-			15	0.65		
effects								
PERIOD	-	-	-	-	2	8.08	12.46	0.0001
FDB	-	-	-	-	1	0.00	0.00	0.98
EXT.FDB	-	-	-	-	1	3.45	5.32	0.033
0-group perch								
model	9	7.84	5.76	0.0001	5	5.70	5.66	0.0019
error	56	1.36			21	1.01		
effects								
PERIOD	7	6.72	4.94	0.0002	3	4.19	4.15	0.019
FDB	1	17.45	12.82	0.0007	1	10.95	10.86	0.0034
EXT.FDB	1	6.05	6.05	0.039	1	4.99	5.00	0.037

Note

a: In 28 out of 66 daytime hauls, and in 2 out of 25 nighttime hauls, zero 1-group smelt were caught. Because zero cannot be log-transformed, a model for the daytime observations was not fitted, and the nighttime model was fitted without the two 'zero' observations. The fitted model represented 'zero'-observations reasonably well: predicted values of 'zero' observations ranged between 2.2 and 4.5, whereas the range of predicted values for 'non-zero'-observations was 1.2 - 65.

6.2c) was affected by the light attenuation coefficient ($P = 0.03$, Table 6.3) and resembled the *VDP* of 0-group smelt. During both daytime and nighttime, 0-group perch seemed to concentrate near the bottom, but less so under clear conditions than under turbid conditions ($P = 0.04$, Table 6.3, Fig. 6.2d and 6.2e). However, this effect of water transparency may have been spurious, because of the positive correlation between water transparency (cf. Table 6.1) and mean length of perch (cf. Table 6.2). It may have been that 0-group perch gradually shifted their behavior from pelagic, as during the larval stage, to more benthic, as during the juvenile and adult stage.

Parameter estimates for the effects of *FDB* and *FDB·EXT* provide a means to calculate local abundance per unit area, if the relative depth, the light attenuation coefficient, the height of the sampled depth stratum (*HEIGHT*) and the bottom depth (*BOTTOM*) are known. The parameterized version of formula [6.3] can be rewritten as

$$CpUE = \mathrm{e}^{(a + b \cdot EXT) \cdot FDB + \mathrm{Constant}} \quad \text{[formula 6.4]}$$

where *CpUE* is the number of fish per haul, *e* is the base of the natural logarithm, *a* is the parameter estimate of the *FDB* effect and *b* of the *FDB·EXT* effect. If all depth strata would have been sampled, the sum of the observations is the local abundance in the sampled surface area (*N*):

$$N = \frac{BOTTOM}{HEIGHT} \cdot \int_{0}^{1} e^{(a+b \cdot EXT) \cdot FDB + Constant} \, dFDB \quad \text{[formula 6.5]}$$

which equals

$$N = \frac{BOTTOM}{HEIGHT} \cdot e^{Constant} \cdot \left\{ \frac{1}{a + b \cdot EXT} \cdot (e^{a+b \cdot EXT} - 1) \right\} \quad \text{[formula 6.6]}$$

If there is no effect of *FDB* or *FDB·EXT*, *a* and *b* approach zero (implicating that there is no vertical gradient in fish density), and formula [6.6] simplifies to

$$N = \frac{BOTTOM}{HEIGHT} \cdot e^{Constant} \quad \text{[formula 6.7]}$$

where $\mathrm{e}^{Constant}$ = *CpUE* (see formula [6.4]). The term {..} in formula [6.6] can be considered as a factor to correct abundance estimates for turbidity-mediated variation in the *VDP*. The magnitude of this correction factor is considerable if the effect of water transparency on the *VDP* is strong. For example, suppose that the sampling instrument is a bottom trawl; then *FDB* is close to zero, and consequently $\mathrm{e}^{Constant}$ equals *CpUE* (cf. [formula 6.3]). For 0-group smelt at daytime, the estimates for *a* and *b* were -8.69 and -481.60 respectively. At $EXT = -2.8$ (Secchi depth = 0.5 m) and at EXT = -1.4 (Secchi depth 1.1 m), the values of the correction factors are 25 and 0.44

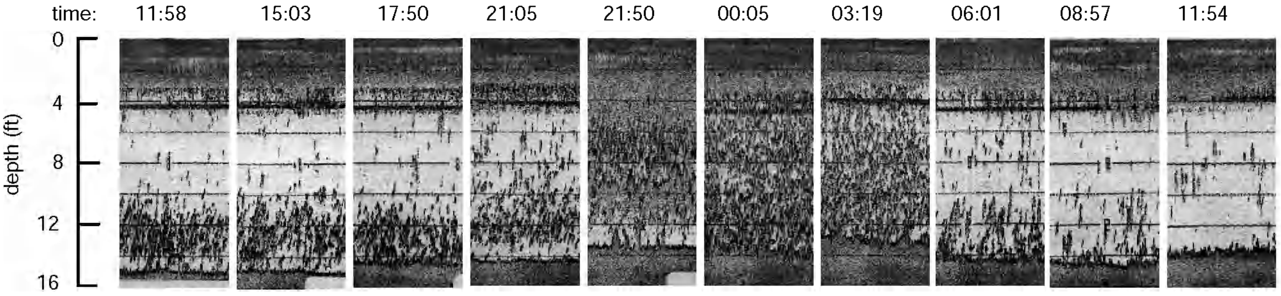

***Figure 6.3**. Hydroacoustic recordings of the sampling day starting on June 29th. The echograms shown are 90 s excerpts of recordings that lasted for 10 minutes each. The speed of the boat was ca 1 m.s^{-1}. Sunset was at 22:03 hr, sunrise at 05:18 hr. Fish were more dispersed over the water column during nighttime than during daytime.*

respectively. For abundance per unit area estimates, the bottom trawl *CpUE* should be multiplied by 25 times the *BOTTOM*-to-*HEIGHT* ratio if Secchi depth is 0.5 m, and by 0.44 times the *BOTTOM*-to-*HEIGHT* ratio if the Secchi depth is 1.1 m.

Hydroacoustics

Daytime and nighttime hydroacoustic observations differed notably. Fish seemed to be more dispersed over the water column during nighttime than during daytime. The change from the daytime to the nighttime pattern occurred in a period of less than 1 hour before sunset, and maximally 45 min after sunrise fish returned to their daytime *VDP* (Fig. 6.3).

At each sampling day, the amount of backscattered sound energy was lower during daytime than during nighttime, resulting in significantly lower *MGREY* values in daytime recordings (Wilcoxon Tests, $P < 0.01$). In daytime observations, *MGREY* of the depth stratum at 0-0.6 m above the bottom was correlated to the bottom *CpUE* of 0-group perch and smelt (Pearson correlation coefficient = 0.37, $P = 0.04$; Fig. 6.4). Daytime mid-water *CpUE* was also correlated to *MGREY* of the corresponding depth stratum (Person correlation coefficient = 0.53, $P = 0.05$; Fig. 6.4). Nighttime *CpUE* and *MGREY* were not correlated (Person correlation coefficients = 0.30, -0.04 and P = 0.43, 0.92 for bottom and mid-water respectively), but they do fit in the general relation between *CpUE* and *MGREY* (Fig. 6.4). Probably, dispersion of fish at night resulted in an increase of the total backscattering cross section (MacLennan & Simmonds 1992) up to a level where the echogram became saturated. We concluded that trawl and hydroacoustic observations were coherent.

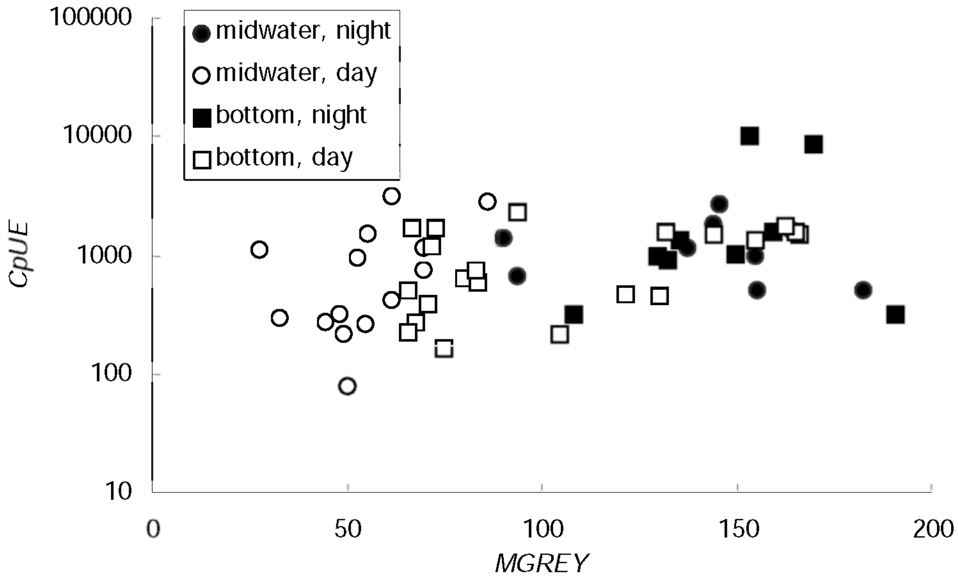

***Figure 6.4**. Correlation between trawl catch per 10 min. haul (CpUE) and hydroacoustic observations (MGREY).*

DISCUSSION

The effect of water transparency on the *VDP* in 5 m deep water was most pronounced for 0-group smelt. During daytime, 0-group smelt concentrated near the surface if the water was turbid (*EXT* ca. -2.8 m^{-1}; Secchi depth ca. 0.5 m) and near the bottom if the water was clear (*EXT* ca. -1.4 m^{-1}; Secchi depth ca. 1.1 m). Rainbow smelt *Osmerus mordax* avoided a light intensity > 0.1 $\mu W \cdot cm^{-2}$ in Lake Memphremagog (Appenzeller & Leggett 1995) by migrating to deeper layers. Assuming a light intensity of 4000 $\mu W \cdot cm^{-2}$ at the surface (cloudy summer midday at 52°N, Golterman, Clymo & Ohnstad 1978), smelt in IJsselmeer exposed itself to a light intensity of > 200 $\mu W.cm^{-2}$ (1 m depth) by staying near the surface under turbid (*EXT* = -2.8 m^{-1}) conditions. Apparently, low water transparency overruled light sensitivity of smelt in IJsselmeer, and made smelt to stay higher up in the water column at a high light intensity. In Lake Memphremagog water transparency varies between 4-8 m Secchi depth (Appenzeller & Leggett 1992), which is probably too high to mediate the *VDP* to the extent that was observed during this study. In other studies on pelagic zooplanktivores, a higher water transparency caused fish to stay at greater depth too, but only through a light-avoidance mechanism (Bohl 1980; Levy 1990b; Rowe 1994; Rudstam & Magnuson 1985).

For 0-group perch, the correlation between water transparency and body length probably caused a spurious effect of water transparency on the *VDP*. This suggestion is corroborated by

Wang & Eckmann (1994), who show that in Lake Constance (Germany) 0-group perch migrate from the pelagic to the nearshore zone in the period July 11 - 18. This is around the same time in the year that we observed 0-group perch concentrating near the bottom.

The echograms strongly suggested that fish were more dispersed in the water column during nighttime than during daytime, a phenomenon that is often observed (eg. Appenzeller & Leggett 1992; Bethke 1993; Bohl 1980; Burczynski, Michaletz & Marrone 1987; Crawford, Hudon & Parsons 1992;Hall *et al.* 1979; Levy 1990a,b). In IJsselmeer, dispersal over the water column occurred in a period shorter than 1 hour before sunset, and fish reverted to their daytime *VDP* in a period of maximally 45 min period after sunrise. This dispersal increases feeding opportunities for the piscivorous bird great crested grebe *Podiceps cristatus*, and consequently in IJsselmeer grebes concentrate their feeding activity in the periods around sunset and sunrise (Piersma, Lindeboom & Van Eerden 1988).

The relationship between water transparency and foraging behavior of piscivorous birds is complex. In clear water, piscivorous birds can more easily detect and catch prey fish. However, a higher water transparency causes smelt to concentrate in the deeper part of the water column, thereby decreasing the predators' foraging efficiency through increased energetic costs associated with deep diving (De Leeuw *et al.* 1998). Furthermore, clear water also causes low prey fish density (cf. Chapter 7). In IJsselmeer, the solitarily pursuit-diving great crested grebe avoids areas with water transparency < 0.4 m Secchi depth, presumably because grebe cannot spot prey fish in turbid conditions (Van Eerden, Piersma & Lindeboom 1993). This study showed that at a water transparency > 0.8 m Secchi depth, foraging efficiency of grebe may decrease through decreased prey availability, setting the optimal water transparency interval for foraging at ca. 0.4 – 0.8 m. As water transparency in IJsselmeer is ca. 0.6 m Secchi depth on average (Lammens 1999), IJsselmeer seems an optimal foraging habitat for grebe, explaining the large numbers that use IJsselmeer for moulting in the months August-September (Winter 1994). Another avian fish-eater in IJsselmeer, smew *Mergus albellus*, adapted to fishing in turbid conditions (< 0.4 m Secchi depth) by developing a social fishing technique (Platteeuw, Van Eerden & Beekman 1999), similar to the fishing technique that is used by cormorants *Phalacrocorax carbo* under turbid conditions (Van Eerden & Voslamber 1995). The effect of water transparency is probably more pronounced for surface-feeding avian piscivores in IJsselmeer that depend on smelt, such as black tern *Chlidonias niger* and black-headed gull *Larus ridibundus* (Buijse *et al.* 1993), than for diving piscivorous birds (cf. Chapter 8).

This study showed that abundance estimates of smelt by bottom trawling are strongly affected by water transparency. If smelt abundance is estimated through volume swept clear by the bottom trawl, and a homogenous smelt distribution in the water column is assumed, the estimate may differ by a factor 0.44 - 25 from the true population, depending on water transparency.

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The following figure should be added to Chapter 6 'Vertical distribution patterns of zooplanktivorous fish in a shallow, eutrophic lake, mediated by water transparency'.

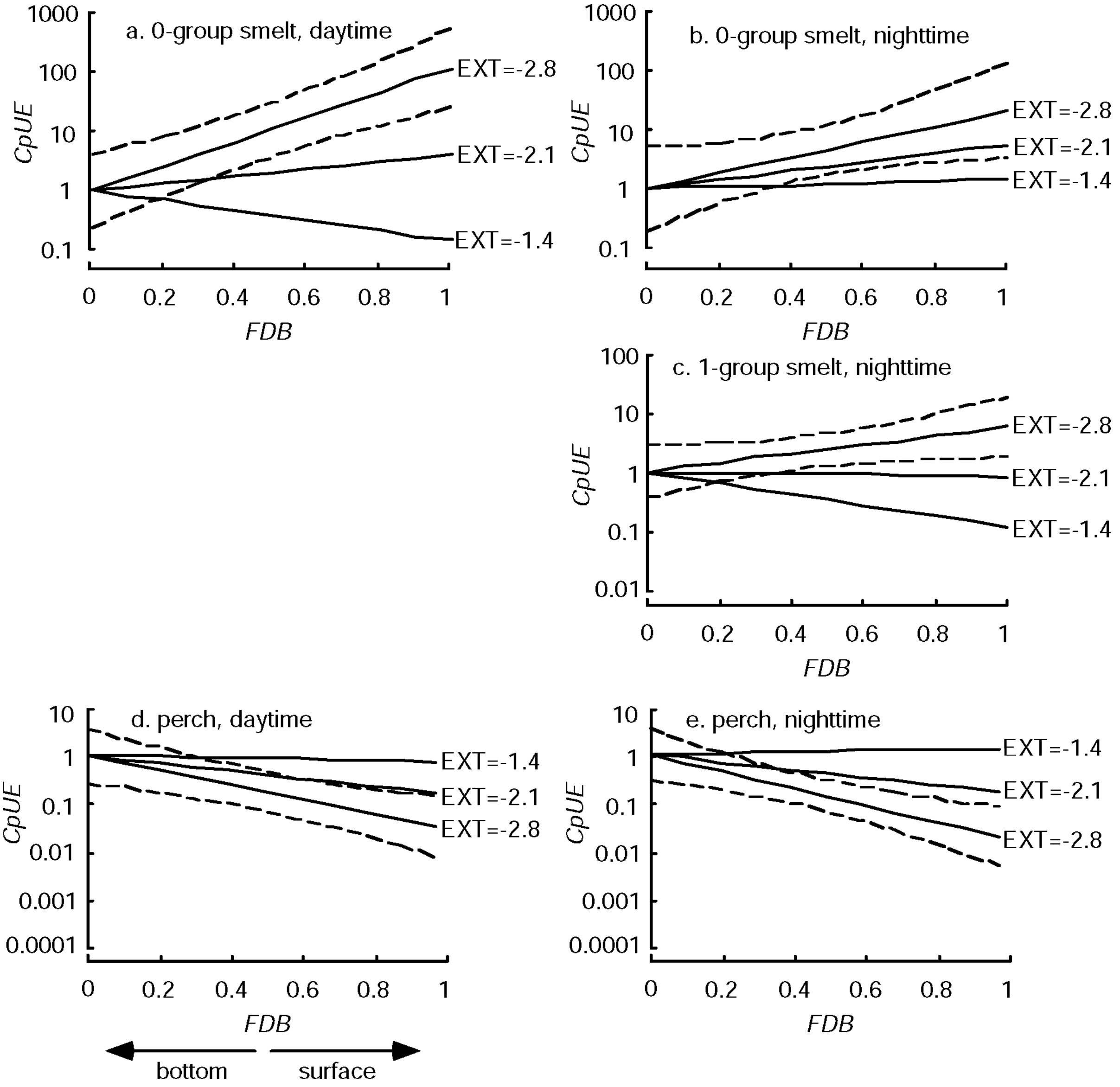

Figure 6.2a-e*. Modeled relationships of catch number (CpUE) vs. fractional distance from bottom (FDB, 0 = bottom, 1 = surface) for 3 levels of water transparency (EXT = -2.8, -2.1, -1.4, corresponding to Secchi disk depth 0.5 m, 0.8 m and 1.1 m respectively). Here, CpUE is expressed as a factorial change from the CpUE at the bottom. The broken lines indicate the estimated 95% confidence limits of the mean for the relationship with EXT = -2.8.*

Chapter 7

Horizontal distribution patterns of prey fish as related to habitat characteristics and spatial scale in a large, shallow lake in The Netherlands

P.J. Mous, W.L.T. van Densen & M.A.M. Machiels

ABSTRACT

The spatial distribution of prey fish species (young-of-the-year smelt, *Osmerus eperlanus*, ruffe, *Gymnocephalus cernua* and young-of-the-year perch *Perca fluviatilis*) in large (180,000 ha), shallow (max. depth 10 m) and eutrophic IJsselmeer (The Netherlands) was studied to assess the consequences for prey-predator interactions. Two factors influencing spatial distribution were studied: habitat heterogeneity and spatial autocorrelation. Two bottom trawl surveys were carried out that differed in mean distance between hauls (ca. 5 km vs. ca. 15 km) and total sampling area (35 km^2 vs. lakewide). Both surveys were carried out during summer and winter. Catch-per-haul was used as an index of local density of prey fish. Variation in water depth and water transparency determined habitat heterogeneity in the open water of IJsselmeer. All species concentrated in deeper areas during winter, and ruffe preferred deeper areas during summer as well, but to a lesser degree than in winter. During summer, perch preferred shallower areas, whereas the spatial distribution of smelt was not affected by depth. Both smelt and ruffe concentrated in areas with a lower water transparency in summer and winter, but spatial distribution of perch was not affected by water transparency. For smelt, the most important prey fish species in IJsselmeer, the effect of water transparency was strong, as both in summer and in winter, smelt were about 200 times as abundant at the most turbid site than at the clearest site. During most surveys and for most species, spatial autocorrelation (on a scale between 0.01-1 and 50 km) was lacking or weak if density was corrected for effects of depth and water transparency. This implies that in the spatial distribution pattern of prey fish in IJsselmeer, aggregations on the scale of large schools (> 10 m diameter) or aggregations of schools were lacking. We inferred that avian and fish predators faced a random variation in the density (integrated over an area of 3000 m^2) of each prey fish species of ca. a factor 3.2. This factor is well within the range of variation reported for other aquatic populations in similar environments. Since spatial autocorrelation in prey fish density was absent or weak, a predator in IJsselmeer would not increase its chance of finding an area with higher food density by migrating over large distances within a homogeneous habitat.

INTRODUCTION

Small fish (< ca. 10 cm *TL*) are the forage base of piscivorous fish and piscivorous birds in IJsselmeer, a large (180,000 ha) eutrophic lake in the Netherlands. The most important prey fish species, smelt *Osmerus eperlanus* (Buijse *et al.* 1983), is exploited by the commercial fishery also. To assess the carrying capacity of IJsselmeer for piscivores and for the commercial fishery, the interaction between prey fish and its predators must be quantified. Besides prey fish density, spatial distribution of prey fish determines food availability for predators (McClatchie, Hutchinson & Nordin 1989; Wanink 1996; Goyke & Brandt 1993; Persson & Eklöv 1995). Therefore, we attempted to describe the spatial distribution pattern and the seasonal variation therein for the three major prey fish species in IJsselmeer: smelt *Osmerus eperlanus*, ruffe *Gymnocephalus cernua* and juvenile perch *Perca fluviatilis* (Buijse *et al.* 1993).

The distribution pattern of fish can be explained from environmental variables (e.g. depth, salinity, substrate; cf. Craig & Babaluk 1993; Jager, Kleef & Tydeman 1993) or habitat type (Bauch 1961). At first sight, the open water of IJsselmeer is a homogeneous habitat. Physical structures are lacking, and there are no large horizontal or vertical gradients in oxygen concentration and temperature. However, there is variation in depth and water transparency. In the northern basin the average depth is 4.5 and maximum depth is 10 m. The bottom type varies with depth: deeper areas are muddy, and shallower areas sandy. Water transparency varies between 0.15 m and ca. 3 m Secchi depth. Because of the variation in depth and water transparency, within-season variation in light intensity at the bottom during daytime amounts to a factor 1000 (Buijse, Schaap & Bult 1992). Buijse, Schaap & Bult (1992) demonstrate that this affects catch-per-haul by trawling (*CpUE*), probably because fish concentrate in darker areas (Chapter 5). However, the separate effects of depth and water transparency on fish density as indexed by *CpUE* have never been quantified.

Aggregations within a habitat further contribute to variation in local prey fish density. The spatial scale of these aggregations determines foraging behavior of predators (Brandt & Kirsch 1993; Schneider 1989; Schneider 1994). If prey fish are highly aggregated, the density averaged over the habitat is a poor indicator of food availability for predators, because then the predators' food availability is more related to the chance of finding an aggregation and to prey handling time (Brandt & Kirsch 1993). The scale of aggregations within a habitat can be described by arbitrary subdividing the habitat in sub-areas, and by assessing differences in density between sub-areas (cf. Fargo & Tyler 1992). A more direct method is to assess spatial autocorrelation in the variance that remains after environmental variables are accounted for. Spatial autocorrelation can be assessed with the variogram (Fig. 7.1), a tool from geostatistics that describes the relationship between variability and distance between sampling locations. Geostatistics is increasingly used to describe spatial distribution in both freshwater and marine aquatic populations (Armstrong *et al.* 1992; Guillard, Gerdeaux & Chautru 1993; Pelletier & Parma 1994; Simard , Marcotte & Bourgault 1993). The variogram can be used to estimate the size of the area wherein species are aggregated (see Gonzalez-Gurriaran, Freire & Fernandez 1993 for an example with brachyurans off northwest Spain).

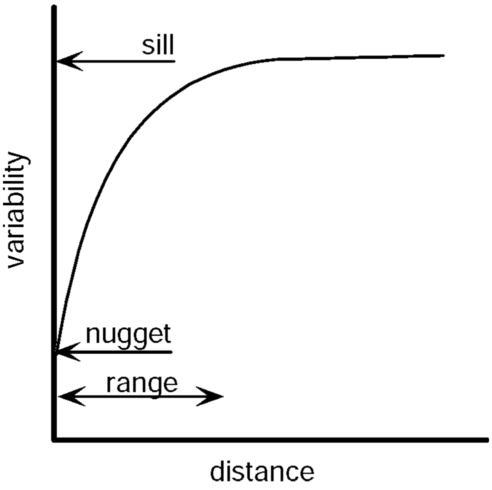

Figure 7.1. The variogram. The variability at distance zero, the nugget, is a measure for sampling error. The range is the distance over which spatial autocorrelation is manifest, and it is a measure for the average size of aggregations. At distances higher than the range, variability is maximal (sill).

In this study, analysis of covariance (ANCOVA) is used to estimate the effects of depth and water transparency on density of small fish, and spatial autocorrelation is assessed by the variogram of the residuals of the ANCOVA model. We compare the amount of spatial variation in small fish density to other systems, and we discuss implications for the foraging behavior of piscivores and the design of fish surveys.

MATERIAL AND METHODS

Study area

IJsselmeer (Fig. 7.2) is a former tidal area that was separated from the Dutch Waddensea by a dyke in 1932. In 1976, the lake was divided by a dyke into two basins: a northern basin of 110,000 ha and a southern basin of 70,000 ha. The mean depth of the northern basin is 4.5 m, with depressions up to 10 m at former tidal channels. The southern basin has a mean depth of 3.5 m, and varies much less in depth. In the period 1985-1994, Secchi depth as measured during fish stock surveys of the R.V. 'Stern' varied between 0.15 m and 3.0 m in the northern basin, and between 0.15 m and 1.3 m in the southern basin. A large part of the variation in Secchi depth is caused by spatial effects, mediated by wind force and wind direction (Fig. 7.3; Lammens 1999). The lake supports commercial fisheries on eel *Anguilla anguilla*, perch *Perca fluviatilis*, pikeperch

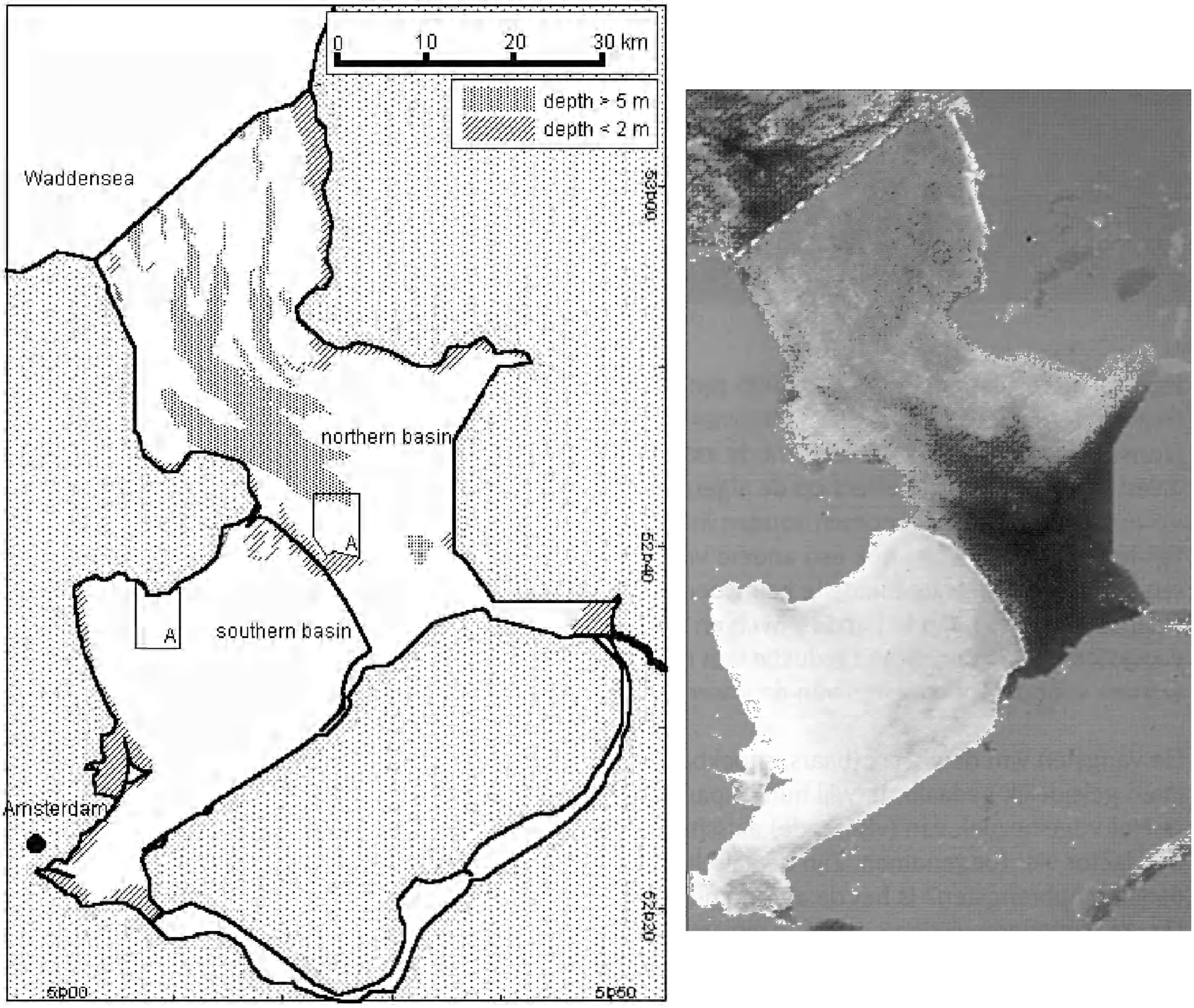

***Figure 7.2**. Left: Maps of IJsselmeer, indicating depth contours and sampling areas of the small scale survey (areas labeled with 'A', see Materials and methods section). Right: satellite image of IJsselmeer (adapted from Lammens & Hosper 1998), where darker areas have a higher water transparency.*

Stizostedion lucioperca and smelt *Osmerus eperlanus*. Other abundant fish species are ruffe *Gymnocephalus cernua*, roach *Rutilus rutilus*, and bream *Abramis brama*. Piscivirous birds (mainly cormorant *Phalacrocorax carbo*, black-headed gull *Larus ridibundus*, grebe *Podiceps cristatus* and goosander *Mergus merganser*) and piscivorous fish (mainly perch, pikeperch and eel) consume ca. 130 kg fish·ha^{-1}·yr^{-1}, of which 70% is smelt, 16% is ruffe and 8% is perch < 15 cm *TL* (Buijse *et al.* 1993).

Survey design and sampling practice

The fish population was sampled with a bottom beam trawl, operated from RV 'Stern' (200 HP). The beam trawl had a mouth width of 3 m and a height of 0.6 m. The cod-end of the net had a mesh size of 2 mm (stretched mesh). The net is non-selective to fish smaller than ca. 10 cm *TL* (Chapter 4). Haul duration was 10 min., and towing speed was 1.5 ± 0.1 m.s^{-1}. The distance over which the trawl was towed was measured with a Doppler log. Speed and towed distance were kept constant by adjusting the throttle. The position of the hauls was recorded with positioning instruments (DECCA and GPS). Per haul, bottom depth and Secchi depth were measured to the nearest 0.1 m. Areas with depth < 2 m could not be sampled by RV 'Stern'.

Small-scale surveys were conducted to study spatial distribution with a high spatial resolution, and large-scale surveys were conducted to study spatial distribution on a lakewide scale. The small-scale survey was conducted in two areas of ca 35 km^2 each (Fig. 7.2). Within each area, 5-7 sampling sites were selected and at each site three hauls were made. The large-scale survey covered the total lake area. Here, a random stratified sampling strategy was followed, where sampling effort was allocated to each stratum according to its surface area. Strata were defined on the basis of depth (more and less than 5 m) and geographic area. Randomization was realized by randomly selecting (without replacement) from a list of geographical positions. To ensure sufficient coverage, only positions at full minutes (latitude and longitude) were included in the list. Details of each survey are summarized in Table 7.1.

Length-frequency distributions (*LFD*) were established for each species in the catch. Total length of smelt and ruffe was measured to the nearest mm, and all other fish species were measured to the nearest cm below. To separate the young-of-the-year (0-group) from the older age classes (≥1-group), the *LFD*s were averaged per survey, per sampling period and per basin, and the average *LFD*s were subjected to Bhattacharya analysis (Sparre & Venema 1992) using the software package FiSAT (Gayanilo, Sparre & Pauly 1995). For ruffe that were sampled during winter, separation into age groups was possible only by assuming that the left part of the *LFD* consisted exclusively of 0-group, because there were usually no separate modi in the *LFD*. Using

Table 7.1. *Sampling details of the small-scale and large-scale surveys. n = number of hauls; h = distance between all possible pairs of sampling positions (km); d = depth (m); s = Secchi depth (m).*

survey/ basin	sampling period	sampling area (km^2)	n	distance between sampling sites (km)			depth (m)			Secchi depth (m)		
				mean	min.	max.	mean	min.	max.	mean	min.	max.
small-scale survey												
north	1-2 Jul 92	35	18	4.4	0.1	8.8	4.6	3.8	5.8	1.2	0.9	1.5
"	17, 20 Aug 92	"	18	5.0	0.1	10.4	4.2	2.7	5.9	0.7	0.6	1.0
"	16-17 Nov 92	"	20	4.7	0.4	9.4	4.5	2.9	5.8	0.6	0.5	0.7
south	28-29 Apr 93	35	15	4.3	0.5	9.7	3.8	3.6	4.0	0.2	0.2	0.3
large-scale survey												
north	29 Aug-8 Sep 94	1100	45	19.4	0.1	50.4	4.5	2.7	5.8	0.6	0.5	1.7
"	21 Nov-15 Dec 94	"	57	19.7	0.1	50.3	4.9	2.7	7.5	1.4	0.7	3.0
south	5-7 Sep 94	700	29	14.1	1.4	34.6	3.9	2.6	4.5	0.6	0.4	0.8
"	12-14 Dec 94	"	27	13.5	1.5	31.3	3.7	3.0	4.3	0.3	0.3	0.6

the fractional distribution of age classes over each length class that resulted from the Bhattacharya analysis, we calculated the number of 0-group and ≥1-group fish in each survey trawl haul (*CpUE*, in number·haul^{-1}).

Estimating the effect of depth and water transparency on local fish density

For each survey and each basin, the effect of depth and water transparency on local density of fish was estimated by analysis of covariance (ANCOVA), using depth and Secchi depth as independent variables, and ln-transformed *CpUE* (*LNCpUE*) as dependent variable. Thus, the ANCOVA model reads:

$$LNCpUE = \text{Constant} + DEPTH + SECCHI + DEPTH{\cdot}SECCHI \quad \text{[formula 7.1]}$$

where *DEPTH* is the effect of depth, *SECCHI* is the effect of water transparency, and *DEPTH·SECCHI* is the effect of the interaction of the two former covariates. If the interaction term reduced variance significantly ($P < 0.05$), the full model was fitted. Non-significant terms were excluded from the model, and the model was refitted with the remaining significant terms. The goodness of fit of the model was checked by residual analysis (cf. Neter, Wasserman & Kutner 1985, p. 109). Residual analysis comprised a test of normality of the residuals (Wilk-Shapiro statistic) and plotting of residuals against each of the independent variables and against the estimated value. Before the ANCOVA model was fitted, dependencies between and variation in the independent variables *DEPTH* and *SECCHI* were assessed. If variation in one of the independent variables was low, the variable was excluded from the ANCOVA model. If there was a strong dependency between the independent variables, only *DEPTH* was included in the ANCOVA model.

***Table 7.2**. Mean number of fish caught per haul (CpUE), mean total length (TL, cm) and standard deviation in total length (s_{TL}) during each survey. The species group 'other' consisted mainly of roach, bream, pikeperch, ≥1-group smelt and ≥1-group perch.*

survey/	0-group smelt			0-group perch			0-group ruffe			≥1-group ruffe			other
basin, period	CpUE	TL	s_{TL}	CpUE	TL	s_{TL}	CpUE	TL	s_{TL}	CpUE	TL	s_{TL}	CpUE
small-scale survey													
north, Jul 92	65	4.3	0.52	2486	4.3	0.64	342	4.0	0.65	166	9.6	0.89	59
north, Aug 92	159	5.4	0.43	4717	5.8	0.52	238	6.8	0.69	52	10.6	0.92	61
north, Nov 92	161	6.9	0.72	2891	6.6	0.48	1051	8.1	0.91	37	12.1	0.72	66
south, Apr 93	460	6.6	0.41	354	6.5	0.62	3658	7.0	0.78	59	11.4	0.74	87
large-scale survey													
north, Sep 94	640	6.0	0.54	18	8.0	0.86	270	7.0	0.94	55	10.5	0.83	119
north, Dec 94	3011	6.7	0.57	17	8.4	0.94	605	8.0	1.05	53	11.2	0.82	98
south, Sep 94	226	6.2	0.48	24	8.4	0.75	334	6.5	0.73	59	10.0	0.90	140
south, Dec 94	657	7.2	0.58	40	8.8	0.79	971	7.2	0.77	165	10.4	0.94	111

Spatial autocorrelation

Spatial autocorrelation was assessed by variograms. Variograms were calculated of the residuals of the ANCOVA models described above, or, if a depth or water transparency effect could not be demonstrated, of *LNCpUE*. Variograms were calculated according to:

$$\gamma(h)=\frac{1}{2N(h)}\sum_{i=1}^{N(h)}[R(x_i+h)-R(x_i)]^2 \quad \text{[formula 7.2]}$$

where γ is a measure of between-haul variability, x_i are the positions of the hauls, $R(x_i)$ is the residual value at location x_i, h is the distance (km) between 2 locations, and $N(h)$ is the number of pairs of positions $(x_i;\ x_i+h)$ (Armstrong *et al.* 1992). For the small-scale surveys, we assumed that h was 0 for the three hauls made at each sampling location. $\gamma(h)$ was averaged over distance classes of 1 km (small-scale surveys) and 4 km (large-scale surveys).

Spatial autocorrelation is expressed by a significant dependency between h and $\gamma(h)$. Dependency was assessed by visual interpretation of the variograms, and calculation of Pearson correlation coefficients. As the number of pairs over which $\gamma(h)$ was calculated differed between distance classes, the Pearson correlation coefficients were weighted according to the number of pairs present in the distance class. All calculations and statistical processing were done with SAS® Software (SAS® Institute Inc. 1989).

RESULTS

Both in the small-scale and the large-scale surveys, more than 90% of the numerical catch consisted of 0-group smelt, 0-group perch, 0-group ruffe, and ≥1-group ruffe (Table 7.2).

Small-scale survey

At the sites in the sampling area in the northern basin, water transparency during summer was lower at the deeper sites (Pearson correlation coefficients -0.97 and -0.62, $P < 0.01$), whereas during winter variation in water transparency was low (Table 7.2). Therefore only *DEPTH* was included as independent variable in the ANCOVA models for the small-scale survey. The density of fish was higher in the deeper parts of the sampling area, except for 0-group perch in July (Table 7.3). Especially ruffe showed a strong preference for the deeper parts of the sampling area in the northern basin: on average, an increase in water depth with 1 m resulted in a 7.5-fold increase in ruffe density. From summer to winter, perch seemed to concentrate gradually more in the deepter parts. In July, they still preferred the shallower parts. In August, they showed a weak preference for the deeper parts, which became strong in November (see the gradual increase in the parameter estimate for *DEPTH*, Table 7.3).

The ANCOVA models fitted the observations reasonably well, as was concluded from the residual analysis. The distribution of the residuals was different from normal in only 4 out of 12 situations (cf. Table 7.3). Inspection of residual plots showed that in these situations, the relationship between *LNCpUE* and *DEPTH* was not linear. Still, also non-parametric tests for correlation showed that the *CpUE* was positively correlated with depth (Spearman correlation coefficients > 0.6, $P < 0.01$). The models also represented zero catches reasonably well, even though zero catches were not included in the analysis. For example, the mean predicted *LNCpUE* for zero catches was 0.1 for ≥1-group ruffe caught during November, whereas the mean predicted *LNCpUE* for non-zero catches was 3.6. Also in other situations, the predicted *LNCpUE* for sites with zero catches was lower than the mean predicted *LNCpUE* of sites with non-zero catches. In the sampling area in the southern basin, both depth and water transparency scarcely varied: the range in depth was and 0.4 m, and the range in Secchi depth was 0.1 m. Therefore, there was no need to correct for the effects of depth or water transparency before variograms were constructed.

Table 7.3. *Small-scale survey, ANCOVA and variogram statistics. n_0 = number of zero catches; s^2 = variance of LNCpUE, F = F statistic, MSE = mean squares of error, b_{DEPTH} = paramater estimate for the DEPTH effect, W = Wilk-Shapiro statistic. Non-nugget = the average of $\gamma(h)$ values where $h \neq 0$. The number of pairs by which the nugget was calculated ranged between 8 and 19. Significance is indicated by asterisks: * $0.01 < P <= 0.05$; ** $P <= 0.01$.*

period/	LNCpUE		ANCOVA model				variogram		
species	n_0	s^2	F	MSE	b_{DEPTH}	W	nugget, $\gamma(h = 0)$	non-nugget, $\gamma(h \neq 0)$	Pearson
northern basin, Jul 92 (n = 18)									
0-gr. smelt	0	0.901	4.66*	0.742	0.47	0.86*	0.48	0.760	0.35
0-gr. perch	0	0.399	10.5**	0.256	-0.41	0.97	0.15	0.209	-0.09
0-gr. ruffe	0	3.69	64.2*	0.781	1.8	0.88*	0.41	0.826	0.29
1-gr. ruffe	3	4.80	22.5**	1.89	2.0	0.94	0.79	1.77	0.22
northern basin, Aug 92 (n = 18)									
0-gr. smelt	0	5.11	33.4**	1.76	1.7	0.81**	0.93	1.68	0.40
0-gr. perch	0	0.727	4.50*	0.596	0.37	0.93	0.22	0.573	-0.02
0-gr. ruffe	0	2.72	43.8**	0.773	1.3	0.92	0.13	0.777	0.06
1-gr. ruffe	2	4.25	37.0**	1.25	1.6	0.84**	0.87	1.18	-0.17
northern basin, Nov 92 (n = 20)									
0-gr. smelt	0	1.99	16.7**	1.09	1.0	0.94	0.29	1.06	0.19
0-gr. perch	0	3.15	101**	0.501	1.7	0.92	0.16	0.471	-0.10
0-gr. ruffe	4	11.0	43.4**	2.87	3.1	0.91	1.67	3.01	0.56
1-gr. ruffe	10	3.56	9.61**	1.29	2.3	0.95	0.90	1.11	-0.16
southern basin, Apr 93 (n = 15)									
0-gr. smelt	0	0.562	-		-	-	0.12	0.902	0.86**
0-gr. perch	0	1.96	-		-	-	0.21	2.70	0.88**
0-gr. ruffe	0	0.199	-		-	-	0.10	0.223	0.10
1-gr. ruffe	2	0.676	-		-	-	0.56	0.594	0.20

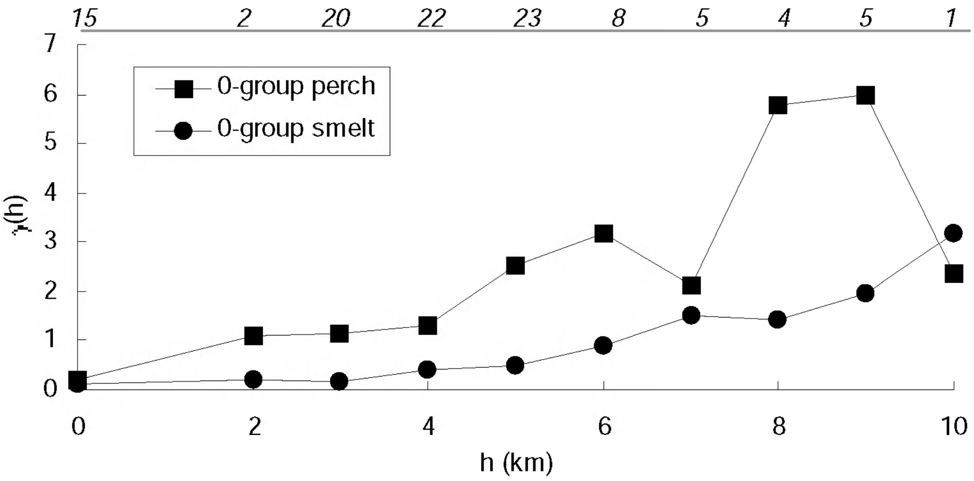

***Figure 7.3**. Small-scale survey. Variograms of 0-group smelt and 0-group perch from the sampling area in the southern basin. Numbers in italics depict the number of pairs that were used to calculate $\gamma(h)$.*

Only in the variograms of 0-group smelt and perch from the southern basin, spatial autocorrelation was demonstrated (Table 7.3). Spatial autocorrelation seemed stronger for perch than for smelt, as was inferred from the steeper slope in the variogram of perch (Fig. 7.3). At higher distances (> 6 km) the variogram of perch became erratic. Both the variograms of 0-group smelt and of 0-group perch did not stabilize around a maximum value at distances up to 10 km. For smelt, the low slope in combination with a low s^2 (cf. Table 7.3) indicated that spatial variation in density was still low.

The variance at a site was always smaller than between sites, as can be inferred from the consistently smaller variability for the nugget than for larger distances (non-nugget) (Table 7.3). This was probably due to the sampling strategy, whereby temporal variation was minimized as the three hauls at each sampling site were completed within ca. 1 hour.

Large-scale survey

During the large-scale survey, the effects of depth and water transparency were not correlated (Pearson correlation coefficient = -0.13 for the first, and -0.14 for the second sampling period; $P > 0.05$). Therefore, depth, water transparency and their interaction were included in the ANCOVA models. In the southern basin, the variation in depth and water transparency was low in both study periods (cf. Table 7.1), so for the construction of the variograms no correction had to be made for habitat heterogeneity.

During summer, less than 15% of the moderate variation in 0-group smelt and 0-group perch density in the northern basin was explained by depth and water transparency. The 0-group smelt preferred the more turbid areas, and 0-group perch the shallower areas (Table 7.4). During winter, 0-group smelt still preferred the more turbid areas, but they also showed a weak preference for deeper areas. Both in summer and in winter, the estimated maximal difference in smelt density due to variation in water transparency was a factor of ca. 200, where in summer this difference was due to a maximal difference in water transparency of 1.2 m Secchi depth, and in winter due to a maximal difference of 2.4 m Secchi depth. The distribution pattern of 0-group perch had completely changed from summer to winter, as 0-group perch had moved from the shallower to the deeper areas, the same as found during the small-scale survey. Both in summer and in winter, the much higher variation in density of ruffe was for a large part (28-57%) explained by depth and water transparency. Both 0-group and ≥1-group ruffe preferred deeper and more turbid areas. During summer, the preference of 0-group ruffe for deeper water was stronger if the water was clearer (Fig. 7.4), as can be inferred from the significant interaction term (Table 7.4).

The ANCOVA models fitted the observations reasonably well. The distributions of the residuals were near normality (Wilk-Shapiro statistics were >= 0.94), and only in two situations a significant ($P < 0.05$) but slight deviance form normality was detected. The residual plots showed no excessive heteroscedasticity or deviances from linearity of effects. During winter, > 15% of all observations consisted of zero catches for 0-group perch and ruffe. Though zero catches could not be included in the ANCOVA models, the models represented the zero catches reasonably well: the mean of predicted *CpUE* for sites with zero catches was generally low, namely 4.5, 2 and 0.73 for 0-group perch, 0-group ruffe and ≥1-group ruffe respectively.

***Table 7.4**. Large-scale survey. ANCOVA statistics. b_{DEPTH}, b_{SECCHI} and $b_{D\cdot S}$ = parameter estimates for the DEPTH, SECCHI and DEPTH·SECCHI effect. NS indicates a non-significant term ($P > 0.05$). Other abbreviations are explained in the caption of Table 7.3.*

period/	LNCpUE		ANCOVA model						variogram
species	n_0	s^2	F	MSE	b_{DEPTH}	b_{SECCHI}	$b_{D\cdot S}$	W	Pearson
northern basin Sep 94 (n = 45)									
0-gr. smelt	1	2.11	6.31*	1.87	NS	-4.43	NS	0.96	0.57*
0-gr. perch	3	1.79	4.49*	1.65	-0.49	NS	NS	0.94*	0.16
0-gr. ruffe	0	3.10	13.6**	1.67	-3.30	-35.9	6.93	0.95	-0.63*
1-gr. ruffe	2	3.95	9.28**	2.83	0.752	-6.79	NS	0.96	0.51
southern basin Sep 94 (n = 29)									
0-gr. smelt	1	0.962	-	-	-	-	-	-	0.81**
0-gr. perch	0	1.64	-	-	-	-	-	-	0.59
0-gr. ruffe	0	1.28	-	-	-	-	-	-	0.81**
1-gr. ruffe	3	2.77	-	-	-	-	-	-	0.64
northern basin Dec 94 (n = 57)									
0-gr. smelt	0	3.38	29.0**	1.69	0.57	-2.1	NS	0.94*	0.88**
0-gr. perch	9	1.89	9.40**	1.60	0.64	NS	NS	0.96	0.35
0-gr. ruffe	14	6.87	29.6**	2.91	2.12	-1.97	NS	0.96	0.46
1-gr. ruffe	23	5.31	14.2**	2.96	1.67	-2.13	NS	0.98	0.20
southern basin Dec 94 (n = 27)									
0-gr. smelt	0	0.502	-	-	-	-	-	-	-0.06
0-gr. perch	0	1.51	-	-	-	-	-	-	0.67*
0-gr. ruffe	0	1.42	-	-	-	-	-	-	0.45
1-gr. ruffe	0	2.03	-	-	-	-	-	-	0.38

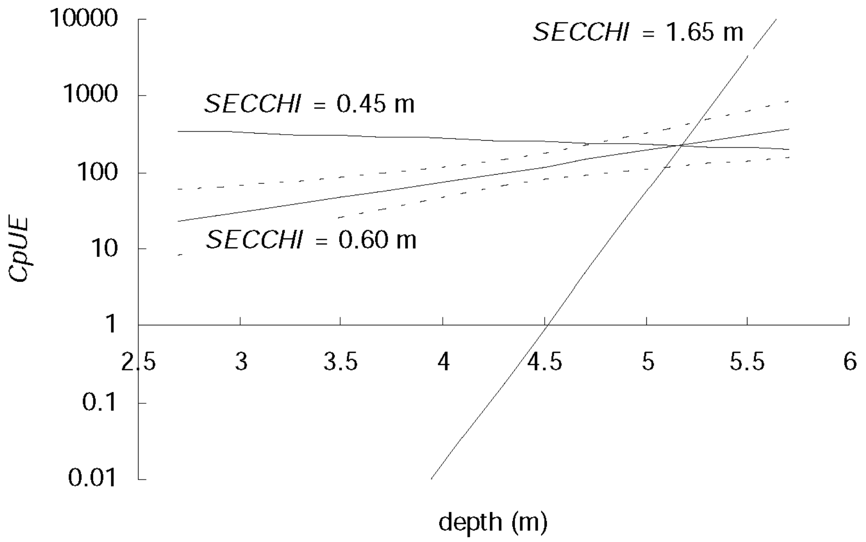

***Figure 7.4**. Large-scale survey, northern basin. Distribution of 0-group ruffe at varying depth and water transparency (SECCHI), as estimated by the ANCOVA model of CpUE. The dashed lines represents the 95% confidence interval of the mean for the relationship at SECCHI = 0.60 m.*

In only 4 out of 12 situations during the large-scale surveys, a significant spatial autocorrelation was found (Table 7.4). Both in summer and winter, variability in density of 0-group smelt in the northern basin became high at distances > ca. 30 km, where much less site pairs contributed to $\gamma(h)$ (Fig. 7.5). This was also found for 0-group smelt in the southern basin during summer, where variability increased at distance > 24 km. Curiously enough, variability in 0-group ruffe density *decreased* with increasing distance in the northern basin during summer, but the low slope of the variogram (Fig. 7.5) indicates that this effect was only weak. In the southern basin, variation in density between sampling sites was generally lower than in the northern basin, even after the effects of depth and water transparency accounted for (see the difference between *MSE* values from the northern basin with s^2 values from the southern basin, Table 7.4). In the southern basin, the slope of the variogram for 0-group ruffe during winter was low, indicating a weak but significant spatial autocorrelation (Fig. 7.6, Table 7.4). Spatial autocorrelation was also demonstrated for 0-group perch in the southern basin during winter. However, the slope in the variogram was low in the first 28 km, and only at the highest distance class (28 km) variability was considerably higher (Fig. 7.5).

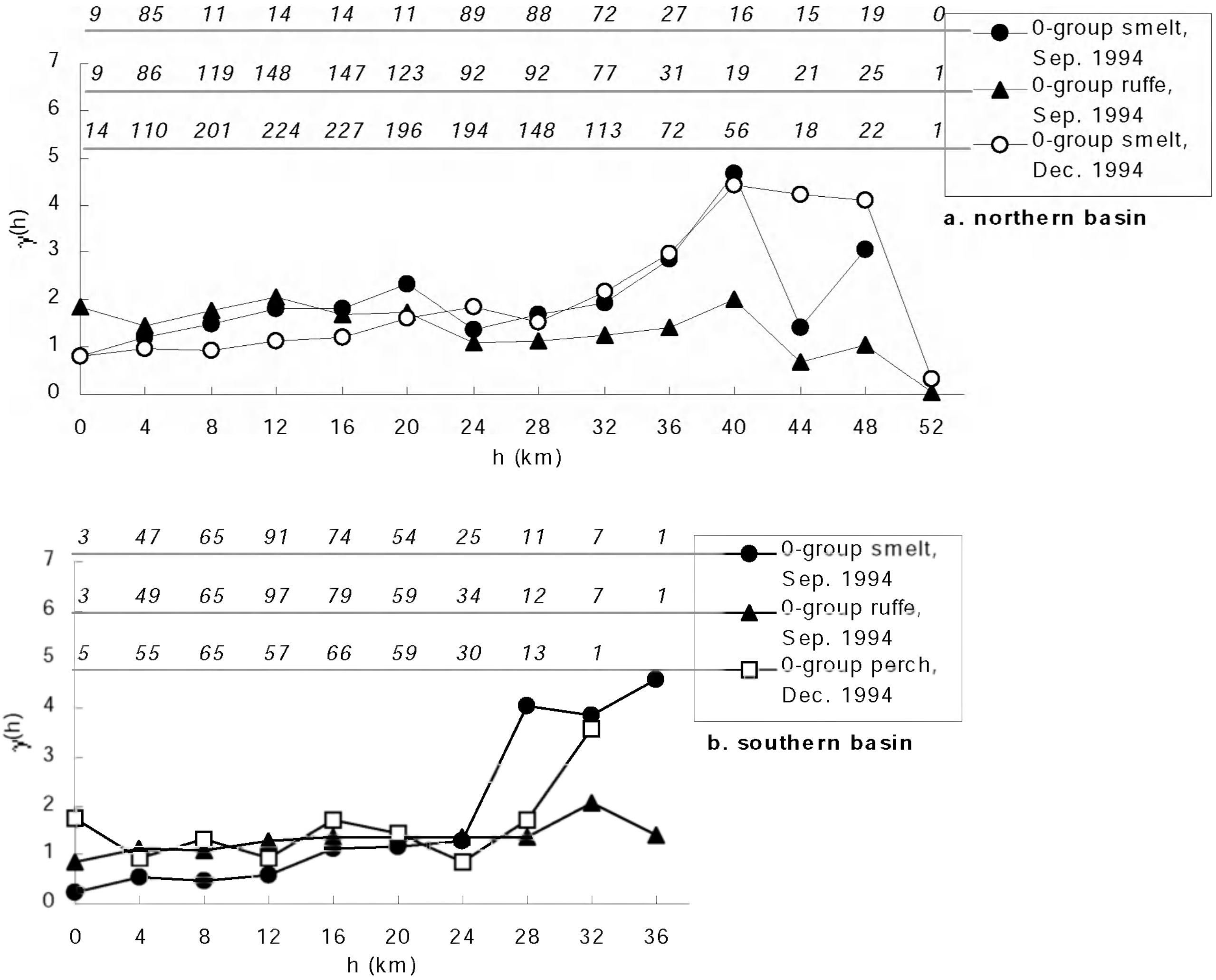

***Figure 7.5**. Variograms with significant Pearson correlation coefficients (cf. Table 7.4) from the large-scale surveys in the northern basin (a), and southern basin (b).*

DISCUSSION

In IJsselmeer, spatial distribution of 0-group smelt, 0-group perch and ruffe was determined by a combination of only two variables: depth and water transparency. With few exceptions, spatial autocorrelation was lacking after effects of depth and water transparency were accounted for.

The effect of depth and water transparency on the density of fish varied between seasons and between species. During winter, all species concentrated in the deeper areas, and this effect was strongest for ruffe. During summer, ≥1-group ruffe concentrated in deeper areas as well, but 0-group ruffe preferred deeper areas only if water transparency was high (Secchi depth > 0.5 m). Probably, when water transparency was high, the high light intensity at the bottom in shallow areas induced 0-group ruffe to migrate to deeper, darker, areas. Ruffe is likely to avoid high light intensity, as its eyes have a *tapetum lucidum* (Ahlbert 1969), an adaptation to low light intensity.

The marked seasonal change in spatial distribution of 0-group perch, with higher density in shallow areas during summer, and in deep areas during winter, is consistent with other studies on perch distribution (Goldspink 1990; Imbrock, Appenzeller & Eckmann 1996). Density of 0-group perch was not affected by water transparency. The 0-group smelt were found to prefer more turbid areas during summer in the large-scale survey. Also in the small-scale survey, more 0-group smelt were caught in more turbid areas during summer. The preference of smelt for turbid areas is also demonstrated by Beekman & Platteeuw (1994).

Since the trawl that we used sampled the bottom layer of the water column only, density per unit area can be derived from catch-per-haul observations only if the vertical distribution pattern is known. Water transparency does not affect the vertical distribution pattern of 0-group perch (Chapter 6), and neither of the bottom-dwelling ruffe (Craig 1977). Hence catch-per-haul of 0-group perch and ruffe was an unbiased index of density. In contrast, 0-group smelt stay near the surface during daytime if water transparency is low (Secchi depth < ca. 0.85 m) (Chapter 8) during summer. Therefore, catch-per-haul was a biased index of 0-group smelt density. Probably, this bias resulted in an underestimation of the effect of water transparency on the density of smelt, because in turbid water the bottom trawl caught more smelt than in clear water, even though it missed the surface-dwelling smelt. Still, the effect of water transparency on the density of smelt was strong: both in summer and in winter, smelt were about 200 times as abundant at the most turbid site than at the clearest site.

Predation risk minimization, foraging opportunities and reproduction are key factors that affect the spatial distribution of fish (Clark & Levy 1988; Levy 1990). Since sampling took place outside the spawning season and since all fish, except ≥1-group ruffe, were immature, reproduction activity could not have affected the spatial distribution in our situation. Predation efficiency of both zooplanktivorous prey fish and piscivorous fish increases with water transparency (Barrett, Grossman & Rosenfield 1992; Benfield & Minello 1996; Gradall & Swenson 1982; Gregory & Northcote 1993). Ruffe is well adapted to inhabit turbid waters (Craig 1987), so probably foraging efficiency of ruffe is less affected by water transparency, but 0-group smelt and 0-group perch have to make a trade-off between foraging efficiency and predation risk minimization. As 0-group smelt preferred turbid areas, and 0-group perch not, smelt and perch must have differed in their strategy to optimize the trade-off. Direct observations by SCUBA diving in deep lakes (up to 40 m depth) in The Netherlands revealed that small perch are actively foraging in schools measuring up to several meters in diameter during daytime. Apparently, small perch adapted to the higher predation risk by schooling behavior (Pitcher & Parrish 1993). In deep, clear lakes smelt are found at depths over 20 m in near total darkness, not showing foraging nor schooling behavior. In contrast to perch, smelt seem to avoid areas where predation risk is high, thereby decreasing their foraging efficiency. Probably smelt adapt to the lower foraging efficiency by staying passive and thus saving energy resources.

Since our sampling instrument yielded fish density estimates that were integrated over an area with a length of ca. 1000 m (the length of the trawl lane) and a width of 3 m (the width of the trawl beam), these dimensions defined the highest attainable spatial resolution. With hydroacoustic sampling, it is possible to study spatial distribution on a finer resolution. In Chapter 6, excerpts of echograms made at IJsselmeer are presented that cover a distance of ca. 100 m. The excerpts are representative for the total echogram, which covered a distance of ca. 600 m. A rough and conservative estimate of the highest spatial resolution, derived from the appearance of the echograms, is 10 m. Within the distance covered by each echogram, spatial autocorrelation seemed absent. Therefore, in IJsselmeer spatial autocorrelation seemed to be weak at a scale up to 50 km, and down to 10 m. Though IJsselmeer is large, and despite the pelagic character of one of the main fish species in IJsselmeer, smelt, fish schools of a dimension as found in herring *Clupea harengus*, mackerel *Scomber scombrus* or rockfish *Sebastes* sp (100-5,000 m^2 surface area; Misund 1993, Kieser *et al.* 1993) were not found in IJsselmeer. Aggregation of fish schools as in North Sea herring *Clupea harengus* that aggregate within a distance of 12 km (Maravelias *et al.* 1996), or as in juvenile capelin *Mallotus villosus* that aggregate within a distance of about 500 m (Simard, Marcotte & Bourgault 1993), was not found in IJsselmeer either. Also compared to other lakes, fish density in IJsselmeer showed little spatial variation: in Lake Sainte-Croix (France), bleak *Alburnus alburnus* aggregated on a scale of 240-280 m (Guillard *et al.* 1992).

From our study, we derived two implications for the feeding behavior of piscivorous fish and piscivorous birds in IJsselmeer. First, since the spatial distribution of prey fish is predictable to some extent, a predator has the possibility to select foraging areas with relatively high prey density according to depth (or geographical position, which is related to depth) and water transparency. Second, within a suitable foraging area, the predator would encounter random variation in forage fish density, without major aggregations. Hence, in IJsselmeer, average prey fish density was probably a good indicator of food availability for predators (cf. Brandt & Kirsch 1993).

Assuming that, within a short sampling period, most variance in *CpUE* observations is caused by spatial variation in density, the variance in log-transformed catch-per-unit-sampling-effort observations can be used to compare spatial variation (including spatial autocorrelation) between species or systems. In this study, the square roots of the *MSE* and s^2 varied between 0.44 and 1.72; the average was 1.15. Considering that the error structure of *LNCpUE* was close to normal, 68.3% of the backtransformed observations were within $e^{\pm 1.15} \cdot e^{\mu}$, where μ is the predicted value of *LNCpUE* (Sokal & Rohlf 1995). Since this estimate of variation includes sampling error, the factor $e^{1.15} = 3.2$ can be considered as a maximum estimate for the spatial variation in density of each species in an area of 3000 m^2 (the area swept by a single haul).

We found only few studies that report variance or residual variance in log-transformed catch-per-unit-sampling-effort observations. In monthly trawl surveys for Dungeness crab *Cancer magister* that were conducted in the estuarine areas of the southern Washington coast, the mean s^2 in log-transformed *CpUE* is 1.23 (minimum 0.31, maximum 3.65), corresponding to a factor 3.0 (McConnaughey & Conquest 1992). The high similarity to the residual variance found in this study was probably caused by the similarity in habitat, as IJsselmeer is an estuarine area as well. The Dungeness crab survey was also conducted in coastal areas, where the estimates for s^2 are considerably higher, with mean s^2 of 8.70 (minimum 2.56, maximum 47.47). The higher s^2 may reflect higher habitat heterogeneity in the coastal area, or a more patchy distribution pattern. The average *MSE* over 4 fish species in ln-transformed *CpUE* observations in Tjeukemeer, a Dutch eutrophic lake with little spatial structure, was 0.90 (minimum 0.52, maximum 1.50) (Van Densen, unpubl. data). This corresponds to a factor 2.6, which is again close to our estimate of spatial variance. Variance in the main zooplankton taxa from 5L samples from two Dutch lakes averaged 0.29 (de Nie, Bromley & Vijverberg 1980) and 0.42 (Verreth 1990), corresponding to a factor 1.7 and 1.9 respectively. These two fully independent estimates are very similar, even though the first variance represents a 'true' variance of repeated samples in a homogeneous lake, and the second variance represents the residual variance after subtracting the observed effect of wind on the distribution of zooplankton. Probably, the factor 1.7-1.9 can be considered as characteristic for 5L samples of zooplankton communities from Dutch lakes. The factor 3.2 that was found during this study can be considered as characteristic for variation in density of fish communities in estuarine or eutrophic lacustrine areas that are sampled by trawl. This factor can be used to estimate the amount of sampling effort needed to obtain a pre-specified level of precision (cf. Cochran 1977).

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Chapter 8

Spatial association of piscivorous birds, black-headed gull *Larus ridibundus* and black tern *Chlidonias niger* with their prey, smelt *Osmerus eperlanus*, in a large, shallow lake in The Netherlands

P.J. Mous, W.L.T van Densen & M.R. van Eerden

ABSTRACT

The strength and the scale of the spatial association between smelt and two of its avian predators, black-headed gull *Larus ridibundus* and black tern *Chlidonias niger*, was assessed. Spatial distribution of smelt was studied by surface trawling, and that of birds by an aerial survey. Birds were also counted from the research vessel during the trawl hauls, allowing for a closer spatial and temporal match between estimates of bird and smelt abundance. The study was conducted in two areas in IJsselmeer, a shallow eutrophic lake in The Netherlands, during August. The spatial scale at which our observations were made ranged within sampling areas between 1 and 20 km, up to ca. 30 km between sampling areas. In one of the two areas, spatial association was present for both bird species at a scale of 5-20 km. A small increase in water transparency, from ca. 0.5 to 0.7 m Secchi depth, resulted in a substantial decrease in the abundance of surface-dwelling smelt, which was associated with a decrease in bird abundance. The spatial distribution of gulls was less extreme than of their prey, smelt: a 10-fold increase in smelt abundance was associated with a 1.5-fold increase in gull abundance. At a spatial scale of less than 5 km, only random variation in abundance of gulls and smelt was observed, and this implied that for smelt random spatial variation was indistinguishable from sampling error. The bird counts that were made during the trawl hauls suggested that, in simultaneous observations on bird and smelt abundance, the strength of the spatial association between birds and their prey was equal to the strength of the association observed at a scale of 5-20 km. In the other sampling area, situated ca. 30 km from the first area, bird abundance was low despite the high abundance of smelt within a section of this area. Probably, at a scale of ca. 30 km, the spatial distribution of black-headed gulls was also governed by the availability of alternative food resources, whereas the low abundance of black terns could have been caused by the higher distance from their roosting site.

INTRODUCTION

The higher trophic levels of the IJsselmeer ecosystem, a 180,000 ha, eutrophic lake in The Netherlands, consist of piscivorous fish, piscivorous birds, and the commercial fishery, which targets piscivorous fish (perch *Perca fluviatilis*, pikeperch *Stizostedion lucioperca*, and eel *Anguilla anguilla*), but also the zooplanktivorous smelt *Osmerus eperlanus* (Buijse *et al.* 1993). Interactions between these components are mainly governed by predation. Both piscivorous fish and birds predate on small fish, of which smelt is the most important in terms of consumed quantity (Buijse *et al.* 1993). To assess whether food availability determined the spatial distribution of two abundant bird species in IJsselmeer, the omnivorous black-headed gull *Larus ridibundus* and the piscivorous black tern *Chlidonias niger*, we studied spatial association between these two bird species with their prey, smelt.

Recently, spatial aspects of predator-prey relationships received considerable attention (Giller, Hildrew & Raffaelli 1992; Goyke & Brandt 1993; Holt 1996; Wootton & Thorpe 1993). The central paradigm in studies on spatial association of predators and their prey is the 'ideal free distribution': predators move to patches where profitability (i.e. feed intake per unit effort) is highest, under the condition that the predators are 'ideal' in their judgement of profitability, and 'free' to move between patches (Begon, Harper & Townsend 1990). The 'ideal free distribution' predicts that predators and their prey are spatially associated. Spatial association is meaningful only if the scale, whereat the association is manifest, is indicated (Schneider 1989; Schneider 1994). For example, foraging cod *Gadus morhua* aggregates with its prey capelin *Mallotus villosus* on a scale as small as 3.5 m, but outside the feeding period, spatial association of cod and capelin is manifest only at a much larger scale (> 4-10 km) (Rose & Leggett 1990).

In IJsselmeer, smelt contributes ca. 70 % to the diet of all piscivores (both birds and fish) (Buijse *et al.* 1993) and about 10-20% to the total value of the yield of the commercial fishery. Many piscivorous birds are attracted to the IJsselmeer area because of the high prey fish availability (Prins *et al.* 1995), so at a spatial scale of 100s km, piscivorous birds can be considered to some extent as 'ideal' predators. However, it is not clear whether spatial association of piscivorous birds and their prey is manifest within IJsselmeer, at a spatial scale of maximally 10s km.

Both black-headed gulls and black terns are most abundant in August of each year (Winter 1994). The population size of black-headed gulls in the IJsselmeer area ranges between 10,000 and 100,000 individuals (Voslamber 1991). Black-headed gulls actively hunt for surface-dwelling smelt, they scavenge from discards of fishing vessels, and they forage in the agricultural areas and garbage lots near IJsselmeer (Voslamber 1991). The annual consumption of smelt by black-headed gull is on average 8.1 kg.ha^{-1} (Buijse *et al.* 1993), which makes it the most important consumer of smelt among the piscivorous bird species in the IJsselmeer area. In contrast to black-headed gulls, black terns forage exclusively on surface-dwelling smelt in IJsselmeer (Schouten 1983). The annual consumption of smelt by black terns is on average 1.1 kg.ha^{-1}. From a single roosting site near the northwestern part of IJsselmeer (Fig. 8.1), terns undertake daily foraging trips. Black terns use IJsselmeer as a resting and foraging area during their migration from their breeding areas in North and East Europe to their wintering areas in tropical West Africa (Schouten 1983). In the period 1989 - 1994, between 90,000 (1993) and 270,000 (1990) terns stayed for a period of 2-3 weeks in IJsselmeer (Karman, Winters & Schobben 1995). As the total Eurasian black tern population is ca. 200,000 (Rose & Scott 1994), IJsselmeer is a key site for the Eurasian black tern population.

The purpose of this study was to test whether black-headed gull and black tern and smelt were spatially associated, and to assess at which scale this association was manifest. Also, the effect of water transparency on the spatial association was assessed, hypothesizing that a higher water transparency would make smelt unavailable for their avian predators, because smelt migrates deeper into the water column at water transparency > 0.8 m Secchi depth (Chapter 6). In two study areas in IJsselmeer, each with a surface area of ca. 16000 ha, the spatial distribution of smelt was assessed by a surface trawl survey, and the spatial distribution of birds was estimated by an aerial survey. Additionally, bird abundance was also estimated by counting from a fisheries research vessel. The field work of the study was conducted in August, because densities of black-headed gull and black tern are highest during this month of the year.

MATERIALS AND METHODS

Sampling was conducted in two sampling areas (*A* and *B*, Fig. 8.1) Area *A*, in the northern basin, was selected because it was close to the roosting site of black terns. Area *B* was selected because it was expected to have a high variation in water transparency, as this area encompasses both the northern and the southern, more turbid basin of IJsselmeer. Area *A* was subdivided in 6 strata, and area *B* in 3 strata (1 stratum in the southern basin, 2 strata in the northern basin). The criteria for the definition of the strata were the 5 m depth contours and geographic consistency. The surface areas of the strata in area *A* were relatively small (cf. Fig. 8.1) because of the high variation in depth. Stratum 5 was geographically not consistent, but we considered the two parts close enough to each other to treat them as a single stratum. In area *B*, the dyke that divides IJsselmeer in a northern and a southern basin formed an obvious stratum boundary. Stratum 2 in area *B* was defined because of its high variation in depth, as there are numerous sandpits, not indicated on the map (Fig. 8.1).

A beam trawl with a mouth width of 3 m, a mouth height of 0.6 m and a stretched mesh size in the cod-end of 2 mm (cf. Chapter 4) was used to sample the fish population in the 0.6 m surface layer (Fig. 8.2). Each haul lasted 10 ± 0.5 minutes, trawling speed was 1.5 ± 0.1 $m \cdot s^{-1}$, and the surface area covered by each haul was ca. 0.3 ha. At the start of the haul, the geographical position and the hauling direction were measured using the ship's navigational instruments (compass and GPS). At the end of the haul, bottom depth and Secchi depth were measured. Weather conditions (wind-force, wind direction and cloudiness) during the haul were recorded as

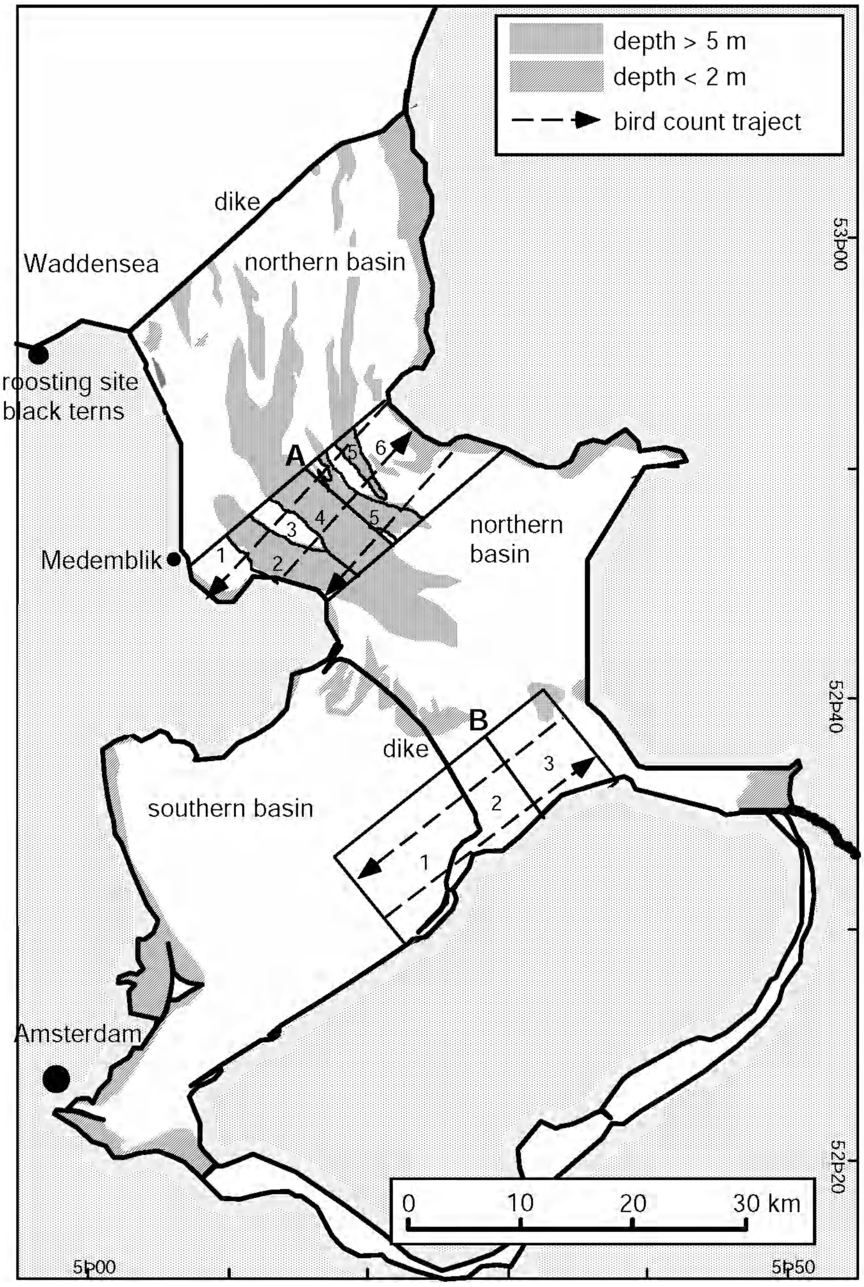

Figure 8.1. Map of IJsselmeer with sampling areas A and B, bird counting trajects and the roosting site of the black terns. Numbers in areas indicate sampling strata.

well. Of each species in the catch, numbers were counted and the length frequency distribution was established. In each area, 27-30 trawl hauls were made to describe the spatial distribution of smelt. The number of haul per stratum was proportional to its surface area. Within each stratum, the starting position of the haul was selected randomly. The trawl was operated from R.V. 'Stern' (200 HP, length 20 m).

Black-headed gulls and black terns were counted from a Cessna 172 airplane, flying at an altitude of 153 m and a speed of 40 $m \cdot s^{-1}$. At each side of the airplane, experienced observers

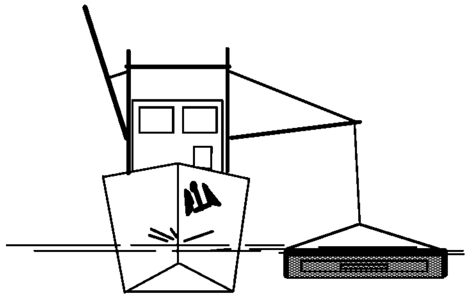

Figure 8.2. Front view of R.V. 'Stern' during a trawl haul (not on scale). The beam trawl is situated at the side of the ship, outside the wake of the propeller.

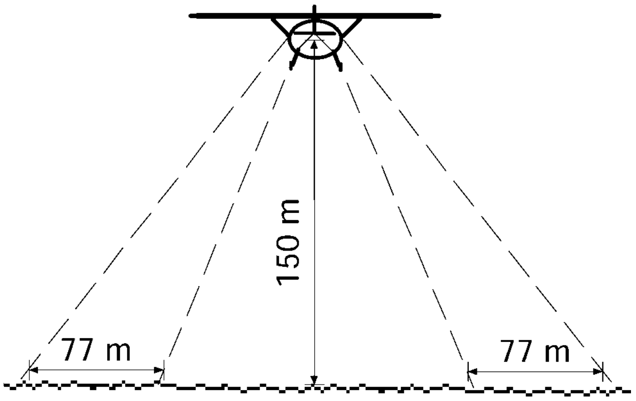

Figure 8.3. Schematic representation of the bird counting set-up (not on scale). Birds were counted within an area enclosed by the dashed lines at both sides of the airplane.

counted the black-headed gulls and black terns within a strip with a width of 77 m along the traject (Fig. 8.3). Three trajects were flown over area *A* and two trajects over area *B* (cf. Fig. 8.1). Bird counts were integrated over time intervals of 15 s, corresponding to a stretch of 600 m. Thus, each bird count represented bird abundance in a surface area of 4.6 ha. The geographical position of each stretch was calculated from the position of the start and end location of the trajects, and from the number of stretches within the trajects. The bird counts from each stretch were allocated to the sampling strata according to their geographical position.

Sampling took place in three consecutive weeks in August 1995. Birds were surveyed in both areas each week. We checked whether there was a difference in bird abundance between the two areas, and whether the difference was consistent between weeks. Due to time constraints, only one area per week could be surveyed for smelt. We restricted our analysis of spatial association to areas that were sampled for birds and smelt within the same week. Smelt were sampled in the first two weeks in area *A*, and in the third week in area *B*. The bird counting trajects were flown on August 7, 15 and 22. On August 7, observations were made at one side of the airplane only. On August 7 and 15, the trajects were flown in the morning. On August 22, it was foggy in the morning, which would have impaired the observations. Therefore, sampling was postponed to early in the afternoon, after the fog lifted.

We analyzed spatial patterns in environmental variables (depth and Secchi depth) and in fish and bird abundance for week 1 and 2 in area *A*, and for week 3 in area *B*. To describe spatial patterns, we assessed between-stratum and between-week variation in the estimated values of abundance, depth and Secchi depth. A correlation matrix of the estimated values was established using Kendall's non-parametric correlation coefficient, τ (Sokal & Rohlf 1981 p. 601). From the correlation analysis, we derived possible causal relationships. For area *A*, estimates with their 95% confidence limits were calculated by constructing an analysis-of-variance (ANOVA) model, using stratum number (*STRATUM*), week number (*WEEK*) and their interaction (*STRATUM.WEEK*) as explaining class variables. For area *B*, only *STRATUM* was used as an explaining variable. To normalize the error distribution, bird and smelt counts were log-transformed (natural logarithms). Assumptions of ANOVA were checked by residual analysis (cf. Neter, Wasserman & Kutner 1985, p. 109).

'Zero' counts, which frequently occurred during the aerial survey, were excluded from the ANOVA. If zero counts comprised more than 20% of the observations in the analysis, we used the generalized linear modeling (*GLM*) approach (McCullagh & Nelder 1989) to analyze the presence or absence of birds in a counting stretch, instead of ANOVA on log-transformed counts. In the *GLM*, a binomial error distribution and a logit link function was used. The zero counts can be included in the analysis, while information on the precise number of birds within a stretch is lost. In ANOVA, partial sums of squares were used for hypothesis testing (SAS® Institute Inc. 1989). In *GLM*, the analogue of partial sums of squares (partial likelihood ratios) was used (SAS® Institute Inc. 1993).

To study spatial distribution at a finer scale than was possible with the ANOVA, a variogram (Armstrong *et al.* 1992; cf. Chapter 7) of log-transformed bird and smelt counts in area *A* was constructed. The variogram relates the distance between sampling locations to the variability in abundance between these sampling locations. The variogram was calculated according to:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [R(x_i + h) - R(x_i)]^2 \quad \text{[formula 8.1]}$$

whereby x_i are the positions of the hauls, $R(x_i)$ is the log-transformed count at location x_i, h is the distance (km) between 2 locations and $N(h)$ is the number of pairs of positions $(x_i; x_i+h)$ (Armstrong *et al.* 1992). Since the geographic positions of each count were spaced irregularly, $\gamma(h)$ was calculated over a varying interval of h, keeping the number of observations within an interval constant. Variograms were calculated only if the proportion of zero counts was less than 20%.

Birds were also counted from the research vessel during a trawl haul, when availability of manpower permitted. This made a direct correlation analysis of bird and smelt abundance possible. The counting area was circular-shaped with a radius of ca. 300 m around the vessel, thus covering a surface area of ca. 86 ha during the haul. Birds that were following the ship and that foraged in the wake of the ship were included in the counts, whereas birds that left the counting area before the haul was completed were excluded from the counts. For each area, the correlation between smelt catch and bird count was assessed by calculating Kendall's τ.

Data processing was done with SAS® Software (SAS® Institute Inc. 1990).

RESULTS

The average depth of the trawled sites per stratum did not differ significantly between weeks. In area *A*, mean depth varied between 3.7 m (stratum *A3*) and 5.8 m (stratum *A4*) (Fig. 8.4a). In area *B*, mean depth per stratum varied less (between 4.1 and 4.5 m, Fig. 8.4b) than in area *A*, but these small differences between strata were significant in both areas (Table 8.1). Also, differences in water transparency were low (Fig. 8.4c, d). Water transparency in the northern basin is usually higher than in the southern basin (cf. Chapter 7, Chapter 9), but during the study period, water transparency in the southern basin was higher (Fig. 8.4d). This was probably a result of the northerly wind. In area *A*, water transparency was higher in the eastern part than in the western part, but the maximum difference was ca. 0.2 m Secchi depth only. The differences in water transparency between strata in both areas were small, but significant (Table 8.1).

Weather conditions remained fairly constant throughout the total sampling period: the wind was mostly northerly, there was intermittent cloud cover with no precipitation (Table 8.2). During week 1, the wind-force was higher (ca. 4 Beaufort) than during week 2 and 3 (1-2 Beaufort).

Of all trawl catches, > 99% of fish in weight and numbers consisted of smelt. The second most abundant fish species in the catch was three-spined stickleback *Gasterosteus aculeatus*. The size structure of smelt caught was simple, with two modi in the length-frequency distribution, at ca. 5 cm and ca. 8 cm *TL* (Fig. 8.5). These modi represented the age 0 and the age 1 group. Age 0 smelt were several orders of magnitude more abundant than age 1 smelt. Smelt caught in the southern basin (stratum *B1*) were ca. 0.5 cm smaller than smelt from the northern basin (Fig. 8.5).

The number of smelt per haul (*CpUE*), an index for abundance, ranged between 16 and 72000. In week 1, smelt were distributed evenly over area *A*. In week 2, abundance of smelt was lower in the two easternmost strata (*A5* and A6) (Fig. 8.6a). This difference in distribution over area *A* between sampling week 1 and 2 was significant ($P < 0.01$ for the interaction term in the ANOVA, Table 8.3). In area *B*, smelt abundance was ca. 20 times higher in the southern basin (stratum *B1*) than in the northern basin (strata *B2* and *B3*) (Fig. 8.6b, Table 8.3).

Table 8.1*. ANOVA tables for depth and Secchi depth.*

studied variable /	area A			area B		
source	df	SS	P	df	SS	P
depth						
model	11	39	0.00	2	0.96	0.04
error	48	13		24	3.2	
STRATUM	5	39	0.00			
WEEK	1	0.61	0.14			
STRATUM·WEEK	5	1.2	0.50			
Secchi depth						
model	11	0.16	0.14	2	0.58	0.00
error	48	0.45		24	0.22	
STRATUM	5	0.11	0.06			
WEEK	1	0.017	0.18			
STRATUM·WEEK	5	0.032	0.64			

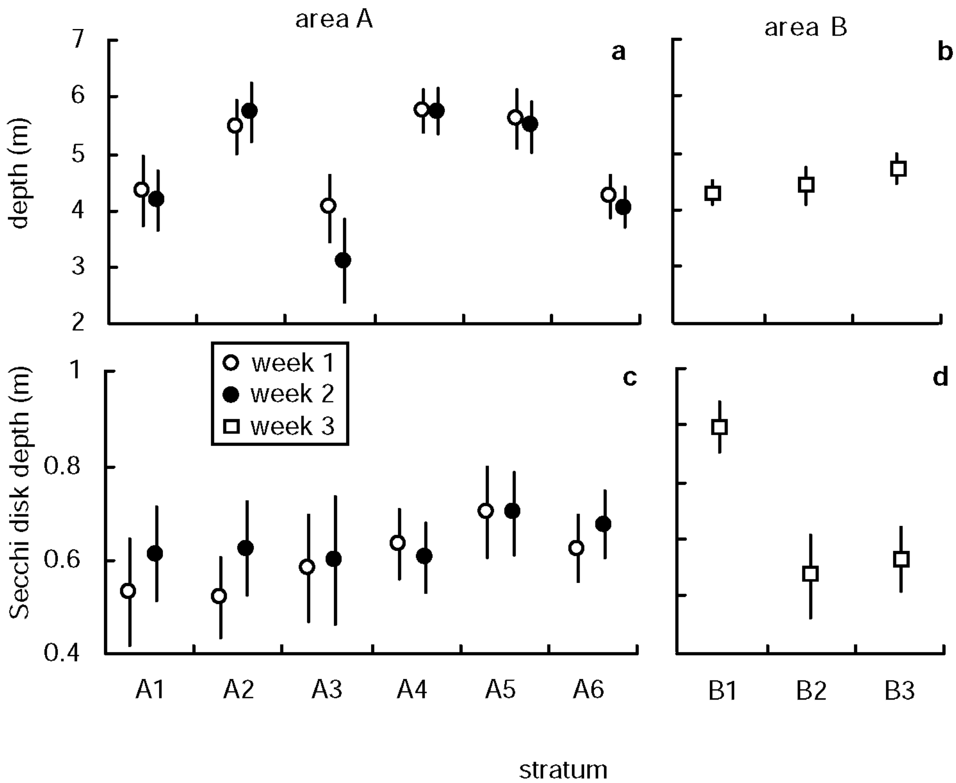

***Figure 8.4**. Model estimates for depth (top) and Secchi depth (bottom), with 95% confidence limits of the means, for area A and B.*

In area *A*, the number of black-headed gulls counted per stretch ranged between 0 and 230, and gulls were present in 229 of 261 stretches. Gulls seemed more evenly distributed over area *A* in week 1 than in week 2 (*P* = 0.12, Table 8.3; Fig. 8.6c). In area *B*, less gulls were counted than in area *A*: Gull counts ranged between 0 and 53 per stretch (see also shaded plot symbols in Fig. 8.6d), whereas gulls were present in only 137 of 174 stretches. Within area *B*, presence was highest in the southern basin (stratum *B1*) (Fig. 8.6d). The difference in mean presence between strata was small, but significant (*P* = 0.08, Table 8.3).

***Table 8.2**. The weather during the smelt sampling weeks and on the days that aerial bird survey was conducted. Wind force in Beaufort, cloudiness in % of sky covered.*

	wind-force		wind direction		cloudiness	
	mean	range	mean	range	mean	range
week 1	3.7	2-5	NNE	N-E	19	0-63
August 7	4		NNE		50	
week 2	2.6	1-4	N	NW-ENE	34	0-88
August 15	2		NW		25	
week 3	1.9	0-4	N	W-ESE	18	0-50
August 22	1		N		0	

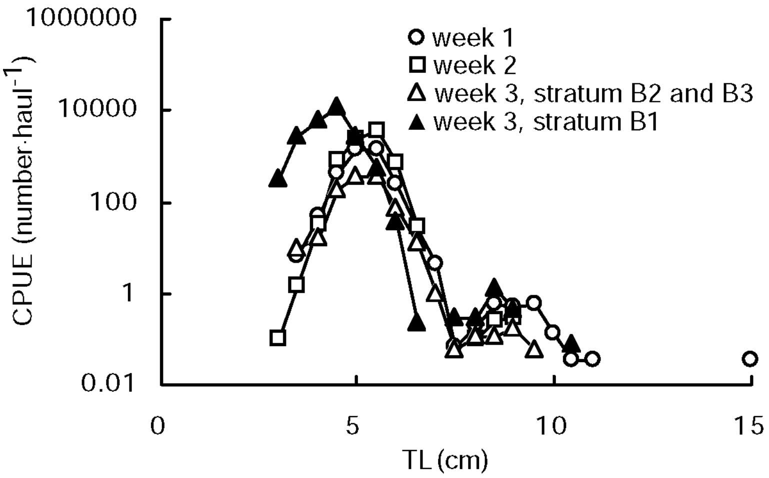

***Figure 8.5**. Length-frequency distributions of smelt caught during the trawl survey. The Y-axis represents the mean number of smelt caught per haul of 10 min.*

The number of terns per stretch varied between 0 and 50 in area *A*, and terns were present in 117 of 261 stretches. Also for terns, spatial distribution seemed more homogeneous in week 1 than in week 2 (Fig. 8.6e), but the difference in tern distribution between week 1 and week 2 (Fig. 8.6e) was not significant ($P = 0.26$, Table 8.3). In area *B*, the maximum number of terns per stretch was only 3, and terns were observed in only 16 of 174 stretches. Presence of terns was low in all strata of area *B*, but the difference in tern presence between the strata (Fig. 8.6f) was significant ($P < 0.01$, Table 8.3).

***Table 8.3**. ANOVA and GLM tables for smelt, black-headed gull and black tern. MLR = maximum likelihood ratio, the GLM analogue of sums of squares (SS). Results of GLM are in italics.*

	area A			area B		
species / source	df	SS/ MLR	P	df	SS/ MLR	P
smelt						
model	11	132	0.00	2	66	0.00
error	48	51		24	38	
STRATUM	5	84	0.00			
WEEK	1	0.048	0.20			
STRATUM·WEEK	5	49	0.00			
black-headed gull						
model	11	45	0.00	*2*	*5.3*	*0.08*
error	217	209		*171*	*175*	
STRATUM	5	22	0.00			
WEEK	1	2.7	0.09			
STRATUM·WEEK	5	8.4	0.12			
black tern						
model	*11*	*58*	*0.00*	*2*	*9.8*	*0.00*
error	*249*	*301*		*171*	*97*	
STRATUM	*5*	*40*	*0.00*			
WEEK	*1*	*2.1*	*0.19*			
STRATUM·WEEK	*5*	*7.9*	*0.26*			

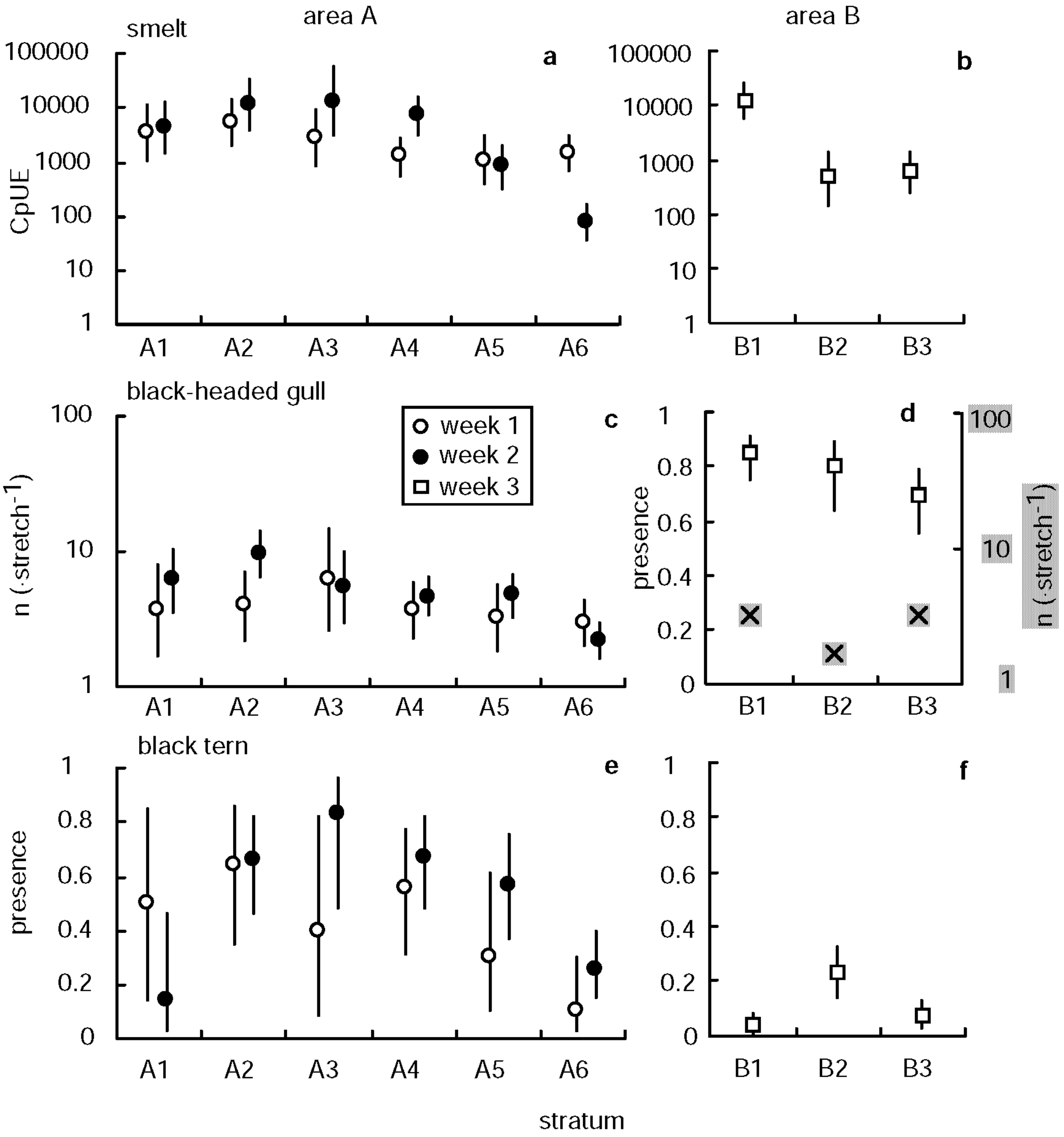

***Figure 8.6**. Mean abundance of smelt (a, b), black-headed gull (c, d) and black tern (e, f) in each stratum, with 95% confidence limits of the estimates. Note the difference in the Y-axes. The Y-axis for smelt depicts CpUE. For gull in area A, the Y-axis depicts the number counted per stretch. The Y-axes of graphs e, f and the left Y axis of d depict the probability of encountering birds in a counting stretch. The shaded plot symbols and the right Y-axis of graph d depict the mean number of birds per counting stretch.*

During each week of the study period, both black-headed gulls and black terns were more abundant in area *A* than in area *B* (Wilcoxon's rank sum tests, $P < 0.01$). This suggested that the distribution of black-headed gulls and black terns remained fairly constant at the spatial scale covering both areas.

The distribution of smelt, gulls and terns over area *A* seemed similar: in week 1, fish and birds were distributed evenly, whereas in week 2, abundance of fish and birds was lower in the easternmost strata and higher in stratum *A2* and *A3*. For area *A*, the correlations between smelt

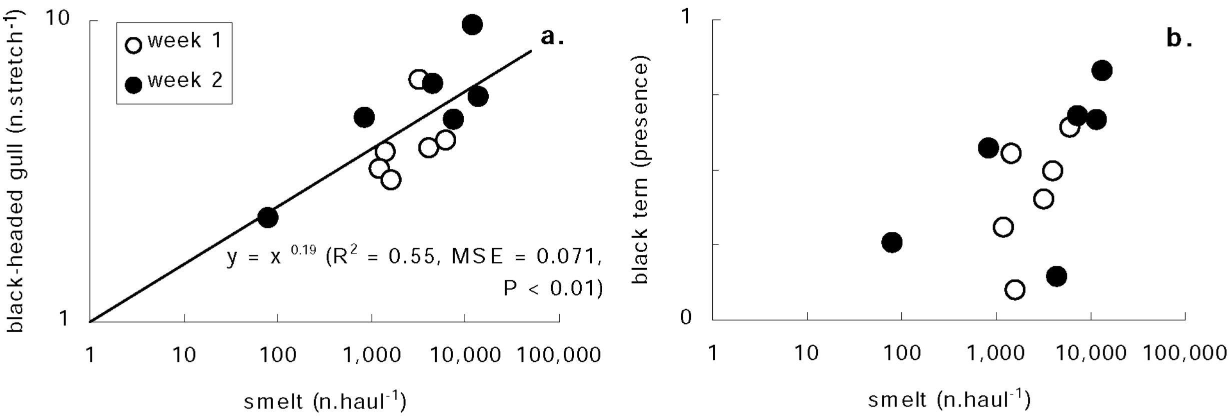

***Figure 8.7**. Relationship between the mean number of smelt per haul and the mean number of black-headed gulls per counting stretch (a) and between smelt and the mean presence of black tern (b) in area A (means are derived from Fig. 8.6a,c,e). For black-headed gulls, the fitted line with regression statistics is indicated.*

and bird abundance were positive (τ = 0.48) and significant (P = 0.03) for both gulls and terns (Table 8.4). However, a 10-fold increase in smelt abundance resulted in an increase of gull abundance with a factor 1.5 only (Fig. 8.7). Within area *A*, smelt abundance was low where water transparency was high (stratum *A5* and *A6*), and correlation between these 2 variables was negative and significant (Table 8.4). The correlation between bird abundance and water transparency was negative as well, but not significant (P = 0.33). None of the correlations with depth were significant (P > 0.20) (Table 8.4), indicating that in area *A* spatial distribution of both surface-dwelling smelt and birds was not affected by depth. Despite the extremely high abundance of surface-dwelling smelt in the southern basin (stratum *B1*), where water transparency was high compared to the rest of area *B* and to area *A*, abundance of birds was low compared to area *A*. Within area *B*, abundance of black-headed gull was indeed higher in stratum *B1*, but presence of black tern was not (Table 8.4).

***Table 8.4**. Correlation coefficients among model estimates per week, per stratum. In each cell, the top value represents Kendall's τ, and the value (between brackets) the associated P-value. Because correlation coefficients for area B were calculated with 3 estimates each, the minimum attainable P-value was 0.12.*

	Secchi depth	smelt	gull	tern
area A				
depth	0.12 (0.58)	0.06 (0.78)	-0.03 (0.89)	0.27 (0.22)
Secchi depth		-0.52 (0.02)	-0.22 (0.33)	-0.22 (0.33)
smelt			0.48 (0.03)	0.48 (0.03)
gull				0.39 (0.07)
area B				
depth	-0.33 (0.60)	-0.33 (0.60)	-1 (0.12)	0.33 (0.60)
Secchi		1 (0.12)	0.33 (0.60)	-1 (0.12)
smelt			0.33 (0.60)	-1 (0.12)
gull				-0.33 (0.60)

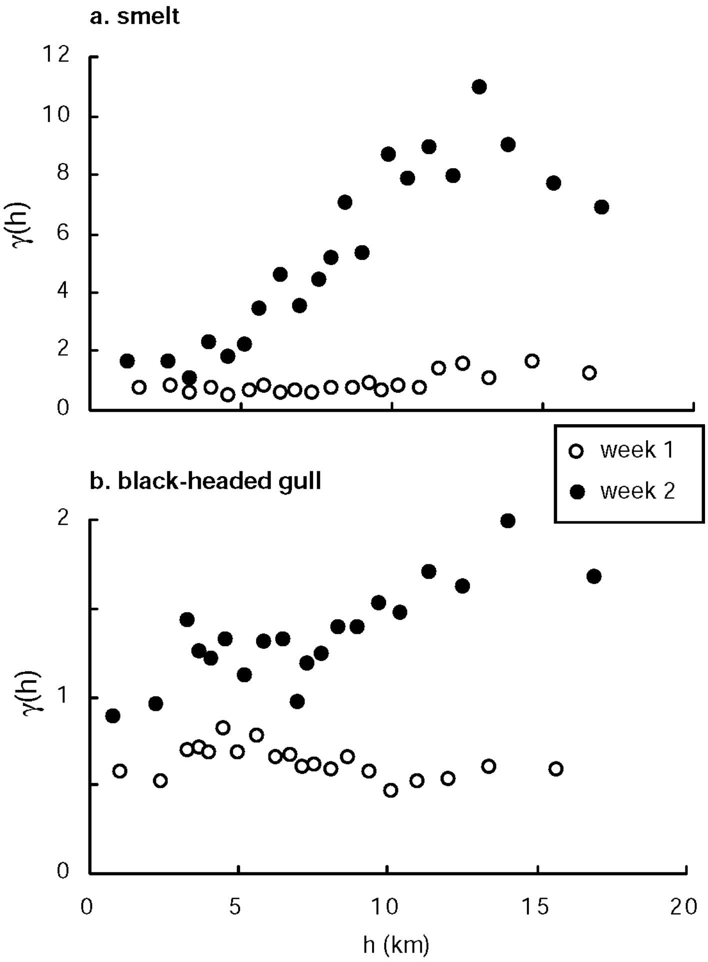

***Figure 8.8**. Variograms of log-transformed smelt (a) and black-headed gull (b) counts in area A. The X-axis represents the distance between sampling locations, the Y-axis is a measure of variance in abundance between sampling locations.*

Variograms of smelt (Fig. 8.8a) and gulls (Fig. 8.8b) from area *A* were similar, and they corroborated the spatial distribution patterns as estimated by ANOVA (cf. Fig. 8.6a,c). In week 1, variability in smelt and gull abundance was constant with varying distance between sampling locations (*h*), indicating that the spatial pattern was governed by random variation in trawled smelt and counted gulls only. In week 2, variability in both smelt and gull abundance increased with increasing *h*, reflecting the between-stratum differences in abundance that were demonstrated in the ANOVA. Within the spatial scale of a single stratum, roughly between 1-5 km (cf. Fig. 8.1), there was no indication that variability increased with increasing *h*. Hence, on this spatial scale, the spatial distribution pattern was governed by random variation in trawled smelt and counted gulls only.

During 72 hauls, bird counts were made from the research vessel during the trawl hauls. Gulls were always present, whereas terns were observed during 35 hauls only. Between 3 and 213 gulls and up to 258 terns were counted per haul. For area *A*, the number of smelt caught per trawl

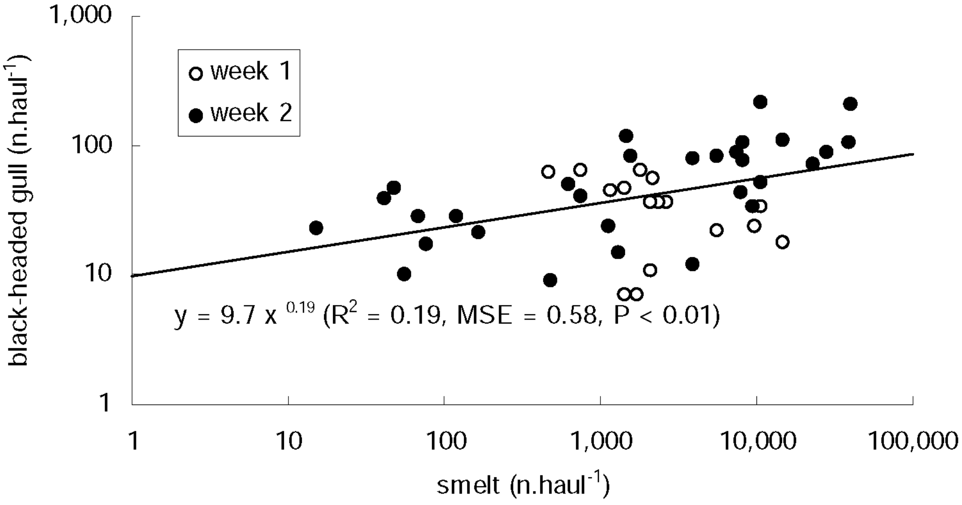

***Figure 8.9**. Relationship between the number of smelt caught per haul and the number of black-headed gulls counted during hauls in area A, with statistics of the fitted line.*

haul was positively correlated with the number of gulls counted during the haul (τ = 0.31, *n* = 46, *P* < 0.01). Spatial association was exactly as weak as was found in aerial survey of the spatial distribution of birds: a 10-fold increase in smelt abundance resulted in an increase of gull abundance with a factor 1.5 only (Fig. 8.9). Furthermore, despite the close temporal and spatial match in sampling birds and fish, only 19% of the variation in log-transformed bird counts was explained by the log-transformed number of smelt caught. For area *B*, the correlation was positive, but not significant (τ = 0.13, *n* = 26, *P* = 0.35). The correlation between terns observed from the ship and smelt abundance was low and insignificant in both area *A* (τ = -0.02, *n* = 46, *P* = 0.84) and area *B* (τ = 0.10, *n* = 26, *P* = 0.55). Hence, although in this survey smelt and birds were sampled simultaneously in closely overlapping sampling areas, spatial association was in general not as strong as found on a higher spatial scale in area *A*.

DISCUSSION

Spatial association black-headed gull and black tern with their prey, smelt, was demonstrated, but the association was not consistent for the two areas studied. In the southern study area (area *B*, cf. Fig. 8.1), spatial association was not manifest, even though variation in smelt abundance was high (cf. Fig. 8.6b). In the northern study area (area *A*, cf. Fig. 8.1), the distribution of smelt changed between two successive weeks, and the distribution of birds changed accordingly. Here, water transparency affected the abundance of surface-dwelling smelt, probably through vertical migration of smelt deeper in the water column (Chapter 6), and through horizontal migration to more turbid areas (Chapter 7). Consequently also food availability of black-headed gull and black tern varied spatially. It was unlikely that, within the narrow range of Secchi depths observed in area *A* (0.5-0.7 m), foraging efficiency of surface-feeding birds was affected by water transparency. Still, the spatial distribution of birds was much less extreme than the distribution of their prey: the 10-fold increase in abundance of smelt was associated with only a 1.5-fold increase in the abundance of black-headed gull. This corroborated the conclusion of Kennedy & Gray (1993), that the spatial distribution of foraging animals is consistently less extreme than the distribution of their resources.

We could only speculate why smelt abundance in the section of the southern basin that was surveyed (stratum *B1*) was even higher than smelt abundance in the more turbid northern basin. Probably, the absence of the prevalent westerly wind caused a large part of the southern basin to clear up, leaving smelt without an alternative, more turbid habitat. The high water transparency in stratum *B1* was atypical, as the southern basin is usually more turbid than the northern basin (cf. Chapter 7, 9).

Bird counts from the ship supported the conclusion that spatial association was present in area *A* and absent in area *B*. Therefore, we concluded that the difference in predator-prey association between area *A* and area *B* was meaningful. Variation in the ability of terns and gulls to detect smelt from the air could not account for the lack of spatial association, because the part with the highest smelt abundance coincided with the area where water transparency was highest. Possibly, gulls and terns did not use area *B* as a foraging area, so that spatial distribution of smelt in area *B* was not relevant to the spatial distribution of gulls and terns. This hypothesis was supported by the consistently lower bird abundance in area *B* during our study period. Probably, the relatively high tern abundance in area *A* was caused by the proximity of the roosting site (cf. Fig. 8.1). The relatively high abundance of gulls in area *A* might have been caused by the presence of a large rubbish dump near the town Medemblik (cf. Fig. 8.1), which presented an additional foraging opportunity for gulls. These effects, that are not related to smelt abundance, resulted in an absence of spatial association between birds and their prey at a scale of ca. 30 km.

The scale whereat prey-predator spatial association of predators with their prey was demonstrated ranged between 5 and 20 km. On a finer scale (1-5 km), variability in smelt and gull abundance did not increase with increasing distance between sampling locations (cf. Fig. 8.8). For smelt, this implied that within this scale interval random spatial variability in abundance was indistinguishable from sampling error (cf. Armstrong *et al.* 1992). In the survey where birds were counted form the research vessel, and where bird counting areas (86 ha) completely overlapped the trawl lanes (0.3 ha), the strength of the prey-predator association was exactly the same as on a scale of 5-20 km. Furthermore, only 20% of the variation in gull abundance observations was explained by variation in smelt abundance, despite the close temporal and spatial match in sampling birds and fish. Concluding, the association between smelt and one of its avian predators, black-headed gull, is manifest only at a scale of 5-20 km in IJsselmeer.

The finest scale whereat spatial association was detected during this study (5 km) is similar to other studies where a similar scale interval to is used. Spatial interdependency of krill and their predators (mammals and birds) is manifest at a scale > 4 km (McClatchie, Hutchinson &

Nordin 1989; Veit, Silverman & Everson 1993. Association of puffins *Fratercula arctica* and common guillemots *Uria aalge* with their prey (capelin *Mallotus villosus*) is highest at the higher end within a scale interval of 0.2-6 km (Schneider 1989). Also, studies on fish piscivores and their prey suggest that fine spatial scales are not meaningful (Brandt & Kirsch 1993; Goyke & Brandt 1993; Horne & Schneider 1994; Rose & Leggett 1990). From the agreement between studies in respect to the minimal scale at which spatial interdependency of predator and prey is manifest, one might suggest that there is little justification to use a finer scale than ca. 5 km for most studies on predator-prey distribution patterns. Of course, this suggestion is valid only in the absence of a steep spatial gradient in environmental characteristics (e.g. perpendicular to a reef).

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Section III

Interactions between the fishery and fish-eating birds

Chapter 9

Interactions in the utilization of small fish by piscivorous fish and birds, and by fishery in IJsselmeer

P.J. Mous, W. Dekker, M.B. van Eerden & W.L.T. van Densen

ABSTRACT

To assess the carrying capacity of IJsselmeer as a foraging area for piscivorous fish and piscivorous birds, and as a fishing ground for a commercial fishery, patterns in production and utilization of small fish (fish < 10 cm *TL*) over a 20-year period are analyzed. Total biological production of small fish was 102 $kg.ha^{-1}.yr^{-1}$ in the northern basin and 116 $kg.ha^{-1}.yr^{-1}$ in the southern basin. The most important categories of small fish species in terms of production were smelt *Osmerus eperlanus*, ruffe *Gymnocaphalus cernua* and juvenile perch *Perca fluviatilis*. Throughout the period 1970-1995, young-of-the-year (0-group) smelt was a keystone species in IJsselmeer, contributing 72% to the total small fish production in the northern basin, and 60% to the total production of small fish of the southern basin. Inter-annual variation in production of 0-group smelt was relatively low, 67% of the annual production estimates varied within a factor 2 around the inter-annual geometric mean. Smelt production was probably balanced by its utilization. Most of the smelt production was utilized by piscivorous fish (mainly perch), followed by the fishery for spawning smelt and the piscivorous birds around IJsselmeer. Growth of zooplanktivorous smelt and benthivorous ruffe was density-dependent, and fast growth of smelt was associated with a large mean length of its preferred food, *Daphnia spp.* As production of smelt, the most important producer, was fully utilized, and since its growth was density-dependent, the capacity of IJsselmeer to sustain small fish production for utilization by piscivorous fish, piscivorous birds and the fishery was probably reached. Management regimes that aim for a higher biological production of piscivorous fish should either include a restriction of the commercial fishery on smelt, or allow that food availability of piscivorous birds decreases.

INTRODUCTION

Small-sized fish (fish < ca. 10 cm *TL*) are an important component of lake ecosystems. Often, they comprise most of the fish production, as the biomass and productivity, as the ratio of biological production and average stock biomass is high compared to that of large and older fish (Sprules *et al.* 1991; Downing & Plante 1993; Randall, Kelso & Minns 1995; Holcik 1996). Many species of small fish are zooplanktivorous, and their predation pressure can ultimately affect water quality through a cascading effect (Carpenter, Kitchell & Hodgson 1985; Hanson & Butler 1994). In IJsselmeer, predatory fish, piscivorous birds, and the commercial fishery all three depend on the production of small fish, so knowledge on the capacity of IJsselmeer to sustain production of small fish is of vital importance for the management of IJsselmeer's natural resources. The concept of carrying capacity is much related to production and utilization patterns. There is no consensus on the meaning of carrying capacity (De Bie 1991), but Begon, Harper & Townsend (1990) give a useful definition: The population density where production is balanced by mortality (utilization), in populations where production or mortality are density-dependent. In this chapter, the carrying capacity of IJsselmeer for the production of small fish is assessed by balancing production against utilization, and by studying density-dependency in the main categories of small fish.

From a steady-state flow model that is representative for an average situation in IJsselmeer over the period 1983-1987 (Buijse *et al.* 1993), it is clear that the zooplanktivorous smelt *Osmerus eperlanus* is the most important small fish species in terms of biological production in IJsselmeer (ca. 130 $kg.ha^{-1}.yr^{-1}$). Other important small fish species are the benthivorous ruffe *Gymnocephalus cernua* (9 $kg.ha^{-1}.yr^{-1}$) and juvenile perch *Perca fluviatilis* (5 $kg.ha^{-1}.yr^{-1}$). The production of smelt, ruffe and juvenile perch together contributes ca. 80% to the total fish production of IJsselmeer. Consumption of small fish by piscivorous fish is 81 $kg.ha^{-1}.yr^{-1}$, of which 83% is consumed by perch, 12% by pikeperch *Stizostedion lucioperca*, and 4% by eel *Anguilla anguilla*. Small fish consumption by piscivorous birds is 48.4 $kg.ha^{-1}.yr^{-1}$, of which 43% was consumed by cormorant *Phalocrocorax carbo*, 21% by black-headed gull *Larus ridibundus* and the remainder by 10 other bird species. The commercial fishery utilizes small fish, as it targets for spawning concentrations of smelt in early spring (catch 9 $kg.ha^{-1}.yr^{-1}$). During the rest of the year, the fishery utilizes small fish production indirectly by targeting consumers of small fish, namely large-sized eel, pikeperch, and perch, for which the catch amounts to 3, 1 and 4 $kg.ha^{-1}.yr^{-1}$ respectively. Not targeted for, but most of the discards of the summer fishery with fykenets for eel consist of small fish (cf. Van Dam *et al.* 1995). Hence, a more intensive exploitation of small fish by the fishery, either directly or indirectly, may have a negative impact on the outcome of the fishery for eel, perch and pikeperch, and on the viability of bird populations.

Production of small fish might strongly vary between years due to yearclass strength variation: in IJsselmeer, yearclass strength of perch varies up to a factor 400, and of pikeperch up to a factor 70 (Buijse, Van Densen & Schaap 1992). In this study, inter-annual variation in the biological production of small fish over a period of ca. 20 years is described to assess the variation in ecosystem dynamics. Utilization of small fish by the fishery and by fish-eating birds, and the temporal variations therein, were assessed through fish auction statistics and published reports.

For perch and pikeperch, water temperature plays an important role in determining year class strength and growth (hence production), but the size of the parental stock does not (Buijse, Van Densen & Schaap 1992). In this study, the possible effect of the size of the parental stock, and of water temperature on biological production of smelt and ruffe was assessed. Also, growth and condition of smelt were studied in relation to seasonal and inter-annual fluctuations in availability of high-quality food for smelt, as indexed by the mean *Daphnia spp.* size in the lake.

In this study, it is demonstrated that smelt was an important producer throughout the 1970s, the 1980s, and the early 1990s in IJsselmeer. Smelt growth was density-dependent, and food-limited. There was evidence that production of small fish was fully utilized by piscivorous fish, piscivorous birds and the fishery. Therefore, it was concluded that the carrying capacity for the production of small fish was reached.

MATERIALS AND METHODS

Intra-annual variation in abundance and body size of small fish was assessed with a repetitive trawl survey program in the period May 1994 - March 1995. Inter-annual variation was assessed with a yearly trawl survey that was conducted in each fall during 1970-1994. All survey hauls were made during daytime. After completion of each survey haul, the geographical position, haul duration, bottom depth and Secchi depth were recorded. A length-frequency distribution (*LFD*) was established for each species in the catch. All length measurements were made in, or recalculated to, total length. Allometric length - weight relationships were used to calculate body weight from total length (Table 9.1).

A length-frequency distribution (*LFD*) was established for each species in the catch. To separate the 0-group (the young-of-the-year) from the ≥1-group (all year classes older than the young-of-the-year class), the *LFD*s were averaged per survey, per sampling period and per basin, and the average *LFD*s were subjected to Bhattacharya analysis (Sparre & Venema 1992). Bhattacharya analysis was performed with the software package FiSAT (Gayanilo, Sparre & Pauly 1995). For ruffe that were sampled during the winter half year, separation into age groups was possible only by assuming that the left part of the *LFD* consisted exclusively of 0-group, because the modi of the 0-group and ≥1-group were not discernable. Using the fractional distribution of age

Table 9.1. *Parameter values for allometric length-weight relationships ($W=a \cdot TL^b$). W=body weight (kg), TL = total length (cm). Parameter values were estimated by regression analysis on length-weight observations ($n > 700$, $R^2 > 0.98$).*

	a	b
smelt	$2.30 \cdot 10^{-6}$	3.37
perch	$4.70 \cdot 10^{-6}$	3.36
ruffe	$6.48 \cdot 10^{-6}$	3.29

classes over each length class, we calculated number of 0-group and ≥1-group fish in each survey trawl haul (*CpUE*, number·haul^{-1}), and successively fish densities (number·ha^{-1}) (see Appendix).

Intra-annual survey

For this survey, conducted during 4 moments within a years time (May 1994, August-September 1994, November-December 1994 and March 1995), a small, fine-meshed beam trawl was used (mouth width 3 m, mouth height 0.6 m, stretched mesh size in cod-end 2 mm). In total, 332 hauls of 10 minutes each were made, during which a distance of ca. 900 m was covered. See Chapter 4 for a detailed description of the gear. Hauls were randomly positioned in 2 depth strata (areas deeper and shallower than 5 m) and 7 geographic strata (3 in the northern basin, 4 in the southern basin; Fig. 9.1). Allocation of observations to strata was proportional to surface area of each stratum. To ensure sufficient coverage within each stratum, only locations at full geographical minutes were allotted a probability of being sampled (cf. Jolly & Hampton 1990). See Table A1 for survey details.

During the first survey in May 1994, we noticed that the bottom trawling did not catch any 0-group fish, and we suspected that 0-group fish inhabited the upper part of the water column only (cf. Chapter 6). Therefore, we made 12 additional hauls at the surface, positioned randomly over the middle stratum of the northern basin. We assumed that the volume swept by the surface hauls represented the 0-group density in the upper half of the water column.

The March 1995 survey was conducted just before and during the smelt fishing season. To allow for near-shore spawning concentrations of smelt, the March 1995 survey was stratified in a near-shore (2 km from the shoreline) and an open-water stratum. In the open-water stratum, the hauls were randomly positioned using the same procedure as in the other intra-annual surveys. In the near-shore stratum, one haul was randomly positioned within stretches along the shore of 5 km length each. Towing direction was always perpendicular to the shore. Preliminary analysis showed that only in the southern basin significantly more smelt in the near shore stratum were caught (ANOVA on ln-transformed *CpUE*, $P < 0.001$). Therefore, *CpUE* observations from the near shore and the open water stratum were pooled for the northern basin, whereas *CpUE* observations from the southern basin were weighted according to the surface area of each stratum in subsequent analyses. To assess the effect of the smelt fishery on smelt density, 12 sampling locations in the northern basin that were sampled before the beginning of the smelt fishing season (on March 10) were sampled again on April 9, after the closing of the fishing season.

The intra-annual survey yielded estimates of variation in stock density, mortality and individual body weight of each age group of small fish over the period May 1994 – March 1995.

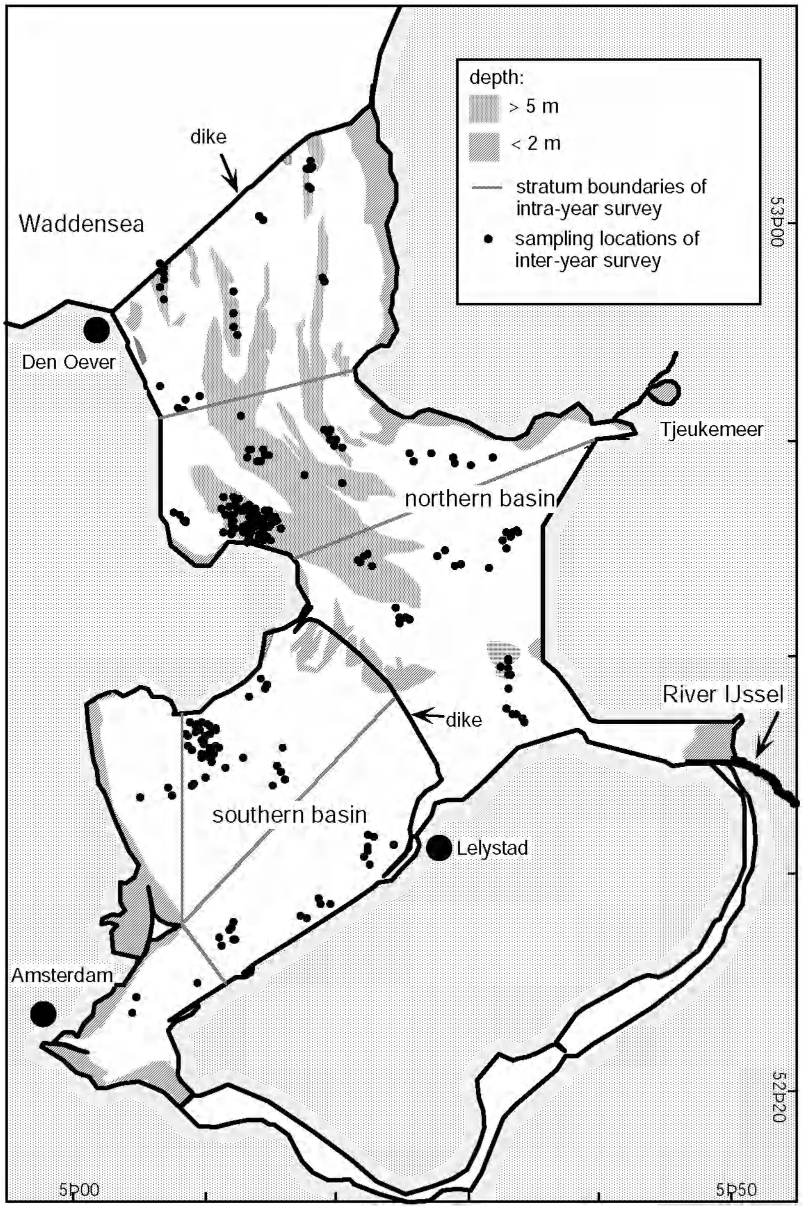

***Figure 9.1**. Map of IJsselmeer, with stratum boundaries of the intra-annual survey and sampling locations of the inter-annual survey*

Inter-annual survey

A bottom trawl was used to estimate inter-annual variation in density and size composition of small fish. The cod-end of the bottom trawl used had mesh size 1.8 cm (stretched mesh), mouth width 8 m, and height 1 m. Towing speed was ca. 1.5 m.s^{-1}. In total, 533 hauls of varying duration (10-45 minutes.haul^{-1}) were made. After 1982, haul duration was standardized (10 minutes.haul^{-1}). A complete description of the gear, including size selectivity characteristics, is given in Chapter 4. Sampling took place at fixed locations throughout the period 1966-1994 (Fig. 9.1), but the number of observations varied between years. Each survey was completed within 4 weeks in the period October-November. For observations on body size, we included *LFD*s as obtained during preliminary surveys in the years 1966-1969.

Production

Biological production (*P*) during the growing season was estimated per age group as the product of average biomass ($\overline{B}$) during the growing season and productivity (*P/B*), which productivity equals the instantaneous growth rate *G*, when assuming exponential growth in individual weight during the season (Ricker 1975):

$$P = G.\overline{B} \quad \text{[formula 9.1]}$$

The instantaneous growth rate (*G*) was estimated from $\ln(W_e/W_b)$, where W_b and W_e are the individual weights at the beginning and end of the growing season (June – November). Average biomass was approximated with $N_h.W(L_h)$, where N_h is fish density (numbers.ha^{-1}) halfway the growing season and W_h is individual weight (kg) corresponding with fish length (cm) halfway the growing season: $L_h = (L_e+L_b)/2$. N_h was reconstructed from fish density as recorded during the survey in fall (N_e) and mortality rate *Z* during the growing season via: $N_h = N_e.e^{-Z/2}$. For 0-group fish *Z* was estimated from density estimates during early summer, late summer and fall surveys.

Mortality rates for ≥1-group fish were estimated from density estimates during the fall surveys: $Z = \ln(N_{0\text{-}group}+N_{\geq 1\text{-}group})_{\text{year=t-1}} - \ln(N_{\geq 1\text{-}group})_{\text{year=t}}$. It was assumed that all mortality took place during the growing season. For ≥1-group smelt in the period 1982 - 1994, when a fykenet fishery for spawning smelt was operated in early spring of every year, instantaneous fishing mortality (*F*) was subtracted from instantaneous total mortality rate (*Z*). This *F* was calculated as the difference in *Z* per year between the reference period 1971 - 1981 and the period 1982 – 1994.

Utilization

Perch and pikeperch are the main fish predators in IJsselmeer, whereas fish consumption by eel is relatively low (Koenders & Mentink 1982; Buijse *et al.* 1993, Dekker & Van Willigen 1993, Paulisse 1993). An estimate for small fish consumption by perch and pikeperch was derived from the catch statistics of the commercial fishery. Perch and pikeperch in the commercial catch are all piscivorous. If the *CpUE* remains constant over a period of years, biological production of the exploited stock must at least equal the commercial catch (Baranoff 1918), and a conservative estimate of consumption then equals the commercial catch multiplied with the inverse of the commonly used gross food conversion efficiency of 0.2 for fresh weight (Pauly 1986). As fishing mortality (*F*) is much higher than natural mortality for these intensively exploited piscivores

(Dekker & Schaap 1993; Dekker 1996), the under-estimation due to this approximation method will be small, but the consumption of piscivores having not yet reached commercial size should be accounted for. Perch first appear in the commercial catch at a length of ca. 25 cm *TL* (Buijse *et al.* 1992), whereas perch are piscivorous at a length of ca. 18 cm *TL* (Buijse & Van Densen 1992; Van Densen, Ligtvoet & Roozen 1996). Pikeperch is piscivorous at a total length of 10 cm *TL* (Buijse & Houthuijzen 1992, Van Densen, Ligtvoet & Roozen 1996), whereas the minimum length in the catch is 37 cm *TL* (Buijse *et al.* 1992). A simple biomass/production model (formula [9.1], Ricker 1975) with F_{perch} = 0.86 yr^{-1}, $F_{pikeperch}$ = 1.5 yr^{-1}, (Dekker & Schaap 1993; Dekker 1996), $M = 0.2$ yr^{-1} and growth parameters as in Buijse *et al.* (1992), predicted that underestimation of consumption amounted to a factor 1.2 for perch and 2.9 for pikeperch. These factors were used to correct the consumption estimates.

Utilization of small fish and prey selection by piscivirous birds in IJsselmeer is extensively studied (Doornbos 1979; Schouten 1983; Van Eerden, Zijlstra & Munsterman 1991; Voslamber 1991; Buijse *et al.* 1993; Van Eerden 1993; Beekman & Platteeuw 1994; Winter 1994; Prins *et al.* 1995; Stam 1996), and basic data form these studies are summarized here.

The commercial catch was estimated through auction statistics. Fishermen were legally obliged to trade their catch through the auction before 1975, but about 10% of the catch was illegally sold directly to wholesalers (Nagtegaal & Snel 1984). After 1975, trading via the auction was no longer obliged, but this policy change was not reflected in a marked change in the auction statistics of commercially most important eel. Hence, we assumed that auction statistics continued to represent a constant proportion of the total catch. A relatively large part of smelt caught is sold directly to wholesalers, and therefore the catch volume sold directly in the years 1990-1993 and 1995 was estimated by interviewing the most important wholesalers.

To estimate the quantity and species composition of small fish caught as discards in eel fykenets, catch composition of experimental fykenet catches was determined in 1983 and 1987. In 1993, a creel survey was carried out to estimate the volume of discards (Dekker, Schaap & Van Willigen 1993). Results of these surveys are summarized here.

Density-dependency

As smelt and ruffe reach sexual maturity during their first year (Willemsen 1977), the stock size of smelt and ruffe in fall is a measure for the size of the spawning stock that will produce the 0-group fish of next year. To investigate whether the 0-group densities of smelt and ruffe were affected by parental stock size, we plotted 0-group fish density against size of parental stock of the previous year, using density estimates from the inter-annual survey.

Population density and growth for the three fish species and the two basins of IJsselmeer were subjected to correlation analysis to assess possible density-dependency of production. Also, we correlated population density and growth with average water temperatures in the 2nd and the 3rd quarters of the year (daily water temperature data from the Netherlands Ministry of Transport, Public Works and Water Management). The subdivision of the summer half year in two parts was meaningful, since the average water temperatures of the 2nd and 3rd quarter were not correlated

(Pearson correlation coefficient was 0.02 and 0.03 for the northern and the southern basin respectively).

Food quality, growth and condition

The correlation of mean length of smelt and 0-group perch as attained in fall with food quality during the growing season as indexed by the average body size of *Daphnia spp.* in the lake was investigated. The size distribution of *Daphnia spp.* was monitored in the northern and the southern basin of IJsselmeer in the years 1987, 1988, 1989 (Zuilekom 1991) and in 1992 (Prins *et al.* 1995). Because mean length of 0-group smelt varied within a narrow range (5.9-7.9 cm), we increased variation in mean length by including data on size and density of 0-group smelt and *Daphnia spp.* from Tjeukemeer, a lake close to IJsselmeer (Fig. 9.1).

In IJsselmeer, the population of large-bodied *Daphnia spp* is high until June, after which the population collapses due to a high predation pressure of zooplanktivorous fish (Prins *et al.* 1995; Veen, Vijverberg & Mooij 1997; Lammens 1999). To assess whether this resulted in a decrease in condition of smelt during the growing season, we studied the seasonal variation in condition of smelt. We measured percentage dry weight of 0-group and ≥1-group smelt that were sampled in the northern basin of IJsselmeer in May, June, August, September and November 1991. Of each length class (0.5 cm width) available in the catch, a sample of several fish weighing in total up to ca. 150 g was collected. The sample was homogenized using a ultrathorax. From the homogenized sample, replicates of 5-10 g material were dried during 10 hours at 70°C, and successively for 4 hours at 103 °C. After being placed for 2-3 hours in an exsiccator, the remaining material was weighed and dry weight was calculated. If the replicates differed more than 5% from each other, the analysis was done again. We used the mean of the replicate observations in our analysis.

A statistical model that explains variation in dry weight by sampling period was constructed to describe the seasonal variation in condition. Since condition of fish varies with length (Craig 1977; Delahunty & de Vlaming 1980; Booth & Keast 1986; Thompson *et al.* 1991 Liao *et al.* 1995; Miranda & Hubbard 1994; Salam & Davies 1994;), length was included as a covariate in the model.

RESULTS

Intra-annual variation in density and body size

For all species and age groups studied, most growth occurred in the period May 1994-September 1994 (Table 9.2). From December to April of the next year, hardly any growth occurred. Apparently, the growing season had ended by the end of November, and did not start until after March.

The 0-group smelt, having an average size of 2.2 cm *TL*, and perch, with an average size of 1.2 cm *TL*, were already present in large numbers in the survey catches of May 1994. The 0-group ruffe were probably not fully recruited at that time, as they were caught in only 3 of 12 surface hauls, and in none of the bottom hauls. Like growth, absolute mortality (in terms of numbers) was low during winter (November-March) compared to summer (May-September). This was probably the result of the slow growth and hence low predation pressure of piscivorous fish in winter. Also, fishing mortality due to discarding was nil during winter, since eelfyke fishery takes place in summer only. The most important cause of winter mortality must have been predation by piscivorous birds (see below). For the calculation of biological production, it was assumed that instantaneous mortality was constant during the growing season (May 20 to November 28), and that all mortality occurred in this period.

***Table 9.2**. Mean density (N, ha^{-1}) and mean total length (L, cm) of the major categories of small fish in the northern and southern basin during May 1994 - March 1995. The dates represent the average date of each sampling period. The 95% confidence interval of the means (CI) is presented as a factor. I.e., the upper confidence limit for mean x with CI y is xy; the lower confidence limit is x/y. Estimates between brackets were based on 12 surface trawl hauls, the other estimates were based on the bottom trawl surveys. The coefficient of variation in length was approximately 10%.*

basin/	0-group smelt			≥1-group smelt			0-group perch			0-group ruffe			≥1-group ruffe		
date	$N.10^3$	CI	L	N	CI	L	N	CI	L	$N.10^3$	CI	L	N	CI	L
northern															
20-May-94	(134)	(2.0)	(2.2)	430	1.9	8.4	(4500)	(2.5)	(1.2)	0.00	-	1.0	331	1.3	10.3
1-Sep-94	132[a]	1.6	5.9	87	1.3	10.4	37	1.5	8.3	0.56	1.5	7.0	83	1.7	11.5
28-Nov-94	32	1.4	6.7	53	1.5	11.3	33	1.5	8.0	1.1	1.8	7.6	83	2.0	11.7
23-Mar-95	23[b]	1.3	6.7	38[b]	1.3	10.5	38	1.3	8.4	0.93	1.3	8.3	95	1.3	11.7
southern															
6-Sep-94	34[a]	1.5	6.7	430	1.4	8.4	48	1.6	6.4	0.64	1.4	8.4	61	1.4	10.1
13-Dec-94	5.1	1.3	7.3	299	1.3	9.2	78	1.6	7.2	2.2	1.7	8.7	339	1.6	10.4
23-Mar-95	2.3[b]	1.5	7.3	119[b]	1.5	9.2	46	1.1	7.3	2.4	1.3	8.9	431	1.3	10.6

Notes

a. *The estimate was corrected for the water transparency-mediated vertical distribution pattern of smelt < ca. 7 cm TL (0-group, cf Chapter 6).*

b. *The estimates were corrected for fishery mortality due to the smelt fykenet fishery.*

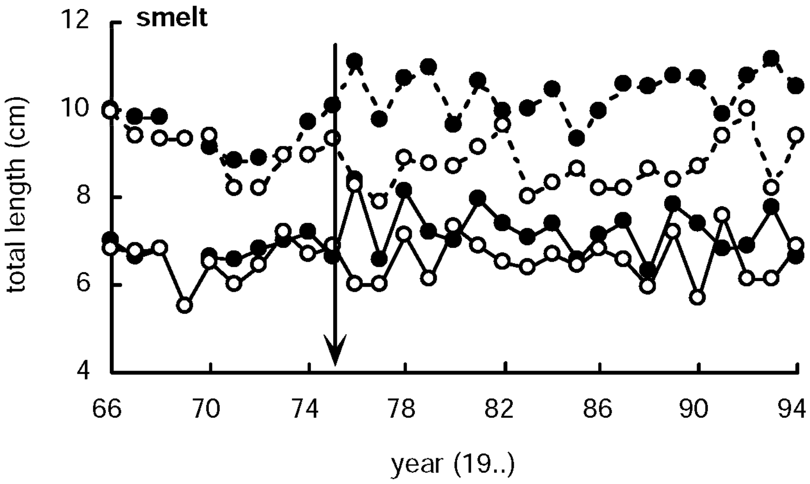

Figure 9.2. Mean total length of 0-group (solid lines) and ≥1-group (dashed lines) smelt in the northern basin (solid plot symbols) and the southern basin (open plot symbols) in fall. The arrow indicates the year when the dike that separates the northern basin from the southern basin was completed (1975).

Inter-annual variation in body size

The 0-group smelt reached a mean length of 6-8 cm and ≥1-group smelt a length of 8-11 cm (Fig. 9.2). Since the building of the dike that separates the northern basin from the southern basin (1975), 0-group smelt in the northern basin was on average 10% (0.7 cm) longer than 0-group smelt from the southern basin. The ≥1-group smelt differed with 15-20% (1.7 cm). The difference in length after dike construction is due to the increase in mean length of smelt in the northern basin from on average 6.8 cm (1966-1975) to 7.2 cm (1976-1994). For ≥1-group smelt, mean length increased from 9.4 to 10.4 cm. The differences were significant for both 0-group and ≥1-group smelt (two-tailed t-tests, $P = 0.04$ and $P < 0.01$).

The mean total length of 0-group perch averaged 7.5 cm (Fig. 9.3). There was no noteworthy difference in length between the northern and the southern basin.

Ruffe (Fig. 9.4) reached a mean total length of 6-8 cm in their first growing season. The mean length of ≥1-group ruffe varied between 9 and 12 cm. After dike construction, 0-group ruffe was on average 0.9 cm longer, and ≥1-group ruffe was on average 1.2 cm longer in the northern basin than in the southern basin. Also here, the difference originated from a faster growth after dike construction in the northern basin: the difference for 0-group ruffe was 1.2 cm and for ≥1-group ruffe 1.4 cm (two-tailed t-tests, $P < 0.01$).

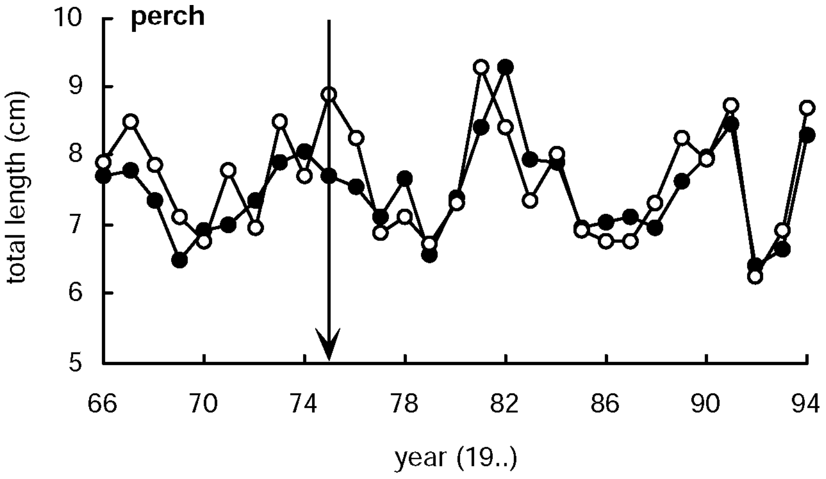

Figure 9.3. Mean total length of 0-group perch in fall. For further explanation, see caption of Fig 9.2.

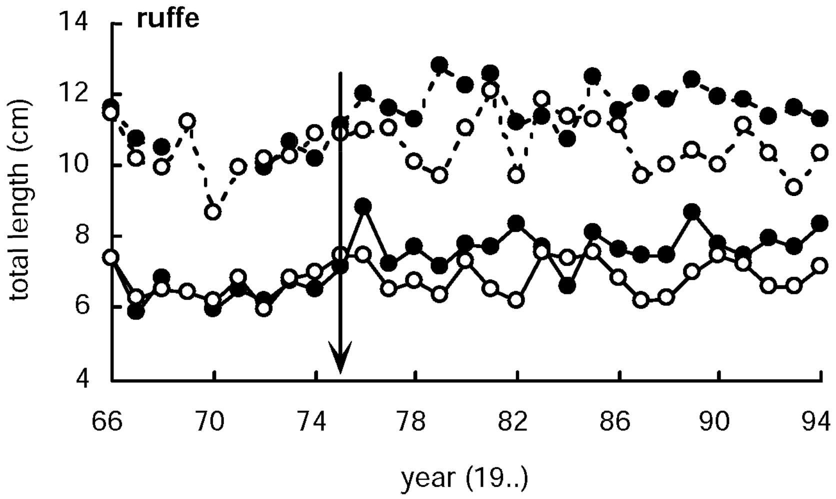

Figure 9.4. Mean total length of 0-group and ≥1-group ruffe in autumn. For further explanation, see caption of Fig. 9.2.

Inter-annual variation in density

Population density in fall differed significantly between years for each species (ANOVA for each species and basin: $R^2 > 0.25$; $P < 0.001$). The models fitted the observations reasonably well, as only two residual distributions were different from normal (Wilk-Shapiro statistic < 0.95, $P < 0.05$). Firstly, the residual distribution for ≥1-group smelt from the northern basin was skewed to the left. Secondly, a single outlier caused deviation from normality for 0-group ruffe from the southern

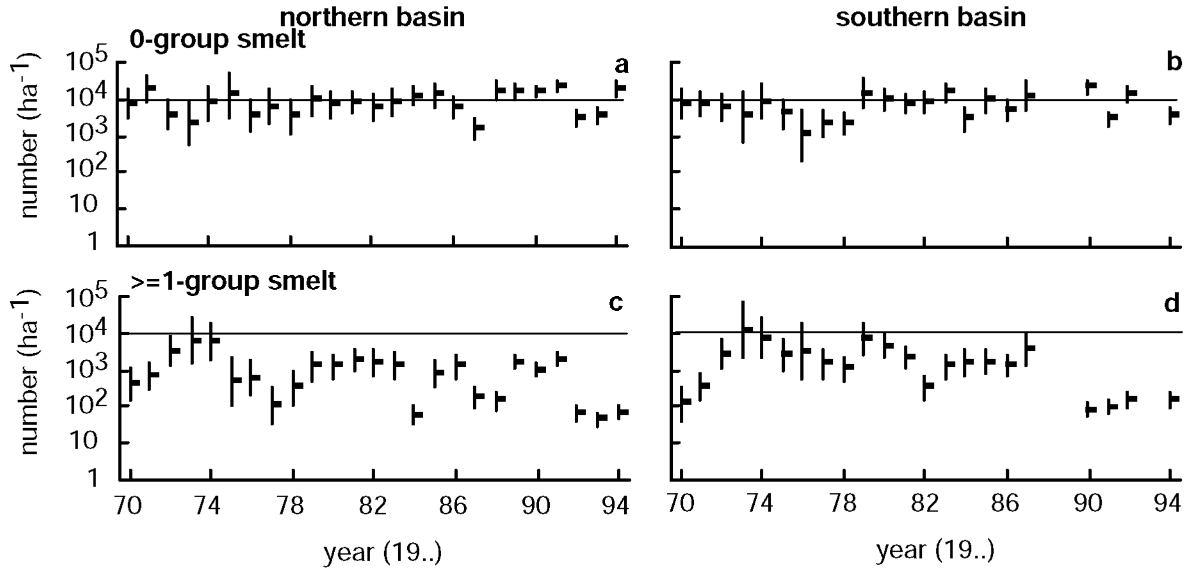

Figure 9.5. Mean smelt density (ha^{-1}), with 95% confidence limits of the mean. A reference line is indicated at a density of 10,000 ha^{-1}.

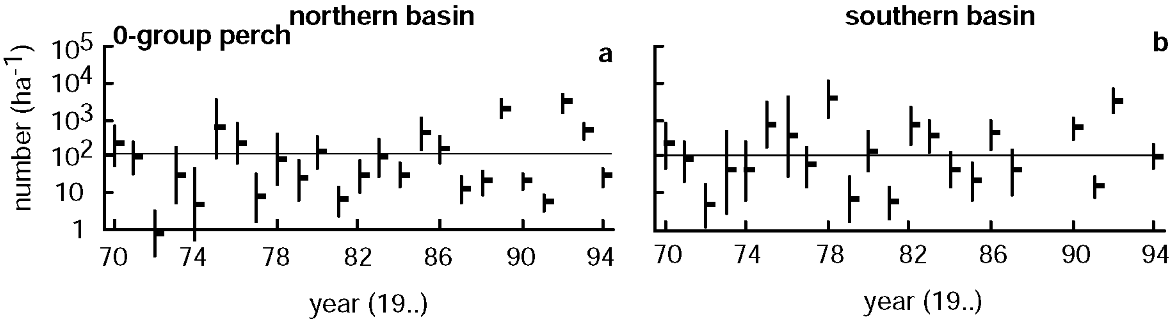

Figure 9.6. Mean 0-group perch density (ha^{-1}), with 95% confidence limits of the mean. A reference line is indicated at a density of 100 ha^{-1}.

basin. The density of 0-group smelt, which showed no trend over the period 1970-1994, varied by a factor of only ca. 10 (1,000-10,000.ha^{-1}) in both basins (Fig. 9.5). The density of ≥1-group smelt (Fig. 9.5 c and d) varied stronger than the density of 0-group smelt. There was no clear decreasing or increasing trend in the density of ≥1-group smelt, though autocorrelation was high for some years (e.g. the period 1970-1975 in both basins). After 1984, density of ≥1-group smelt was frequently low at ca. 100 ha^{-1}. Correlation between smelt density of the northern and of the southern basin over the period 1975-1994 was low and insignificant (0-group: Pearson = -0.1; ≥1-group: Pearson = 0.13, $P > 0.1$).

Density of 0-group perch fluctuated much more than the density of smelt, up to a factor 1000 in both basins (Fig. 9.6). As with smelt, there was no trend over the period 1970-1994. Correlation of 0-group perch density between basins was high and significant (Pearson correlation coefficient = 0.68, $P < 0.01$).

The 0-group ruffe were 2.5 times more abundant, and ≥1-group ruffe were 6.3 times more abundant in the southern basin than in the northern basin over the period 1970-1994 (Fig. 9.7).

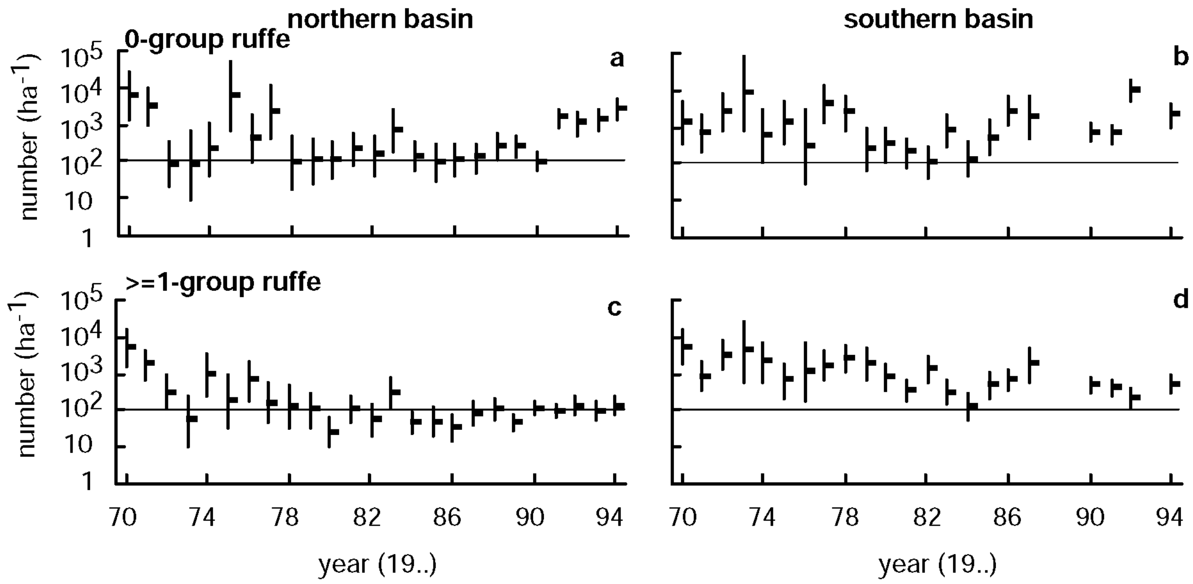

Figure 9.7. Mean ruffe density (ha^{-1}), with 95% confidence limits of the mean. A reference line is indicated at a density of 100 ha^{-1}.

Only ≥1-group ruffe showed a clear decreasing trend over the period 1970-1994 (Fig. 9.7c, d). In the northern basin, ≥1-group ruffe density seemed to have stabilized after 1982. Correlation between ruffe density of the northern and of the southern basin over the period 1975-1994 was low and insignificant (0-group: Pearson = 0.18; ≥1-group: Pearson = 0.04, $P > 0.1$).

Production

The mortality rate (Z) of 0-group smelt during summer, calculated as $\ln(N_{May\ 20}) - \ln(N_{November\ 28})$ (cf. Table 9.2), was low ($Z = 1.4$ growing season^{-1}). This was caused by the low estimate of the density in May, as compared to the density in September. It is possible that this low density estimate at the start of the growing season was caused by sampling bias, as surface hauls were only made in the middle part of the northern basin. Therefore, total mortality rate was also calculated under the assumption that the daily mortality rate during the period May 20 – November 28 was the same as the daily mortality rate during the period September 1 – November 28 ($Z = 0.0161$ day^{-1}). Under this assumption, $Z = 3.1$.growing season^{-1} in the northern basin, and $Z = 4.0$.growing season^{-1} in the southern basin. Under the assumption of the high values for Z, production was ca. 2 times higher in the northern basin, and nearly 4 times higher in the southern basin than if the low values for Z were used for production estimates (Table 9.3). We think that the higher production estimates were more realistic (cf. Buijse *et al.* 1993).

The 0-group smelt dominated production of small fish. The contribution of 0-group smelt production to the total small fish production was 72% in the northern basin, and 60% in the southern basin. The 1-group smelt contributed little to the total production, because of their marginal growth. In the southern basin, production of 0-group perch and ruffe was higher than in

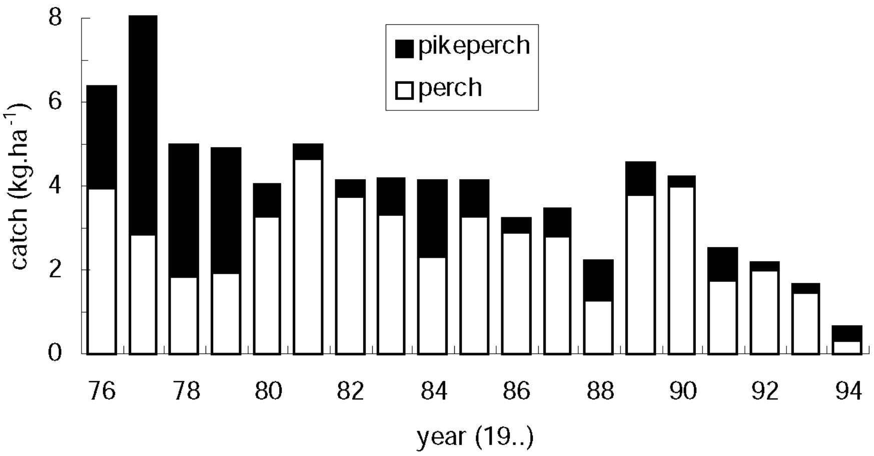

Figure 9.8. *Annual landings (kg.ha^{-1}) of perch and pikeperch in 1976-1994 (auction statistics).*

the northern basin. Variation in 0-group smelt production was low compared to other species groups: over the period 1976-1994, 67% of the annual production estimates varied within a factor of ca. 2 around the geometric mean (sd_G 1.9 in the northern, and 2.3 in the southern basin). Due to the high inter-annual variation in density, variation in 0-group perch production was high (sd_G 5.7 in the northern, and 6.9 in the southern basin).

Utilization by piscivorous fish and birds

The catch statistics for perch and pikeperch (Fig. 9.8) that were used to calculated total consumption were multiplied with 1.1 to allow for fish that were traded without using the services

Table 9.3.. *Summary statistics of yearly production (kg.ha^{-1}) over the period 1976-1994 in the northern and the southern basin. mean = arithmetic mean, mean$_G$ = geometric mean, sd$_G$ = back-transformed standard deviation of ln-transformed annual production estimates, min., max. = minimum and maximum production estimated.*

	northern basin					southern basin				
	mean	mean$_G$	sd$_G$	min.	max.	mean	mean$_G$	sd$_G$	min.	max.
smelt, 0-group, high M	72.9	61.0	1.9	14.0	166.0	70.1	54.5	2.3	7.2	134.7
smelt, 0-group, low M	31.8	26.6	1.9	6.1	72.4	18.9	14.7	2.3	1.9	36.4
smelt, ≥1-group(a)	4.8	2.6	3.4	0.3	16.4	3.3	2.0	2.9	0.3	16.0
perch, 0-group (b)	12.9	3.0	5.6	0.3	95.8	23.2	5.8	6.8	0.2	137.7
ruffe, 0-group (c)	6.8	3.3	3.4	0.9	35.2	11.6	5.8	3.6	0.6	60.4
ruffe, ≥1-group(a)	4.4	1.5	3.4	0.3	50.8	7.7	5.2	2.6	0.9	24.9

Notes

a. *Mortality estimates for ≥1-group fish were calculated from the inter-annual survey (see Materials and methods section).*

b. *Mortality rate was estimated as $\ln(N_{May 20,\ 1994}) - \ln(N_{November\ 28,\ 1994}) = 4.9$ growing season^{-1}. This mortality rate was also applied to 0-group perch from the southern basin.*

c. *For 0-group ruffe, the intra-annual survey resulted in a negative estimate for summer mortality. Hence, the estimate for ≥1-group ruffe was adopted.*

of the auction (cf. Nagtegaal & Snel 1984). Assuming a gross food conversion ratio for wet weight of 0.2 (Pauly 1986), and a multiplication factor of 1.2 for perch and 2.9 for pikeperch to allow for fish consumption by perch and pikeperch that were smaller than the minimum legal size, fish consumption by perch and pikeperch in 1976-1994 averaged 38 $kg.ha^{-1}.yr^{-1}$ (range 8-102 $kg.ha^{-1}.yr^{-1}$).

Cormorants *Phalacrocorax carbo* contribute ca. 40 % to the total fish consumption by birds in IJsselmeer (Table 9.4) (Buijse *et al.* 1993). Ca. 75% of their food consisted of ruffe and perch. For all piscivorous bird species combined, smelt was the most important prey fish, and ca. 40% of the smelt extraction by birds was consumed by black-headed gull. Still, as black-headed gull uses a variety of terrestial and aquatic food resources, including discards of the commercial fishery (Voslamber 1991), black-headed gull was probably not strongly dependent on the smelt stock (cf. Chapter 8). Overwintering mergansers and migrating black terns are more directly dependent on smelt (Chapter 8; Doornbos 1979; Schouten 1983; Beekman & Platteeuw 1994; Stam 1996), though their annual consumption is about 4 times less than the annual consumption by black-headed gull (cf. Table 9.4).

Cormorant is the only fish-eating bird species that showed a clear trend in population density in the 1980s and early 1990s (Winter 1994; Prins *et al.* 1995). The number of breeding pairs in the three colonies around IJsselmeer increased by nearly a factor 4 from 1978 to 1993 (Fig. 9.9), after which it dropped by one-third in 1994. The drop was probably caused by the extremely bad breeding season of 1993: cormorants had a breeding success of 0.2 young per breeding pair (Van Eerden 1993), as compared to 0.5-2.6 young in the period 1981-1987 (Van Eerden, Zijlstra & Munsterman 1991). The low breeding success was caused by starvation of the chicks, as the unusually high water transparency observed during spring of 1993 negatively affected feeding efficiency of cormorants on smelt, the most important food for chicks (Van Eerden 1993). Low density of smelt, as observed in fall 1992 (Fig. 9.5) was probably an important factor as well. The spring of 1993 was probably the only period since 1980 during which food limitation of piscivorous birds was apparent. In 1994-1998, the number of breeding pairs of cormorant stabilized at ca. 11,000.

Table 9.4*. Fish consumption by birds (*$kg.ha^{-1}.yr^{-1}$*). Table adjusted from Buijse et al. 1993. Data are representative for the 1990's (cormorants) and the late 1980's.*

predator	prey smelt	ruffe	roach	bream	eel	perch	pike-perch	*total*
cormorant, *P. carbo*	1.7	8.4	3.1	0.0	0.2	7.3	0.0	*20.7*
black-headed gull, *Larus ridibundus*	8.1	1.0	0.0	0.0	0.0	1.0	0.0	*10.1*
grebe, *Podiceps cristatus*	4.6	0.6	0.1	0.1	0.0	0.4	0.0	*5.7*
goosander, *Mergus merganser*	2.7	0.6	1.5	0.0	0.0	0.8	0.0	*5.6*
red-breasted merganser, *Mergus serrator*	0.3	0.0	0.0		0.8	0.0		*1.1*
black tern, *Chlidonias niger*	1.1	0.0				0.0		*1.1*
smew, *Mergus albellus*	0.9	0.1						*1.0*
other	0.9	0.4	0.7	0.5	0.0	0.5	0.0	*3.0*
total	*20.3*	*11.1*	*5.4*	*0.6*	*0.9*	*10.0*	*0.0*	*48.3*

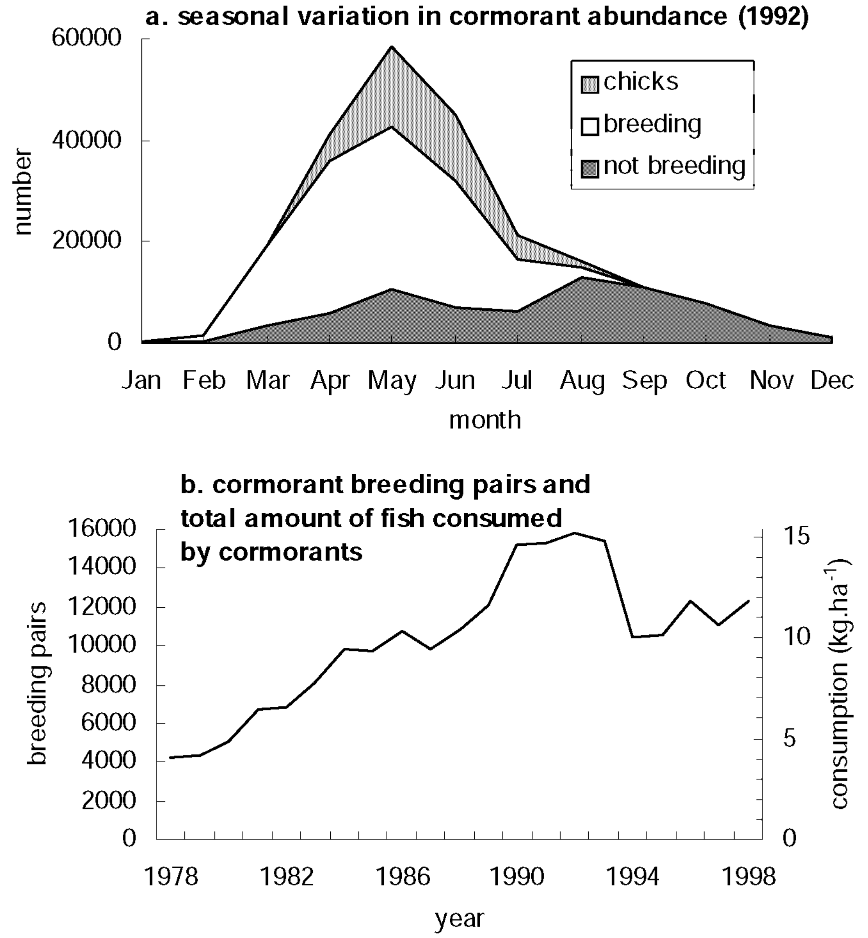

***Figure 9.9**. Seasonal variation in number of cormorants around IJsselmeer in the year 1992 (a), and inter-annual variation in breeding pairs and fish consumption (b). The number of breeding pairs in the IJsselmeer area over the period 1978-1998 is derived from van Eerden & Gregersen (1995), Timmerman & Prins (1996) and SOVON. The relationship between predation pressure exerted by breeding cormorant pairs on the one hand and the total cormorant predation pressure (including chicks and non-breeding cormorants) on the other hand was estimated from cormorant abundance surveys conducted in 1992. Assuming that daily fish consumption for each cormorant was 0.4 kg (cf Platteeuw, Koffijberg & Dubbeldam 1995; Platteeuw & van Eerden 1995), the total annual predation of the cormorant population was estimated at 175 kg per breeding pair.*

Utilization of small fish production by the fishery

Smelt is the only small fish species that is targeted for by the commercial fishery (Fig. 9.10). Already before the transition from a marine into a freshwater system by the construction of a dike in 1932, a commercial fishery on smelt existed. After 1932, the fishery was practiced irregularly, and only larger smelt (ca. > 10 cm *TL*) were landed to satisfy a small domestic market. In 1982, an export market for all size classes of smelt developed. This was the beginning of an intensive fykenet fishery on spawning aggregations of smelt, which took place for a period of 4-6 weeks

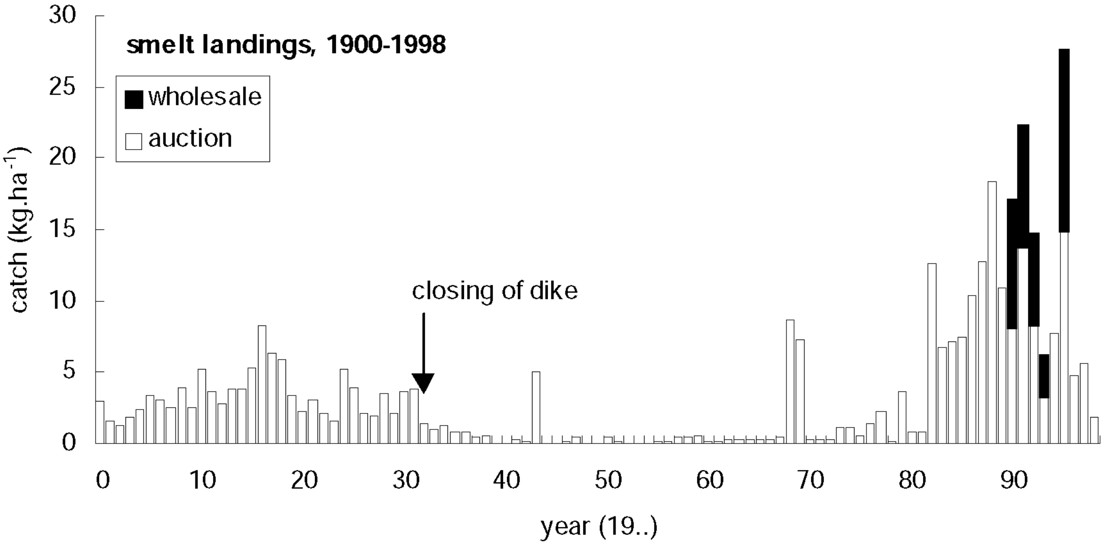

***Figure 9.10**. Annual catch of smelt (kg.ha^{-1}.yr^{-1}) over the period 1900-1998. In the years 1990-93 and 1995, statistics on both the amount fish sold directly to wholesalers and the amount of fish traded at the auction were collected. In these years, between 47 and 62% (mean 54%) of the total amount of smelt caught were auctioned. The year when the dike that separated IJsselmeer from the Waddensea was completed (1932) is indicated).*

during March-April. The fykenet fishery targeted for the total smelt population, including the youngest age group (Janss 1991). The fishery landed between 5 and 30 kg.ha^{-1}.yr^{-1}.

After the development of the smelt fykenet fishery in 1982, survival of 0-group smelt dropped significantly. Instantaneous mortality rates (*Z*, year^{-1}) were 1.15 (northern basin) and 1.35 (southern basin) higher than before (Table 9.5; two-tailed t-test, $P < 0.05$). Hence, fishing mortality (*F*) must have amounted to 1.15 year^{-1} for the northern basin and 1.35 year^{-1} for the southern basin. This implies that during the period of 4-6 weeks when the smelt fishery took place, ca. 70% of the population was caught each year. The trawl surveys before and after the smelt fishing season of 1994 (see Materials and Methods) corroborated these estimates of *F*. The density of 0-group smelt differed significantly before and after the fishing season (ANOVA on ln-transformed catch numbers, $P < 0.01$). *Z* over the fishing season (March 10 - April 9) was estimated at 1.59 (95% *CL*s: 0.54-2.64). Assuming that the natural mortality was negligible, the *F* was equal to *Z*. Density of ≥1-group smelt fell below trawl detection level during the fishing season: before the

***Table 9.5.** Mean total instantaneous mortality rate (yr^{-1}) of smelt from fall to fall of the next year in the periods 1970-1981 and 1982-1994. Z was estimated as $\ln(N_{0\text{-group, year=t-1}}+N_{\geq 1\text{-group,year=t-1}})-\ln(N_{\geq 1\text{-group,year=t}})$, where $N_{0\text{-group}}$ and $N_{\geq 1\text{-group}}$ represent population density estimates in fall (cf Fig. 9.5 a-d).*

basin	1971-1981		1982-1994	
	mean	sd	mean	sd
north	2.05	1.20	3.20	1.27
south	1.10	1.05	2.45	1.49

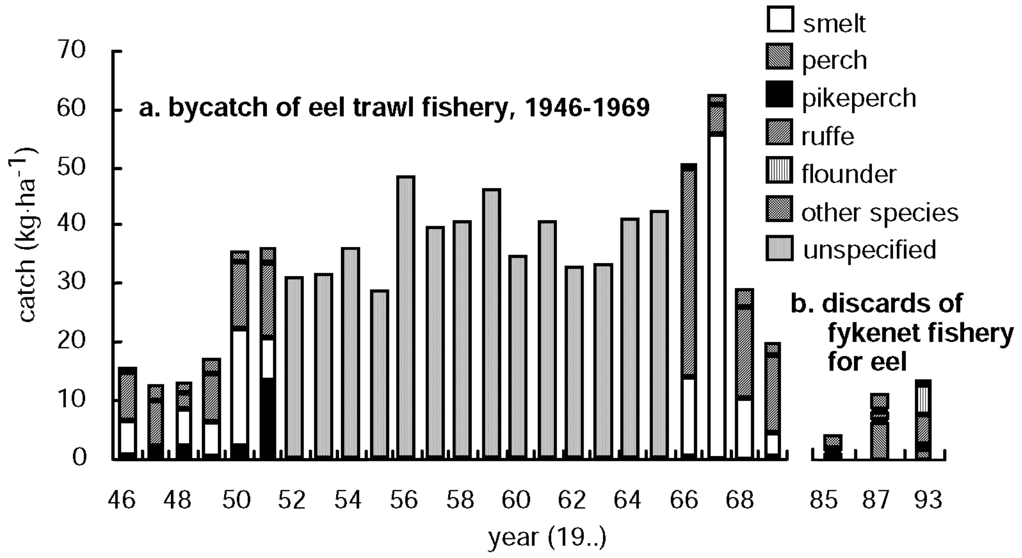

***Figure 9.11**. Yearly bycatch of the eel trawl fishery (a) and the eel fykenet fishery (b). To estimate species composition of the eel trawl bycatch, the species composition of survey trawl catches made in summer 1946-1951 (De Beaufort 1954) and 1966-1969 (Steinmetz & Oudelaar 1971) were used. The survey gear was similar to the gear used by the commercial fishery. Total weight of the eel trawl bycatch was obtained from auction statistics. The yearly eel fykenet bycatch of 1983, 1987 and 1993 was estimated by experimental fykenets and a creel survey among the fishermen (Dekker, Schaap & van Willigen 1993).*

fishing season, only 2 of 13 hauls consisted of zero catches, whereas after the fishing season, 9 of 13 hauls contained no ≥1-group smelt. Catch numbers of 0-group perch, 0-group ruffe and ≥1-group ruffe did not decrease significantly over the smelt fishing season (ANOVA on ln-transformed catch numbers; Wilcoxon's test, $P > 0.10$). This confirmed our observations that bycatch in the fykenet fishery for smelt was small.

Before 1970, smelt and other small fish were also caught as bycatch in the trawl fishery for eel. This bycatch was sold at the auction as trash fish (Fig. 9.11). The bulk of these trash fish consisted of smelt and ruffe, but substantial numbers of perch and pikeperch juveniles were also

***Table 9.6**. Summary of smelt production and utilization estimates (kg.ha^{-1}.yr^{-1}). Minimum and maximum over the indicated period are between brackets.*

	northern basin	southern basin
production (1976-1994)		
0-group smelt	73 (14 – 166)	70 (7.1 – 135)
≥1-group smelt	5 (0.34 - 16)	3 (0.32 – 16)
utilization		
piscivorous fish[a] (1976-1994)	38 (8-102)	
piscivorous birds (1983-1987)	ca. 20	
fishery[b] (1982-1994)	19 (6 – 34)	

Notes

a. Most of the fish (> ca. 90%) consumed by perch and pikeperch consist of smelt (Willemsen 1977; Buijse & Houthuijzen 1992; Buijse & Van Densen 1992; Buijse et al. 1993)

b. Corrected auction statistics, assuming that 54% of the total catch was auctioned.

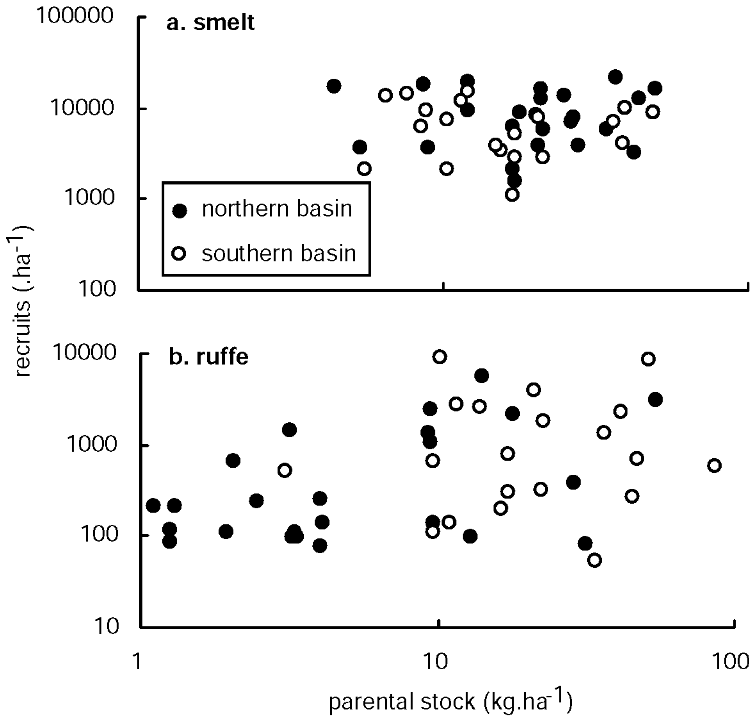

***Figure 9.12**. Scatterplots of recruitment vs. parental stock size over the period 1970-1993. The population stock size (weight of 0-group and ≥1-group fish combined) during fall was used as a measure for the parental stock size; the density of 0-group fish (.ha^{-1}) in fall of the next year was used as a measure for recruitment.*

caught (De Beaufort 1954). Because of its hypothesized negative effects on the gillnet and fykenet fishery for adult perch and pikeperch, the eel trawl was banned in 1970. After 1970, the eel trawl was replaced by a fykenet fishery for eel. Similar to the eel trawl fishery, the fykenet fishery caught other species along with the target species. However, this non-target catch was not sold at the auction, but discarded. As discarded fish do not survive (Willemsen 1985), the fykenet fishery causes fishery mortality in small fish.

Compared to the bycatch of the eel trawl fishery (13-62 kg.ha^{-1}.year^{-1}), the bycatch of the eel fykenet fishery (4-14 kg.ha^{-1}.year^{-1}) was low (Fig. 9.11). The eel fykenets caught less smelt, more perch, and in 1993 a substantial amount of flounder (ca. 36% of the total bycatch). The catch of smelt in the fykenets was underestimated, since the fishermen removed gilled smelt during the hauling process, before the catch could be measured. Still, the bycatch after the trawl ban in 1970 seemed orders of magnitude smaller than before 1970. Thus, the exploitation pattern of smelt has changed dramatically in almost 50 years: from intensive exploitation by a trawl fishery until 1970, and low exploitation rates until 1981, to the intensive exploitation of spawning smelt by a fykenet fishery.

The balance between production and utilization

Smelt was the most important small fish species in terms of production and consumption. Although variation in the production of smelt was large, and although there were uncertainties in the consumption estimates, it was clear that the estimate of smelt production was low compared to its total utilization. Thus, the major part of smelt production must have been utilized by piscivorous fish, birds and by the fishery (Table 9.6).

Factors affecting production

Recruitment

Only for ruffe, a stock-recruitment relationship could be proven (Fig. 9.12). In the northern basin, the parental stock was frequently low (< ca. 5 kg.ha^{-1}), which resulted in a lower recruitment (linear regression of ln-transformed 0-group ruffe density on ln-transformed density of parental stock: R^2 = 0.21, P = 0.02). With only one exception, parental stock density in the southern basin was higher than 9 kg.ha^{-1}, which was apparently sufficient to guarantee reproduction. Possibly, the variation in parental stock size of smelt in the period 1970-1993 was too low to detect a stock-recruitment relationship. Though the smelt fishery extracted smelt that had not reproduced yet (cf. Janss 1991), there was no evidence that this practice decreased recruitment of smelt. With a smelt stock in fall of at least 4.4 kg.ha^{-1}, the lowest stock size over the period 1970-1993 in both basins, recruitment seemed to be guaranteed. Earlier studies on perch and pikeperch recruitment in IJsselmeer already showed that there was no significant stock-recruitment relationship (Buijse, Van Densen & Schaap 1992) within the observed variation in the parental stock size in IJsselmeer.

***Table 9.7**. Pearson correlation coefficients for correlation between density (N), mean total length (TL) and water temperature in the 2nd (Q2) and 3rd quarter (Q3). The correlation coefficients were calculated from estimates over the period 1976-1994. Asterisks indicate significance: * 0.05 < P<0.1, ** 0.01 < P < 0.05, *** P < 0.01.*

basin/ species	N*TL	N*Q2	N*Q3	TL*Q2	TL*Q3
northern basin					
smelt, 0-group	-0.44*	-0.04	0.22	0.25	-0.04
smelt, ≥1-group	-0.32	-0.09	0.47*	0.55	-0.10
perch, 0-group	-0.44*	0.58**	0.02	-0.18	0.53**
ruffe, 0-group	0.07	0.06	0.28	0.52**	0.35
ruffe, ≥1-group	-0.13	0.14	0.20	0.03	-0.08
southern basin					
smelt, 0-group	-0.25	0.37	0.17	-0.36	0.24
smelt, ≥1-group	-0.58**	-0.35	-0.47*	0.22	0.29
perch, 0-group	-0.28	0.60**	0.06	-0.03	0.47**
ruffe, 0-group	-0.17	0.16	-0.09	-0.14	0.17
ruffe, ≥1-group	-0.55**	-0.08	-0.26	-0.47*	0.07

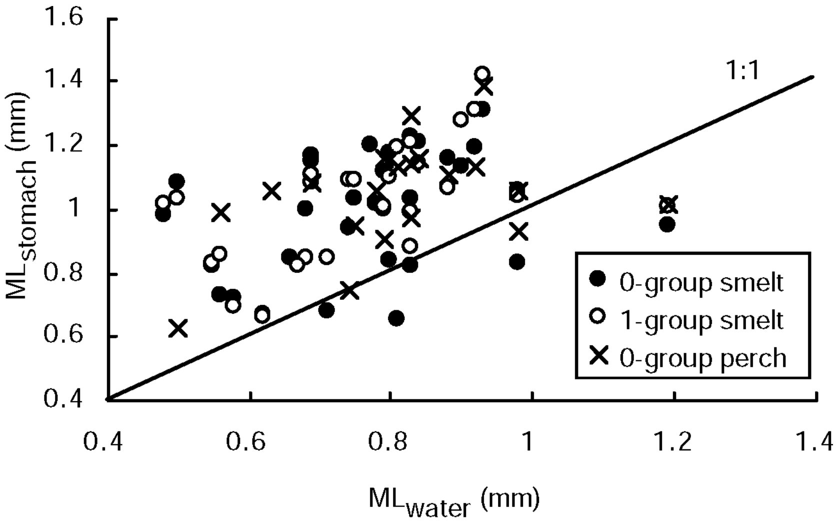

***Figure 9.13**. Relationship between mean length of Daphnia spp available in the water column (ML_{water}) and the mean length of Daphnia spp encountered in stomachs of 0-group smelt ($ML_{stomach}$), ≥1-group smelt and 0-group perch. The 1:1 line represents non-selectivity. Data from Houthuijzen (1989).*

Growth in relation to density, water temperature, and food availability

Slow growth was associated with high population density for each species and in both basins, except for 0-group ruffe in the northern basin (Table 9.7). Density and mean length of smelt and ruffe were in some situations correlated with water temperature, but the correlations were not consistent between basins (Table 9.7). Therefore, we did not consider them further. A higher mean water temperature during the 2nd quarter had a positive effect on density of 0-group perch in both basins. Apparently, high temperatures during spawning and during the first months in the life

***Table 9.8**. Pearson correlation coefficients for ln-transformed 0-group smelt density (lnN), smelt length (L) and Daphnia length (DL). Asterisks indicate the significance level. *: 0.05<P<0.1 **: 0.01<P<0.05, *** P<0.01.*

	IJsselmeer		IJsselmeer and Tjeukemeer	
	L	DL	L	DL
lnN	-0.31	-0.77	-0.66***	-0.74***
L		0.83**		0.82***

***Table 9.9.** ANCOVA table for PDW - length relationships in smelt. Effect mean squares are type III. df = degrees of freedom, MS = mean squares, P = significance level.*

source	df	MS	P
model	6	69.9	0.0001
error	43	1.09	
TL	1	133	0.0001
TL^2	1	106	0.0001
MONTH	4	38.0	0.0001

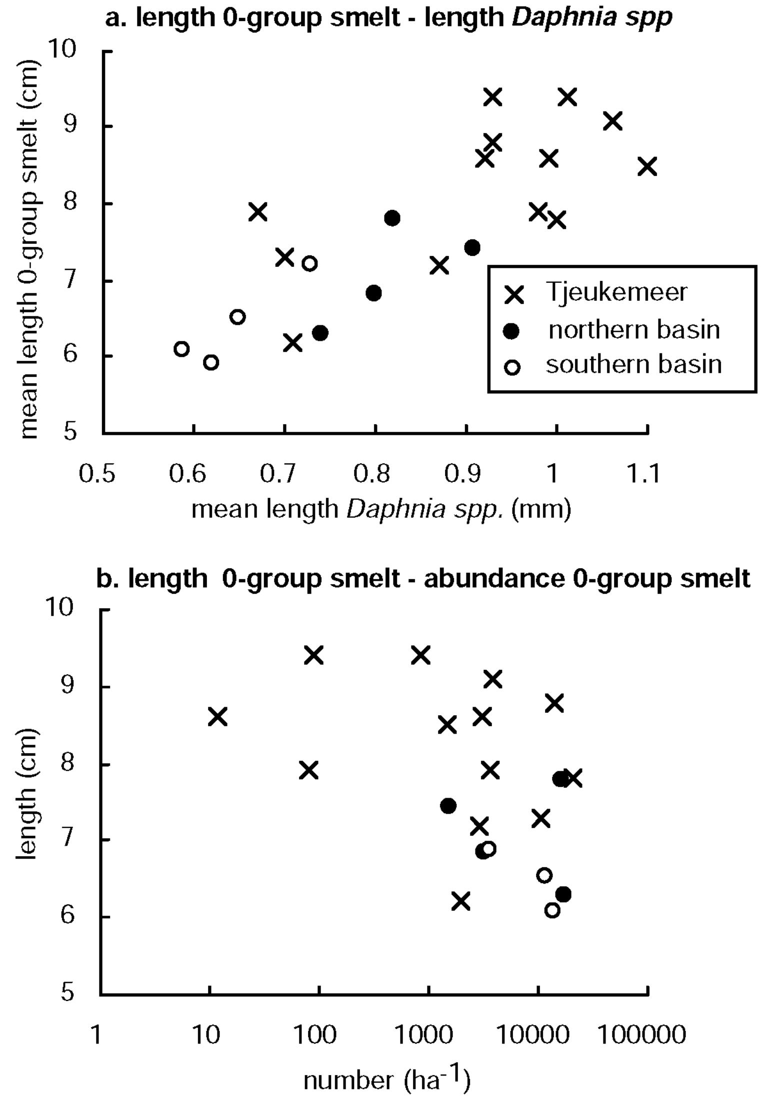

***Figure 9.14**. Top panel (a): Relationship between length of 0-group smelt at the end of the growing season and mean length of Daphnia spp in August-September in IJsselmeer and Tjeukemeer. Bottom panel (b): Relationship between length of 0-group smelt at the end of the growing season and 0-group smelt density at the end of the growing season.*

of the newborns favored reproduction success (see also Buijse, Van Densen & Schaap 1992). Growth of 0-group perch was positively affected by 3rd quarter mean water temperature; this correlation was consistent between the basins. The dependence of first-year growth on the mean temperature of the 3rd quarter was to be expected, since during the 3rd quarter 0-group perch gained ca. 90% of its weight attained at the end of the growing season. In conclusion, 0-group perch density and growth were positively affected by temperature, whereas growth of smelt and ruffe seemed to be governed by density-dependent resource limitation only.

In IJsselmeer, smelt and 0-group perch selected towards the larger bodied *Daphnia spp.* (Fig. 9.13). Also in Tjeukemeer, a 2000 ha lake nearby IJsselmeer, both smelt and 0-group perch select for larger *Daphnia spp*, and growth is slower in the absence of their preferred food item

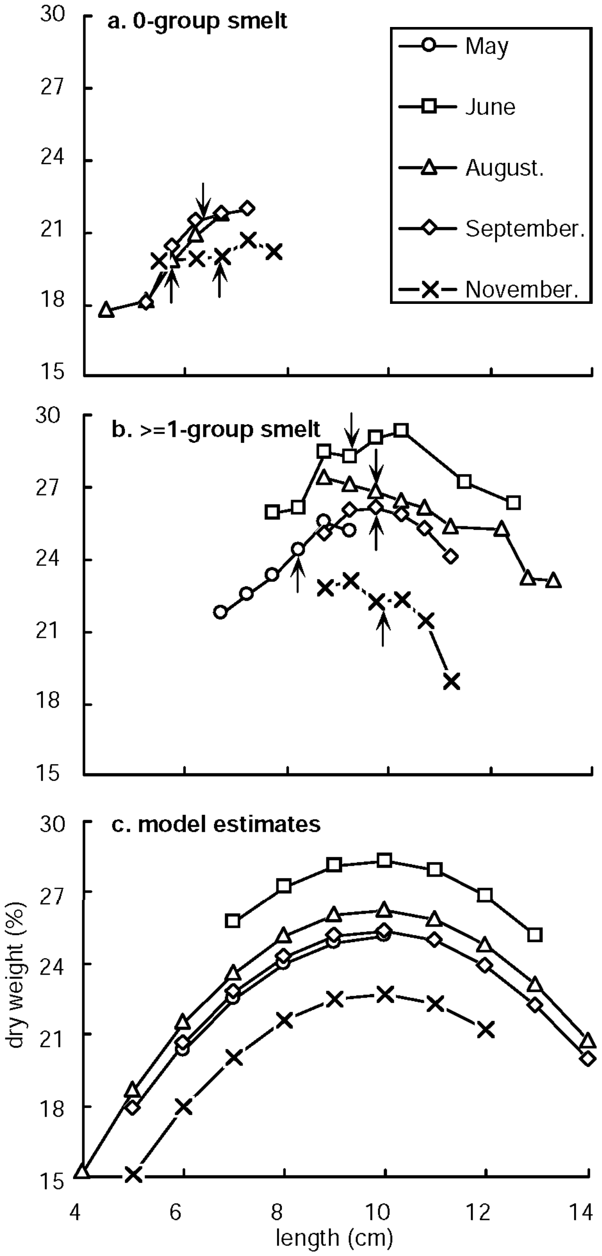

***Figure 9.15**. Seasonal variation in the relationship between dry weight (as % of total wet body weight) and total length of 0-group smelt (a) and ≥1-group smelt (b). The mean length of the age class in each month is indicated by arrows. The lower panel (c) represents the modeled relationship.*

(Van Densen 1985; Lammens *et al.* 1985). The relationship between growth and mean *Daphnia spp* length (Fig. 9.14a), and between smelt growth and density seemed to be the same for IJsselmeer and Tjeukemeer (Fig. 9.14b), which confirmed density-dependent growth mediated by *Daphnia spp* (Table 9.8). As production and consumption rate of zooplanktivorous fish were about the same in the northern and the southern basin (cf. Table 9.3), the lower availability of large-bodied *Daphnia spp* in the southern basin must have been caused by a lower potential production of *Daphnia spp.*

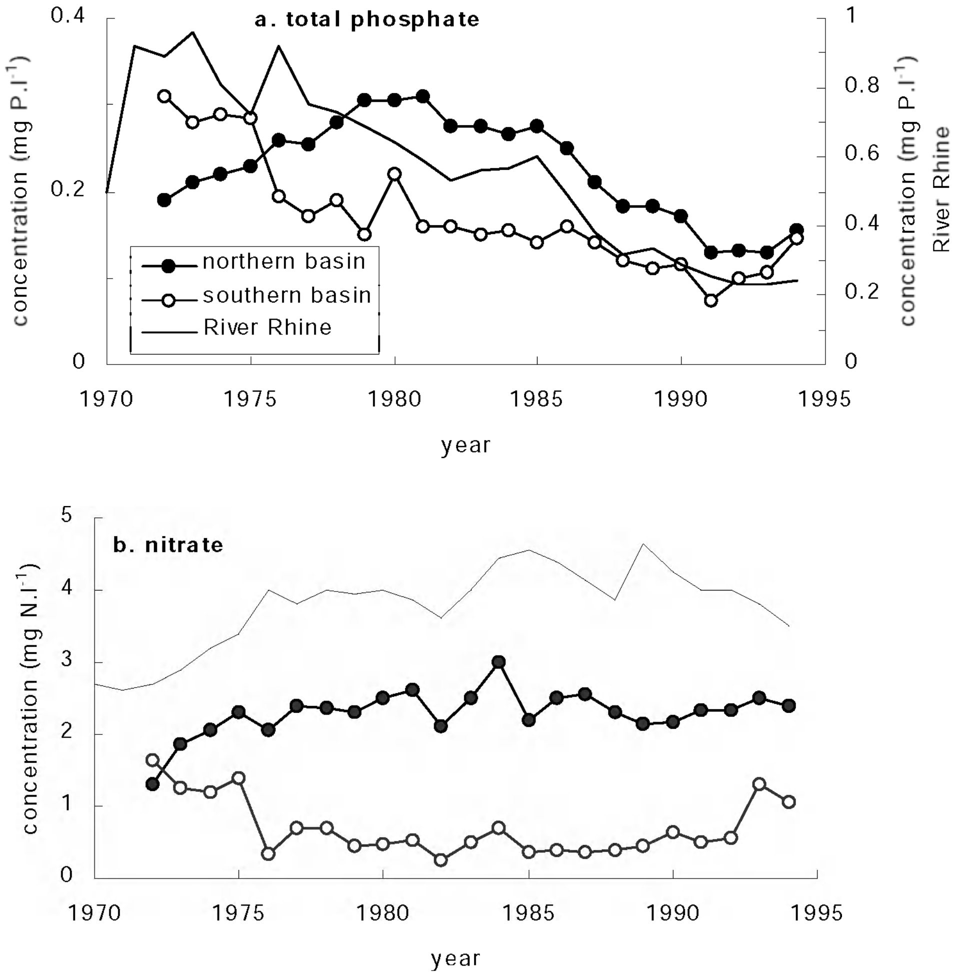

Figure 9.16*. Total phosphate (a) and nitrate (b) concentration in IJsselmeer and in River Rhine. Source: Netherlands Ministry of Transport, Public Works and Water Management.*

Condition, as indexed by percentage dry weight (*PDW*), of 0-group smelt increased with length, but was lower at the end of the growing season (November) (Fig. 9.15a). For ≥1-group smelt, the relationship between *PDW* and length were parabolic (Fig. 9.15b). Condition was maximal at ca. 10 cm *TL* in June, and at the end of the growing season condition was ca. 20% lower than in June. Growth of ≥1-group smelt stopped in August. An ANCOVA model with *PDW* of 0-group and ≥1-group smelt as dependent variable, and length (*TL*) and month (*MONTH*) as independent variables ($PDW = \text{Constant} + TL + TL^2 + MONTH$) explained 98% of the variation in *PDW* ($P = 0.0001$) (Table 9.9, Fig. 9.15c).

In general, seasonal variation in condition of smelt reflected seasonal variation in food availability. The decrease in *PDW* of smelt > 10 cm *TL* was probably caused by an increasing shortage of food, i.e. zooplankton of proper sizes. Hence, the capacity of IJsselmeer to sustain production of larger zooplanktivorous smelt must have been low. Smelt > 15 cm *TL*, which occurred at very low density (<< $1.ha^{-1}$) in IJsselmeer, often contained 0-group smelt in their stomachs (P.J. Mous, pers. obs.). These very large smelt were probably the few survivors that succeeded in switching to piscivory.

DISCUSSION

Throughout the period 1970-1995, zooplanktivorous smelt was a keystone species in IJsselmeer. In the northern basin, smelt comprised ca. 72% (cf. Table 9.3), and in the southern basin 60% of the total production of small fish (102 $kg.ha^{-1}.yr^{-1}$ in the northern and 116 $kg.ha^{-1}.yr^{-1}$ in the southern basin). Total small fish production, which probably comprised the larger part of total fish production, was within the range reported for lakes of similar trophic status: according to the relationship between total phosphorus concentration (TP) and fish production of Downing, Plante & Lalonde (1990), total fish production in IJsselmeer was estimated to range between 10 and 130 $kg.ha^{-1}.yr^{-1}$.

Production of 0-group smelt in the northern and the southern basin, was relatively stable: 67% of the annual production estimates for each species were within a factor 2 around the inter-annual mean. Such stability, here pertaining to a single species of a single age group, is reported for the major producers in other ecosystems: in Windermere, 67% of the annual production estimates of the perch population varied within a factor 1.8 (Craig 1980) around the inter-annual mean over a 12-year period, and in Danube River, this factor was 2.5 for the total fish population over a 5-year period (Holcik 1996). Variation in the production of 0-group perch in IJsselmeer was extremely high (ca. a factor 6), due to the high variation in yearclass strength (cf. Buijse, Van Densen & Schaap 1992). The relatively stable production of smelt formed a stable forage base for piscivorous fish and birds in IJsselmeer.

In IJsselmeer, probably all of the smelt production was utilized by piscivorous fish and birds, and by the fishery. There are few studies that attempt to balance production against utilization. Brandt *et al.* (1991) estimate that in Lake Michigan (USA), about 50% of alewife *Alosa pseudoharengus* production is utilized by a commercial fishery and piscivorous salmonids. Of a total fish production of 243 kg $C.ha^{-1}.yr^{-1}$ in a Sri Lankan reservoir, 22% was utilized by avian piscivores, mainly cormorants *Phalacrocorax spp*, grey pelican *Pelecanus philippensis* and storks, and 9.9% by the fishery (Piet, Vijverberg & Van Densen 1999). For the same Sri Lankan reservoir, Pet *et al.* (1996) propose to introduce a piscivore, barramundi *Lates calcarifer* to utilize the excess fish production, enabling the development of a new fishery. In Lake Victoria (East Africa) the idea of introducing a large predator (Nile perch *Lates niloticus*) to utilize production of haplochromines was put into practice, which resulted in major changes in the fish community and in other components of the ecosystem (Witte *et al.* 1992; Ogutu-Ohwayo 1990; Wanink & Goudswaard 1994). In accordance with Parsons (1996), we think that in most situations fish production is balanced by utilization, and that changes in utilization generally affect the food web structure.

Growth of both zooplanktivorous smelt and benthivorous ruffe was food limited in IJsselmeer, and in both fish species growth suddenly increased in the northern basin after the closing of the dike that separates the northern basin from the southern basin in 1975 (cf. Fig. 9.2 and Fig. 9.4). The closing of the dike separated the southern basin from the inflow of nutrient-rich water of River IJssel, a tributary of the River Rhine (Fig. 9.16). Consequently, the average residence time of water became more than 4 times as short in the northern basin than in the southern basin (Prins *et al.* 1995). Probably, the increased nutrient loading of the northern basin after 1975 was passed on in the food chain to primary and secondary production, causing increased food availability and faster growth for smelt and ruffe.

Predation pressure by smelt on zooplankton probably caused a decrease in food quality (i.e. zooplankton size), which in turn decreased smelt growth, as was suggested by the negative relationship between smelt density and smelt growth, and the positive relationship between smelt growth and *Daphnia spp* body size. The existence of this mechanism has also been demonstrated for 0-group yellow perch *Perca flavescens* in Oneida Lake, USA (Mills *et al.* 1989; Mills, Sherman & Robson 1989). The relationships between *Daphnia spp* body size, smelt growth and smelt density were consistent over both basins of IJsselmeer and Tjeukemeer, which suggests that zooplankton body size is a suitable measure for the level of particulate zooplanktivory. Thus, we agree with Mills & Schiavone (1982) and Mills, Green & Schiavone (1987), that zooplankton body size could be a useful, although rough, indicator for abundance of fish, even for comparing between systems. A possible explanation for a difference in *Daphnia spp* length between the two basins at equal predation pressure of zooplanktivorous smelt was a difference in zooplankton production between the two basins. As nutrient loading is much higher in the northern basin than in the southern basin (Prins *et al.* 1995), this explanation seemed justified.

In IJsselmeer, smelt reach sexual maturity in one year (Willemsen 1977). This fast rate of maturation has also been observed in other Eurasian smelt populations that inhabit shallow lakes (Belyanina 1969; Ivanova & Polovkova 1972; Ivanova 1981; Ivanova & Volodin 1982). The ability of slow-growing smelt to reach sexual maturity after its first summer is probably a key factor for its success in IJsselmeer, enabling it to withstand high predation and fishing mortality. Production of larger smelt was probably not only limited by food availability but also by mortality through starvation, as indicated by the low condition of smelt > 10 cm *TL*. Probably, only smelt that managed to switch to piscivory by feeding on their own offspring in early summer survived, explaining the low density of larger smelt (> 15 cm *TL*) in IJsselmeer. This critical switch from zooplanktivory to piscivory is also demonstrated for pikeperch (Buijse & Houthuijzen 1992).

Especially in late spring, when smelt biomass is at its minimum, strong interaction between the smelt fishery and other users may occur. This was illustrated by the food shortage experienced by cormorants in early 1993, which was primarily caused by an exceptionally weak yearclass of smelt, but was probably worsened by the smelt fishery in early spring. As the mechanisms that determine year class strength are mostly beyond control by management measures (Borchardt 1988; Buijse, Densen & Schaap 1992; Luecke *et al.* 1990; Mooij 1996), an occasional conflict between smelt fishery and cormorants cannot be avoided through wildlife or fishery management.

In IJsselmeer, small fish production was probably balanced by utilization, and growth of the main small fish producers was density-dependent. Therefore, the carrying capacity of the system for the smelt fishery, piscivorous fish and piscivorous birds was probably reached. This conclusion is also supported by observations on the population dynamics of piscivorous birds and the status of the fishery: the breeding success of the cormorant population depending on IJsselmeer is now relatively low compared to other populations (Van Eerden & Gregersen 1995), the increase of the cormorant population was apparently halted in the early 1990s (cf. Fig. 9.11), and there is strong evidence that the IJsselmeer fishing fleet suffers from over-capacity (Buijse 1992; Taal & De Wilde 1997). Management scenarios that would aim for a higher utilization of small fish are probably not viable, as there is little scope for further maximizing small fish production by management of the IJsselmeer bird populations or fish stocks. These conclusions are valid only for the IJsselmeer ecosystem in its present state. A change in the ecosystem structure could result in a change in its carrying capacity. This was illustrated by the increase in smelt growth in the northern basin, explained here by a man-induced increase in nutrient loading.

There probably is scope to optimize utilization of small fish production through fishery management. Buijse *et al.* (1992) show that improved management of the gillnet fishery could increase the yield of perch and pikeperch by a factor ranging between 1 and 1.3. As this results in a higher production of piscivorous fish, predation pressure on small fish will become higher. This will be at the expense of small fish utilization by either the fishery for spawning smelt or by piscivorous birds. Consequently, improved management of the gillnet fishery is viable only if either the intensity of the smelt fishery is decreased, or if one allows less piscivorous birds around the lake.

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APPENDIX - CALCULATING FISH DENSITY FROM CATCH-PER-UNIT-EFFORT OBSERVATIONS

Intra-annual survey

For the estimation of fish density from *CpUE* observations made during intra-annual survey (Table A.1), *CpUE* observations were corrected for the swept area and expressed as numbers.ha^{-1} first. Next, ANCOVA models were constructed of ln-transformed *CpUE* observations, using bottom depth (*DEPTH*) and water transparency (*SECCHI*) as independent variables. Thus, the deterministic part of the model reads:

$$\ln(CpUE)=\text{Constant}+b_1.DEPTH+b_2.SECCHI+b_3.DEPTH.SECCHI \quad \text{[formula A.1]}$$

where b_1, b_2 and b_3 are the parameter estimates. ANCOVA statistics and parameter estimates are presented in Table A.2. The models were used to calculate estimates of ln(*CpUE*) for each observation. The density estimates were calculated as the arithmetic means of back-transformed estimated values. Because allocation of sampling locations was proportional to surface area of strata, the density estimates were unbiased in respect to water transparency- and depth-mediated distribution patterns. Using this method, it was implicitly assumed that unexplained variance was caused by sampling error rather than by random spatial variation in density. Population density of smelt was also corrected for water transparency-mediated vertical distribution (Chapter 6, see Results section). Estimates of 0-group fish density in May 1994 were calculated as geometric means of surface trawl *CpUE* observations.

***Table A.1**. Sampling conditions during the intra-annual survey. n = number of hauls. NS = near shore; OW = open water.*

Basin/	sampling period	n	depth (m)			Secchi depth (m)		
Survey			mean	min.	max.	mean	min.	max.
northern basin								
a	17-26 May 94	39	4.6	2.8	6.2	1.09	0.6	1.6
b	29 Aug-8 Sep 94	45	4.5	2.7	5.8	0.66	0.5	1.7
c	21 Nov-15 Dec 94	57	4.9	2.7	7.5	1.48	0.7	3.0
d, NS	8-30 Mar 95	38	4.2	3.0	5.6	0.77	0.4	1.3
d, OW	8-30 Mar 95	57	4.9	2.9	6.6	0.67	0.4	1.3
southern basin								
a		0	-	-	-	-	-	-
b	5-7 Sep 94	29	3.9	2.6	4.5	0.66	0.4	0.8
c	12-14 Dec 94	27	3.7	3.0	4.3	0.33	0.3	0.6
d, NS	20-23 Mar 95	21	3.5	2.7	4.2	0.24	0.2	0.5
d, OW	21-23 Mar 95	19	4.1	3.2	4.6	0.20	0.2	0.2

Inter-annual survey

To obtain population density estimates from *CpUE* observations made during the inter-annual survey, four sources of bias were corrected for. First, *CpUE* observations were corrected for the swept area and expressed as numbers.ha^{-1}. Second, *CpUE* observations were corrected for size selectivity of the trawl gear, which was caused by cod-end mesh penetration of small fish. This was necessary for smelt only; the selectivity curve is presented in Chapter 4. Third, *CpUE* observations were corrected for depth- and water transparency-mediated variation in spatial distribution patterns (see below). Finally, smelt *CpUE* was corrected for the vertical distribution pattern, assuming the vertical distribution pattern of smelt > ca. 7 cm *TL* as observed during summer 1992. The vertical distribution pattern was corrected for by multiplying *CpUE* with 0.42 times the water depth : net height ratio (cf. Chapter 6).

Correction for depth- and water transparency-mediated distribution patterns was necessary, because the sampling locations of inter-annual survey did not adequately represent the IJsselmeer habitat in respect to depth and water transparency. Most sampling locations were situated in the deeper areas of the northern basin (cf. Fig. 9.1). Hence, the mean depth of all sampling locations in the northern basin was on average ca. 1 m deeper than the actual mean

***Table A.2**. ANCOVA statistics and parameter estimates of models which relate ln(CpUE) of the most important small fish species caught during the intra-annual survey to DEPTH (in m) and SECCHI (in m) (see text). n_0 = number of hauls with zero individuals in the catch, s^2 = total variance of ln(CpUE), MSE = mean squares of error of the model, F = F-statistic of the model. The significance level of F is coded as: * = $0.05 \leq P < 0.1$, ** = $0.01 \leq P < 0.05$, *** = $P < 0.01$, NS = not significant. Dependent variables that did not contribute significantly to the model were omitted, and the model was refitted without these variables. An independent variable was also excluded from the model if variation in the variable was low (cf. Table A.1). This was the case for DEPTH in the southern basin, and SECCHI in all surveys in the southern basin except intra-annual survey-b.*

Species/	northern basin								southern basin					
Survey	n_0	s^2	MSE	F	INT	b_1	b_2	b_3	n_0	s^2	MSE	F	INT	b_2
smelt, 0-group														
b	1	4.50	1.98	19***	35.5	-3.69	-43.1	6.97	1	1.14	1.04	3.8*	12.8	-3.30
c	0	3.67	1.70	34***	8.7	0.779	-2.10	NS	0	0.546				
d	0	1.95	1.52	9.9***	22.7	-2.54	-21.4	4.26	0	1.78				
smelt, >=1-group														
a	13	3.85	1.87	9.8***	19.2	-3.21	-24.9	5.55						
b	6	0.884	0.834	3.4*	3.0	0.315	NS	NS	1	0.683	-	NS	-	-
c	12	1.53	1.23	9.7***	-0.7	0.640	NS	NS	0	0.362				
d	41	0.935	0.833	4.6	3.5	0.266	-1.97	NS	1	1.47				
perch, 0-group														
b	3	1.78	1.65	4.52	5.7	-0.494	NS	NS	0	1.65	-	NS	-	-
c	9	1.88	1.61	9.3***	0.2	0.638	NS	NS	0	1.49				
d	14	1.60	1.28	8.4***	11.1	-1.22	-14.4	2.44	0	0.531				
ruffe, 0-group														
b	0	3.11	1.67	14***	23.9	-3.33	-36.1	6.99	0	1.28	0.846	16***	9.79	-6.04
c	14	6.87	2.96	29***	-3.2	2.13	-1.97	-	0	1.41				
d	6	5.36	2.17	45***	14.7	-0.942	-24.4	3.65	0	0.525				
ruffe, >=1-group														
a	2	4.08	2.30	15***	5.5	0.820	-4.13	NS						
b	4	3.10	2.44	6.4***	4.4	0.627	-5.33	NS	3	2.77	0.82	62***	11.1	-12.8
c	25	4.06	2.22	14***	-0.8	1.39	-2.19	NS	0	2.07				
d	23	2.24	1.29	19***	15.0	-1.63	-22.6	3.71	1	0.578				

depth of the northern basin (Table A.3). This implies that the habitat consisting of the former tidal channels is over-represented compared to the former sandbanks. Furthermore, until 1987 the choice of sampling locations was biased towards locations, with low water transparency at the moment of sampling. The reasoning behind this strategy was that low water transparency presented better sampling conditions, because of a higher vulnerability of fish to the trawl. Indeed, Buijse, Schaap & Bult (1992) show that *CpUE* is low if the water is clear. However, the low *CpUE* in clear water was probably caused by a low local density of fish, as some fish species avoid areas where water transparency is high (Chapter 7; Ryder 1977). It is therefore impossible to evaluate whether *CpUE* of the survey trawl was affected by variation in population density or by variation in gear vulnerability, and this sampling strategy may have caused an over-estimation of population density. After 1987, sampling took place without taking water transparency into consideration. This change in sampling strategy partly explains the frequent occurrence of high mean water transparency at the sampling stations after 1987 (Table A.3).

To correct for depth- and water transparency-mediated distribution patterns, fish density was first described as a function of depth and water transparency, using *CpUE* observations from intra-annual survey-c. This survey, which was carried out during the same period in the year as inter-annual survey, was not biased in respect to depth and water transparency. With the parameter estimates (Table A.1), *CpUE* observations were scaled to values corresponding to the lakewide mean depth (4.5 m) and the lakewide mean Secchi depth (0.75 m). The values 4.5 and 0.75 were assumed to be representative for the period 1970-1994 (Prins *et al.* 1995). The formula used for the correction reads:

$$\ln(CpUE)'=\ln(CpUE)-b_1\cdot(DEPTH-4.5)-b_2\cdot(SECCHI-0.75)-b_3\cdot(DEPTH\cdot SECCHI-4.5\cdot 0.75) \quad \text{[formula A.2]}$$

where $\ln(CpUE)'$ is the corrected value, and b_1, b_2 and b_3 are the parameter estimates of the spatial distribution models. If an independent variable in the model was not significant, its associated parameter value was set to zero. The back-transformed mean of $\ln(CpUE)'$ was an estimate for the population density at a depth of 4.5 m and a Secchi depth of 0.75 m. This estimate represents the value most likely to occur if an *CpUE* observation at a randomly chosen location in fall of a particular year would have been made. Only if parameters b_1, b_2 and b_3 all have value zero, the back-transformed mean of $\ln(CpUE)'$ represents a density estimate representative for the basin as a whole. In other situations, a raising factor was applied to the back-transformed mean of $\ln(CpUE)'$ to obtain a density estimate representative for the basin. The raising factor was calculated as the ratio of the arithmetic mean of predicted *CpUE* values to the geometric mean of predicted *CpUE* values of intra-annual survey-c.

Because parameter estimates were unavailable for the southern basin, we could not correct these *CpUE* observations for depth- and water transparency-mediated spatial distribution patterns. However, for the southern basin geometric means of *CpUE* observations were probably relatively unbiased estimates for population density, because depth and water transparency were almost constant during the study period (cf. Table A.3). Furthermore, the average depth and water transparency of sampling locations were close to the average depth and water transparency of the southern basin (cf. Prins *et al.* 1995). Only in the years 1988, 1989 and 1993 the average water transparency of the sampling stations was relatively high. Therefore, population density estimates of these years were not calculated for the southern basin.

Three assumptions underlied our method to correct for spatial distribution patterns. First, it was assumed that the major small fish species were distributed as during intra-annual survey-c (cf. Table A.2). As *CpUE* generally increased with increasing depth and decreasing water transparency during the young fish surveys in fall (Buijse, Schaap & Bult 1992), this assumption seemed valid. Second, it was assumed that inter-annual variation in depth and water transparency was caused by sampling artifacts, rather than by an intern-annual variation in the true mean depth and water transparency. For water transparency, this assumption was probably too rigid. However, because variation in annual average water transparency does not show a trend (Prins *et al.* 1995), this assumption did probably not obscure any significant trend in small fish density. Third, it was assumed that unexplained variation in *CpUE* was caused by sampling error rather than by random spatial variation in density

***Table A.3**. Sampling conditions (mean over sampling stations, ± standard deviation) during inter-annual survey in the period 1970-1994. n = number of survey hauls.*

	northern basin			southern basin		
Year	n	depth (m)	Secchi depth (m)	N	depth	Secchi depth (m)
1970	6	4.5±1.15	0.27±0.08	3	3.0±0.42	0.23±0.03
1971	9	5.0±0.94	0.65±0.42	4	2.6±0.46	0.29±0.09
1972	7	6.4±0.94	0.58±0.30	4	3.6±0.38	0.21±0.05
1973	3	6.9±1.40	0.50±0.26	1	3.8	0.25
1974	5	5.7±1.16	0.49±0.15	2	3.8±0.07	0.35±0.07
1975	3	5.0±1.27	0.42±0.16	3	3.5±0.45	0.25±0.05
1976	6	5.5±1.34	0.42±0.07	1	3.5	0.3
1977	5	5.3±0.83	0.41±0.12	4	3.6±0.15	0.25±0.10
1978	5	5.6±1.19	0.84±0.21	5	3.3±0.51	0.15±0.00
1979	7	5.9±0.99	0.50±0.12	3	3.7±0.57	0.32±0.03
1980	10	5.8±0.87	0.59±0.27	5	3.8±0.46	0.23±0.06
1981	12	5.8±0.92	0.58±0.20	7	3.8±0.53	0.32±0.12
1982	9	5.8±0.92	0.56±0.34	5	3.7±0.45	0.25±0.00
1983	8	5.9±1.11	0.60±0.23	6	4.1±0.64	0.39±0.04
1984	19	6.0±0.81	0.78±0.24	5	3.9±0.26	0.36±0.05
1985	10	6.2±1.35	0.63±0.24	5	4.2±0.40	0.21±0.02
1986	13	6.3±1.06	0.55±0.17	7	3.9±0.22	0.21±0.07
1987	16	5.8±1.07	1.12±0.46	3	3.7±0.29	0.27±0.03
1988	19	5.7±0.80	0.98±0.27	12	3.9±0.32	0.66±0.16
1989	33	5.8±0.59	0.83±0.43	15	4.0±0.28	0.86±0.16
1990	38	5.8±0.71	0.64±0.29	15	3.9±0.26	0.23±0.04
1991	39	5.6±0.65	0.80±0.33	15	3.8±0.17	0.35±0.19
1992	26	5.5±0.74	0.61±0.15	12	3.9±0.21	0.29±0.02
1993	30	5.5±0.93	0.84±0.32	14	4.2±0.68	0.52±0.08
1994	28	5.4±0.91	1.01±0.54	11	4.0±0.26	0.30±0.08

Chapter 10

Management regimes for the fisheries and for the fish-eating birds of IJsselmeer

P.J. Mous, M.A.M. Machiels & W.L.T. van Densen

ABSTRACT

A simulation model for the top predators and their interactions in the IJsselmeer ecosystem was developed to evaluate various management regimes. The components of the model were prey fish (smelt *Osmerus eperlanus*, ruffe *Gymnocephalus cernua*, small perch *Perca fluviatilis* and small pikeperch *Stizostedion lucioperca*), piscivorous fish, a fykenet fishery and a gillnet fishery, and a piscivorous bird, cormorant *Phalacrocorax carbo*. Processes incorporated in the model comprised density-independent growth of prey fish, density-dependent growth of piscivorous fish, density-independent and stochastic recruitment, fishing mortality, and fish mortality caused by predation exerted by piscivorous fish and by cormorants. Field data on the IJsselmeer ecosystem from the 1980s and early 1990s (cf. Chapter 9) were used to parameterize the model. The management measures evaluated were: reduction of fishing effort in the fykenet and gillnet fishery, enlargement of the legal minimum mesh size of gillnets, and a theoretical complete removal of cormorants. The effects of these measures were compared with a reference situation representative for a management situation as in the 1980s and early 1990s. A 75% reduction in the number of eel fykenets has the strongest positive effect on the total value of the catch (+16%). The present day direct exploitation of smelt reduces the positive effects of restrictions in the effort of the fykenet and gillnet fishery. After complete removal of cormorants, the value of the value of the total catch increases moderately with 16%. The effect of effort and mesh size regulations on food availability for cormorants is moderate too, varying between -23% and +76%. Stochastic recruitment and cyclic trends in predator and prey abundance strongly obscures the effects of management measures, as evaluated here, on the fish stocks, on the outcome of the fishery and on the prey availability for cormorants.

INTRODUCTION

The fish stock of IJsselmeer represents a valuable asset, as it is utilized by ca. 100 fishing companies who extract ca. 10 million dfl worth of fish annually (Taal & De Wilde 1997). Furthermore, the fish stock provides a forage base for piscivorous birds (Buijse *et al.* 1993), thereby contributing to the lakes function as a nature conservation area (cf. De Groot 1992). Problems arise if functions conflict, for example if fishermen perceive fish predation by piscivorous birds as a threat to commercially important fish stocks. It is the task of the authority responsible for the management of the lake ecosystem to design a management strategy that optimizes the value of the lake to the human population, taking into consideration as many functions as possible. Such a strategy was developed for the Dutch Waddensea, where the cockle fishery explicitly takes the requirements of another user of cockles, eider *Somateria mollissima*, into consideration (Dankers & De Vlas 1992).

The design of an integrated management strategy requires prediction of the effects of alternative management measures on the components of the ecosystem. The most commonly used management tools in fisheries science (yield-per recruit and surplus production models) are single-species oriented (Ricker 1975; Gulland 1983; Thompson 1992; Jacobson, Lo & Barnes 1994). Simulation models are often used to evaluate the effects of management measures (De Wit & Goudriaan 1978; Jørgensen 1993). In fisheries, simulation models amongst others are used to determine effective fish stocking and harvesting strategies (Johnson BM *et al.* 1992), to perform bioeconomic analyses of fishery management (Johnson BL *et al.* 1992), to explore possibilities for a more complete utilization of reservoir fish production (Pet, Machiels & Van Densen 1996), and to compare short-term losses to long-term benefits after the implementation of a new management measure (Pelletier & Laurec 1992). Dynamic simulation models that account for interactions allow for studying effects of management measures on a larger part of the ecosystem.

In this chapter, a dynamic simulation model is presented to assess the effects of fishery and wildlife management on the higher trophic levels in the ecosystem of the northern basin of IJsselmeer, a eutrophic lake in the Netherlands with a surface area of 112,000 ha and a mean depth of 4.5 m. Presently, most IJsselmeer fish stocks are overfished (Dekker & Van Willigen 1993; Dekker & Schaap 1993), and the profitability of the fishery is low (Taal & De Wilde 1997). There has been a debate on the effect on the total commercial catch of the increasing population of the fish-eating cormorant *Phalacrocorax carbo* and of discarding by the fishery (Dekker, Schaap & Van Willigen 1993; Van Dam *et al.* 1995). There is agreement that there is a large scope to enhance the profitability of the fishery by a more rational exploitation. In 1996, the IJsselmeer fishermen agreed to a 50% reduction in fishing effort, under the condition that the anticipated effects of this measure on the fish stocks would benefit the fishery rather than the IJsselmeer cormorant population. Thus, there clearly is a need for a tool that predicts the effects of management measures on the fish stocks, the fishery, and the fish-eating birds of the IJsselmeer ecosystem.

With an earlier model of the gillnet fishery in IJsselmeer, the effects of various management measures on the output of the fishery was evaluated (Buijse *et al.* 1992). This model considered only two fish species, perch *Perca fluviatilis* and pikeperch *Stizostedion lucioperca*, and a limited number of ecological and exploitation processes: recruitment, growth, natural mortality and gillnet fishery mortality. Interaction between species was not modeled. We extended this model by incorporating the following components and processes: the stocks of prey fish (smelt *Osmerus eperlanus* and ruffe *Gymnocephalus cernua*), the commercial fishery for spawning smelt in early spring, the mortality due to discarding in the fishery with fykenets for eel (cf. Dekker, Schaap & Van Willigen 1993), and the predation on fish by piscivorous fish and by the most important avian piscivore of IJsselmeer, cormorants (Buijse *et al.* 1993).

The management measures that were implemented in the model correspond to the measures that the fishery management has at its disposal: control of fishing effort through a licensing system, gear regulations (e.g. a minimum mesh size for gillnets), and a closed fishing season (Hamelynck, Van Santvoort & Janssen 1992). We studied the effects of effort reductions in detail, since effort reduction is the most feasible management measure in the IJsselmeer fishery. Although a reduction of the cormorant population has never been proposed officially, the IJsselmeer fishermen have high expectations of this measure. Therefore, we assessed whether a theoretical removal of cormorants would have a beneficial effect on the outcome of the IJsselmeer fishery, and how large this effect would be. Additional simulation runs were made with stochastically varying recruitment of fish to assess to what extent effects of management would become obscured due to high year-to-year variance in the fish stocks (cf. Buijse 1992; Pelletier & Laurec 1992; Van Densen & Buijse 1992).

MATERIALS AND METHODS

The modeled ecosystem (cf. Chapter 9) comprised four fish species (smelt, perch, pikeperch and ruffe), one piscivorous bird species (cormorant) and three types of fishery (fykenet fishery, smelt fykenet fishery, and gillnet fishery for perch and pikeperch). For reasons explained in the discussion section of this chapter, eel was not included in the model. The eel *fishery* was included, because of the effect of the fykenets on the stocks of other fish through discarding. The modeled processes encompassed growth, recruitment and predation (Fig. 10.1).

Parameter values that control growth, mortality and recruitment of the fish stocks were derived from published reports and from Chapter 9. The model output consisted of species composition and size distribution of the fish population in the lake, of the commercial catch and of the fish consumed by cormorants. The model output was validated by comparison of model output with the situation of the IJsselmeer system in the 1980s and 1990s.

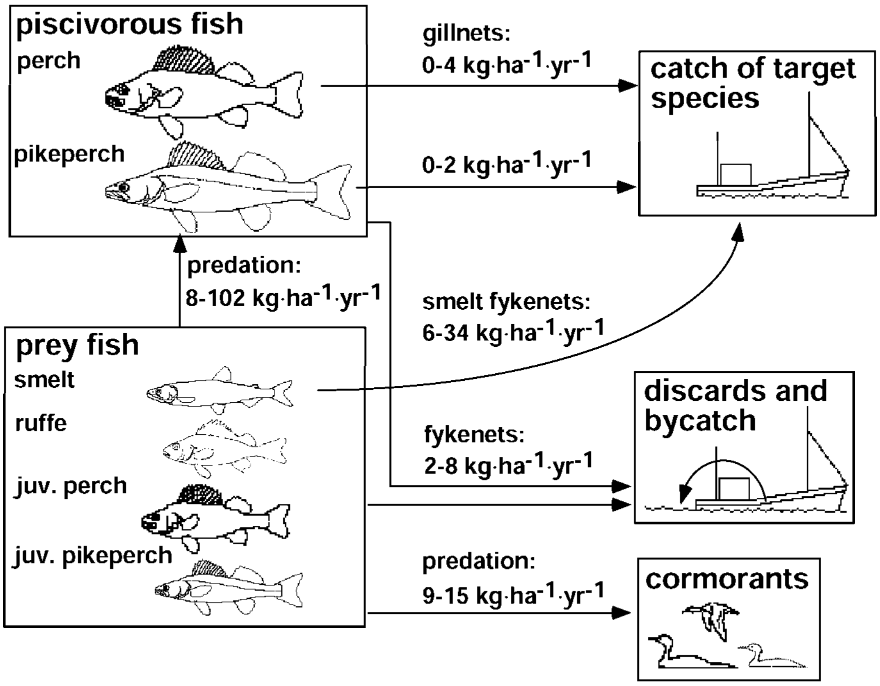

***Figure 10.1**. The modeled part of the IJsselmeer ecosystem. Arrows indicate predator-prey relationships. Predation rates present the observed range for the period 1980s and early 1990s (Chapter 9).*

Model structure

As some of the modeled processes were highly length-dependent (e.g. gillnet mortality and predation mortality), the model was length-based. In this way the shape of the length-frequency distributions of age classes was efficiently controllable (Buijse *et al.* 1992; Walters *et al.* 1993; Pet, Machiels & Van Densen 1996). Our method differed from other models (e.g.; Johnson BM *et al.* 1992; Rice, Crowder & Rose 1993; DeAngelis *et al.* 1993; McGarvey 1994; Scheffer *et al.* 1995), where the elementary state variable represents an individual fish or a group of fish with length attributes (mean, standard deviation) attached to it. The simulation method used here was recursive numerical integration of state variables over a specified time step, according to model-specific expressions for rates of change (De Wit & Goudriaan 1978). The elementary state variable in our model was the number of fish of species i, age class j that occupy length class k (Fig. 10.2). The number of fish in a length class decreased through mortality, and increased through recruitment and growth. Growth also caused the number of fish in a length class to decrease, namely when fish shifted from the length class under consideration to the higher length class.

The population of each fish species was divided over 8 age classes and each age class was divided over 12 length classes. The width of the length classes in the model was dependent on the mean length and standard deviation in length of the age class under consideration, and varied between 0.5 cm for small fish and 4 cm for larger fish. Where necessary, body weight of the

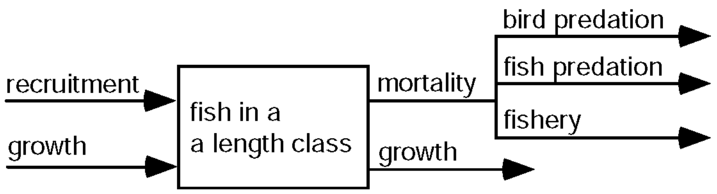

***Figure 10.2**. The conceptual framework of the simulation model.*

modeled fish was calculated from length by an allometric length-weight relationship (Table 10.1). After reaching day 365 during the simulation run, the contents of age-indexed length-frequency distributions were shifted one age group higher.

The simulation time step was set at two days, because sensitivity analysis showed that a greater time step resulted in deviations in the biomass of the most dynamic species in the model, smelt (Table 10.2). The components and processes of our simulation model are described in the sections below and in Fig. 10.3. The model was implemented in Turbo Pascal v. 7.0 (Borland International Inc. 1992). The model output was processed with SAS v. 6 (SAS Institute Inc. 1990).

Simulation of dispersion in length growth of fish

To simulate dispersion in length growth within age classes of fish, Buijse *et al.* (1992) and Pet, Machiels & Van Densen (1996 use the fractional boxcar train method. Originally, the fractional boxcar train method was used to simulate dispersion in the development time of organisms. For this purpose, the developmental axis of a development stage is broken up into a number of classes or boxcars, and at each time step in the simulation a certain fraction of the number of organisms is shifted from one boxcar to the next (Goudriaan & Roermund 1993). For simulation of dispersion in length growth, the length trajectory is sub-divided in length classes (the analogue of the boxcars). The distribution of the population number over the length classes is of interest here, rather than the dispersion in development time. Because of this fundamental difference, the original boxcar train method was adapted by Buijse *et al.* (1992). Fish of a particular age class are stored in an array of length classes. Length increase of fish in this age class is cumulated in a variable (*LINC*). When, after several time steps, *LINC* equals a certain fraction (*FR*) of the width of a length class, the same fraction (*FR*), but now of the number of fish in each length class is shifted to the next length

***Table 10.1.** Parameter estimates for the length-weight relationships $W=a.L^b$ of smelt, ruffe, perch and pikeperch. W=body mass (in kg), L=total length (cm), n = number of observations by which the length-weight relationship was estimated, R^2 = fraction of variance explained by the linear relationship on log-transformed length and weight.*

species	a	b	n	R^2
smelt	$2.30\cdot10^{-6}$	3.37	996	0.98
ruffe	$6.48\cdot10^{-6}$	3.29	700	0.99
perch	$4.70\cdot10^{-6}$	3.36	16706	0.99
pikeperch	$4.64\cdot10^{-6}$	3.17	9171	0.99

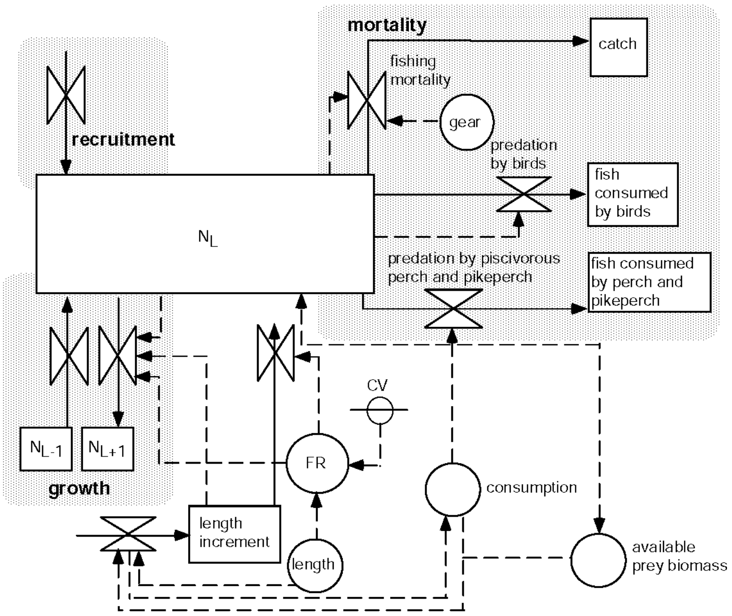

***Figure 10.3**. Relational diagram of the most important components and processes in the model, according to Forrester's conventions (De Wit & Goudriaan 1978). State variables are represented by rectangles, rates of change by valves, auxiliary variables by circles and parameters by circles with cross bars. The solid arrows indicate the flow of material and the dashed arrows represent the flow of information. N_k = the number of individuals in length class k, CV = the coefficient of variation of the length-frequency distribution of the age class, FR = fractional boxcar train variable. See text for further details.*

class. Also at this time step, *LINC* is set to zero. Thus, growth in length is translated to a fractional shift of individuals from one length class to the next. If $FR = 1$, there is no dispersion. When $FR < 1$, the dispersion increases with smaller *FR*, and the dispersion is maximal if $FR = 0.5$.

Buijse *et al.* (1992) present a formula for *FR* that controls the dispersion in length according to pre-specified values for the standard deviation in length for each age class. Pet, Machiels & Van Densen (1996) changed this formula so that it controls dispersion according to a pre-specified, constant coefficient of variation. This formula is used for modeling a fishery with fish populations that are not age-structured. We now present a formula that controls dispersion according to a pre-specified, constant coefficient of variation in an age-structured population.

The deduction of the formula starts with expressions for the increase in variance and mean length of an age class that results from a shift from one length class to the next:

$$s_a^2 = s_b^2 + dL^2.(FR - FR^2) \quad \text{[formula 10.1]}$$

$$L_a = L_b + dL.FR \quad \text{[formula 10.2]}$$

where *dL* = the width of size classes, s^2 = the variance in length of the age class, *L* = the mean length of the age class. The suffixes *b* and *a* refer to the state of the variables *b*efore and *a*fter the transfer. Formulas 1 and 2 are combined into:

$$CV_{fr,a} = \frac{\sqrt{s_b^2 + dL^2.(FR - FR^2)}}{L_b + dL.FR} \quad \text{[formula 10.3]}$$

where CV_{fr} = the fractional coefficient of variation. To simulate a population in which the CV_{fr} is constant:

$$CV_{fr} = \frac{\sqrt{CV_{fr}^2.L_b^2 + dL^2.(FR - FR^2)}}{L_b + dL.FR} \quad \text{[formula 10.4]}$$

which can be rearranged to:

$$FR = \frac{dL - 2.L_b.CV_{fr}^2}{dL.(1 + CV_{fr}^2)} \quad \text{[formula 10.5]}$$

In Fig. 10.4, it is shown how length-frequency distributions are generated using formula 10.5 with constant CV_{fr} and *dL*.

***Table 10.2**. Modeled annual average biomass of the four fish species, with the simulation time step (dt) set to 1, 2, 3, 5 and 10 days. The biomass is expressed as a percentage relative to the biomass that resulted from a simulation run with a time step of 1 day.*

species	dt = 1	dt = 2	dt = 3	dt = 5	dt = 10
smelt	100	100	108	108	112
perch	100	100	100	100	98
pikeperch	100	100	100	100	99
ruffe	100	100	100	99	101

***Table 10.3**. Seasonalized Von Bertalanffy growth parameters.*

species	L_{inf} (cm)	K (yr^{-1})	C[d]	t_s[d] (day 1-365)
smelt[a]	13.9	0.73	1	200
ruffe[b]	13.9	0.73	1	200
perch[c]	54.2	0.14	1	200
pikeperch[c]	94.4	0.21	1	200

Notes

a. *Parameter estimates from Van Der Weide (1991), based on growth of the 1988 and 1989 age classes. The model estimates the length of age 0 and age ≥1 smelt as observed over the period 1982-1994 (see Chapter 9) reasonably well.*

b. *Length attained by ruffe after 1,2 and 3 growing seasons were almost equal to those of smelt (Willemsen 1977, Van Der Weide 1991, Chapter 9), hence the similarity in growth parameters to those of smelt.*

c. *Parameter estimates from Buijse et al. 1992. In this study, separate sets of parameters were calculated for males and females. However, the difference in growth between the sexes was small, so we arbitrarily decided to use the parameter estimates for female perch and pikeperch.*

d. *Since growth stops in winter, we used C = 1. We assumed that growth was maximal on July 20 (day 200), this is roughly halfway the growing season (cf. Chapter 9).*

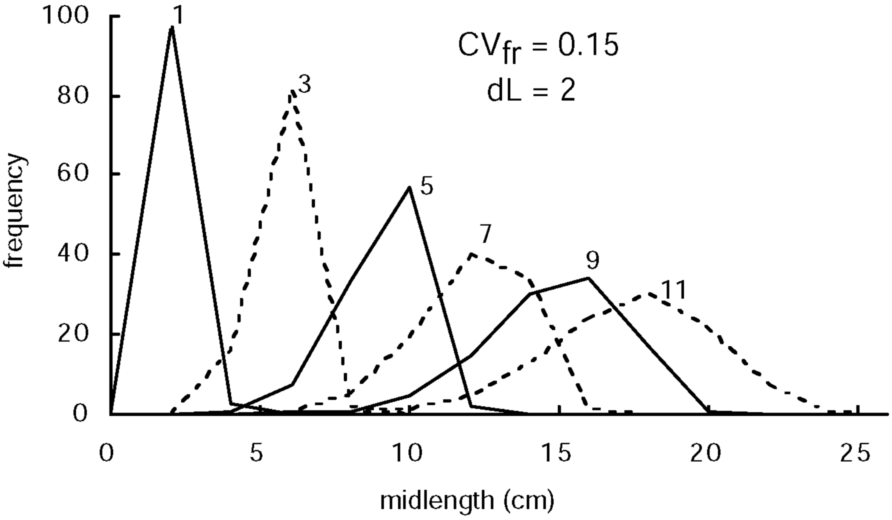

Figure 10.4. *Length-frequency distributions after 1, 3, 5, 7, 9 and 11 shifts. Note that FR in formula 2 dictates at which LINC the contents of each length class must be transferred to the next length class by a fraction FR. The growth rate model determines at which time in the simulation LINC reaches the value dL.FR.*

Growth

A seasonalized Von Bertalanffy function was used to calculate growth in length during each time step *dt*:

$$\frac{dL}{dt} = (L(t) - L_{\text{inf}}).(-K - C.K.\cos(2.\pi.(\frac{t-t_s}{365}))) \quad \text{[formula 10.6]}$$

where *L(t)* = total length (cm) at time *t* (expressed as fraction of the year), L_{inf}= theoretical length at infinite age (cm), *K* = daily growth constant (d^{-1}), *C* = the amplitude of the seasonal oscillation in growth (between 0 and 1) and t_S = the 'summer point', or the day where growth is maximal. If *C* = 0, the formula simplifies to the ordinary Von Bertalanffy growth equation. If *C = 1*, growth becomes zero in winter. Formula [6] is the first derivative of the seasonalized Von Bertalanffy length equation (Sparre & Venema 1992):

$$L(t) = L_{\text{inf}}.(1 - e^{-K.(t-t_0) - \frac{C.K}{2.\pi}.\sin(2.\pi.(\frac{t-t_s}{365}))}) \quad \text{[formula 10.7]}$$

During the simulation run, growth of piscivorous perch and pikeperch was set to zero if the available prey biomass was too low to balance the calculated growth (see text below). Growth parameters are summarized in Table 10.3, and growth curves are depicted in Fig. 10.5.

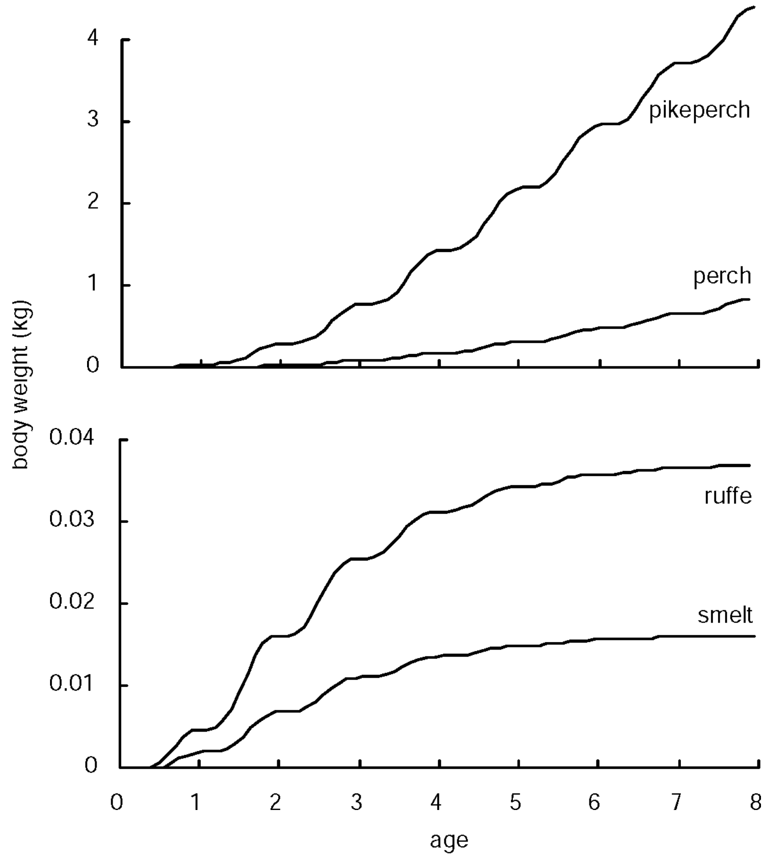

Figure 10.5. Body weight (in kg) as a function of age, calculated from seasonalized Von Bertalanffy length growth equations and allometric length-weight relationships. The growth curves for perch and pikeperch represent the maximum attainable growth, i.e. growth was not food-limited.

Recruitment

Recruitment was modeled by adding the length-frequency distribution of a new age class on July 1 (simulation time) each year. The coefficient of variation (*CV*) of the Gaussian length-frequency distribution was set to 10% (Buijse *et al.* 1992; Ebert, Schroeder & Dixon 1993). The value of the input variable for the number of new recruits (*R*) was derived from the inter-annual geometric mean density and inter-annual standard deviation of age 0 fish as measured during the IJsselmeer surveys, which were conducted in fall over the years 1982-1994 (Table 10.4). With preliminary simulation runs using varying *R*, a value of *R* was obtained that resulted in a number of surviving age 0 fish in fall (simulation time) that corresponded to the densities observed in the field.

The value of *R* for constant recruitment was set to the inter-annual arithmetic mean. The arithmetic mean (*AM*) was calculated as:

$$AM = GM \cdot 10^{0.2172 \cdot s^2} \quad \text{[formula 10.8, Ricker 1975 p. 275]}$$

where *GM* is the inter-annual geometric mean and s^2 is the squared standard deviation of the natural logarithms of the fall abundance estimates over the years 1982-1994. For simulation runs with stochastic recruitment, *R* was randomly selected from a log-normal distribution with mean log(*GM*) and variance s^2.

Fishing mortality

In the model, the smelt fykenet fishery was operated in the period March 15 - April 19. For smelt, an instantaneous fishing mortality rate of 0.0386 day^{-1} was used for all size classes. This implies that ca. 75% of the smelt stock present just before the start of the season was removed (cf. Chapter 9). The fishing mortality rate for non-target species (perch, pikeperch and ruffe) due to smelt fykenets was set to zero, because discarding as observed in the field was negligible.

In the model, the fykenet fishery, which causes mortality through discarding, took place from May 1 to November 1. This fishing season corresponded to the period during which ca. 90% of the annual eel catch was realized (Nagtegaal & Snel 1984). The instantaneous fykenet fishing mortality ($F_{fykenet}$) is unknown, and probably depends on the season and the species that is caught. We calibrated $F_{fykenet}$ in preliminar simulation runs until the annual weight of discards equaled ca. 10 $kg.ha^{-1}$, which corresponds to the observed annual weight of discards for 1993 (Van Dam *et al.* 1995). Calibration resulted in $F_{fykenet}$ = 0.00272 day^{-1} or 0.5 $(\text{fishing season})^{-1}$. We used the same $F_{fykenet}$ value for all species and body sizes in the model.

***Table 10.4**. Observed recruitment and model inputs for recruitment. s^2 is the variance of the natural logarithms of the abundance estimates over the years 1982-1994 (cf. Chapter 10). N_{GM} and N_{AM} are the geometric and arithmetic mean abundance of age 0 fish as measured during the surveys in fall in the period 1982-1994. R_{180} is the model input value for recruitment on day 180. N_{270} is the modeled number of surviving age 0 fish on day 270 for simulation runs with constant recruitment and all variables are to values which were representative for the IJsselmeer situation in the period 1982-1994.*

species	observed (fall 1982-1994)[a]			model input		simulation result
	N_{GM}	s^2	N_{AM}[b]	$R_{180,GM}$[c]	$R_{180,AM}$[d]	N_{270}
smelt	7300	0.57	9700	20000	26000	12000
perch	70	3.3	360	100	540	400
pikeperch[e]	5.0	1.3	10	8.1	16	11
ruffe	230	1.4	460	350	700	520

Notes

a. See Chapter 9

b. Calculated by substituting N_{GM} and s^2_{obs} in formula 10.8.

c. Used as input for simulation runs where recruitment was random

d. Used as input for simulation runs where recruitment was constant, calculated by substituting $R_{180,GM}$ and s^2_{obs} in formula 8.

e. Observed abundance of age 0 pikeperch from Buijse, Schaap & Bult (1992).

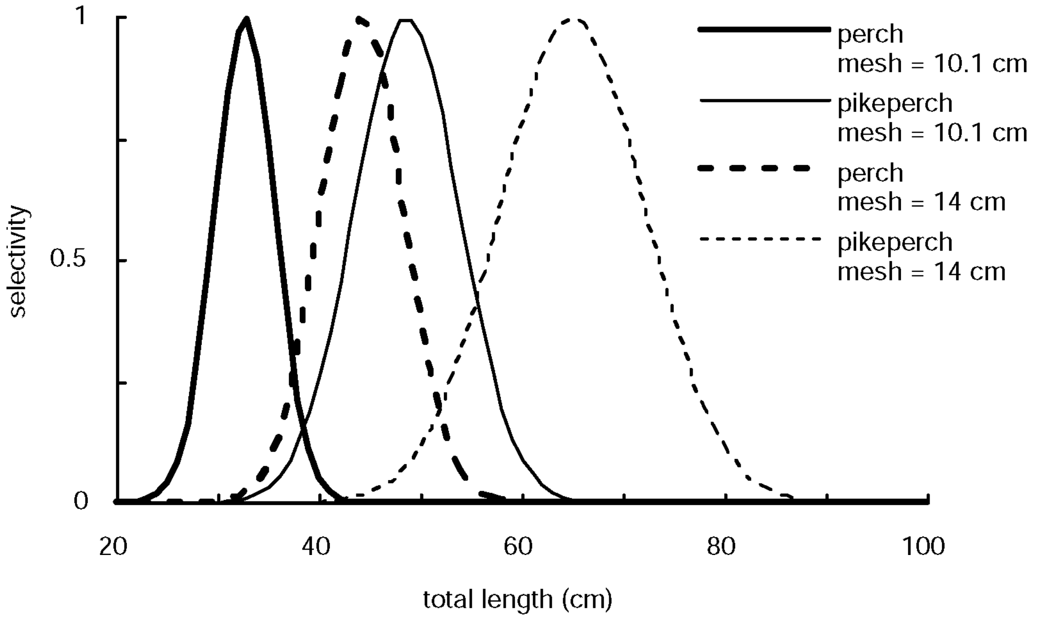

Figure 10.6. *Selectivity of 10.1 and 14 cm (stretched mesh) gillnets for perch and pikeperch (redrawn from Buijse et al. 1992).*

The fishing season of the gillnet fishery in the model started on July 1 and lasted 258 days. In the model of Buijse *et al.* (1992), a seasonal variation in fishing intensity was build in, with the gillnet fishing effort concentrated in winter as observed during the 1970s and 1980s. However, we encountered substantial numbers of gillnets during various summer field trips in the early nineties. Probably, the IJsselmeer fishermen recently tended to use gillnets throughout the fishing season to compensate for the declining eel catches. Hence, we decided to use a constant instantaneous gillnet fishing mortality throughout the fishing season.

To model size-selectivity of the gillnet fishery, a selection curve following a normal distribution was assumed (cf. Buijse *et al.* 1992; Fig. 10.6). The gillnet fishing mortality ($F_{gillnet}$), expressed as the mortality to the size class in the optimum of the selection curve, was established by calibration. At $F_{gillnet}$ = 2 for both perch and pikeperch, the modeled catch approached the observed catch of perch (0 - 4 kg.ha^{-1}.yr^{-1}) and pikeperch (0 - 2 kg ha^{-1}.yr^{-1}) (cf. Fig. 10.1). In the period 1984-1992, the fishing mortality ranged between 0.4 and 2.1 (fishing season)$^{-1}$ for pikeperch of age classes 2-5 and between 0.1 and 1.9 (fishing season)$^{-1}$ for perch of age classes 3-6 (Dekker & Schaap 1993). The observed fishing mortality rates relate to a length range of fish rather than to the modal length in the selection curve, so the observed fishing mortality for fish with this modal length must have been higher. Thus, the calibrated fishing mortality was probably close to the observed fishing mortality.

Predation mortality caused by piscivorous perch and pikeperch

Mortality of prey fish was modeled by calculating the food requirement of piscivorous perch and pikeperch and subtracting the required amount from the prey fish population. It was assumed that at the length where perch and pikeperch become piscivorous, perch and pikeperch switched from 0% to 100% piscivory, and that predators were gape-limited.

The length where perch become piscivorous in the model was set at 20 cm *TL*. In IJsselmeer, perch switch from a diet of invertebrates to fish at a total body length between 10 and 20 cm (Buijse & Van Densen 1992). This was compensated to some extent by the model assumption that perch > 20 cm *TL* feed exclusively on fish, whereas perch > 20 cm *TL* are observed to supplement their diet with invertebrates (Buijse & Van Densen 1992). Pikeperch is dependent on fish to a much larger extent than perch (Willemsen 1977; Van Densen, Ligtvoet & Roozen 1996), and in IJsselmeer pikeperch switches to piscivory at ca. 10 cm *TL* (Buijse & Houthuijzen 1992). Consequently, the length at which pikeperch become piscivorous was set at 10 cm *TL* in the model.

The individual consumption rate of piscivorous fish was calculated from their individual growth rate in terms of weight, assuming a gross food conversion efficiency of 20% (Pauly 1986). Thus, the individual consumption rate *dC/dt* was calculated as:

$$\frac{dC}{dt}=\frac{1}{0.20}\cdot\frac{dW}{dt}=\frac{1}{0.20}\cdot\left(a\cdot L(t)^{b}\right)' \quad \text{[formula 10.9]}$$

where *a* and *b* are the length-weight relationship parameters (Table 10.1) and *dW/dt* is the individual weight growth rate. After substitution with formula [10.6], formula [10.9] transforms into:

$$\frac{dC}{dt}=\frac{1}{0.20}\cdot a\cdot b\cdot L(t)^{b-1}\cdot\frac{dL}{dt} \quad \text{[formula 10.10]}$$

In the model, all individuals in an age class of piscivores had the same growth rate. Hence, consumption rate was constant between individuals of the same age class, irrespective of length. To calculate the consumption over a period *dt* for a length class of piscivorous perch or pikeperch, the individual consumption rate was multiplied by the number of individuals that were present in the length class.

***Table 10.5**. Parameter estimates for the total length - mouth gape (TL, GAPE, in cm) and the total length - body depth (TL, BDEPTH, in cm) relationships used in the model. n = number of observations by which the length-weight relationship was calculated, R^2 = fraction of variance explained by the relationship.*

	GAPE = a·TL+b				*BDEPTH* = a·TL+b			
species	a	b	n	R^2	a	b	n	R^2
smelt					0.179	-0.033	133	0.94
perch	0.117	-0.140	94	0.87	0.322	-0.600	94	0.98
pikeperch	0.113	0.274	96	0.94	0.260	-0.278	96	0.98
ruffe					0.312	-0.403	48	0.95

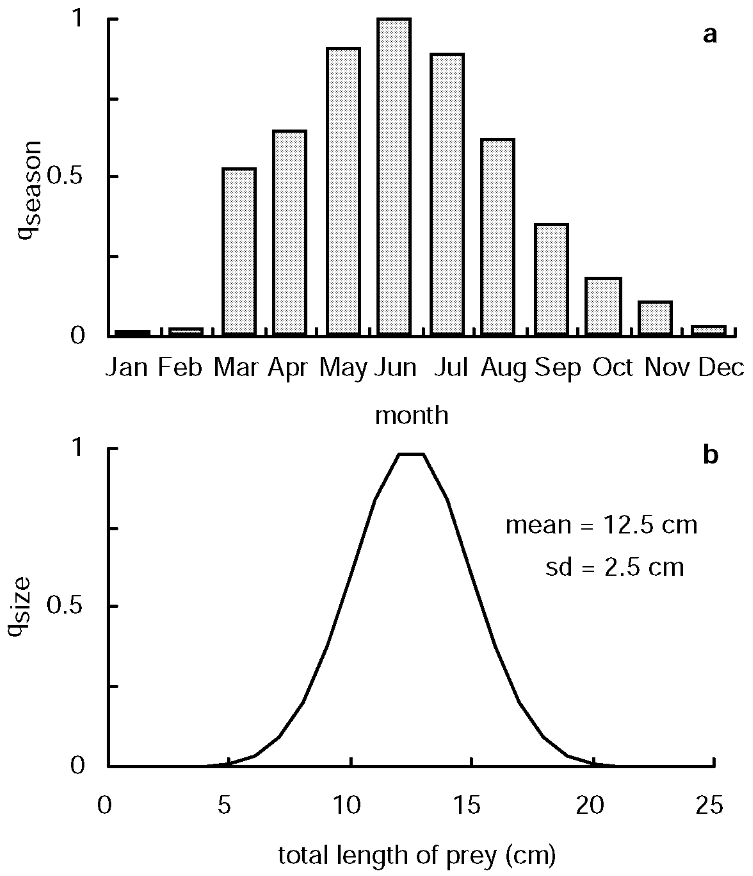

***Figure 10.7**. Modeled seasonal variation in cormorant predation pressure (a) (data from Van Dam et al. 1995) and modeled prey size preference of cormorants (b).*

Following Hambright (1991), we assumed that prey selection by piscivorous perch and pikeperch was determined by the mouth gape of the predator (*GAPE*) and the body depth of the prey (*BDEPTH*) only (Table 10.5), whereby the population of prey fish consisted of smelt and ruffe, and small perch and pikeperch. For each length class of piscivore, the available prey biomass was calculated by determining the biomass of fish fulfilling the criterion $BDEPTH < GAPE$. If the amount of available prey was less than the food requirement for an age and length class of piscivores, the growth rate was set to zero for the species and age class under consideration. In this manner, food-limited growth of piscivores was modeled. If biomass of available prey was sufficient to balance predator growth, the population of available prey fish was reduced by a factor equaling the food requirement : available prey fish biomass ratio. Inter-annual variation in diet composition of piscivorous perch and pikeperch in IJsselmeer corresponded only weakly to the inter-annual variations in biomass composition of prey fish (Benneheij 1996; Van Oostenbrugge 1996). However, the model assumption was corroborated by the Lake Erie situation, where seasonal and inter-annual variation in the diet of walleye *Stizostedion vitreum* and yellow perch *Perca flavescens* did follow the variation in composition of the available prey fish stock (Hartman & Margraf 1992; Knight, Margraf & Carline 1984).

Fish mortality caused by cormorants

In the model, fish predation by the cormorant population is linearly related to the amount of available prey. In this way the model simulates that numbers of cormorants decrease in a situation of food scarcity, as was observed by Van Eerden & Gregersen (1995). Predation by cormorants is maximal in June and minimal in January. We modeled inter-seasonal variation in cormorant predation pressure by multiplying the instantaneous predation mortality rate with a time-dependent factor $q_{seasonal}$, which varied between 0 and 1 (cf. Chapter 9; Fig. 10.7 a). Though in some water bodies large prey (up to 30 cm *TL*) are consumed in considerable numbers (Veldkamp 1995), most of the prey fish caught by cormorants measure between 5 and 20 cm *TL* (Dirksen *et al.* 1995; Van Eerden & Voslamber 1995). Hence, prey size preference (q_{size}) was modeled with a selection curve following a normal distribution, with an optimum at 12.5 cm fish length and a standard deviation of 2.5 cm (Fig. 10.7b). Combining prey size preference with the seasonal variation in cormorant predation pressure, the instantaneous mortality rate caused by cormorants was calculated as $p_{cormorant,opt} \cdot q_{seasonal} \cdot q_{size}$, where $p_{cormorant,opt}$ is the instantaneous mortality rate caused by cormorants at optimum prey size during the month with the highest cormorant predation pressure. In preliminar simulation runs, we calibrated $p_{comorant,opt}$ to 0.00822.day^{-1}, so that the annual prey fish extraction was at the observed prey fish extraction of ca. 10 kg.ha^{-1} (cf. Chapter 9).

Model initialization

Before assessing the effectiveness of management measures with the model, a virtual fish population that included all age classes was generated with and initialization run. To allow for predation of the oldest age class (8 years) on the youngest cohort of fish, a simulation period of 16 years was used for initialization. During initialization, all variables that affect growth, mortality and recruitment were set to values that were representative for the IJsselmeer situation in the 1980s

***Table 10.6**. Management objectives and measures that were simulated with the model.*

Objective		Measure
1	Improve recruitment of perch and pikeperch to the fishery by reduction of mortality caused by discarding, optimization of the gillnet fishery.	50% reduction in fykenet and gillnet fishing effort (*FG50*)
2	Increase smelt availability to birds and piscivorous fish, reduction of discarding, optimization of the gillnet fishery.	50% reduction in fykenet, smelt fykenet, and gillnet fishing effort (*SFG50*)
3	Improve recruitment of perch and pikeperch to the fishery by a strong reduction of mortality caused by discarding.	75% reduction in eel fykenet fishing effort (*F75*)
4	Optimization of the gillnet fishery, notably for pikeperch, reduction of variable costs of the fishery enterprise.	75% reduction in gillnet fishing effort (*G75*),
5	Optimization of the gillnet fishery, notably for pikeperch, keeping employment in the gillnet fishery at its present level.	Increase of the legal minimum gillnet mesh size from 10.1 cm to 14 cm (stretched mesh) (*MESH*)
6	Assess the effects on the fish stocks of predation by cormorants.	Theoretical removal of cormorants (*COR*)

and early 1990s. Catch and population characteristics were stable over the last 5 years of the initialization run. For subsequent simulation runs, which typically started by implementation of a new management measure (see below), a period of 16 years was simulated as well.

Management objectives and measures

Five fisheries management objectives were identified, and for each objective, management measures were proposed. The effectiveness of the proposed management measures was assessed with the model. The management measures that were implemented comprised restrictions in effort, restrictions in mesh size of gillnets, and combinations of these measures (Table 10.6). To assess the effects on the fish stocks of predation by cormorants, a simulation run was made with a theoretical removal of cormorants. The first measure, the 50% reduction of fykenet and gillnet fishing effort was actually implemented in 1996 (Taal & De Wilde 1997). Effects of the management measures were presented in relation to the situation at the end of the initialization run (reference situation).

Buijse (1992) postulated that it is difficult to demonstrate the effectiveness of altered management because of the variation in year-class strength. To test this hypothesis for the 50% fykenet and gillnet effort reduction, 10 simulation runs that featured stochastic recruitment were done, and the simulation results were compared with output from a simulation run were recruitment was kept constant. The same initial population was used at the start of each simulation run.

RESULTS

The reference situation

In the reference simulation run, the dominant fish species were smelt and perch, which comprised most of the biomass in the lake, of the commercial catch and of the food of cormorants (Table 10.7). The mean length of perch and pikeperch caught with gillnets in the model was similar to the observed mean length in the fishery. The proportion of smelt in the diet of cormorants (33%) in the model, representing the remaining 67%, was high compared to the percentage observed in the field (5%, cf. Chapter 9). The relative proportions of perch, ruffe and pikeperch in the food of cormorants in the model were the same as observed in the lake. Prey fish availability was sufficient to support growth of piscivorous perch and pikeperch as shown in Fig. 10.5.

The biomass-size distribution (Fig. 10.8a) of the fish community on simulation day 270 (corresponding to September 28) was compared to the biomass-size distribution as observed during trawl surveys that were conducted in IJsselmeer during fall (Fig. 10.8b). In the biomass-size distribution as observed during the trawl survey, small perch was more abundant than in the modeled population, because of exceptional strong year classes of perch in 1989, 1992, 1993 (cf. Chapter 9). Furthermore, both ruffe and larger perch seemed more abundant in the observed biomass-size distribution. This difference was probably caused by sampling bias, resulting from over-representation of the deeper part of the lake in the sampling program (cf. Chapter 7). Apart of these differences, the simulated biomass-size distribution was roughly similar to the observed biomass-size distribution. Smelt dominated in the smallest size classes, the larger size classes were dominated by ruffe, perch and pikeperch successively.

***Table 10.7**. Modeled fish population and annual fish extraction characteristics with model variables set to values representative for the period 1982-1994 in IJsselmeer. Population characteristics are annual means.*

	biomass (kg·ha^{-1})	body length (cm)		body mass (g)		age (years)[a]	
		mean	sd	mean	sd	mean	sd
population in the lake							
smelt	14.1	6.2	1.7	1.4	1.2	0.3	0.5
perch	11.2	8.8	4.8	19.7	51.9	0.8	1.0
pikeperch	3.1	20.6	12.1	168.3	323.5	1.0	1.0
ruffe	3.9	7.1	2.2	5.6	5.6	0.7	0.8
catch of target fish							
smelt	14.0	7.5	1.0	2.1	1.2	1.0	0.2
perch	2.5	28.9	2.6	395.5	118.2	4.7	0.9
pikeperch	1.7	43.8	4.0	785.2	227.6	2.7	0.6
ruffe	0	0		0		0	
fykenet discards / bycatch							
smelt	5.7	5.6	1.4	1.0	1.1	0.1	0.3
perch	5.6	8.5	4.9	19.3	51.0	0.7	1.0
pikeperch	1.6	20.0	11.3	163.7	201.5	0.9	0.9
ruffe	1.9	6.9	2.4	5.5	5.8	0.6	0.8
consumption by cormorants							
smelt	2.7	8.4	1.6	3.4	2.3	0.9	0.6
perch	2.9	10.7	2.2	16.0	11.6	1.3	0.5
pikeperch	0.1	12.3	2.6	15.3	9.5	0.4	0.5
ruffe	2.6	9.8	1.7	13.1	6.8	1.6	0.8

Note

a. When recruiting to the population, the age of fish was set to zero. At January 1, the age of each cohort was increased by one.

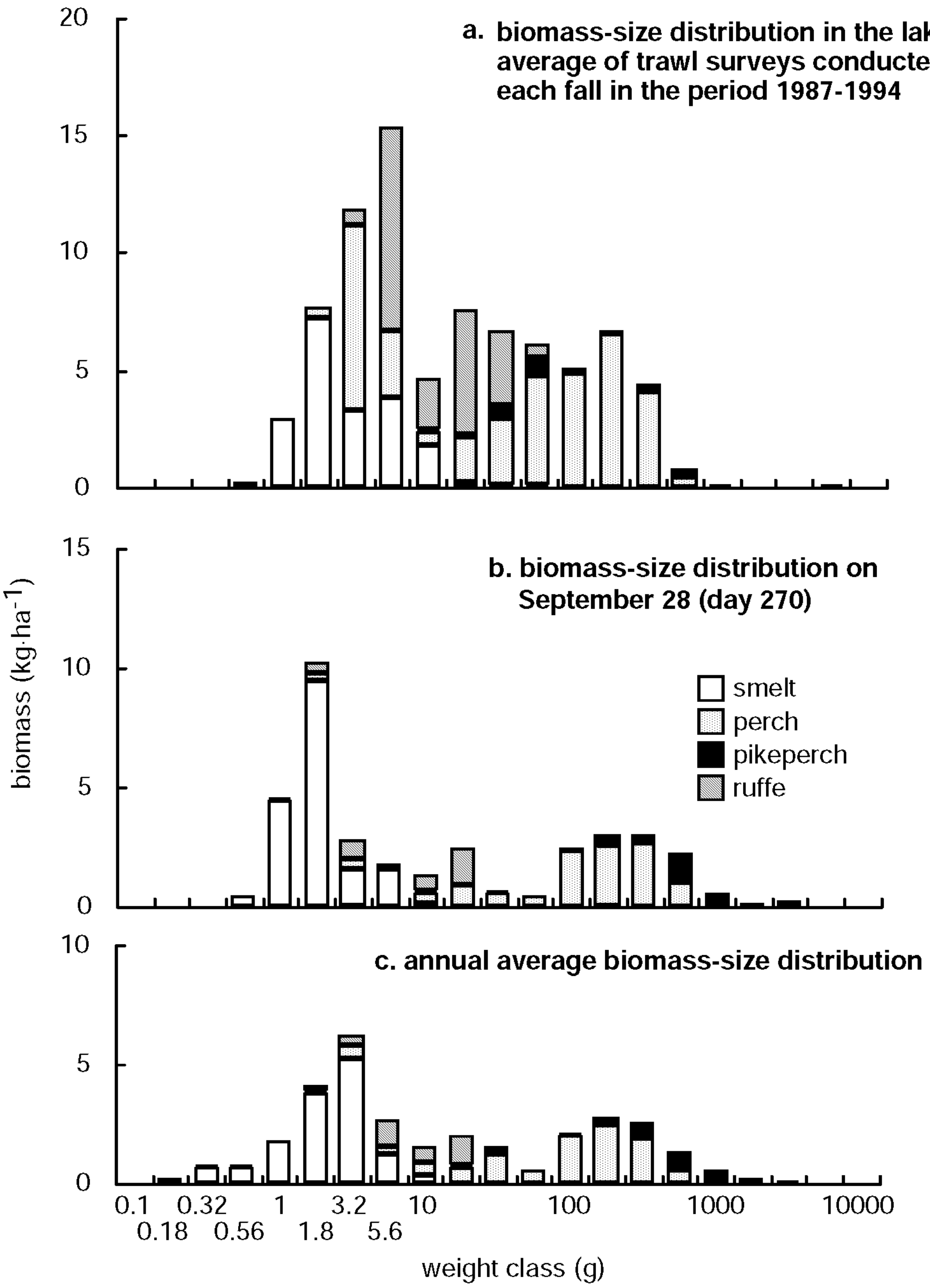

***Figure 10.8**. Biomass-size distribution of the fish population in the lake (a), simulated biomass-size distribution in the reference situation on September 28 (day 270) (b), and averaged over a simulation year (c).*

The change in population numbers and biomass of a year class over a period of 8 years showed characteristic differences between species (Fig. 10.9). For smelt, mortality of age 1 and older was ca. 1.5 yr^{-1} (excluding mortality caused by the smelt fykenet fishery). Modeled mortality was close to the observed mortality over the growing season of ca. 1.8 yr^{-1} (cf. Chapter 9). Stock biomass of smelt was dominated by age 0 fish. The development in the biomass of ruffe showed a plateau, and both age 0 and age 1 contributed significantly to the population. This difference in stock structure between smelt and ruffe was observed in the field as well (cf. Chapter 9). Total

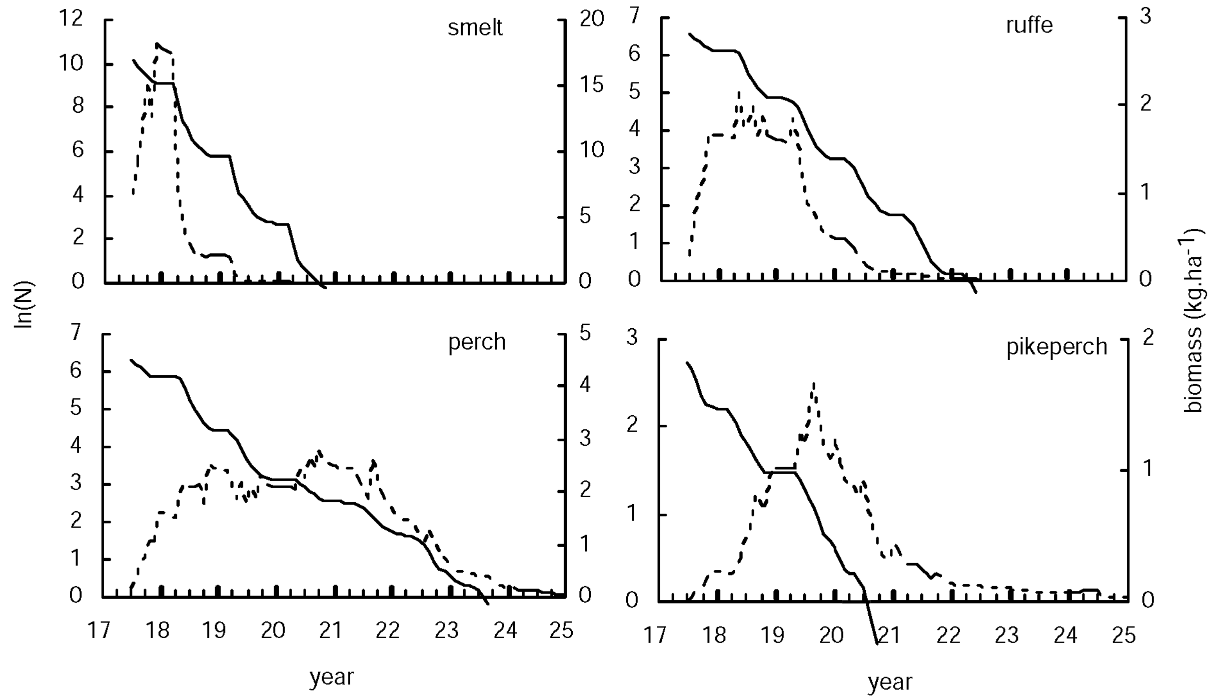

Figure 10.9. *Variation in abundance (solid lines) and biomass (dashed lines) of the age class born in year 17. Abundance is expressed as the natural logarithm of the number of fish per ha (ln(N), left Y-axis), biomass in kg.ha*$^{-1}$ *(right Y-axis). All model variables set to values of the reference situation. Note the different scales on the Y-axes.*

mortality of ruffe was lower than of smelt, mainly because of the high fishery mortality of smelt. The cohort biomass of perch remained relatively stable between age 1 and age 4. Total mortality was high during age 0, age 1 and age 2, because of high predation mortality. Mortality was relatively low during age 3 and age 4, because these larger perch were less vulnerable to predation by larger piscivores. Due to gillnet fishery mortality, total mortality increased again at age 5 and 6. For pikeperch, biomass was maximal at age 2. At higher age, the pikeperch biomass decreased sharply because of gillnet fishery mortality. In general, we concluded that the modeled fluctuation in population numbers and biomass of age classes was realistic.

The size and species compositions of the catch by the professional fishery and of the cormorant diet are depicted in Fig. 10.10. The fykenet catch showed the widest size range because the fykenet fishery was not size-selective, and because it was practiced throughout the growing season. The smelt fykenet fishery was also not size-selective, but because it was practiced during the spawning season only, the size range of the catch was smaller than the size range of discarded smelt. Because cormorants consumed only fish between 5 and 20 cm *TL*, only larger smelt and smaller perch than present on average in the lake were present in the diet (cf. Fig. 10.8c). Because the size range of ruffe present in the lake matched the selection range of cormorant feeding behavior, the proportion of ruffe in the diet of cormorants was high compared to the proportion of ruffe in the lake (cf. Fig.10.8c).

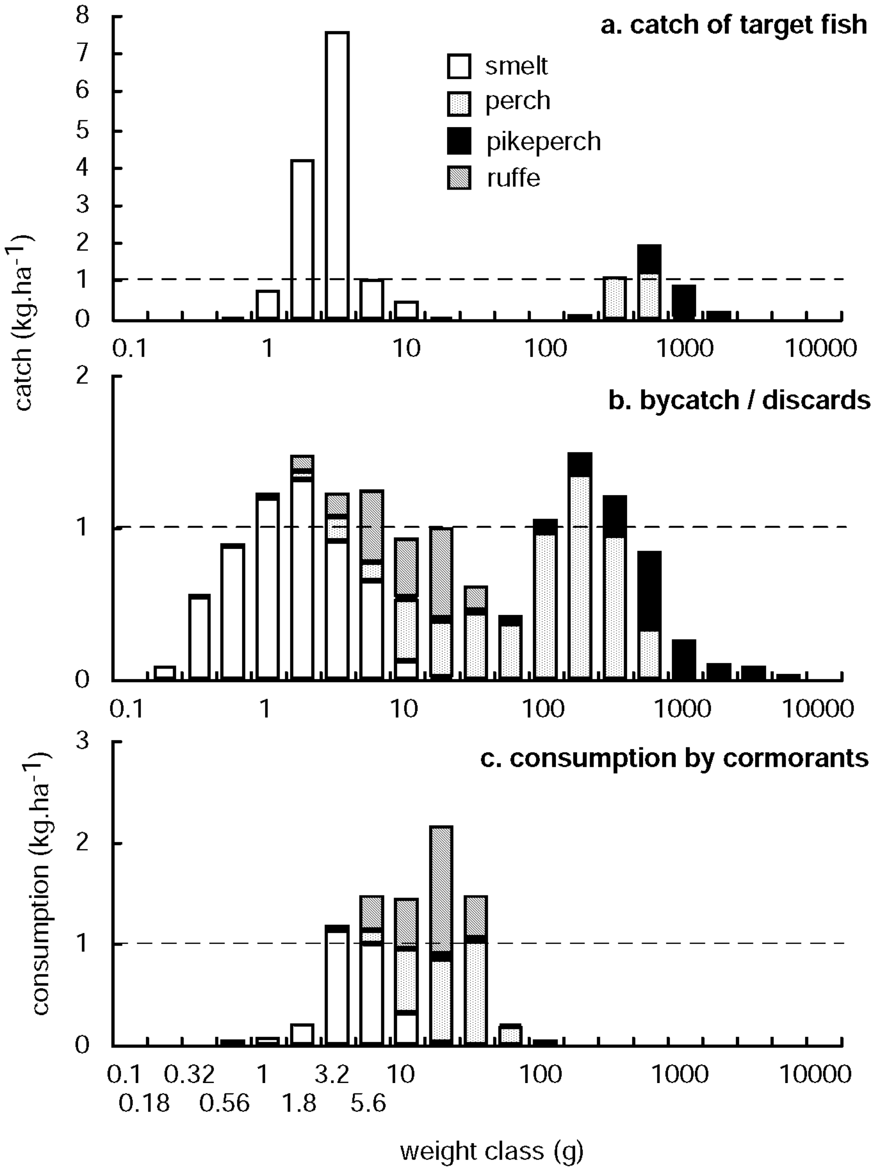

***Figure 10.10**. Biomass-size distributions of the catch of target fish, caught by gillnets (perch, pikeperch) and by smelt fykenets (a), bycatch / discards, caught by eel fykenets (b), and fish consumed by cormorants (c). Reference lines are positioned at 1 kg.ha^{-1}.*

Effects of management measures

After implementation of the management measures, except measure *G75* and *MESH*, inter-annual variation in mean annual population biomass showed a cyclic trend (Fig. 10.11). This was caused by an increase in the biomass of piscivores, resulting in increased predation mortality of juveniles of these piscivores, and in depletion of the stock of prey fish, thus causing slower growth of piscivores. So predation pressure decreased, and the stock of prey fish increased again. Mean length of each species in the population showed a cyclic trend as well (Table 10.8). Even after

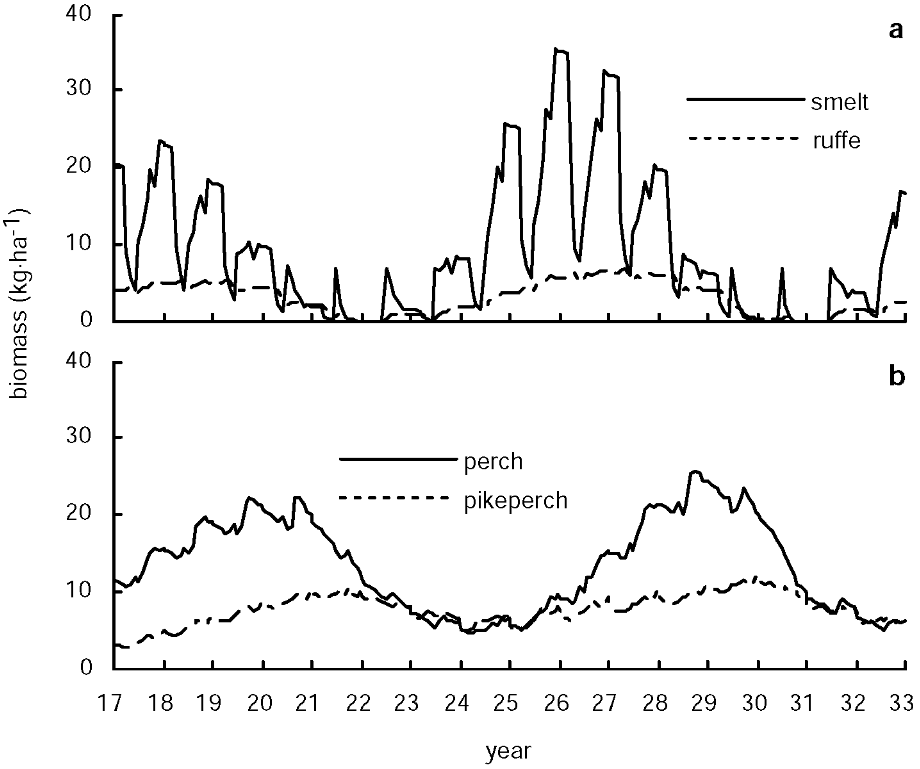

***Figure 10.11**. Variation in biomass after reduction in eel fykenet and gillnet fishing intensity by 50%. The management measure was implemented in year 17. The small irregularities that occurred on a time scale of less than 3 months result from the method we used to simulate dispersion in growth (see Materials and Methods section).*

extension of the simulation period with 48 years, the amplitude of the biomass variation did not change significantly. Inter-annual means of one complete cycle (the last 8 years of the simulation) were used for comparison with the reference situation, since the inter-annual mean over a period of one completed cycle equals the converged biomass values (McGarvey 1994).

The effects of the management measures on population biomass and on biomass of fish extracted annually are summarized in Fig. 10.12. The effects of management measures were evaluated from the relative changes from the reference situation (Tables 10.9, 10.10, 10.11 and 10.12).

All management measures resulted in an equal or higher mean length of fish in the population (Table 10.9). The increase in mean length varied between 0 and 53%. Management measures that involved a decrease in the fykenet fishery for eel (measures *FG50*, *SFG50*, *F75*) had generally stronger effects on the population than the other management measures. All measures, except measure *SFG50*, resulted in a lower smelt biomass. This was a consequence of the higher predation pressure of piscivorous perch and pikeperch. In measure *SFG50*, the reduction by 50% in fishing effort of the smelt fykenet fishery was apparently sufficient to cause an increase in smelt biomass, despite the higher predation pressure. Changes in total fish biomass varied between -2% (*MESH*) and +62% (*SFG50*).

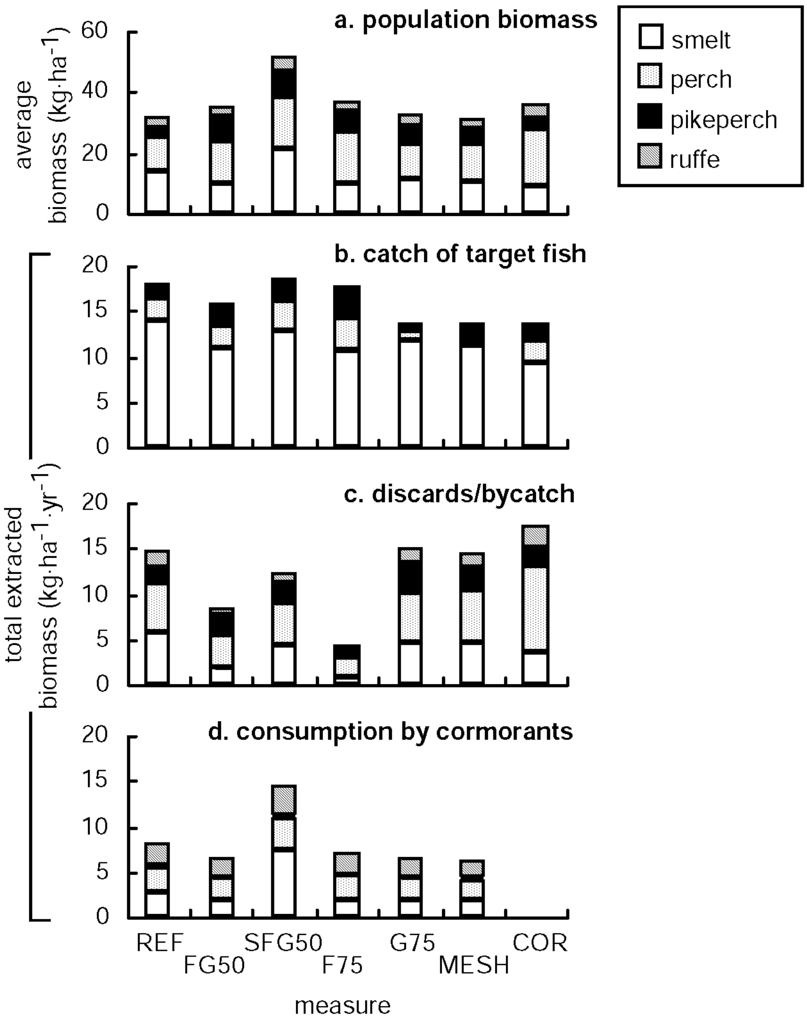

Figure 10.12*. Consequences of management measures for the population biomass (a), the amount of annually extracted fish (b, c), and for the consumption by cormorants (d), compared to the reference situation (REF).*

Table 10.8*. Coefficient of variation (CV = sd/mean) in total biomass and mean length. The coefficients refer to the variation in mean annual values in the last 8 years of the simulation period. Because more age groups contributed significantly to the perch and pikeperch populations than to the smelt and ruffe populations, the relative amplitude of the cyclic patterns of perch and pikeperch were lower than for the short-lived smelt and ruffe. Because food limitation in growth of piscivores did not occur after implementation of measures G75 and MESH, the CV was negligible compared to the other simulation runs.*

population		management measures					
		FG50	*SFG50*	*F75*	*G75*	*MESH*	*COR*
biomass							
	smelt	0.83	0.62	0.99	0.04	0.11	0.91
	perch	0.49	0.64	0.46	0.03	0.07	0.56
	pikeperch	0.20	0.26	0.26	0.00	0.00	0.23
	ruffe	0.73	0.48	0.87	0.02	0.06	0.63
mean length							
	smelt	0.08	0.02	0.08	0.00	0.00	0.12
	perch	0.36	0.24	0.35	0.00	0.01	0.28
	pikeperch	0.12	0.12	0.12	0.00	0.00	0.05
	ruffe	0.13	0.09	0.13	0.00	0.01	0.17

Mean length of fish in the catch by the commercial fishery (smelt caught in smelt fykenets, perch and pikeperch caught in gillnets) changed by -1 to +29% (Table 10.10). The changes were relatively small compared to the changes in the population, except for the relatively large increase in mean length of perch and pikeperch after implementation of measure *MESH*. Because the profitability of the fishery depends on the value of the catch, rather than on the biomass caught, the change in total annual catch value was calculated. The effect of the management measures on the

***Table 10.9**. Relative change[a] (%) in biomass and mean length in the population after implementation of management measures.*

population	management measures					
	FG50	*SFG50*	*F75*	*G75*	*MESH*	*COR*
biomass						
smelt	-26	+50	-30	-17	-21	-35
perch	+22	+60	+58	-1	+4	+67
pikeperch	+169	+164	+109	+109	+73	+14
ruffe	-17	+26	-13	-12	-15	+26
total	*+11*	*+62*	*+16*	*+1*	*-2*	*+12*
mean length						
smelt	+14	+13	+16	+10	+10	+22
perch	+34	+20	+53	+2	+3	+43
pikeperch	+33	+29	+30	+22	+19	+6
ruffe	+11	+9	+18	+1	+0	+25

Note

a. Relative changes were calculated as follows: the mean over the last 8 years of the simulation period was calculated, and the result was expressed as a relative change compared to the mean annual value before implementation of the management measure.

***Table 10.10**. Relative change (%) in biomass and mean length in the catch of target fish after implementation of management measures. The change in value was based on the mean price over the years 1993 and 1994 (0.90, 7.60 and 9.90 dfl.kg^{-1} for smelt, perch and pikeperch respectively).*

catch of target fish	management measures					
	FG50	*SFG50*	*F75*	*G75*	*MESH*	*COR*
biomass[a]						
smelt	-22	-8	-24	-16	-20	-33
perch	+5	+35	+46	-57	-77	-3
pikeperch	+35	+36	+113	-46	+9	+11
tot. catch of target fish	*-13*	*+2*	*-2*	*-24*	*-25*	*-24*
tot. value of target fish	*+8*	*+24*	*+51*	*-42*	*-32*	*-6*
tot. value inc. bycatch[c]	*-5*	*+12*	*+16*	*-26*	*-19*	*+16*
mean length[b]						
smelt	+11	+8	+16	-1	-1	+18
perch	+4	+4	-1	+6	+28	-1
pikeperch	+5	+5	+1	+6	+29	+1

Notes

a. Relative changes were calculated as follows: First, the mean over the annual total catch in the last 8 years of the simulation period was calculated. Next, the result was expressed as a relative change compared to the annual total catch before implementation of the management measure.

b. Relative changes were calculated as described in (a), but instead of annual total catch, the mean length of individuals in the annual total catch was used.

c. Includes, besides target fish, perch and pikeperch above minimum legal size (22 cm TL for perch, 42 cm TL for pikeperch) that were caught in eel fykenets. The proportion of perch above minimum legal size in bycatch / discards was 47%, and of pikeperch 14% (cf Fig. 10.10b).

total value of target fish varied considerably from –42% to +51%. However, if the bycatch of the fykenet fishery (perch and pikeperch above minimum legal size) was accounted for, the change in total value was only moderate, ranging between –26% and +16%. Mostly, gains in catches of piscivorous fish were partly decreased by losses due to a lower smelt catch. Furthermore, a higher catch in the gillnet fishery was associated with a lower bycatch in the fykenet fishery (see *FG50*, *SFG50*, *F75*). On the other hand, a lower catch in the gillnet fishery was partly compensated by a higher bycatch in the fykenet fishery (*G75*, *MESH*). Of the management measures that were simulated, the 75% reduction in the fykenet fishing effort (*G75*) had the strongest positive effect on the value of the total catch (+51% in catch of target fish, +16% in catch of target fish and bycatch).

After the theoretical removal of cormorants (measure *COR*), the population biomass of perch increased considerably (+67%), but the gillnet catch of perch remained stable (-3%). At the same time, discards/bycatch of perch increased considerably (+68%). Hence, most of the extra production of perch ended up in the fykenets. The larger population of perch caused an increase in

***Table 10.11**. Relative change (%) in biomass and mean length in discards/bycatch after implementation of management measures.*

bycatch / discards		management measures				
	FG50	*SFG50*	*F75*	*G75*	*MESH*	*COR*
biomass[a]						
smelt	-63	-20	-83	-16	-19	-34
perch	-39	-19	-60	-2	+3	+68
pikeperch	+32	+31	-48	+102	+67	+14
ruffe	-59	-36	-78	-12	-16	+34
total	*-43*	*-16*	*-70*	*+3*	*-1*	*+18*
mean length[b]						
smelt	-5	+5	-9	-1	-2	-7
perch	+4	+7	+23	-1	-1	+22
pikeperch	+26	+23	+23	+18	+15	+2
ruffe	-8	+1	-10	-2	-3	+6

Notes

a. See footnote (a) of Table 10.9.

b. See footnote (b) of Table 10.9.

***Table 10.12**. Relative change (%) in biomass and mean length of fish consumed by cormorants after implementation of management measures.*

consumption by cormorants	*FG50*	*SFG50*	management measures *F75*	*G75*	*MESH*	*COR*
biomass[a]						
smelt	-22	+178	-23	-26	-31	-100
perch	-18	+24	-10	-13	-17	-100
pikeperch	-33	-27	-37	-32	-32	-100
ruffe	-17	+33	-8	-17	-22	-100
total	*-19*	*+76*	*-14*	*-19*	*-23*	*-100*
mean length[b]						
smelt	-7	+3	-8	-2	-2	-
perch	-1	-2	+4	+1	0	-
pikeperch	+1	+2	-1	+2	+2	-
ruffe	-2	-3	+1	0	0	-

Notes

a. See footnote (a) of Table 10.9.

b. See footnote (b) of Table 10.9.

the predation mortality in smelt, which resulted in a lower smelt catch (-33%). Overall, the theoretical removal of cormorants resulted in an increase in total catch value (including bycatch) of 16%.

The model suggested that the exploitation of smelt reduced the scope to increase the production of the gillnet fishery for perch and pikeperch. Without a reduction in the effort in the fykenet fishery for smelt, a 50% reduction of the effort of both the gillnet fishery and of the eel fykenet fishery would increase the catch of perch with only 5%, and the catch of pikeperch with 35%. When also the fishing effort of smelt fykenets was reduced (50%), the increase in the catch of pikeperch was about the same (36%), but the perch catch increased much stronger, namely with 35%.

As was expected, a reduction in fishing effort of fykenets resulted in a decrease in the total amount of bycatch/discards (Table 10.11, measure *FG50*, *SFG50*, *F75*). In measure *FG50* and *SFG50*, bycatch of pikeperch increased, because of the ca. 2.5-fold increase in population biomass of pikeperch (cf. Table 10.10).

Most management measures resulted in a moderate decrease (14 - 23%) of cormorant consumption (Table 10.10). Only measure *SFG50* (a 50% reduction in all three types of fisheries) resulted in an increase of cormorant consumption. This was mainly caused by the higher consumption of smelt by the cormorants. The species composition of all fish consumed by the cormorants after implementation of the other management measures hardly changed. Changes in the mean length of fish consumed by cormorants were small.

Trends in population biomass that resulted from simulation runs featuring stochastic recruitment, differed strongly from each other, and from the trend with constant recruitment (Fig. 10.13). The coefficient of variation (*CV*) in fish biomass per year as found with constant recruitment ranged from 0.32 for total biomass until 0.79 for smelt biomass (Table 10.13). Most of this variance can be attributed to interactions between trophic groups and negative feed-back within species. The *CV*s from the simulation runs corresponded reasonably well with the *CV* in fish biomass as found during 25 years of trawl surveys (1970-1994). The only exception was pikeperch, where an extremely high *CV* (1.73) was observed in the lake, whereas the *CV* for pikeperch biomass in the

Table 10.13*. Coefficient of variation (CV = sd/mean) in annual biomass as estimated from trawl surveys conducted in IJsselmeer during fall over the period 1970-1994*[a]*, as modeled with constant recruitment (R) (cf. Fig. 11.13, top graph), and as modeled with stochastic recruitment (cf Fig. 11.13, lower 10 graphs).*

			modeled, stochastic R		
	observed (1970-1994)	modeled, constant R	mean over 10 simulation runs	min.	max.
smelt	0.71	0.79	1.00	0.76	1.40
perch	0.59	0.44	0.60	0.35	0.94
pikeperch	1.73	0.25	0.42	0.24	0.65
ruffe	0.66	0.68	0.93	0.58	1.34
total	0.39	0.32	0.58	0.38	0.88

Note

a. Data are available at the Fish Culture and Fisheries Group, Wageningen University

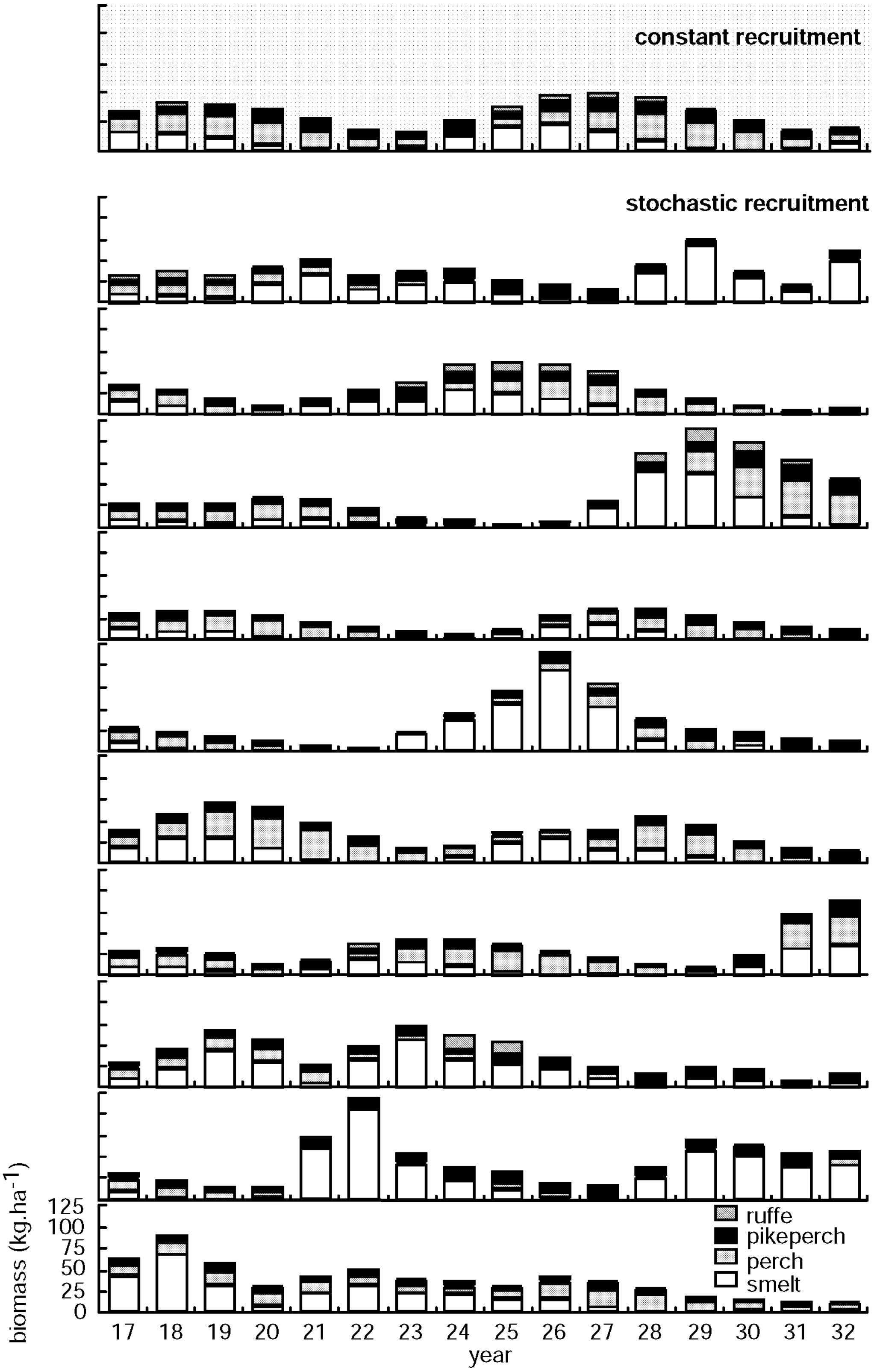

Figure 10.13. *Annual mean biomass in year 17-32, after implementation of a 50% reduction in eel fykenet and in gillnet fishing effort at the beginning of year 17. The top graph represents a simulation run with constant recruitment. The 10 lower graphs represent simulation runs with stochastic recruitment. Trends in catch, bycatch/discards and cormorant consumption (not presented here) resembled the trends in population biomass.*

model, with constant recruitment, was low (0.25). The *CVs* as found with the 10 runs with stochastic recruitment were on average ca. 50% higher than the *CVs* for constant recruitment. Possibly, the feed-back mechanisms in the lake ecosystem were more effective in stabilizing stock biomass than model outcome shows. Anyway, stochastic recruitment, as well as interactions and feed-back mechanisms in the fish community, contribute to a large variance around a possible trend in the fish stocks, the commercial catch, in bycatch/discards, and in food availability for cormorants. So they strongly obscured the effects of the management measure.

DISCUSSION

The simulation exercises suggested that in IJsselmeer, cormorants have a moderate, negative effect on the fishery. After a simulated removal of all cormorants, the total value of smelt catch, the catch of perch and pikeperch in gillnets, and the bycatch of the fyknet fishery, was 18% higher. Food consumption by cormorants increased considerably after a simultaneous decrease in the gillnet, eel fykenet and the smelt fykenet effort, mainly because of the 178% increase in smelt consumption. However, the effect of the other management measures on the food availability for cormorants was moderate: the simulated management measures resulted in a decrease of 14-23% in fish consumption by cormorants.

Effects of the fishery management measures on the outcome of the gillnet and smelt fykenet fishery were strong. Especially measures that were directed towards the eel fykenet fishery had a strong positive effect on the catch. The strongest effect on the value of the catch (+51%) resulted from the strongest decrease (75%) in eel fykenet fishing effort. Measures directed exclusively towards the gillnet fishery always reduced the value of the total catch. However, losses in the gillnet fishery were partly compensated by gains in the bycatch of target species above minimum legal size in the fykenet fishery. The exploitation of smelt reduced the positive effects of restrictions in the effort of the fykenet and gillnet fishery. Without a reduction in smelt fykenet effort, a 50% reduction of the gillnet and eel fykenet fishing effort resulted in an increase in the catch of perch with only 5%. If the smelt fykenet effort was reduced also, the perch catch increased stronger, namely by 36%.

The decrease in pikeperch catch with 46% after a 75% reduction in the gillnet fishery simulated here was similar to the reduction in the pikeperch catch found with the model of Buijse *et al.* (1992) (ca. 50%). The reduction in perch catch (57%) was higher in the present model than in the model of Buijse *et al.* (1992) (ca. 30%). This difference was probably caused by predation pressure exerted by both piscivorous fish and cormorants that was incorporated in the present model. The effect of predation on the catch of perch was stronger than on the catch of pikeperch, due to the slower growth of perch, making it vulnerable for predation during a longer part of its life history.

The occurrence of food-limited growth in piscivorous fish, and predation on juveniles of piscivorous fish species, resulted in a cyclic pattern in fish population biomass, whereby low biomass of piscivorous fish coincided with a high prey fish biomass and vice versa. This was in agreement with population dynamics theory, which states that a time-lag in density-dependent responses result in cyclic trends in population biomass (Begon, Harper & Townsend 1990). Food limitation of piscivorous fish is demonstrated for walleye *Stizostedion vitreum* in another large lake, Lake Erie (Knight, Margraf & Carline 1984; Hartman & Margraf 1992). The effect of predation on juveniles of piscivorous fish was demonstrated for yellow perch *Perca flavescens* (Hartman & Margraf 1993) and walleye (Santucci & Wahl 1993).

The cyclic trends in fish biomass and the variability caused by stochastic recuitment suggested that effects of management measures show up in biomass and catch averages after long periods only. Thus, this study corroborated the conclusion of Hastings (1996), that population models are likely to produce fluctuations in population biomass over long periods, and that changes in input parameters in the model may become apparent only after long transient periods. Pelletier & Laurec (1992) demonstrate that random variation in recruitment obscures the effects of improved fishery management significantly. Because of these obscuring effects, and because the effects of management measures simulated here were only moderate, especially on the total value of the catch, there is serious doubt about time series of commercial catch statistics or of survey trawl data clearly showing the effectiveness of fishery management measures.

Eel, which contributed 62% in value to the total catch of the commercial fishery over the period 1990-1993, was not included in our model. Notwithstanding its economic value, eel is not of direct importance for the functioning of the higher trophic levels in the IJsselmeer ecosystem. The importance of eel as a prey fish is negligible, whereas its role as a piscivore is limited as well: fish predation by eel accounts for only about 3% of the total amount of fish consumed (Buijse *et al.* 1993). Furthermore, the problem in the eel fishery (declining eel catches) cannot be solved by gear and effort regulations alone, because the problem is at least partly caused by declining immigration of glass eel (Van Dam *et al.* 1995). Finally, lack of quantitative data on the IJsselmeer eel stock (cf. Dekker & Van Willigen 1993) would have made parameterization of the eel component in the model difficult. Population dynamics characteristics of eel populations in the wild are difficult to study: age determination is laborious (Vøllestad *et al.* 1988), variability in growth between individuals is high (Panfili, Ximénès & Crivelli 1994), and its migration routes are not known (McDowall 1988).

Lower trophic levels (e.g. zooplankton, fytoplankton, invertebrate benthos) were not included in the model, although they affect population dynamics of prey fish in IJsselmeer (Chapter 9), and although fishery management could eventually affect functions of the lake through effects on water quality (Carpenter, Kitchell & Hodgson 1985; Hanson & Butler 1994). Even though density-dependency in the growth of smelt and ruffe through food-limitation was observed in IJsselmeer (Chapter 9), it was not modeled because variation in growth of prey fish species was small (Chapter 9). Because only moderate management measures were simulated, we think that this omission did not invalidate our model.

This model is not suitable to evaluate the effects of drastic measures (e.g. complete ban on the fishery). A drastic measure would probably result in a structural change in the ecosystem. For instance, fish species that were not included in our model could become dominant. Since the modeling of structural dynamics of ecosystems (including changes in species flocks) is still in an experimental stage (Jørgensen & Nielsen 1994; Jørgensen 1995), we opted to simulate the effects of less drastic measures only.

Notwithstanding the confinements of the simulation model presented here, the model yielded realistic output values for population biomass, catch, and fish consumed by cormorants without having to use correction factors or expressions that summarize multiple undefined sources of fish mortality ('natural mortality'). In our model, fish mortality was dependent on fishing effort, and predation by piscivorous fish and birds only. Also, the model corroborated our earlier conclusion that prey fish production was balanced by utilization of the fishery, piscivorous fish, and piscivorous birds (cf. Chapter 9).

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Curriculum Vitae

Peter Mous werd op 29 juni 1966 in Den Haag geboren. In 1984 behaalde hij het VWO diploma aan het Chr. Lyceum te Alphen aan den Rijn, en begon hij aan een studie Zoötechniek aan de Lanbouwuniversiteit Wageningen. Na voltooiing van een doctoraalonderzoek over de reproductie van Nijlbaars in het Victoriameer, Oost Afrika, behaalde hij in 1989 zijn doctoraaldiploma. Na verschillende contracten die overwegend met tropische visserij te maken hadden begon hij in 1992 aan een promotieonderzoek over de interacties tussen de visserij, visbestanden en vogels in het IJsselmeer. Sinds 1998 werkt Peter voor The Nature Conservancy in Indonesië, waar hij betrokken is bij een marien natuurbeschermingsproject in Komodo National Park.